



Shrews, lagomorphs, and rodents (excluding Cricetidae) from the Pliocene Panaca Formation, southeastern Nevada, USA

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ABSTRACT

About 2,500 specimens of small mammal fossils were collected from 12 localities in the Pliocene Panaca Formation in Meadow Valley, southeastern Nevada. The most common taxa in the Panaca small mammal fauna are cricetid and heteromyid rodents, and lagomorphs. This assemblage of small mammals indicates that the Panaca local fauna represents the early Blancan Land Mammal Age. This paper describes and compares the small mammal taxa of the Panaca local fauna except for the cricetids, which are described in a separate paper in this volume.

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KEY WORDS: early Blancan; NALMA; small mammals; local fauna

INTRODUCTION

The Panaca local fauna (l.f.) described by Chester Stock (1921) is located in Meadow Valley, south of Panaca in Lincoln County, southeastern Nevada (Figure 1). Stock named the sediments the Panaca Formation. The fossils from Panaca described by Stock include *Plihippus* sp., *?Teleoceras* sp., and *Pliauchenia* (now considered *Hemiauchenia*), genera that were generally assigned to the Hemphillian North American Land Mammal Age (NALMA), although precise age of the Panaca l.f. was questionable (Stirton 1940; Macdonald and Pelletier 1956). Later, G.E. Hazen and H.S. Gentry, working for the Frick Laboratory of the American Museum of Natural History (F:AM) during the 1940s, collected more fossils from Meadow Valley, noting that most of the fossils they found from the Panaca area were younger than the fossils col-

lected earlier by Stock. Later still, both small and large mammals were collected by T. Galusha and R. Emry, working for the American Museum of Natural History (AMNH). Some of those fossils were described by May (1981), Repenning (1987), and White (1987, 1991). Mou (1997) described a new species of arvicolid rodent from the Panaca l.f., and later (1998) described the enamel schmelzmuster of the new arvicolid rodent. Virtually all of these small mammals collected from the Panaca area are indicative of Blancan NALMA. More recently, Lindsay et al. (2002) resumed collection of small mammals in Meadow Valley, placing them in a magnetostratigraphic framework to shed light on placement of the Hemphillian/Blancan boundary in these deposits, and concluding that they are of Blancan NALMA.

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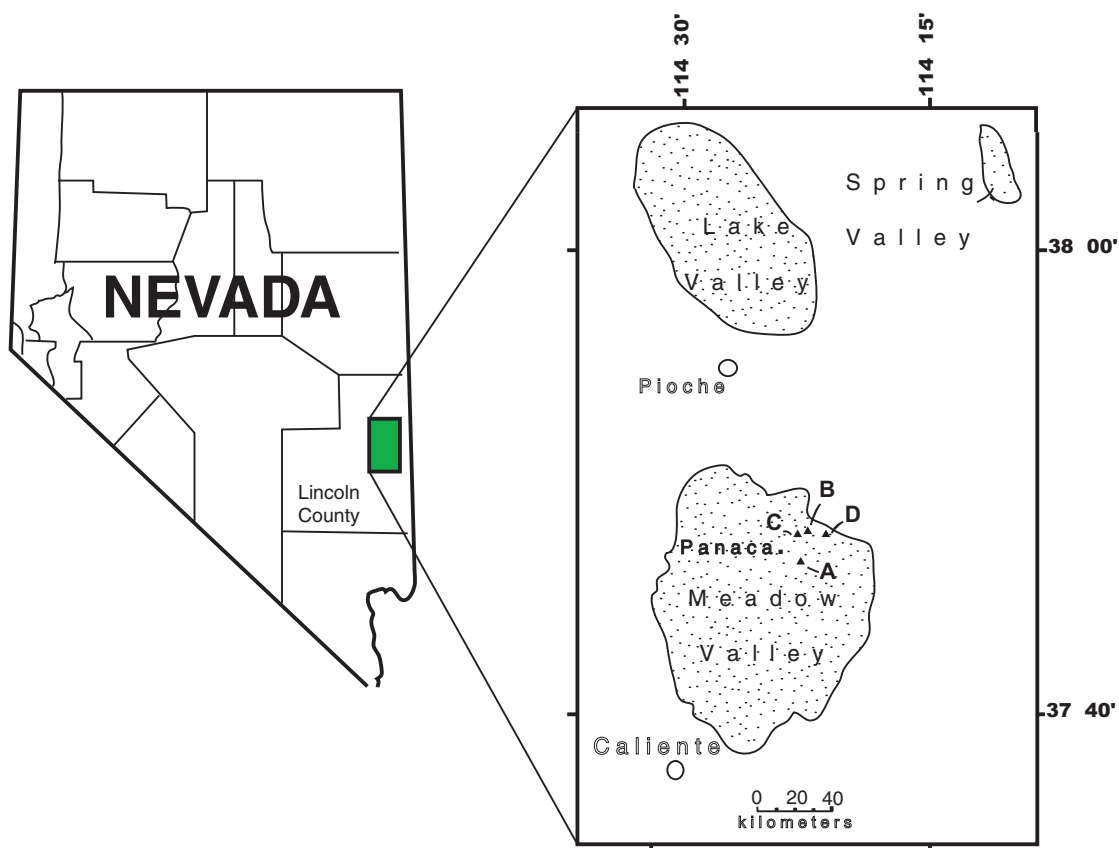


FIGURE 1. Location of the Panaca local fauna, southeastern Nevada. A= Little Hogback section, B=Limestone Corner section, C=Double Adobe Section, D=Rodent Hill section.

This report describes and places the small mammals of the Panaca l.f. in the evolutionary-chronologic context of Meadow Valley sediments, framed in the earlier chronological study of the Panaca Fm. (Lindsay et al. 2002).

GEOLOGIC SETTING

The fossils reported herein are from the Panaca Formation, which is generally considered to be fine-grained basin fill that is exposed in basins of eastern Nevada (Phoenix 1948; Ekren et al. 1977; Pederson et al. 2000). The Panaca small mammal fauna is derived from 12 sites in the vicinity of Panaca, near the northern margin of Meadow Valley. These sites were placed in five stratigraphic sections (Figure 2) arranged according to the paleomagnetic and stage-of-evolution correlations described in Lindsay et al. (2002, figure 7). These sites are correlated within the limits of chrons C3n.2r through C3n.3r of the Geomagnetic Polarity Time Scale (GPTS), which places them between 4.60-4.96 Ma, based on the calibration of Berggren et al. (1995). We were unable to locate and place

one other site, Rodent Quarry #2 of Galusha and Emry. We equate Rodent Quarry #1 of Galusha and Emry with our locality UALP 9504, the Fejfar site. One of our small mammal sites, UALP 9502, is identical with the AMNH Double Butte Quarry of Hazen and Gentry.

As noted by Lindsay et al. (2002) the stratigraphic-chronologic framework for the Panaca Fm. is constrained by an ash bed that overlies our highest small mammal site and has been identified as the Healdsburg Tephra by A. Sarna-Wojcicki of the United States Geological Survey (USGS, Menlo Park). That tephra has been dated 4.69 Ma, using the 27.84 Ma monitor for the Fish Canyon sanidine interlaboratory standard. The Healdsburg Tephra is shown in the upper part (marked as XXXX in Figure 2) of the Rodent Hill section.

All of the small mammal sites currently known from the Panaca Fm. are considered early Blancan NALMA whereas the large mammals reported from the Panaca Fm. by Stock (1921) are considered Hemphillian NALMA. Based on the location given by Stock (1921), we believe the fossils collected and reported by Stock were from stratigraphic lev-

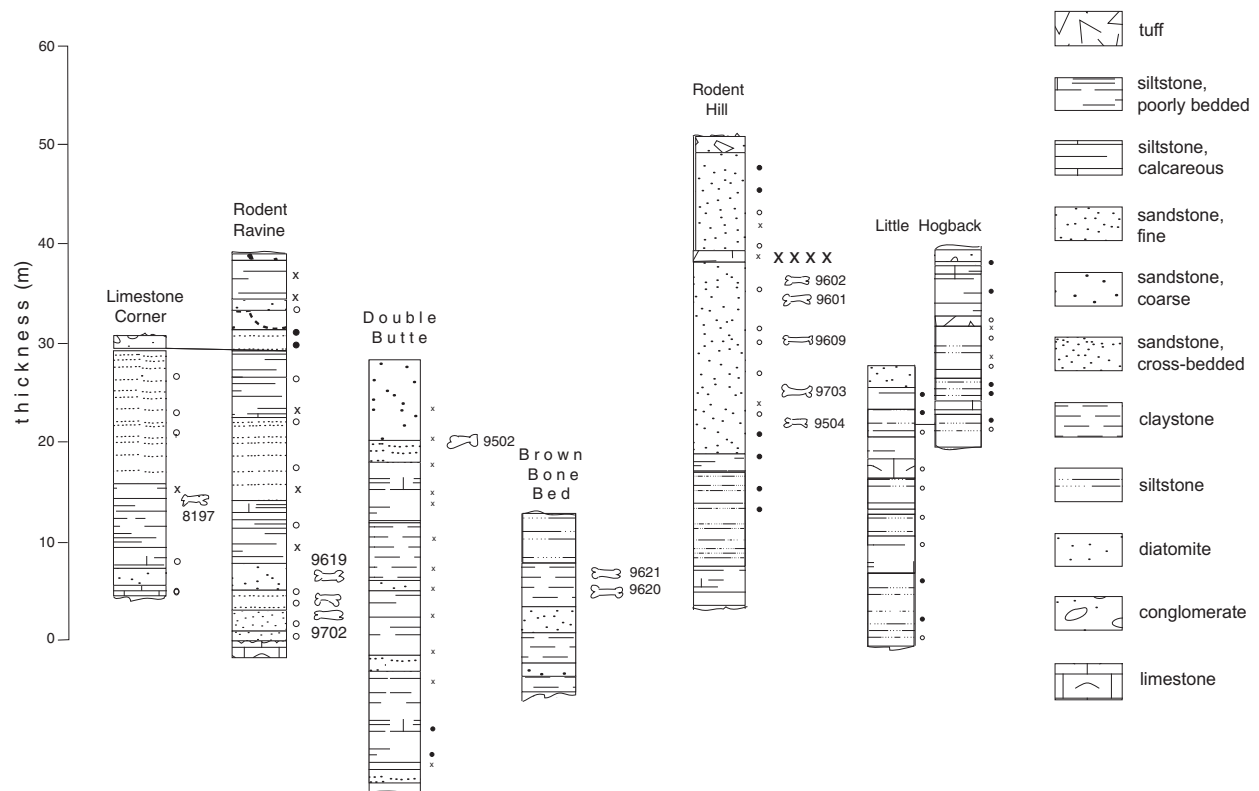


FIGURE 2. Stratigraphic section in the vicinity of Panaca that have yielded vertebrate fossils (bone symbols). Sections are arranged according to the correlations in Figure 7 of Lindsay et al. (2002). Note that we have not indicated any fossil site in the Little Hogback section, which is where we believe fossils were collected by Stock (1921). Small circles and X's to the right of the sections indicate magnetic polarity determinations (open circle = reversed polarity, closed circle = normal polarity, x = indeterminate polarity).

els below our lowest small mammal site (e.g., in magnetozone B+) in the Little Hogback section (Figure 2). Note that the rate of sediment accumulation in the Little Hogback section is lower than in the other sections as it is farther from the edge of the basin where most of the fossil sites are located. We searched the lower exposed strata in the area of the Little Hogback section very thoroughly but were unable to find any identifiable fossils, or any sediment that would yield small mammals from that area. See Lindsay et al. (2002) for more details on the geology and chronology of the Panaca l.f.

METHODS AND MATERIALS

All of the small mammals (about 2,500 identifiable specimens) collected during this study were identified by the author and compared with the small mammals collected from the Panaca Fm. by Galusha and Emry for the AMNH. All specimens listed below in materials examined are from the UALP collection unless indicated otherwise. Due to the limit of this paper, description of the largest

group, the cricetids, is reported in Mou (this volume).

Most of the identified small mammals are isolated teeth that were picked from fine or coarse concentrate after multiple washing of sediment in screen boxes. Specimens were mounted (using polyvinyl acetate dissolved in acetone) on the head of a half-inch straight pin embedded into a small cork, to facilitate handling and measurement; a half-dram glass vial was placed over the pin for safety in storage. Measurements were made to the nearest 0.01 mm with the aid of a reticule mounted in a microscope. All measurements are maximum dimensions regardless of wear, and transverse dimensions are perpendicular to anteroposterior dimensions. When applicable, the means, standard deviations and coefficients of variance were computed for each sample. Dental terminology follows Korth (1994) unless differences are noted and discussed in the text. Upper teeth are abbreviated with capital letters (e.g., M1) and lower teeth are abbreviated with lower case letters (e.g., m1).

Institutional abbreviations are: American Museum of Natural History (AMNH), Frick Laboratory of American Museum of Natural History (F:AM), University of Kansas (KU), San Bernardino County Museum (SBDM), University of Arizona Laboratory of Paleontology (UALP), University of Michigan Museum of Paleontology (UMMP), U.S. Geological Survey (USGS). Locality data are available to qualified researchers from the Department of Geosciences, University of Arizona, which is the repository for all UALP specimens. In the Materials examined sections, the acronym UALP has been removed to save space.

SYSTEMATIC PALEONTOLOGY

Order INSECTIVORA Cuvier, 1817
 Family SORICIDAE Vacq'dAzyr, 1792
 Tribe NEOMYINI Repenning, 1967
 Genus PARANOTOSOREX new genus

Type species. - *Paranotosorex panacaensis* new species.

Included species. Type species only.

Diagnosis. Size is similar to *Notiosorex crawfordi* with dentition 1-4-3/1-2-3 (incisor-antemolars-molars). The upper incisor is non-bifid. P4, M1, and M2 have strong posterior emargination of the basal outline. The lower incisor has one low scalloped cuspule. The entoconid on m1 and m2 are small, well separated from the metaconid with a low entoconid crest. The talonid of m3 is reduced with a low cristid obliqua, joining a low, transversely elongated cusp to the posterior side of the protoconid-metaconid wall below the media notch, in contrast to the crescentic basin of *Notiosorex crawfordi*. The mandibular articulation has a narrow interarticular area between the two condyles with a distinct lingual emargination relative to the condyles of *Sorex*. The upper condyle is oval, and the lower condyle is elongate and offset lingually from the plane of the lower sigmoid notch but without a groove. There is light pigmentation on the tips of the P4, M1, lower incisor, lower antemolars, m1, and m2.

Differential diagnosis. *Paranotosorex* n. gen. differs from *Notiosorex* by its oval upper condyle on the mandibular articulation and less lingual offset of the lower condyle. It differs from *Megasorex* by its smaller size as well as the two differences for *Notiosorex* and from all other shrews by its Neomyini tribal characters.

Etymology. *Para*, close to, implying morphologically close to *Notiosorex*.

Occurrence. Known only from the Panaca l.f., southeastern Nevada.

Paranotosorex panacaensis new species
 Table 1; Figure 3

Holotype. UALP 22849, left mandible with m1-m3 and complete coronoid process and condyles from UALP locality 9702.

Etymology. *panaca*, name of the town near type locality; *ensis*, Latin "of place."

Diagnosis. as of the genus.

Material examined. UALP loc. 8197: 21218, I; 21219, L maxillary with P4; 21220, L maxillary with M1-M2; 21221, R maxillary with P4-M1; 21222, R dentary with m2-m3; 21223, mandible with i-m2; 21225, L dentary with m1-m3 and complete posterior area; 21431, RM1; 23381, dentary with i-m2. **UALP loc. 9601:** 22855, L dentary with m2-m3. **UALP loc. 9602:** 22859, R dentary with two antemolars (including p4) and m1; 22860, R dentary with incisor, p4 and m1; 22861, R dentary with m3; 22862, Left maxillary with M1-M2; 22864, LM1 or M2; 22894, L dentary with m1-m3 and complete posterior area. **UALP loc. 9620:** 22873, m1; 22874, m1; 22875, Lm2. **UALP loc. 9702:** 22890, L maxillary with I-P4; 22891, L maxillary with M1-M2; 22892, LM1; 22893, I; 22850, R dentary with posterior area and m2-m3; 22886, Rm1; 22887, Rm2; 22889, i.

Description. A maxillary fragment (UALP 22890) with incisor and four antemolar teeth indicates that the upper dentition of this species is 1-4-3. The incisor is falciform and bicuspid. Its anterior cusp is non-bifid, and the posterior cusp is very low and flat. A thin basal cingulum is present on the labial side but is absent on the lingual side. No pigmentation is seen on the three available incisors.

The first three upper antemolars are unicuspid and minute, with well-developed cingula on both labial and lingual sides. The anterior two antemolars are subequal in size, whereas the posterior antemolar is slightly smaller. No pigmentation is seen on the three teeth.

The P4 is slightly smaller than the M1 and appears trapezoidal in occlusal view. The alveolus beneath this broken P4 suggests that it had strong posterior emargination of the basal outline and a broadly curving hypoconal flange. The protocone of the P4 is small but distinct on the anterior border. The parastyle is small, joining the low anterior cingulum that connects with the protocone lingually. The paracone is the largest cusp, separated from the metacone by a broad notch. A low, narrow cin-

TABLE 1. Measurements (in mm) of shrews from the early Blancan Panaca local fauna. N=number of specimens, M=mean, OR=observed range.

Locality		Length			Width		
		N	M	OR	N	M	OR
<i>Paranotiosorex panacaensis</i> n. gen. and sp.							
8197	P4	2	1.48	1.44-1.52	2	1.72	1.72-1.72
	M1	2	1.50	1.48-1.52	2	1.74	1.72-1.76
	M2	1	1.40	-----	1	1.60	-----
	m1-m3	1	3.72	-----	--	----	-----
	m1	3	1.40	1.40-1.40	3	0.93	0.92-0.96
	m2	4	1.30	1.20-1.40	3	0.91	0.88-0.92
	m3	2	1.00	1.00-1.00	2	0.62	0.60-0.64
9601	m2	1	1.36	-----	1	0.96	-----
	m3	1	1.00	-----	1	0.68	-----
9602	M1	1	1.56	-----	1	1.88	-----
	M2	1	1.44	-----	1	1.68	-----
	m1	3	1.48	1.48-1.48	3	0.95	0.92-0.96
	m2	1	1.36	-----	1	0.92	-----
	m3	2	0.98	0.92-1.04	1	0.64	-----
9620	m1	2	1.54	1.52-1.56	2	0.90	0.88-0.92
	m2	1	1.40	-----	1	0.92	-----
9702	I-P4	1	4.60	-----	--	----	-----
	P4	1	1.64	-----	0	----	-----
	M1	1	1.50	-----	1	1.76	-----
	m1-m3	1	3.82	-----	--	----	-----
	m1	2	1.50	1.48-1.52	2	0.98	0.96-1.00
	m2	3	1.39	1.36-1.40	2	0.86	0.84-0.86
	m3	2	0.98	0.96-1.00	2	0.62	0.60-0.64
<i>?Paranotiosorex</i> sp.							
9504	P4-M2	1	4.28	-----	--	----	-----
	P4	2	1.52	1.52-1.52	2	1.76	1.72-1.80
	M1	1	1.48	-----	1	1.72	-----
	M2	2	1.38	1.36-1.38	2	1.56	1.56-1.56
	m1-m3	1	3.76	-----	--	----	-----
	m1	1	1.44	-----	1	1.00	-----
	m2	2	1.34	1.32-1.36	2	0.92	0.88-0.96
	m3	2	0.96	0.92-1.00	2	0.64	0.64-0.64
<i>Sorex meltoni</i>							
9621	M1	1	1.12	-----	1	1.24	-----
	m1-m3	1	3.04	-----	--	----	-----
	m1	2	1.24	1.20-1.28	2	0.78	0.76-0.80
	m2	1	1.20	-----	1	0.76	-----
	m3	1	0.92	0.96-1.00	2	0.56	0.60-0.64

gulum is present at the posterior side of the metacone. The hypocone is slightly lingual to the protocone. Very light pigmentation is seen on the crown of the P4 below the notch between the paracone and metacone.

M1 is wider than long, with strong emargination of the posterior basal outline. A W-shaped ectoloph is well developed, with the posterior V distinctively larger, higher, and more elongated posteriorly relative to the anterior V. The metacone is

larger and higher than the paracone, and both are much higher than the protocone. The parastyle and metastyle are prominent whereas the mesostyle is slightly less developed. The hypocone is small, low, close and slightly lingual relative to the protocone. The hypoconal flange is elongated posteriorly and slightly higher anteriorly. A narrow and low posterior cingulum is present. No pigmentation is seen on two specimens, whereas light pigmenta-

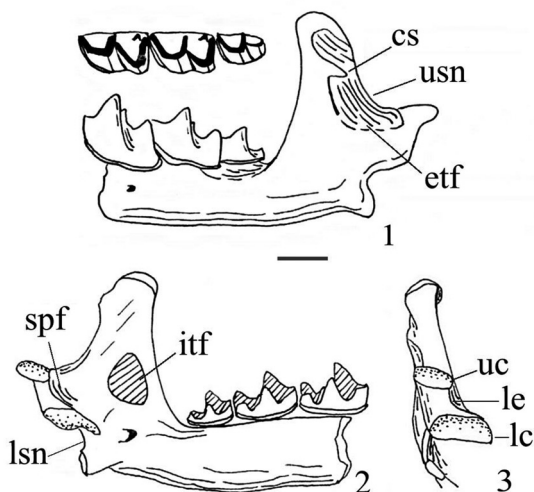


FIGURE 3. Holotype of *Paranotiosorex panacaensis*, n. gen. and sp., UALP 22849, a left mandible with m1-m3. cs=coronoid spicule, usn=upper sigmoid notch, etf=external temporal fossa, spf=super pterigoid fossa, itf=internal temporal fossa, lsn=lower sigmoid notch, uc=upper condyle, le=lingual emargination, lc=lower condyle. 3.1, occlusal and labial views. 3.2, lingual view. 3.3, posterior view. The scale bar is 1 mm.

tion is seen on the ridge of the ectoloph of one specimen (UALP 22892).

M2 is similar to M1 except for the following characters: smaller, anterior and posterior Vs subequal on the W-shaped ectoloph, less strong emargination of the posterior basal outline, and less developed hypoconal flange. No pigmentation is seen on the two specimens.

Two mandibles from UALP loc. 9702 and one from UALP loc. 9602 preserve a complete coronoid process and condyles. The lingual condylar emargination is open, without a filled bony plate (as seen in the Blarinini). Consequently, the two condyles are separated by a narrow interarticular area. The upper condyle is oval, and the lower condyle is elongated, offset lingually from the plane of the lower sigmoid notch to a greater extent than in Blarini or Soricini, but no grooves are developed as in other species of Neomyini. The coronoid process is slightly deflected labially, and the tip of the coronoid process is slightly curved anteriorly as in *Notiosorex*. A coronoid spicule is prominent (Figure 3.1). The superior pterygoid fossa is shallowly basined. A pterygoid spicule is absent, but a tiny pterygoid boss can be seen. The internal temporal fossa is subtriangular, and the external temporal fossa is very shallow with the ventral margin below

the level of the upper sigmoid notch. The mental foramen is located below m1, slightly anterior to the hypoconid or between the protoconid and hypoconid.

UALP 22859 indicates the lower dentition of *P. panacaensis* n. gen and sp. is 1-2-3. The lower incisor on this specimen is broken, but UALP 22889 shows that the lower incisor is procumbent and elongated, with one low cusplule on the cutting edge. The first antemolar is unicuspid, smaller than the second antemolar (p4). The p4 has a characteristic Soricinae pattern, with an L-shaped posterolabial crest and a posterolingual basin. No pigmentation is seen on the antemolars of UALP 22859. However, UALP 23381 has light pigmentation on the tips of the incisor and antemolars.

The trigonid and talonid of m1 are subequal anteroposteriorly, with the trigonid distinctly higher than the talonid. The paraconid is anterior to the protoconid and metaconid. It is also lower and farther from the protoconid than the metaconid. In the talonid, the hypoconid is high and prominent; a small but distinct entoconid is present on the lingual border, slightly anterior to the hypolophid and well separated from the metaconid. The entoconid is low and can be detected most securely from the lingual side (Figures 3.1 and 3.2). The anterior cingulum and the cingulum labial to the hypoconid are slightly more prominent than the posterior cingulum and the labial cingulum beneath the protoconid. UALP 22894 is exceptional in that the cingulum is uniform and better developed. Light pigmentation is seen only on one m1, UALP 23381.

The m2 is similar to m1 except that it is smaller, and the paraconid and metaconid are subequal in length. Light pigmentation is seen only on one m2, UALP 23381.

The m3 is much smaller than m1 or m2. Compared to m2, the protoconid and metaconid are closer, and the metaconid is slightly smaller than the paraconid. The talonid of m3 is reduced to a short and narrow basin, with a minute hypoconid and a low cristid obliqua joining the posterior wall of the protoconid-metaconid below the median notch. Reduction of the talonid is similar to that of *Notiosorex crawfordi*. Anterior and labial cingula are moderately developed.

Discussion. The occlusal pattern of p4 and the deep, pocketed internal temporal fossa exclude *P. panacaensis* n. gen and sp. from the subfamily Heterosoricinae. The lingual emargination of the mandibular articulation indicates that *P. panacaensis* n. gen and sp. is not a member of the subfamilies Limnoecinae or Crocidurinae. All of these

characters strongly suggest that this shrew belongs to the subfamily Soricinae.

Strong emargination of the posterior basal outline on P4, M1, and M2 of *P. panacaensis* n. gen and sp. is similar to that seen in the tribe Soricini; however, the following diagnostic characters of Soricini (Repenning 1967) are not found in *P. panacaensis* n. gen and sp.: 1) mandibular condyles are separated, the interarticular area is broad with no conspicuous lingual emargination; 2) lower condyle is not offset lingually beyond the plane of the mandible at the lower sigmoid notch; 3) superior pterygoid fossa of the mandible is a shallow pit rather than a deep basin; 4) internal temporal fossa is large and triangular; 5) coronoid process is not deflected labially; 6) m1 has a strong entoconid crest; and 7) the upper dentition is usually 1-6-3.

P. panacaensis n. gen and sp. has the following characters that are similar to those of the tribe Blarini: 1) mandibular condyles are widely separated, and the lower condyle is offset lingually beyond the lower sigmoid notch; 2) internal temporal fossa is small and oval; 3) coronoid process is slightly deflected labially; 4) no spicule is developed in the superior pterygoid fossa; and 5) m1 and m2 have no (or a very low) entoconid crest. However, members of the tribe Blarini usually have a bony plate filling the lingual emargination of the mandibular articulation so that the interarticular area looks broad, and most species of this tribe lack emargination of the posterior basal line on P4, M1, and M2, as seen in *Blarina* and *Paracryptotis*. However, some species of *Cryptotis* (e.g., *Cryptotis parva*) do not have a bony plate in the interarticular area, and the upper molars have moderate emargination. But *Cryptotis* is more primitive than *P. panacaensis* n. gen and sp. in that it retains five antemolar teeth in the upper dentition, whereas *Paranotiosorex* n. gen. has only four.

The lingual emargination of interarticular area in the mandible, lack of bony plate filling the interarticular area, lingual offset of the lower condyle, low external temporal fossa, and the 1-4-3 upper dentition suggest that *P. panacaensis* n. gen and sp. belongs in the tribe Neomyini. Only two genera of Neomyini, *Notiosorex* and *Megasorex*, have been reported from North America. *Megasorex* is significantly larger than *Notiosorex*, and *P. panacaensis* n. gen and sp. is similar to *Notiosorex crawfordi* (living species) in all characters except the shape of the upper mandibular condyle. *P. panacaensis* n. gen and sp. has an oval upper condyle, whereas *N. crawfordi* has a triangular upper condyle. Also, the offset of the lower condyle from

the lower sigmoid notch is stronger in *N. crawfordi* where a distinct groove is seen between the condyle and notch. Two fossil species of *Notiosorex* (*N. jacksoni* Hibbard 1950 and *N. repenningi* Lindsay and Jacobs 1985) have been reported in North America. *N. jacksoni* is from the early Blancan Fox Canyon local fauna (Hibbard 1950) of Kansas and the Beck Ranch local fauna (Dalquest 1978) of Texas. Measurements of *P. panacaensis* n. gen and sp. are smaller than those of the holotype and paratype of *N. jacksoni* given by Hibbard (1950). According to Hibbard (1950), there is no posterior cingulum on P4, M1, or M2 of *N. jacksoni*, and this was the primary reason he erected a new species of *Notiosorex*. The entoconid and entoconid crest on lower molars and the talonid on m3 of *N. jacksoni* were not described. A lower jaw collected later from the Fox Canyon fauna (Hibbard 1953, figure 4.3B) shows a triangular upper condyle of the mandible in *N. jacksoni*. The other fossil species, *N. repenningi*, from the early Blancan Concha fauna of Mexico (Lindsay and Jacobs 1985) is much larger than *P. panacaensis* n. gen and sp. *N. repenningi* has a triangular upper mandibular condyle, a small but distinct entoconid, and a low entoconid crest on m1 and m2. The talonid of m3 is reduced to a posterior distinct entoconid and a low entoconid ridge on the lingual side. The labial cingula on the lower molars of *N. repenningi* are very deep. *P. panacaensis* n. gen and sp. can be distinguished from the three species in *Notiosorex* by the shape of the upper mandibular condyle. Based on this character, as well as those discussed above, *P. panacaensis* n. gen and sp. is considered a new species in a new genus.

Some Eurasian Neomyini, such as *Nectogale* and *Soriculus*, have an oval upper mandibular condyle. However, their dental morphology differs from *P. panacaensis* n. gen and sp. in that they have: 1) bifid upper incisors; 2) accessory cuspids on p4 and lower molars in *Nectogale*; 3) a reduced labial cingulum on lower molars in *Nectogale*; and 4) upper dental formula 1-5-3 in *Soriculus*.

Tedford (1961) suggested that *Hesperosorex* from the middle Clarendonian Ricardo local fauna of California might be ancestral to *Notiosorex*. *Hesperosorex* is more primitive in having lower crown height, retaining the entoconid on m3, and having less reduction of m3 relative to m1. The upper mandibular condyle of *Hesperosorex* is oval, and the lower condyle has an extreme lingual offset, resulting in a groove between the condyle and the lower sigmoid notch. There is no lingual emargination on the interarticular area in *Hesperosorex*, in

contrast to *Notiosorex* and *Paranotiosorex* n. gen. Because *Hesperosorex* already has a greater offset of the lower condyle, it is probably not the direct ancestor of *Paranotiosorex* n. gen.

There is much more intraspecific variation in dental morphology of shrews within the recent specimens of *N. crawfordi* in the mammal collection at the University of Arizona than anticipated. Of the 11 specimens examined, eight have a small entoconid on the m1 and m2, and the entoconid crest is low. But, the other three specimens have a large entoconid with a distinctively high crest. The former characters are the same as those of *P. panacaensis* n. gen and sp., and the latter are identical to the diagnosis of *N. crawfordi* given by Repenning (1967) who compared four recent specimens from Texas and California in the Museum of Vertebrate Zoology at the University of California, Berkeley.

There are three possible explanations for this phenomenon: 1) misidentification of the eight specimens in the University of Arizona collection; 2) sexual dimorphism; and 3) intraspecific variation. The UALP specimens are identified correctly; examination of the mandibular structure of the eight specimens indicated that the condyles are identical. Thus they can belong only to the tribe Neomyini. The only other species of this tribe living in North America is *Megasorex gigas*, which is significantly larger with a slight posterior emargination on p4, and a less reduced talonid on m3. All of these characters eliminate the possibility that the *Notiosorex* specimens were misidentified specimens of *Megasorex*. There is a single species of *Notiosorex*, *N. crawfordi*, presently recognized in North America. Therefore, the possibility of misidentification of *N. crawfordi* is ruled out, unless an unnamed species of *Notiosorex* is hiding in North America. All three of the *Notiosorex* specimens with a strong entoconid and high entoconid crest examined are female, but females also occur among the other eight specimens, which argues against sexual dimorphism as an explanation for the morphological variation. Therefore, it seems likely that the variation in dental morphology seen among living specimens of *N. crawfordi* results from intraspecific variation strongly suggesting that caution is needed when dental morphology is used to identify shrews.

Dalquest (1972) erected a new genus and species, *Beckiasorex hibbardi*, from the Beck Ranch local fauna of Texas. *Beckiasorex* is similar in size to *N. crawfordi*, and has a mandibular articulation identical to that of *Notiosorex*. Dalquest

(1972) stated that *B. hibbardi* most closely resembles *N. jacksoni* except for its smaller size, reduced entoconid, and low entoconid crest. It is very likely that *B. hibbardi* represents a new species of *Notiosorex* rather than a new genus.

Occurrence. Known only from the Panaca l.f., southeastern Nevada.

?*Paranotiosorex* sp.

Table 1

Material examined. UALP loc. 9504: 22853, R maxillary with P4-M2; 22854, R dentary with i plus p4-m3; 22867, R dentary with m2-m3; 22869, LM2; 22870, L maxillary with last two antemolar teeth and alveoli of incisor and anterior two antemolar teeth; 22871, I; 22872, i.

Description. The isolated upper incisor (UALP 22871) is considered the same species as the other specimens from this locality. It is falciform and bicuspid, and the anterior cusp is non-bifid. A thin cingulum is present on its labial side of the tooth. Dark pigmentation is seen on the tip of the anterior and posterior cusps.

A left maxillary (UALP 22870) indicates that the upper dentition of this shrew is 1-4-3. The third antemolar tooth is unicuspid and tiny, slightly smaller than the third antemolar of *Paranotiosorex panacaensis* n. gen and sp. The P4, M1, and M2 are all similar to those of *P. panacaensis* except for their slightly smaller size and presence of dark pigmentation on the tips of the paracone and metacone.

The posterior part of the mandible on UALP 22854 is broken, but lingual emargination of the interarticular area is preserved, and the lower condyle has the same lingual offset as seen in *P. panacaensis* n. gen and sp. The mental foramen is located beneath the m1, slightly anterior to the hypoconid. The lower dentition is 1-2-3, as in *P. panacaensis* n. gen and sp. The p4 is unicuspid, with occlusal features characteristic of the Soricinae. The m1 has a high trigonid and slightly smaller talonid. The entoconid is small but distinct relative to the metaconid; the entoconid crest is short and very low. Labial cingulum is more developed than in *P. panacaensis* n. gen and sp. The m2 is similar to m1 except for its smaller size. The m3 is reduced in both the trigonid and talonid. The talonid is confined to a crescentic basin with a small posterior cuspule. Dark pigmentation is present on the tip of p4 and the protoconid of m1. Light pigmentation is seen on the protoconid of m2.

Discussion. The following features indicate that this shrew belongs in the tribe Neomyini: 1) lingual

emargination of the interarticular area in the mandible; 2) lingual offset of the lower mandibular condyle; 3) small entoconid and low entoconid crest; and 4) upper dentition of 1-4-3. The dental morphology of this taxon is similar to that of *Notiosorex* and *Paranotiosorex* n. gen. It differs from *P. panacaensis* n. gen. and sp. in having dark pigmentation, and the talonid of m3 lacks a distinct cusp. It may represent a different species of *Paranotiosorex* n. gen., or a different genus (the diagnostic upper mandibular condyle is absent).

Occurrence. Known only from the Panaca l.f., southeastern Nevada.

Tribe SORICINI Fischer de Waldheim, 1817

Genus SOREX Linnaeus, 1758

Sorex meltoni Hibbard, 1956

Table 1; Figure 4

Material examined. UALP loc. 9621: 22848, L dentary with p4-m2 and alveolus of m3; 22851, RM1; 22852, Rm3; 22882, R dentary with m2-m3; 22883, R dentary with m1.

Description. This shrew is quite small. Occlusal outline of M1 is rectangular, with moderate emargination of the posterior basal margin. The posterior V is larger and slightly higher than the anterior V on the W-shaped ectoloph. The hypocone is small and slightly lingual relative to the protocone. The hypoconal flange is flat, without curving upward distally, and a posterior cingulum is present. Pigmentation cannot be detected securely because of the overall dark brown tooth color, although the tips of the paracone and metacone appear to be darker, possibly caused by pigmentation.

The posterior part of the mandible (UALP 22848) is broken but the small pit of the superior pterygoid fossa is preserved, indicating a lingual emargination of the interarticular area. The lower condyle is oval, extending labially to the lower sigmoid notch. The coronoid process is not deflected labially, and it expands distally with a small external temporal boss. The external temporal fossa extends to about the level of the upper sigmoid notch. The internal temporal fossa is large and triangular. The mental foramen is beneath the m1, below the notch between the paraconid and protoconid.

The p4 is unicuspid, with an L-shaped crest and a large, deep posterolingual basin. The p4 has a prominent posterolingual cingulum. The trigonid of m1 is longer than the talonid, with the metaconid slightly higher than the entoconid, and the entoconid higher than the paraconid. The entoconid is

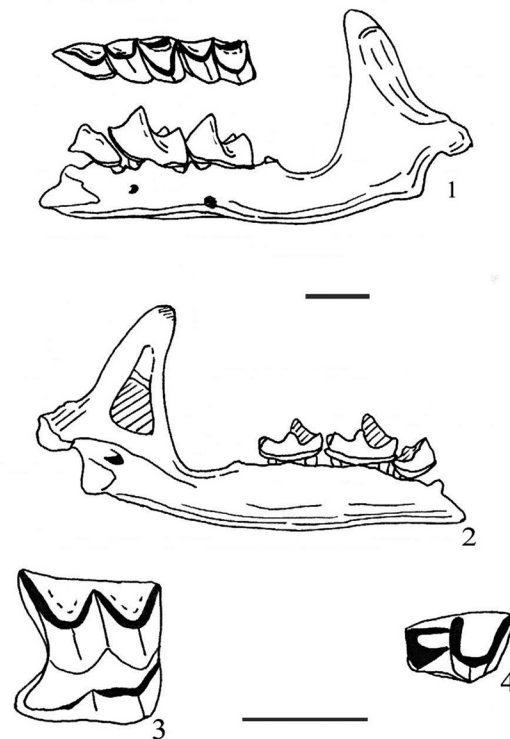


FIGURE 4. *Sorex meltoni* from the Panaca local fauna. 4.1, occlusal and labial views of UALP 22828, a left mandible with p4-m2. 4.2, lingual view of the same specimen as 1. 4.3, occlusal view of UALP 22851, a right M1. 4.4, occlusal view of UALP 22852, a right m3. The scale bars equal 1 mm.

posterior to the metaconid with a high entoconid crest. The labial cingulum on m1 is thin beneath the protoconid. The lingual cingulum is well developed. The m2 is similar to m1 but smaller and with subequal height of the entoconid and paraconid. The labial cingulum is present beneath the protoconid, and the lingual cingulum is well developed. The m3 is the smallest tooth. The talonid is smaller than the trigonid, with a V-shaped ridge on the distinct sublabial hypoconid. A labial cingulum is well developed on m3. No pigmentation can be detected on the lower cheek teeth due to the dark tooth color, although the tips of cusps on p4, m1, and m2 are more heavily colored, which may be caused by pigmentation.

Discussion. These specimens are assigned to the genus *Sorex* because of the following characters: 1) occlusal morphology of the p4 is like that seen in the subfamily Soricinae; 2) mandibular condyles have morphology characteristic of the tribe Soricini; 3) mental foramen is below m1, located anterior to the protoconid; 4) m1 has a high entoconid and

well-developed entoconid crest; 5) m3 is slightly reduced and has a basined heel; and 6) posterior outline of M1 has a slight but distinct emargination.

Eight species of *Sorex* are recognized from North America during the Pliocene and early Pleistocene (Hibbard 1937a, 1953, 1956; Hibbard and Bjork 1971). In many of the published descriptions of these species the morphology of the mandibular condyles and dentition are incomplete, making species identifications difficult. Repenning (1967) questioned the generic and tribal assignment of *S. dixonensis* Hibbard 1956 and *S. leahyi* Hibbard 1956 because these species display mandibular condyles characteristic of the tribe Neomyini (see Hibbard 1956, figures 3-4).

The Panaca material is most similar to *Sorex meltoni* Hibbard and Bjork (1971) from the Hagerman local fauna. *S. meltoni* differs from *S. taylori* Hibbard 1937a in having a more reduced m3 and less developed labial cingulum on m1; from *S. hagermanensis* Hibbard and Bjork (1971), in smaller and lacking the entoconid on m3; from *S. powersi* Hibbard and Bjork (1971), in being smaller and having a higher entoconid crest on m1 and m2 (the entoconid crest of *S. powersi* was not described, but the entoconid crest seen in the illustration [Hibbard and Bjork 1971, figures 4.1C, D] is low); from *S. sandersi* Hibbard (1956) in being smaller; and from *S. rexroadensis* Hibbard (1953) by having a different internal temporal fossa.

Range. Early and middle Blancan NALMA.

Occurrence. Known from the Panaca l.f. Extended range includes the Hagerman local fauna, Glens Ferry Formation, Idaho.

Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE Gray, 1821

Virtually all fossil leporid systematics is based on the p3 and P2, therefore only these teeth were selected for detailed study. The deciduous premolars change both in occlusal size and enamel pattern, so these teeth were also excluded from the study.

Leporids radiated explosively throughout North America during the Pliocene, which is reflected by their high diversity and abundance in Blancan faunas. Five species of the genus, *Hypolagus*, are recorded from the Panaca l.f., plus two species of the genera *Pewelagus* (N=47) and *Lepoides* (N=45), which are the most common leporids in the local fauna. These seven species of leporids represent the extinct subfamily Archaeolaginae; in contrast, the extant subfamily of leporids, Leporinae, is represented in the Panaca l.f. by only a

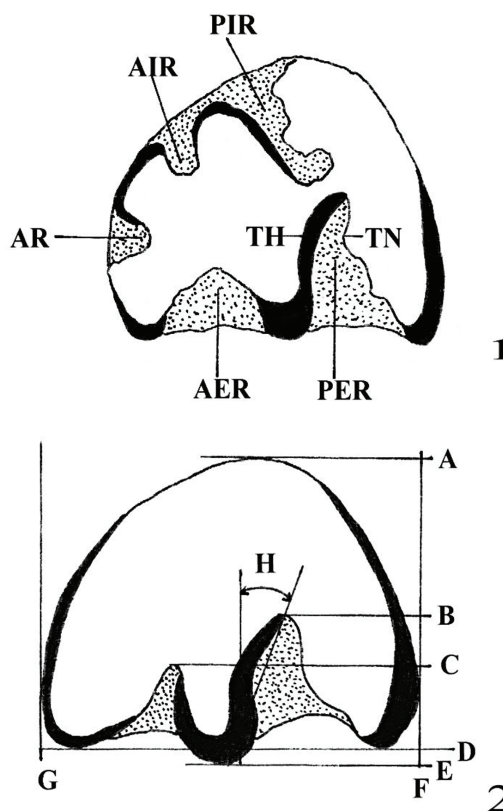


FIGURE 5. 5.1, the nomenclature of tooth structure on the occlusal surface of p3 of a leporid. AR=anterior reentrant; AIR=anterointernal reentrant; PIR=posterointernal reentrant; AER=anteroexternal reentrant; PER=posteroexternal reentrant; TH=thick enamel in PER; and TN=thin enamel in PER. 5.2, diagram of the occlusal surface of an archaeolagine p3 showing the measurements. Anteroposterior length F-G; width A-E; depth of anteroexternal reentrant (AER) C-E; depth of posteroexternal reentrant (PER) B-E; deflection of PER H; line of orientation D.

handful of specimens (N=5) assigned to two extinct genera. These nine leporid taxa are outnumbered only by the Rodentia, some of which also radiated explosively during the Pliocene.

The procedure for study of leporids follows that of White (1987). In this method the maximum length and width of each p3 is measured with a dial caliper calibrated to 0.01 mm. The occlusal enamel pattern is then drawn on an index card using a microscope and camera lucida. Measurements of other features, including angles, are taken from the drawings. Abbreviations for the measurements, developed by White (1987), are shown in Figure 5.

Subfamily ARCHAEOLAGINAE Dice, 1929
 Genus HYPOLAGUS Dice, 1917
Hypolagus edensis Frick, 1921
 Table 2; Figure 6.1-6.9

Material examined. UALP loc. 8197: 21233-21237, five isolated p3s. **UALP loc. 9504:** 21519, p3; 21520, palate with RP3-M3 and LP3-M3 and L dentary with p2-m3; 22146-22148, three isolated p3s. **UALP loc. 9601:** 22175-22179, five isolated p3s; 22180, Lp3-P4; 22181-22184, four isolated p3s; 22186-22187, two p3s; 22191, p3; 22210, p3. **UALP loc. 9602:** 22219, L dentary with p3-m3; 22221, R dentary with l-m2; 22222, p3; 22223, p3; 22225-22227, three isolated p3s; 222230-22231, two p3s; 22234-22238, five isolated p3s; 22241, p3. **UALP loc. 9702:** 22334-22337, four isolated p3s; 22339-22346, eight isolated p3s; 22362, p3.

Description. *Hypolagus edensis* is a small leporine. The p3 of *H. edensis* has no AR, and its AER is shallow with a relatively smooth outline. On one immature specimen (UALP 21520) a deeply incised AIR is connected to the PER, but near the base of the crown the AIR is absent and the AER is deeply incised. In the sample of 52 p3s, the TH is straight (40.4%), weakly sigmoid (32.7%), or sigmoid (26.9%) and TN is folded in 28.8% of the sample. Size of p3, along with depth ratios of AER and PER relative to width of the tooth, and deflection of PER are given in Table 2.

Discussion. The p3 of *H. edensis* is distinguished from that of all other species of *Hypolagus* by a deeply incised AER. *H. edensis* differs from *Pewelagus dawsonae*, another small leporid species in the Panaca l.f., by having a relatively smooth outline of the PER.

Range. Late Hemphillian and early to middle Blancan NALMAs.

Occurrence. UALP loc. 8197 in the Limestone Corner section, UALP locs. 9504, 9601, and 9602 in the Rodent Hill section, UALP loc. 9702 in the Rodent Ravine section of the Panaca l.f., southeastern Nevada. The extended range includes the late Hemphillian NALMA of Arizona and California and the Blancan NALMA of California, Idaho, Texas, and Washington (White 1987; White and Morgan 1995).

Hypolagus tedfordi White, 1987
 Table 2; Figures 6.10-6.12

Material examined. Limestone Corner F:AM loc.: F:AM 108711, Rp3, **UALP loc. 9601:** 22188, Lp3, **UALP loc. 9602:** 22240, Lp3, **UALP loc. 9621:** 22393, Rp3.

Description. *H. tedfordi* is a small leporine whose p3 has a triangular cross section. In occlusal view, the p3 PER and AER are both shallow, PER is weakly deflected posteriorly, and the TH is sigmoid in 2 of 4 specimens. The TN is unfolded in all specimens, and the AER is not crenulated.

Discussion. *H. tedfordi* differs from other known species of *Hypolagus* except *H. fontinalis* in its markedly shallow (weakly incised) PER. It is distinguished from *H. fontinalis* by its significantly smaller size (White 1987). White (1987) also mentioned that *H. tedfordi* usually has an anteriorly deflected PER, whereas *H. fontinalis* has a posteriorly deflected PER. In the three p3s assigned to *H. tedfordi* from the Panaca l.f., each PER is weakly deflected posteriorly. Thus, in *H. tedfordi* there is some variation in the deflection of the PER.

H. tedfordi was found only in the Clarendonia and Hemphillian faunas, previously. The occurrence of *H. tedfordi* in the Panaca l.f. extends its geological range into early Blancan NALMA.

Range. Clarendonian to early Blancan NALMAs.

Occurrence. F:AM loc. in the Limestone Corner section, UALP locs. 9601 and 9602 in the Rodent Hill section, UALP loc. 9621 in the Brown Bone section of the Panaca l.f., southeastern Nevada. The extended range includes late Clarendonian NALMA of California and the Hemphillian NALMA of Arizona and California (White 1987).

Hypolagus cf. *H. ringoldensis* Gustafson, 1978
 Table 2; Figures 7.1-7.5

Material examined. UALP loc. 8197: 21238-21240, three isolated p3s; **Limestone Corner F:AM loc.:** F:AM 108716, right p3. **UALP loc. 9601:** 22214, left p3; **UALP loc. 9602:** 22220, right p3. **UALP loc. 9619:** 22324, left p3; **UALP loc. 9702:** 22355, right p3. **UALP loc. 9620:** 22389, left p3; **UALP loc. 9621:** 22392, right p3.

Description. *Hypolagus* cf. *H. ringoldensis* is a relatively large leporid with variable development of the AR; five p3 specimens in the sample of 10 from the Panaca Fm. have a thin AR that is very shallow but filled with cementum; TH is weakly sigmoid in all specimens and crenulation is absent on the enamel wall of AER.

Discussion. This taxon resembles *Hypolagus ringoldensis* because of its large size and variable development of the AR. This taxon is questionably referred to *H. ringoldensis* because it expands the known characteristics of that species; e.g., the TH is weakly sigmoid, and development of internal reentrants is variable. It may represent a new spe-

TABLE 2. Measurements (in mm) of the adult p3s of lagomorphs from the early Blancan Panaca local fauna. M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range, N=number of specimens.

Taxon	Statistics	Length	Width	Relative depth	Relative depth of AER	Deflection of PER	PER (degrees)
<i>Hypolagus edensis</i>	M	2.31	1.97	33.8	46.3	14.4 post	
	SD	0.165	0.134	3.347	4.047		
	CV		7.13	6.80	9.90	8.73	
	OR		1.92-2.75	1.70-2.20	27.8-41.4	35.6-53.8	0-32 post
	N		43	42	36	36	36
<i>H. tedfordi</i>	M	2.31	1.99	20.9	41.5	12.25	
	SD	0.085	0.175	1.395	3.672		
	CV	3.69	8.81	6.68	8.74		
	OR	2.20-2.40	1.80-2.20	19.7-22.9	36.2-44.4	0-24 post	
	N	4	4	4	4	4	4
<i>H. cf. H. ringoldensis</i>	M	3.38	2.86	26.1	59.4	0.4 ant	
	SD	0.256	0.309	4.673	2.676		
	CV	7.58	10.83	17.87	4.51		
	OR	3.00-3.70	2.40-3.30	21.0-32.4	55.8-61.5	11 ant-13 post	
	N	6	6	4	4	4	5
<i>H. gidleyi</i>	M	3.1	2.5	19.0	56.9	0	
	N	1	1	1	1	1	1
<i>H. regalis</i>	M	3.00	2.60	27	54	15 ant	
	N	1	1	1	1	1	1
<i>Pewelagus dawsonae</i>	M	2.36	2.00	33.1	45.8	16.3 post	
	SD	0.144	0.162	5.107	3.200		
	CV	6.10	8.09	15.44	6.99		
	OR	2.00-2.60	1.75-2.55	24.6-48.6	39.0-56.1	6-25 post	
	N	42	42	35	35	35	35
<i>Lepoides lepoides</i>	M	3.90	3.30	26.4	58.2	8.85 post	
	SD	0.229	0.275	5.631	2.932		
	CV	5.85	8.33	21.54	5.05		
	OR	3.50-4.20	3.00-4.00	19.2-38.1	53.7-62.3	1-18.5 post	
	N	11	11	10	10	10	10
<i>Nekrolagus progressus</i>	M	3.16	2.73	18.9	56.5	1.75 post	
	SD	0.428	0.330	3.70	1.258		
	CV	13.56	12.12	19.58	2.23		
	OR	2.80-3.70	2.40-3.10	15.6-22.9	55.3-57.8	7 ant-9 post	
	N	4	4	3	3	3	4

cies, but the sample is too small and the morphology too variable to identify consistent characters. *Hypolagus* cf. *H. ringoldensis* differs from most other leporids recovered from the Panaca l.f. by its larger size. It differs from *H. regalis* in the absence of a strongly anteriorly deflected PER, and the AER is not as deeply incised. *Hypolagus* cf. *H. ringoldensis* differs from *H. oregonensis*, known only from the late Hemphillian of Oregon (White 1987), in larger size and TH is not usually sigmoid.

Range. Late Hemphillian and early Blancan NALMAs.

Occurrence. UALP loc. 8197 and F:AM loc in the Limestone Corner section, UALP locs. 9601 and 9602 in the Rodent Hill section, UALP locs. 9619 and 9702 in the Rodent Ravine section, and USLP locs 9620 and 9621 in the Brown Bone Bed section of the Panaca l.f., southeastern Nevada. The extended range of *H. ringoldensis* includes the Hemphillian NALMA of Nebraska, Florida, and Ari-

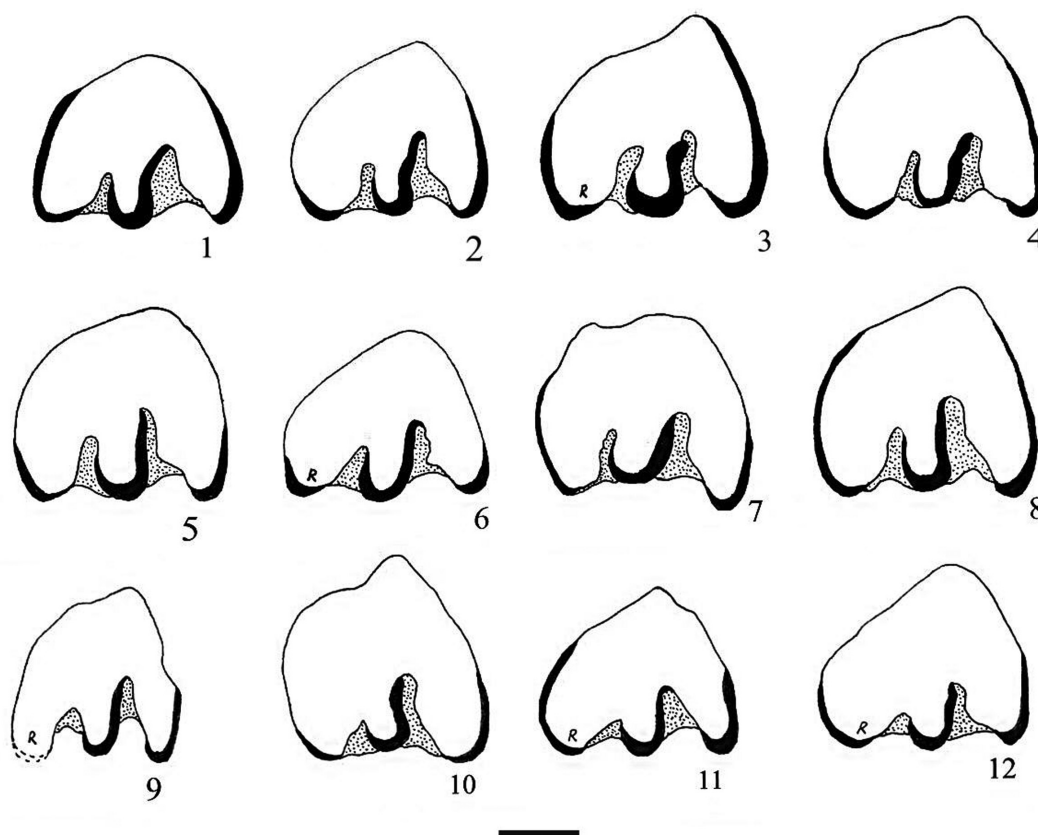


FIGURE 6. Enamel patterns of the occlusal surface of p3s of *Hypolagus edensis* and *H. tedfordi*. The letter "R" indicates a right p3 and the drawing was reversed. 6.1-6.8, *Hypolagus edensis*, UALP 21519, 22147, 22146, 22177, 22222, 22230, 22335, and 22342. 6.9, *Hypolagus* cf. *H. edensis*, UALP 22343. 10-12, *Hypolagus tedfordi*, UALP 22393, 33340, 22188. The scale bar equals 1 mm.

zona, the Blancan NALMA of Texas, Kansas, and Washington (White 1987).

Hypolagus gidleyi White, 1987

Table 2; Figure 7.6

Material examined. UALP loc. 9602: 22239, left p3.

Description. The p3 is semicircular in cross section. Occlusal view of p3 shows that PER is more deeply incised than AER, it lacks an AR, the TH is straight and the TN and enamel wall of AER are not crenulated.

Discussion. This specimen is identified as *H. gidleyi* because its size is smaller than *H. ringoldensis* and larger than *H. edensis* plus other small species of *Hypolagus*. It differs from *Hypolagus regalis* in lacking a strong anteriorly deflected PER; it differs from *Hypolagus oregonensis* in its straight TH. Size and morphology of the specimen place it with *H. gidleyi*.

Range. Late Hemphillian to middle Blancan NALMAs.

Occurrence. UALP locality 9602 in the Rodent Hill section in the Panaca l.f., southeastern Nevada. The extended range of *H. gidleyi* includes the Hemphillian NALMA of Texas and New Mexico, the Blancan NALMA of Idaho, Nebraska, Texas and Washington (White 1987).

Hypolagus regalis Hibbard, 1939

Table 2; Figure 7.7

Material examined. UALP loc. 9504: 22149, Rp3; UALP loc. 9601: 22193, Rp3.

Description. The p3 is of medium size, with AER well incised across the occlusal surface, but less incised than the PER; the PER strongly deflected anteriorly, and the AER and TH are not crenulated. Specimen UALP 22193 is an immature tooth with AIR and PIR that do not extend to the base of the crown.

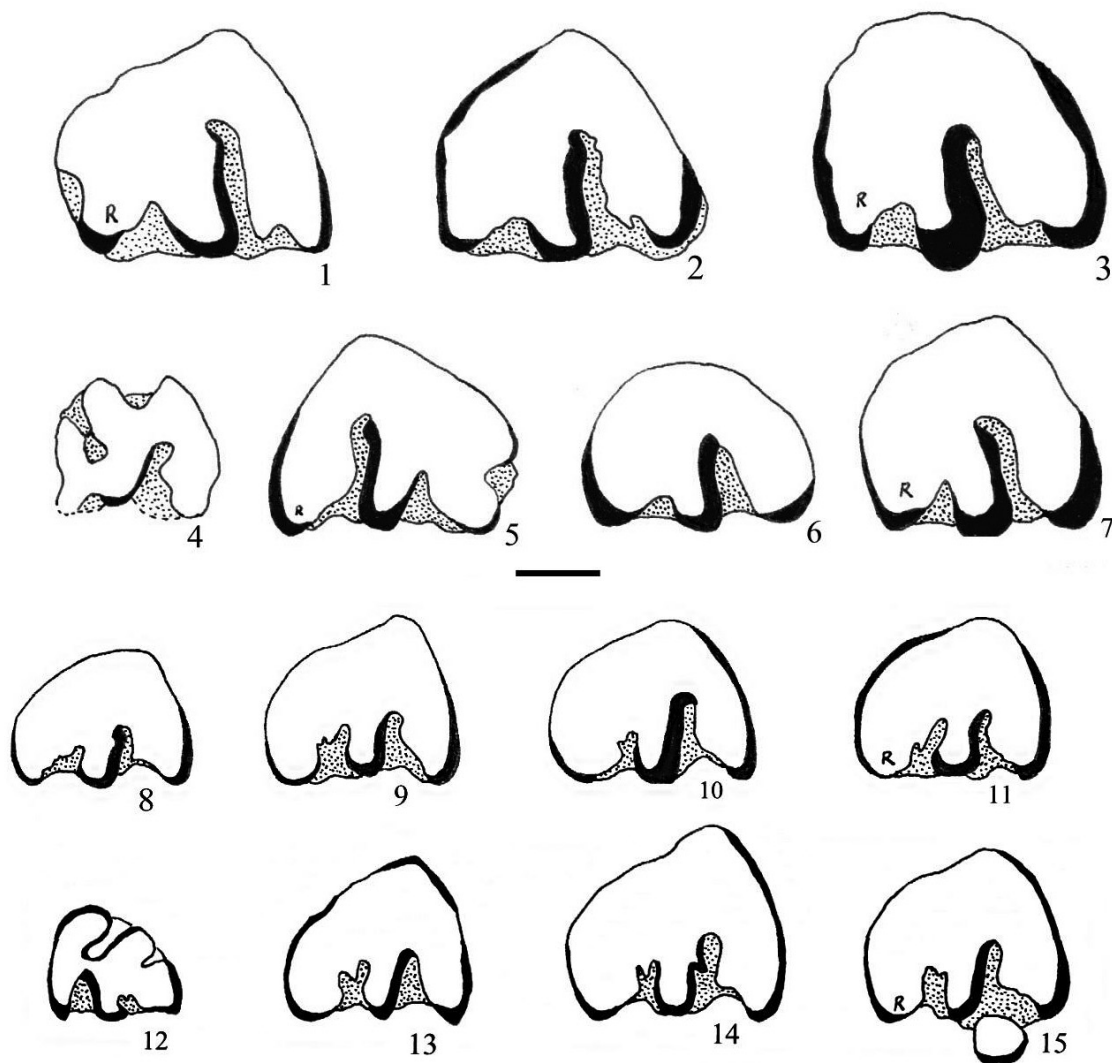


FIGURE 7. Enamel patterns on the occlusal surfaces of p3s of *Hypolagus* cf. *H. ringoldensis*, *Hypolagus gidleyi*, *Hypolagus regalis*, and *Pewelagus dawsonae*. The letter "R" indicates a right p3 and the drawing was reversed, or it was drawn from the bottom. 7.1-7.5, *Hypolagus* cf. *H. ringoldensis*. UALP 22329, 21240, F:AM 108716, and UALP 22324 (immature, illustrated by 4 and 5). 7.6, *Hypolagus gidleyi*. UALP 22239. 7.7, *Hypolagus regalis*. UALP 22149. 8-15: *Pewelagus dawsonae*. UALP 21228, 21229, 21510, 22185, 22158 (immature), 22248, 22243, 22354. The scale bar is 1 mm.

Discussion. *H. regalis* is characterized by having a strong anterior deflection of PER on p3; it differs from *H. voothiesi* in having a more deeply incised AER and with PER more strongly deflected anteriorly. *H. regalis* differs from *H. arizonensis* in being slightly larger (White 1987).

Range. Late Hemphillian and early Blancan NALMAs.

Occurrence. UALP locs. 9504 and 9601 in the Rodent Hill section of the Panaca l.f., southeastern Nevada. The extended range of *H. regalis* includes

the Hemphillian NALMA (Santee l.f.) of Nebraska, the Blancan NALMA of Kansas (Rexroad and Wendell Fox l.f.s), and Texas (Beck Ranch l.f.)

Pewelagus White, 1984

Pewelagus dawsonae White, 1984

Table 2; Figure 7.8-7.15

Material examined. UALP loc. 8197: 21226-21232, seven isolated p3s. UALP loc. 9504: 21508-21510, three isolated p3s; 22150, p3; 22151, Rp3-p4; 22158, p3; UALP loc. 9601: 22185, p3; 22189, p3; 22190, p3; 22192, p3;

22195, p3; **UALP loc. 9602:** 22216, p3; 22218, L dentary with p3-m2; 22220, p3; 22223, p3; 22228-22229, two p3s; 22242-22245, four isolated p3s; 22248-22250, three isolated p3s; 22252-22253, two p3s; **UALP loc. 9703:** 22395, p3. **UALP loc. 9619:** 22323, Lp3; **UALP loc. 9702:** 22338, p3; 22347-22354, eight isolated p3s; 22360-22361, two p3s. **UALP loc. 9620:** 22394, Rp3.

Description. *Pewelagus* is small; p3s have a triangular cross section with PER and AER deeply incised across the occlusal surface. AER has two folds (39 of 43) or more crenulations (4 of 43). TH is sigmoid (N=18), straight (N=15), or weakly sigmoid (N=10) and TN is folded in 40.5% of the sample. Dimensions and deflection of PER are given in Table 2.

Discussion. Two species of *Pewelagus* are known, *P. dawsonae* and *P. mexicanus*; the former is distinguished from the latter by being smaller and with TN that is usually crenulated (White 1987). *P. dawsonae* differs from small species of *Hypolagus* in having two or more crenulations on AER.

White (1987) had identified a p3 from the Limestone Corner F:AM locality as *P. dawsonae*. The localities in the Panaca Fm. that produce large samples of lagomorphs (e.g., Locs. 8197, 9504, 9601, 9602, and 9702) are dominated by *P. dawsonae* and *H. edensis*. This sympatry suggests that *P. dawsonae* and *H. edensis* probably occupied different niches. Based on its greatly enlarged tympanic bullae and narrow choanae, White (1987) suggested that *P. dawsonae* inhabited burrows for protection from predators. My results support that interpretation.

Range. Blancan NALMA.

Occurrence. UALP loc. 8197 and F:AM loc in the Limestone Corner section, UALP locs. 9504, 9601, 9602, and 9703 in the Rodent Hill section, UALP locs. 9619 and 9702 in the Rodent Ravine section, and UALP loc. 9620 in the Brown Bone Bed section of the Panaca l.f., southeastern Nevada. The extended range of *Pewelagus* includes the Blancan NALMA of California (Layer Cake, Vallecito Creek, and Coso Mountains l.f.s) and Texas (Red Corral and Blanco l.f.s).

Lepoides White, 1987

Lepoides lepoides White, 1987

Table 2; Figure 8.1-8.6

Material examined. Limestone Corner locality

F:AM: AMNH(F:AM) 10716, p3; AMNH(F:AM) 10717, p3; AMNH(F:AM) 10718, palate;

AMNH(F:AM) 10719, p3; AMNH(F:AM) 10720, palate; AMNH(F:AM) 10721, mandible; AMNH(F:AM) 10722, p3; AMNH(F:AM) 10725, p3; AMNH(F:AM) 10727, palate; AMNH(F:AM) 10728, palate; AMNH(F:AM) 10730, mandible; AMNH(F:AM) 10731, p3. **UALP loc. 9504:** 21367, L and R dentaries with p3-m3; 22143, P2; 22144, P2; **UALP loc. 9601:** 22159, partial palate with L and R P2-M2; 22160, L dentary with p3-p4; 22162-22165, four isolated p3s; 22169, P2; 22171-22173, three isolated P2s; 22209, P2; **UALP loc. 9602:** 22215, L maxillary with P2-M3; 22255-22260, six isolated P2s; **UALP loc. 9609:** 22399, L maxillary with P2-P4. **UALP loc. 9619:** 22322, RP2; 22326, partial palate with L P2-M3 and R P2-M1; 22327, R dentary with p4-m2; 22328-22329, two dentaries with incisor and full cheek teeth; 22330, L maxillary with P2-M2; 22331, P2; 22332, L maxillary with P4-M1; **UALP Loc. 9702:** 22333, L dentary with incisor and full cheek teeth; 22366, R maxillary with P2-M2.

Description. *Lepoides* is significantly larger than other fossil archaeolagines. The P2 has three reentrants; the p3s are semicircular to triangular in cross section, with an AR, AER, and deeply incised PER. The PER is strongly deflected posteriorly; TH is sigmoid in 91.7% of the sample, and TN is folded in 75% of the sample (N=12). One dentary (UALP 22160) has an AIR in addition to the AR, AER, and PER. In this specimen the PER is inclined 58.7% of the occlusal width, with a slight posterior deflection, and the AER is inclined 21.7% of the occlusal width. The TN is not folded and the AER is not crenulated on this specimen. It is assigned to *Lepoides* based on its size and the posterior deflection of the PER.

Discussion. *Lepoides* is distinguished from other large lagomorph species in the Panaca l.f. in having a posterior deflection of PER.

Range. Late Hemphillian and early Blancan NALMAs.

Occurrence. F:AM locality in the Limestone Corner section, UALP locs. 9504, 9601, 9602, and 9609 in the Rodent Hill section, and UALP locs. 9619 and 9702 in the Rodent Ravine sections of the Panaca l.f., southeastern Nevada. The extended range of *Lepoides lepoides* includes the Hemphillian NALMA of Nebraska (Santee l.f.; White 1987) and late Hemphillian (Silver Springs l.f.; Kelly 1998) and early Blancan NALMAs of Nevada.

Subfamily LEPORINAE Trouessart, 1880

Genus *Nekrolagus* Hibbard, 1939

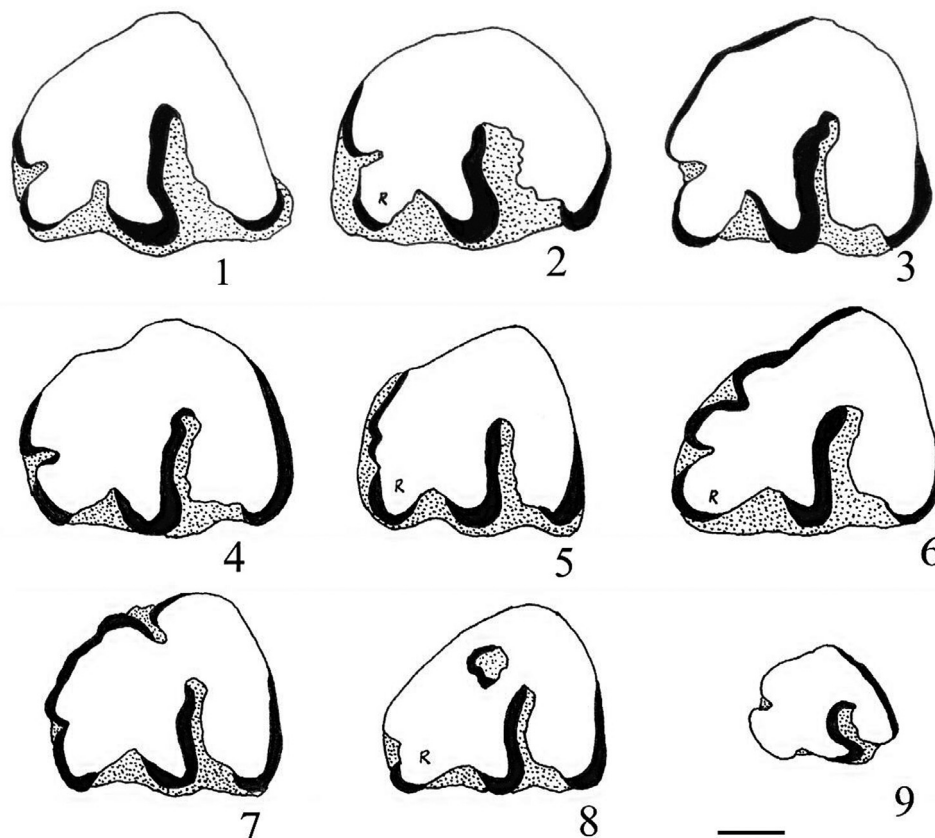


FIGURE 8. Enamel patterns on the occlusal surface of p3s of *Lepoides lepoides*, *Nekrolagus progressus*, ?*Pronotolagus* sp. 8.1-8.5, *Lepoides lepoides*, UALP 22139, 22140, 22163, 22333, 22329. 8.6, ?*Lepoides lepoides*, UALP 22160. 8.7-8.8, *Nekrolagus progressus*, UALP 22217, F:AM 108715. 8.9, ?*Pronotolagus* sp., UALP 21511. The scale bar is 1 mm.

Nekrolagus progressus Hibbard, 1939
Table 2; Figures 8.7-8.8

Material examined. Limestone Corner F:AM loc.: AMNH(F:AM) 108715, R p3; **UALP loc. 8197:** 21241, L p3; **UALP loc. 9601:** 22174, L p3; **UALP loc. 9602:** 22217, L dentary with i, p3-m1.

Description. *Nekrolagus progressus* is near the size of *Sylvilagus floridanus* and *Hypolagus vetus*. *N. progressus* differs from all other lagomorphs from the Panaca l.f. in having either a PIR or an enamel lake in the position of the PIR. The p3s of *N. progressus* usually with a shallow AR; the PER is deeply incised across the occlusal surface and may be slightly deflected anteriorly or posteriorly; the AER is shallow and uncrenulated; TH is smooth except for one specimen (UALP 22217) with a slightly sigmoid TH; TN is smooth except for one immature specimen (UALP 21241) in which

TN is folded. One specimen (F:AM 10875) develops an enamel lake on the occlusal surface when the PIR is pinched off (Figure 5.8).

Range. Late Hemphillian and early Blancan NALMAs.

Occurrence. F:AM loc. and UALP loc. 8197 in the Limestone Corner section, UALP locs. 9601 and 9602 in the Rodent Hill section of the Panaca l.f., southeastern Nevada. The extended range of *Nekrolagus progressus* includes the Blancan NALMA of Kansas (Rexroad 3 l.f., Wendell Fox l.f., and Deer Park l.f.), Washington (White Bluffs l.f.), and Texas (Beck Ranch l.f.; White 1991).

Pronotolagus White, 1991
?*Pronotolagus* sp. White, 1991
Table 2; Figure 8.9

Material examined. **UALP loc. 9504:** 21511, Rp3.

TABLE 3. Measurements (in mm) of cheek teeth of *Pliogeomys parvus* from the early Blancan Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		N	Length				Width				
			M	SD	CV	OR	N	M	SD	CV	OR
8197	m3	1	0.70	----	----	----	1	1.00	----	----	----
9502	P4	2	1.34	----	----	1.20-1.48	2	1.48	----	----	1.36-1.60
	M1	1	0.96	----	----	----	1	1.52	----	----	----
	M2	3	0.89	0.061	6.84	0.84-0.96	3	1.35	0.042	3.08	1.32-1.40
	m1	2	0.98	----	----	0.96-1.00	2	1.54	----	----	1.52-1.56
	m2	3	0.88	0.080	9.09	0.80-0.88	2	1.32	----	----	1.28-1.36
	m3	1	1.00	----	----	----	1	1.32	----	----	----
9504	M1	1	1.04	----	----	----	1	1.76	----	----	----
	M2	2	0.86	----	----	0.84-0.88	2	1.78	----	----	1.72-1.84
9601	M2	1	0.88	----	----	----	1	1.44	----	----	----
9602	M2	4	0.83	0.050	6.06	0.80-0.90	4	1.67	0.055	3.30	1.59-1.7
	p4	2	1.50	----	----	1.40-1.60	2	1.56	----	----	1.56-1.56
	m3	1	1.00	----	----	----	2	1.50	----	----	1.40-1.60
9620	M3	0	----	----	----	----	1	1.44	----	----	----
	p4	1	1.60	----	----	----	1	1.56	----	----	----
	m1	2	1.01	----	----	1.00-1.02	2	1.66	----	----	1.60-1.72
	m2	2	1.02	----	----	1.00-1.04	2	1.44	----	----	1.40-1.48
	m3	1	0.96	----	----	----	1	1.60	----	----	----

Description. *Pronotolagus* is a medium to large leporid whose p3 lacks AR and with AIR more deeply incised than PIR (when the PIR is present). The AER is shallow and wide; PER is incised less than half the occlusal width (White 1991). UALP 21511 (length is 2.1 mm, width is 1.65 mm) is slightly smaller than *P. apachensis* with a small but distinct AIR; the PER is deeply incised; the AER is shallow and unfolded; TH is strongly sigmoid and TN is folded.

Discussion. Presence of AIR and absence of AR in UALP 21511 indicate this specimen is *Pronotolagus*. Size of UALP 21511 is close to that of *P. apachensis* but p3 of that species lacks a strongly sigmoid TH. *Pronotolagus* differs from *Notolagus* in having a less deeply incised AIR and the AIR often unites with AER in *Notolagus*, forming an isolated column in the anterior part of the tooth.

Occurrence. UALP loc. 9504 in the Rodent Hill section in the Panaca l.f., southeastern Nevada. The extended range of *Pronotolagus* is late Clarendonian of California (Apache Canyon l.f.) and early Hemphillian of Nebraska (LeMoyné l.f., White 1991).

Order RODENTIA Bowdich, 1821
 Family GEOMYIDAE Bonaparte, 1845
 Subfamily GEOMYINAE Bonaparte, 1845
Pliogeomys Hibbard, 1954a
Pliogeomys parvus Zakrzewski, 1969

Table 3; Figures 9-10

Materials examined. UALP loc. 8197: 21410, m3; 21419, m3. UALP loc. 9502: 21566-21567, two P4s; 21572-21573, two M2s; 21574, m1 or m2; 21575, m2; 21576. M1; 21577, M1 or M2; 21579-21581, three isolated p4s; 21582-21583, two m1s; 21584-21585, two m2; 21586, M2; 21587, m3;

21588, m2; 23563, M1. UALP loc. 9504: 23138, M1; 23267-23268, two M2s. UALP loc. 9601: 23261, M2. UALP loc. 9602: 23169, m3; 23172, m3; 23262-23263, two p4s; 23265, M2; 23266, ?M2; 23269, ?M2; 23380, M2. UALP loc. 9620: 23237, M3; 23256, m1; 23257-23258, two m2s; 23259, m1; 23260, m3; 23264, p4.

Description. Sample from the Panaca l.f. is restricted to isolated teeth; the sample is described by the type of tooth.

P4: Specimen UALP 21566 (Figure 9.1) is unworn and provides a framework for loph-cusp unions; the protoloph and metaloph are connected by a prominent loph directed from the hypostyle of the metaloph to join the protoloph slightly lingual to the midline; the posterior cingulum is very low and short, about two-thirds of the length of the metaloph; dentine tracts are developed low on the sides of the protoloph with the tract on the lingual side higher than that on the labial side; dentine tracts on the metaloph cannot be determined because of breakage. UALP 21567 (Figure 9.2) is slightly worn with protoloph and metaloph joining as before; reentrant angles are V-shaped and narrow, with shallow lingual valleys and deep labial valleys; dentine tracts on the sides of the metaloph are much higher than those on the protoloph; posterior enamel surface is thin (broken on this specimen); a remnant anterior root is present.

M1 and M2: These teeth are similar in occlusal view, both with a thin protoloph and a transversely shorter and anteroposteriorly wider metaloph; the lingual side is slightly wider than the labial side (Figures 9.3 and 9.4). M2s are slightly shorter than M1s in anteroposterior length. The protoloph has three transversely elongated and subequal cusps.

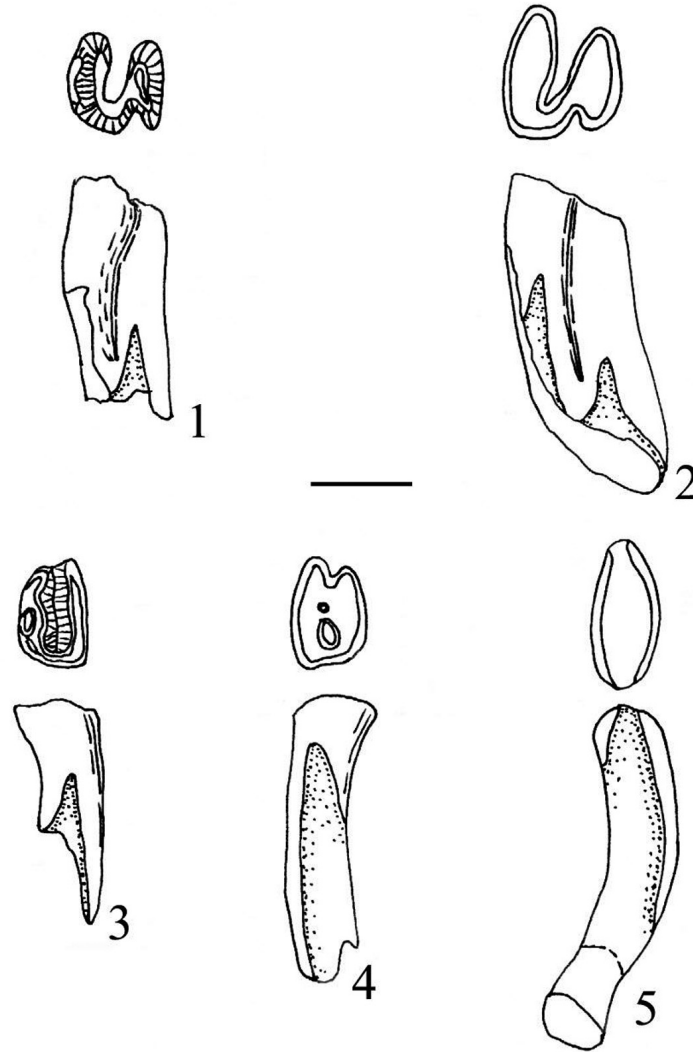


FIGURE 9. Upper cheek teeth of *Pligeomys parvus* from the Panaca local fauna. 9.1-9.2, occlusal and lingual views of P4s, UALP 21566, 21567. 9.3, a right M1, UALP 21572. 9.4-9.5, M2s, UALP 21586, 23267. The scale bar is 1 mm.

The metaloph has three unequal cusps (large medial hypocone, small lingual hypostyle, and middle size labial metacone). The lophs are joined lingually after early wear and then joined labially; small ephemeral enamel islets may form in early wear (Figure 9.4). Dentine tracts are well-developed, interrupted after moderate wear; the posterior enamel plate is completely lost after advanced wear. In most of the M2s the enamel base is much higher on the posterior side relative to the anterior side, with the base of the posterior enamel plate about 1.0 mm below the dentine tract. However, four specimens from UALP locality 9602 (23265, 23266, 23269, and 23390) have the enamel base

on the posterior face only slightly higher than on the anterior face.

p4: Unworn teeth have an enamel cap on the occlusal surface, with small, indistinct cusps; on worn specimens the protolophid is subcircular in outline, shorter transversely and longer anteroposteriorly than the metalophid; the two lophids are connected medially by a short prominent loph. Dentine tracts are high on the sides of the teeth, higher on the labial side, and slightly higher on the metalophid than on the protolophid.

m1 and m2: Occlusal outline of m1 and m2 are similar, with the anteroposterior length slightly greater on the labial side. The metalophid has

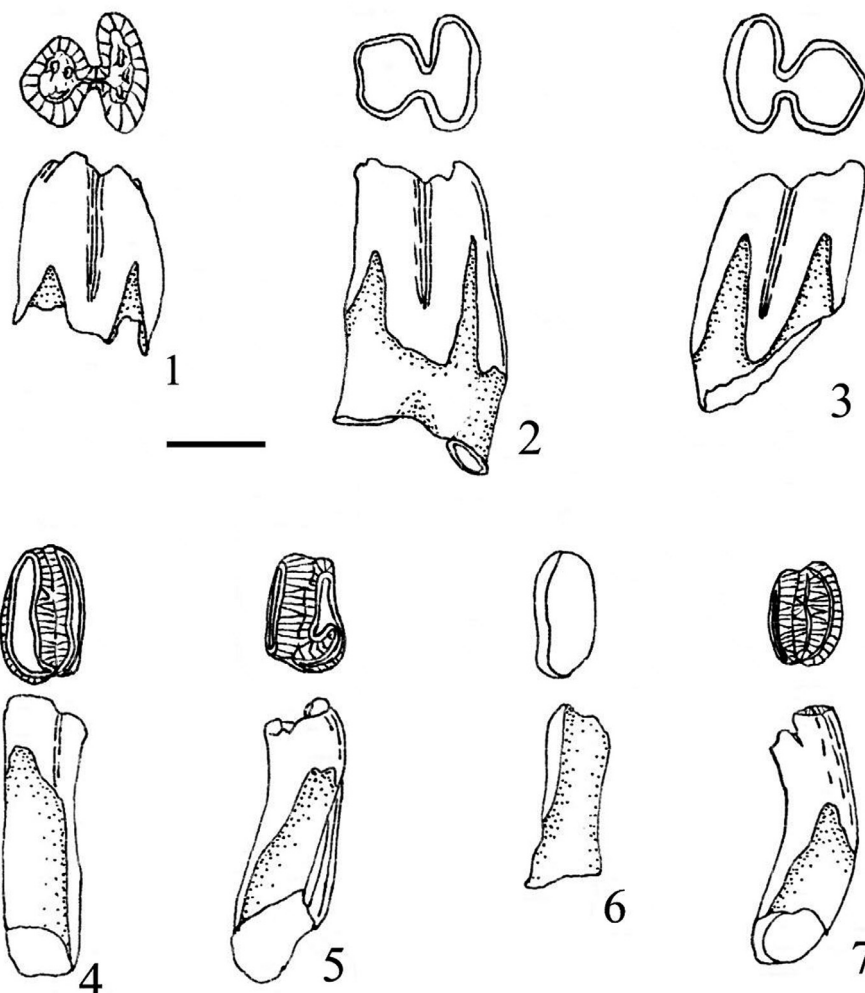


FIGURE 10. Lower cheek teeth of *Pliogeomys parvus* from the Panaca local fauna. 10.1-10.3, occlusal and labial views of p4s, UALP 23264, 23263, 21579. 10.4, a left m1, UALP 23256. 10.5, a right m2, UALP 23257. 10.6, a right m1 or m2, UALP 21574. 10.7, a right m3, UALP 23172. The scale bar is 1 mm.

three cusps (large medial protoconid, small labial anteroposteriorly-elongated protostylid, and lingual metaconid). An anterior cingulum is well developed, joining the protostylid and the metaconid after passing anterior to the protoconid. Initially, the hypolophid is much thinner anteroposteriorly than the metalophid, with three indistinct, transversely elongated cusps. The two lophids join labially in early wear and join again (lingually) in moderate wear. The enamel base is much higher on the anterior plate than on the posterior plate, so the anterior enamel band is removed after the tooth is worn through about one-third of its height. Dentine tracts are well developed but not as narrow as seen on upper cheek teeth. Unworn and slightly

worn teeth are open at the base, but worn teeth have a large single root.

m3: This tooth is smaller than m1 or m2. It has a long and low anterior cingulum that continues to the lingual side of the metaconid. The hypolophid is very thin anteroposteriorly, shorter transversely, and lower than the metalophid. Cusps are indistinct, and roots are undeveloped on four available specimens.

Discussion. The geomyid occlusal pattern of cheek teeth and the presence of roots on the p4s of well-worn molars indicate that this taxon is more primitive than modern *Geomys*, which is characterized by evergrowing teeth (Hibbard 1954a). Three species of *Pliogeomys* have been recorded in

TABLE 4. Measurements (in mm) of cheek teeth of *Perognathus mclaughlini* from the early Blancan Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		N	Length				OR	N	Width			
			M	SD	CV	OR			M	SD	CV	OR
8197	P4	2	1.00	----	----	1.00-1.00	2	1.13	----	----	1.08-1.18	
	M1	1	0.88	----	----	----	1	1.12	----	----	----	
	M2	1	0.76	----	----	----	1	1.12	----	----	----	
	p4	2	0.82	----	----	0.76-0.88	2	0.82	----	----	0.80-0.84	
	m1	1	1.04	----	----	----	1	1.12	----	----	----	
	m2	1	0.88	----	----	----	1	1.00	----	----	----	
	m3	1	0.76	----	----	----	1	0.88	----	----	----	
9504	P4	7	0.98	0.069	7.03	0.88-1.08	7	1.19	0.078	6.54	1.08-1.28	
	M1	2	0.92	----	----	0.92-0.92	2	1.28	----	----	1.28-1.28	
	M2	4	0.83	0.038	4.61	0.80-0.88	4	1.09	0.034	3.15	1.04-1.12	
	p4	9	0.76	0.037	4.91	0.72-0.80	9	0.80	0.022	2.80	0.76-0.84	
	m1	8	1.06	0.060	5.77	0.96-1.16	8	1.08	0.049	4.53	1.04-1.16	
	m2	9	0.90	0.024	2.68	0.88-0.94	9	1.06	0.040	3.76	1.00-1.12	
	m3	5	0.72	0.018	2.34	0.70-0.74	5	0.86	0.036	4.18	0.84-0.92	
9601	P4	1	1.00	----	----	----	1	1.20	----	----	----	
	M2	0	--	----	----	----	1	1.08	----	----	----	
	p4	1	0.80	----	----	----	1	0.76	----	----	----	
9602	M2	2	0.95	----	----	0.92-0.98	2	1.08	----	----	1.08-1.08	
	P4	3	1.03	0.081	7.82	0.96-1.12	3	1.20	0.080	6.67	1.12-1.28	
	M1	5	0.96	0.049	5.10	0.88-1.00	5	1.26	0.022	1.73	1.24-1.28	
	M2	5	0.78	0.036	4.56	0.72-0.80	5	1.06	0.022	2.07	1.04-1.08	
	p4	3	0.76	0.040	5.26	0.72-0.80	3	0.83	0.023	2.79	0.80-0.84	
	m1	4	1.03	0.020	1.94	1.00-1.04	4	1.06	0.023	2.18	1.04-1.08	
	m2	3	0.89	0.061	6.84	0.84-0.96	3	1.07	0.046	4.33	1.04-1.12	
9616	P4	1	1.00	----	----	----	1	1.16	----	----	----	
9620	M2	1	0.78	----	----	----	1	1.04	----	----	----	
	m1	1	1.08	----	----	----	2	1.08	----	----	1.04-1.12	
	m2	1	0.92	----	----	----	1	1.08	----	----	----	
9702	P4	3	0.97	0.023	2.34	0.96-1.00	3	1.10	0.020	1.82	1.08-1.12	
	M1	2	0.91	----	----	0.88-0.94	2	1.16	----	----	1.16-1.16	
	M2	1	0.76	----	----	----	1	1.04	----	----	----	
	p4	2	0.76	----	----	0.72-0.80	2	0.81	----	----	0.80-0.82	
	m1	2	1.10	----	----	----	2	1.12	----	----	1.08-1.16	
	m2	1	0.88	----	----	----	1	1.04	----	----	----	

North America and Mexico; these are *P. buisi* (genotype) from the late Hemphillian Buis Ranch local fauna of Oklahoma (Hibbard 1954a), *P. parvus* from the middle Blancan Hagerman local fauna of Idaho (Zakrzewski 1969), and *P. carranzai* from the late Hemphillian Yepomera local fauna of Chihuahua (Lindsay and Jacobs 1985). *P. parvus* is significantly smaller than *P. buisi*, and the roots of p4 are not as well developed as in *P. buisi* (Zakrzewski 1969). *P. carranzai* is characterized by its very high crown, high dentine tracts, and the shallow median groove on the upper incisor. No upper incisor of a pocket gopher has been found in the Panaca l.f. Size of p4 and m2 from the Panaca l.f. are similar to *P. parvus* from the Hagerman l.f. (Zakrzewski 1969, table 2) although m1 is slightly larger and m3 is distinctly larger than those from the Hagerman l.f. These differences are considered within the range of intraspecific variation because the sample size of geomyids from both the Panaca and Hagerman l.f.s is small, and large variation is seen in the Idaho sample. Notice that the geomyid teeth from UALP loc. 9502 are slightly smaller than those from other Panaca sites. *P. carranzai* is higher crowned and larger than the Panaca geomyid. Also, dentine tracts on the sides of p4 (Lindsay and Jacobs 1985, figure 6a) of *P. carranzai* are much higher

than those from the Panaca l.f. Martin et al. (2002) considered *P. carranzai* a species of *Geomys*. Size, crown height, and development of dentine tracts indicate that the Panaca geomyid should be assigned to *P. parvus*.

Dalquest (1983) erected a new genus of Geomyinae, *Progeomys*, from the Coffee Ranch local fauna (type Hemphillian) in Texas. So far, only the genotypic species *Progeomys sulcatus* has been found in North America. This taxon is characterized by a strongly rooted p4 and absence of, or very incipient, development of dentine tracts on the cheek teeth. The Panaca *Pliogeomys* is more advanced than *P. sulcatus*, both in root loss and development of dentine tracts.

Range. Early to middle Blancan NALMA.

Occurrence. UALP locality 8197 in the Limestone Corner section, UALP locality 9502 in the Double Butte section, UALP locs. 9504, 9601, and 9602 in the Rodent Hill section, and UALP locality 9620 in the Brown Bone bed section of the Panaca l.f., southeastern Nevada. Extended range of *Pliogeomys parvus* includes the Hagerman local fauna of Idaho

Family HETEROMYIDAE Allen and Chapman, 1893

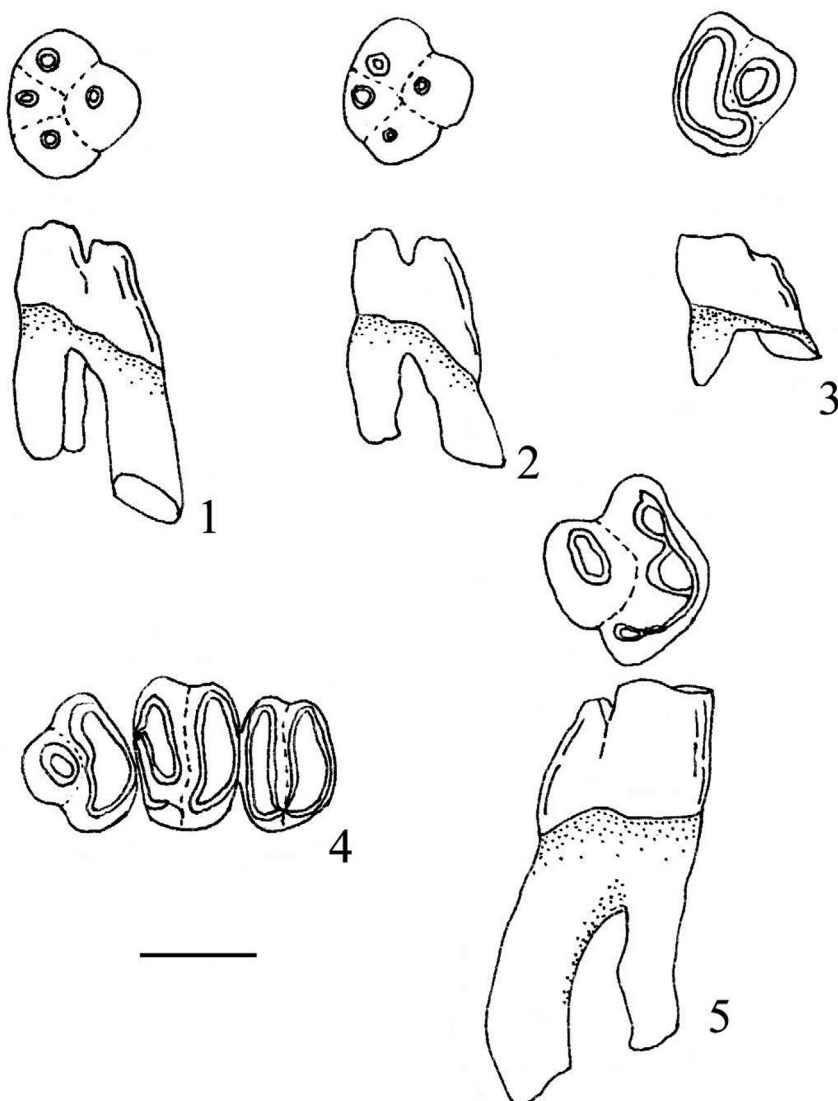


FIGURE 11. Upper cheek teeth of *Perognathus mclaughlini* and *Oregonomys* sp. from the Panaca local fauna. 11.1-11.3, occlusal and lingual views of P4s, UALP 23037, 23038, and 21285. 11.4, occlusal view of a left P4-M2, UALP 23093. 11.5, *Oregonomys* sp., occlusal and lingual view of a left P4, UALP 23064. The scale bar is 1 mm.

Subfamily PEROGNATHINAE Wood, 1935

Perognathus Wied-Neuwied, 1839

Perognathus mclaughlini Hibbard, 1949

Table 4; Figures 11.1-11.4 and 12.1-12.3

Materials examined. UALP loc. 8197: 21276, RdP4; 21277, P4; 21278, LM1; 21279, RM2; 21280-21281, two p4s; 21282, Rm1; 21283, Rm3; 21284, Lm2; 21285, P4. **UALP loc. 9504:** 21530-21531, two P4s; 21532, m1; 21533, L dentary with p4, m2-m3; 21555, edentulous dentary; 23028-23029, two L dentaries with incisor, p4-m2; 23030, L dentary with incisor, p4 and m1; 23031, R dentary with p4 and m3; 23032, L dentary with incisor,

p4-m2; 23033, edentulous dentary; 23037-23042, six P4s; 23043-23044, two M1s; 23045-23048, four m1s; 23049, R dentary with p4-m2; 23050, L dentary with incisor, m2-m3; 23051-23053, three p4s; 23054-23057, four m1s; 23058-23061, four m2s; 23062-23063, two m3s; 23065, M1; 23378-23379, two edentulous dentaries. **UALP loc. 9601:** 23066, LP4; 23067, LM2; 23068, Lp4; 23069-23070, two M1s. **UALP loc. 9602:** 23071-23073, three P4s; 23074-23078, M1s; 23079-23083, M2s; 23084, L dentary with p4-m1; 23085, R dentary with m1-m3; 23086, R dentary with p4; 23087, p4; 23088-23089, two m1s; 23090-23092, three m2s. **UALP**

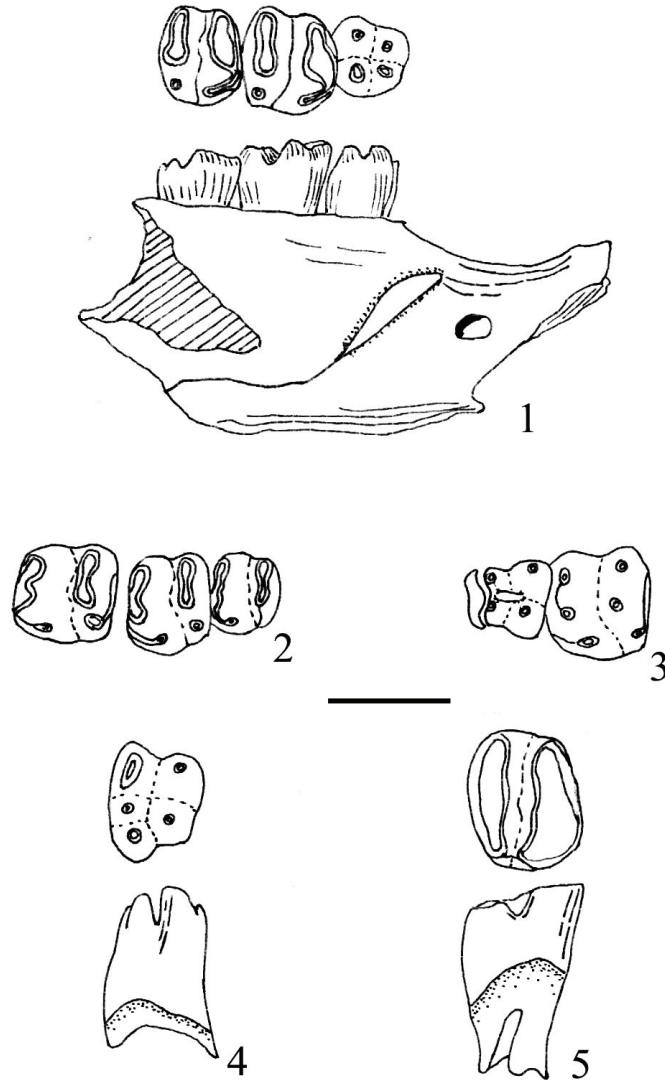


FIGURE 12. Lower cheek teeth of *Perognathus* and ?*Cupidinimus* from the Panaca local fauna. 12.1, occlusal and labial views of a left dentary fragment with p4-m2, UALP 23049. 12.2, occlusal view of left m1-m3, UALP 23085. 12.3, *Perognathus* cf. *P. gidleyi*, occlusal view of left p4-m1, UALP 23030. 12.4, ?*Cupidinimus*, occlusal and labial views of a right p4, UALP 21561. 12.5, ?*Cupidinimus*, a right m1, UALP 23270. The scale bar equals 1 mm.

loc. 9616: 23249, RP4. **UALP loc. 9702:** 23093, L maxilla with P4-M2; 23094-23095, two P4s; 23096, LM1; 23097, Rp4; 23098, Rm1; 23099, Rm2; 23376, R dentary with p4-m1; 23377, L dentary with incisor. **UALP loc. 9620:** 23250, LM2: 23251-23252, two m1s; 23253, left m2; 23254, m1.

Description. Dental terminology for heteromyids follows Lindsay (1972, figure 19). Cheek teeth are brachylophodont. Upper teeth have three distinct roots (lingual, anterolabial, and posterolabial), and lower teeth have two distinct transverse roots (anterior and posterior).

P4: Four cusps are present; a protocone on the protoloph, a metacone, hypocone and hypostyle on the metaloph; accessory cuspules are absent on both lophs. The protoloph and metaloph are joined medially after moderate wear; the protocone is conical, very circular. The hypocone is the largest cusp on the metaloph, the metacone and hypostyle are subequal; the hypostyle is located slightly more anterior relative to the metacone, making a smooth curved posterior outline of the metaloph; on UALP 21285 (Figure 11.3) the hypostyle is located more anteriorly, resulting in an L-shaped outline of the

metaloph. Nine of the 16 P4s are slightly inflated on the lower part of the crown. The base of the enamel is lower on the protoloph.

M1: Teeth are strongly bilophodont with the protoloph slightly wider transversely than the metaloph. The protoloph is relatively straight whereas the metaloph is slightly curved, especially on its posterior side. Three cusps are present on the protoloph, with the medial protocone largest and the lingual protostyle the smallest cusp; three cusps are also present on the metaloph, with the medial hypocone largest, and the lingual hypostyle the smallest. The protostyle and hypostyle are not connected until very late wear (i.e., after the other cusps are connected). The transverse valley is open lingually until wear has obliterated all of the cusps; it is open labially until very late wear. An anterior cingulum is distinct until moderate wear, connecting the protostyle to the anterolingual base of the paracone.

M2: Slightly smaller and otherwise similar to the M1, except that the protoloph is distinctly wider transversely than the metaloph. Cusps are similar to those on M1. The lophids are joined lingually after early wear, forming a distinct U-shaped occlusal outline (Figure 11.4). Both anterior and posterior cingula are distinct until moderate wear.

Dentary: The masseteric crest is high, as in other species of *Perognathus*, and the mental foramen is located below it; the average diastemal length (between the incisor and p4) is 2.73 mm (N=6); average mandibular depth below the p4 on the labial side is 2.70 mm (N=7); average alveolar length, p4-m3, is 3.90 mm (N=4).

p4: Four well-developed cusps are present, two on the protolophid and two on the metalophid; accessory cuspules are absent. Labial cusps (protostylid and hypoconid) are closer than the lingual cusps (metaconid and entoconid), making an asymmetrical occlusal outline. The metalophid is slightly wider transversely than the protolophid. The transverse valley is slightly wider and deeper on the lingual side of the tooth. The two lophids lack a median ridge, with the exception of UALP 23028 and UALP 23030 (both from UALP loc. 9504) with a narrow ridge joining the protoconid and hypoconid. Union of the protolophid and metalophid occurs in moderate to late wear, joining initially on the labial side, followed (soon after) by union on the lingual side.

m1: Occlusal outline is subquadrate, with two subequal lophids, each with three cusps. The metalophid is angular, reflecting strong flexure of the anterior cingulum near the anterolabial corner of the tooth; the hypolophid is straight, gently rounded

posteriorly. The protoconid and hypoconid are larger than the metaconid and ectoconid, the hypostylid is smaller than the protostylid. Lophids are united medially during late wear, forming an H-shaped enamel pattern on well-worn specimens. The transverse valley is moderately deep, slightly deeper on the lingual side, and open labially and lingually. A low posterior cingulum is distinct on 3 of 17 specimens (18%), connecting the metaconid and hypostylid (Figure 12.2). UALP 23030 has a subrectangular occlusal outline, with the protostylid located more posteriorly than in other m1s. Other features of this tooth, however, are inseparable from those assigned to *P. mclaughlini*.

m2: This tooth is subrectangular in occlusal outline, transversely wider than long, with the metalophid slightly wider than the hypolophid due to reduction of the hypostylid. Cusps are similar to those on m1. The transverse valley is open on both sides, deeper on the lingual side, and lophids unite medially as in m1.

m3: Size is similar to the p4; the protostylid is much reduced, and the hypostylid is absent. The metalophid is distinctly wider than the hypolophid, and the lophids are closely appressed, slightly tighter on the lingual side. The lophids are not united on any of the available specimens although they would unite medially with greater wear. The anterior cingulum is much reduced, weakly joining the protostylid and the protoconid. The transverse valley is open on both sides.

Discussion. The p4 is the most diagnostic tooth of this small perognathine, with asymmetrical occlusal outline, absence of cuspules, and labial initial union of the lophids. The p4 is asymmetrical in four small fossil perognathines: *P. mclaughlini*, *P. henryredfieldi*, *P. rexroadensis*, and *P. pearlettensis*.

P. henryredfieldi in late Hemphillian of Arizona (Jacobs 1977) is significantly smaller than the Panaca perognathine, and the roots of p4 are fused proximally in *P. henryfieldi* which distinguishes it from the Panaca perognathine. *P. pearlettensis* is a small species (alveolar length of p4-m3 is only 3.1 mm; Hibbard 1941a), although range of some teeth overlap those of *P. mclaughlini*; also, accessory cuspules may be present on p4 of *P. pearlettensis*. As noted by Jacobs (1977), initial union of lophids on p4 of *P. pearlettensis* is central rather than labial as in *P. mclaughlini*. *P. rexroadensis* is rather similar in morphology to *P. mclaughlini*, although "*P. rexroadensis* is larger and the m3 possesses a larger pos-

terior loph for the size of the tooth than in the m3 of *P. mclaughlini*." (Hibbard 1950). The Panaca small perognathine is closer in size to *P. mclaughlini* than to *P. rexroadensis*, and the occlusal pattern of the Panaca small perognathine m3 is more like that of *P. mclaughlini*. It is therefore assigned to *P. mclaughlini*.

Some other fossil species of *Perognathus* (e.g., *P. gidleyi*, *P. stevei*, *P. dunklei*, and *P. furlongi*) are similar in size to *P. mclaughlini*, but they all have p4s that are bilaterally symmetrical, and the initial union of p4 lophids is medial. In addition, *P. gidleyi* has lingual fusion of lophs in M1 and M2 (Tomida 1987); *P. stevei* normally has an anteroconid on p4 and frequently has a hypostylid on its p4 metalophid (Martin 1984); *P. maldei* has better development of an H-pattern on its lower molars (Zakrzewski 1969); and *P. furlongi* is more brachydont with strong inflation of the lower part of the crown, and the M1 transverse valley is open lingually until very late wear (Wood 1935; Lindsay 1972). The features above distinguish *P. mclaughlini* from similar size species of *Perognathus*.

Martin et al. (2002) reviewed the features of small perognathine rodents, similar to *P. mclaughlini*, in their identification of a small perognathine from the Deer Park assemblages in Kansas. They assigned the Deer Park B perognathine to *P. cf. gidleyi*, based partly on central union of the p4 lophids although their sample included only one moderately worn p4 with the metalophid much narrower than the hypolophid. In general, small perognathine rodents are very difficult to identify and with better samples these fossil species will likely be identified more securely. Until then, identifications of small samples are often based on features that might be considered individual variation, such as central or medial union of p4 lophids. In comparison with *P. mclaughlini* from its type locality (Saw Rock Canyon local fauna, Kansas), specimens of *P. mclaughlini* from Panaca have a shorter transverse width on the lower molars, and m1 is more quadrate in occlusal outline in the Panaca specimens. These differences are considered to result from intraspecific variation, because the other dental features are so similar.

Range. Late Hemphillian and early Blancan NALMAs.

Occurrence. UALP locality 8197 in the Limestone Corner section, UALP locs. 9504, 9601, and 9602 in the Rodent Hill section, UALP locs. 9619 and 9702 in the Rodent Ravine section, and UALP locality 9620 in the Brown Bone Bed section of the

Panaca l.f., southeastern Nevada. Extended range of *Perognathus mclaughlini* includes late Hemphillian NALMA of Arizona (Redington l.f., Jacobs 1977) and Oklahoma (Buis Ranch l.f., Hibbard 1954a) and early Blancan NALMA of Kansas (Saw Rock Canyon l.f., Hibbard 1949)

Oregonomys Martin, 1984

Oregonomys sp.

Figure 11.5

Material examined. UALP loc. 9504: 23064, left P4.

Description. A large, relatively worn, brachylophodont upper premolar with protoloph elongated transversely is assigned to this genus. The protoloph is oriented obliquely relative to the metaloph, with the labial side of the protoloph placed more anteriorly than the lingual side. The metaloph has three cusps (a large medial hypocone, a labial metacone, and minute lingual hypostyle), and with the hypostyle oriented anteroposteriorly and placed slightly anterior relative to the hypocone. The transverse valley is deeper labially, partly closed lingually by the hypostyle. The posterior cingulum is well rounded, joining the hypostyle, the posterior hypocone and the metacone. Three large roots are present, fused at their bases.

Discussion. The transverse elongation of the protoloph suggests that an accessory cuspule may have been present initially, erased by early wear. The size and suspected multicusped protoloph characterize this P4 as a species of *Oregonomys*. Three species (*O. pebblespringensis*, *O. sargenti*, and *O. magnus*) of *Oregonomys* are known. The Panaca specimen is excluded from *O. sargenti* whose hypostyle is not placed anteriorly, and whose union of lophs is more medial than in the Panaca P4. Size of the P4 places it in the range of measurements (see Martin 1984, tables 10 and 12) for both *O. pebblespringensis* (larger) and *O. magnus* (smaller). Occlusal pattern of the Panaca P4 is very close to that of *O. magnus*, although the P4 pattern of *O. pebblespringensis* is also possible. More specimens are needed to clarify species identification.

Range. Late Hemphillian to middle Blancan NALMAs.

Occurrence. UALP locality 9504 in the Rodent Hill section, Panaca l.f., southeastern Nevada. Extended range of *Oregonomys* includes fauna from the Dalles Formation near Arlington and McKay Reservoir in northern Oregon (Martin

1984), and the Hagerman local fauna of Idaho (Zakrzewski 1969).

?*Cupidinimus* sp. Wood, 1935
Figures 12.4-12.5

Materials examined. UALP locality. 9502: 21561, left p4; 21564, left M1. UALP locality 9504: 23270, right m1.

Description. Cheek teeth are mesodont, with steep crowns and deep roots. The M1 is moderately worn with cusps obliterated on the loph; the protoloph is slightly wider transversely and straighter than the metaloph. The lophs are joined lingually by apparent fusion of the protostyle and hypostyle; the base of the protoloph is slightly lower than the base of the metaloph. The transverse valley is moderately wide and deep on the labial side. A low but broad dentine tract is present on the lingual side of the tooth.

The p4 (Figure 12.4) is only slightly worn, with five distinct cusps (protoconid and protostylid on the protolophid; metaconid, hypoconid, and hypostylid on the metalophid). The protoconid and protostylid are more robust than the transversely elongate metaconid and the hypostylid; the hypoconid is smaller and medial on the metalophid. The m1 (Figure 12.5) is high crowned with a subrectangular occlusal outline, wider than long; width of the metalophid and hypolophid are subequal, each with the remnant of three cusps. The metalophid is elongated anteroposteriorly on the labial side, reflecting a well-developed anterior cingulum that would join the protostylid and the metaconid in unworn teeth. Union of the lophids occurs medially initially, in late wear, then labially; height of the labial reentrant above the base of the crown is 0.60 mm, the ratio of this height to the transverse width is 0.42, within the range of this character in *Cupidinimus* (0.36 to 0.67, Barnosky 1986). There is no dentine tract on the sides of the tooth; base of the metalophid is markedly higher than the base of the hypolophid. There are two well-developed transversely-elongated roots.

Discussion. These teeth are very similar to *Prodipodomys* from the Panaca Fm. based on the occlusal outline; however, these teeth are distinctly lower crowned, and the transverse valleys extend transversely wider, across the tooth, compared to the teeth of *Prodipodomys*. *Cupidinimus* is known primarily from faunas older than Blancan NALMA.

Occurrence. UALP locality 9502 in the Double Butte section, and UALP locality 9504 in the Rodent Hill section of the Panaca l.f., southeastern Nevada.

Subfamily DIPODOMYINAE Coues, 1875

Prodipodomys Hibbard, 1939

The classification of Korth (1994) for the Subfamily Dipodomysinae is followed except that *Dipodomys minor* Gidley 1922 is recognized here as *Prodipodomys minor*.

There has been confusion among taxonomists for a number of years regarding the distinction between *Dipodomys*, the modern kangaroo rat, and its presumed ancestor, *Prodipodomys*. Gidley (1922) erected the fossil species *Dipodomys minor* on the basis of a mandibular fragment with p4 and the alveoli of m1-m3 from the Benson local fauna of Arizona. Gazin (1942) later removed *D. minor* from *Dipodomys* and established for it a new genus, *Prodipodomys*, mainly on the basis of alveoli for two well-developed roots of m1 in the holotype specimen; Gazin interpreted *Prodipodomys* as the primitive rooted ancestor of derived and rootless *Dipodomys*. This opinion was followed by Hibbard (1953), who noted that premolars of *Dipodomys* were often rooted in adult animals with late tooth wear, and later (Hibbard 1954b) that some extant species of kangaroo rat also have rooted molars late in life. The distinction between *Dipodomys* and its ancestor *Prodipodomys* was clarified by Zakrzewski (1981), who emended the diagnosis of both fossil genera based on crown height rather than root loss. Zakrzewski (1981) pointed out that roots of *Dipodomys* are generally a tubular continuum of the crown; primitive species may possess more than one root but they are generally fused into a single columnar root, also in primitive species the p4 is two rooted, and the P4 is 3-rooted. Of greater significance, Zakrzewski (1981) pointed out the crown height of teeth in adults of *Dipodomys* generally exceeded the length of the root, whereas the crown height in adults of *Prodipodomys* is approximately the same as the root length. Also, dentine tracts are well-developed, and the anterocone of P4 is lost in early wear of *Dipodomys*, whereas dentine tracts are absent or poorly developed, and a distinct anterocone is generally present on P4 of *Prodipodomys*.

Characteristics of *P. minor* were never securely established because the taxon was based on a single specimen that lacked features of crown height and root length. A large sample of *P. minor* from the Panaca l.f. provides better characterization for the species. Following Zakrzewski's (1981) criteria for differentiation of *Prodipodomys* and *Dipodomys*, I conclude that it is appropriate to assign the sample of this taxon from the Panaca Fm. to *Prodipodomys*, as *P. minor*. The reasons

TABLE 5. Measurements (in mm) of cheek teeth of *Prodipodomys minor* from the early Blancan Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		N	M	Length			N	M	Width		
				SD	CV	OR			SD	CV	OR
9504	P4	3	1.08	0.069	6.42	1.00-1.12	4	1.33	0.100	7.52	1.20-1.44
	M1	8	0.88	0.070	7.89	0.76-0.96	9	1.38	0.075	5.44	1.24-1.48
	M2	5	0.74	0.046	6.13	0.68-0.80	5	1.14	0.035	3.04	1.12-1.14
	M3	8	0.80	0.058	7.20	0.72-0.88	8	0.99	0.093	9.35	0.84-1.12
	p4	2	1.08	0.00	0.000	1.08-1.08	2	1.20	0.00	0.00	1.20-1.20
	m1	7	0.93	0.030	3.25	0.88-0.96	7	1.29	0.049	3.78	1.24-1.36
	m2	8	0.83	0.028	3.41	0.80-0.88	8	1.23	0.077	6.28	1.08-1.28
	m3	2	0.60	----	----	0.56-0.64	2	0.88	----	----	0.88-0.88
	9601	M1	1	0.84	----	----	----	1	1.40	----	----
	M3	2	0.82	----	----	0.80-0.84	2	0.90	----	----	0.88-0.92
	m1	0	----	----	----	----	1	1.36	----	----	----
	m2	2	0.80	----	----	0.80-0.80	1	1.28	----	----	----
9602	M3	1	0.80	----	----	----	1	1.00	----	----	----
	m1	2	0.86	----	----	0.84-0.88	2	1.28	----	----	1.28-1.28
	m2	3	0.79	0.023	2.94	0.76-0.80	3	1.23	0.023	1.88	1.20-1.24
9702	P4	2	0.88	----	----	0.88-0.88	2	1.28	----	----	1.28-1.28
	M1	1	0.84	----	----	----	1	1.32	----	----	----
	M3	1	0.72	----	----	----	1	0.92	----	----	----
	p4	3	0.81	0.023	2.84	0.80-0.84	3	1.07	0.061	5.73	1.00-1.12
	m1	2	1.00	----	----	1.00-1.00	2	1.46	----	----	1.44-1.48
	m2	1	0.88	----	----	----	1	1.20	----	----	----
	m3	1	0.56	----	----	----	1	0.84	----	----	----
8197	P4	2	1.06	----	----	1.00-1.12	2	1.40	----	----	1.36-1.44
	M1	3	0.86	0.060	6.98	0.80-0.92	3	1.36	0.080	5.88	1.28-1.40
	M2	1	0.92	----	----	----	1	1.40	----	----	----
	p4	0	----	----	----	----	1	1.36	----	----	----
	m1	1	0.88	----	----	----	1	1.40	----	----	----
	m2	1	0.76	----	----	----	1	1.28	----	----	----
	m3	1	0.60	----	----	----	1	1.00	----	----	----
9502	M3	1	0.68	----	----	----	1	0.88	----	----	----
	p4	1	0.84	----	----	----	1	1.16	----	----	----
	m3	1	0.68	----	----	----	1	1.08	----	----	----

are: 1) The dentine tracts on the sides of cheek teeth are low (<1 mm); 2) The p4s and m1s have two distinct roots; 3) Crown height of these teeth is comparable to that of *P. kansensis* from the Edson Quarry fauna in Kansas (Hibbard 1937b), and much lower than that of any species of *Dipodomys*.

Height of the dentine tract on these teeth is measured relative to the base of the enamel on the labial side of the tooth. However, it should be noted that the enamel base usually has a different height on the anterior and posterior surfaces. For upper molars, the posterior enamel base is slightly higher than the anterior enamel base; the opposite pattern applies for the lower molars. Since height of a dentine tract for heteromyid teeth is usually referenced to the enamel base on the side that is higher, regardless of its location on the anterior or posterior side of the tooth, I chose the higher enamel base as the reference for the base of the dentine tract. For p4, I chose the posterior enamel base because it is higher than the anterior enamel base. In contrast, height of crown is measured relative to the lower base of the enamel for P4. Worn specimens will have lower average crown height, so height of crown should be measured only on unworn or slightly worn teeth. This procedure differs from that of Zakrzewski (1970) and Tomida

(1987) who included all of the available specimens to characterize crown height in heteromyids.

Prodipodomys minor Gidley, 1922
Table 5-6; Figures 13-14

Emended diagnosis. A small heteromyid rodent with hypsolopodont and rooted cheek teeth. The P4 and M1 have three roots; M2 and M3 have a single root; p4 has two roots; m1 has one or two roots; m2 and m3 have a single root. Incipient dentine tracts occur on the sides of p4. Crown height of teeth is significantly lower than in *Dipodomys*.

Materials examined. UALP locality 8197: 21406, L maxillary with P4-M1; 21407-21408, two M1s; 21409, LM2; 21411, Lp4; 21412, Rm2; 21413, m3; 21414, RP4; 21418, Lm1; 21420, m3. **UALP locality 9502:** 21578, Rm3; 21589, Rm3. **UALP loc. 9504:** 21525, P4; 21534, M1; 21536, m2; 21538-21542, five M3s; 21551, R maxillary with P4-M2; 23100, L maxillary with P4-M2; 23101, R dentary with p4-m3; 23102-23103, two P4s; 23104, R maxillary with M1-2; 23105-23108, four isolated M1s; 23109-23111, three isolated M2s; 23112, M3; 23114-23115, two M3s; 23116, Lp4-m1; 23117, p4; 23119-23120, two m1s; 23121, m2; 23122, m1; 23123-23124, two m2s; 23125, m1; 23128, m1; 23129, m3; 23131, M3; 23133, m3; 23139, M1. **UALP loc. 9601:** 23179, M1; 23182, Lm1; 23183-

TABLE 6. Measurements of dentine tracts (in mm) of cheek teeth of *Prodipodomys* from the early Blancan Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Tooth	N	M	SD	CV	OR
<i>Prodipodomys minor:</i>					
P4	4	0.32	0.065	20.41	0.24-0.40
M1	9	0.61	0.166	27.24	0.40-0.88
M2	4	0.42	0.192	45.67	0.20-0.60
M3	11	0.05	0.067	141.93	0.00-0.20
p4	4	0.17	0.115	66.50	0.00-0.28
m1	8	0.53	0.222	41.86	0.20-0.84
m2	11	0.37	0.119	31.78	0.20-0.64
m3	3	0.00	0.000	0.00	0.00-0.00
<i>Prodipodomys tihenii:</i>					
P4	12	0.36	0.111	30.70	0.20-0.48
M1	12	0.81	0.049	6.05	0.72-0.92
M2	9	0.52	0.194	37.70	0.40-1.00
M3	3	0.27	0.456	166.87	0.00-0.80
p4	6	0.56	0.181	32.26	0.20-0.68
m1	7	0.78	0.056	7.19	0.68-0.84
m2	8	0.55	0.070	12.75	0.44-0.64
m3	10	0.13	0.150	119.32	0.00-0.32

23184, two M3s; 23186, Rm2. **UALP loc. 9602:** 23146, Rm3; 23149-23150, two m2s; 23151, m1; 23152, m2; 23168, m1. **UALP loc. 9616:** 23231, RM1; 23232, LM3. **UALP loc. 9620:** 23241, Lp4; 23242, Rm2. **UALP loc. 9621:** 23247, LM3; 23248, m3. **UALP loc. 9702:** 23191-23192, two P4s; 23193, LM1; 23194, LM3; 23195-23196, two P4s; 23197, p4; 23198, m1; 23199, Lm2; 23200, Lm3; 23222, m1.

Description. *Prodipodomys minor* is a small species within the genus; alveolar length of the maxilla is 3.92 mm; occlusal length of p4-m3 is 3.6 mm, whereas alveolar length of the dentary is 4.6 mm; diastemal length, between p4 and the incisor, is 3.2 mm; depth of the mandible below m1 is 3.00 mm; mandibular foramen is lingual to the incisor; masseteric crest is strong and high, with the mental foramen below it; lower incisor has no groove.

P4: Occlusal surface includes a narrow protoloph and a transversely wide metaloph; on unworn specimens (e.g., UALP 21414 and 23102) the protoloph has a minute accessory cuspule labial to the protocone (Figure 13.2). The metaloph has three cusps (large medial hypocone, labial metacone, and lingual hypostyle). The hypostyle is displaced anteriorly, about equidistant from the hypocone and the protocone, and remaining isolated until late wear; the hypostyle is circular on most specimens, anteroposteriorly-elongated on three specimens (UALP 21414, 23153 and 23271). The lophs are

connected medially, then lingually, after pronounced wear. A low dentine tract is present on the lingual side, measured in four specimens (Table 6). Three well-developed roots are present, united basally, separate distally.

M1: Occlusal surface is bilobed, transversely wider than long. The protoloph has three cusps (labial paracone, medial protocone, and lingual proto-style); the metaloph has three cusps (labial metacone, medial hypocone, and lingual hypostyle). The metaloph is transversely narrower than the protoloph and is inflated posteriorly at the hypocone, presenting a gently rounded posterior margin. The hypostyle joins the protostyle after early wear, producing a U-pattern in occlusal view. Dentine tracts are low, measurable on nine specimens (Table 6). Roots are short relative to the height of crown; 8 of 11 specimens have three roots broadly joined at the base, the lingual root is smaller than the posterolabial root and transversely-elongated anterolabial root; 2 of 11 specimens have two roots, with labial roots fused in UALP 23105, lingual and anterolabial roots fused in UALP 23193.

M2: Occlusal pattern as in M1, but size is significantly smaller and transverse width of the metaloph is more reduced relative to the protoloph than on M1. The hypostyle is more reduced than on M1. Lophs are joined lingually initially; in one specimen (e.g., UALP 21409) the lophs are initially united lingually, then labially, producing an enamel islet in

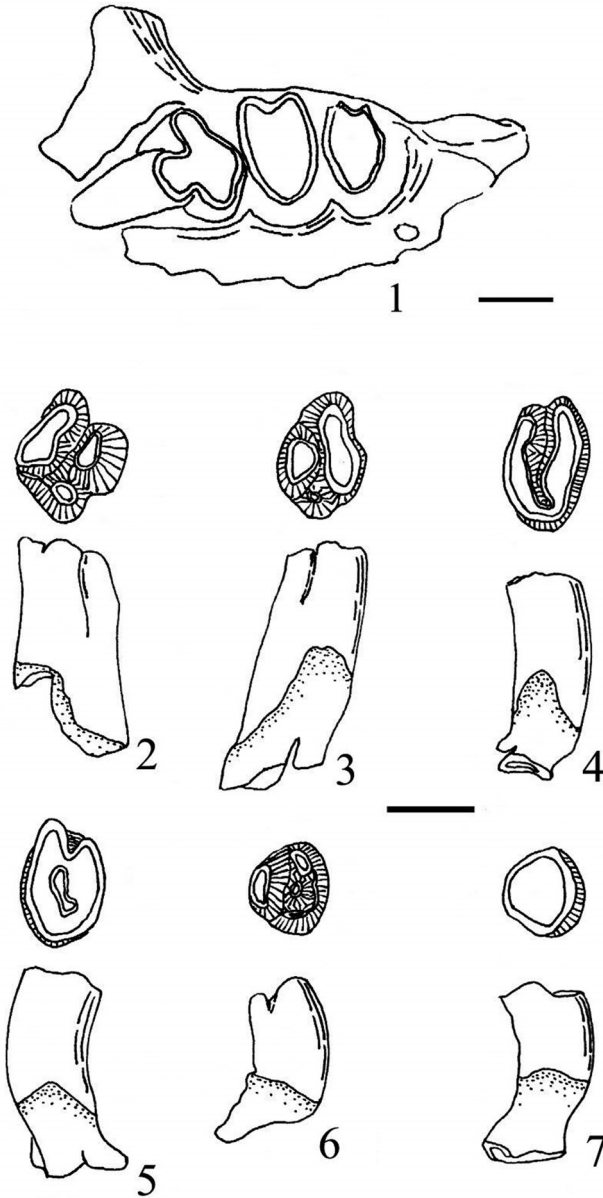


FIGURE 13. Upper cheek teeth of *Prodidipodomys minor* from the Panaca local fauna. 13.1, occlusal view of a left maxillary with P4-M2, UALP 23100. 13.2-13.3, occlusal and lingual views of P4s, UALP 23102, 23191. 13.4, a right M1, UALP 23107. 13.5, a left M2, UALP 21409. 6-7, M3s, UALP 23183, 23112. The scale bar is 1 mm.

the center (Figure 13.5). Roots are small, more fused at the base, tending toward a single root, with a shallow groove on the labial side.

M3: Size is greatly reduced, relative to M1. Occlusal pattern becomes semicircular after early wear. The metaloph is short, more inflated posteriorly, with indistinct cusps; base of the metaloph is strongly flexed posteriorly (Figures 13.6 and 14.7). The protostyle is elongated anteroposteriorly, joining the metaloph in early wear. Dentine tracts are

absent in 9 of 12 specimens. The roots are fused into a single columnar root, with a shallow groove on the posterolabial side; one very small M3 (UALP 23540: length = 0.72. width = 0.64) has a semicircular occlusal pattern with lophs joined both lingually and labially, forming a deep basin in the middle of the tooth.

p4: Occlusal pattern is bilobed, with a lingual protoconid and labial protostylid on the protolophid, and three cusps (lingual metaconid, medial hypoconid,

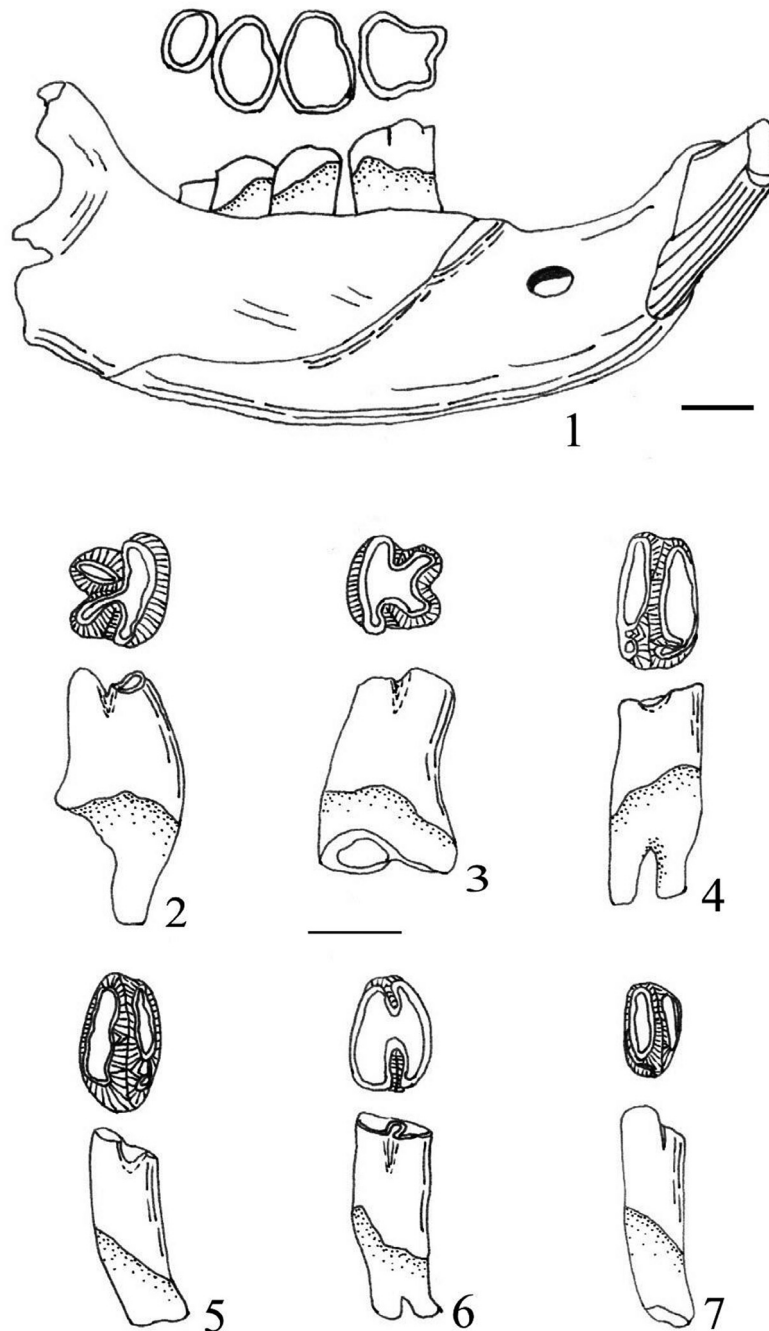


FIGURE 14. Lower cheek teeth of *Prodiplomys minor* from the Panaca local fauna. 14.1, occlusal and labial views of a right dentary with p4-m3, UALP 23101. 14.2-14.3, occlusal and labial views of p4s, UALP 23197, 23117. 14.4, a right m1, UALP 23168. 14.5-14.6, m2s, UALP 23152, 23126. 14.7, a left m3, UALP 23129. The scale bar is 1 mm.

and labial hypostylid) on the metalophid. The metalophid is transversely wider and straighter than the protolophid. The protoconid and protostylid are elongated posteromedially, and joined medially with the metalophid in early wear. A deep anterior groove on the protolophid persists until late wear.

The metaconid is the largest cusp on the metalophid, with subequal hypoconid and hypostylid. The transverse valley is wider lingually than labially, and these valleys become shallow reentrants after moderate wear, persisting almost to the base of the crown. A very low dentine tract is present on both

sides of the tooth, measurable on four specimens (Table 6). Two transversely wide roots are well developed and fused proximally at the base of the crown.

m1: The occlusal pattern is bilobed, with metalophid transversely wider and flexed relative to the more straight and narrow hypolophid. The largest cusp on the metalophid is the medial protoconid, with a smaller metaconid and a much smaller protostylid. An anterior cingulum joins the metaconid and the protostylid, passing anterior to the protoconid. The largest cusp on the hypolophid is the medial hypoconid, with a smaller entoconid and a much smaller and lower hypostylid. The lophids are united medially after moderate wear, forming an H-pattern. Dentine tracts are better developed on m1 than on other lower molars, and are usually present on the metalophid, measurable in 11 specimens (Table 6). The roots are fused proximally, separate distally, tending toward a relatively small, single, curved root; 8 of 12 specimens have a shallow groove on the labial side of the root.

m2: The m2 is smaller than m1, with a similar occlusal pattern. The protostylid and hypostylid are both more reduced than on m1, and the lophids are joined labially at a later wear stage than the lingual union of lophids. Low dentine tracts were measured on 11 specimens (Table 6). Roots are fused proximally, separated posteriorly, tending toward a relatively small, columnar, and posteriorly curved root. Eight out of 12 specimens have a shallow groove on the labial side of the root.

m3: The m3 is distinctly smaller and transversely narrower than m2. The metalophid has three cusps (metaconid, protoconid, and a much reduced protostylid). The hypolophid is lower and transversely narrower than the metalophid, it lacks a hypostylid. On unworn specimens, 2 of 3 have a low anterior cingulum, and one (UALP 21420) has a cingulum joining the protostylid and protoconid. A dentine tract is absent. Roots are fused proximally to become a long single root lacking grooves.

Discussion. Size of *Prodipodomys minor* is similar to that of *P. kansensis* and *P. griggsorum* from Kansas; it is significantly smaller than other species of *Prodipodomys* and of two fossil species of *Dipodomys* (*D. hibbardi* and *D. gidleyi*). *P. minor* is considered a derived species of *Prodipodomys* based on fusion of the roots in both upper and lower molars.

Prodipodomys kansensis from the Hemphillian Edson Quarry local fauna of Kansas (Hibbard 1937b and Zakrzewski 1970) differs from *P.*

minor in having two well-developed roots on m1 with no dentine tracts on cheek teeth, a large mandibular foramen labial to m3, and a slight groove on the lower incisor. *Prodipodomys griggsorum* is slightly higher crowned than *P. kansensis*, but is considered more primitive than other species of *Prodipodomys* because of its better developed (e.g., more primitive) roots. The M1 and M2 of *P. griggsorum* have three well-developed roots, and the m1 has two roots.

Other species of *Prodipodomys* from Blancan faunas are significantly larger than *P. minor*. In addition, *P. centralis* has better developed roots on M1 and M2; its p4 has accessory cuspules and a well-developed ridge between the two lophids (Hibbard 1941b, 1954b, and 1972). *P. tihenii* from the Borchers local fauna of Kansas (Hibbard 1943) has p4 and m1 with two roots, plus m2 and m3 are single-rooted; this is similar to roots of *P. minor*, however, dentine tracts on P4 and p4 of *P. tihenii* are slightly higher than those of *P. minor* (Zakrzewski 1970, table 1). *P. idahoensis* from the Hagerman local fauna of Idaho also has higher dentine tracts (Zakrzewski 1969, figure 5A) than *P. minor*. Unfortunately, the coefficient of variance (CV) for height of the dentine tracts is very high for most of the species of *Prodipodomys* due to the small range of height.

Range. Blancan NALMA.

Occurrence. UALP locality 8197 in the Limestone Corner section, UALP loc. 9502 in the Double Butte section, UALP locs. 9504, 9601, and 9602 in the Rodent Hill section, UALP locs. 9616 and 9702 in the Rodent Ravine section, and UALP locs. 9620 and 9621 in the Brown Bone Bed section, of the Panaca l.f., southeastern Nevada. Extended range of *P. minor* includes the Benson local fauna, San Pedro Valley, Arizona (Gidley 1922).

Prodipodomys tihenii Hibbard, 1943
Table 6-7; Figures 15-16

Materials examined. UALP locality 8197: 21276, R deciduous P4; 21415, LM1; 21416, Lm1. UALP loc. 9502: 21562, P4; 21565, LM2; 21568-21571, four isolated P4s. UALP loc. 9504: 21526, Rp4; 21527, m1; 21552, R maxillary with P4-M1; 21553, M2; 21554, L edentulous dentary; 21528, m2; 21529, m3; 21536, M2; 22912, deciduous P4; 23113, m3; 23118, deciduous p4; 23132, m3; 23134, L maxillary with P4-M1; 23135, P4; 23136, M1; 23137, M2; 23140, M3; 23141, Rp4; 23142-23144, three isolated m1s; 23145, R maxillary with P4-M2. UALP loc. 9601: 23176, LP4; 23177-23178, two M1s; 23180, M1; 23181, RM2; 23185,

TABLE 7. Measurements (in mm) of cheek teeth of *Prodipodomys tihen* from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality	N	M	Length			N	M	Width			
			SD	CV	OR			SD	CV	OR	
8197	M1	1	1.08	---	---	---	1	1.52	---	---	---
	m2	1	0.96	---	---	---	1	1.46	---	---	---
9502	P4	5	1.14	0.092	8.11	1.04-1.28	5	1.54	0.049	3.18	1.48-1.6
	m2	1	0.96	---	---	---	1	1.44	---	---	---
9504	P4	5	1.27	0.078	6.05	1.16-1.36	5	1.58	0.046	2.88	1.52-1.64
	M1	3	1.08	0.04	3.70	1.08-1.12	3	1.65	0.058	3.51	1.58-1.68
	M2	3	0.97	0.061	6.28	0.92-1.04	3	1.49	0.046	3.09	1.44-1.52
	M3	1	1.00	---	---	---	1	1.24	---	---	---
	m1	3	1.17	0.083	7.10	1.08-1.24	2	1.58	---	---	1.56-1.60
	m2	1	1.04	---	---	---	1	1.48	---	---	---
	m3	1	0.75	---	---	---	1	1.24	---	---	---
9601	P4	1	1.04	---	---	---	1	1.48	---	---	---
	M1	3	1.09	0.023	2.11	1.08-1.12	3	1.52	0.04	2.63	1.48-1.56
	M2	1	0.96	---	---	---	1	1.40	---	---	---
	m2	1	1.08	---	---	---	1	1.48	---	---	---
9602	m3	3	0.78	0.085	10.88	0.68-0.84	4	1.09	0.082	7.57	1.00-1.20
	P4	4	1.12	0.057	5.05	1.08-1.20	4	1.55	0.038	2.57	1.52-1.60
	M1	4	1.06	0.095	8.98	1.00-1.20	5	1.59	0.033	2.10	1.56-1.64
	M2	1	0.96	---	---	---	1	1.40	---	---	---
	M3	2	0.94	---	---	0.88-1.00	2	1.34	---	---	1.28-1.40
	p4	4	1.28	0.057	4.42	1.20-1.32	5	1.42	0.092	6.47	1.28-1.52
9616	m1	1	1.20	---	---	---	1	1.60	---	---	---
	m2	5	1.03	0.033	3.24	1.00-1.08	4	1.42	0.061	4.26	1.40-1.52
	m3	2	0.74	---	---	0.74-0.74	3	1.16	0.069	5.97	1.08-1.20
	P4	3	1.28	0.00	0.00	1.28-1.28	3	1.60	0.040	2.50	1.56-1.64
	M1	1	1.08	---	---	---	1	1.56	---	---	---
9620	M2	1	1.00	---	---	---	1	1.52	---	---	---
	M1	0	---	---	---	---	1	1.52	---	---	---
	M2	1	0.92	---	---	---	1	1.44	---	---	---
	p4	1	1.20	---	---	---	2	1.36	---	---	1.32-1.40
9621	m1	1	1.20	---	---	---	1	1.60	---	---	---
	M1	0	---	---	---	---	1	1.52	---	---	---
	M2	1	0.88	---	---	---	1	1.48	---	---	---
	M3	2	0.94	---	---	0.88-1.00	2	1.34	---	---	1.28-1.40
9702	p4	1	1.20	---	---	---	1	1.44	---	---	---
	m3	1	0.72	---	---	---	1	1.08	---	---	---
	P4	4	1.19	0.03	2.53	1.14-1.20	4	1.60	0.066	4.14	1.50-1.64
	M1	4	1.11	0.038	3.45	1.08-1.16	4	1.68	0.073	4.35	1.60-1.76
	M2	5	0.93	0.044	4.72	0.88-0.96	5	1.40	0.078	5.55	1.28-1.48
9703	p4	1	1.12	---	---	---	1	1.24	---	---	---
	m1	3	1.15	0.092	8.06	1.04-1.20	3	1.65	0.061	3.70	1.64-1.72
	m2	3	1.09	0.023	2.11	1.08-1.12	3	1.48	0.12	8.11	1.36-1.60

Rm2; 23187-23190, three isolated m3s. **UALP loc. 9602:** 23094, deciduous P4; 23147, m1; 23148, m2; 23153, L maxillary with P4-M2; 23154-23155, two P4s; 23156-23159, four isolated M1s; 23161-23162, two M3s; 23163-23167, five isolated p4s; 23169-23171, three isolated m1s; 23173-23175,

three isolated m3s. **UALP loc. 9616:** 23223-23225, three isolated P4s; 23226, RM1; 23227, LM2; 23228, Rp4; 23229, Rm1; 23230, Rm2. **UALP loc. 9619:** 23233, P4; 23234, m1. **UALP loc. 9620:** 23235, LM1; 23236, LM2; 23238-23239, two p4s; 23240, Rm1. **UALP loc. 9621:**

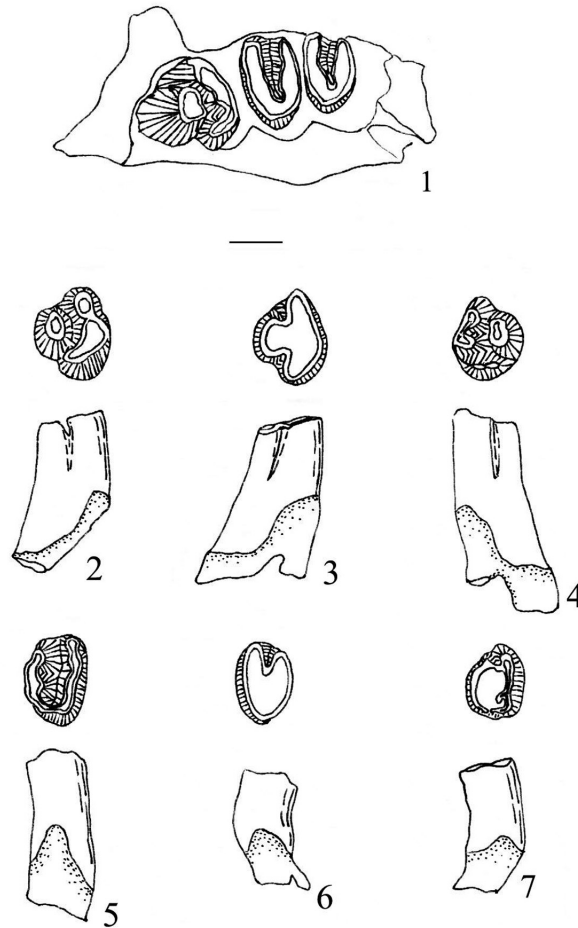


FIGURE 15. Upper cheek teeth of *Prodidipodomys tihenii* from the Panaca local fauna. 15.1, occlusal view of a left maxillary with P4-M2, UALP 23153. 15.2-15.4, occlusal and lingual views of P4s, UALP 23223, 23201, 23154. 15.5, a right M1, UALP 23157. 15.6, a left M2, UALP 23137. 15.7, a right M3, 23161. The scale bar is 1 mm.

23243, Rp4; 23244, LM1; 23245, Rp4; 23246, m3. **UALP loc. 9702:** 23201-23204, four isolated P4s; 23205-23208, four isolated M1s; 23209-23213, five isolated M2s; 23214, Rm3; 23215, Rp4; 23216-23218, three isolated m1s; 23219-23221, three isolated m2s. **UALP loc. 9703:** 23255, M3.

Description. *Prodidipodomys tihenii* is larger than *P. minor*, sharing many morphological features with that species.

dP4: Crown height is very brachydont. Two small cuspules are on the anterior cingulum with the lingual cuspule larger than the labial cuspule. The protoloph has two cusps (a labial paracone and a medial protocone); the metaloph has three cusps (a labial metacone, medial hypocone, and a lingual hypostyle that is elongated anteroposteriorly). The posterior roots are not preserved.

P4: Subtriangular occlusal pattern with a conical protoloph and transversely wider metaloph. The transverse occlusal outline of the protoloph increases lingually with wear. The protoloph and metaloph are broadly joined medially although the initial union may be slightly labial to the midline. The hypostyle is elongated anteroposteriorly, joining the protocone after moderate wear. Dentine tracts are low on the lingual side of tooth. Three roots are present, with the posterior roots fused at the base.

M1: Bilophodont occlusal pattern with the protoloph slightly wider transversely and less inflated posteriorly than the metaloph. The protoloph has three cusps (labial paracone, medial protocone, and lingual protostyle); the metaloph has three cusps (labial metacone, medial hypocone, and lingual hypostyle). The protoloph has a gently

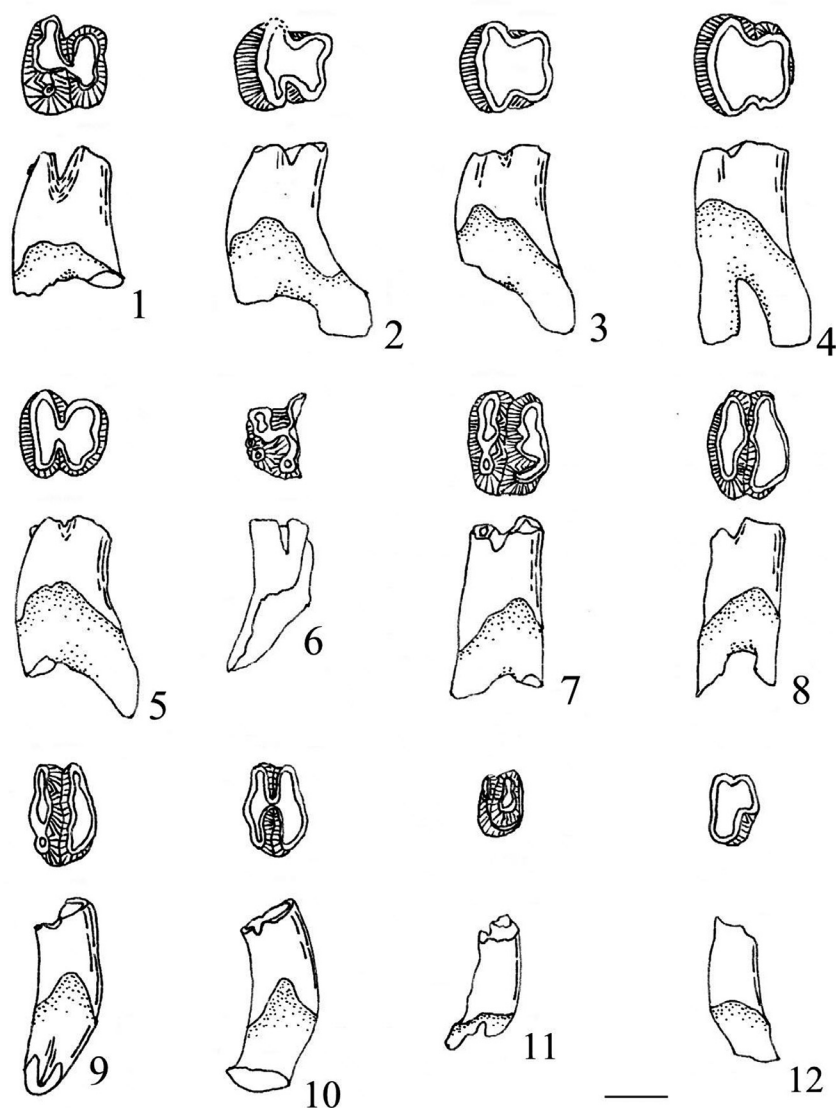


FIGURE 16. Lower cheek teeth of *Prodidipodomys tiheni* from the Panaca local fauna. 16.1-16.6, occlusal and labial views of p4s, UALP 23228, 23243, 23238, 23166, 23215, 23239. 16.7-16.8, m1s, UALP 21527, 23229. 16.9-16.10, m2s, UALP 23147, 23148. 16.11-16.12, m3s, 21420, 23132. The scale bar is 1 mm.

rounded posterior margin. Lophes are joined lingually during early wear, forming a U-shape occlusal pattern. The transverse valley is deeper lingual to the midline. Dentine tracts are low on all specimens. Three roots are well-developed, with slight fusion at the base of the lingual and anterolabial roots; the anterior root is largest, and the posterolabial root is smallest. UALP 23136 has a bifurcated lingual root.

M2: Occlusal pattern is similar to that of M1, but smaller and the transverse width of the metaloph is shorter than the protoloph width. The lophes are joined lingually in early wear, forming a U-shape

occlusal pattern. Dentine tracts are low on all specimens (Table 6). Roots are variable with 3 of 11 having three separate roots, 4 of 11 having two roots (anterolabial and lingual roots fused), 3 of 11 having V-shaped roots, and 1 of 11 having a single root with a deep labial groove.

M3: Smallest cheek tooth of upper dentition, with indistinct cusps on both lophes. The occlusal pattern is oval, becoming semicircular in late wear. The metaloph is inflated posteriorly and well rounded; the protoloph is straight, slightly wider transversely than the metaloph. Lophes are joined both lingually and labially after early wear, forming a deep

enamel islet medially (Figure 15). Dentine tracts are low on 1 of 3 specimens. Two specimens have a single root, one specimen has two roots.

dp4: Brachydont tooth with three transverse lophids in the occlusal pattern. The anterior lophid has the anterior cingulum lacking cusps; the protolophid and metalophid are joined medially after early wear, forming an H-pattern.

p4: Bilophodont occlusal pattern with the protolophid transversely narrow relative to the metalophid. The protolophid has a shallow anterior inflection between the protoconid and protostylid that is reduced with wear, and a minute accessory cuspule is present between the protoconid and protostylid in 3 of 9 specimens (UALP 21526, 23215, and 23229). The metalophid has three cusps (lingual metaconid, medial hypoconid, and small labial hypostylid). Lophids are joined medially after early wear. A broad dentine tract is low on both labial and lingual sides of the metalophid. Two transversely elongate roots are present.

m1: Bilophodont occlusal pattern with the metalophid flexed and slightly wider transversely relative to the straighter hypolophid. Three cusps occur on the metaphid (a lingual metaconid, a larger and medial protoconid, and much smaller labial protostylid). The anterior cingulum joins the metaconid and protostylid, passing anterior to the protoconid. Three cusps are present on the hypolophid (a lingual entoconid, a larger medial hypoconid, and a much smaller labial hypostylid). The lophids are joined medially after early wear, forming an H-pattern. Dentine tracts are low on both sides of the tooth. Two transversally elongated roots are present, fused at the base and separate distally.

m2: Occlusal pattern as in m1, but smaller. The protostylid and hypostylid are smaller and lower than in m1. Dentine tracts are low on both sides of the tooth. Roots are variable: 3 of 8 specimens have a single root with a labial groove, 3 of 8 specimens have a V-shaped root, and 2 of 8 specimens have a single root, lacking a groove.

m3: Smallest cheek tooth in the lower dentition. The metalophid has two indistinct cusps (lacking the protostyle) and a weak anterior cingulum; the hypolophid is shorter, lower and transversely narrower than the protolophid, lacking the hypostylid. A dentine tract is low on 4 of 10 specimens. A single root, curved posteriorly, is present.

Discussion. Cheek teeth of *Prodipodomys tihenii* from the Panaca l.f. are significantly larger and slightly higher crowned than those of *P. minor*; they

also have slightly higher dentine tracts. The P4 of *P. tihenii* has a hypostyle that is more elongated anteroposteriorly and connects with the protocone in early wear, in contrast to *P. minor* whose hypostyle is isolated until later wear. The M1 and M2 of *P. tihenii* are similar to those of *P. minor* in the development of cusps and lophids. A minute accessory cuspule occurs on the protolophid of p4 in some specimens of *P. tihenii*; this is probably a highly variable feature, but no accessory cuspules were seen on the equivalent p4 sample of *P. minor* from the Panaca l.f. Tomida (1987) reported a similar small accessory cuspule on one specimen of *Dipodomys hibbardi* from the 111 Ranch local fauna of Arizona. The m1 and m2 of *P. tihenii* are very similar to those of *P. minor* from the Panaca l.f., but dentine tracts are significantly higher on the *P. tihenii* specimens. Also, roots are better developed on m1 specimens of *P. tihenii*, in comparison to those of *P. minor*.

Prodipodomys tihenii is similar in size to *P. centralis* from the Rexroad local fauna of Kansas and *P. idahoensis* from the Hagerman local fauna of Idaho. Unworn p4s of *P. centralis* are characterized by the resemblance to p4s of the extant heteromyid *Liomys* (Hibbard 1941b). An additional difference between *P. tihenii* and *P. centralis* mentioned by Hibbard (1972) is that the former has a deeper depression dorsal and labial to the mandibular foramen. Zakrzewski (1981) noted higher dentine tracts in specimens of *P. tihenii* relative to specimens of *P. centralis* from the Borchers local fauna of Kansas. Similarly, the dentine tracts of *P. tihenii* from the Panaca l.f. are closer to those of *P. tihenii* than to *P. centralis* from The Borchers local fauna measured by Zakrzewski (1981, table 1).

P. tihenii and *Dipodomys hibbardi* have very similar occlusal patterns on P4 and p4, but the former is more primitive in its lower crown height, lower dentinal tracts, and better-developed roots. Similarity of the occlusal pattern suggests that *P. tihenii* may be close to the ancestry of *Dipodomys hibbardi*.

In the Panaca l.f., both *P. tihenii* and *P. minor* were usually found at most of the localities. Their relative abundances are similar, and there is no significant change morphologically in these samples through the stratigraphic levels.

Range. Blacan NALMA.

Occurrence. UALP locality 8917 in the Limestone Corner section, UALP localities 9504, 9602, and 9703 in the Rodent Hill section, UALP locs. 9616, 9619, and 9702 in the Rodent Ravine section, UALP locs. 9620 and 9621 in the Brown Bone Bed

section, UALP loc. 9502 in the Double Butte section, of the Panaca l.f., southeastern Nevada. Extended range of *P. tihen* includes the Borchers local fauna, Kansas (Hibbard 1941a).

SUMMARY

Both Hemphillian and Blancan mammals are recorded from the Panaca Fm.; however, the Blancan mammals greatly outnumber the Hemphillian mammals, both in number of specimens and number of taxa. All of the small mammals reported above are from sites that are interpreted to be of Blancan NALMA.

The most common small mammals from the Panaca Fm. are cricetid and heteromyid rodents, plus some of the rabbits. The cricetid rodents are excluded from this report, as they greatly exceed the number of taxa known from these deposits. They are described in a separate report by Mou (this volume). Complete faunal list of the Panaca l.f. can be seen in Lindsay et al., tables 1 and 2 (2002). The shrews, rabbits, geomyid, and heteromyid rodents of the Panaca l.f. are described in this report.

The Panaca shrews include *Paranotosorex panacaensis*, new genus and species, plus an incisor and maxillary fragment of a shrew, *?Paranotosorex* sp. that do not fit into the morphology of *P. panacaensis* and might represent another species. *Paranotosorex*, n. gen. is distinguished from the extant desert shrew *Notiosorex crawfordi*, which has a range confined to the deserts of the southwest United States and northern Mexico, based primarily on having an oval upper articulation and less offset lower articulation of the mandible. Other than *Notiosorex*, shrews (*Sorex*, *Cryptotis*, and *Blarina*) are widespread throughout North America during the late Cenozoic.

Rabbits underwent an explosive diversification during the Hemphillian and Blancan NALMAs, reflected in five species of the genus *Hypolagus* (*H. edensis*, *H. tedfordi*, *H. cf. H. ringoldensis*, *H. gidleyi*, and *H. regalis*), one species of *Pewelagus* (*P. dawsonae*), one species of *Lepoides* (*L. lepoides*), one species of *Nekrolagus* (*N. progressus*), and possibly a species of *Pronotolagus* (*?Pronotolagus* sp.) recorded from the Panaca l.f. This diversity of rabbits greatly exceeds the modern diversity of rabbits in North America, but is not unusual relative to many Blancan faunas (White 1991), although it exceeds that of the Blancan Taunton local fauna of Washington (White and Morgan 1995) and the Irvingtonian Vallecito local fauna of California (White 1984). The extinct genera *Pewel-*

agus and *Lepoides* are the most abundant rabbits in the Panaca l.f., with most of the other taxa recorded from only a handful of specimens. The record of *H. tedfordi* in the Panaca l.f. is a range extension; *H. tedfordi* is known primarily from Clarendonian and Hemphillian NALMAs.

The only gopher recorded from the Panaca l.f. is *Pliogeomys parvus*, also recorded from the Blancan Hagerman local fauna of Idaho.

Heteromyid rodents from the Panaca l.f. include a good sample of *Perognathus mclaughlini*, a small perognathine; one tooth of *Oregonomys* sp. (a P4); and three teeth of *?Cupidinimus* sp. and very good samples of two dipodomys species, *Prodipodomys* (*P. minor* and *P. tihen*). The Panaca record of *?Cupidinimus* sp. is a range extension: *Cupidinimus* is known primarily from Barstovian, and Clarendonian NALMAs.

Age of the Panaca l.f. is considered early Blancan. This is based in part on the faunal assemblage and in part on the correlation of the Panaca l.f. sequence with the interval of chrons C3n.2r through C3n.3r (Lindsay et al. 2002, figure 10) of the GPTS. The magnetic polarity sequence of the Panaca sections are placed relative to the GPTS with the Healdsburg Tephra, dated 4.69 Ma (using the 27.84 Ma monitor for the Fish Canyon sanidine interlaboratory standard), located above the fossil sites near the top of chron C3n.2n in the Rodent Hill section. Details of the magnetostratigraphy are explained in Lindsay et al. (2002). The Panaca l.f. represents one of the earliest Blancan faunas, according to the correlation of the Hemphillian-Blancan boundary near the top of chron C3n.4n, as interpreted by Lindsay et al. (2002). Stage of evolution of the small mammal assemblage, especially the arvicolid rodents, also supports a very early Blancan age (Mou 1997, 1998).

Small mammals of the Panaca l.f. are most similar to the Hemphillian Redington l.f. in Arizona (Jacobs 1977), the Hemphillian Edson l.f. in Kansas (Hibbard 1939), the Blancan Saw Rock Canyon l.f. in Kansas (Hibbard 1952 and 1964; Zakrzewski 1970), the Blancan Deer Park l.f. in Kansas (Martin et al. 2002), the Blancan Verde l.f. in Arizona (Czaplewski 1990), the 111 Ranch l.f. in Arizona (Tomida 1987), the Blancan Hagerman l.f. in Idaho (Zakrzewski 1969), and the Blancan Arroyo Seco l.f. in California (White 1984).

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