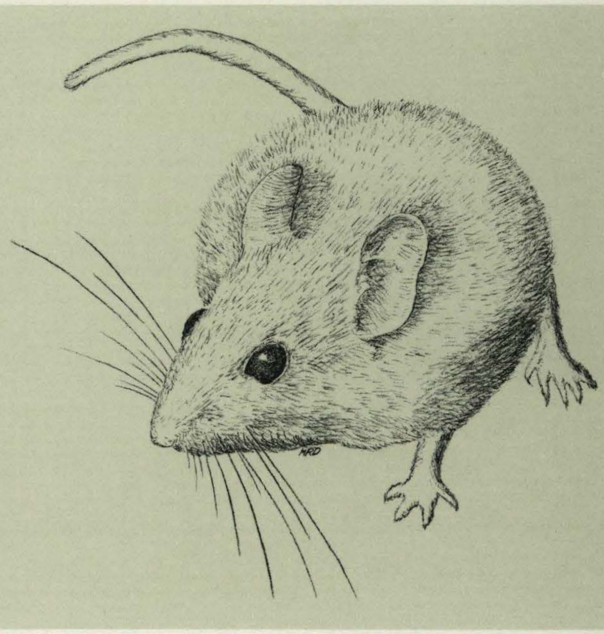
PEROMYSCUS OF THE LATE TERTIARY IN OREGON

By

J. Arnold Shotwell



BULLETIN NO. 5

of the

MUSEUM OF
NATURAL HISTORY

University of Oregon
Eugene, Oregon

June 1967

1872

The *Bulletin* of the Museum of Natural History of the University of Oregon is published to increase the knowledge and understanding of the Natural History of Oregon. Original articles in the fields of Archaeology, Botany, Ethnology, Geology, Paleontology and Zoology appear irregularly in consecutively numbered issues. Contributions arise primarily from the research programs and collections of the Museum of Natural History and the Oregon State Museum of Anthropology. However, in keeping with the basic purpose of the publication, contributions are not restricted to these sources and are both technical and popular in character.

J. ARNOLD SHOTWELL, *Director*
Museum of Natural History
University of Oregon

Communications concerning manuscripts and purchase of copies of the *Bulletin* should be addressed in care of the Museum of Natural History, University of Oregon, Eugene, Oregon 97403. A list of previous issues of the *Bulletin* will be found inside the back cover.

PEROMYSCUS OF THE LATE TERTIARY IN OREGON

PEROMYSCUS OF THE LATE TERTIARY IN OREGON

by

J. ARNOLD SHOTWELL

Bulletin No. 5

Museum of Natural History
University of Oregon
Eugene, Oregon
June 1967

Funds for publication of Bulletin No. 5 provided by the National Science Foundation grant GB 3971.

PEROMYSCUS OF THE LATE TERTIARY IN OREGON

by

J. ARNOLD SHOTWELL

Museum of Natural History

University of Oregon

ABSTRACT

Samples of *Peromyscus* from six late Tertiary localities in Oregon are described. Variation and progressive changes are discussed for the time, Barstovian through Hemphillian. Two new species, *P. pagei* and *P. valensis* are described. The diversity of late Tertiary species in Oregon and the Northern Great Basin is compared with that of living species in North America today.

INTRODUCTION

Fossil species of the genus *Peromyscus* are common in the Tertiary as early as late Miocene (James 1963). However, we still have very little understanding of the history of this common small mammal. Recently excavation techniques have been developed which produce abundant small mammal fossils from consolidated sediments. Previously, recovery of small mammals from Tertiary beds has been largely fortuitous. As a result most of the described Tertiary species of *Peromyscus* are known only from the type and possibly several other specimens. *Peromyscus russelli* (James 1963) is a notable exception. Thus our knowledge of variation in fossil species is minimal and accounts in a large part for the present lack of a generally acceptable phylogenetic picture. Collections made over the last ten years by field parties of the Museum of Natural History of the University of Oregon have been aimed at procuring quantitatively useful samples of fossil vertebrates from a single geographic area representing a late Tertiary sequence. Specimens of a number of species of *Peromyscus* are common in these samples.

The recent works of Hooper (1957) and Hershkovitz (1955, 1962) have described the nature of variation in the dentition of a number of living Western Hemisphere cricetids including *Peromyscus* and also suggested some functional roles of various structures of the dentition. These works and our new material provide a basis for a step towards an understanding of the history of *Peromyscus*.

ACKNOWLEDGEMENTS

I am grateful to the Museum of Paleontology, University of California, Berkeley, Los Angeles County Museum of Natural History and the Museum of Comparative Zoology, Harvard, for the loan of important type specimens and comparative material. This study is a small part of a broad study of late Tertiary faunal change suported by grants G21820 and GB 3971 of the National Science Foundation. The illustrations are by Mildred R. Detling.

MATERIALS AND METHODS

Materials from six localities are used in the present study. Five of these localities are in a single geographic area of southeastern Oregon in the Northern Great Basin. The sixth is from the vicinity of the Columbia River to the north. Most of the specimens discussed below have been produced from three localities in the Northern Great Basin. These three localities represent a sequence of late Tertiary faunas of late Miocene (Barstovian, Quartz Basin) early Pliocene (Clarendonian, Black Butte) and middle Pliocene (Hemphillian, Little Valley) age. They also represent a sequence of samples of a single type of association previously referred to as stream-bank (Shotwell 1964). Three other Hemphillian (mid-Pliocene) localities, Juniper Creek Canyon and Bartlett Mountain in the same geographis area as the three sequencial localities and McKay Reservoir near the Columbia River to the north, provide useful information concerning the local diversity of *Peromyscus* in the Pliocene. Figure 1 is a map showing the localities referred to in this study. Measurements of the teeth were made using a Gaertner measuring microscope.

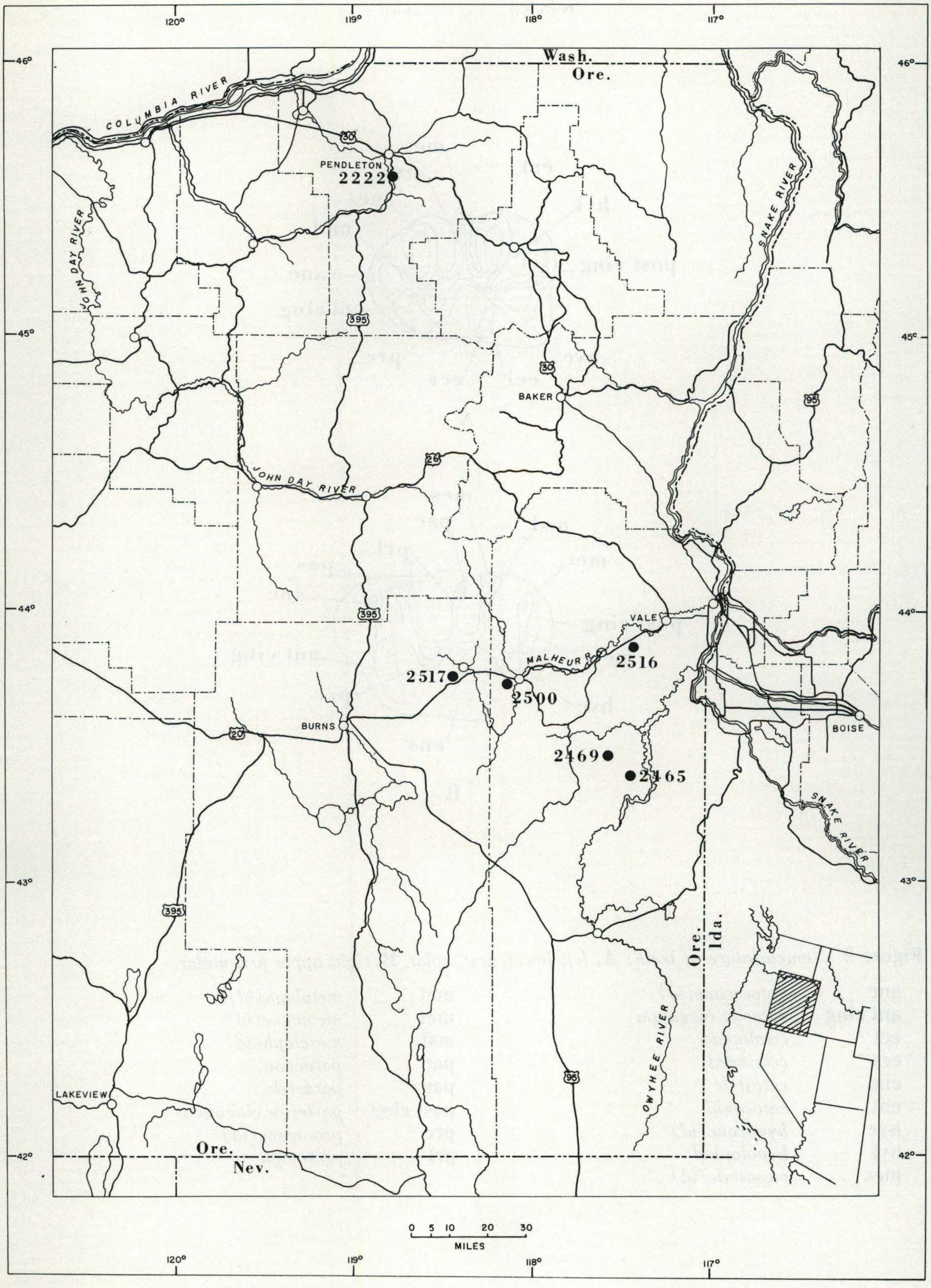
The entire collection from the six localities may be sorted into three groups of specimens. Group one mice exhibit cuspate, brachyodont teeth, group two, includes more lophiodont higher crowned forms, and group three lophiodont high crowned forms. The most abundant species of group one are small animals, however, larger forms are also known. Group two includes mice of about the same size as the larger forms from the first group. Group three mice are very large. The three groups segregated are thus also roughly size groups with a broad range of size in group one. Mice of groups two and three tend to have proportionately narrower teeth than those of group one. The small mice of group one are the most abundant and occur in all the localities. There are 191 specimens from the three sequence localities and 37 from the other localities. They form a close knit group on the basis of size, although they vary considerably in characteristics of the teeth other than size.

Within all three groups of *Peromyscus* variations of dental pattern, relative size of the dental elements and characteristics of the mandible occur. The purpose of this study is to determine the nature of these variations, their correlation with each other and other factors when possible, and their significance to an understanding of the history of this group in the Northern Great Basin.

The Northern Great Basin species of *Peromyscus* will be analyzed by groups. New species present in our collections will be described as they are encountered in the discussion. Group one species will be considered first. Frequencies of occurrence of variants will be those of the three sequential localities, Quartz Basin (Barstovian), Black Butte (Clarendonian) and Little Valley (Hemphillian) unless otherwise indicated. They provide the most useful quantitative samples and represent a late Tertiary sequence of similar communities. Species will be considered in their time order within groups and sub groups.

The appendicular skeletal elements of all of the species discussed are similar enough to living species that assignments are not difficult. Proportional differences do exist but will be described at a later date.

Figure 1. *Locality map; 2222, McKay Reservoir, Hemphillian; 2517, Bartlett Mountain, Hemphillian; 2500, Black Butte, Clarendonian; 2516, Little Valley, Hemphillian; 2469, Juniper Creek Canyon, Hemphillian, 2465, Quartz Basin, Barstovian.*


120°
119°
118°
117°
46°
45°
44°
43°
42°
Wash.
Ore.
COLUMBIA RIVER
30
PENDLETON
2222
JOHN DAY RIVER
395
30
BAKER
SNAKE RIVER
95
26
JOHN DAY RIVER
395
VALE
MALHEUR R.
2516
2517
2500
BURNS
20
BOISE
2469
2465
SNAKE RIVER
395
Ore.
Ida.
OWYHEE RIVER
95
LAKEVIEW
Ore.
Nev.
0 5 10 20 30
MILES

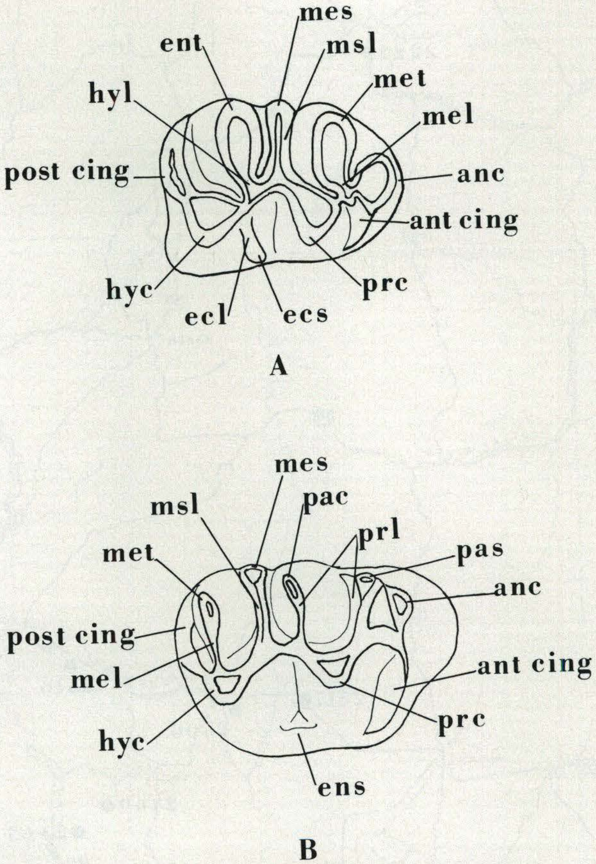


Figure 2. *Nomenclature of teeth;* **A,** *left lower first molar,* **B,** *right upper first molar.*

anc	*anterocone(id)*	**mel**	*metaloph(id)*
ant cing	*anterior cingulum*	**met**	*metacone(id)*
ecl	*ectolophid*	**msl**	*mesoloph(id)*
ecs	*ectostylid*	**pac**	*paracone*
ens	*entostyle*	**pas**	*parastyle*
ent	*entoconid*	**post cing**	*posterior cingulum*
hyc	*hypocone(id)*	**prc**	*protocone(id)*
hyl	*hypolophid*	**prl**	*protoloph*
mes	*mesostyle(id)*		

GROUP ONE

SMALL SPECIES

PEROMYSCUS PAGEI n.sp.[1]

TYPE: UO22623, a left mandible with M1-3.

HYPODYM: All from UOloc 2465; UO22972 right mand. M1-3; UO22617 right mand. M1-2; UO22637 right mand. M2-3; UO22645 right mand. M1-3; UO22662 left mand. M1-2; UO22622 left mand. M1-2; UO22635, UO 22632, UO22640, UO22644, UO22658, UO 22724 all lower first molars; UO22670 right mand. M3; UO22633 left max. M2-3; UO 22648 right max. M1-2; UO22646 left max. M1-2; UO22653 right max. M1-2; UO22641 left max. M2-3; UO22654 right max. M1; UO 22656, UO22661, UO22674, UO22675, UO 22643, UO22630, UO22659, UO22609, UO 22613, UO22652, UO22608, UO22663, UO 22669, UO22636, UO22665, UO22660, UO 226642, UO22673, UO22616, UO22634, all upper first molars; UO22626, UO22722, UO 22631, UO22639, UO22647, UO22676, all upper second molars; UO22687, UO22969, UO22686, all upper third molars.

TYPE LOCALITY: Quartz Basin UOloc 2465

AGE: Barstovian

DIAGNOSIS: A small species with complex low crowned teeth. Anteroconid of the M_1 a single cusp situated internal to the midline of the tooth in the form of a loop which is appressed with the metaconid, anterocone of M^1 bifurcated assymetrically, paraloph of M^1 single present in most specimens, parastyle often present, reduced hypocone (id) on third molars

DESCRIPTION: In the lower first molar the anteroconid is a single cusp and situated internal to the midline of the tooth giving an assymetrical appearance to the anterior portion of the tooth. There is no anterior cingulum internal to the anteroconid but it is well developed externally, sloping smoothly down to the base of the protoconid but not closing off the first external valley. The anteroconid and metaconid are appressed resulting in a narrow first internal valley. The metaconid and entoconid are connected to the other cusps at their anterior borders. There is a mesolophid on all specimens terminating in a mesotylid. An ectostylid and less often an ectolophid is apparent on a few specimens. The posterior cingulum slopes from the hypoconid to the base of the entoconid. There is a thickening of the cingulum at the position of the hypoconulid. This is reflected on the posterior face of the tooth in a hypoconal groove.

In the lower second molar the anterior cingulum extends the full width of the anterior border of the tooth. It connects high on the metaconid at its internal terminus and low on the protoconid at its external end. The metaconid and protoconid are connected to the center of the anterior cingulum by lophids. A small anterior internal lake is bounded by the anterior cingulum, metaconid and the lophid connecting the metaconid to the anterior cingulum. There is a well developed mesolophid terminating in a mesostylid. A low ectolophid is occasionally present. The entoconid is connected by a single lophid at its anterior end. The posterior cingulum extends from the hypoconid to a point low on the entoconid. A hypoconulid is present as is also a hypoconal groove on the posterior face of the tooth.

The lower third molar is similar to the second but with a greatly reduced hypoconid. This results in a posterior narrowing of the occlusal outline of the tooth. The internal valleys are closed off by a cingulum extended from the protoconid to the reduced hypoconid and continuous with the posterior cingulum. The mesolophid connects to this cingulum close to the hypoconid. Three small lakes are thus formed on the internal side of the tooth. The anterior lake is bounded by the mesolophid and protoconid, the central and smallest by the mesolo-

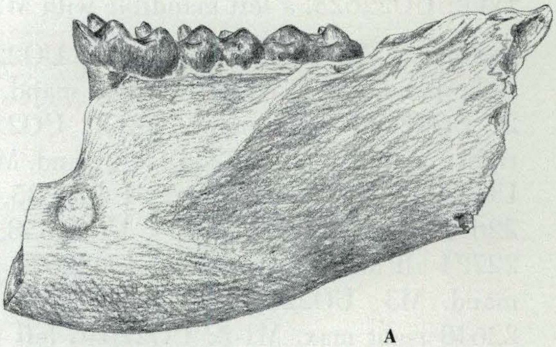
---

[1] This species is named for Mr. and Mrs. Ralph Page who for many years lived near Quartz Basin. At the time of our work in Quartz Basin the Page Ranch was owned by Mr. Jean Morcom who allowed us to use the facilities.

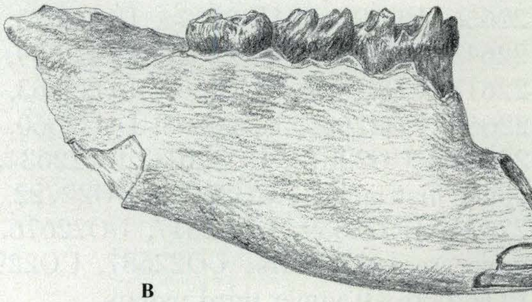
phid and hypolophid and the posterior by the hypolophid and posterior cingulum. In addition a very small lake appears in early wear anterior to the protoconid but is soon lost with wear.

In some specimens of the upper first molar the anterocone is slightly bifurcated assymetrically. The larger portion of the cusp is external and the smaller more centrally located. The bifurcation is expressed on the anterior face of the tooth only in early wear. The larger segment of the anterocone is displaced externally and tends to line up with the paracone and metacone. In other specimens a bifurcation of the anterocone is not distinct. The anterior mure is connected to the smaller segment of the anterocone. The paraloph and protoloph I connect to the anterior mure. Protoloph I is sometimes weak. It is strong when the paraloph is reduced or missing. Protoloph II is usually well developed. A parastyle is often present but may be replaced by a cingulum. The parastyle may be present even when there is no paraloph. The first internal valley is open. A well developed mesoloph is present on all the specimens and terminates in a mesostyle. An entostyle is often present located close to the hypocone. The metacone is connected by metaloph II in all specimens. The posterior cingulum extends from the hypocone to a point low on the metacone. A hypoconule is apparent in later wear with an accompanying shallow hypoconal groove on the posterior face of the tooth.

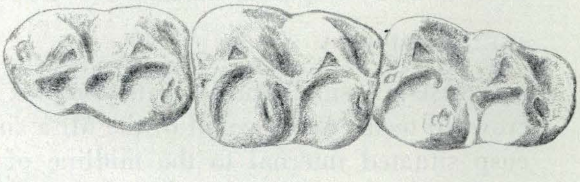
The anterior cingulum of the upper second molar forms the entire anterior border of the tooth. Externally it terminates in a well developed parastyle. Internally it connects low on the protocone. On some specimens the internal portion of the anterior cingulum is absent. Protolophs I and II are present on all specimens. Protoloph I connects to the anterior central margin of the protocone which extends to the center of the anterior cingulum. A narrow but prominent valley is formed between the anterior cingulum and the paracone. It is partially



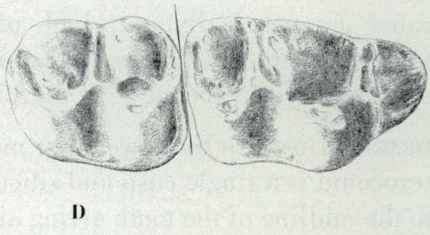
A



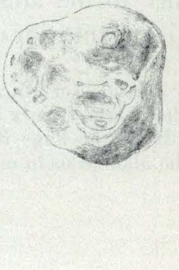
B



C



D



E

blocked by the low connection between the parastyle and paracone. The mesoloph is well developed and terminates in a mesostyle on all specimens. An entostyle is often present but no entoloph. The metacone is connected by a central metaloph. The posterior cingulum connects low on the metacone. The hypoconule and hypoconular groove are poorly developed or missing.

The anterior portion of the third upper molar is similar to that of the M^2. The posterior moiety of the tooth is much reduced with virtually no metacone and a reduced hypocone. As in the lower third molar the posterior cingulum is extended by an external cingulum to the anterior cusp (paracone). The metacone exists only as a point on this cingulum. A metaloph connects to the mure forming two lakes one between the metaloph and paracone and one between the metaloph and posterior cingulum. A small mesoloph may invade the anterior of these two lakes and sometimes isolates a segment of the lake into another very small lake.

DISCUSSION: The only known fossil species of *Peromyscus* which is comparable with *P. pagei* is *P. russelli* James. This species is larger than *P. pagei*. The known size ranges apparently do not overlap. These two mice are very similar and differ, other than size, primarily in the frequency of occurrence of accessory lophs and styles which are more common in *P. pagei*. The lingual valleys of the lower third molars and the labial valleys of the upper third molars of *P. pagei* are closed by a cingulum whereas these are apparently open in *P. russelli*. In *P. russelli* the lingual extension of the anterior cingulum of the M^2 is stronger. *P. pagei* and *P. russelli* are contemporaneous species both with complex dentitions and differing in much the same way living species with complex dentitions do.

Figure 3. Peromyscus pagei; **A**, **B**, *internal and external views of mandible type specimen UO 22623, x9,* **C**, *occusal view* $LM_{1\text{-}3}$, *UO22623, x18,* **D**, $RM^{1\text{-}2}$ *UO22653, x18,* **E**, RM^3, *UO22680, x18, all specimens from Quartz Basin UOloc, 2465 anterior to right in all but* **A**.

The frequency of occurrence of accessory structures and variants of *P. pagei* appear in in Table 2. Measurements are presented in Table 1. Measurements of the type specimen, lower dentition, follow:

UO22623-type mandible	AP	Tr
M^1	1.39	0.94
M^2	1.23	1.02
M^3	1.23	0.92

PEROMYSCUS DENTALIS Hall 1930A

Clarendonian Black Butte localities 2337 and 2500 represent similar environments and are in the same local stratigraphic position and not far apart. UOloc 2500 was worked with improved techniques which produced a considerable quantity of *P. dentalis* material whereas UOloc 2337 produced one specimen. The difference is solely due to the collecting techniques employed. The specimen from UOloc 2337 was described by Shotwell and Russell (1963).

The mandible fragments from these localities indicate that this portion of the skeleton is similar to previously known specimens. The mental foramen is anterior and labial to the M1. The groove between the M3 and the coronoid process is occupied by several foramina, one much larger than the others.

Fifty one specimens from UOloc 2500 (Black Butte) are assigned to *P. dentalis*. This large sample provides information on variation and on the character of the M_3 and upper cheek teeth previously not known.

In the lower first molar the individual cusps are high and very cuspate. The anteroconid and metaconid are appressed but with a narrow valley between. In about one half of the specimens the anterior cingulum is not well defined and appears as a sharpening of the large anteroconid towards the protoconid. In others it is present and forms a loop as in *P. pagei*. The metaconid is connected to the anteroconid by a narrow metalophid. On about one third of

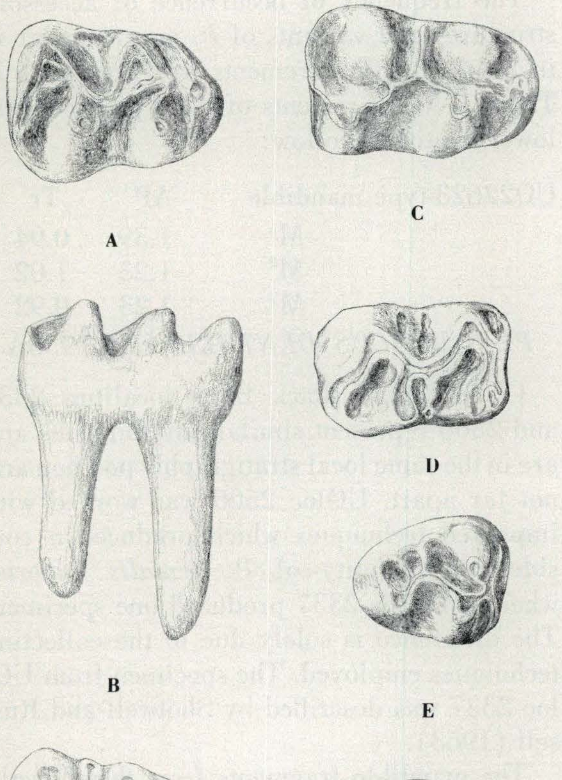


Figure 4. Peromyscus dentalis, *selected variants,* **A** *and* **B,** *LM_1, UO24486,* **C,** *RM_1, UO25097,* **D,** *RM_2, UO24864,* **E,** *LM_3, UO24531,* **F,** *RM^1, UO 24542,* **G,** *LM^1, UO25096,* **H,** *RM^3, UO24562,* **I,** *LM^2, UO24851, all from Black Butte UOloc 2500, all x18 with anterior to right.*

the specimens there is a mesolophid and mesostylid. An ectostylid is present on less than half of the specimens. The posterior cingulum connects low on the entoconid.

The anterior cingulum of the second lower molar is strong, externally sloping to the base of the protoconid. Internally the anterior cingulum connects at about the middle of the anterior face of the metaconid sometimes recurving enough to form a very small valley. The metaconid connects anteriorly to the anterior cingulum. The remainder of the cusps interconnect similarly to those of the M_1. Mesostylid or ectostylid occur on some specimens rarely both and neither is well developed when present. The posterior cingulum connects low on the entoconid. A hypoconulid is present as is a hypoconular groove.

The anterior portion of the third lower molar is similar to that of M_2. Posteriorly the entoconid is reduced and connects the posterior border of the protoconid and metaconid forming a lake. The posterior cingulum connects the much reduced hypoconid with the entoconid. The cingulum connects high on the entoconid thus forming another but smaller lake. A hypoconular groove is present.

The upper dentition of *P. dentalis* has not been previously described. Two variants are also seen in the upper first molar with several intermediate specimens. Several specimens are simple teeth with no accessory lophs or styles. Other specimens have well developed mesoloph and paralophs with mesostyles and parastyles and in other characteristics quite similar to *P. pagei.* Some specimens have very weak mesolophs and no paralophs or styles. On some specimens a poorly developed bifurcation of the anterocone can be seen but this is lost in early wear. On some specimens a short protoloph I is present.

Only the more complex variant of the upper second molar is present in the available material. The tooth is similar to that of *P. pagei,* however, somewhat simpler. No parastyle is present. The mesostyle is less well developed but a mesoloph is present on all the specimens and often short.

The third upper molar differs from *P. pagei* in the lack of a protoloph I. The lophs of the posterior moiety are reduced from the condition in *P. pagei.*

P. dentalis apparently has been derived from a species very much like *P. pagei.* They are about the same size. The primary differences in their tooth characters are those of a trend toward simplicity and reduction of the posterior moiety of the third molars.

The type of *P. dentalis,* from the Clarendonian Fish Lake fauna of Nevada, lacks accessory structures. In size it is close to the Black Butte specimens and is especially close to those individuals without accessory structures. It is concluded here that the Black Butte material simply provides a more complete picture of that species. Measurements of the Black Butte specimens are presented in Table 1. Measurements of the type specimen of *P. dentalis,* a mandible with first and second molars, are as follows:

	AP	Tr
M_1	1.46	0.97
M_2	1.32	1.03

PEROMYSCUS VALENSIS n.sp.[2]

TYPE: UO26920 mandible with incisor, M1-2

HYPODYM: UO25610 mand. M1-3; UO25611 mand. frag. M1-2; UO25625 mand. M1-3; UO25612-25622 all lower M1; UO25624 and 25625 lower M1; UO25626-25632 all lower M2; UO25633-25636 all lower M3; UO25641 and 25642 max. M1-2; UO25650 and 25651 max. M1-2; UO25637 max. M1-3; UO25638-25640 all upper M1; UO25643-25649 all upper M1; UO25652-25663 all upper M2; UO 25664 max. M2-3; UO25665 upper M3.

TYPE LOCALITY: UOloc 2516, Little Valley

AGE: Hemphillian

DIAGNOSIS: A small *Peromyscus,* the size of *P. dentalis.* Mandible lighter than *P. dentalis* but heavier than living species. Third molars relatively smaller than those of *P. dentalis,* similar to living species. Occurrance of accessory lophs and cusps much less frequent than in *P. dentalis.*

DESCRIPTION: The lower first and second molars are similar to those of *P. dentalis* except in the frequency of occurence of accessory cusps. In *P. valensis* the mesolophid, mesostyle and ectostylid appear in fifteen to twenty percent of the specimens whereas in *P. dentalis* about fifty percent have these accessory cusps. The upper first molar of *P. valensis* does not have a paraloph which is present in about one half of those of *P. dentalis.* The mesoloph appears less frequently in *P. valensis* but the mesostyle occurs with about the same frequency in both species. All of the known upper second molars of *P. dentalis* have a mesoloph while only one fourth of those of *P. valensis* have this accessory cusp.

The lower third molar of *P. valensis* is smaller than in *P. dentalis.* The hypoconid and entoconid are joined in a posterior lophid very similar to the posterior loop of many living cricetids. Other cusps of the posterior moiety of the tooth are absent. The posterior moiety is narrow resulting in a triangular occlusal outline. In the upper third molar the hypocone-protocone valley is represented by a notch. The hypocone and metacone appear as cusps accessory to the anterior moiety and form a single loop or small loph. The tooth is nearly round in occlusal outline.

P. antiquus is a much larger form although in some respects similar. Measurements of the Little Valley specimens are presented in Table 1. Measurements of the type lower dentition are as follows:

---

[2] This species takes its name from Vale, Oregon, which is near the type locality.

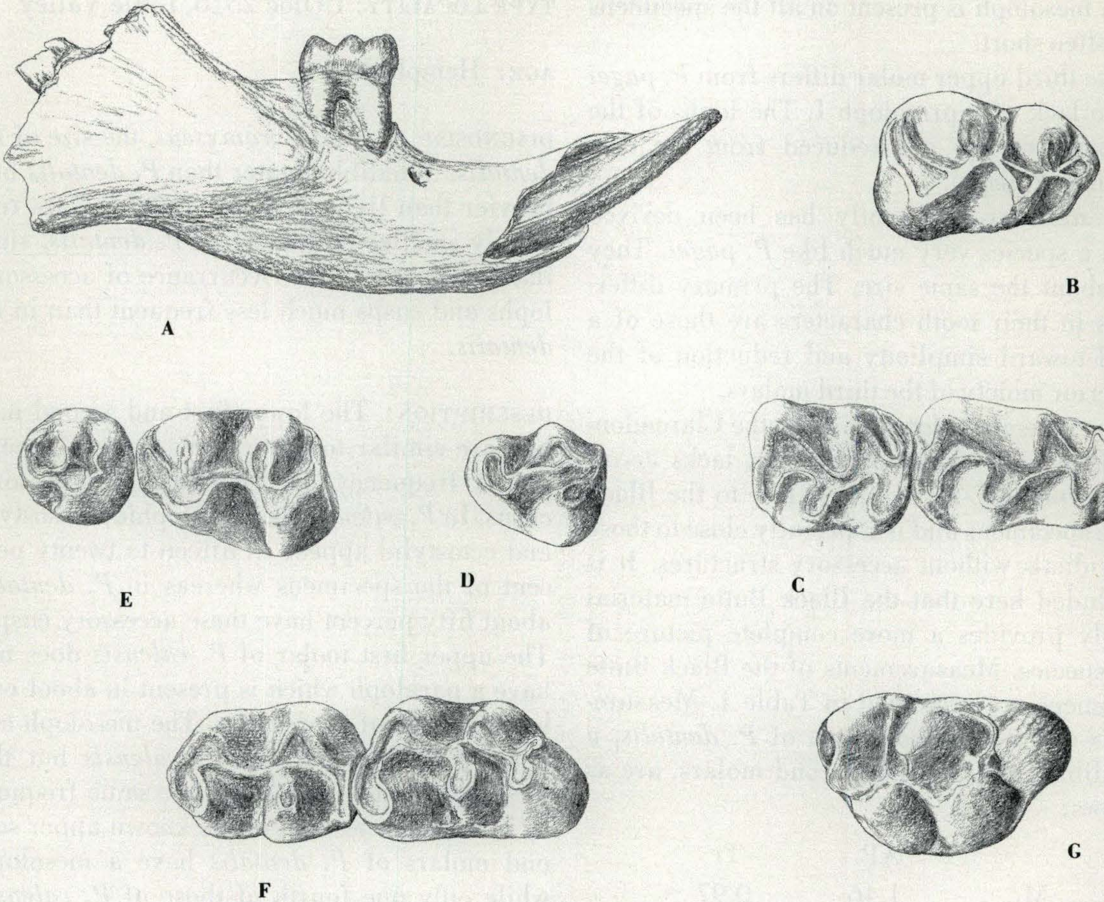


Figure 5. Peromyscus valensis; **A,** *right mandible, lateral view, UO26938, x9,* **B,** *RM_1, UO26939, x18,* **C,** *type specimen LM_{1-2}, UO26920, x18,* **D,** *LM_3, UO25634, x18,* **E,** *RM^{1-2}, UO25664, x18,* **F,** *LM^{1-2}, UO 25641, x18,* **G,** *RM^1, UO25648, x18, all specimens from Little Valley UOloc 2516, anterior to right.*

UO25641	AP	Tr
M^1	1.50	0.96
M^2	1.14	0.90

PEROMYSCUS cf. *VALENSIS*

At McKay Reservoir, an Hemphillian locality near the Columbia River, a species of *Peromyscus* is well represented and is close if not conspecific with *P. valensis*. The specimens from McKay Reservoir tend to have an anterior groove on the anterconid of the lower first molar. The frequency of the occurrence of accessory structures is similar to that in the Little Valley sample.

PEROMYSCUS cf. *VALENSIS*

Peromyscus is not common at Bartlett Mounttain, an Hemphillian site west of Little Valley in the Juntura Basin, however, the small sample available indicates a species close to *P. valensis*.

TABLE I

MEASUREMENTS OF THE TEETH

LOWER MOLARS

			M_1 AP			M_1 Tr				M_2 AP			M_2 Tr				M_3 AP			M_3 Tr		
Species	Locality	No. sp.	Range	X	s	Range	X	s	No. sp	Range	X	s	Range	X	s	No. sp.	Range	X	s	Range	X	s
P. pagei	2465	11	1.26-1.53	1.39	0.081	0.92-1.07	0.98	0.045	6	1.23-1.28	1.25	0.021	0.99-1.04	1.02	0.020	5	1.14-1.23	1.17	0.040	0.85-0.93	0.89	0.035
P. dentalis	2500	10	1.30-1.53	1.43	0.072	0.84-1.03	0.97	0.060	8	1.19-1.32	1.24	0.046	0.83-1.00	0.93	0.060	5	0.94-1.14	1.02	0.089	0.68-0.92	0.84	0.107
P. valensis	2516	18	1.25-1.56	1.40	0.086	0.76-1.02	0.90	0.072	12	1.11-1.36	1.19	0.072	0.85-1.03	0.94	0.052	5	0.86-1.03	0.94	0.089	0.76-0.85	0.79	0.040
P. valensis	2517	2	1.30-1.41	1.36	0.077	0.91-0.96	0.94	0.035	5	1.21-1.35	1.22	0.062	0.95-1.04	0.99	0.040	2	0.96-1.03	0.99	0.050	0.79-0.91	0.85	0.085
P. valensis	2222	4	1.42-1.57	1.50	0.075	0.81-1.11	0.93	0.150	4	1.20-1.26	1.23	0.030	0.90-0.96	0.93	0.030	1		0.99			0.73	
P. large sp.	2465	2	1.77-1.80	1.78	0.022	1.10-1.20	1.15	0.071	5	1.57-1.70	1.67	0.058	1.24-1.36	1.29	0.053	1		1.65			1.24	
P. large sp.	2500	1		1.65			1.12									1		1.41			1.24	
P. antiquus	2516																					
P. antiquus	2517								3	1.67-1.80	1.72	0.075	1.20-1.31	1.25	0.063	2	1.54-1.68	1.61		1.15-1.34	1.23	
P. antiquus	2222															2	1.17-1.22	1.19		0.89-0.91	0.90	
P. esmeraldensis	2500	6	1.67-1.87	1.76	0.081	0.98-1.09	1.03	0.049	14	1.31-1.56	1.40	0.071	1.05-1.22	1.14	0.048	9	1.13-1.44	1.28	0.103	0.89-1.01	0.96	0.040
P. cf. *esmeraldensis*	2516								3	1.41-1.46	1.43	0.029	0.97-1.02	1.00	0.014							
P. cf. *esmeraldensis*	2222	9	1.61-1.90	1.73	0.096	0.99-1.17	1.08	0.060	2	1.48-1.52	1.50		1.05-1.13	1.09								
P. cf. *esmeraldensis*	2517	2	1.64-1.66	1.65		0.94-0.98	0.96									2	1.15-1.18	1.17		0.92-0.95	0.93	
P. cf. *pliocenicus*	2469	1		2.26			1.29		2	1.87-1.93	1.90		1.39-1.43	1.41		1		1.58			1.22	
P. cf. *pliocenicus*	2516								1		2.32			1.87		1		1.90			1.45	
P. cf. *pliocenicus*	2222																					

s is estimated using $s = \frac{range}{\sqrt{n}}$ after Parratt 1961

TABLE I continued

MEASUREMENTS OF THE TEETH

UPPER MOLARS

		M^1							M^2							M^3						
			AP			Tr				AP			Tr				AP			Tr		
Species	Locality	No. sp.	Range	X	s	Range	X	s	No. sp	Range	X	s	Range	X	s	No. sp.	Range	X	s	Range	X	s
P. pagei	2465	23	1.51-1.74	1.63	0.062	0.93-1.15	1.03	0.059	12	1.10-1.29	1.22	0.054	0.98-1.13	1.04	0.043	5	0.96-0.97	0.96	0.004	0.92-0.98	0.95	0.026
P. dentalis	2500	9	1.46-1.68	1.54	0.073	0.94-1.05	1.00	0.036	7	1.15-1.25	1.21	0.037	0.93-1.05	0.99	0.045	1		0.96			0.92	
P. valensis	2516	11	1.40-1.68	1.55	0.084	0.84-1.11	0.98	0.081	16	1.02-1.28	1.14	0.074	0.85-1.07	0.96	0.062	4	0.77-0.86	0.80	0.045	0.77-0.94	0.84	0.085
P. valensis	2517								7	1.15-1.33	1.26	0.067	0.96-1.14	1.05	0.068	2	0.77-0.95	0.86		0.79-0.94	0.86	
P. valensis	2222	1		1.35			0.95		1		1.29			1.05								
P. large sp.	2465	2	2.08-2.12	2.10		1.23-1.31	1.27		4	1.33-1.62	1.49	0.15	1.16-1.40	1.24	0.12	1		1.10			1.12	
P. large sp.	2500								1		1.49			1.29								
P. antiquus	2516	2		1.78		1.25-1.26	1.26		2	1.45-1.48	1.47		1.13-1.19									
P. antiquus	2517															2	1.35-1.36	1.36		1.15-1.33	1.24	
P. antiquus	2222																					
P. esmeraldensis	2500	12	1.64-1.87	1.74	0.066	0.99-1.22	1.08	0.066	12	1.29-1.54	1.38	0.072	0.94-1.19	1.07	0.072	7	1.08-1.24	1.15	0.060	0.94-1.06	0.98	0.045
P. cf. *esmeraldensis*	2516	1		1.72			1.19		1		1.43			1.08								
P. cf. *esmeraldensis*	2222																					
P. cf. *esmeraldensis*	2517	2	1.45-1.64	1.55		0.93-1.04	0.99									1		0.95			0.90	
P. cf. *pliocenicus*	2469	3	2.15-2.28	2.22		1.47-1.59	1.54		1		1.92			1.47								
P. cf. *pliocenicus*	2516								1		2.10			1.74								
P. cf. *pliocenicus*	2222								2	2.10-2.15	2.12		1.47-1.84	1.66								

s is estimated using $s = \frac{range}{\sqrt{n}}$

COMPLEXITY

The basic pattern of the molars of *Peromyscus* is one of four alternating cusps. In the upper and lower first molars an additional anterior cusp is present. While in the upper and lower third molars the posterior cusps may be reduced or absent. Anterior or posterior cingula are present and vary in their development. The basic cusps also vary in their form. Accessory structures, lophs and styles, may appear between the major cusps. When present they complicate the dental pattern depending on how many are present and their degree of development. Complexity is thus another variation of the dentition. The various samples used in this study differ in the frequency of occurrence of accessory structures rather than in their simple presence or absence.

The accessory lophs, when present, occupy the valleys between the basic cusps and are directed towards the margin of the tooth. In their fullest development they terminate on the margin and fuse with their respective stylar cusp, a small pillar-like accessory structure which appears on the margin of the tooth. Accessory lophs and styles may appear independently, that is one may be present when the other is not. These structures take their names from their position on the tooth, thus paraloph, parastyle, mesoloph mesostyle entostyle, entoloph, ectolophid and ectostylid. Figure 2 illustrates the nature and position of these structures when present. The paraloph and parastyle are found only in the upper teeth. The ectoloph and ectostyle are found in the upper teeth. Their equivalents in the lower teeth are the ectostylid and ectolophid. When the structures are indicated for lower teeth the suffix *id* is used and when they are indicated for both uppers and lowers the convention loph (id) or style (id) is employed.

In describing the frequency of appearance of these accessory lophs and styles they may be noted independently or the frequency of occurrence of various combinations appearing on individual teeth may be indicated. Table 2 indicates the frequency of occurrence of the accessory structures of the upper and lower first and second molars. The data are recorded as percentages to allow comparisons. The frequency of accessory structures decrease across the table for all structures and all teeth from *P. pagei* to *P. valensis*, a progression from oldest to youngest. Mesostyles and mesolophs tend to be more abundant on the upper molars than mesostylids and mesolophids of the lower molars. However, ectostylids and ectolophids of the lower molars are more abundant than are entostyles and entolophs of the uppers.

Style(id)s and loph(id)s of the same tooth position (viz. mesostyle-mesoloph) may occur together or independently. When they occur together the loph may reach the style on the border of the tooth or it may be short, thus the loph and style may be fused or separate. Other possible combinations include the loph or style appearing alone or neither loph or style present. Five combinations of loph and style are thus possible: 1. loph and style present and connected, 2. loph and style present but not connected, 3. loph only present, 4. style only present, 5. neither loph or style present. These are similar to combinations recognized by Hooper (1957) in his work on living species of *Peromyscus.* The combinations from 1-5 represent a series from most complex to least complex although combinations 3 and 4 may be equivalent. Frequencies of occurrence of these combinations give a more accurate indication of complexity and are presented for the three sequence species in Table 3. Only the most complex combinations of mesostyle(id) and mesoloph(id) occur in the dentition of *P. pagei.* In *P. dentalis* all combinations of mesostyle(id) and mesoloph(id) occur. The available sample is about equally split between complex and simple combinations. All combinations are also present in *P. valensis,* however, the simplest are the most abundant. The more complex combinations of ectostylid and ectolophid occur in the lower dentitions of *P. pagei* and *P. dentalis* but not in *P. valensis.* Complex combinations of the entostyle and entoloph of

TABLE 2

FREQUENCY OF OCCURRENCE OF STYLE(ID)S AND LOPH(ID)S $\frac{\text{M1-2}}{\text{M1-2}}$

		UOloc 2465	UOloc 2500	UOloc 2516	UOloc 2500
		P. pagei	*P. dentalis*	*P. valensis*	*P. esmeraldensis*
mesostyle(id)	M_1	100	55.6	22.2	16.7
	M_2	100	25.0	25.0	0
	M^1	100	44.4	40.0	20.0
	M^2	100	66.7	20.0	0
mesoloph(id)	M_1	100	44.4	16.7	100
	M_2	100	37.5	8.3	81.9
	M^1	100	66.7	20.0	100
	M^2	100	100	6.7	100
ectostylid	M_1	54.6	55.6	11.1	16.7
	M_2	50.0	50.0	0	0
entostyle	M^1	43.5	0	0	0
	M^2	33.3	16.7	0	0
ectolophid	M_1	27.3	22.2	0	66.7
	M_2	50.0	12.5	0	50.0
entoloph	M^1	0	0	0	20.0
	M^2	0	0	0	0
no. specimens	M_1	11	9	18	6
	M_2	6	8	12	11
	M^1	23	9	10	10
	M^2	12	6	15	11
Totals		52	32	55	38

TABLE 3

FREQUENCY OF LOPH AND STYLE COMBINATIONS

		P. pagei				*P. dentalis*				*P. valensis*			
	Combination	M_1	M_2	M^1	M^2	M_1	M_2	M^1	M^2	M_1	M_2	M^1	M^2
meso	1	100	100	100	100	33.3	25.0	33.3	33.3	5.5		10	
	2					11.1		11.1	33.3	5.5	8.3		
	3						12.5	22.2	33.3	5.5		10	6.7
	4					11.1				11.1	16.7	20	20
	5					44.4	62.5	33.3		72.2	75.0	60	73.3
ento-ecto	1	27.3	50.0				12.5						
	2					22.2							
	3												
	4	27.3		43.5	33.3	33.3	37.5		16.7	11.1		10	
	5	45.4	50.0	56.5	66.7	44.4	50.0	100	83.3	88.9	100	90	100

TABLE 4

FREQUENCY OF JOINT OCCURENCES OF STYLE(ID) AND LOPH(ID) COMBINATIONS

		P. pagei				*P. dentalis*				*P. valensis*			
m	e	M_1	M_2	M^1	M^2	M_1	M_2	M^1	M^2	M_1	M_2	M^1	M^2
1	1	27.3	50.0				12.5						
1	2					22.2							
1	4	27.3		43.5	33.3								
1	5	45.4	50.0	56.5	66.7	11.1		33.3	33.3	5.5		10	
2	4					11.1	12.5		16.7				
2	5							11.1	16.7	5.5	8.3		
3	5						12.5	22.2	33.3	5.5		10	6.7
4	4									5.5			
4	5					11.1				5.5	16.7	20	20
5	4					22.2	37.5			5.5		10	
5	5					22.2	25.0	33.3		66.7	75.0	50	73.3
Totals		11	6	23	12	9	8	9	6	18	12	10	15

the upper dentition do not occur in any of the samples since entolophs are absent. The ectolophid does not occur alone in any of the samples and is unknown in any combination in the *P. valensis* sample. A reduction in frequency of complex combinations of accessory lophs and styles from *P. pagei* through *P. valensis* is present as well as a complimentary increase in the frequency of simple combinations or lack of these structures.

The mesostyle(id) and mesoloph(id) occur near the middle of the tooth while the ecto and ento style(id) and loph(id) occur on the posterior portion of the tooth. Combinations of both groups of accessory structures can thus occur jointly on a single tooth. Table 4 indicates the frequency of occurrence of joint combinations of accessory structures in the samples. Combinations are arranged in the table with the most complex at the top and simplest at the bottom. Although there are five recognized combinations of each of the two pairs of structures it was noted in Table 3 that one of the combinations, ectolophid or entoloph alone, does not occur in any of the samples, thus only twenty types of joint occurrence are expected. It is clear from Table 4 that not all these joint combinations occur in the samples. Only a total of eleven are present among all three samples. Table 2 indicates that the entoloph of the upper dentition does not occur in any of the samples so that combinations of the posterior accessory structures of the upper dention are limited to two, presence or absence of the entostyle. However, in the lower dentition both ectostylid and ectolophid occur but only in four combinations as noted above.

The more complex combinations of ectostylid-ectolophid occur jointly only with equally complex combinations of mesostylid-mesolophid. Complex combinations of ectostylid-ectolophid do not occur with simpler combinations of mesostylid-mesolophid. This accounts for eight of the nine missing joint combinations. In *P. dentalis* and *P. valensis* joint combinations occur in which the ectostylid is the only accessory structure present but these are relatively simple combinations. No combination of mesolophid and ectostylid appears on any teeth in the samples. Table 4 emphasizes the strong trend from a few (3) complex joint combinations in *P. pagei* to most of the combinations seen (9) in *P. dentalis* with the frequencies of occurence spread over the entire range of complexity, to *P. valensis* which exhibits seven of the joint combinations but has the frequencies of occurrence heavily concentrated in the simpler ones. In other words there is a trend from highly complex teeth to relatively simple teeth in this time sequence.

There are additional accessory structures which do not occur on all the molars. Two of these are the parastyle and paraloph of the upper first molar. This pair of structures is similar in their development and combinations of occurrence to the other accessory structures. However, as in the case of the entoloph the paraloph does not occur alone on any of the upper molars of the samples used here, thus only four combinations are possible. Table 5 indicates the frequency of joint occurrence of the various combinations of paraloph and parastyle with those of the mestostyle-mesoloph and entostyle on the upper first molar. The pattern of these combinations is similar to that of the other accessory structures, both in the distribution of complexity and the lack of certain possible joint occurrences. Forty four combinations might be expected but only twelve appear. The paraloph-parastyle appears to be limited in complexity, relative to the mesostyle-mesoloph, in much the same way as the ectostylid-ectolophid of the lower dentition was limited relative to the mesostylid-mesolophid combinations.

In the upper second molar, as well as the other upper molars, the anterior external cusp is joined to the anterior internal cusp at their posterior borders by a small loph referred to as protoloph II. In some specimens an additional anterior connection is also present and is termed protoloph I. The frequency of occurrence of this structure relative to combinations of the mesostyle-mesoloph and entostyle is presented in Table 6. Protoloph I occurs on all of the upper second molars of the *P. pagei* sample, none of the upper second molars of *P. dentalis*, and twenty five percent of those of *P. valensis*. Allowing for the small sample size of *P. dentalis* it appears that protoloph I may follow a similar pattern of reduced frequency in time as do the other accessory structures.

TABLE 5

FREQUENCY OF JOINT OCCURRENCE OF PARA, MESO AND ENTO STYLE AND LOPH COMBINATIONS IN M^1

p	m	e	*P. pagei*	*P. dentalis*	*P. valensis*
4	1	4	4.4		
1	1	4	39.2		
4	1	5	8.7		10.0
1	1	5	47.7	33.3	
5	2	5		11.1	
5	3	5			10.0
4	3	5		11.1	
1	3	5		11.1	
5	4	5			20.0
4	5	4			10.0
4	5	5			20.0
5	5	5		33.3	30.0
Total specimens			23	9	10

The nonrandom distribution of joint occurrences of accessory structures in each of the samples suggests that there is some genetic relationship between the appearance and development of the accessory structures. A degree of interdependence is apparent. This may indicate a rather simple genetic basis for the accessory structures and account for their similar occurrence, independently, among many cricetids.

THIRD MOLARS

Changes in morphology of the dentition of late Tertiary *Peromyscus* are apparent and form recognizable trends. These morphological changes can be recognized in characteristics other than those involved in complexity of tooth pattern. In searching for such trends the first and second molars appear to be less useful than the third molars. This is not uncommon in cricetids. It has previously been recognized that there is an apparent reduction in size of the lower third molar relative to the other molars particularly in anterior-posterior diameter, although strong statistical evidence was not available (see Wilson 1936, p. 33). The materials used in this study, although

TABLE 6

OCCURRENCE PROTOLOPH I ON M^2

		Present			Absent		
m	e	*P. pagei*	*P. dentalis*	*P. valensis*	*P. pagei*	*P. dentalis*	*P. valensis*
1	4	4					
1	5	8				2	
2	4					1	
2	5					1	
3	5			1		2	
4	5			1			2
5	5			1			10
Totals		12	0	3	0	6	12
No. sp.		12	6	15	12	6	15

not providing the type of statistical evidence most desirable, do provide reasonably well controlled samples from which consistent character changes in the M_3 are recognized.

The lower third molars of *P. pagei* from the earliest step of the sequence (Quartz Basin, Barstovian) are similar to the lower second molars in their anterior moiety but are somewhat modified in the posterior moiety. The entoconid, one of the four major cusps, is reduced to the size and development of a large stylar cusp. The hypoconid, the other major cusp of the posterior moiety is but little reduced and the accessory lophs and cusps are present. The posterior narrowing of the occlusal outline, so noticeable in these teeth, is apparently a reflection of the reduction of the entoconid. In the next younger sample of the sequence, *P. dentalis* from Black Butte (Clarendonian), similar modifications of the major cusps occur with possibly additional reduction of the hypoconid. In the youngest sample of the sequence, *P. valensis* (Little Valley, Hemphillian), the hypoconid and entoconid are joined in a posterior lophid very similar to the posterior loop of many cricetids. Other features of the posterior moiety of the tooth are absent. This later change may in part also reflect the simpler teeth of this stage of the sequence. The hypoconid portion of the loop forms the posterior border of the tooth. The posterior moiety of the tooth is noticeably narrower than in the earlier samples and in fact the occlusal outline in worn specimens is triangular rather than rectangular. Through this sequence there is a marked reduction of the major cusps of the posterior moiety of the lower third molar until in *P. valensis* of the Hemphillian essentially the character of living species of *Peromyscus* is reached.

A similar sequence of reduction and modification of cusps is also evident in the upper third molar. This tooth is relatively smaller than the lower third molar. The upper third molar occludes only with the lower third whereas the lower third occludes with both the upper third and posterior moiety of the upper second molar. This is a general characteristic of the occlusion of *Peromyscus* cheek teeth. The lower teeth occlude somewhat anterior to the upper teeth. Thus the lower first molar occludes only with the upper first. The upper first occludes with both the lower first and second. The lower second with the upper first and second, the upper second with the lower second and third. The situation in the third molar has already been described. The consistently smaller size of the upper third molar as compared with the lower third is thus a function of the total cheek tooth occlusion.

The upper third molars of *P. pagei* in the earliest step of the sequence display a greatly reduced hypocone more so than the comparable hypoconid of the lower third molars. Similarly the metacone is reduced to a stylar cusp. The anterior moiety is, however, essentially like that of the upper second molar. A valley exists between the hypocone and protocone as in the other upper cheek teeth. Upper third molars in the subsequent *P. dentalis* have this valley greatly reduced and the hypocone reduced to virtually a stylar cusp. By the Hemphillian *P. valensis,* the hypocone-protocone valley is represented by only a notch. The hypocone and metacone appear as accessory cusps to the anterior moiety and form a single loop or small loph. These changes in expression of characters are reflected in the occulusal shape of the tooth. At the beginning of the sequence the upper third molar presents a much rounded triangular occlusal outline but by the Hemphillian it is nearly round, similar to the condition of the living species.

The progressive reduction and modifications of the posterior moiety of the third molars and the resulting change of occlusal outline in mice of group one appear to be accompanied by size reduction relative to the other molars especially in the lower third molar (Table 1). Since much of the material used in this study consists of isolated teeth, direct comparisons between first molars and third molars on an individual basis is not possible. However, the lower first molars of mice from group one of the three sequence localities are nearly the same size as indicated by the means of anterior-posterior measurements. Difference then of size in the third molars will thus also indicate relative size differences. The means of anterior-posterior measurements of the third lower molar in *P. pagei* are much greater than those for *P. valensis*. The mean measurement of the intermediate *P. dentalis* is slightly less than that for the Barstovian species. This data suggests an absolute and relative size reduction in the lower M3 from Barstovian to Hemphillian. The fact that these are means of unassociated individual teeth detracts from the significance of any conclusions which may be drawn from them.

MANDIBLES

The smaller species of *Peromyscus* of group one (*P. pagei, P. dentalis, P. valensis*) and the modern species living in the Northern Great Basin today have first and second molars in the same size range. Using this as a basis for size other aspects of the dentition and skeleton may be compared. Reduction in the third molars during the time involved has already been described.

The incisor and mandible may be compared using the size grouping based on the tooth size already noted. The mandible of *P. pagei* is much deeper below the first molar than that of subsequent species. The incisor is also deeper but about the same width. Table 7 indicates the differences.

TABLE 7

Species	Depth of ramus below M1	Depth of incisor	Width of incisor
P. pagei	3.6	1.37	0.62
P. dentalis	3.3	no data	no data
P. valensis	3.0	1.15	0.60
P. rubidens	2.7	1.02	0.50

The figures in Table 7 are based on single comparable specimens so that they are only suggestive not necessarily conclusive. However, they verify impressions gained by observation. There is an apparent progression from a heavy jawed form to one with a delicate jaw. The differences between *P. pagei* and living species, the extremes of the progression, are quite striking. Even with the number of progressive differences so far described, complexity, third molar reducation, size of jaw and incisor there are basic similarities in all the specimens. The first and second molars are, of course, similar in size, the position of the posterior end of the incisor is similar. On all of the species there is a foramen between the third molar and the ascending ramus of the lower jaw. The mental foramen is situated similarly on all the species.

GROUP ONE

Large Species

Specimens representing significantly larger species with brachydont cuspate dentitions are known from Quartz Basin, Black Butte and Little Valley. They are, however, not as abundant as the smaller ones.

PEROMYSCUS sp.

The larger species of *Peromyscus* from UOloc 2465 (Quartz Basin) is only slightly larger than *P. russelli* but obviously larger than *P. pagei.* The most prominent feature of the M_1 of the larger species, other than its greater size, is the closing off of the first internal valley by the anterior cingulum, resulting in the formation of a small lake. The anteroconid and metaconid do not appear to be appressed as in *P. pagei.* As in *P. pagei* the metaconid and entoconid are connected on the anterior borders to the other cusps of the tooth. All specimens have mesolophid and mesostylid. A low ectolophid is present but apparently no ectostylid. The hypoconulid is prominent as is the hypoconal groove. The major cusps of the M_2 give the appearance of being tipped anteriorly. Other features are as in *P pagei,* with the hypoconulid and hypoconal groove well developed. Only one specimen of an M_3 is known for the large species. Other than its greater size the most prominent feature is the posterior internal extension of the anterior cingulum to the ectolophid. This extended cingulum completely isolates the protocone from the border of the tooth.

The anterocone of the M^1 is lophid rather than conid and bifurcated as in the smaller species. The anterior cingulum extends externally and posteriorly to the protocone connecting about midway up its side. The broad first external valley is thus partially cut off forming a lake. A poorly developed paraloph invades this basined valley. The first internal valley is

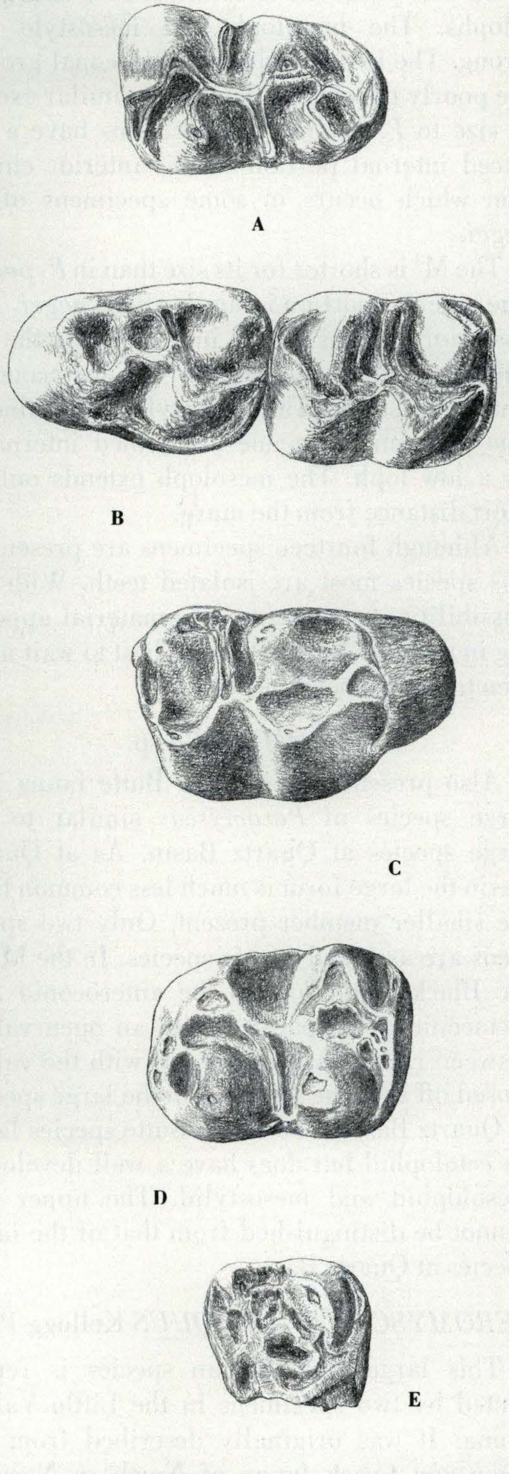


Figure 6. Peromyscus *large sp.*; **A,** *LM_1, UO22649,* **B,** *RM_{2-3}, UO22621,* **C,** *RM^1, UO22638,* **D,** *LM^2, UO22610, LM^3, UO22629, all x18, all specimens from Quartz Basin UOloc 2465, anterior to right.*

open. The paracone is connected by both protolophs. The mesoloph and mesostyle are strong. The hypoconule and hypoconal groove are poorly developed. The M^2 is similar except in size to *P. pagei.* All specimens have a reduced internal portion of the anterior cingulum which occurs in some specimens of *P. pagei.*

The M^3 is shorter for its size than in *P. pagei.* The anterior portion is similar to *P. pagei.* The posterior portion differs in not having the extended posterior cingulum. The metacone is small and stylar. The mesostyle is prominent. The paracone-metacone are joined internally by a low loph. The mesoloph extends only a short distance from the mure.

Although fourteen specimens are present of this species most are isolated teeth. With the possibility of more complete material appearing in the near future it seems best to wait until then to erect a new species.

PEROMYSCUS sp.

Also present in the Black Butte fauna is a large species of *Peromyscus* similar to the large species at Quartz Basin. As at Quartz Basin the large form is much less common than the smaller member present. Only two specimens are assigned to this species. In the M_1 of the Black Butte species the anteroconid and metaconid are separated with an open valley between rather than appressed with the valley closed off as is the situation in the large species at Quartz Basin. The Black Butte species lacks an ectolophid but does have a well developed mesolophid and mesostylid. The upper M2 cannot be distinguished from that of the large species at Quartz Basin.

PEROMYSCUS cf. *ANTIQUUS* Kellogg 1910

This large Hemphillian species is represented by two specimens in the Little Valley fauna. It was originally described from the Thousand Creek fauna of Northern Nevada. The known material suggests that *P. antiquus* lacks the accessory structures seen in the earlier large species reported above, and thus indicates that a similar progression of complex to simple dentition also occurs in the large species. *P. antiquus* is also represented in the Bartlett Mountain and McKay Reservoir faunas.

GROUP TWO

PEROMYSCUS cf. *ESMERALDENSIS*
(Wood) 1964

UOloc 2500 of the Clarendonian Black Butte fauna includes a common large mouse. It is distinct in that the cusps are very high and strongly lophid in character. Small accessory lophs and styles are prominent and result in a complex pattern. The base of the valleys are as low as in other *Peromyscus* teeth so that "high-crowned" may not be a proper description. Early wear in these teeth is similar to that of species of *Peromyscus* with lower cusps, that is; among the major cusps of the dentition the protocone, protoconid, and hypocone and hypoconid quickly wear to a flat tritating surface while the other major cusps remain cuspate in form until later wear. In *P. esmeraldensis* the cusps of the teeth wear differentially as noted above but only in early wear. In subsequent wear all the cusps present flat tritating surfaces and the teeth thus take on the appearances of those of microtines, alternating triangles and all. Sixty molars from UOloc 2500 are assigned to this species.

The first lower molar has a complex occlusal pattern. The anteroconid is divided into two equal sized cusps. The division is primarily on the posterior face of the cusp with only occasionally a shallow broad groove on the anterior face. The anterior cingulum drops off sharply on the labial side to the base of the protoconid. The lingual anteroconid cusp and the metaconid are close but separated by an open, narrow reentrant valley. The metaconid and protoconid connect anteriorly in a mure. This anterior mure connects to the cusps of the anteroconid in a variety of ways. In most specimens one lophid connects from the mure to the lingual cusp of the anteroconid. This, of course, is the border to the first reentrant valley. In a number

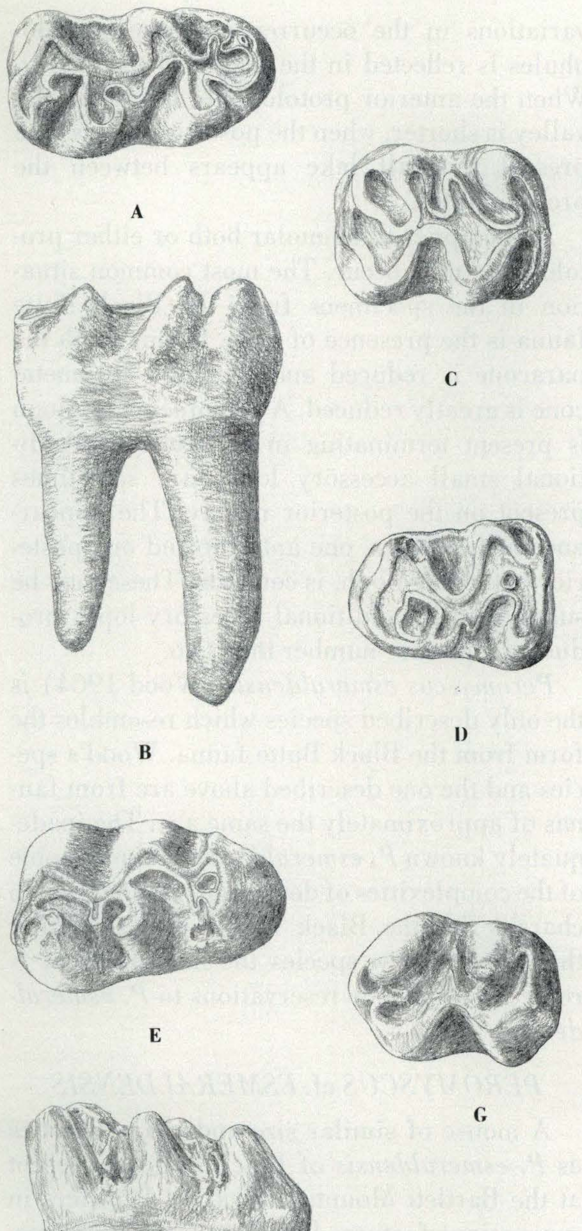


Figure 7. Peromyscus *cf.* esmeraldensis; **A** *and* **B,** *LM_1, UO22885,* **C,** *RM_2, UO24518,* **D,** *LM_3, UO 24853,* **E** *and* **F,** *LM^1, UO22886,* **G,** *RM^2, UO 25081,* **H,** *RM^3, UO24557, all x18, all specimens from Black Butte UOloc 2500, anterior to right.*

of specimens the mure is Y shaped with the other branch extending to the labial cusp of the anteroconid. In some specimens this branch is not complete and may be directed labially taking the appearance of a paralophid with a short lophid extending posteriorly from the labial anteroconid and terminating between the arms of the Y. In some specimens when the arms of the Y connect to the two anteroconid cusps a short paralophid appears at the junction of the arms.

A mesolophid is present on all the specimens of lower first molars present. It varies considerably among the specimens, however, most of this variation may be attributed to differences in stage of wear. In little worn specimens the mesolophid is spur-like and short. It appears at the connection of the entoconid and central mure. At this stage of wear the mesoloph borders a deep invagination of the anterior internal face of the entoconid. This invagination of enamel is lost from the occlusal pattern with wear. In later wear there is thus only the mesolophid. In one specimen the mesolophid extends to the border of the tooth and connects to an angular extension of the metaconid. None of the specimens exhibit a mesostylid but almost all have an ecotostylid but no ectolophid or only a slight irregularity in the enamel at that point. The posterior cingulum extends to the base of the entoconid. A well developed hypoconulid is present, only slightly smaller than the hypoconid. From this hypoconulid a small spur-like lophid extends anteriorly toward the entoconid.

The lower second molar reflects many of the characteristics of the first molar. The anterior portion is, of course, reduced to the anterior cingulum which is primarily labial. However, the cingulum extends a short distance lingually exhibiting a small valley between it and the metaconid in early wear. In later wear the metaconid appears to form the anterior lingual face of the tooth. The invagination into the entoconid present on the M_1 at the mesolophid is not present on the M_2. The hypoconulid is developed similarly to that cusp in the lower first molar.

In the third lower molar the protoconid is attached by both protolophids creating a small lake in that position. The entoconid is greatly reduced and tends to connect anteriorly by a cingulum with the metaconid resulting in a long diagonal lake in later wear. Similarly the posterior cingulum connects to the entoconid forming a much smaller posterior lake.

The upper first molar parallels the lower first molar in many aspects. There is incipient twinning of the anterocone. The labial cusp is in line with the paracone and metacone. The lingual cusp of the anterocone is connected to the anterior mure. A paraloph is usually present connecting it also to the mure, but seldom reaching more than halfway to the border of the tooth. An additional loph sometimes connects the labial cusp to the anterior mure as in the lower first molar. In later wear the mure appears to broadly connect to both cusps. A small parastyle is present in less than half of the specimens. The protocone and hypocone are lophid and join to form a W shaped composite loph which includes the posterior cingulum. The mesoloph is short and spur-like. On a few specimens a mesostyle is present. The paracone and metacone are stylar in appearance and connects by lophs on their posterior sides to the protocone-hypocone loph. The posterior cingulum connects high on the metacone. A small lake is formed by the posterior cingulum. There is no apparent development of the hypoconule.

The upper second molar is similar to the upper first molar except in its anterior moiety. The anterior cingulum extends from the protocone to the base of the paracone forming most of the anterior face of the tooth. At its inception on the protocone a distinct ridge appears on the anterior face of the protocone. The paracone has only a posterior connection to the mure. There is thus a long curved diagonal valley in the anterior moiety of the tooth which opens just anterior to the paracone. This valley also appears on the upper third molar, however, variations in the occurrence of the protolophules is reflected in the length of the valley. When the anterior protolophule is present the valley is shorter, when the posterior one is also present a small lake appears between the protolophules.

In the upper third molar both or either protolophule may occur. The most common situation in the specimens from the Black Butte fauna is the presence of both. In this tooth the paracone is reduced and lophoid. The metacone is greatly reduced. A prominent mesoloph is present terminating in a mesostyle. Additional small accessory lophs are sometimes present on the posterior moiety. The appearance of two lakes, one anterior and one posterior to the mesoloph, is common. These may be subdivided by additional accessory lophs producing a greater number than two.

Peromyscus esmeraldensis (Wood 1964) is the only described species which resembles the form from the Black Butte fauna. Wood's species and the one described above are from faunas of approximately the same age. The inadequately known *P. esmeraldensis* includes some of the complexities of dental morphology which characterize the Black Butte species. Rather than erect a new species the new material is referred with some reservations to *P. esmeraldensis.*

PEROMYSCUS cf. *ESMERALDENSIS*

A mouse of similar size and characteristics as *P. esmeraldensis* of Black Butte is present at the Bartlett Mountain locality. It differs in some minor features from the Black Butte species. Most notable is the close contact of the anteroconid and metaconid in the lower first molar. These two cusps are in contact forming a small lake between them and the anterior mure. The anteroconid is twinned but in some specimens appears to be divided laterally into three cusps. On one specimen of lower first molar there is a bump in the enamel on the posterior face of the entoconid giving it a trefoil appearance. Other elements of the dentition are not well enough represented to allow

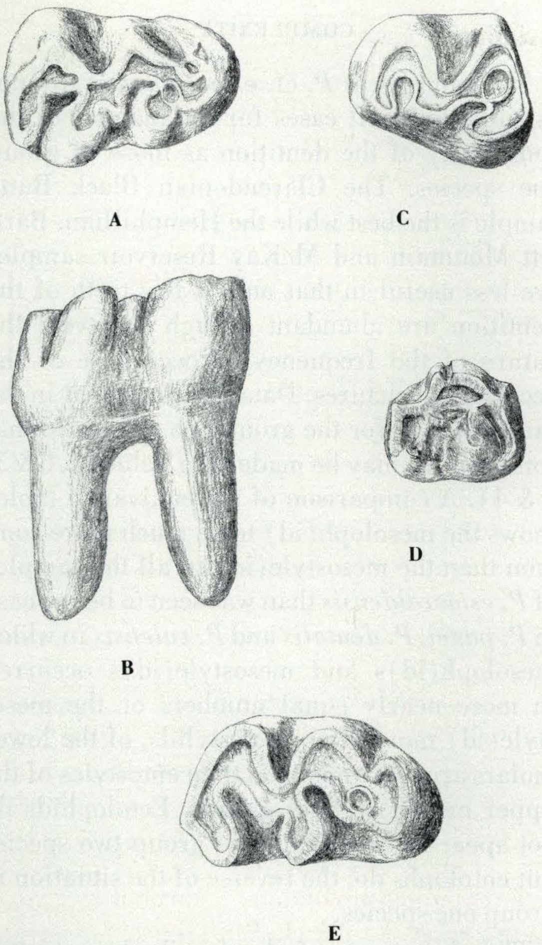


Figure 8. Peromyscus *cf.* esmeraldensis; **A** *and* **B,** *LM_1, UO25591,* **C,** *LM_3, UO26940,* **D,** *LM^3, UO 25078,* **E,** *LM^1, UO24957, all x18, all specimens from Bartlett Mountain UOloc 2517, anterior right.*

recognition of consistent differences with the Black Butte species. The nature of the lower first molar suggest such differences do exist but cannot be well characterized with the available specimens. This species is thus referred to *P.* cf. *esmeraldensis* primarily to reflect its similarities with the Black Butte species.

PEROMYSCUS cf. *ESMERALDENSIS*

At Little Valley lophiodont high crowned mice are rare. Only five specimens are present in the sample available.

PEROMYSCUS cf. *ESMERALDENSIS*

P. cf. *esmeraldensis* is also present in the McKay Reservoir fauna. The lower first molar differs from both the Black Butte and Bartlett Mountain species in having a single cusped anteroconid. The anteroconid and metaconid are closely appressed, even more so than in the Bartlett Mountain species, in fact the only separation is in a shallow groove on the face of the tooth. In later wear the anteroconid, anterior cingulum and metaconid are completely fused and appear as an anterior loop. A mesolophid is present on most of the specimens. Stylids are rare except on the M_1. The hypoconulid is well developed and approaches the hypoconid in size.

Again sufficient material is not present to characterize a new species. However, the material available from McKay Reservoir suggests significant differences from that previously described to indicate a probable new species. It apparently includes some of the differences seen between the Bartlett Mountain and Black Butte species and also exhibits additional differences.

Peromyscus teeth of group two are represented by ninety specimens from the localities used. The second group is not present in the earliest of the sequence localities (Barstovian Quartz Basin) but makes its first appearance in the Clarendonian Black Butte sample. In this sample these subhyposodont mice are as common as those of group one. In the succeeding Hemphillian samples the abundance of group two mice varies considerably from sample to sample. At Little Valley they are not as common as group one, at Bartlett Mountain they are about as abundant and at McKay Reservoir they are more abundant. The latter two localities represent a different association and a different geographical area respectively. Measurements of dentition of group two mice are found in Table 1.

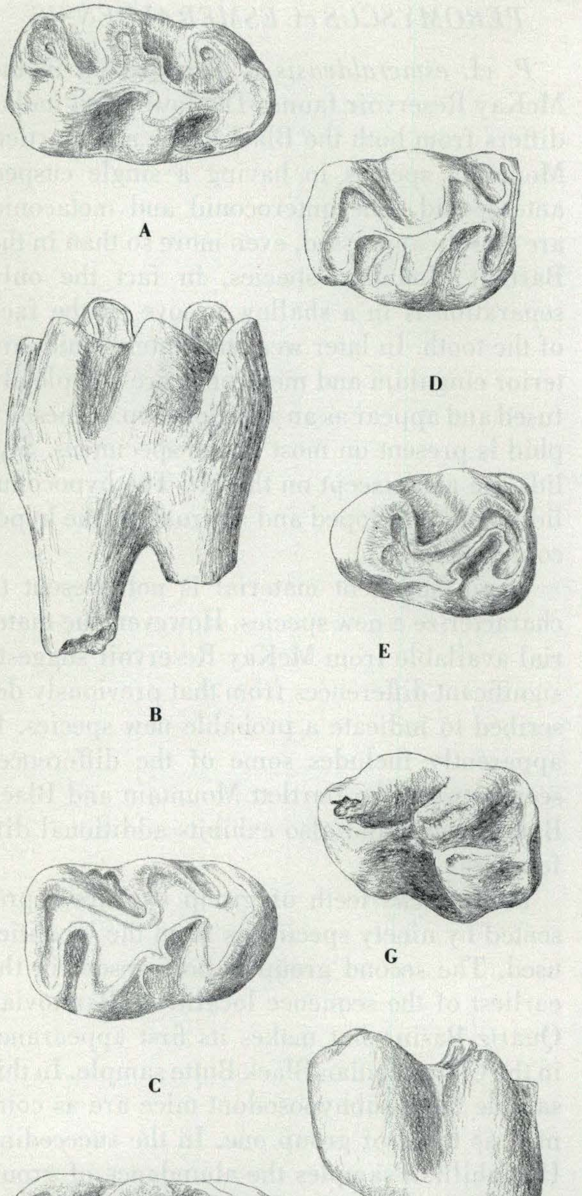


Figure 9. Peromyscus *cf.* esmeraldensis; **A** *and* **B,** *LM$_1$, UO24916,* **C,** *LM$_1$, UO24603,* **D,** *LM$_2$, UO 24602,* **E,** *LM$_3$, UO26941,* **F,** *RM^1, UO24588,* **G** *and* **H,** *RM^2, UO26942, all x18, all specimens from McKay Reservoir, UOloc 2222, anterior right.*

COMPLEXITY

The samples of *P.* cf. *esmeraldensis* are not as suitable in all cases for an analysis of the complexity of the dentition as those of group one species. The Clarendonian Black Butte sample is the best while the Hemphillian, Bartlett Mountain and McKay Reservoir samples are less useful in that only a few teeth of the dentition are abundant enough to reveal the nature of the frequency of occurence of the accessory structures. Data are presented in the same form as for the group one species so that comparisons may be made (see Tables 2, 8 & 3, 9 & 4). A comparison of the equivalent tables shows the mesoloph(id) to be much more common than the mesostyle(id) in all the samples of *P. esmeraldensis* than was seen to be the case in *P. pagei, P. dentalis* and *P. valensis* in which mesoloph(id)s and mesostyle(id)s occurred in more nearly equal numbers or the mesostyle(id) more often. Ectostylids, of the lower molars are more common than entostyles of the upper molars in both groups. Ectolophids do not apear in the samples of group two species but entolophs do, the reverse of the situation in group one species.

The frequency of the five loph and style combinations (Tables 3 and 8) reveal more clearly the difference between the group one and group two species. In the mesostyle(id) mesoloph(id) combinations, combinations 1 and 2 are rare in group two mice. The most common combination is 3 (mesoloph(id) alone). It occurs in three fourths of the specimens. In combinations of the ectostylid-ectolophid, combination 3 occurs in the group two mice but is not known in those of group one. Comparison of Tables 4 and 9, the frequency of joint occurrences of combinations, emphasizes the more lophid character of group two species as contrasted with the more cuspate group one species. Comparisons of relative complexity between contemparaneous species of group one and two are difficult to evaluate since the types of joint combinations are so different. If the data of Tables 4 and 9 are abstracted in terms

TABLE 8

FREQUENCY OF LOPH AND STYLE COMBINATIONS IN *P. esmeraldensis*

		UOloc 2500				UOloc 2517				UOloc 2222			
	Combination	M$_1$	M$_2$	M^1	M^2	M$_1$	M$_2$	M^1	M^2	M$_1$	M$_2$	M^1	M^2
meso	1	20											
	2			9.1									
	3	80	81.8	90.9	100	100	84.6	100		70			100
	4									10			
	5		18.2				15.4			20	100	100	
ento-ecto	1												
	2			27.3									
	3			63.7				100					
	4	100	27.3			100	23			20			
	5		72.7	9	100		77			80	100	100	100
no. specimens		5	11	11	11	2	13	4		10	1	2	

TABLE 9

JOINT OCCURRENCES OF STYLE(ID) AND LOPH(ID) COMBINATIONS IN *P. esmeraldensis*

		UOloc 2500				UOloc 2517				UOloc 2222			
m	e	M$_1$	M$_2$	M^1	M^2	M$_1$	M$_2$	M^1	M^2	M$_1$	M$_2$	M^1	M^2
1	4	1											
2	2			1									
3	2			2									
3	3			7				4					
3	4	4	3			2	3			1			
3	5		6	1	11		8			6			3
4	4									1			
5	5		2				2			2	1	2	
Totals		5	11	11	11	2	13	4		10	1	2	3

of mesostyle(id)-mesoloph(id) combinations and compared the difficulty of making such a comparison is more evident. (see Table 10)

The *P. dentalis* sample and the sample of *P. esmeraldensis* from the Black Butte fauna (Clarendonian) both came from the same excavation and are of about the same abundance. These two samples provide the best opportunity to compare contemparaneous representatives of group one and group two *Peromyscus*. These along with other samples are compared in Table 10. *P. dentalis* has about eighty percent of the teeth in the sample about equally split between the most complex mesostyle(id) mesoloph(id) combinations and the simplest. Whereas in *P. esmeraldensis* nearly ninety percent of the specimens in the sample are found in a single combination consisting of the mesoloph (id) alone. A small part of the sample is equally divided between the most complex and simplest combinations. No combinations involving the metastyle(id) alone are represented. In

TABLE 10

FREQUENCY OF JOINT OCCURRENCES IN TERMS OF COMBINATIONS OF MESOSTYLE(ID)-MESOLOPH(ID)

	Group one species		Group two species		
	P. dentalis	*P. valensis*	UOloc 2500	UOloc 2517	UOloc 2222
1-2	43.8	7.3	5.3	0	0
3	15.5	5.5	89.4	89.5	62.5
4	3.2	16.4	0	0	6.3
5	38.5	70.8	5.3	10.5	31.2
no. sp.	32	55	38	19	16

TABLE 11

RATIO OF NUMBER OF ACCESSORY STRUCTURES TO NUMBER OF SPECIMENS

Species	Fauna	Age	strct/specimen	no. specimens
P. pagei	Quartz Basin	Barst.	2.56	52
P. dentalis	Black Butte	Clar.	1.44	32
P. valensis	Little Valley	Hemp.	0.42	55
P. cf. *valensis*	Bartlett Mt.	Hemp.	0.60	15
P. esmeraldensis	Black Butte	Clar.	1.53	38
P. cf. *esmeraldensis*	Bartlett Mt.	Hemp.	1.28	9
P. cf. *esmeraldensis*	McKay R.	Hemp.	0.72	14
P. cf. *esmeraldensis*	Little Valley	Hemp.	0.40	5

terms of the abundance of the simplest combinations *P. dentalis* might be considered to have the less complex teeth since it has the higher representation of simple teeth, however, in terms of the abundance of the most complex combinations it also has the higher representation. A ratio of number of accessory structures per tooth for each sample provides a more useful comparison of complexlity. Table 11 lists the ratios for the samples of group one and two species using only the structures which may appear on any tooth. *P. dentalis* and *P. esmeraldensis* of the Black Butte fauna appear close in degree of complexity as represented by a ratio of the number of accessory structures per tooth.

The reduction in complexity through time within group one is well iluustrated in Table 11. A reduction in the species of group two from Clarendonian to Hemphillian is not so clear. The Hemphillian sample from the Bartlett Mountain fauna appears to have a similar complexity to that of *P. esmeraldensis* from the Clarendonian Black Butte fauna. The group two species from the Hemphillian McKay Reservoir indicates a much reduced complexity in Tables 10 and 11. The apparent ambiguity between the McKay Reservoir sample and the Bartlett Mountain sample, both Hemphillian in age, may be due to contemporaneous diversity of environment. As noted earlier the Quartz Basin, Black Butte and Little Valley samples represent similar faunal associations (stream bank) as does the McKay Reservoir. The Bartlett Mountain sample represents a quite different terrestrial association. This may well explain the apparent ambiguity noted and may explain why no such ambiguity has appeared in the group one species as represented by the Quartz Basin, Black Butte and Little Valley samples. However, the *P. valensis* material from Bartlett Mountain is of about the same complexity as that from McKay Reservoir and Little Valley suggesting that if the ambiguity in the *P.* cf. *esmeraldensis* sample from Bartlett Mountain is to be explained by environmental difference the difference is not of the nature that it effected *P. valensis*. Since the *P.* cf. *esmeraldensis* sample is quite small the possibility of error is high and extrapolation of the data may be unjustified.

THIRD MOLAR

The lower third molar of group two mice in the sample from Black Butte (Clarendonian) have a small hypoconid and a much reduced entoconid. The entoconid suggests a stylar cusp. The tooth is definitely divided into anterior and posterior moieties. A cingulum extends from the hypoconid around the posterior border and anteriorly from there to the metaconid. In some individuals this cingulum does not extend beyond the entoconid. Very few lower third molars of group two are present in our samples of Hemphillian faunas. McKay Reservoir has produced the only specimens. In these the hypoconid and entoconid are somewhat reduced from that of the Clarendonian form. These cusps appear as a single L shaped loop. The reduction in posterior moiety of the lower third molars of group two thus parallel those observed in group one of the same faunas.

The upper third molars of group two mice from the Black Butte (Clarendonian) locality display a reduced hypocone. A cingulum extends around the posterior border of the tooth from the posterior border of the hypocone and extends anteriorly to the paracone. Two stylar cusps occur along this cingulum, one at the position of a hypoconule and the other at the position of a metastyle or possibly metacone. On some specimens the cingulum does not extend anteriorly to the paracone. In the Hemphillian specimens of group two upper third molars the posterior moiety is obviously reduced from that of specimens from the Clarendonian. The hypocone is much smaller with a small stylar metacone. On some specimens these posterior cusps form a circular loph. Specimens are available only from the Hemphillian Bartlett Mountain fauna. Again the changes in tooth character in the Clarendonian-Hemphillian in mice of group two parallels that of those of group one at the same time.

GROUP THREE

PEROMYSCUS cf. *PLIOCENICUS*

Wilson 1937

The Juniper Creek Canyon fauna (UOloc 2469) includes eight molar teeth and a fragmental mandible of a large *Peromyscus*. Only one specimen of the lower first molar is present. The stage of wear of the specimen is such that the metaconid and anteroconid are one feature not unlike an anterior loop. A small lake in this loop indicates that the metaconid and anteroconid were partially separated in earlier wear. It is not possible to determine from the specimen if the anteroconid was twinned or not. The narrowness of the anterior mure suggests that the anteroconid was a single cusp. In *P. pliocenicus* (Wilson 1937) the anteroconid is twinned. No stylids are present. The mesolophid is represented by a slight irregularity in the enamel at the appropriate position.

The lower second molar, represented by two specimens, has a short but prominent anterior, lingual cingulum apparently not present in *P. pliocenicus*. The hypoconulid is as large as other cusps but separated from the entoconid by only a shallow valley. These two cusps join in later wear. One specimen has a well developed mesostylid whereas the other does not.

A single lower third molar also has an anterior cingulum as in the second molar. The entoconid is greatly reduced. At the stage of wear of the specimen only an anterior post meta-

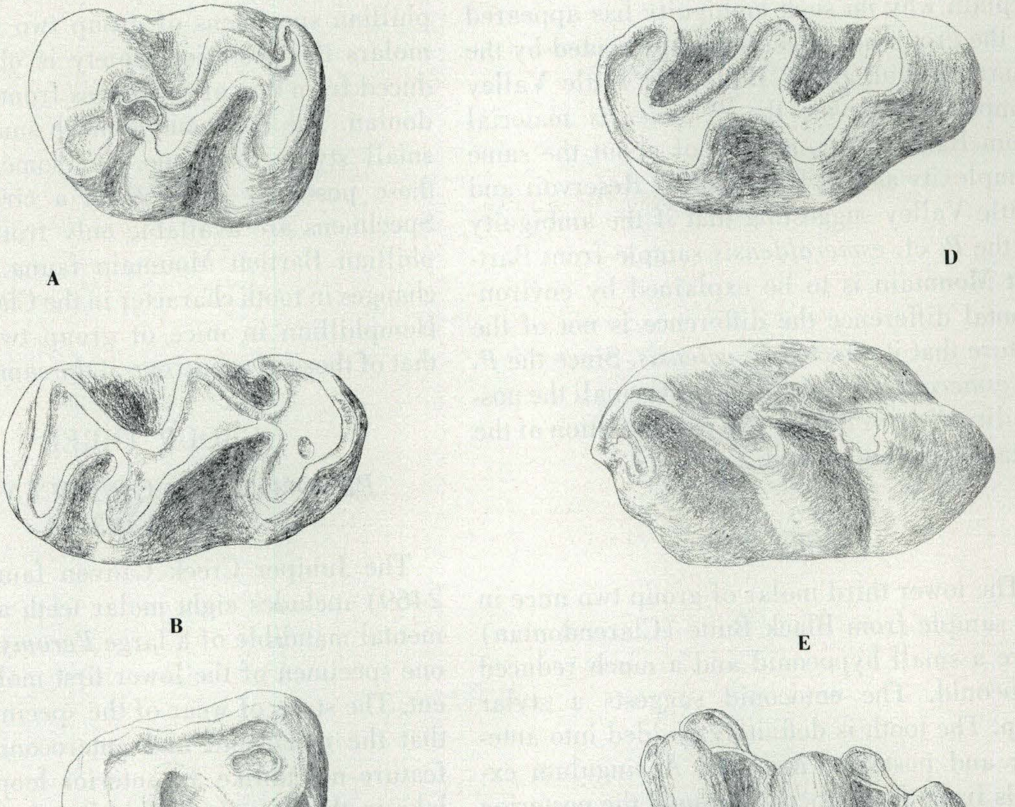


Figure 10. Peromyscus *cf.* pliocenicus; **A,** *LM_2, UO21717,* **B,** *LM_1, UO21719,* **C,** *RM_3, UO21720,* **D,** *RM^1, UO21728,* **E** *and* **F,** *LM^1, UO21716,* **G,** *LM^1, UO21723,* **H,** *LM^2, UO21721, all x18, all specimens from Juniper Creek Canyon UOloc 2469, anterior right.*

conid lake is present. In earlier wear there probably was at least a posterior lake.

The upper first molar is represented by three specimens. The anterocone appears to be a single cusp which became broad with wear. No anterior cingulum appears not even the short one as present in *P. pliocenicus*. The anterocone and paracone are separated by a shallow valley and are distinguished throughout wear. No styles or accessory lophs are present. The posterior cingulum connects high on the metacone. In many aspects this tooth is reminiscent of the upper first molar of *P. esmeraldensis* but is larger.

A single specimen is available of the upper second molar. The anterior cingulum is represented by a small ridge on the face of the protocone. No styles or accessory lophs are present. There are no other distinctive features.

This very large *Peromyscus* is similar to *P. pliocenicus* in gross characteristics but is slightly smaller. It differs in some significant features which when better material is known may justify separation into a new species. With these reservations it is referred to *P. pliocenicus*.

PEROMYSCUS cf. *PLIOCENICUS*

A large *Peromyscus* is represented in the Little Valley fauna by a mandible with the incisor and second and third molars and an upper second molar. The teeth are all significantly larger than those of the Juniper Creek fauna described above. In characteristics they are close to the Juniper Creek species. The upper second molar is similar in size to those of the McKay Reservoir species but the accessory structures are not present. This species is referred to *P. pliocenicus* merely to reflect its general character.

PEROMYSCUS cf. *PLIOCENICUS*

Two large upper second molars representing *Peromyscus* are present in the McKay Reservoir fauna. Both are unlike this tooth in *P. pliocenicus* in that they have accessory lophs. In overall occlusal pattern the M^2 is very close to the much smaller *P. esmeraldensis* from the Black Butte fauna. The anterior cingulum is simple and connects rather low on the paracone. The paracone is connected posteriorly. It has an accesorry loph on the anterior face as well as one on the posterior face. They give an occlusal pattern which might be called a double trefoil. The end of the posterior cingulum is inflated and does not connect to the metacone. However, in later wear connection is made. The tooth represents a large species similar to *P. pliocenicus* but retains many of the characteristics of the smaller *P. esmeraldensis*.

COMPLEXITY

Peromyscus species of group three are represented by only twelve specimens which may represent as many as three species. This does not provide adequate material for an analysis of the frequency of accessory structures. Those accessory structures observed parallel combinations seen in *P. esmeraldensis* in their tendency to be primarily lophoid.

THIRD MOLAR

Only two lower third molars are available and no upper third molars. The posterior moiety is reduced to a loop similar to that seen in *P. valensis*.

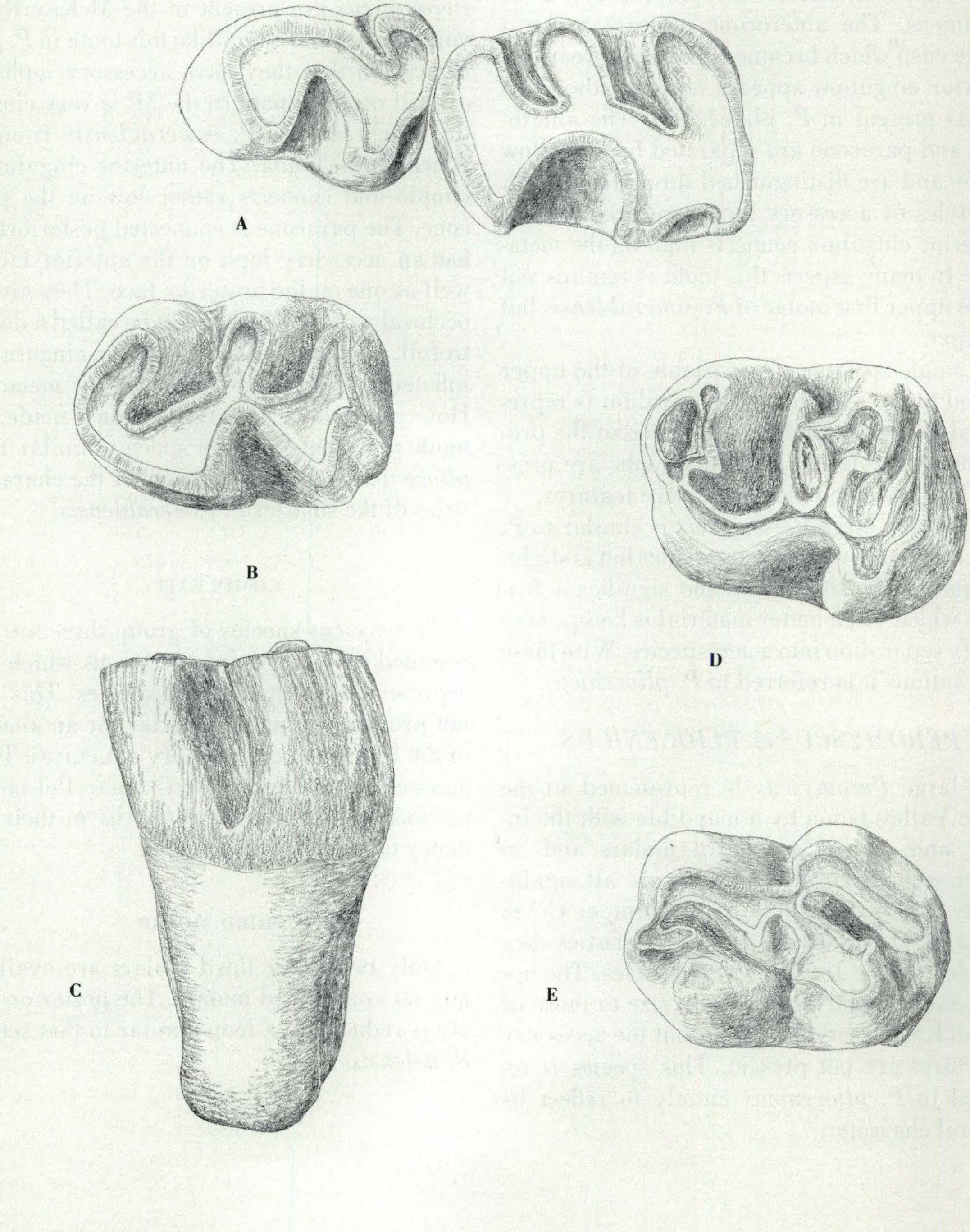


Figure 11. Peromyscus *cf.* pliocenicus; **A,** *RM$_{2-3}$ UO25667,* **B** *and* **C,** *RM^2, UO25666,* **D,** *RM^2, UO26943,* **E,** *LM^2, UO24594, all x18,* **A-C** *from Little Valley UOloc 2516,* **D-E** *from McKay Reservoir UOloc 2222, anterior right.*

SUMMARY

One of the most striking observations made on the series of species studied here is the chronologic reduction in the complexity of the dental pattern. This is apparent in all the material where a sequence is available. The significance of these observations is revealed in a review of variation of complexity in living cricetines. Hershkovitz (1955, p. 644) has commented that, "In cricetines a well-developed, functional mesoloph(id) is always associated with brachyodont, bunodont molars of primarily forest-dwelling species." In speaking of living forms in particular he goes on to say, "A mesoloph(id) is vestigial or absent in specialized high flat-crowned molars of cricetines inhabiting open country, scrubland and secondary forests (usually coniferous). Regressive loss of the mesoloph is associated with the evolution of grazers and grain-eaters from browsers and fruit-eaters." In summarizing the results of his study of dental variations of living *Peromyscus* Hooper (1957, p. 48) remarks; "There are not enough data to permit reliable generalizations regarding geographic trends in the characters studied. The few data at hand suggest that the populations that inhabit arid situations, such as in the Southwestern United States, Northwestern Mexico, and the Yucatan Peninsula have simpler teeth, with fewer and smaller styles and lophs, than populations of the same species that live in denser cover in more humid areas. This is in harmony with a current hypothesis, namely that the mesoloph(id) is vestigial or absent in molars of cricetines inhabiting open country and scrubland. (Hershkovitz 1955:644)." Hershkovitz (1962, p. 82) amends this statement with, "Actually, the phenomenon exemplifies more than a hypothesis. It is a demonstration of a basic principle in cricetine evolution." Hershkovitz' conclusion is drawn from his knowledge of the diverse character of living cricetids. Hershkovitz and Hooper thus recognize an apparent functional relationship in the degree of complexity of cricetid teeth and in particular the teeth of *Peromyscus*. These characteristics are in turn related to differences of environment of the living species.

Very similar differences of environment are recognized for the area of the fossil samples studied here. However, these differences are chronologic rather than geographic. That is the general environment of the area of these samples may be said to progress from a more humid wooded one to a condition of semi-arid scrubland at the end of the sequence. (see Shotwell 1963 for references) The trend from complexity to simplicity of dentition of *Peromyscus* in time in this sequence correlates with this environmental trend. Mice of this genus living in the Northern Great Basin today have simple teeth comparable to the Hemphillian specimens.

Qualitative changes are observed in the third molars in all three groups of mice in the period of time reflected in our sequence of samples. These changes, which in general represent a gradual reduction of the cusps of the posterior moiety, lead to the condition to be seen in living species of *Peromyscus*. Measurements of isolated teeth of group one mice indicate that there is apparently an accompanying reduction in the absolute and relative size of the third molars. This is thus an evolutionary trend common to all three groups of mice segregated for the purposes of this study.

The three groups of mice utilized here may represent evolutionary steps themselves. Group one mice occur throughout the sequence studied and live in the geographic area of the study today. Group two mice represent a probable evolutionary step from some point in the history of group one and provide a subhypsodont dentition. Group three mice apparently present another evolutionary step in their higher crowned more lophiodont teeth but are close to group two.

All three groups are present in the Northern Great Basin in the Hemphillian. Group two first appears in the Clarendonian and group one is present in the earliest step of our sequence (Barstovian). Group three first appears in the Hemphillian. Groups two and three do not occur in known subsequent faunas of the Northern Great Basin nor are they represented in the modern fauna. However, several living species of *Peromyscus* in Central America may represent these groups. Mice of the genus *Peromyscus* living in the Northern Great Basin today represent only group one.

Discussion of the Northern Great Basin species of *Peromyscus* has been carried on to this point by the use of broad groupings rather than attempting subgeneric assignments. The broad groupings were made in such a way that they are as natural as any formal taxonomic categories. These categories are probably not equal, nor are the recognized subgenera of living species, with which they may be compared. Since the previously known materials are limited and species have been typified on such poor or small numbers of specimens, strict adherence to these as taxa in the erection of new species and in the assignment of new specimens would result in a taxonomy which could not allow for the variation we see in living species of this genus. Furthermore an attempt to understand the types of variation and history of the group would be thwarted or certainly more difficult. I have thus approached this problem almost as if no fossil species of *Peromyscus* had been named previously, with the hope that once some general aspects of the nature of their variation and history were evident then taxonomic applications could be made and the available names used by broadening the diagnoses of the original authors, if necessary. Taxonomic rules are designed to prevent chaos and not to perpetuate our ignorance. New knowledge can be reflected in the systematics of a group without doing violence to the rules of nomenclature. Such a procedure which, although not orthodox, is possible and in this case justified.

The ninety living species of *Peromyscus* are assigned to five subgenera; *Peromyscus*, *Haplomylomys*, *Ochrotomys*, *Podomys* and *Megadontomys*. Group one of this study would presumably include mice of the subgenera, *Peromyscus*, *Haplomylomys* and *Ochrotomys*. Hooper (1957 p. 51-52) has questioned these as separate natural groups as a result of his studies. The primary basis of segregation of these three subgenera is the frequency of occurrence of accessory lophs and cusps a characteristic which Hooper has shown to vary greatly within species. Group three mice are similar in size to species of *Peromyscus* assigned to the subgenus *Megadontomys*. Wilson (1937) in describing a new Hemphillian species of *Peromyscus* from the Kern River of California, *P. pliocenicus*, to which our group three mice are compared, recognized the similarity in size to *Megadontomys* but felt that the development of accessory folds of living species of this subgenus disallowed assignment of *P. pliocenicus* to *Megadontomys*. In addition he felt that it is highly improbable that any modern subgenera were differentiated as early as middle Pliocene (Hemphillian). The data presented in this study and the results of Hooper's work indicate that the persence of the accessory folds need not be given such weight in taxonomic assignments. In addition some of our group three mice are more complex than the typical *P. pliocenicus* material. It is clear that a development of mice of the genus *Peromyscus* similar to those living today assigned to the subgenus *Megadontomys* occurred by the Hemphillian and could be the progenerators of this subgenus. I have not had the opportunity to compare our material with representatives of *Megadontomys* and doubt very much if this would be useful until both better fossil material is available and the living species are better represented in collections. Group two mice may compare with living species of the subgenus *Podomys*. This suggestion is based on the subhypsodont nature of the dentition and size. No matter what the eventual result of such assignments may be the important fact is that the wide diversification of modern species of *Peromyscus* is similar to that established in this genus by the Hemphillian in the Northern Great Basin, and possibly in other areas of North America.

The assignment of all of the species referred above to *Peromyscus* indicates a range from Barstovian to recent for the genus. As has been demonstrated above several characteristics of the Barstovian species, depth of jaw and relative size and character of the third molar, are quite different than those of living species. These differences are, however, progressive changes and occur in several apparently distinct lines of *Peromyscus.* Segregation of each stage in these changes into separate new genera or subgenera has the effect of reflecting the history of this group but lumps what appear to be only distantly related species together. The time of occurrence would be the most significant characteristic in common to such groupings. Making distinctions using the progressive characters noted in this study would likely be arbitrary in actual practice and age of occurrence would be the determining factor in taxonomic assignments. Recognizing the several lines of this group and segregating each of them using the progressive characters could be pursued but would result in a multiplicity of genera, at least six new genera or perhaps subgenera. If these species are as diverse as such an arrangement indicates then the living *Peromyscus* would appear as a polyphyletic group which may well be the case. As noted above the various lines as recognized in the late Tertiary species of this study have counterparts in the living subgenera of *Peromyscus.* This problem is quite similar to that of the late Tertiary ground squirrels in which their diversification either parallels or progenerates the diversification in the living species and subgenera of the genus *Spermophillus* (also the case in *Canis, Felis, Mustella,* etc.). With the application of mass collecting techniques to late Tertiary rocks many more quantitatively useful samples of small mammals will be available in the near future and from wider geographic areas. I prefer to maintain the assignment of the late Tertiary species to *Peromyscus* recognizing the different possible lines informally until more adequate means for a realistic assignment are available. The varying character of the appendicular skeleton in late Tertiary rodents may provide highly useful evidence in making the distinctions required in a more formal classification or may simply further becloud the relationships.

Wood (Clark, Dawson and Wood 1964) has resurrected the genus *Copemys* and assigned all of the pre-Hemphillian species to it. The Hemphillian species are ignored in his reassignments. The resulting gap makes the distinction between *Copemys* and *Peromyscus* possible although unrealistic. It also groups a number of species and lines together which are less like each other than are some species of *Copemys* and what would then be called *Peromyscus.* For instance *P. dentalis* and *P. esmeraldensis* both assigned to *Copemys* by Wood would appear more closely related than *P. den talis* and *P. maniculatus,* hardly a reasonable arrangement. James (1963) describes a skull of *P. russelli* which he finds to be sufficiently modern in its characters to be included in *Peromyscus.*

The known west American species of late Tertiary *Peromyscus* fit the groupings employed here as follows:

GROUP ONE

- *P. russelli* James 1963, Barstovian and Clarendonian of southern California
- *P. longidens* Hall 1930B, Barstovian of southern California
- *P. dentalis* Hall 1930A, Clarendonian, Oregon and Nevada (also possibly Barstovian James 1963)
- *P. antiquus* Kellogg 1910, Hemphillian, Nevada
- *P. pagei* n. sp., Barstovian, Oregon
- *P. valensis* n. sp., Hemphillian, Oregon

GROUP TWO

- *P. esmeraldensis* (Wood 1964), Claredonian, Oregon and Nevada
- *P.* cf. *esmeraldensis*, Hemphillian, Oregon

GROUP THREE

P. pliocenicus Wilson 1937, Hemphillian, southern California

P. cf. *pliocenicus*, Hemphillian, Oregon

CONCLUSIONS

The late Tertiary sequence of *Peromyscus* from the Northern Great Basin described here indicates trends in three aspects; trend toward simplicity of dentition from early complex forms, reduction of the development of the cusps of the posterior moiety of the third molars accompanied by an apparent relative size reduction in the third molar, and the development of a delicate mandible from an early massive one. On a broader scale group two mice may be derived from those of group one and group three mice are very probably derived from group two. Some of these developmental trends may not be typical of *Peromyscus* in North America, whereas others appear to at least reflect those of western North America. Complexity vs. simplicity and the close tie to environment which is apparent may not follow the same sequence or at least at the same times as those of the Northern Great Basin. James (1963) recognizes simple and complex forms in the Barstovian of California and Hooper's study refers to living species in southern areas with complex teeth. The reduction of the third molars is apparently typical of the known fossil materials. Species with unreduced third molars do not exist today. The dates of first appearance of group two mice and those of group three agree with those of other areas. Both of these groups or parallels to them, extinct in the Northern Great Basin today, still exist in southern areas. The diversity of complexity of dentition and major groupings seen in the Northern Great Basin of the Hemphillian exists today in other areas of North America.

Two characteristics recognized in this late Tertiary sequence of the Northern Great Basin thus appear to occur in other areas at different times, that is the trend from complexity to simplicity and the last occurrence of groups two and three, while third molar reduction and mandible reduction, occur contemporaneously with those of other areas. Too few large samples of *Peromyscus* from other areas and also too few samples from controlled sequences exist now to extend this discussion. However, it seem obvious that some aspects of the morphologic differences in *Peromyscus* are closely related to regional environmental conditions while others must be attributed to more general factors. If the characteristics of complexity, accessory lophs and styles, have a simple genetic basis they may have appeared independently a number of times. Their appearance in the samples from one area later than in another may not therefore indicate genetic exchange but simply the delayed occurrence of a particular set of environmental conditions.

REFERENCES CITED

Clark, J. B., M. R. Dawson, A. E. Wood, 1964, Fossil Mammals from the Lower Pliocene of Fish Lake Valley, Nevada: Bull. Mus. Comp. Zool. v. 131, no. 2, pp. 29-63

Hall, E. R., 1930 A, Rodent and Lagomorphs from the Later Tertiary of Fish Lake Valley, Nevada: Univ. Calif. Pub. Bull. Dept. Geol. Sci., v. 19, no. 12, pp. 295-312

————, 1930 B, Rodents and Lagomorphs from the Barstow Beds of Southern California: Univ. Calif. Pub. Bull. Dept. Geol. Sci., v. 19, no. 13, pp. 313-318

Hershkovitz, P., 1955, South American Marsh Rats, Genus *Holochilus,* with a summary of Sigmodont Rodents: Fieldiana, Zool. v. 37, pp. 639-688

————, 1962, Evolution of Neotropical Cricetine Rodents (Muridae): Fieldiana, Zool, v. 46, 524 pp.

Hooper, E. T., 1957, Dental Patterns in Mice of the Genus *Peromyscus*: Misc. Pub. Mus. Zool., Univ. Mich. no. 99, pp .7-59

James, G. T., 1963, Paleontology and Non-marine stratigraphy of the Cuyama Valley Badlands, California: Univ. Cal. Pub. Geol. Sci. v. 45, pp. 1-154

Kellogg, L., 1910, Rodent Fauna of the Late Tertiary Beds of Virgin Valley and Thousand Creek, Nevada: Univ. Calif. Pub. Dept. of Geology, v. 5, no. 29, pp. 421-437

Parratt, L. G., 1961, Probability and experimental errors in Science: Wiley, New York, 255 p.

Shotwell, J. A., 1963, Pliocene Mammalian Communities of the Juntura Basin: Trans. Amer. Philos. Soc., N.S., v. 53, pt. 1, pp. 7-21

————, 1964, Community Succession in Mammals of the Late Tertiary in *Approaches to Paleoecology*: ed. Imbrie, J. & N. Newell. John Wiley & Sons, pp. 135-150

Shotwell, J. A. and D. E. Russell, 1963, Mammalian Fauna of the Upper Juntura Formation, the Black Butte local fauna: Trans. Amer. Philos. Soc., N.S., v. 53, pt. 1, pp. 42-69

Wilson, R. W., 1936, A Pliocene Rodent Fauna from Smiths Valley, Nevada: Carn. Inst. Wash. Pub. 473, pp. 15-34

————, 1937, New Middle Pliocene Rodent and Lagomorph Faunas from Oregon and California: Carn. Inst. Wash. Pub., no. 487, pp. 1-19

Wood, A. E., 1936, The Cricetid Rodents described by Leidy and Cope from the Tertiary of North America: Amer. Mus. Nov. no. 822, pp. 1-8

PUBLICATIONS

Museum of Natural History
University of Oregon
Eugene, Oregon

Bulletins	*Titles*	*Price*
No. 1	Cenozoic Stratigraphy of the Owyhee Region, Southeastern Oregon; Kittleman, L. R. *et al.*, 45 pp., 9 plates 11 figures, (December 1965)	$1.50
No. 2	Notes on some Upper Miocene Shrews from Oregon, Hutchison, J. H., 23 pp., 17 figures, (March 1966)	$1.25
No. 3	A New Archaic Cetacean from the Oligocene of Northwest Oregon, Emlong, D., 51 pp., 15 figures, (October 1966)	$1.50
No. 4	The Archaeology of a Late Prehistoric Village in Northwestern California; Leonhardy, Frank C., 41 pp., 17 figures, (March 1967)	$1.00
No. 5	*Peromyscus* of the Late Tertiary in Oregon; Shotwell, J. Arnold, 11 figures, (June 1967)	$1.25