LATE TERTIARY GEOMYOID RODENTS OF OREGON

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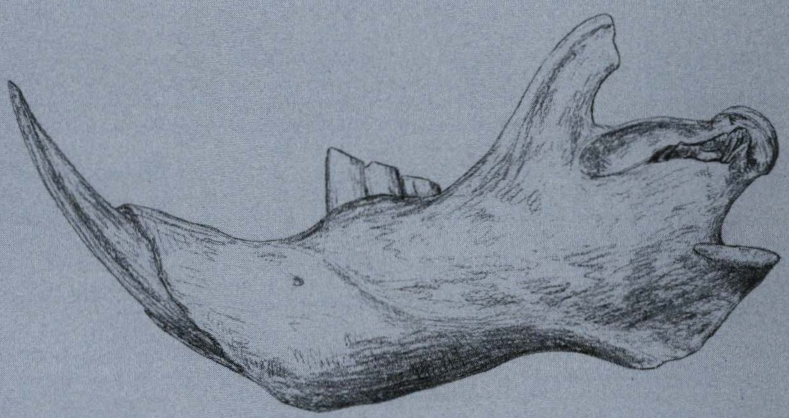

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ABSTRACT

The geomyoid rodents of the late Tertiary of Oregon are described and their relationships discussed. Most of the material involved is new. A new genus, *Parapliosaccomys*, is recognized and three new species, *Parapliosaccomys oregonensis*, *Adjidaumo quartzi*, and *Pseudotheridomys pagei*.

INTRODUCTION

Disaggregation and screening of sediments from a number of localities in Oregon from Barstovian to Blancan in age has produced large numbers of specimens of small mammals. Since the results of these excavations are to be used in quantitative sequential studies, not only is taxonomic assignment of both dental and appendicular skeletal material necessary but an understanding of the relationships of species from one step in the sequence to those of the next is required. However several groups of small mammals are so abundant and so imperfectly known that a consideration of their taxonomic problems as separate reports seemed necessary. Shotwell (1958, 1961, 1967) and Hutchison (1966) have previously published similar reports on other taxonomic groups from these same collections. These works will be incorporated in faunal and paleoecological studies as a final step in this program.

The development of efficient sediment disaggregation techniques (see R. L. Wilson, 1965) allows the collection of large numbers of small fossil mammals to be recovered from Tertiary rocks.

Assignment of skeletal material from these collections of disassociated elements presents some formidable problems. The small size and usual large amounts of material alone makes handling and comparisons troublesome. Late Tertiary small mammals are fortunately, in many cases, members of extant families and already possess skeletal characteristics which are distinct in much the same way as their modern counterparts. Thus it is not difficult to separate skeletal elements of sciurids, cricetids, geomyoids, etc., even when size is not a distinguishing characteristic.

We have found that if all the small mammal skeletal material is considered at once, by elements, that assignments are relatively easy for the bulk of the material. Since only a few species of mammals of the same size are present in any one fauna, segregation of elements by size first expedites the work considerably. If this procedure is followed for a number of sites at the same time, assignment of troublesome elements can be made with more confidence. This is made possible by recognition of the consistent mutual occurrence of unassigned skeletal elements and identified dental elements over several collections. Still some material m u s t remain unassigned. It usually represents low density species whose chance

occurrence is such that dental elements are not seen. When two species of similar size occur, both representing families without living relatives, for which previous collecting has not yielded associated dental and skeletal material, assignment is at best tenuous. Once firm assignments are made for the bulk of the specimens then future collections can be handled from a comparative approach and the amount of material requiring assignment by mutual occurrence or some other deductive approach is greatly reduced. There is nothing new in this approach, vertebrate paleontologists have always used some version of it. Small mammals have not usually been handled in this way because either too little skeletal material was available, the worker felt it was of little significance to his immediate goals, or he was so unfamiliar with the skeleton of small mammals that the effort required to make the comparisons, which usually involve preparation of the complete skeletons of modern forms, discouraged him from proceeding.

Appendicular skeletal materials of most of the geomyoids discussed below have been recovered. Most consistent in the materials available are the elements of the hind limb. As a result comparative descriptions of these elements is included. It is believed that information concerning the hind limb will be useful in revealing the locomotor habits of members of this group. Fore limb elements are much more poorly represented and thus comparisons over more than a very few of the species discussed is not possible. Living species used for comparison include, *Perognathus parvus*, *Microdipodops megacephalus*, *Dipodomys ordii*, *Liomys salvini*, *Heteromys desmarestianus*, *Thomomys umbrinus*, and *Thomomys bulbivorus*.

Localities from which material is discussed in this report range from Arikareean to Blancan in age. Their geographic positions are indicated on the map of figure 1. Their ages are as follows:

Arikareean

Haystack Valley UO 2275 (John Day)

Barstovian

Quartz Basin UO2465

Red Basin UO 2495

Mascall UC 4830

Clarendonian

Black Butte UO 2500

Hemphillian

Little Valley UO 2516
Bartlett Mountain UO 2517
Otis Basin UO 2347
Juniper Creek Canyon UO 2469
Thousand Creek UC 1103
Krebs Ranch I UO 2322
Krebs Ranch II UO 2323
McKay Reservoir UO 2222

Blancan

Wildhorse Butte UO 2396
Hagerman Idaho UO 2437 (east of map area)

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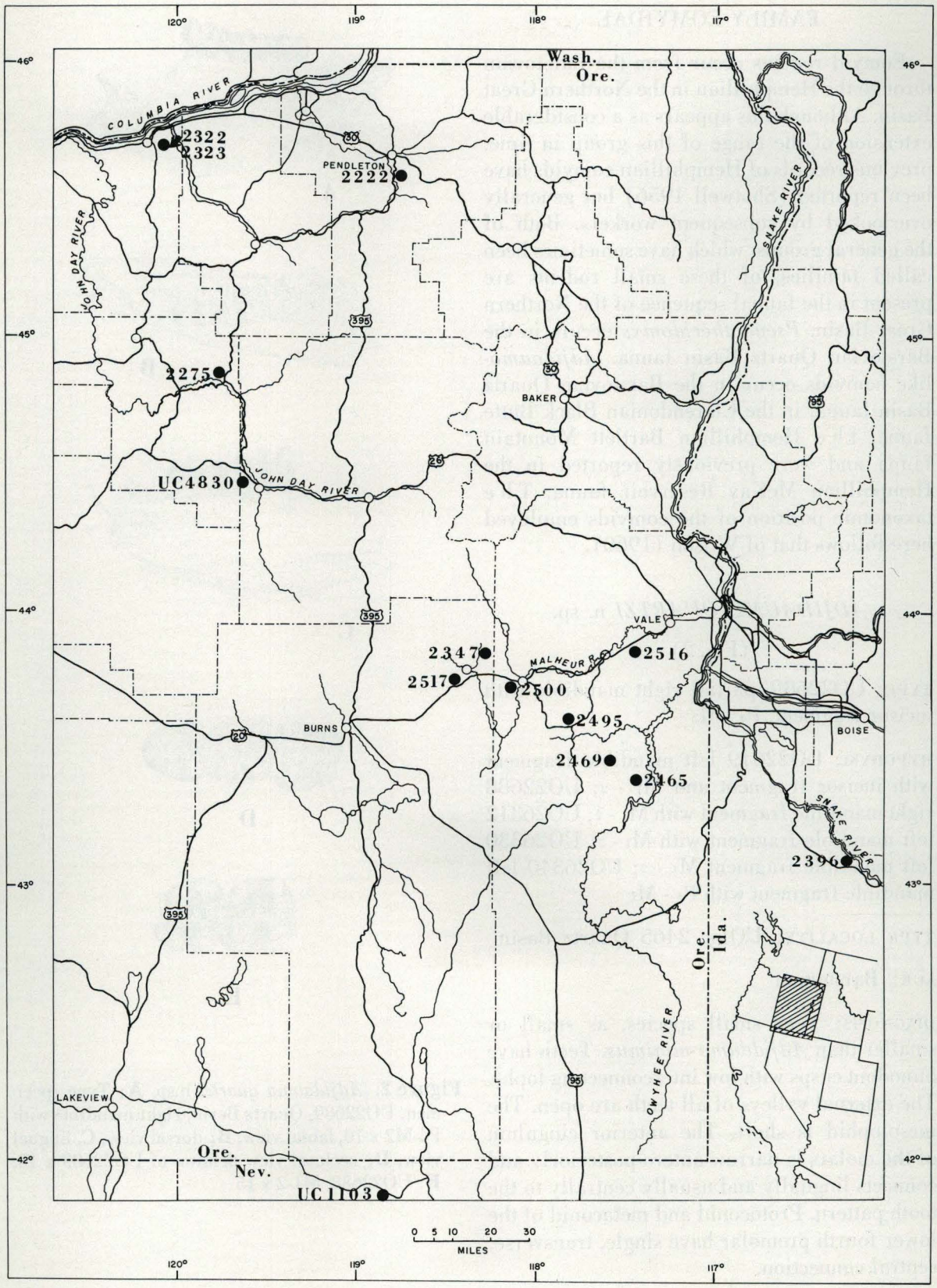
I am grateful to Drs. Reid Macdonald, Los Angeles County Museum of Natural History, Seth Benson, Museum of Vertebrate Zoology, University of California, Don Savage, Museum of Paleontology, University of California and William Clemens, University of Kansas, Museum of Natural History, for the loan of fossil and recent geomyoids in their care. This phase of the study was supported by National Science Foundation grants G21820 and GB 3971. The illustrations are by Mildred Detling.

Figure 1. Location of sites from which geomyoid material is discussed. See text for additional information.


120°
119°
118°
117°
46°
45°
44°
43°
42°
Wash.
Ore.
COLUMBIA RIVER
2322
2323
PENDLETON
2222
JOHN DAY RIVER
SNAKE RIVER
395
30
2275
BAKER
84
UC4830
JOHN DAY RIVER
26
VALE
2347
MALHEUR R.
2516
2517
2500
2495
BURNS
BOISE
2469
2465
SNAKE RIVER
2396
Ore.
Ida.
OWYHEE RIVER
LAKEVIEW
Ore.
Nev.
UC1103
0 5 10 20 30
MILES

FAMILY EOMYIDAE

Eomyid rodents occur from the Barstovian through the Hemphillian in the Northern Great Basin. Although this appears as a considerable extension of the range of this group in time, previous records of Hemphillian eomyids have been reported (Shotwell 1956) but generally overlooked by subsequent workers. Both of the general groups, which have sometimes been called families, of these small rodents are present in the faunal sequence of the Northern Great Basin. *Pseudotheridomys* occurs in the Barstovian Quartz Basin fauna. *Adjidaumo*-like eomyids occur in the Barstovian Quartz Basin fauna, in the Clarendonian Black Butte fauna, the Hemphillian Bartlett Mountain fauna and were previously reported in the Hemphillian McKay Reservoir fauna. The taxonomic position of the eomyids employed here follows that of Wilson (1960).

ADJIDAUMO QUARTZI n. sp.

(Fig. 2)

TYPE: UO22689, partial right mandible with incisor fragment, P_4 - M_2

HYPODYM: UO22619 left mandible fragment with incisor fragment and M_{1-2}; UO22688 right mandible fragment with M_{1-2}; UO26312 left mandible fragment with M_{1-2}; UO26330 left mandible fragment M_{1-2}; UO26340 left mandible fragment with P_4 - M_1

TYPE LOCALITY: UOloc 2465 Quartz Basin

AGE: Barstovian

DIAGNOSIS: Very small species, as small or smaller than *Adjidaumo minimus*. Teeth have bunodont cusps with low interconnecting lophs. The external valleys of all teeth are open. The mesolophid is short. The anterior cingulum of the molars is narrow antero-posteriorly and connects lingually and usually centrally to the tooth pattern. Protoconid and metaconid of the lower fourth premolar have single, transverse, central connection.

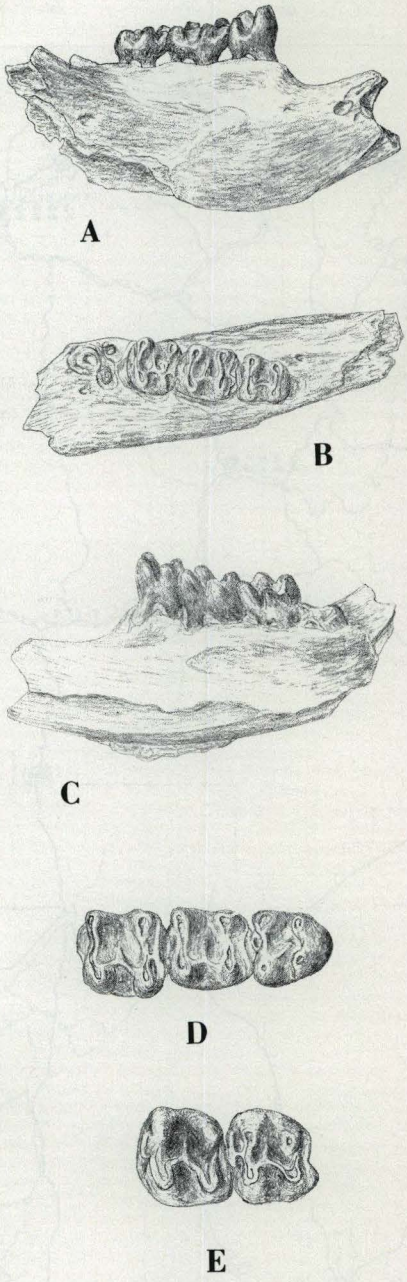


Figure 2. *Adjidaumo quartzi* n.sp. **A**; Type specimen, UO22689, Quartz Basin, right mandible with P4-M2 x 10, labial view, **B**; dorsal view, **C**, lingual view, **D**; occlusal view dention of UO22689 x 15, **E**; UO22688, M1-2 x 15

DESCRIPTION: The protoconid and metaconid of the lower fourth premolar are close together and connected to form a single transverse metalophid with the individual cusps at the ends. This loph occupies the entire anterior third of the tooth and is expanded on the anterior surface. The result is not unlike the parallel situation in some spermophillids. There is no mesostylid. The mesolophid is very short. It forms a small lingual extension of the mesoconid which is weakly connected to the protometaconid nearest the protoconid. The entoconid is connected to the mesoconid by a narrow lophid and to the hypoconid by a narrow rather high hypolophid. The mesoconid is very nearly in the center of the tooth. The tooth is two rooted. There is a small posterior cingulum.

The lower first and second lower molars are similar in cusp arrangement. There is an anterior cingulum which connects low on the metaconid lingually and extends labially to the margin of the tooth. It is connected to the metalophid near its midpoint on four specimens but on UO22688 and UO26330 the anterior cingulum is an isolated transverse ridge. The metalophid is much lower than on the P_4 and the metaconid and protoconid are more widely separated. The mesolophid is prominent but extends less than halfway to the lingual margin of the tooth. There is no mesostylid. There is a well developed hypoconulid which connects to the hypolophid. The posterior cingulum is represented by a sharpened edge on the posterior border of the tooth. The molars have two small anterior roots and one larger posterior root.

On the mandible a large mental foramen lies anterior to the P_4, there is also a small one just posterior to it and below the P_4. The incisor crosses the tooth row at the M_3 and ends posteriorly in a small capsule just above the level of the occlusal surface of the teeth. The angle is slightly inflected. The incisor face is slightly rounded. The masseteric crest is reduced and terminates in a rugose low tubercle below the posterior border of the P_4. There is a distinct depression above the anterior end of the tubercle and below the P_4. On the lingual side of the mandible there is a deep elongated pit extending from just anterior and lingual of the P_4 to the anterior border of the M_1. It is bordered on its lingual side by a crest. There is no pit between the M_3 and the ascending ramus.

COMPARISONS: This species is quite similar to *Adjidaumo minimus* of the Oligocene. The very small mesolophid of the lower molars apparently segregates *A. quartzi* from other known species as well as the single central transverse connection between the protoconid and metaconid of the lower fourth premolar.

The lingual pit on the mandible below the fourth premolar appears also in *Leptodontomys*. This Pliocene genus also has small mesolophids on the lower molars and a similar development of the anterior cingulum occurs on these teeth. *Leptodontomys* is somewhat more lophiodont particularly in the case of the lower fourth premolar. The Quartz Basin species could well be ancestral to the known species of *Leptodontomys*.

TABLE 1

MEASUREMENTS OF DENTITION

Adjidaumo quartzi

	P_4		M_1		M_2	
	AP	T	AP	T	AP	T
UO22689	0.60	0.64	0.78	0.72	0.72	0.77
UO22619			0.81	0.79	0.76	0.81
UO22688			0.83	0.77	0.81	0.75
UO26312					0.68	0.72
UO26330			0.71	0.66	0.74	0.72
UO26340	0.59	0.59	0.68	0.69		

LEPTODONTOMYS sp.

(Fig. 3)

The Clarendonian Black Butte fauna contains an eomyid referable to the genus *Leptodontomys*. UOloc 2500 produced seventeen isolated teeth representing all elements of the check teeth and an edentulous mandible fragment.

In the lower premolar the protoconid is lophiodont rather than bunodont. The connec-

tion between the protoconid and metaconid is weak. There is a small anterior cingulum extending from the center of the anterior face of the tooth toward the base of the metaconid.

In the lower first and second molars the anterior cingulum is connected at the center of the tooth extending both lingually and labially forming a T. The posterior cingulum is connected to the hypoconid only, much in the same way seen in many cricetids, and terminates low on the entoconid. The valleys are open and relatively shallow. The third lower molar is quite similar to the other molars but lacks the posterior cingulum. The lower premolar is two rooted whereas the lower molars have the typical three rooted eomyid pattern, one large root posteriorly and two small roots anteriorly.

The upper premolar has a small stylar cusp and several cuspids on its anterior face. The major cusps are more strongly connected than in the lower premolar and the posterior cingulum is more developed connecting to the hypocone. There are very small lateral accessory cusps, ectostyle and mesostyle, present on the single specimen available.

The upper first and second molars are similar to the lower molars but have the typical cricetid root arrangement. The anterior cingulum is T-shaped as in the lowers, however, on some specimens both lingual and labial arms of the T are not present. Some specimens have an ectostyle, The posterior cingulum conects to the hypocone in the same way as in cricetids. The upper third molar is smaller than the first and second and lacks the posterior cingulum. In other characteristics it is similar to the other molars.

The lower fourth premolar of *Leptodontomys oregonensis* from McKay Reservoir has a stronger protoconid-metaconid connection than in the Black Butte species. The anterior cingulum of *L. oregonensis* does not apparently connect to either the protoconid or metaconid and the protoconid is cuspate rather than lophiodont. The posterior cingulum in *L. oregonensis* is not highly developed as in the Black Butte species.

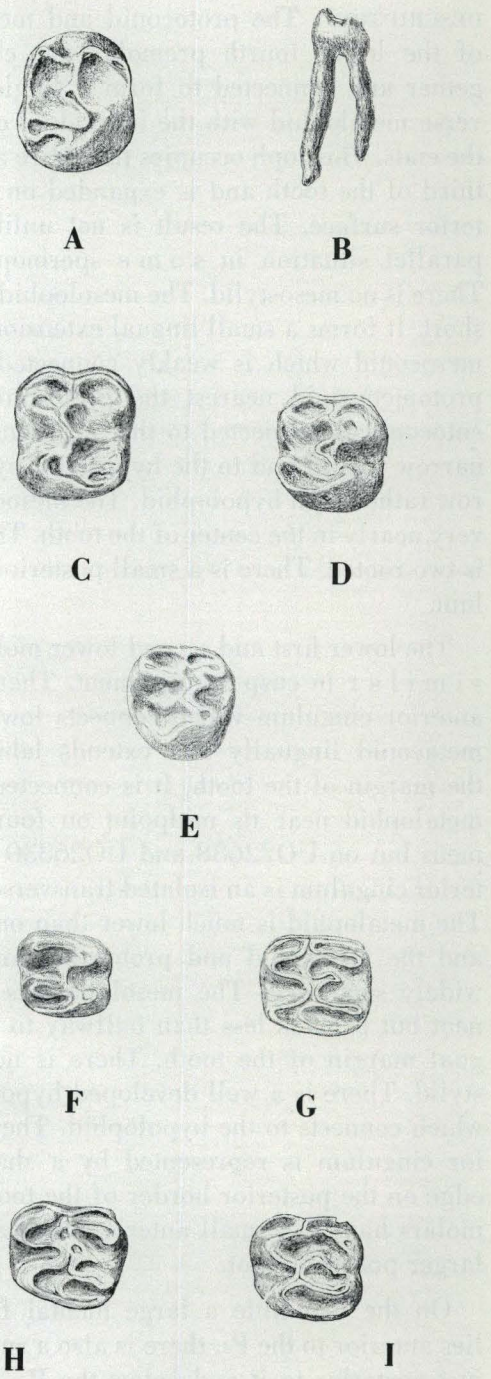


Figure 3. *Leptodontomys* sp. Black Butte fauna, UOloc 2500, **A**; UO24450, P_4 occlusal view x 15, **B**; lateral view x 7.5, **C**; UO25278, $M_{1\ or\ 2}$ x 15, **D**; UO25283, $M_{1\ or\ 2}$ x 15, **E**; UO24454, M_3 x 15, **F**; UO24456, P^4 x 15, **G**; UO24892, $M^{1\ or\ 2}$ x 15, **H**; UO24453, $M^{1\ or\ 2}$ x 15, **I**; UO25273, M^3 x 15

TABLE 2
MEASUREMENT OF DENTITION
Leptodontomys sp.

		AP	T
UO25274	P_4	0.59	0.68
UO24450	P_4	1.02	0.89
UO25278	M_1	1.02	1.00
UO24454	M_3	0.73	0.85
UO24455	$M_{1 \text{ or } 2}$	0.80	0.77
UO25284	$M_{1 \text{ or } 2}$	1.01	0.94
UO25279	$M_{1 \text{ or } 2}$	0.76	0.83
UO25283	$M_{1 \text{ or } 2}$	0.87	0.84
UO24852	P^4	0.71	0.77
UO24456	P^4	0.75	0.78
UO25285	$M^{1 \text{ or } 2}$	0.81	0.89
UO24452	$M^{1 \text{ or } 2}$	0.95	0.90
UO24849	$M^{1 \text{ or } 2}$	0.87	0.94
UO25282	$M^{1 \text{ or } 2}$	0.77	0.86
UO24453	$M^{1 \text{ or } 2}$	0.85	1.00
UO24892	$M^{1 \text{ or } 2}$	0.78	0.92
UO25273	M^3	0.80	0.87

LEPTODONTOMYS sp.

(Fig. 4)

Three speciments of eomyids occur in the Hemphillian Bartlett Mountain fauna, a lower premolar, a lower fiirst or second molar and a lower third molar. The premolar is similar to that described from the Black Butte fauna but is higher crowned. The protoconid is cuspate rather than lophiodont as in the Black Butte species. The anterior cingulum is not developed as in *Leptodontomys oregonensis* and the Bartlett Mountain specimen is higher crowned. The molars are similar to the Black Butte species but higher crowned.

PSEUDOTHERIDOMYS PAGEI n. sp.

(Fig. 5)

TYPE: UO22715 mandible with P_4, $M_{2\text{-}3}$ and fragmental incisor

HYPODYM: UO22708 mandible fragment with P_4-M_2, UO22971 maxilla with P^4-M^3, UO22719, mandible fragment P_4-M_3; UO22711, mandible fragment $M_{1\text{-}2}$; UO22717, mandible fragment P_4-M_1; UO22709, mandible fragment P_4; UO22716 mandible fragment P_4; UO22712, mandible fragment M_1; UO22723, mandible fragment, $M_{1 \text{ or } 2}$; UO22718, mandible fragment M_1; UO22704, maxilla fragment; UO22725 maxilla fragment P^4; UO22713 maxilla fragment $M^{1 \text{ or } 2}$; UO22720 maxilla fragment P^4; UO22710 maxilla fragment $M^{1 \text{ or } 2}$; UO22721 maxilla fragment P^4;

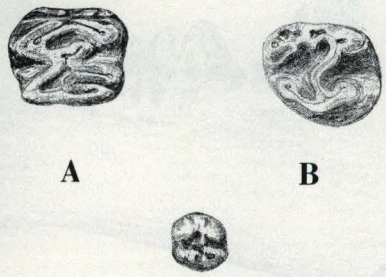


Figure 4. *Leptodontomys* sp. Bartlett Mountain fauna UOloc 2517, **A**; UO27007, $M_{1 \text{ or } 2}$ x 15, **B**; UO25192, M_3 x 15, **C**; UO24956, P_4 x 15

TYPE LOCALITY: UOloc 2465 Quartz Basin.

AGE: Barstovian.

DIAGNOSIS: Size is that of *Pseudotheridomys hesperus* Wilson (1960). All lophs extend to the margin of the tooth. In the lower dentition two anterior valleys (the metaconid and post metaconid) are closed off by the junction of the lophids forming two anterior lakes. In the same manner the posterior (post entoconid) valley is closed off to form a lake. The post mesolophid valley remains open. In the upper dentition the post metacone valley is the only one forming a lake except in extreme wear. Strongly developed mesostyles and stylids are present on all teeth.

DESCRIPTION: On the P_4 the ectolophid is not cut through as in *P. hesperus* except in early wear. The connection is narrow throughout wear. In some specimens (UO22708) the connection of mesolophid to metaconid is incomplete but only in an early stage of wear. In none of the specimens is the anterior valley open. In the first lower molar all valleys other than the central are closed except in one specimen (UO22718) in which only the anterior

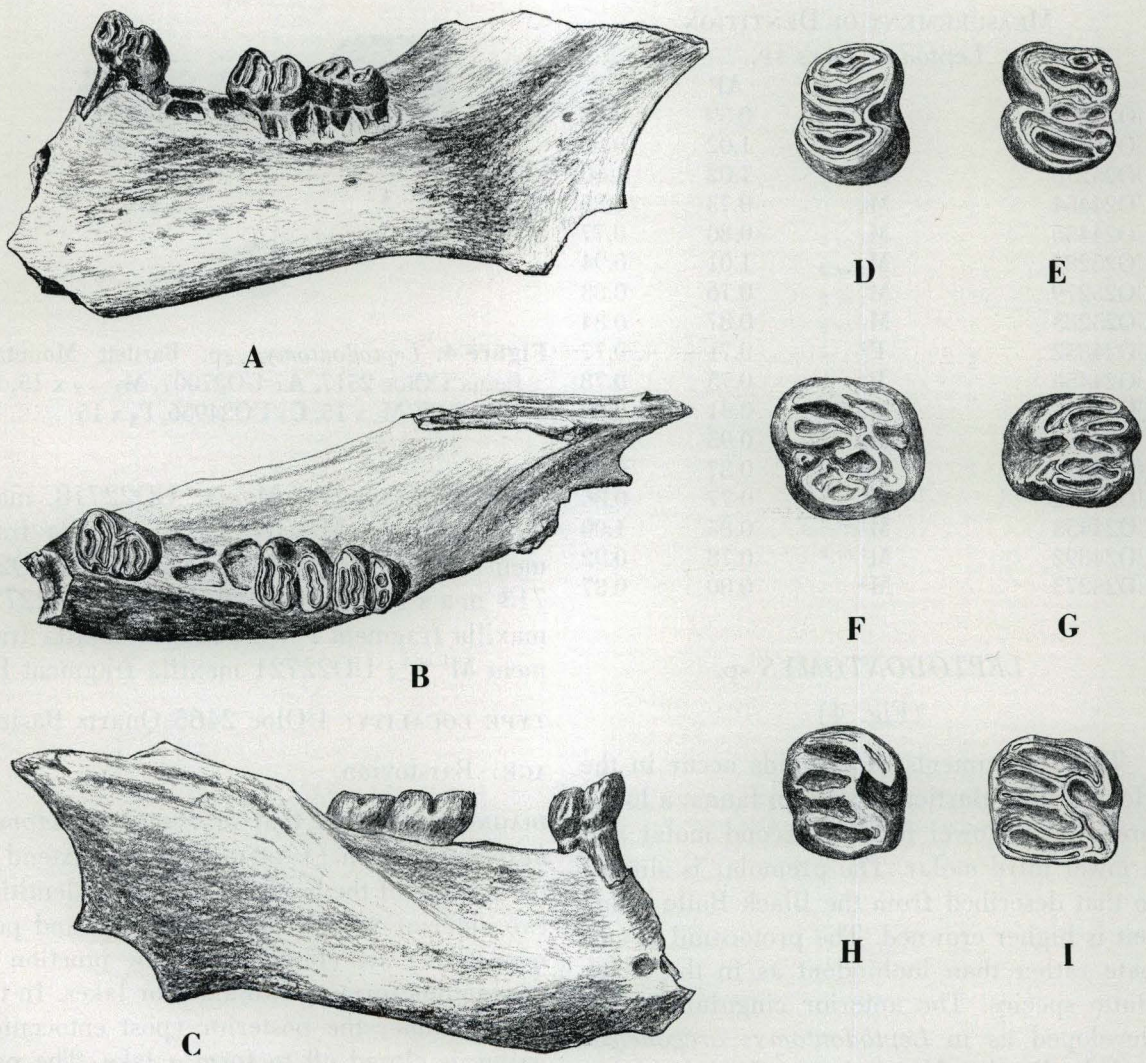


Figure 5. *Pseudotheridomys pagei* n.sp. Quartz Basin fanua, UOloc 2465, **A**; Type specimen UO22715, right mandible with P_4, M_{2-3}, lingual view x 10, **B**; dorsal view x 10, **C**; labial view x 10, **D**; UO22716, P_4 x 15, **E**; UO22718, $M_{1 \text{ or } 2}$ x 15, **F**; UO22721, P^4 x 15, **G**; UO22720, P^4 x 15, **H**; UO22713, $M^{1 \text{ or } 2}$ x 15, **I**; UO22710, $M^{1 \text{ or } 2}$ x 15

valley is closed and exceptionally small. Connection between the anterior and posterior moieties is tenuous but consistent. The second lower molar is similar to the first but appears to be shorter antero—posteriorly than the first. In one specimen (UO22711) the anterior fossettid is subdivided by an accessory lophid. The third lower molar differs from the other cheek teeth in that the ectolophid is not evident and a strong connection between the entoconid and metastylid joins the anterior and posterior portions of the tooth pattern on the lingual border rather than more centrally as in the other cheek teeth. The posterior valley is subdivided by a small accessory lophid.

In comparison with *P. hesperus* the Quartz Basin species differs primarily in the consistent lingual closure of the two anterior valleys and the posterior valley. This is accompanied by consistent but often weak connection between the posterior and anterior portions of the tooth pattern.

The mandible is well preserved in several specimens. It is relatively shallow. The mental foramen is located well down on the side of the jaw and anterior to the fourth premolar. The masseteric crest is distinct with a somewhat irregular upper border and terminates just below the fourth premolar. The groove between the third molar and the ascending ramus is broad and shallow. No foramina are present in the groove. A small laterally expanded foramen is present at the extreme posterior end of the groove and open posteriorly. The incisor appears to cross the dentition at a point between the second and third molars and terminates just above the occlusal level of the teeth. The incisor is flat on its medial side and somewhat inflated on the lateral side. The enamel ends abruptly at the medial side of the face of the incisor and less definitely on the lateral face. The face of the incisor is flat adjacent to the medial side and curves gradually into the lateral face on that side of the tooth.

In the upper cheek teeth the posterior valley is the only one closed until very late wear. In the upper fourth premolar the transverse lophs all reach the border of the tooth. The metaloph is only weakly connected to the mesostyle. The posterior portion of the tooth varies in the five specimens present. In one the lake valley is closed off much in the same way as in the lower teeth (UO22720). In another the valley is open posteriorly, in still another the central portion of the valley is open posteriorly and the external portion is blocked to form a small lake just posterior to the metacone which is much enlarged. In one specimen the anterior portion of the tooth differs in that there is an extension of the anterior cingulum lingually resulting in an invagination of the pattern just anterior to the protocone.

The upper third molar is present in only one specimen. It, however, is well worn or partially damaged. It is apparently shorter antero-posteriorly than the other molars.

In late wear the two anterior and posterior valleys of all the teeth are closed. *P. hesperus* apparently does not possess a mesostyle on the P^4 which is so well developed in the Quartz Basin species. There is no division of the pattern of the upper molars into posterior and anterior moieties. This is a result of the well developed mesoloph and mesostyle which thus makes a pattern of five transverse lophs on each tooth extending to the edge of the tooth the two posterior ones usually being joined at their labial ends to form a lake. The chief differences between the two American species are somewhat parallel to those seen in the European species as summarized by Wilson (1960). These differences may reflect possible differences in age.

TABLE 3

MEASUREMENT OF DENTITION

Pseudotheridomys Pagei

	P_4		M_1		M_2		M_3	
	AP	T	AP	T	AP	T	AP	T
UO22708	0.99	0.89	0.97	0.94	0.91	0.90		
UO22715	1.06	0.78			0.95	0.95	0.94	0.84
UO22719	0.98	0.85	1.00	0.95	0.90	0.93		
UO22711			1.02	1.01	0.89	0.98		
UO22716	1.01	0.87						
UO22709	0.99							
UO22718			1.00	0.96				
UO22717	0.99	0.85	1.00	0.96				

	P^4		M^1		M^2		M^3	
	AP	T	AP	T	AP	T	AP	T
UO22710			1.00	0.98				
UO22713			1.02	1.00				
UO22971			0.95	0.99	0.76	0.93	0.65	0.92
UO22720	0.93	1.00						
UO22725	1.03	1.08						
UO22721	1.02	0.99						

PSEUDOTHERIDOMYS PAGEI

A fragmentary maxilla with the second and third molars intact (UO24414) was recovered from the Barstovian Red Basin Quarry at UOloc 2495 indicating the presence of the new species in that fauna.

FAMILY HETEROMYIDAE

Heteromyid and geomyid rodents are common in most Northern Great Basin Tertiary faunas. The nature of previous samples of these faunas has been such that the forms represented are still, in most cases, only poorly known. Furthermore a workable classification and phylogeny of these mammals still does not exist. As a result the assignment of them to positions in a phylogeny and the recognition of migrant and resident forms is not possible without reassessment of the known material and study of the available new material.

Wood (1935) reviewed the heteromyids and later the geomyids (Wood 1936). A number of papers subsequently, by him, have dealt with these groups. Reeder (1956) more recently has reviewed the heteromyids in an unpublished thesis of which only a small part has thus far appeared in print. A number of new names were proposed by Reeder and thus are not yet available. His conclusions and observations, however, are useful in any attempt to work with these rodents. Wilson (1936, 1939, 1949, and 1960) has made frequent reference to particular heteromyids and geomyids in his work. The accuracy and perceptiveness of his descriptions and views makes these works invaluable to any worker attempting to find his way in this group. As emphasized by Reeder, one of the chief difficulties in determining relationships among heteromyids, and I might add geomyids too, is the use of a classification based on living forms and projected into the Miocene. This was, perhaps, a useful starting point in organizing the fragmentary early information on these rodents but is no longer satisfactory without considerable modification.

A further deterent to a more realistic classification has been the tendency of workers to immediately segregate heteromyids and geomyids in their studies and thus invoke a separation disproportionate to the real differences involved. This has resulted in a confused literature, artificial gaps in the record, and an over indulgent invocation of parallism as an explanation of the results. These have, in turn, become the basis for hypotheses which have governed the subsequent assignment of materials, thus compounding the confusion.

I have attempted here, with the advantage of new material representing a particularly crucial period of time in geomyoid evolution, to take a different point of view dictated by the material, in an effort to find a satisfactory classification of these rodents for the purposes of the work described here. This has, of course, required some examination of geologically earlier materials since any such change must be applicable and reasonable beyond the extent of the immediate objective of this work. However, the extent of early material seen by me is limited and I have relied on published descriptions for some of it.

The new material is described below by age and grouped by subfamilies with discussions concerning apparent interrelationships at appropriate places. Measurements of the upper fourth premolars of a number of the species discussed appear in Table 4.

SUBFAMILY PEROGNATHINAE

PEROGNATHUS sp.

A single lower molar (UO25272) in the Clarendonian Black Butte fauna (UOloc 2500) represents a small species of *Perognathus*. The specimen has two roots. Protostylid and hypostylid are both small. There is a strong anterior cingulum. The metaconid and protoconid connect at their anterior borders early in wear. The entoconid and hypoconid connect centrally. Also present are an astragalus (UO27004) and several upper incisors.

PEROGNATHUS sp.

(Fig. 7)

A small species of *Perognathus* is well represented in the Hemphillian Little Valley fauna (UOloc 2516). It is comparable in size with *P. parvus* living there today.

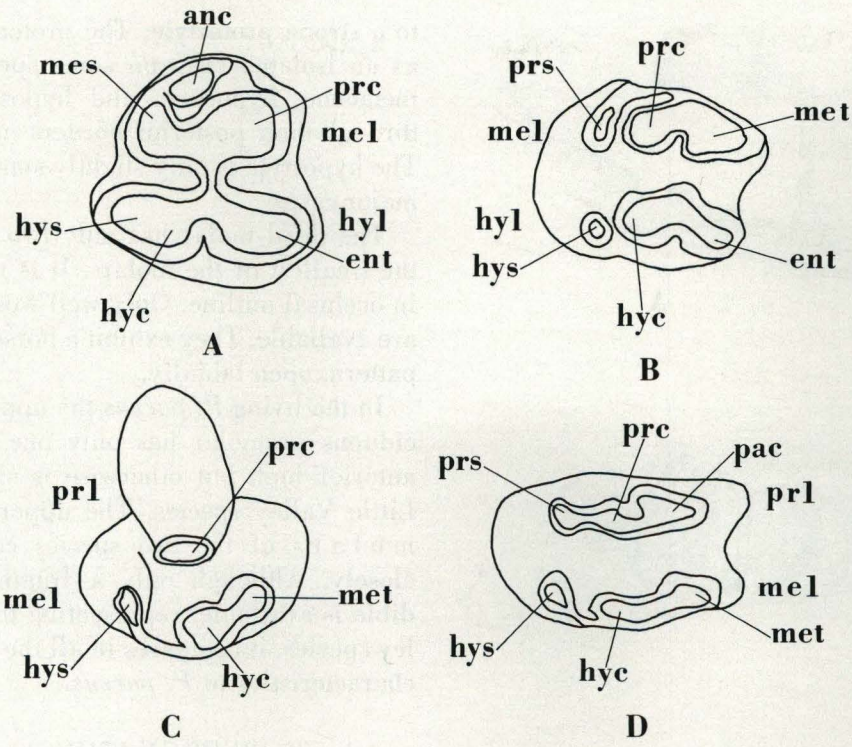


Figure 6. Nomenclature of teeth, **A**; lower left fourth premolar, **B**; lower left molar, **C**; upper left fourth premolar, **D**; upper left molar

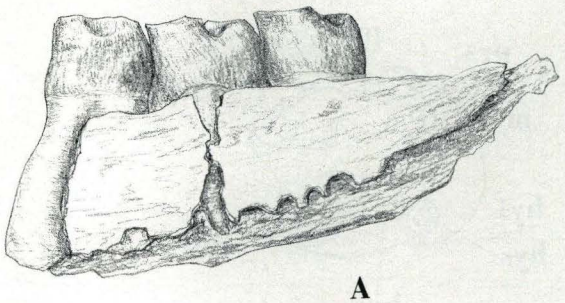
anc—anteroconid
anl—anterolophid
ent—entoconid
hyc—hypocone(id)
hyl—hypolophid
hys—hypostyle(id)
mes—mesoconid
met—metacone
mel—metaloph(id)
pac—paracone(id)
prc—protocone(id)
prl—protoloph
prs—protostyle(id)

The lower fourth premolar has four simple cusps of which the antero-lingual is the largest. The four cusps join in the middle of the tooth.

The first and second lower molars possess two broad roots. The metaconid and protoconid connect anteriorly early in wear and are about equal in size. The anterior cingulum connects the anterior border of the protoconid to the protostylid. The hypoconid and entoconid connect centrally. The hypostylid remains isolated until late wear. The third molar is apparently single rooted. It is more lophiodont than the other molars. The hypostylid is absent.

The upper deciduous fourth premolar has three lophs. There are two small cusps on the anterior loph. The central loph consists of a large cusp with a very small stylar cusp labial to it. Two large connected cusps are on the posterior loph. A smaller stylar cusp is connected by a posterior cingulum and is situated slightly anterior to the other cusps of the posterior loph.

The upper fourth premolar has three roots. The protocone is large, centrally located and isolated until very late wear. Hypostyle, hypocone, and metacone are arranged in a gentle cresent. The hypostyle is nearly as large as the other cusps.



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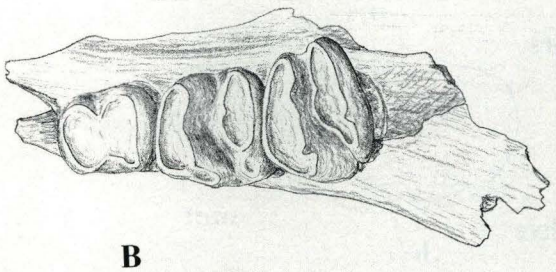

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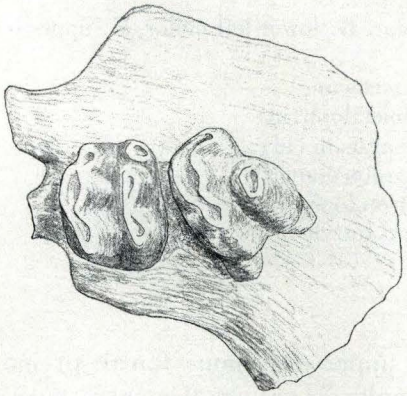

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Figure 7. *Perognathus* sp. Little Valley fauna UO loc 2516, **A**; UO25942, left mandible fragment with P_4-M_2, labial view x 15, **B**; dorsal view x 15, **C**; lingual view x 15

The upper first and second molars possess three roots. The first molar is the larger tooth. In both teeth the paracone and protocone are connected on their posterior borders when a connection exists. It is not always present. The anterior cingulum connects from the paracone to a strong protostyle. The protocone appears as an isolated cusp on some specimens. The metacone, hypocone, and hypostyle connect through their posterior borders in early wear. The hypostyle is only slightly smaller than the major cusps.

The third molar has only two roots and is the smallest of the molars. It is nearly round in occlusal outline. Only well worn specimens are available. They exhibit a horseshoe shaped pattern, open labially.

In the living *P. parvus* the upper fourth deciduous premolar has only one cusp on the anterior loph but otherwise is similar to the Little Valley species. The upper and lower molars of the two species compare very closely. Although only a fragmentary mandible is available, representing the Little Valley species, it compares in all the recognizable characteristics to *P. parvus*.

PEROGNATHUS sp.

Four specimens in the Hemphillian Bartlett Mountain fauna UOloc 2517 sample represent a small species of *Perognathus*. They appear to be slightly lower crowned than the Little Valley species but are otherwise similar.

PEROGNATHUS SARGENTI Shotwell 1956

(Fig. 8)

This species known only from the Hemphillian McKay Reservoir (UOloc 2222) presents problems of assignment which are not yet resolved. It is the size of *Diprionomys*, much larger than any *Perognathus*. The molars are close to those of *Perognathus*. The lower fourth premolar, however, is highly molariform. It is basically a *Perognathus* premolar in character but has a well developed protostylid and hypostylid. A strong anterior cingulum is present so that the appearance of the tooth is that of a molar with the exception of a strong groove on the anterior face of the tooth separating the protoconid and mesoconid. The teeth are lower crowned than other known geomyoids of the Hemphillian with the exception

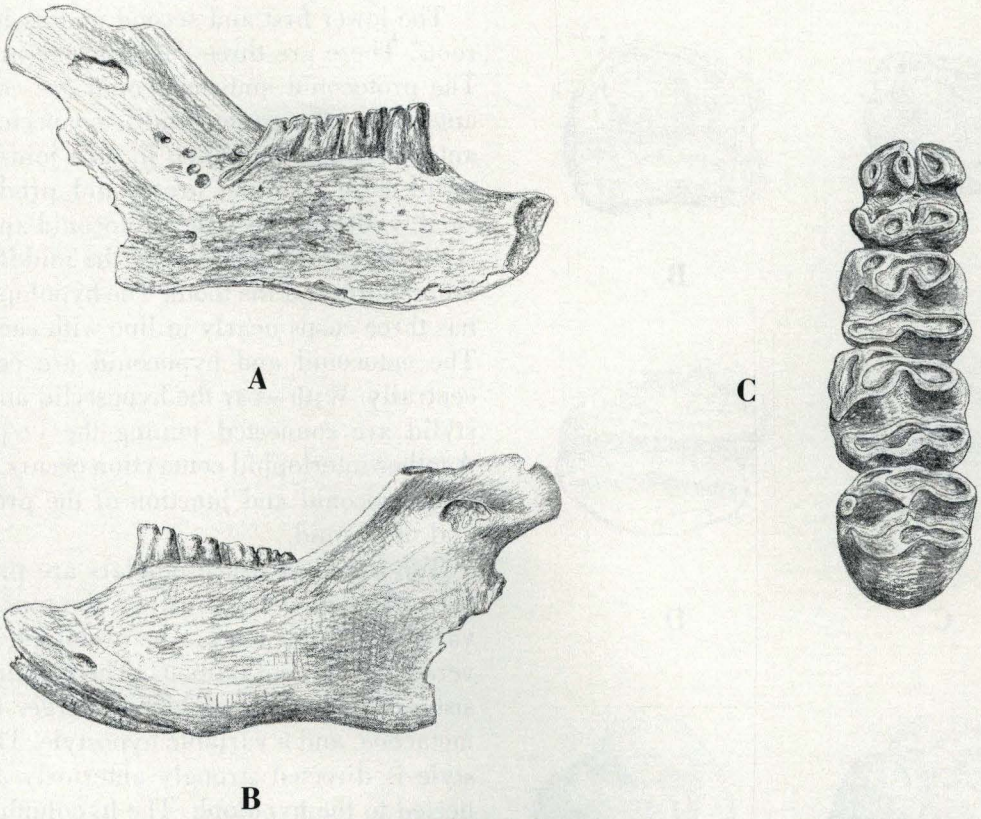


Figure 8. *Perognathus sargenti*, McKay Reservoir fauna UOloc 2222, **A**; Type specimen, UO3637, left mandible with P_4-M_3, lingual view x 5, **B**; labial view x 5, **C**; occlusal view of dentition x 15

of *Perognathus*. In this characteristic *P. sargenti* has the appearance of Barstovian species. Assignment to *Perognathus* still seems to be possible but questionable. The type specimen is refigured as the original drawings were of limited value due to the small scale.

PEROGNATHUS sp.

A typical *Perognathus* also occurs at McKay Reservoir (UOloc 2222) and is similar to the species occurring at Little Valley.

PEROGNATHUS sp.

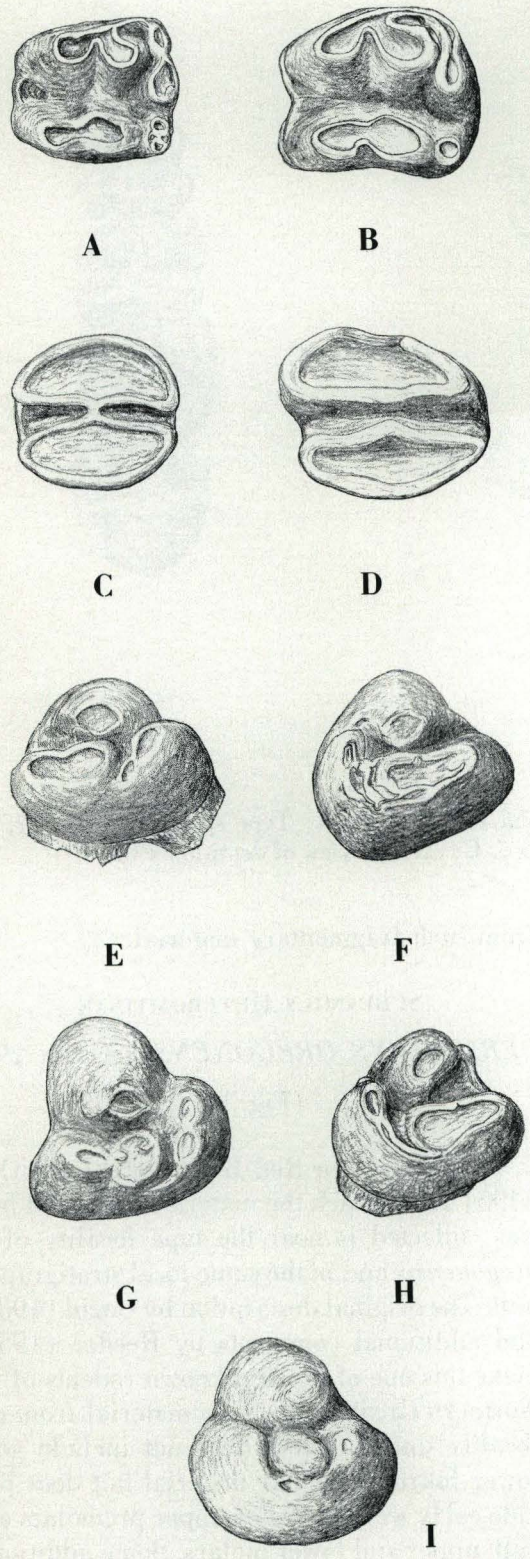
A fragmental mandible with a partial P_4 and M_2 (UO8425) and an isolated molar (UO26949) of *Perognathus* are known from the Hemphillian Krebs Ranch II fauna, UOloc 2323. The species represented is typical in size and character so far as can be determined from such fragmentary material.

Subfamily Heteromyinae

PERIDIOMYS OREGONENSIS Gazin 1932

(Fig. 9)

The Barstovian Red Basin locality (UOloc 2495) from which the material described here was collected is near the type locality of *P. oregonensis* and in the same local stratigraphic unit. The original description by Gazin (1932) and additional comments by Reeder (1956) make this one of the best known rodents of the Northern Great Basin. New material from our locality unfortunately does not include good lower fourth premolar material but does provide early wear stages of upper premolars and both upper and lower molars. Some additional information is thus available.



The lower first and second molars have two roots. There are three cusps on the metaloph. The protoconid and mesoconid are connected anteriorly. The protostylid is connected to the anterior cingulum which in turn joins the anterior border of the protoconid producing a small valley between the protoconid and protostylid. The protostylid is in the middle of the labial border of the tooth. The hypolophid also has three cusps nearly in line with each other. The entoconid and hypoconid are connected centrally. With wear the hypostylid and protostylid are connected joining the l o p h i d s. Another interlophid connection occurs between the hypoconid and junction of the protoconid and metaconid.

Ten upper fourth premolars are present in the collection. They illustrate the considerable variation in this tooth. The protoloph is transversely ovate and bulbous. The metaloph consists of a hypocone, which is larger than the metacone, and a variable hypostyle. The hypostyle is directed strongly anteriorly and connected to the hypoloph. The hypoloph may be a simple loph or in some cases consist of as many as three small cusps .In some specimens these cusps reach the size of the hypostyle proper. Six of the available ten specimens are at a stage of wear which illustrates the character of the variants. At least five of these have two cusps, two of the five specimens have three. The protoloph and metaloph connect late in wear at the hypocone.

The upper first molar is larger than the second. Each has one lingual and two labial roots. The lingual and labial ends of the valley between lophs are of about the same depth. In wear, connection between the lophs occurs in a number of places so that several small lakes may occur.

Figure 9. *Peridiomys oregonensis*, Red Basin, UO loc 2495, **A**; UO22877, $M_{1 \text{ or } 2}$, **B**; UO24413, $M_{1 \text{ or } 2}$, **C**; UO24207, $M_{1 \text{ or } 2}$, **D**; UO22870, $M_{1 \text{ or } 2}$, **E**; UO22879, P^4, **F**; UO24195, P^4, **G**; UO24203, P^4, **H**; UO24199, P^4, **I**; UO24196, P^4, all x 15

HIND LIMB: A single, slightly crushed, calcaneum (UO26997) is the only element of the hind limb of *Peridiomys oregonensis* present in our collection (see fig. 25M). The cuboid facet is ovoid with a groove entering it similar to that of *Pliosaccomys* of the Black Butte fauna but more rounded as in *Diprionomys*. The trochlear process is well separated and well defined similar to *Diprionomys* in this respect.

PERIDIOMYS OREGONENSIS

Four upper cheek teeth of *P. oregonensis* occur in the sample from Quartz Basin, UOloc 2465 indicating the presence of this species in this Barstovian fauna.

DIPRIONOMYS sp.

A single worn first or second lower molar (UO24465) of *Diprionomys* occurs in the Clarendonian Black Butte fauna at UOloc 2500. No specific assignment below genus can be made.

DIPRIONOMYS PARVUS Kellogg 1910

(Fig. 10 & 11)

This species is well represented in the Hemphillian Little Valley sample from UOloc 2516 and a considerable amount of new information is thus available concerning the dentition.

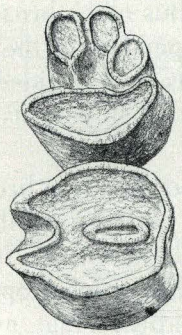
The lower fourth premolar is high crowned but has two well developed roots. The metalophid consists of a mesoconid and protoconid with one or two accessory cusps connecting the anterior borders of the major cusps. The posterior portions of the cusps are separated by a shallow valley. The protoconid is slightly larger than the mesoconid and is situated more anteriorly. The hypolophid consists of three cusps, entoconid, hypoconid, and hypostylid, all of which are slightly compressed anteroposteriorly. The entoconid and hypoconid are of about equal size while the hypostylid is much smaller. The protoconid and entoconid are well separated whereas the mesoconid and hypostylid are only separated in early wear. The internal valley is thus much broader than the external and also persists to the base of the enamel. This results in a decidedly assymetric occlusal pattern which persists through wear.

The lower first molar has two broad well separated roots. None of the available teeth are so little worn that the cusps can be distinguished on the metalophid or hypolophid. The available specimens indicate that a lake is formed by connections between the lophids at both the protoconid and metaconid. The remaining open valley extends down the internal side of the tooth nearly to the base of the enamel. A much shallower valley is apparent on the external side. On the second lower molar the roots are connected on the internal side. The least worn specimen does not reveal the character of individual cusps, however, it is apparent that the initial connection of the lophids is at the metaconid and that an internal valley is well developed. A second connection of the lophids occurs at the protostylid forming a lake.

The third lower molar has a single simple root. A worn specimen displays an ovoid occlusal outline with a small lake. The tooth is smaller than the other molars.

The upper fourth premolar is large and has two roots. The broad posterior root appears bifurcate in some specimens. The protoloph consists of a protocone with a prominent antero-lingual accessory cusp. The shape of the protocone, which is transversely broad, suggests that a labial accessory cusp might also be present in earlier wear. On one specimen an antero-labial accessory cusp is present. The occlusal outline of the protoloph is thus broad and rectangular. The metaloph apparently has three cusps with the hypostyle well developed and directed somewhat anteriorly. The protoloph is connected at a point between the hypostyle and hypocone.

In the upper molars the cusps are united in a U-shaped loph open at the styles, hypostyle,



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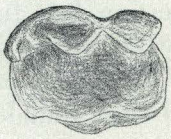

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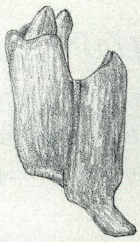

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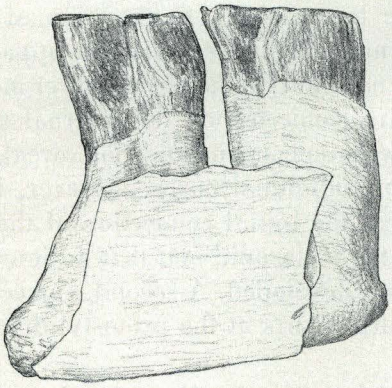

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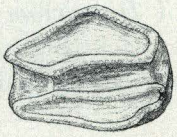

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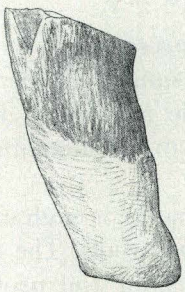

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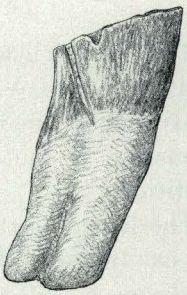

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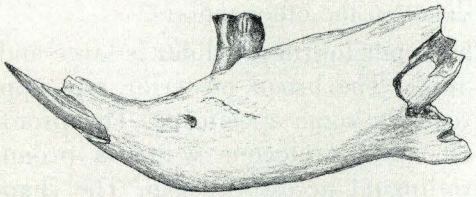

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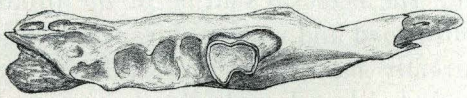

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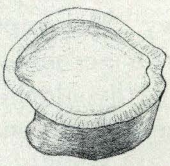

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and protostyle forming the two ends of the U. The paracone, protocone, and metacone occur as points on this loph while the hypocone is isolated. On some specimens the hypocone is connected to the U-shaped loph by a diminutive loph. Within the interloph area is a deep pit closed off at the styles. A lake is thus persistent through much of the wear of the upper molars.

The lower incisor has a rounded anterior face. The masseteric crest of the mandible rises dorsally as it progresses anteriorly, terminating below and anterior to the fourth premolar in a rugosity. The mental foramen is slightly anterior and ventral to the termination of the masseteric crest. The diastema is noticeably flat.

HIND LIMB: The distal end of the tibia-fibula is the only representation of that compound element present (see UO26972, fig. 24). The tibia and fibula are completely fused distally. It is close to *Liomys* and differs from *Heteromys* in the same manner as does *Liomys*. In *Heteromys* the groove for the flexor tibialis opens into the medial fossa for the trochlea of the astragalus. In *Liomys* and *Diprionomys* this groove is well separated from the fossa by a high septum which forms the medial border of the fossa. The grooves for the peroneus brevis and longus of the lateral maleolus are well developed and separated by strong processes. The relative size of these grooves is the same as in *Liomys*.

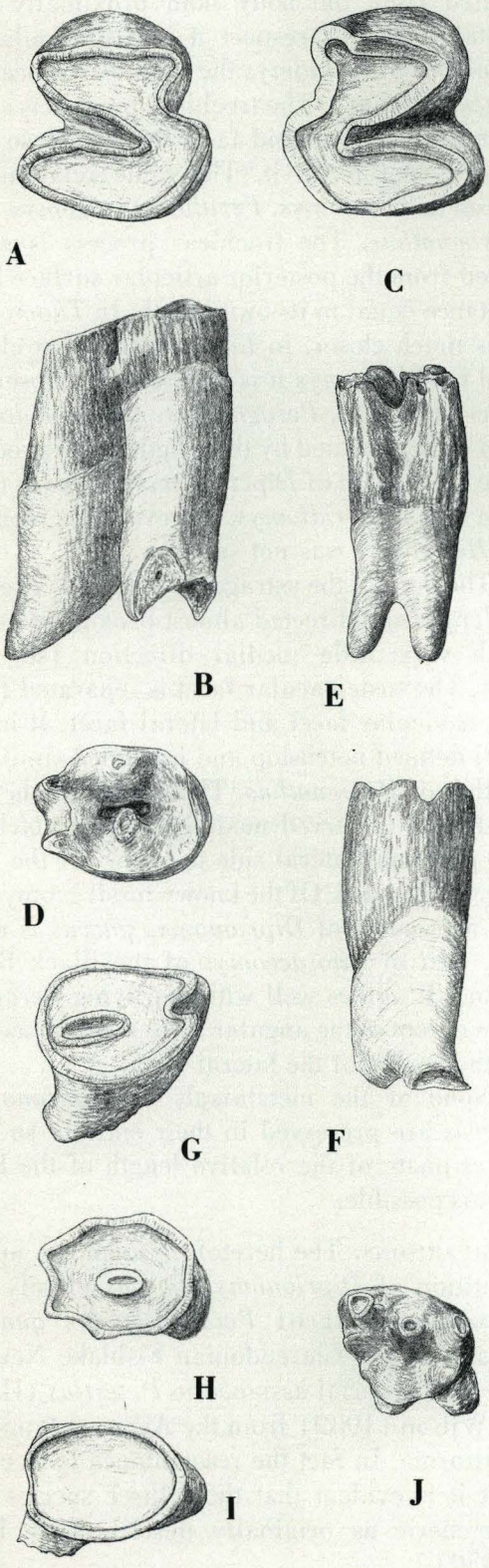
The calcaneum of *Diprionomys parvus* is slightly smaller than that of *Liomys salvini*. (see UO26971, fig. 25N). The cuboid facet is a well rounded hexagon in outline similar to *Thomomys* and not greatly different from *Peridiomys*. The trochlear process is well separated from the body both proximally and distally. In this respect it is also similar to *Thomomys*. In *Liomys* the trochlear process is not well defined. The trochlear process is separated from the cuboid facet by a notch so that it does not reach it. The same relationship exists in *Thomomys*, *Peridiomys*, *Liomys*, and *Perognathus*. The trochlear process is separated from the posterior articular surface by a distance equal to its own length. In *Thomomys* it is much closer, in *Liomys* somewhat closer and in *Peridiomys* it is only slightly closer. In *Microdipodops*, *Perognathus*, and *Dipodomys* it is well separated by the length of the process. The calcaneum of *Diprionomys parvus* is most like that of *Peridiomys*, however, this element of *Heteromys* was not seen.

The neck of the astragalus is close to *Liomys* in length and directed almost proximo-distally with very little medial direction (see fig. 26). The sustentacular facet is separated from the navicular facet and lateral facet. It has a well defined notchstop and is shaped similarly to that of *Perognathus*. The border of the lateral facet is curved medially with a notch on the proximal lateral side to allow for the passage of a tendon. Of the known fossil geomyoids the astragulus of *Diprionomys parvus* is most like that of *Pliosaccomys* of the Black Butte fauna. It agrees well with the living *Perognathus* except in the angular medial distal section of the border of the lateral facet.

None of the metatarsals of *Diprionomys parvus* are preserved in their entirety so that no estimate of the relative length of the hind foot is possible.

COMPARISONS: The heretofore unknown upper dentition of *Diprionomys parvus* closely approaches that of *Perognathoides quartus* (Hall) of the Clarendonian Fishlake Nevada site and material assigned to *P. tertius* (Hall) by Wilson (1939) from the Avawatz fauna of California. In fact the resemblance is so close that it is evident that these three species are congeneric as originally described by Hall (1930).

Figure 10. *Diprionomys parvus* Little Valley fauna, UOloc 2516, lower dention, **A**; UO25991, right P_4-M_1, occlusal view x 15, **B**; lingual view x 15, **C**; UO25992, left P_4, x 15, **D**; UO25594, left mandible I, P_4, labial view x 5, **E**; dorsal view x 5, **F**; UO 26016, left $M_{1 \text{ or } 2}$, occlusal view x 15, **G**; labial view x 15, **H**; lingual view x 15, **I**; UO26023, right M_2, occlusal view x 15, **J**; lingual view x 15, **K**; labial view x 15, **L**; UO27008, x 15

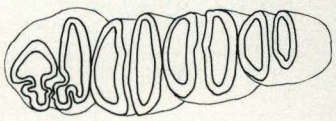


The appearance of accessory cusps arranged along the anterior border of the lower fourth premolar is strikingly like that of the much older *Gregorymys*. In *Periodiomys oregonensis* the cusps of the anterior lophid of the lower premolar also are first connected anteriorly. As in *Diprionomys parvus* the lophids of the lower premolar of *P. oregonensis* are connected labially and remain separated lingually. In both species the lophids of the lower molars are connected both centrally and labially. On the type specimen of *P. oregonensis* the connection is first central in the second and third molars but has not yet occurred in the first. Here connection would have been central and labial at about the same time. The teeth of *D. parvus* are much higher crowned and more lophiodont than are those of *P. oregonensis*, however, the difference in their age (Hemphillian and Barstovian) may indicate that these differences are those that would be expected. They are otherwise similar in basic plan and suggest a close relationship.

Among living heteromyids *Heteromys* and *Liomys* resemble *Diprionomys parvus* most closely. In *Liomys*, *Diprionomys parvus* and *Heteromys* lower teeth the lingual valley extends nearly to the base of the enamel whereas the labial valley is quite shallow (see fig. 12).

Figure 11. *Diprionomys parvus* Little Valley fauna, UOloc 2516, upper dentition, **A**; UO26073, right P^4, occlusal view, **B**; labial view, **C**; UO26012, left P^4, **D**; UO26014, right $M^{1 \text{ or } 2}$, occlusal view, **E**; labial view, **F**; lingual view, **G**; UO26004, left M^2,**H**; UO26022, right $M^{1 \text{ or } 2}$, **I**; UO26024, right M^2, **J**; UO26028, M^3, all x 15

Figure 12. *Liomys salvini*, little worn dentition, UCMVZ 131194, **A**; occlusal view left lower dentition, **B**; labial view anterior to left, **C**; lingual view, anterior to right, **D**; upper right dentition occlusal view, **E**; labial view, anterior to right, **F**; lingual view anterior to left, all x 10
Heteromys desmarestianus, little worn dentition, UCMVZ 98369, **G**; left lower dentition, occlusal view, **H**; labial view, anterior to left, **I**; lingual view, anterior to right, **J**; upper right dentition, occlusal view, **K**; labial view, anterior to right, **L**; lingual view, anterior to left, all x 10



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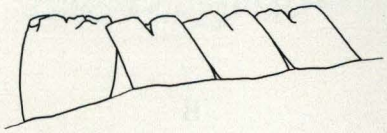

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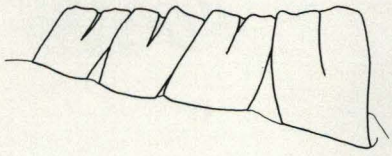

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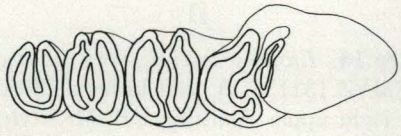

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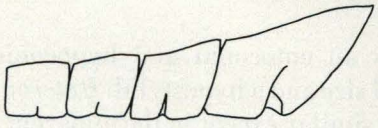

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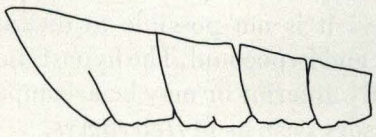

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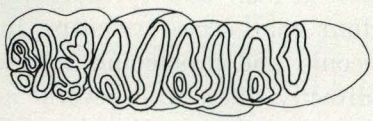

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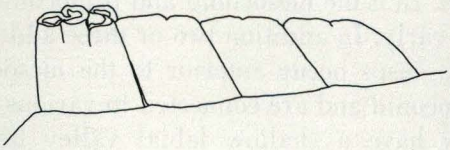

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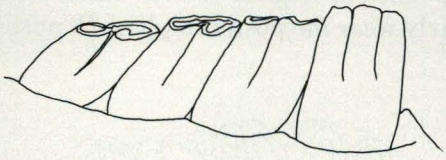

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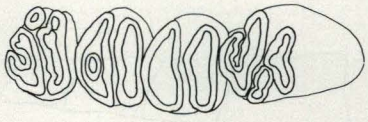

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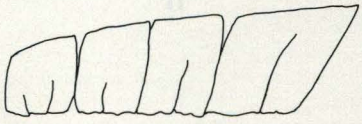

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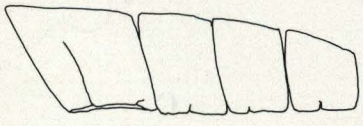


L

On the anteroloph of the P_4 of *D. parvus* the mesoconid and protoconid are well separated and connect at their anterior borders through three or four small accessory cusps. In *Liomys* the mesoconid and protoconid connect transversely directly often with several accessory cusps present on the anterior faces. The protoconid is the larger cusp. The anteroloph of the P_4 of *Heteromys* is somewhat more complicated. In it the mesoconid and protoconid connect early. In addition two or three additional large cusps occur anterior to the mesoconid-protoconid and are connected in various ways. They have a shallow labial valley between them and the mesoconid and a deep lingual valley between them and the protoconid. Thus two persistent lingual valleys occur on the P_4. In early wear the posteroloph of *D. parvus* displays an entoconid and hypoconid of about equal size and a hypostylid. *Heteromys* appears to be similar except in the apparent addition of an accessory cusp anterior to the hypostylid although this may just be a more anteriorly situated hypostylid. Even in unerupted teeth of *Liomys* it is not possible to distinguish entoconid and hypoconid. The hypostylid is situated slightly anterior or may be accompanied by an accessory cusp as in *Heteromys*.

The anteroloph and posteroloph of *D. parvus* connect at their labial edge and centrally sometimes creating a small enamel lake be-

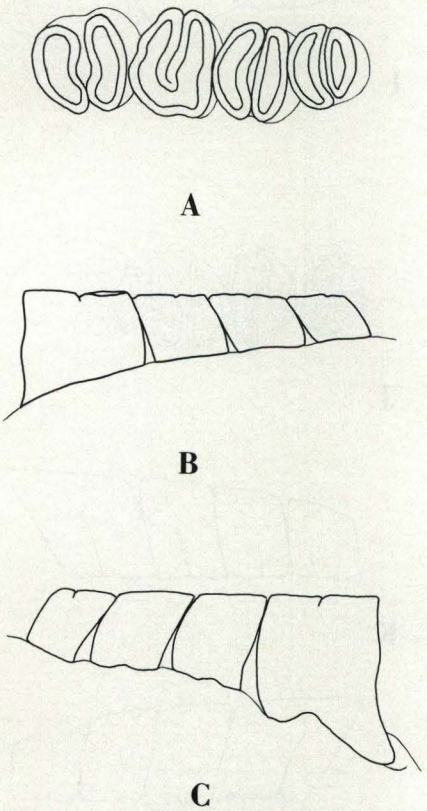


Figure 13. *Liomys salvini*, well worn dentition, UCMVZ 98419, **A**; left lower dentition occlusal view, **B**; labial view, anterior to left, **C**; lingual view, anterior to right, all x 10

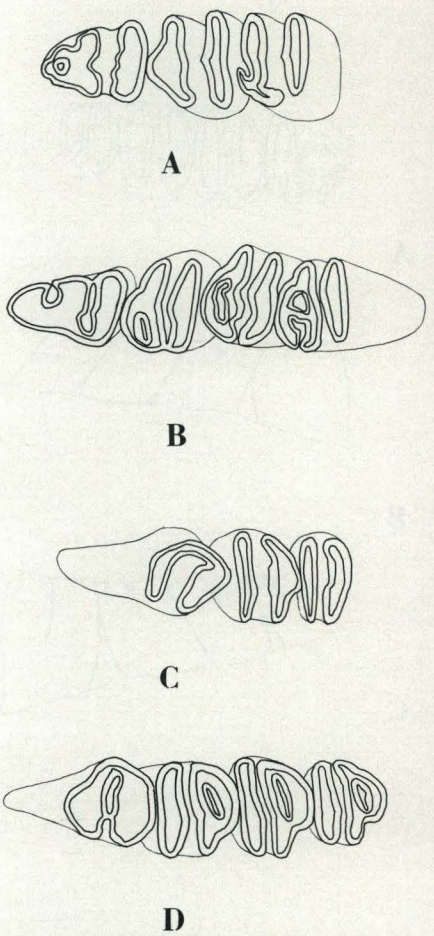


Figure 14. *Liomys salvini*, very young dentition, UCMVZ 131155, **A**; left lower dentition DP_4-M_2, **C**; right upper dentition DP^4-M^2, *Heteromys desmarestianus*, very young dentition, **B**; left lower dentition DP_4-M_3, **D**; right upper dentition DP^4-M^3, anterior to left on all specimens, all x 10

tween these points until late wear. The broad lingual valley remains open. In *Liomys* the connections is primarily labial so that moderately worn lower premolars of *Liomys* and *D. parvus* have a similar pattern (see fig. 13). In *Heteromys* two lingual valleys are open throughout wear although the labial valleys close early. The resulting occlusal pattern is thus unlike the other two genera.

The lower molars of *D. parvus* and *Liomys* consist of two simple transverse lophs which connect labially early. In *D. parvus* an additional connection is made between the protoconid and hypoconid in early wear isolating a small persistent enamel lake. In *Liomys* this second connection may occur much later in wear. The lower molars of *Heteromys* have an antero-posteriorly broad anterior loph (metaloph) which displays a persistent lake between the protostylid and protoconid unlike *D. parvus* and *Liomys*. The lophids connect labially early in wear. A secondary connection does not appear to occur.

The protoloph of the upper fourth premolar of *D. parvus* is broad and almost rectangular due to the development of lateral accessory cusps. In *Liomys* the protoloph is also broad but lophiodont and ovoid in occlusal outline. In *Heteromys* the protoloph has a flat anterior face and is also broadened but is triangular in occlusal outline. The metaloph of *D. parvus* and *Liomys* are similar whereas that of *Heteromys* is complicated by accessory lophs. The protoloph of *D. parvus* is connected to the metaloph through the hypostyle in later wear. In *Liomys* and *Heteromys* the protoloph is isolated from the metaloph until late wear. It apparently has a more central connection but no specimens were seen which were worn enough to reveal the exact nature of the connection.

The labial and lingual valleys of the upper molars of *D. parvus* are relatively short. The labial valley is longer in *Liomys* and much longer in *D. parvus* and *Heteromys*. In *Diprionomys* and *Liomys* connection between the protoloph and metaloph occurs early in wear at two points on the occlusal surface. One is at the lingual edge, the other medial to the labial border at about the point of the medial edge of the paracone. The result is a persistent central enamel lake and a small labial groove. In *Heteromys* only the lingual connection occurs. In late wear as the base of the labial valley is reached it appears that the connection becomes gradually broader. The metaloph of the molars of *D. parvus* and *Liomys* is simple and comparable, however, in *Heteromys* additional cusps create a persistent lake.

The palate in *Liomys* and *Heteromys* is smooth and not as wide as in *Dipodomys* or as narrow as in *Thomomys* or *Parapliosaccomys*. The teeth are in a straight line and the tooth lines diverge posteriorly. Complete palate material of *D. parvus* is not available so that direct comparisons of this feature are not possible. However, the palate of *D. quartus* is known and it compares closely with that of *Liomys* and *Heteromys* in width, smoothness, and divergence of the tooth lines. The alveolar area, however, is raised considerably above the palate surface. Partial palate material of *D. parvus* indicates that this raised alveolar area is also present in it. The mandibles of all three species examined compare well.

In size, height of crown of the teeth, and general dental characteristics it appears that these three rodents are closely related as has previously been suggested. In more specific details *D. parvus* is closer to the species of *Liomys* examined than *Heteromys* both in dental and appendicular skeletal features.

DIPRIONOMYS cf. *PARVUS*

In the Hemphillian Juniper Creek Canyon site (UOLoc 2469) *Diprionomys*, probably *D. parvus*, occurs represented by a lower fourth premolar (UO21727) and a fragmental upper molar (UO21728).

DIPRIONOMYS cf. *PARVUS*

Diprionomys is well represented in the Hemphillian Bartlett Mountain fauna, UOloc 2517. The material avaliable in most instances is

close to that from Little Valley, however, the upper premolars assigned do not have the well developed accessory cusps seen in the Little Valley specimens. They are smaller and may indicate the presence of another *Diprionomys* such as *D. minimus*. Since they are isolated teeth assignment is questionable.

Both upper and lower deciduous premolars are present in the collection from Bartlett Mountain. The lower deciduous premolar is very similar to that of *Perognathoides halli* as illustrated by Reeder (1956, fig. 87a). The posterior portions of the teeth are very much alike, however, there are minor differences anteriorly. There are three antero-lingual cusps on the Bartlett Mountain species rather than two as in *Perognathoides halli*. They decrease in size anteriorly. The labial side of the tooth consists of two and possibly three cusps rather than a lophid as in *P. halli*, however, this may be simply a wear difference since with wear the separate cusps merge to form a lophid. The central oblique cusp extends to the labial border in *D. parvus* rather than occurring entirely within the central basin of the tooth. A deciduous lower premolar from Little Valley is deeply worn on the labial side but little worn lingually. Those characteristics remaining agree with those of the Bartlett Mountain species.

The two upper deciduous premolars have damaged anterior ends but most of the characteristics are recognizable. One is well worn and the other in early wear. The tooth consists of three transverse lophs, the two posterior lophs are the largest and of about the same transverse width. The posterior loph consists of two strongly connected cusps as is the middle loph. These two lophs are connected by a cingulum at their lingual ends. This cingulum continues anteriorly, but much reduced, to the anterior loph, however, the major connection to the anterior loph is on the labial side. The anterior loph which is missing on one specimen and damaged on the other appears to have consisted of a single broad cusp.

Several geomyoid hind foot elements are present in the Bartlett Mountain fauna. Their size and similarity to those elements of *Liomys* suggest that they may represent *Diprionomys*. They include the cuboid, navicular and ectocunieform elements not known from Little Valley. All are close to *Liomys*. The cuboid has a smaller angle between the deep tendon groove and facet for MT IV. The proximal-distal length is short as in *Liomys* and *Perognathus*. On the ectocunieform the navicular facet is slightly rounder than *Liomys* but otherwise close.

Subfamily Geomyinae

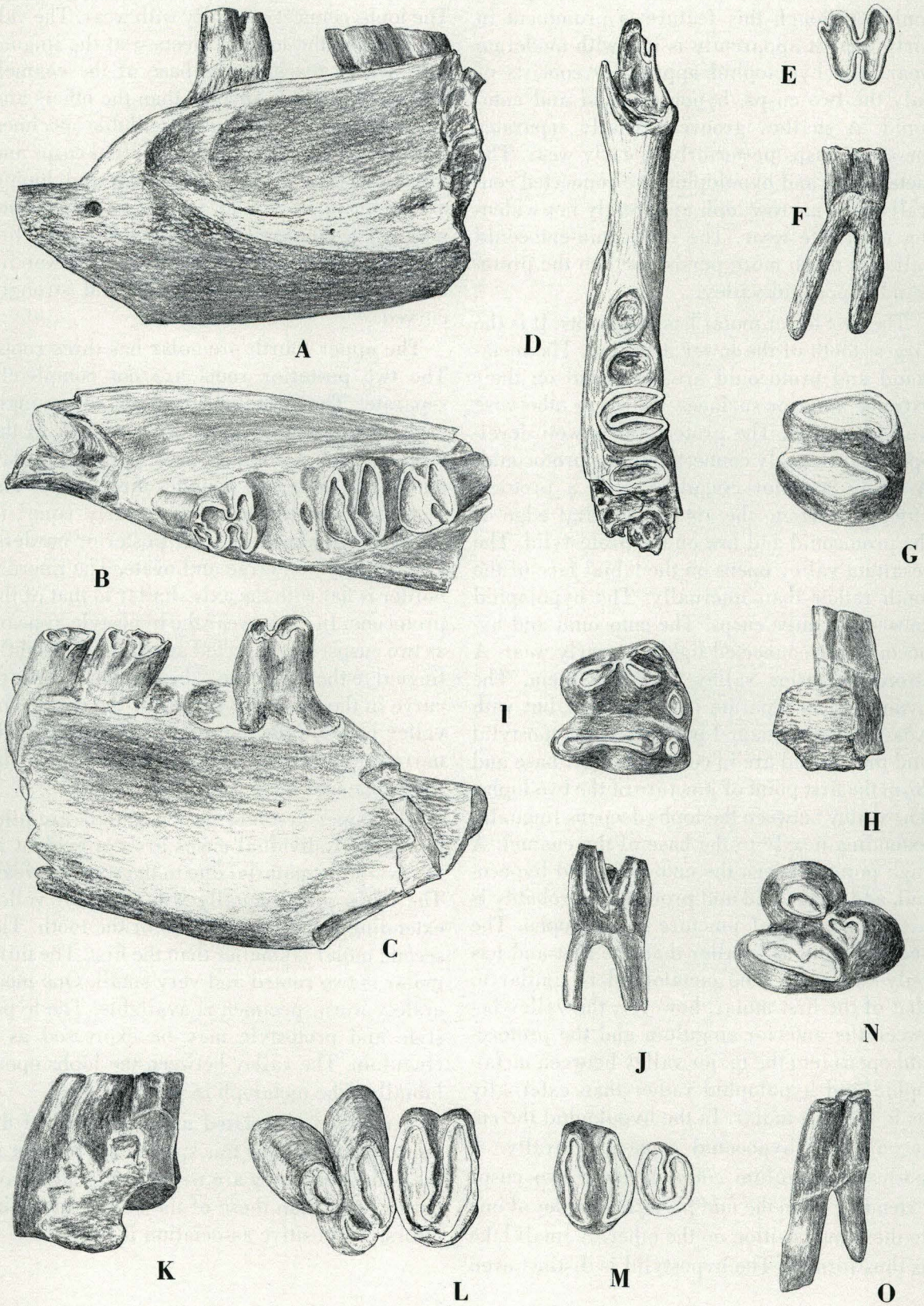
PRODIPODOMYS? MASCALLENSIS Downs 1956

(Fig. 15)

A small rodent here assigned to *Prodipodomys mascallensis* is well represented in the Barstovian Quartz Basin fauna, UOloc 2465. The mandible is relatively heavy and deep for the size of the animal. The masseteric crest is sharp and curves strongly dorsally nearly reaching the diastema. It terminates just anterior to the anterior root of the fourth premolar. The mental foramen is below the lowest point of the diastema and in one specimen is represented by two openings. The diastema is short.

The lower fourth premolar has two very long roots. The metalophid consists of a large protoconid with a smaller mesoconid. Extending antero-medially from the mesoconid is a lophid including an anteroconid. This lophid, or possibly anterior cingulum, forms a nearly com-

Figure 15. *Prodipodomys mascallensis*, Quartz Basin fauna, UOloc 2465, **A**; UO22740, left mandible with P_4, M_{2-3}, labial view x 10, **B**; dorsal view x 10, **C**; lingual view, x 10, **D**; UO22743, left mandible with M_1, dorsal view, x 10, **E**; UO22738, left P_4, occlusal view x 10, **F**; labial view x 10, **G**; UO22732, M_3, occlusal view, x 15, **H**; labial view x 10, **I**; UO22736, right M_1 occlusal view x 15, **J**; lingual view x 10, **K**; UO22731, left P^4-M^1, labial veiw x 10, **L**; occlusal view x 15, **M**; UO22970, left M^{2-3} x 15, **N**; UO22728, right P^4 occlusal view x 15, **O**; lingual view x 10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plete lake between it and the mesoconid-protoconid. Although this feature is prominent in early wear it apparently is lost with moderate wear. The hypolophid apparently consists of only the two cusps, hypoconid and and entoconid. A shallow groove partially separates these two cusps posteriorly in early wear. The metalophid and hypolophid are connected centrally by a narrow loph apparently not widening until late wear. The metaconid-entoconid valley is much more persistent than the protoconid-hypoconid valley.

The first lower molar has four roots. It is the largest tooth of the lower dentition. The metaconid and protoconid are connected on their extreme anterior surfaces. They are otherwise well separated. The protostylid is well developed and strongly connected to the protoconid. A strong anterior cingulum, with a protoconule, connects to the anterior medial edge of the protoconid and low on the protostylid. The resultant valley opens on the labial face of the tooth rather than internally. The hypolophid consists of three cusps. The entoconid and hypoconid are connected lightly in early wear. A strong posterior valley separates them. The hypostylid is separate in early wear but with wear joins the enamel pattern. The hypostylid and protostylid are in contact at their base and form the first point of juncture of the two lophs. The valley between the lophs deepens lingually extending nearly to the base of the enamel. A high point between the entoconid and hypoconid, and metaconid and protoconid probably is a second point of juncture of the lophs. The second molar is smaller than the first and has only two roots. The metalophid is similar to that of the first molar, however, the valley between the anterior cingulum and the protoconid opens into the major valley between metalophid and hypolophid rather than externally as in the first molar. In the hypolophid the entoconid and hypoconid connect centrally. A posterior cingulum connects these two cusps extending from the mid posterior border of one to the same position on the other. A small lake is thus formed. The hypostylid is distinct even after connection with wear to the hypoconid. The lophs connect centrally with wear. The valley between the lophs is deepest at the lingual side nearly reaching the base of the enamel. The third molar is smaller than the others and possess two roots. The only available specimen is well worn, however, the individual cusps and lophs are still evident. The cusp and lophid arrangement is similar to that of the second molar. The connection of the lophs is more lingual than in the second molar. The lower incisor is ovoid in cross section and strongly curved.

The upper fourth premolar has three roots. The two posterior roots are not completely separate. The protoloph consists of a single cusp, ovate in early wear, with the axis of the cusp somewhat oblique. It is posteriorly flattened. The metaloph includes three cusps. The metacone and hypocone are nearly equal in size and are joined on their posterior borders. The hypostyle is large and ovate. The internal border is flat with the axis similar to that of the protocone. In early wear the hypostyle appears as two cusps. It is directed anterior and slightly lingual to the hypocone. This results in a sharp curve in the posterior border of the tooth. The valley between the hypostyle and protocone is narrow and shallower than that between the protocone and metacone.

The upper first and second molars are bilophiodont. Individual cusps are not evident in the available material due to the stage of wear. The lophs join lingually with a labial valley extending nearly to the base of the tooth. The second molar is smaller than the first. The third molar is two rooted and very small. One moderately worn specimen is available. The hypostyle and protostyle may be expressed as a cingulum. The valley between the lophs opens labially. The metaloph is much reduced.

A number of isolated upper incisors of the appropriate size for this species are present in the collection. They are without sulci and have flatter faces than those of the known lower incisors. No positive association is available.

HIND LIMBS Only the calcaneum and astragalus have been recognized. The calcaneum (UO-26989) is similar to that of *Pliosaccomys* of the Clarendonian Black Butte fauna (see fig. 25 K & L). It has a heart-shaped cuboid facet. The trochlear process is relatively close to the posterior articular surface and well defined. The sustentaculum astragali is directed proximally. The astragalus is also similar to that of *Pliosaccomys* and in fact cannot be separated from it.

COMPARISONS: The species compares favorably with *Prodipodomys? mascallensis* Downs (1956) from UCloc 4830 of the Barstovian Mascall fauna in a number of characteristics. The new material is, for the most part, less worn so that differences observed may only reflect stages of wear. The known Mascall specimen, a mandible with complete dentition, is at a stage of wear in which the two lophids of each of the molars have already united in at least two places, both lingual and central. Reeder (1956) in examining this specimen concluded that the lingual connection was made first the other later. On this basis, plus the lack of great reduction of the third molar, he concluded that this species should be assigned to *Peridiomys* rather than *Prodipodomys* (Reeder 1956, p. 224). In the new material, which is much less worn, first contact between lophs of the first molar is at the styles, or lingual, on the second and third molars it is central with a lingual connection soon afterward in the course of wear. The new material also indicates that the teeth are higher crowned than estimated by Reeder for the Mascall specimen.

The lower fourth premolars appear to differ, however, this again may represent wear and variation. The Mascall specimen exhibits a shallow groove on the anterior face of the tooth. The Quartz Basin specimens, less worn, exhibit an extension of a reduced mesoconid which may be an anterolophid with a small anteroconid included. This lophid blocks any expression of the anterior valley in the face of the tooth.

The posterior portion of the mandible is not present in either the Quartz Basin or Mascall material so that it cannot be determined if the mandibular foramen is situated as in *Prodipodomys kansensis* and *P. idahoensis*.

Some noteworthy similarities exist between the Quartz Basin species and *Proheteromys sulculus* Wilson (1960). Although the later species does not exhibit the central connection of cusps in the lower premolar it does present an anteroconid between the mesoconid and protoconid. *P. sulculus* tends to have an early connection between the proto and hypostyles in the first lower molar and a more central connection in the second and third molars. *P. sulculus* lacks the hypostyle present in the Quartz Basin species. The basic plan of the upper fourth premolar of *P. sulculus* is similar to that of the Quartz Basin species in that both have a single cusped protocone connected to the posterior loph through the entostyle. The Quartz Basin species is much higher crowned, however. The protostyle-hypostyle connection is not so strong in the latter species as in *P. sulculus*. The mental foramen of the mandible of *P. sulculus* is apparently situated more anteriorly than in the new material. The incisor of *P. sulculus* is somewhat flattened rather than convex as in the Quartz Basin species.

Peridiomys oregonensis is a larger form than the Quartz Basin species and lower crowned. The lower premolar of *P. oregonensis* has its interloph connection between the external cusps rather than centrally as in the new material.

In both general and specific characteristics the Quartz Basin species closely approximates the known specimen of *Prodipodomys ? mascallensis*. Its assignment to a genus is not clear. The lower premolar is fundamentally different than that of *Peridiomys*, although some other characteristics suggest relationships at a more distant level. Similarly *Proheteromys sulculus* suggests relationships but these again are apparently distant. Similar suggestive relationships can also be noted with much older forms as *Dikkomys*, *Grangerimus* and *Gregorymys*. Among younger forms this species represents

some aspects of *Prodipodomys* and *Pliosaccomys*. The central connection of the cusps of the lower fourth premolar is seen in both *Prodipodomys* and *Pliosaccomys* although the metalophid is more complex in the known species of *Pliosaccomys*. The Quartz Basin specimen has about the degree of complexity of that of *Pliosaccomys wilsoni*. The lophids of the lower molars of *Pliosaccomys* tend to connect first labially then centrally whereas in *Prodipodomys* presumably they connect centrally first. In the Quartz Basin species this varies with the position in the jaw, the lophids of M_1 connecting differently than M_2. The anterior face of the lower incisors of *Pliosaccomys* are flattened and those of *Prodipodomys* more rounded. The lower third molar of *Pliosaccomys* is not noticeably reduced but in modern dipodomyines it is greatly reduced. The Quartz Basin species has a relatively smaller lower third molar than that of *Pliosaccomys* but not reduced to the degree of the living *Dipodomys*.

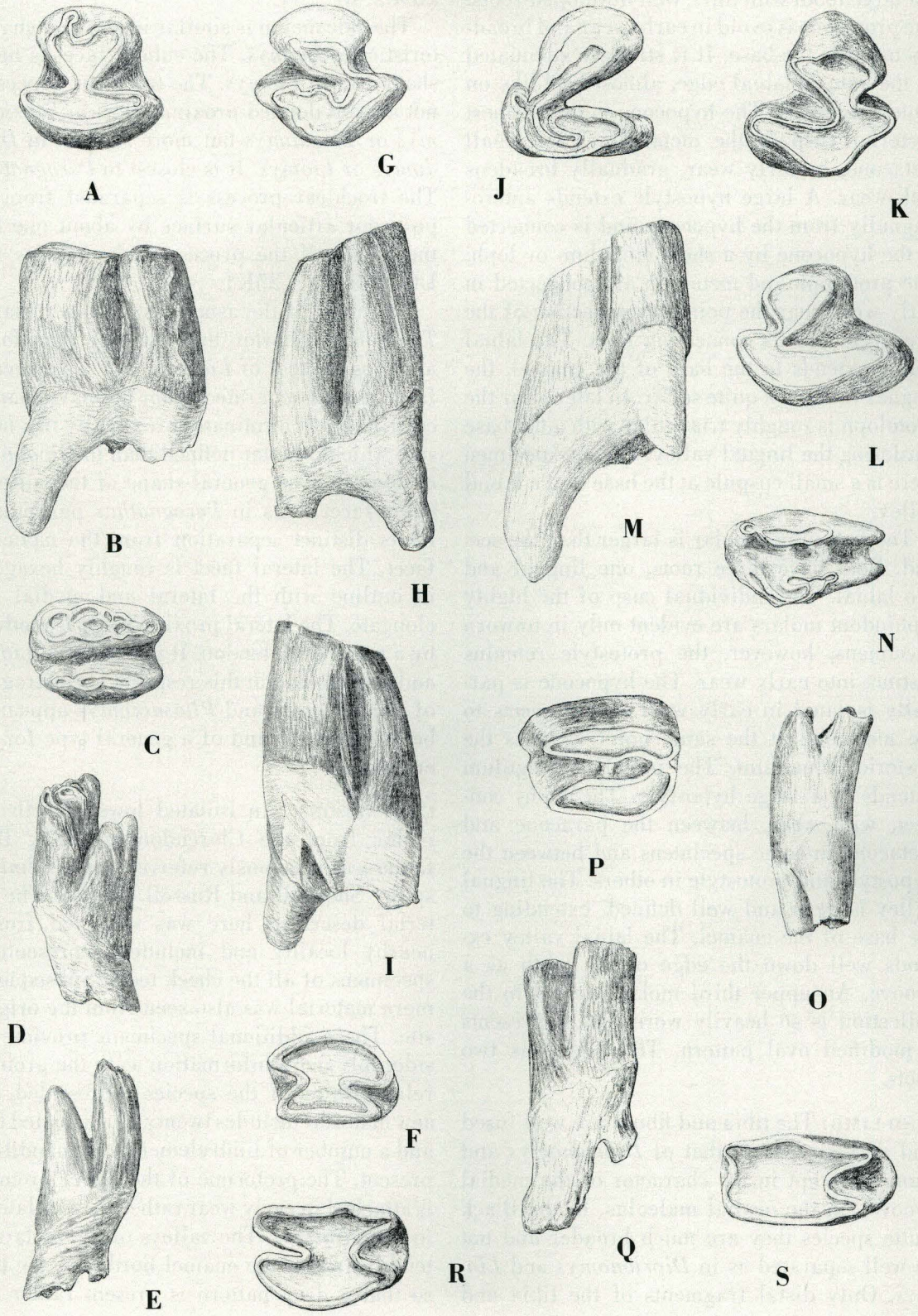
The Quartz Basin species as well as the Mascall species, if they are different, both occupy a similar phylogenetic position. This position is one in a group of rodents which has relationships with apparently both heteromyids and geomyids. No known genus is entirely satisfactory for these species.

PLIOSACCOMYS sp.

A species of *Pliosaccomys* is well represented in the Clarendonian Black Butte fauna at UOloc 2500. The lower fourth premolar is high crowned as are the other teeth and possess two roots. The metalophid consists of two cusps, protoconid and mesoconid, which are subequal in size. These cusps are well separated by an anterior valley. Accessory cusps appear on the anterior tips of each of the cusps and on one specimen an "anteroconid" blocks the anterior valley. On specimens in which the anterior valley is evident it extends well down the face of the tooth. The individual cusps of the hypolophid are not distinct on any of the available specimens. The hypoconid and protoconid are not separated posteriorly at the stage of wear seen. There may be a hypostylid present but there is no direct evidence of it. The valley between the entoconid and protoconid extends nearly to the base of the enamel. The other valley is not as deep. The valleys are broadly open. The hypolophid and metalophid connect centrally. This connection becomes very little wider with wear.

The first and second lower molars have two roots. In some specimens the posterior root is bifurcate. The molars are highly lophiodont with individual cusps recognizable only in very early wear. The lophs are deeply separated and narrow antero-posteriorly. The protoconid and metaconid are of about equal size and are connected through their anterior borders. The protostylid is large in some specimens doubled and connected by the anterior cingulum to the protoconid producing a shallow valley between the protostylid and protoconid which at some stage of wear appears as a lake in the occlusal pattern. The hypolophid is shorter than the metalophid. Hypoconid and entoconid are of about the same size and connected through their anterior borders. The hypostylid is large. The valley between the lophids extends nearly to the base of the enamel both lingually and labially. The lophids connect with wear from a point between the entoconid and hypoconid to the edge of the metaconid. The third molar has three roots, two posterior. The only specimen available is in late wear and displays a strong central connection of the lophs. The hypolophid appears to be reduced.

Figure 16. *Pliosaccomys* sp. Black Butte fauna, UOloc 2500, **A**; UO24478, left P_4, occlusal view, **B**; labial view, **C**; UO24467, left $M_{1\text{ or }2}$ occlusal view, **D**; labial view, **E**; lingual view, **F**; UO24891, M_3, **G**; UO24476, right P^4 occlusal view, **H**; labial view, **I**; lingual view, **J**; UO24472, left P^4, **K**; UO24459, right P^4,**L**; UO 24462, left P^4, occlusal view, **M**; lingual view, **N**; UO24460, left $M^{1\text{ or }2}$, occlusal view, **O**; lingual view, **P**; UO24461, right $M^{1\text{ or }2}$ occlusal view, **Q**; labial view, **R**; UO24458, left $M^{1\text{ or }2}$, **S**; UO24468, left $M^{1\text{ or }2}$, all x 15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The fourth premolar of the upper dentition is a large tooth with three well developed roots. The protocone is ovoid in early wear and broadens towards the base. It is strongly attenuated on the anterio-labial edge, almost keel-like on some specimens. The hypocone is the furthest posterior cusp of the metaloph. The small metacone, in early wear, gradually broadens with wear. A large hypostyle extends anterolingually from the hypocone and is connected to the hypocone by a short cingulum or loph. The protoloph and metaloph are connected in early wear near the point of connection of the hypostyle and its connecting loph. The labial valley extends to the base of the enamel, the lingual valley not quite so far. In later wear the protoloph is roughly triangular with a flat base bordering the lingual valley. On one specimen there is a small cuspule at the base of the labial valley.

The first upper molar is larger than the second. Both have three roots, one lingual and two labial. The individual cusp of the highly lophiodont molars are evident only in unworn specimens, however, the protostyle remains distinct into early wear. The hypocone is partially isolated in early wear and connects to the metacone at the same point as does the posterior cingulum. The posterior cingulum extends to a large hypostyle. The lophs connect, with wear, between the paracone and metacone in some specimens and between the hypostyle and protostyle in others. The lingual valley is deep and well defined, extending to the base of the enamel. The labial valley extends well down the edge of the tooth as a groove. An upper third molar present in the collection is so heavily worn that it presents a modified oval pattern. The tooth has two roots.

HIND LIMB: The tibia and fibula are well fused and very similar to that of *Diprionomys* and *Liomys* except in the character of the medial grooves on the medial maleolus. In the Black Butte species they are much broader and not as well separated as in *Diprionomys* and *Liomys*. Only distal fragments of the tibia and fibula are present in our collections (see UO-26982, fig. 24).

The calcaneum is similar in size and characteristics to *Liomys*. The cuboid facet is heart-shaped as in *Liomys*. The trochlear process is not as well defined proximally as in *Diprionomys* or *Thomomys* but more so than in *Dipodomys* or *Liomys*. It is closest to *Perognathus*. The trochlear process is separated from the posterior articular surface by about one half the length of the process as in *Liomys* (see UO26981, fig. 25K).

The neck of the astagalus is longer than in *Thomomys*, shorter than that of *Dipodomys* and close to that of *Liomys*. The sustentacular facet is well separated from the navicular facet distally. It terminates proximally in a notch stop which is better defined than in *Dipodomys* or *Liomys*. The general shape of the sustentacular facet is as in *Perognathus* particularly in its distinct separation from the navicular facet. The lateral facet is roughly hexagonal in outline with the lateral and medial side elongate. The lateral proximal side is modified by a notch for a tendon. It is similar to *Liomys* and *Dipodomys* in this respect. The astragalus of *Diprionomys* and *Pliosaccomys* appears to be very similar and of a general type for heteromyids.

COMPARISONS: An isolated lower fourth premolar from the Clarendonian Black Butte fauna was previously referred to *Cupidinimus* sp. by Shotwell and Russell (1963). The material described here was collected from a nearby locality and included representative specimens of all the cheek teeth. Subsequently more material was also seen from the original site. These additional specimens provide considerably more information as to the probable relationships of the species represented. The new material includes twenty four isolated teeth and a number of limb elements, no mandible is present. The protocone of the upper premolar is attached in early wear rather than isolated as in *Cupidinimus*. The valleys of the molars extend nearly to the enamel border of the tooth so that a deep pattern is present rather than

TABLE 4
MEASUREMENTS OF UPPER FOURTH PREMOLARS

Species	number	locality	AP greatest	AP occlusal	T greatest	T occlusal
Peridiomys oregonensis	UO24198	2495	1.64	1.38	1.44	1.44
	UO22879	2495	1.30		1.51	
	UO24203	2495	1.30		1.49	
	UO24196	2495	1.41		1.60	
	UO24195	2495	1.22		1.50	
	UO24199	2495	1.32		1.46	
	UO22744	2465	1.64	1.38	1.42	
Diprionomys parvus	UO26073	2516		1.54		1.74
	UO26012	2516		1.46		1.53
	UO26072	2516		1.32		1.37
	UO26013	2516		1.56		1.61
	UO26011	2516		1.25		1.18
Prodipodomys mascallensis	UO22728	2465	1.23	0.89	1.29	1.02
	UO22731	2465		0.98	1.39	1.09
Pliosaccomys sp.	UO24476	2500	1.40	0.96	1.58	1.11
	UO24474	2500	1.35	1.35	1.58	1.58
	UO24472	2500		1.19	1.53	1.21
	UO24462	2500	1.31	1.31	1.53	1.53
	UO24475	2500		1.38		1.32
	UO24459	2500		1.25		1.49
Pliosaccomys magnus	UO24436	2517		1.55		1.75
Parapliosaccomys oregonensis	UO26096	2222		1.20		1.41
	UO26095	2222		1.27		1.40
	UO25370	2222		1.40		1.47

elevated as in *Cupidinimus*. The lower premolars are elongated antero-posteriorly particularly the anterior loph and much more so than in *Cupidinimus*. Variations in the point of contact in the course of wear of the anterior and posterior lophs of the molars are similar to those of *Cupidinimus*. It is evident that the earlier assignment of this species to *Cupidinimus* was erroneous.

In comparison with the Barstovian Quartz Basin species, assigned to *Prodipodomys mascallensis*, a number of gross similarities are evident. Both species have strongly bilophiodont molars but the valleys separating the lophs are much deeper in the Black Butte species. The lower premolars of both species have cusps joining in the center of the tooth. However, the anterior loph of the Black Butte species is proportionally longer anteroposteriorly than that of the Quartz Basin form. The lateral and medial valleys are much more broadly open in the Black Butte species. In the latter species the metaconid and protoconid of the lower fourth premolar are much more equal in size and both have accessory cusps. In the lower molars of both species the lophs connect centrally with wear. The tendency for an early lingual connection of lophs in the upper molars seems to be stronger in the Quartz Basin species. It varies considerably in the Black Butte species. The younger species is larger and higher crowned than the older form. A number of the differences enumerated are those which may reflect an evolutionary step, particularly when the difference in age of the two species is considered plus the gross similarities.

Many characteristics of the Black Butte species are close to those of *Pliosaccomys*. The elongated anterior loph of the lower fourth premolar, the early connection of the anteriorly flattened protocone of the upper fourth premolar, the deep valley in the molars extending to the enamel base, the apparently little

reduced third molars, all strongly indicate close relationship with *Pliosaccomys*. The lower fourth premolar is not as complicated as that of the Hemphillian *P. dubius* and the central connection of lophs of the lower molars is not as frequent in *P. dubius*. The available material indicates a strong relationship between *Pliosaccomys dubius* and the Black Butte species. The species are not con-specific but are very probably con-generic. *Pliosaccomys wilsoni* James (1963) is of approximately the same age as the Black Butte species, however, early labial connection of the lophs of the lower molars in the California species differs from the Black Butte species in the same way as does *P. dubius*.

The species could be assigned here to *Prodipodomys* due to the central connection of lophs in the lower molars and the absence of flat-faced incisors in the sample. Similarities to *Pliosaccomys* are strong, however, for example the early connection of proto and metaloph of the P^4, and assignment is therefore made to *Pliosaccomys*.

PLIOSACCOMYS MAGNUS (Kellogg) 1910
(Figs. 17 & 18)

Diprionomys magnus Kellogg, L. 1910 U. C. Bull. Dept. Geol., Vol. 5, No. 29, p. 434

Cupidinimus magnus (Kellogg), Wood, A. E., 1935 Ann. Carn. Mus., Vol. 24, p. 145

Dipodomys or *Prodipodomys magnus* (Kellogg), James, G. T., 1963 U. C. Publ. Geol. Sci., Vol. 45, p. 106

This species is well represented at Bartlett Mountain. The materials consist primarily of unassociated teeth and skeletal elements. The dentition is high crowned and without enamel failure.

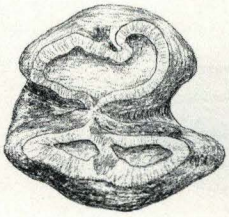
The lower fourth premolar has two roots. On the metalophid are two major cusps, possibly with small accessory cusps in very early wear, however, the available material is worn to a point where these smaller cusps are included in the occlusal pattern of the major cusps. An anterior valley separates the major cusps and extends down the face of the tooth a short distance. Three cusps make up the hypolophid. The hypoconid and entoconid are large and well defined. The hypostylid is quite small. In early wear the cusps are connected centrally. The metalophid wears to a single circular cusp narrowly connected to an ovoid hypolophid. The deciduous lower fourth premolar has a pattern similar to that of *P. dubius*. It is highly cuspate with cusps weakly connected to a low central lophid.

In the lower first and second molars the cusps are strongly lophiodont. Individual cusps are not well separated even in unworn teeth. A strong anterior cingulum connects from a point between the metaconid and protoconid of the metalophid and extends around to a strong protostylid. The metalophid is much higher than the hypolophid which is lophiodont and consists of three cusps. The lophs first contact labially, with wear, but at a point internal enough to leave a shallow groove down that side of the tooth. The lingual valley is deep and extends nearly to the base of the enamel. The roots of the molars are separated only on the labial side.

Only one speciment of an upper fourth premolar in the collection from Bartlett Mountain can be assigned to this species with confidence. This specimen is worn to the point that individual cusps are lost. The protoloph is triangular and attenuated at the anterior labial angle as in other *Pliosaccomys*. The anterior border of the metaloph is flat but strongly curved on the posterior border. The protoloph has a narrow connection to the metaloph apparently between the hypostyle and hypocone. The resultant worn occlusal pattern is Z-shaped. The third root is only poorly developed.

The upper first and second molars are high

Figure 17. *Pliosaccomys magnus,* Bartlett Mountain fauna, UOloc 2517, lower dentition, **A**; UO 26058, right P_4, occlusal view, **B**; lingual view, **C**; UO24943, P_4, **D**; UO24979, DP_4, **E**; UO27009, anterior moiety P_4, **F**; UO26037, right $M_{1\text{ or }2}$, occlusal view, **G**; lingual view, **H**; labial view, **I**; UO25229, right $M_{1\text{ or }2}$, occlusal view, **J**; posterior lingual view, **K**; UO26036, right $M_{1\text{ or }2}$, **L**; UO 26068, left M_3, **M**; UO26067, right M_3, all x 15



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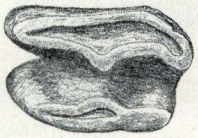

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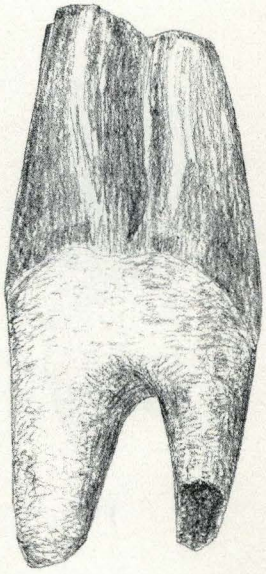

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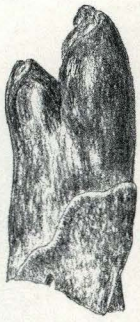

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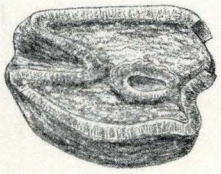

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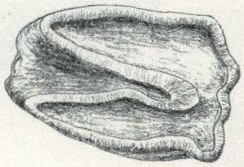

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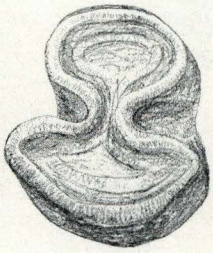

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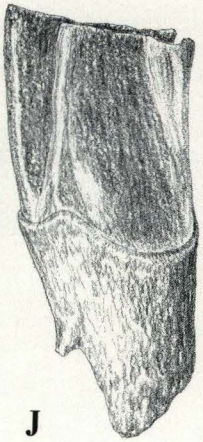

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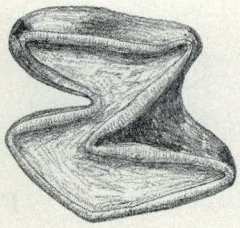

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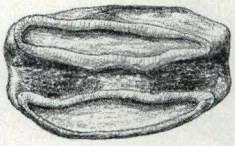

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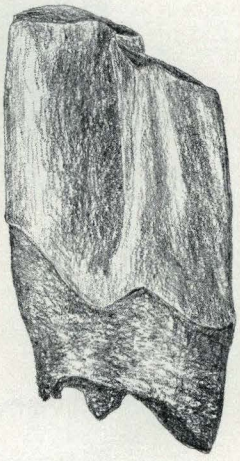

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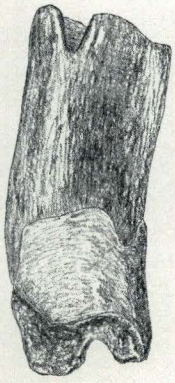

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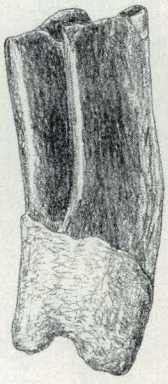

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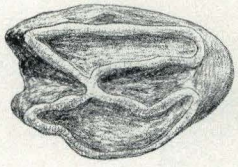

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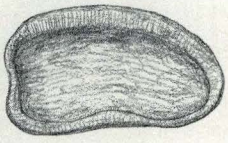

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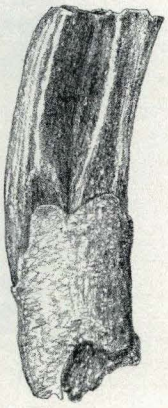


H

I

crowned teeth. They are much wider than long. The protoloph consists of three poorly defined but equal sized cusps with apparently no anterior cingulum. The hypostyle, of the metaloph, is directed somewhat anteriorly and is ovoid. The metacone is also ovoid whereas the hypocone is rounded. Connection between the lophs occurs between the paracone and metacone slightly internally so that a narrow extension of the valley beyond this point extends to the base of the enamel. Connection is also made and about at the same time between hyopstyle and protostyle.

COMPARISON: The lower premolar is similar to that of *Pliosaccomys magnus* (Kellogg) from the Hemphillian Thousand Creek fauna in that the anterior loph is very nearly round in late wear and has an anterior groove in earlier wear. The molars are close to *P. dubius* but little worn molars of P. *magnus* are not known from the type locality. Those in the type specimen of *P. magnus* are well worn and appear not to taper noticeably lingually as they do in *P. dubius*. In the Bartlett Mountain species no specimens are available of lower molars which are worn to the extent of the known specimens of *P. magnus* so that comparison of this characteristic is not possible. The lower molars of the Bartlett Mountain specimens have an anteriorly directed anterior cingulum similar to that of *P. dubius* but not so much as seen in *P. wilsoni.*

Two lower milk premolars are present in the collection from Barlett Mountain. They are very close to one referred to *P. dubius* by Wilson. The cusps of the *P. dubius* material appear to be somewhat lengthened antero-posteriorly but this is apparently due to the state of wear of the specimen. The cusps of the Bartlett Mountain species are highly conical but the arrangement and interconnection of the cusps and lophs is identical with those of *P. dubius.*

The available evidence indicates that the Bartlett Mountain species should be called *Pliosaccomys magnus.* The geographic proximity and similarities where they can be seen in the limited material available lead to this conclusion. It is not impossible that all three occurrences represent the same species.

Pliosaccomys magnus is larger and much higher crowned than *Pliosaccomys* sp. from the Clarendonian Black Butte fauna. The time relationship, the close geographic proximity and the similarity of many aspects of the dentition strongly tempt one to suggest a direct evolutionary step between the two forms. Since, however, both collections are primarily isolated teeth, although occurring in close association and carefully collected, some caution is indicated. Furthermore since associated dentitions in mandibles and palates with incisors representing these forms will most certainly be found in the near future it is best at this point to indicate that the Black Butte species very probably represents a developmental stage through which *P. magnus* passed and may be its immediate ancestor although such a step would have been rather large.

Figure 18. *Pliosaccomys magnus*, Bartlett Mountain fauna, UOloc 2517, upper dentition, **A**; UO 24436, left P^4, occlusal view, **B**; labial view, **C**; UO27010, $M^{1 \text{ro} 2}$, **D**; UO24960, right $M^{1 \text{or} 2}$ occlusal view, **E**; lingual view, **F**; labial view, **G**; UO25233, left $M^{1 \text{or} 2}$ occlusal view, **H**; labial view, **I**; lingual view, all x 15

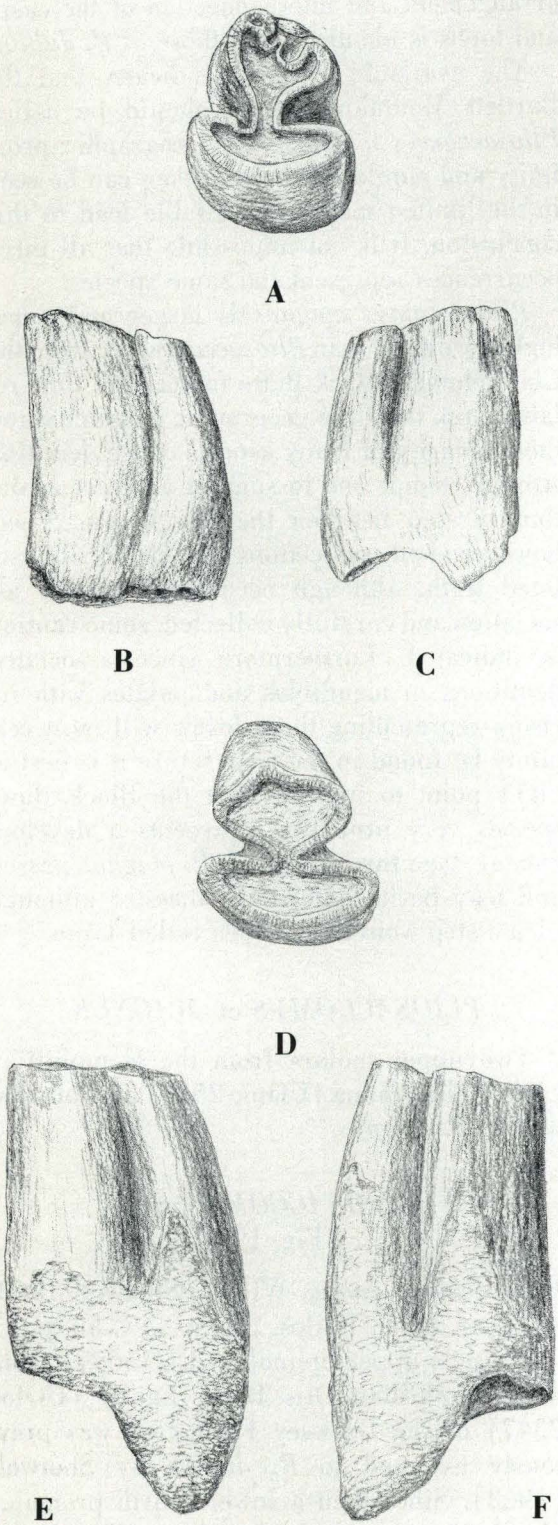
PLIOSACCOMYS cf. *MAGNUS*

Two upper molars from the Hemphillian Little Valley fauna (UOloc 2516) are referred here to *P. magnus.*

PLIOSACCOMYS sp.
(Fig. 19)

Pliosaccomys dubius Wilson, Shotwell 1963, Trans. Amer. Philos. Soc. n. s., v. 53, p. 73

A single upper premolar (UO15687) from the Hemphillian Otis Basin Fauna (UOloc 2347) of the Drewsey Formation was previously assigned to *P. dubius* by Shotwell (1963). Since then a lower fourth premolar (UO26078) and a calcaneum (UO26951) have been recovered at the same locality. The



calcaneum is slightly smaller than that of *Parapliosaccomys oregonensis* n. sp. but considerably larger than that of *Pliosaccomys* from the Clarendonian Black Butte Fauna. The lack of enamel failure or dentine tracks on the available teeth suggest that it does not represent the McKay species but is best referred to *Pliosaccomys*.

PARAPLIOSACCOMYS OREGONENSIS

n. gen. n. sp.
(Figs. 20-23)

Pliosaccomys dubius Wilson, Shotwell, 1956, Bull. G.S.A., Vol. 67, p. 730

GENOTYPE: *P. oregonensis*

DIAGNOSIS: as in *P. oregonensis*

HOLOTYPE: UO 3631 complete left mandible with incisor, P_4-M_1.

REFERRED MATERIAL: 3 mandibles, $4DP_4$ $18P_4$, 44_M, $4DP^4$, $24P^4$, 56^M, a rostral fragment (UO27005) and a number of skeletal elements.

TYPE LOCALITY: UOloc 2222 McKay Reservoir Oregon.

AGE: Hemphillian

DIAGNOSIS: about the size of *Pliosaccomys dubius* and the smaller species of *Thomomys*. Upper incisors asulcate with flat anterior faces. Lower incisors also with flat anterior faces. Cheek teeth with dentine tracts due to enamel failure extending somewhat more than halfway up the sides of the columns of unworn teeth. Roots present on teeth in late wear. Character of the unworn teeth as in *Pliosaccomys*, but with shallower molar patterns. There is no pit between the third lower molar and the ascending ramus. The rostrum is arched.

DESCRIPTION: The mandible of *Parapliosaccomys oregonensis* is very close to that of the

Figure 19. *Pliosaccomys* sp. Otis Basin fauna, UO loc 2347, **A**; UO26078, left P_4 occlusal view, **B**; labial view, **C**; lingual view, all x 15, *Pliosaccomys* sp. Krebs Ranch I fauna, UOloc 2322, **D**; UO26948, left P_4, occlusal view, **E**; labial view, **F**; lingual view, all x 15

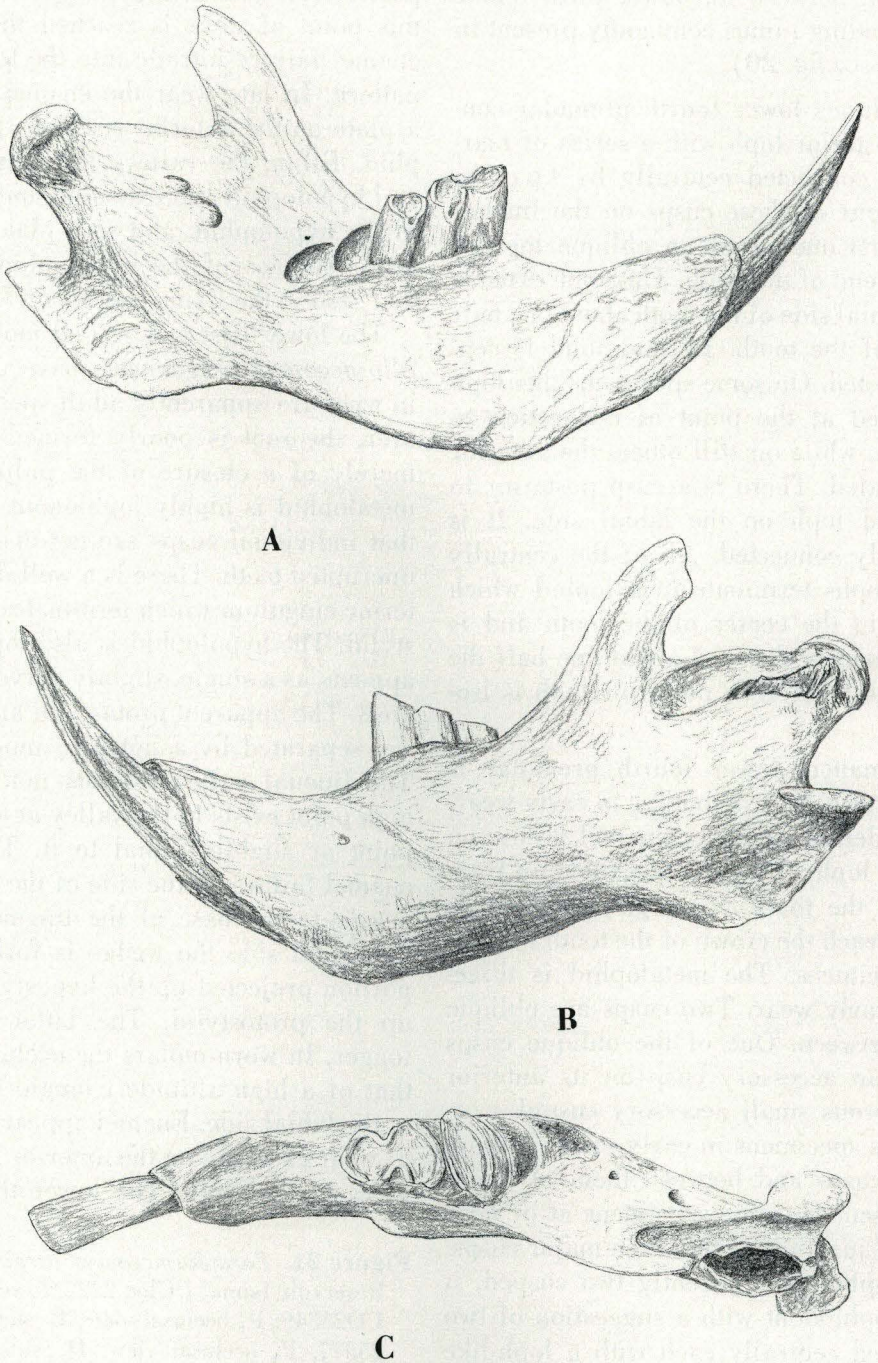


Figure 20. *Parapliosaccomys oregonensis* n.sp. McKay Reservoir fauna, UOloc 2222, Type specimen UO 3631, left mandible with I—P_4—M_1,**A**; lingual view, **B**; labial view, **C**; dorsal view, all x 5

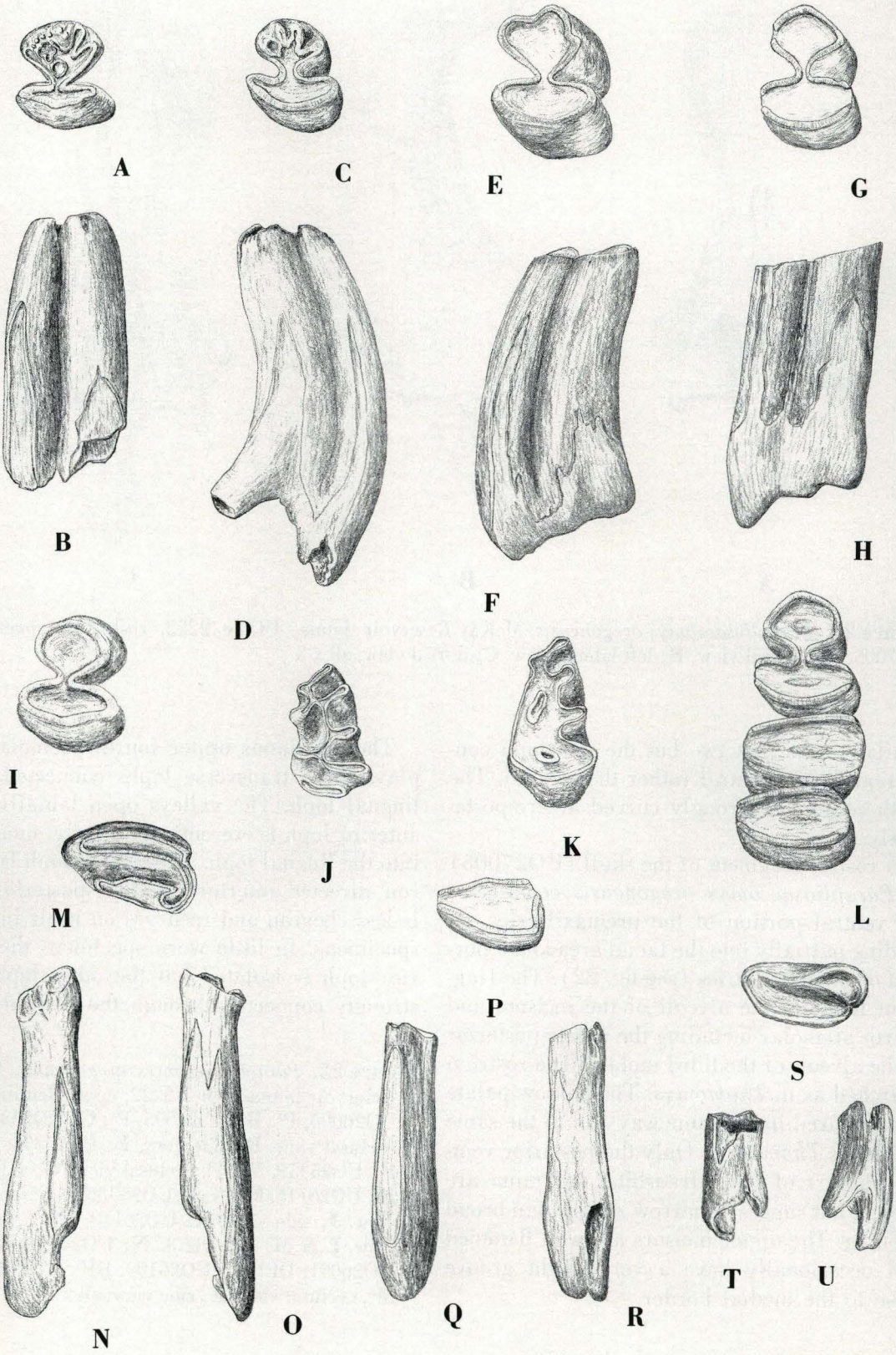
smaller species of *Thomomys*. It lacks the pit or depression between the lower third molar and the ascending ramus commonly present in *Thomomys* (see fig. 20).

The deciduous lower fourth premolar consists of a posterior loph with a series of marginal cusps connected centrally by l o p h s. There are four of these cusps on the lingual side. The first one forms an oblique loph at the anterior end of the tooth. This loph extends along the labial side of the tooth about one half the length of the tooth. Its mid-point is centrally connected. On some specimens this loph is interrupted at the point of connection to the midloph, while on still others the anterior loph is isolated. There is a cusp posterior to the extended loph on the labial side. It is also centrally connected. All of the centrally connected lophs terminate in a lophid which is situated in the center of the tooth and is antero-posteriorly directed about one half the length of the tooth. The posterior loph is isolated.

The permanent lower fourth premolar is very high crowned. It is rootless in early wear. It displays dentine tracts by enamel failure on the edges of lophs. These tracts extend up from the base of the tooth as wedge-shaped areas but do not reach the crown of the tooth in little w o r n specimens. The metalophid is three-cusped in early wear. Two cusps are oblique with one between. One of the oblique cusps may have an accessory cusp on its anterior face. Numerous small accessory cuspules occur on some specimens in early wear, both on the major cusps and between them. A small lake is present on some specimens at or near the point of juncture of the three major cusps. The hypolophid is apparently two cusped, it is highly lophiodont with a suggestion of two cusps located centrally each with a loph-like extension. The fusion is so complete in unworn teeth that no cusp identities can be made. The metalophid and hypolophid are joined in unworn teeth. The juncture is narrow, central, and remains so with wear. Continued wear soon produces an occlusal pattern of a round metalophid narrowly connected to an antero-posteriorly flattened hypolophid. Soon after this point of wear is reached the wedges of enamel failure intrude into the tooth occlusal pattern. In late wear the enamel is found as a plate on the anterior surface of the metalophid, filling the valleys between metalophid and hypolophid and extending out to the edges of the hypolophid, and as a plate on the posterior surface of the hypolophid, not unlike that seen in the living species of *Thomomys*.

The lower first and second molars of *Parapliosaccomys oregonensis* have a single root in what are apparently adult specimens. However, the root is poorly formed and consists merely of a closure of the pulp cavity. The metalophid is highly lophiodont to the extent that individual cusps are not evident even on unerupted teeth. There is a well developed anterior cingulum which terminates at the protostylid. The hypolophid is also lophiodont and appears as a single, slightly curved, transverse crest. The apparent protostylid and hypostylid are separated by a notch in most specimens. The lingual valley extends much deeper. A high point exists in the valley at about the mid point or slightly labial to it. The wedge of enamel failure on the side of the tooth extends nearly to the base of the lingual valley. On the labial side the wedge is forked with one portion projected up the hypostylid, the other up the protostylid. The latter extension is longer. In worn molars the occlusal pattern is that of a high altitude triangle with the base at the labial side. Enamel appears at this stage of wear as plates on the anterior and posterior faces of the tooth. The lower third molar is

Figure 21. *Parapliosaccomys oregonensis*, McKay Reservoir fauna, UOloc 2222, lower dentition, **A**; UO25349, P_4 occlusal view, **B**; side view, **C**; UO 25377, P_4 occlusal view, **D**; side view, **E**; UO 24904, P_4 occlusal view, **F**; side view, **G**; UO 26085, P_4 occlusal view, **H**; side view, **I**; UO 26084, P_4, **J**; UO24624, DP_4, **K**; UO26089, DP_4, **L**; UO3630, right P_4-M_2, **M**; UO2411, $M_{1 \text{ or } 2}$, occlusal view, **N & O**; side views, **P**; UO25334, $M_{1 \text{ or } 2}$, occlusal view, **Q & R**; side views, **S**; UO 26153, M_3, occlusal view, **T & U**; side views, all x 10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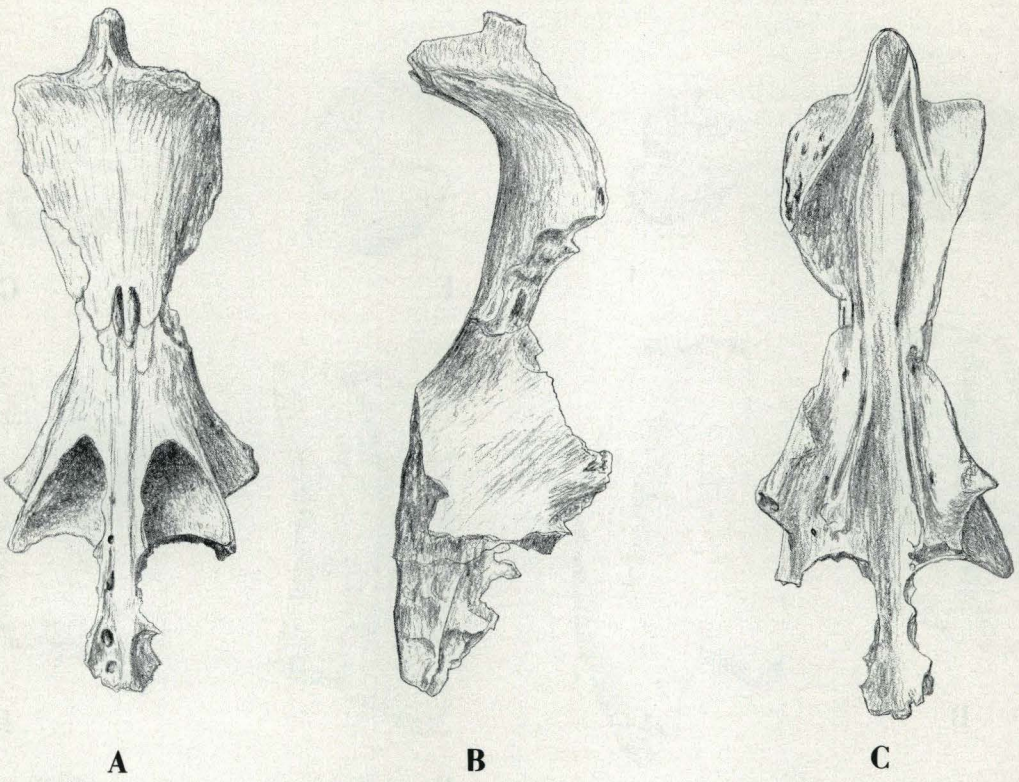


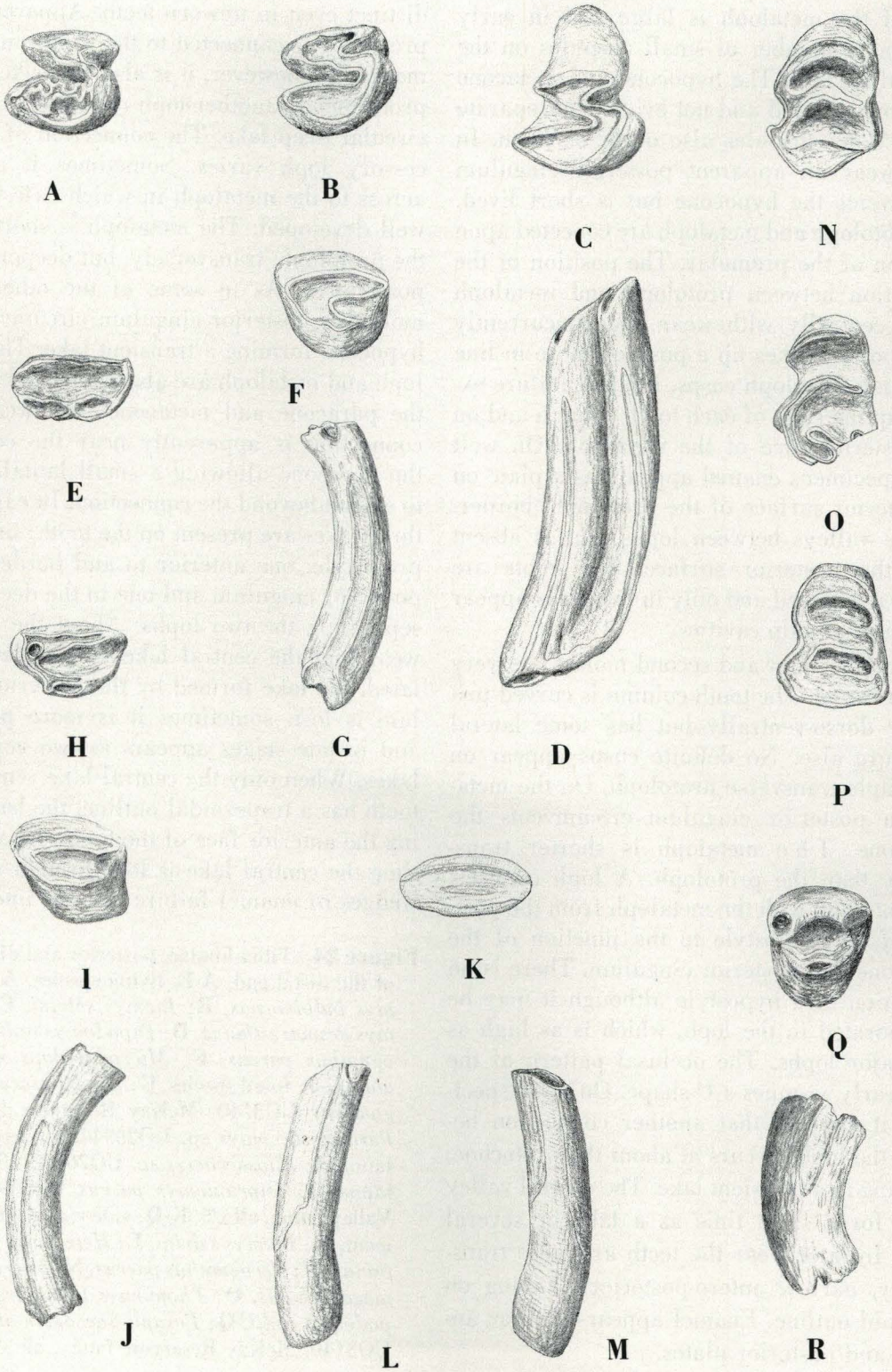
Figure 22. *Parapliosaccomys oregonensis,* McKay Reservoir fauna, UOloc 2222, rostral fragment, UO 27005, **A**; ventral view, **B**; left lateral view, **C**; dorsal view, all x 5

similar to the first two but the interloph connection is first central rather than labial. The tooth column is strongly curved antero-posteriorly.

A rostral fragment of the skull (UO27005) of *Parapliosaccomys oregonensis* consists of the ventral portion of the premaxillaries extending partially into the facial area and a portion of the maxillaries (see fig. 22). The fragment includes the alveoli of the incisors and fourth premolar including the palate posterior to the alveoli of the third molars. The rostrum is arched as in *Thomomys*. The narrow palate is sculptured in the same way and to the same degree as *Thomomys*. Only the posterior ventral borders of the infraorbital foramina are present but suggest a narrow rather than broad opening. The upper incisors are well flattened and occasionally have a very slight groove close to the medial border.

The deciduous upper fourth premolar displays three transverse lophs connected by a lingual loph. The valleys open labially. The anterior loph is cresentic anteriorly, moulding into the lingual loph. The central loph is chevron, directed anteriorly and the posterior loph is less chevron and recurves on itself in some specimens. In little worn specimens the anterior loph is isolated but the other lophs are strongly connected through the lingual loph.

Figure 23. *Parapliosaccomys oregonensis,* McKay Reservoir fauna, UOloc 2222, upper dentition, **A**; UO26096, P^4, **B**; UO26095, P^4, **C**; UO25370, P^4, occlusal view, **D**; side view, **E**; UO25374, $M^{1 \text{ or } 2}$, **F**; UO25359, $M^{1 \text{ or } 2}$, occlusal view, **G**; side view, **H**; UO26116, $M^{1 \text{ or } 2}$, **I**; UO25356, $M^{1 \text{ or } 2}$, occlusal view, **J**; side view, **K**; UO26110, $M^{1 \text{ or } 2}$, occlusal view, **L & M**; side views, **N**; UO24623, DP^4, **O**; UO26091, DP^4, **P**; UO26100, DP^4, **Q**; UO26131, M^3, occlusal view, **R**; side view, all x 10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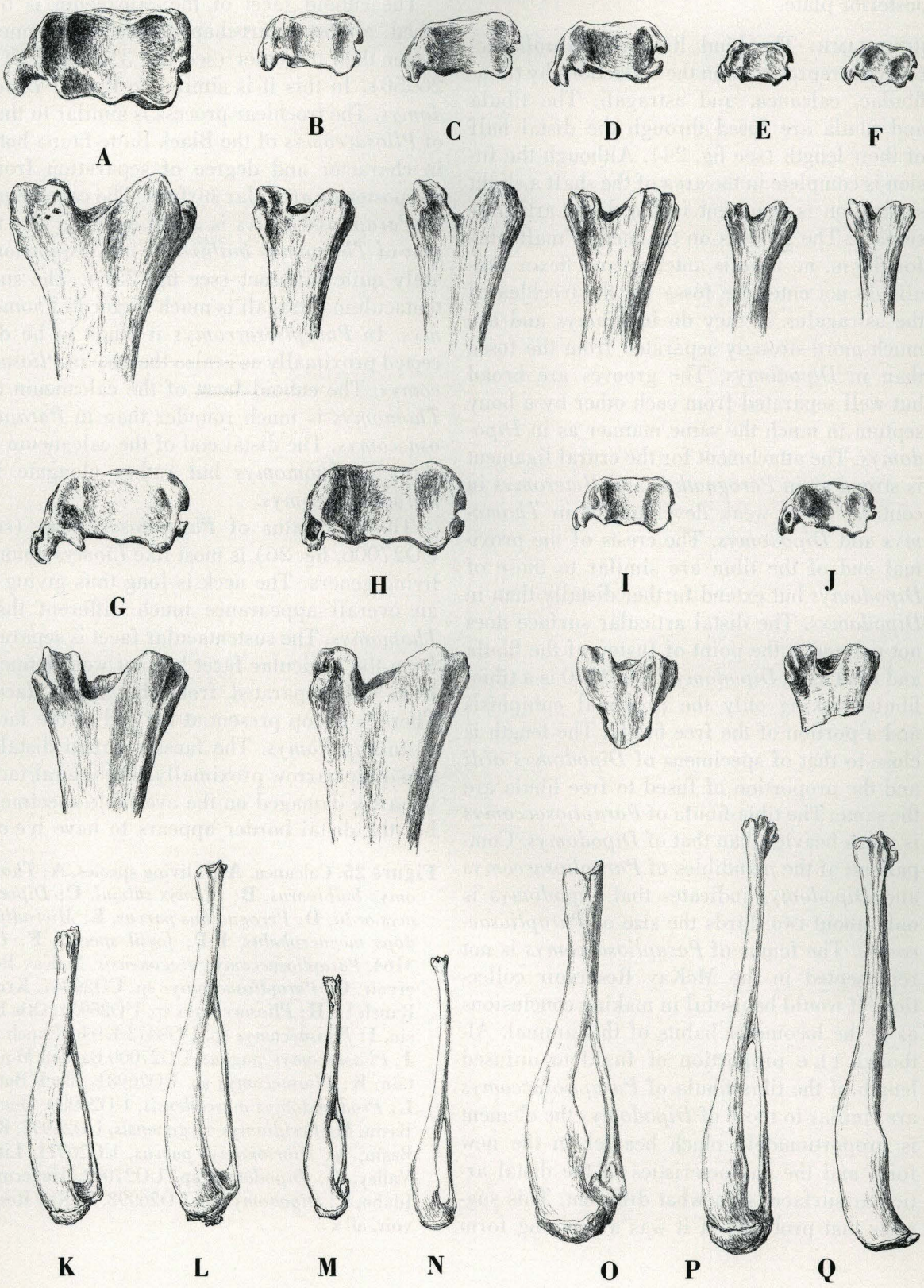
The column of the permanent upper fourth premolar curves dorsoventrally. The protoloph is a single lophiodont cusp. The hypostyle of the metaloph is large and in early wear has a number of small cuspules on the occlusal surface. The hypocone and metacone are strongly fused and not evident as separate cusps. Many cuspules also occur on them. In early wear an apparent posterior cingulum circumvents the hypocone but is short lived. The protoloph and metaloph are conected upon eruption of the premolar. The position of the connection between protoloph and metaloph moves centrally with wear and concurrently the hypostyle takes up a position more in line with other metaloph cusps. Enamel failure extends up the edge of each tooth column and on the posterior face of the metaloph. On well worn specimens enamel appears as a plate on the anterior surface of the protoloph, bordering the valleys between lophs, but is absent from the posterior surface. The roots are poorly developed and only in late wear appear as closure of pulp cavities.

The upper first and second molars are very high crowned. The tooth column is curved primarily dorso-ventrally but has some lateral curvature also. No definite cusps appear on the simple transverse protoloph. On the metaloph a posterior cingulum circumvents the hypocone. The metaloph is shorter transversely than the protoloph. A loph connects the protoloph with the metaloph from the position of the protostyle to the junction of the hypocone and posterior cingulum. There is no indication of a hypostyle although it may be incorporated in the loph, which is as high as the major lophs. The occlusal pattern of the tooth early assumes a U-shape. On some specimens it appears that another connection between the lophs occurs at about the protocone, resulting in a transient lake. The central valley exists for a short time as a lake or several lakes. In later wear the teeth are wide transversely, narrow antero-posteriorly taking on an ovoid outline. Enamel appears then as anterior and posterior plates.

The upper third molar is strongly curved dorso-ventrally. It is not as high crowned as the other molars. The individual cusps are not distinct even in unworn teeth. Apparently the protostyle is connected to the protocone in the main loph, however, it is also connected to the protocone by another loph resulting in a small circular deep lake. The connection of this accessory loph varies. Sometimes it connects across to the metaloph in which case it is not well developed. The metaloph is shorter than the protoloph, transversely, but deeper antero-posteriorly. As in some of the other upper molars, a posterior cingulum circumvents the hypocone forming a transient lake. The protoloph and metaloph are also connected between the paracone and metacone with wear. This connection is apparently near the center of the paracone allowing a small labial portion to extend beyond the connection. In early wear three lakes are present on the tooth; one at the protostyle, one anterior to and bordering the posterior cingulum and one in the deep valley separating the two lophs. About the stage of wear that the central lake is completely isolated, the lake formed by the posterior cingulum is lost, sometimes it is more persistent and in late stages appears as two very small lakes. When only the central lake remains the tooth has a trapezoidal outline, the base forming the anterior face of the tooth. At about the time the central lake is lost through wear the wedges of enamel failure intrude into the oc-

Figure 24. Tibia-fibulae, posterior and distal views of the distal end, **A-E,** living species, **A**; *Thomomys bulbivorous*, **B**; *Liomys salvini*, **C**; *Heteromys desmarestianus*, **D**; *Dipodomys ordii*, **E**; *Perognathus parvus*, **F**; *Microdipodops megacephalus*, **G-J**; fossil species, **G**; *Parapliosaccomys oregonensis* UO3140, McKay Reservoir fauna, **H**; *Parapliosaccomys* sp. UO26944, Krebs Ranch II fauna, **I**; *Pliosaccomys* sp. UO26982, Black Butte fauna, **J**; *Diprionomys parvus* UO26972, Little Valley fauna, all x 5, **K-Q**; side views complete element, **K**; *Liomys salvini*, **L**; *Heteromys desmarestianus*, **M**; *Perognathus parvus*, **N**; *Microdipodops megacephalus*, **O**; *Thomomys bulbivorus*, **P**; *Dipodomys ordii*, **Q**; *Parapliosaccomys oregonensis* UO3140, McKay Reservoir fauna, all x 2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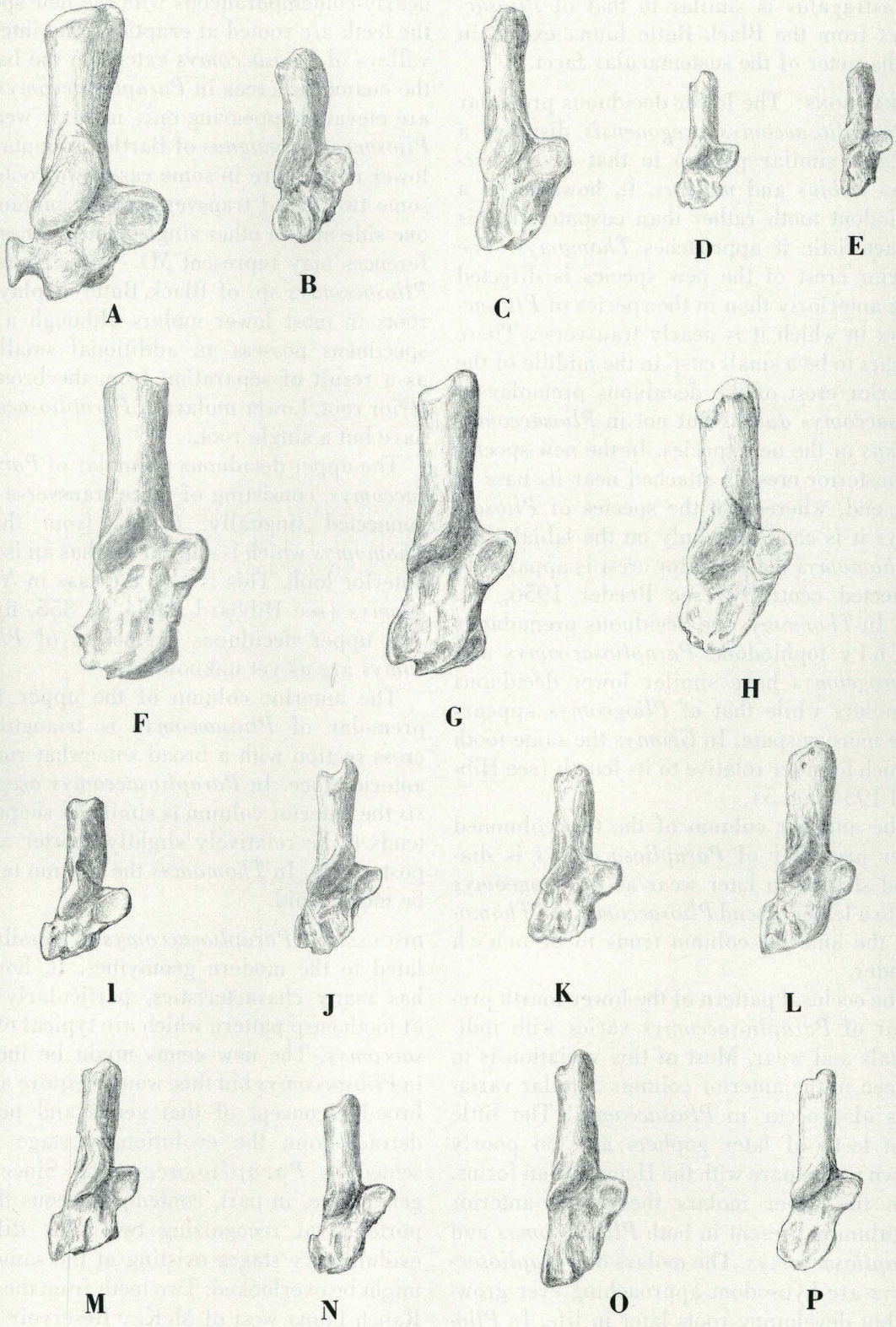
clusal pattern. The result is an anterior plate of enamel opposed by a strongly crescentic posterior plate.

HIND LIMB: The hind limb of *Parapliosaccomys* is represented in the collections by tibia-fibulae, calcanea, and astragali. The tibula and fibula are fused through the distal half of their length (see fig. 24). Although the fusion is complete in the area of the shaft a slight separation is apparent in the distal articular surface. The grooves on the medial malleolus for the m. m. tibialis anterior and flexor tibialis do not enter the fossa for the trochlea of the astragalus as they do in *Liomys* and are much more strongly separated from the fossa than in *Dipodomys*. The grooves are broad but well separated from each other by a bony septum in much the same manner as in *Dipodomys*. The attachment for the crural ligament is strong as in *Perognathus* and *Heteromys* in contrast to its weak development in *Thomomys* and *Dipodomys*. The crests of the proximal end of the tibia are similar to those of *Dipodomys* but extend further distally than in *Dipodomys*. The distal articular surface does not narrow at the point of fusion of the fibula and tibia as in *Dipodomys*. UO 3140 is a tibia-fibula lacking only the proximal ephiphisis and a portion of the free fibula. The length is close to that of specimens of *Dipodomys ordi* and the proportion of fused to free fibula are the same. The tibia-fibula of *Parapliosaccomys* is much heavier than that of *Dipodomys*. Comparison of the mandibles of *Parapliosaccomys* and *Dipodomys* indicates that *Dipodomys* is only about two thirds the size of *Parapliosaccomys*. The femur of *Parapliosaccomys* is not represented in the McKay Reservoir collections It would be useful in making conclusions as to the locomotor habits of this animal. Although the proportion of fused to unfused length of the tibia-fibula of *Parapliosaccomys* are similar to those of *Dipodomys* the element is proportionately much heavier in the new form and the characteristics of the distal articular surfaces somewhat different. This suggests that probably if it was a jumping form it mixed this gait with scampering perhaps as in *Perognathus*.

The cuboid facet of the calcaneum is bilobed almost heart-shaped one lobe much larger than the other (see UO 3164 and UO-26950). In this it is similar to that of *Dipodomys*. The trochlear process is similar to that of *Pliosaccomys* of the Black Butte fauna both in character and degree of separation from the posterior articular surface. The calcaneum of *Parapliosaccomys* is about equal in size to that of *Thomomys bulbivorus* but proportionately quite different (see fig. 25F). The sustentaculum astragali is much larger in *Thomomys*. In *Parapliosaccomys* it tends to be directed proximally as is also the case in *Pliosaccomys*. The cuboid facet of the calcaneum of *Thomomys* is much rounder than in *Parapliosaccomys*. The distal end of the calcaneum is short in *Thomomys* but rather elongate in *Parapliosaccomys*.

The astragalus of *Parapliosaccomys* (see UO27006, fig. 26) is most like *Liomys* among living genera. The neck is long thus giving it an overall appearance much different than *Thomomys*. The sustentacular facet is separate from the navicular facet but not well defined. It is well separated from the lateral facet. There is a stop present at the end of the facet as in *Dipodomys*. The facet is broad distally and quite narrow proximally. The lateral facet is partly damaged on the available specimens but the distal border appears to have been

Figure 25. Calcanea, **A-E**; living species, **A**; *Thomomys bulbivorus*, **B**; *Liomys salvini*, **C**; *Dipodomys ordii*, **D**; *Perognathus parvus*, **E**; *Microdipodops megacephalus*, **F-P**; *fossil species*, **F**; *UO* 3164, *Parapliosaccomys oregonensis*, McKay Reservoir, **G**; *Parapliosaccomys* sp. UO26947, Krebs Ranch II, **H**; *Pliosaccomys* sp. UO26951, Otis Basin, **I**; *Pliosaccomys* sp. UO8473 Krebs Ranch II, **J**; *Pliosaccomys magnus*, UO27000 Bartlett Mountain, **K**; *Pliosaccomys* sp. UO26981, Black Butte, **L**; *Prodipodomys mascallensis*, UO26989, Quartz Basin, **M**; *Peridiomys oregonensis*, UO26997, Red Basin, **N**; *Diprionomys parvus*, UO26971, Little Valley, **O**; *Dipodomys* sp. UO27002, Hagerman Idaho, **P**; *Dipodomys* sp. UO26998, McKay Reservoir, all x 5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angular rather than curved, similar to *Liomys*. The astragalus is similar to that of *Pliosaccomys* from the Black Butte fauna except in the character of the sustentacular facet.

COMPARISONS: The lower deciduous premolar of *Parapliosaccomys oregonensis* displays a basically similar pattern to that of *Pliosaccomys dubius* and *magnus*. It, however, is a lophiodont tooth rather than cuspate. In this characteristic it approaches *Thomomys*. The anterior crest of the new species is directed more anteriorly than in the species of *Pliosaccomys* in which it is nearly transverse. There appears to be a small cusp in the middle of the posterior crest of the deciduous premolar of *Pliosaccomys dubius* but not in *Pliosaccomys magnus* or the new species. In the new species the posterior crest is attached near its base at each end, whereas in the species of *Pliosaccomys* it is connected only on the labial side. In *Thomomys* the posterior crest is apparently connected centrally (see Reeder 1956, fig. 90). In *Thomomys* the deciduous premolar is highly lophiodont. *Parapliosaccomys* and *Neterogeomys* have similar lower deciduous premolars while that of *Pliogeomys* appears to be more cuspate. In *Geomys* the same tooth is much broader relative to its length (see Hibbard 1954, fig. 5).

The anterior column of the two columned lower premolar of *Parapliosaccomys* is diamond shaped in later wear as in *Pliogeomys* and to a lesser extend *Pliosaccomys*. In *Thomomys* the anterior column tends to be much rounder.

The occlusal pattern of the lower fourth premolar of *Parapliosaccomys* varies with individuals and wear. Most of this variation is to be seen in the anterior column. Similar variations also occur in *Pliosaccomys*. The little worn teeth of later gophers are too poorly known to compare with the Hemphillian forms.

In the lower molars the strong anterior cingulum is present in both *Pliosaccomys* and *Parapliosaccomys*. The molars of *Parapliosaccomys* are hypsodont approaching ever growing but developing roots later in life. In *Pliosaccomys dubius* and *magnus*, which are nearly contemporaneous with the new species, the teeth are rooted at eruption. The interloph valleys of *Pliosaccomys* extend to the base of the enamel whereas in *Parapliosaccomys* they are elevated appearing only in early wear. In *Pliosaccomys magnus* of Bartlett Mountain the lower molars are in some cases two rooted, in some two broad transverse roots combined at one side and in other single rooted. These differences may represent M1 - M2 differences. *Pliosaccomys* sp. of Black Butte displays two roots in most lower molars although a few specimens possess an additional small root as a result of separation from the broad anterior root. Lower molars of *Parapliosaccomys* have but a single root.

The upper deciduous premolar of *Parapliosaccomys*, consisting of three transverse lophs connected lingually, differs from that of *Thomomys* which is similar but has an isolated anterior loph. This is also the case in *Neterogeomys* (see Hibbard, 1954, p. 355, fig. 5). The upper deciduous premolars of *Pliosaccomys* are as yet unknown.

The anterior column of the upper fourth premolar of *Pliosaccomys* is triangular in cross section with a broad somewhat rounded anterior face. In *Parapliosaccomys oregonensis* the anterior column is similarly shaped but tends to be relatively slightly shorter anteroposteriorly. In *Thomomys* the column tends to be more ovoid.

DISCUSSION: *Parapliosaccomys* is possibly related to the modern geomyines. It, however, has many characteristics, particularly those of tooth cusp pattern which are typical of *Pliosaccomys*. The new genus might be included in *Pliosaccomys* but this would require a much broader concept of that genus and possibly detract from the evolutionary stage represented by *Parapliosaccomys*. Since these genera are, in part, contemporaneous the importance of recognizing two quite different evolutionary stages existing at the same time might be overlooked. Two teeth from the Krebs Ranch fauna west of McKay Reservoir (Shot-

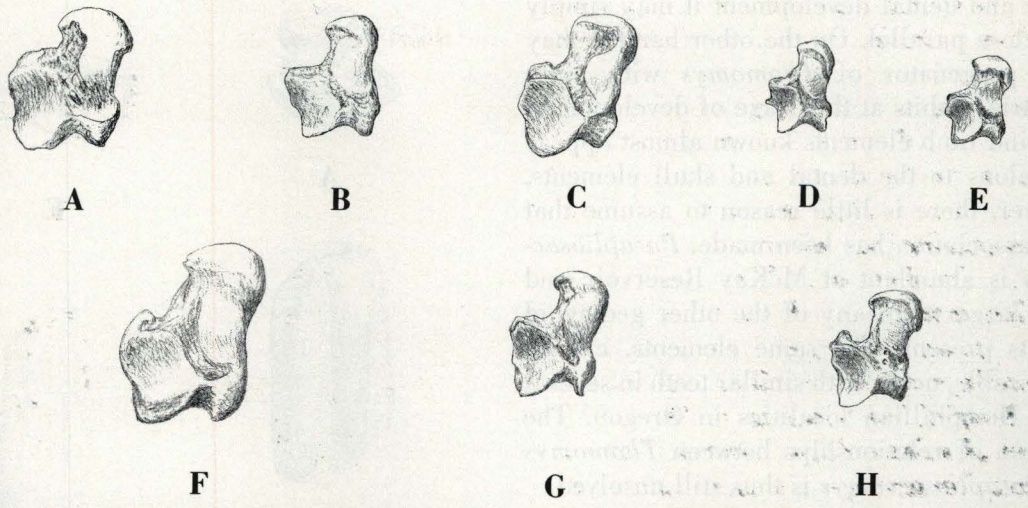

Figure 26. Astragali ventral view, **A-E**; living species, **A**; *Thomomys bulbivorus*, **B**; *Liomys salvini*, **C**; *Dipodomys ordii*, **D**; *Perognathus parvus*, **E**; *Microdipodops megacephalus*, **F-H**; fossil species, **F**; *Parapliosaccomys oregonensis* UO27006, McKay Reservoir fauna, **G**; *Pliosaccomys* sp. UO27013, Black Butte fauna, **H**; *Diprionomys parvus* UO27014, Little Valley fauna, all x 5

well 1958) provoke some caution into this discussion. One is a lower fourth premolar from Krebs Ranch I (UOloc 2322, fig. 19D) the other a lower molar from Krebs Ranch II (UOloc 2323). These two faunules are essentially contemporaneous but apparently represent divergent habitats. Tibia-fibula and calcanea from Krebs Ranch II (UOloc 2323, fig. 25G) compare closely with those of *P. oregonensis*. There is no reason other than their common characteristics to consider them as representing the same species. The importance of them to this discussion is the fact that they represent rather high crowned forms, higher than *Pliosaccomys* but lower than *Parapliosaccomys*, which have roots but display dentine tracks. This is a combination of characteristics not typical of either known *Pliosaccomys* or *Parapliosaccomys*. These specimens are contemporaneous or possibly slightly younger than the fauna of McKay Reservoir, the type locality of *Parapliosaccomys*. Two possible explanations are obvious; these teeth simply represent a species of *Parapliosaccomys* reflecting a diversity of crown height and dentine track development or, they represent a species of *Pliosaccomys* which has progressed to the point of the appearance of dentine tracks. The first explanation would not effect the present discussion significantly since such an occurrence would not be unexpected. The second explanation would indicate that the modern type of geomyine may have been derived from more than one of a number of closely related Hemphillian genera which may also be the case. The significance of these specimens canot be fully assessed until more material representing them is available. Our attempts to enlarge upon the material have, so far, been unsuccessful.

With its arched rostrum, dentine tracks in the teeth and nearly ever growing teeth, *Parapliosaccomys* is more geomyine-like than is *Pliosaccomys* but both genera have many features in common, in fact, are certainly either of immediate common ancestory or possibly one derived from the other in the Clarendonian or late Barstovian. The known skeletal elements of *Parapliosaccomys* indicate a possible scampering-hopping locomotion and do not suggest a subterranean form such as *Thomomys* although they may well have occupied burrows as does *Dipodomys*. Although *Parapliosaccomys* approaches *Thomomys* in its

palate and dental development it may simply be a close parallel. On the other hand it may be a progenator of *Thomomys* with more terrestrial habits at this stage of development. The hind limb elements known almost appear anomalous to the dental and skull elements, however, there is little reason to assume that a misassociation has been made. *Parapliosaccomys* is abundant at McKay Reservoir and much larger than any of the other geomyoid rodents present. The same elements, closely comparable, occur with similar teeth in several other Hemphillian localities in Oregon. The problem of relationships between *Thomomys* and *Parapliosaccomys* is thus still unsolved.

THOMOMYS sp.
(Fig. 27)

A small gopher appears in the Blancan Wildhorse Butte locality (UOloc 2396). It is represented by six isolated teeth and two fragmentary mandibles. The pit between the ascending ramus and the third molar is poorly developed as in living small species of *Thomomys*. The premolar and molar teeth are without roots. An unworn upper fourth premolar indicates that the tooth is highly lophiodont, individual cusps are not apparent and the metaloph consists of a number of very small antero-posteriorly directed lophs. The protoloph attaches to the metaloph at its lingual edge but it is obvious that this connection progresses labially with later wear until the attachment is at least labial to the apparent position of the hypostyle. The protoloph is strongly flattened antero-posteriorly at this early stage but expands down the column until in later wear it is ovoid. In early wear a subsidiary lophid appears on the antero-lingual side of the protoloph so that in some stages of wear the protoloph may approach a subtriangular shape somewhat attenuated at the point of the subsidiary loph as is the case with *Pliosaccomys*. A worn specimen of the upper fourth premolar displays a transversely ovoid protoloph and metaloph connected towards the lingual side of the tooth, not centrally. Enamel

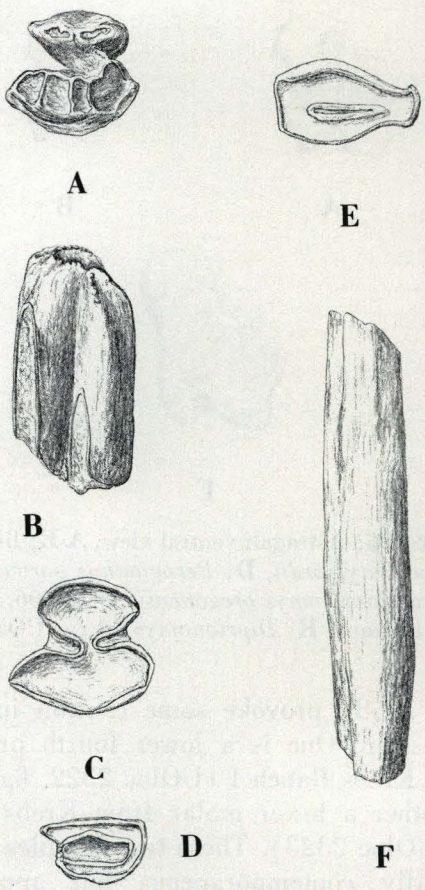

Figure 27. *Thomomys* sp. Wildhorse Butte UOloc 2396, **A**; UO27012, P^4 occlusal view, **B**; side view, **C**; UO26185, P^4 occlusal view, **D**; UO27011, M^3 occlusal view, **E**; UO26184, $M^{1 \text{ or } 2}$ occlusal view, **F**; side view, all x 10

failure occurs at the edges of each of the columns of the tooth but appears to be due to extreme thinning of the enamel rather than complete loss as in *Parapliosaccomys*.

One molar displays the lingual constriction of the column seen in living species of *Thomomys* whereas others lack this constriction as in *Thomomys gidleyi* Wilson (1933). The enamel failure of these teeth is similar to that of the upper fourth premolar. A little worn upper molar strongly resembles the same tooth in *Parapliosaccomys* and *Pliosaccomys*. The protoloph and metaloph are connected both lingually and labially creating a deep lake between the lophs. The metaloph is much nar-

rower, transversely, than the protoloph suggesting a posible reduction or loss of the hypostyle.

The available specimens compare favorably with those from the Hagerman fauna which presumably represent *Thomomys gidleyi*. Both species are small and may well represent the same taxon.

Subfamily Dipodomyinae

DIPODOMYS sp.

At Krebs Ranch II, UOloc 2323, a fragmental skull (UO8302), sulcate incisors and an isolated lower molar apparently represent a species of *Dipodomys*. The skull lacks the rostal area along with the palate. The auditory bulla although obviously enlarged are missing. A fragment of the right inner ear remains. The cranium elements are present. The character of the remains of the inner ear compare closely with that of *Dipodomys*. The supra occipital area of the skull is much broader between the enlarged bulla than in living *Dipodomys* possibly suggesting less expanded bulla. The presence of isolated sulcate incisors, similar in character and size to those of *Dipodomys*, further strengthens the impression that the species present is close to *Dipodomys*. The isolated lower molar (UO25941) has an occlusal pattern close to early wear patterns of *Dipodomys ordii*. It is relatively high crowed but has partially fused roots. The enamel is much more extensive on the anterior face than the posterior. The base of the enamel, raises abruptly on the lateral margins of the tooth as an incipient dentine tract. The pattern is apparently shallow not extending to the base of the enamel, at least in part, as in *Pliosaccomys*.

The conclusion based on the above evidence is that a species assignable to *Dipodomys* or certainly a similar form is present in the Krebs Ranch II fauna.

A calcaneum (UO 8473, fig. 25I) may also belong to this species. It is more like *Pliosaccomys* from the Black Butte Fauna than *Dipodomys*, however, it has some characteristics not seen in *Pliosaccomys*. The sustentaculum astragali is directed strongly laterally rather than proximally as in *Pliosaccomys*. The portion of the calcaneum distal to the posterior articular surface is short as in *Pliosaccomys* and *Diprionomys* rather than elongate as in *Dipodomys*. *Parapliosaccomys* is present in the fauna and has a somewhat similar appearance but is much larger. There is a possibility that this particular specimen represents a *Diprionomys* species not otherwise represented in the small sample availabe.

?DIPODOMYS sp.

Several dental and skeletal elements from McKay Reservoir (UOloc 2222, Hemphillian) are assigned here to *Dipodomys*. The dental elements are poor specimens and well worn. They are rooted. No dentine tracts are present. One, a lower fourth premolar (UO25940), has a simple anteroloph at the existing stage of wear rather symmetrical and with a slight anterior groove. A small fragment of a sulcate incisor is present. The skeletal elements are much more definitive. The tibia-fibula (UO-26955) consists of the fused distal ends of the two elements. It is a little larger than *Dipodomys ordii* but in most respects very similar. A calcaneum (UO26998, fig. 25P) is close to *Dipodomys* both in characteristics and proportions. This suite of specimens is only significant in that the presence of *Dipodomys* is apparent. The material, however, is inadequate to make an assignment to species and is only suggestive of genus.

?DIPODOMYS sp.

Several skeletal elements from the Bartlett Mountain fauna (UOloc 2517) of the Drewsey Formation (Hemphillian) indicate the presence of a geomyoid rodent close to *Dipodomys*. A distal fragment of a fused tibia-fibula (UO-26958) is most like *Dipodomys*. The lateral malleolus is, however, not well enough preserved to make a more positive identification. A calcaneum (UO26956) is also close to *Dipodomys* but lacks the indentation of the cu-

boid facet which is well developed in *Dipodomys*. Several well worn tooth specimens, probably all from a single individual, may represent the same species, however, at their advanced stage of wear it is not possible to segregate them with confidence from other similarly sized geomyoid rodents present in the fauna.

A small upper premolar of medium crown height occurs in the Bartlett Mountain fauna. The protoloph and metaloph are fused in early wear at the entostyle. The protoloph is two cusped. The metaloph is three cusped with a well developed hypostyle and posterior cingulum. The early connection of protoloph and metaloph, the medium crown height and orientation of the protoloph sugest a dipodomyine.

?DIPODOMYS sp.

A calcaneum, UO27002, from the Hagerman fauna UOloc 2437, is close to *Dipodomys* (see fig. 25O). Hibbard (1962) has described *Prodipodomys idahoensis* from this same fauna. It is entirely possible that the calcaneum noted here represents that species.

GEOMYINE RELATIONSHIPS

Not until the Hemphillian does the above record include species which approach the characteristics of modern geomyines. It may be useful at this point to re-examine earlier geomyine occurrences in order to indicate something of the history of this group. *Dikkomys mathewi* (Wood 1936) of the lower Harrison of Nebraska was assigned to the geomyinae by Wood. Characteristics of the lower fourth premolar include centrally connected cusps, unequal cusps on the anterior loph with at least accessory cusps on one of the major cusps. This form strongly resembles the *Pliosaccomys* sp. from Black Butte in its dental pattern. The molar teeth are likewise very similar to later geomyines. Characteristics of the skull and mandible apparently are not yet known. Black (1961) has suggested that *Dikkomys* and *Pliosaccomys* are not of the same line of development. This was based on an apparent difference between the means of connection between anterior and posterior lophs of the molars. In *Dikkomys* the loph appear in illustrations to definitely have central connections first, in the course of wear. Black states that in *Pliosaccomys* union of the lophs begins at the buccal margin and spreads inward. I presume that the discussion concerns lower molars. In *Pliosaccomys* the first union of the lophs often does occur on the margin of the tooth, however, at the same time or nearly so connection is also made centrally. This apparently also happens in *Dikkomys* (see Galbreath 1948). The difference in *Dikkomys* and *Pliosaccomys* in this respect is not a fundamental difference of tooth character but an indication of subsequent high development of the protostylid and hypostylid resulting in junction of the lophids at the margin of the tooth also and usually first, in the course of wear. Thus it appears to me that the condition in *Pliosaccomys* is simply a developmental step from that described for *Dikkomys* and that the two genera may well represent the same line of development. *Dikkomys* is too poorly known as yet to be very certain of its phylogenetic position. However, it now appears to be a form closely related to later geomyines.

No other early geomyines have been recognized. However, another subfamily, the entoptychinae, are well represented in early Miocene faunas, particularly the John Day, and are not known later in the record. In the broadest sense this subfamily includes *Entoptychus*, *Pleurolicus*, *Grangerimus* and *Gregoromys* but there is far from any agreement on this arrangement. Hibbard (1954, p. 357) suggests that *Gregoromys* has an ancestral relationship to the geomyinae due to the pattern of the deciduous lower premolar, which is very much like that of the Pliocene geomyines, the presence of a faint groove in the upper incisor of some species, and development of the skull and dental pattern. On the other hand Reeder (1956) considers *Gregoromys* to be a heteromyine in the line of *Heteromys* and *Peridiomys oregonensis*. The character of the lower fourth

premolar of *Diprionomys parvus* of which new material is described above, compares closely with *Gregoromys* in the appearance of a number of additional accessory cusps and the nature of the connection of the lophids supporting Reeder's contention. Reeder further suggests that *Grangerimus* from the John Day may also be a heteromyine possibly also in the *Heteromys* line. However, the character of the lower premolar of *Grangerimus* is that of more centrally connected cusps with an anterior groove separating the major cusps of the anterior loph and possibly accessory cusps on these lophs a characteristic of later geomyines and dipodomyines.

It is difficult to see the difference, if any, between *Grangerimus* and *Pleurolicus sulcifrons*, and the two were considered close by Wood (1936). A skull of *Pleurolicus sulcifrons* from the John Day formation (UO2810) provides useful information as to the possible relationships of this form. The specimen consists of the entire anterior portion of the skull to a point just posterior to the M^3's. The rostrum is not arched as in *Entoptychus* or the modern gophers. It more closely approaches heteromyines in the character of the arching although the anterior end does not sharply recurve as in modern heteromyines. The cheek tooth rows curve gently outward as in some heteromyids (dipodomyines), not in a straight line diverging posteriorly as in *Entoptychus* and living gophers. The palate is not deeply sculptured and is much like modern heteromyines in this characteristic. The incisors are semi-flattened and much narrower in cross-section than those of *Entoptychus*. The incisors curve dorsally nearly to the roof of the rostrum as in heteromyines and *Entoptychus* but not in living geomyids. The infraorbital foramen is located more ventrally than in geomyines but this may merely reflect the lack of strong arching of the rostrum. The character of the opening is similar to that in *Thomomys*. Temporal ridges are present and are developed to about the same degree as in large species of *Thomomys*. This specimen indicates little affinity with *Entophychus*. Its strongest relationships are with the heteromyines and dipodomyines. It possesses some characteristics observed in modern geomyines. The close appression of the anterior and posterior lophs of the lower premolar, rather than the separated and expanded character of the anterior lophid of *Dikkomys*, *Pliosaccomys*, *Parapliosaccomys* and the more recent gophers suggests that it is more closely related to the dipodomyines which characteristically have this appressed anteroloph-posteriorloph relationships as seen in *Dipodomys*.

The above remarks suggest that *Entoptychus* may be the only representative of the entoptychinae and that it is as closely related to the heteromyines as the geomyines, representing a rodent which early adopted a gopher-like habitus but otherwise is not closely related to modern gophers.

The interrelationships of *Prodipodomys*, *Pliosaccomys*, *Parapliosaccomys* and *Dipodomys* are certainly not clear now. They appear to have many characteristics in common. *Prodipodomys* has been distinguished in part by the occurrence of the mandibular foramen lingual to the incisor. However, on the type specimen of *Pliosaccomys dubius* the same arrangement is present. This and the dental characteristics suggest a close relationship between *Prodipodomys* and *Pliosaccomys* in fact they may represent a single group. The relationship of *Dipodomys* to *Prodipodomys* and *Pliosaccomys* still is in question. The occurrence of *Dipodomys* in Barstovian localities of Southern California suggests that it could not be derived from *Prodipodomys*, however, the assignment of specimens to *Dipodomys* in these instances is based primarily on the presence of dentine tracts on the teeth. The poor dental material from Oregon which has been assigned to *Dipodomys*, in this report, primarily on the basis of skeletal elements does not display dentine tracts. Many specimens of living *Dipodomys* species do not show the dentine tracts either. I do not believe that a very close relationship between *Dipodomys* and *Prodipodomys* can be denied or demonstrated at this time.

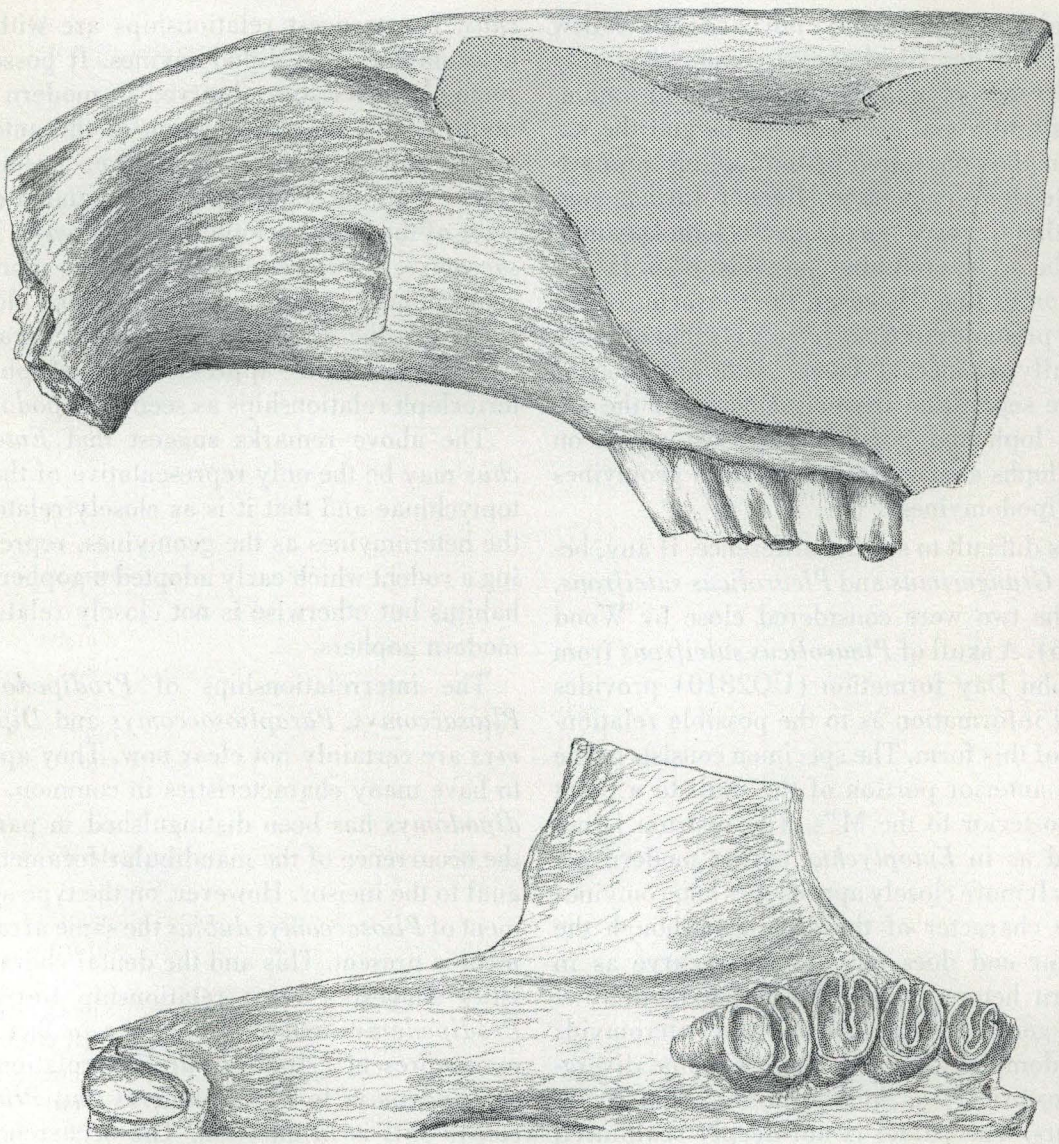

Figure 28. *Pleurolicus sulcifrons*, UO2810, John Day fauna, left lateral and ventral view of skull fragment x 5.

There appears to be a close early relationship between the dipodomyinae and the geomyinae, both with probable early deriviation from the heteromyinae but distinctly separate as early as the Arikareean. A designation of geomyids and heteromyids as separate families thus does not seem reasonable. Wilson (1949, p. 110) pointed out that the heteromyidae and the geomyidae are closely related and that an argument can be made for uniting them in a single group. It appears at this time that recognition of all the subfamilies, entoptychinae, geomyinae, heteromyinae, dipodomyinae, and perognathinae in a single family provides the best arrangement considering our present knowledge.

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