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Cricetid rodents from the Pliocene Panaca Formation, southeastern Nevada, USA

Yun Mou

ABSTRACT

Very large samples of cricetids were collected from 12 localities in the Pliocene Panaca Formation in Meadow Valley, southeastern Nevada. The most common cricetids in the Panaca small mammal fauna are *Mimomys panacaensis*, *Nevadomys* n. gen., and *Repomys*. Present also are *Peromyscus* and *Onychomys*. Enamel microstructure of molars of *M. panacaensis* and *Nevadomys* n. gen. were examined under the scanning electronic microscope. *Nevadomys* n. gen. was probably derived from North American *Paramicrotoscoptes*. The characters of these cricetids, including stage of evolution, indicate that the Panaca local fauna represents the early Blancan land mammal age.

Yun Mou, 8159 East Pima Ridge Drive, Tucson, AZ 85715. yunmou2001@yahoo.com

KEY WORDS: cricetid; arvicoline; schmelzmuster; early Blancan; NALMA

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 Stock (1921) described included *Pliohippus* sp., ?*Teleoceras* sp., and *Pliauchenia* (now considered *Hemiauchenia*), genera that were assigned generally 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 collected earlier by Stock. Later still, both small and large mammals were collected from the Panaca area by T. Galusha and R. Emry, working for the AMNH. Some of those fossils were described by May (1981), Repenning (1987), and White (1987, 1991). Mou (1997, 1998) described a new species of arvicoline rodent from the Panaca l.f., based on its enamel schmelzmuster. All of the 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

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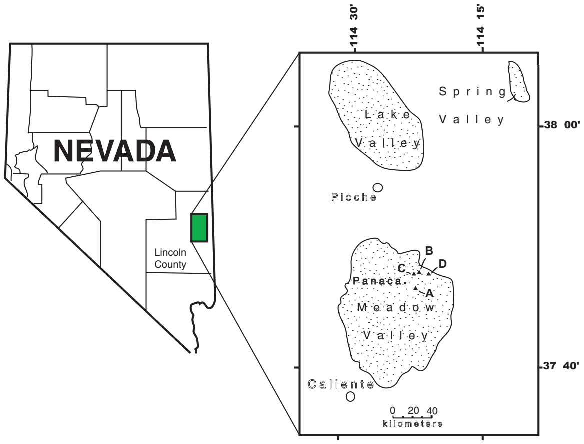

FIGURE 1. Location of the Panaca local fauna, southeastern Nevada. A= Little Hogback section, B=Limestone Corner section, C=Double Adobe Section, D=Rodent Hill section.

these deposits, and concluding that they are of Blancan NALMA.

Arvicolines are high-crowned, grass eating rodents in the cricetid family. Partly due to the nature of their diet, they exhibit gradual evolution in their dental morphology through geological time. The earliest such rodents living in North America are represented by the Hemphillian *Paramicrotoscoptes* and *Goniodontomys* (Wilson 1937; Hibbard 1959; Martin 1975; Repenning 1987). These two genera are in the Subfamily Prometheomyinae rather than Subfamily Arvicolinae (Korth 1994). The earliest true arvicoline in North America is the late Hemphillian *Promimomys minor*, considered to be an immigrant closely related to Eurasian *Promimomys cor* (Repenning 1968; Koenigswald and Martin 1984; Repenning 1987). The arvicolines became abundant during the early Blancan and have thrived since then. Because of their rapid evolution and wide distribution, they have provided an important source for ordering biochronologic events in late Tertiary terrestrial deposits in Europe and North America.

Repenning (1987, 2003) provided a thorough biochronologic review of North American arvicolines. He divided the Blancan land mammal age into five stages based on immigration events. The first appearance of *Mimomys*, represented by *Mimomys* (*Ophiomys*) *mcknighti* and *Mimomys* (*Ogmodontomys*) *sawrockensis*, is considered the beginning of Blancan land mammal age. Repenning et al. (1990) compared this biochronological framework with the mammalian biochronology of Europe.

However, the taxonomy of *Mimomys* in North America has been controversial. *Mimomys* was first recognized in Europe (Forsyth Major 1902). Since then, three subgenera and fifteen species have been found in Europe (Fejfar et al. 1990; Fejfar and Heinrich 1989). Repenning and others (Repenning 1987; Fejfar and Repenning 1992; Repenning et al. 1995) considered North American *Ophiomys*, *Cosomys*, and *Ogmodontomys* as subgenera of *Mimomys* and correlated them with faunal exchanges between Eurasia and North America, which in turn had implications relative to late Cenozoic climate changes (Repenning 1980; Repenning et al. 1995). Koenigswald and Martin (1984) and Martin et al. (2002) pointed out that *Ophiomys*, *Cosomys*, and *Ogmodontomys* have enamel microstructure that differs from that of European *Mimomys*, and thus considered that these three subgenera were endemic North American arvicoline rodents rather than immigrants from Europe.

The most diagnostic teeth of arvicolines are the first lower molar (m1) and the last upper molar (M3). However, it should be noted that there are considerable intraspecific variations in the dental morphology of these rodents, and the occlusal morphology may change markedly through wear, even on a single tooth. Therefore, a reliable identification requires a large sample, preferably including both m1s and M3s. Fortunately, abundant arvicoline rodents have been collected from the Panaca l.f. Repenning (1987) referred two specimens from the Rodent Hill locality near Panaca that were collected by the F:AM to two species: *Mimomys* (*Ophiomys*) *magilli* and *Pliopotamys meadensis*. Based on these identifications, he placed the Panaca l.f. in the middle Blancan (Repenning 1987). Further collection from another locality near Panaca by University of Arizona paleontologists yielded a large sample of arvicoline teeth. Mou (1997) could not recognize the above two species from this sample; instead, she erected a new species, *Mimomys panacaensis*, represented by this population. A combination of characters of this new species excludes it from any of the three arvicolines (e.g., *Ophiomys*, *Cosomys*, and *Ogmodontomys*). *M. panacaensis* shows a number of primitive characters, including small size, low dentine tract, and 47% of M3s with three roots. Mou (1997) suggested that the evolutionary stage of *M. panacaensis* is close to that of *M.* (*Ophiomys*) *mcknighti*, and thus it should represent early Blancan instead of middle Blancan. Mou (1998) later studied the enamel microstructure of

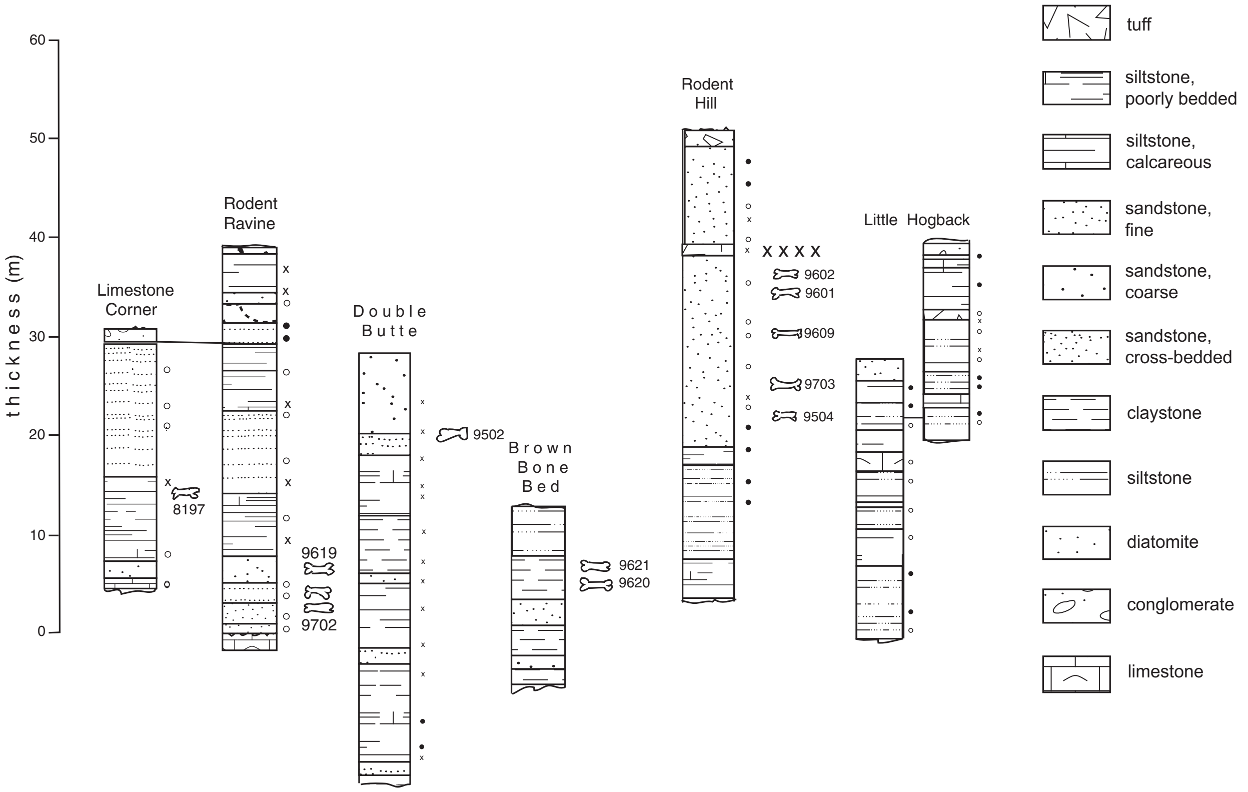

FIGURE 2. Stratigraphic section in the vicinity of Panaca that yielded vertebrate fossils (bone symbols). Sections are arranged according to the correlations in Figure7 of Lindsay et al. (2002). Note that we have not indicated any fossil site in the Little Hogback section, which is where we believe fossils 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).

M. panacaensis.and found its primitive schmelzmuster comparable to that of early European *Mimomys*, suggesting that *M. panacaensis* probably was an immigrant from Eurasia.

In later field seasons, more fossil sites were found in Panaca, and each site produced large sample of arvicoline teeth. These samples permitted a more clear and reliable identification of these rodents. In addition to *M. panacaensis*, a new genus *Nevadomys* n. gen., including three new species, is recognized from the Panaca l.f.

GEOLOGIC SETTING

All of the fossils reported herein are from the Panaca Fm., generally considered to be fine-grained basin fill 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. All of these sites have been 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). Rodent Quarry #2 of Galusha and Emry could not be correlated. Rodent Quarry #1 of Galusha and Emry correlates with locality UALP 9504, the Fejfar site. One of the 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 the author's highest small mammal site and has been identified as the Healdsburg Tephra by A. Sarna-Wojcicki of the USGS (Menlo Park). That tephra has been dated at 4.69 Ma, using the 27.84 Ma monitor for the Fish Canyon sanidine interlaboratory standard.

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), the author believes the fossils collected and reported by Stock were from stratigraphic levels below our lowest small mammal site (e.g., in magnetozone B+) in the Little Hogback section in 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. Very thorough search of the lower exposed strata in the area of the Little Hogback section did not locate any identifiable fossils or any sediment that would yield small mammals. 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 from the Panaca Fm. 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 included here in materials examined are from the UALP collection unless indicated otherwise.

Most of the identified small mammals are isolated teeth that were picked from fine or coarse concentrate after multiple washings 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. Transverse dimensions are perpendicular to anteroposterior dimensions. When applicable, the means, standard deviations and coefficients of variance were computed for each sample. Upper teeth are abbreviated with capital letters (e.g., M1), and lower teeth are abbreviated with lower case letters (e.g., m1).

Five stages of tooth wear were used: young—crown not worn, roots not yet developed; slightly worn—crown slightly worn, roots developed but short; moderately worn—crown worn down about halfway, roots long but not closed; worn—crown worn down more than halfway, roots closed; well worn—crown almost worn out, roots closed.

In this study, 24 teeth from different localities within the formation were examined for their schmelzmuster. The teeth were embedded in epoxy resin and ground with coarse and fine silicon-carbide abrasives. The grinding surface was parallel to the occlusal surface throughout the entire grinding and polishing procedure. After polishing, the exposed enamel surface was etched in 5% HCL for 15-20 seconds. All of the specimens were then coated and examined under the scanning electronic microscope (SEM).

Institutional abbreviations: 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 RODENTIA Bowdich, 1821
Family CRICETIDAE de Rochebrune, 1883
Subfamily SIGMODONTINAE Wagner, 1843
Tribe PEROMYSCINI Hershkovitz, 1966
Genus PEROMYSCUS Gloger, 1841

The terminology for the cusps and lophs follows Tomida (1987, figure16) except that the stylar cuspule associated with the anteroloph is named as the parastyle for upper molars, and the stylar cuspule associated with the anterolophid in the lower molars is named as the metastylid.

Peromyscus hagermanensis Hibbard, 1962
(Tables 1-2; Figures 3-4)

Material examined. UALP Locality 9702: left maxillary fragment with M1-M2: 23016; M1s: 23017-23020; 23023; left mandible with m1-3: 23015; m1s: 23021, 23022; m2s: 23024-23026; m3: 23027. Locality 9616: right mandible fragment with m1-m2: 22921. Locality 9619: M2: 22922; m2: 22923. Locality 8197: maxillaries with M1-M2: 21243, 21249; M1s: 21225, 21244-21248, 21250-21252; M2s: 21254, 21256-21260, 21272; m1s: 21261-21264; m2s: 21266-21271; m3s: 21273-21274. 21276. Locality 9620: right M1: 22924; right M2: 22925; left m2: 22926; m3s: 22928-22929. Locality 9621: M2s: 22930-22935; right mandible fragment with m1-2: 22936; m1s: 22937-22940; m2s: 22942-22947; m3s: 22941, 22948-22950. Locality 9504: right maxillary with M1-M3:

TABLE 1. Measurements (in mm) of molars of *Peromyscus hagermanensis* from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		Length					Width				
		N	M	SD	CV	OR	N	M	SD	CV	OR
9702	M1	3	1.69	0.014	8.59	1.52-1.78	5	1.05	0.052	4.98	1.00-1.12
	M2	1	1.10	----	----	------	1	0.94	----	----	------
	m1	4	1.50	0.126	8.42	1.40-1.68	4	0.99	0.068	6.90	0.92-1.08
	m2	3	1.23	0.061	4.98	1.16-1.28	4	0.98	0.077	7.82	0.88-1.04
	m3	1	1.04	----	----	------	1	0.88	----	------	----
9616	m1	1	1.60	----	----	------	1	0.96	----	------	----
	m2	1	1.20	----	----	------	1	0.96	----	------	----
9619	m2	1	1.20	----	----	------	1	0.96	----	------	----
9504	M1	9	1.68	0.126	7.50	1.52-1.84	9	1.01	0.084	8.36	0.88-1.12
	M2	8	1.25	0.099	7.95	1.16-1.36	8	1.00	0.066	6.60	0.92-1.08
	M3	3	0.80	0.144	18.03	0.68-0.96	3	0.82	0.125	15.23	0.72-0.96
	m1	7	1.46	0.092	6.29	1.36-1.64	7	0.95	0.079	8.35	0.88-1.12
	m2	8	1.19	0.094	7.91	1.12-1.34	8	0.95	0.067	7.04	0.84-1.04
	m3	3	0.91	0.061	6.74	0.84-0.96	3	0.75	0.061	8.18	0.68-0.80
9601	M1	2	1.64	----	----	1.56-1.72	2	1.04	----	----	0.92-1.16
	M2	1	1.38	----	----	------	1	0.96	----	----	----
	m1	7	1.57	0.063	4.02	1.48-1.64	7	1.01	0.075	7.39	0.88-1.08
	m2	4	1.33	0.050	3.78	1.28-1.40	4	1.03	0.02	1.94	1.00-1.04
	m3	2	1.02	0.085	8.32	0.96-1.08	2	0.88	0.00	0.00	------
9602	M1	13	1.75	0.068	3.89	1.64-1.88	13	1.08	0.062	5.74	0.96-1.16
	M2	5	1.36	0.063	4.65	1.28-1.36	5	1.04	0.057	5.53	0.96-1.10
	M3	2	0.80	----	----	0.76-0.84	2	0.84	----	------	0.84-0.84
	m1	8	1.57	0.106	6.79	1.42-1.72	9	1.02	0.082	8.12	0.84-1.12
	m2	11	1.33	0.038	2.88	1.24-1.36	11	1.02	0.048	4.72	0.94-1.08
	m3	3	1.10	0.035	3.15	1.08-1.14	3	0.84	0.08	9.52	0.76-0.92
8197	M1	9	1.72	0.098	5.70	1.52-1.84	11	1.01	0.062	6.15	0.92-1.12
	M2	8	1.28	0.093	7.28	1.16-1.40	8	1.03	0.049	4.76	1.00-1.12
	M1	4	1.48	0.033	2.21	1.44-1.52	5	0.94	0.46	4.87	0.88-0.96
	m2	6	1.24	0.080	6.45	1.20-1.36	6	0.97	0.067	6.84	0.88-1.06
	m3	2	0.98	----	----	0.96-1.00	3	0.80	----	------	0.76-0.84
9620	M1	1	1.64	----	----	------	1	0.96	----	----	------
	M2	1	1.16	----	----	------	1	0.92	----	----	------
	m2	1	1.16	----	----	------	1	0.96	----	----	------
	m3	2	0.96	----	----	0.92-1.00	2	0.80	0.00	0.00	0.80-0.80
9621	M2	4	1.17	0.143	12.29	1.04-1.36	6	0.98	0.038	3.88	0.92-1.00
	m1	2	1.40	0.057	4.04	1.36-1.44	4	0.88	0.033	3.71	0.84-0.92
	m2	6	1.18	0.075	6.34	1.12-1.32	6	0.93	0.073	7.92	0.84-1.04
	m3	3	0.96	0.040	4.17	0.92-1.00	3	0.79	0.058	7.28	0.76-0.86
Total	M1	37	1.72	0.134	7.83	1.52-2.08	41	1.05	0.097	9.28	0.88-1.44
	m1	33	1.52	0.098	6.44	1.36-1.72	37	0.97	0.077	7.99	0.84-1.12

TABLE 2. Frequencies of occurrence of styles (-ids) and lophs (-ids) on the first upper and lower molars of *Peromyscus hagermanensis* from the Panaca Formation. N=sample size.

Locality		N	Parastyle (-id)	Anteroloph (-id)	Mesostyle (-id)	Mesoloph (-id)
9702	M1	3	0	0	0	1 (33%)
	m1	1	0	0	1	1
8197	M1	8	7 (86%)	1 (13%)	6 (75%)	6 (75%)
	m1	1	0	0	0	1
9504	M1	3	2 (67%)	0	3 (100%)	3 (100%)
	m1	0	--	--	--	--
9601	M1	1	1	0	0	1
	m1	7	0	0	2 (29%)	1 (14%)
9602	M1	15	12 (80%)	1 (7%)	11 (73%)	12 (80%)
	m1	10	0	0	3 (30%)	0
Total	M1	40	28 (70%)	2 (5%)	25 (63%)	26 (65%)
	m1	35	0	0	5 (14%)	4 (11%)

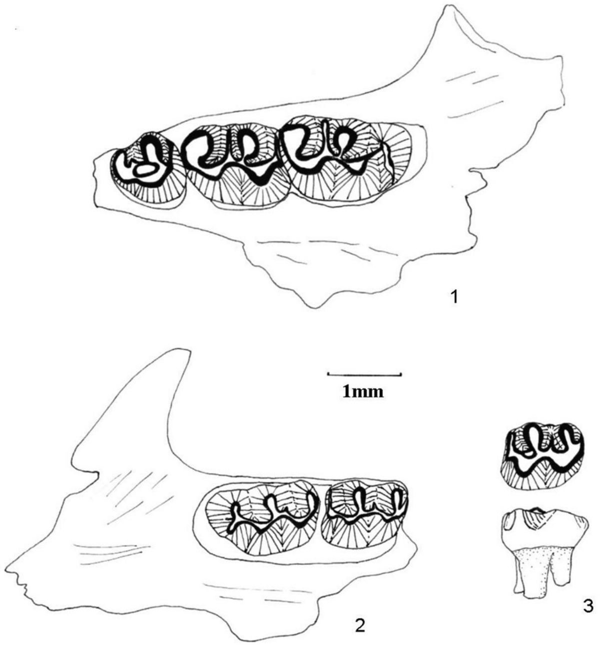

FIGURE 3. The upper molars of *Peromyscus hagermanensis* from the Panaca local fauna. 1**:** occlusal view of UALP 21550, a right maxillary fragment with M1-M3 from Locality 9504. 2**:** occlusal view of UALP 22896, a left maxillary fragment with M1-M2 from Locality 9504. 3: occlusal and lingual views of UALP 22987, a left M2 from Locality 9602.

21550; left maxillary fragment with M1-M2: 22896; right maxillary fragment with M1-2: 21556; M1s: 21547, 22897, 22898, 22916, 22917; M2s: 21546, 22899, 22908, 22910, 22918-22919; M3s: 22900, 22901; right mandible fragment with m1-3: 21557; mandible fragments with m1-2: 22905, 22913, 22914; left mandible fragment with m2-3: 22915; m1s: 22902-22904; m2s: 21548, 22907, 22909, 22920; left m3: 22911. Locality 9601: M1s: 22951-22952; right M2: 22953; m1s: 22954-22956, 22958-22961; m2s: 22962-22965; m3s: 22966-22968. Locality 9602: M1s: 22971-22985; M2s: 22986-22990; M3s: 22991-22992; right mandible fragments with m1-m2: 22969, 22970; m1s: 22993-23001; m2s: 23002-23010; m3s: 23011-23013.

Description. Cheek teeth are brachydont, with moderately high cusps in young individuals. On the maxillary, posterior margin of the incisive foramina extends to the position of the anterocone of M1. The mandibular depth below m1 of five specimens is averaged 3.07 mm, and the width of the lower incisor of six specimens is averaged 0.59 mm. The mental foramen is located on the border of the labial and dorsal surface of the dentary, anterior to the root of m1. The masseteric crest is strong, with its anterior margin located at the upper margin of the mental foramen. The alveolar length of the lower cheek teeth row of seven specimens

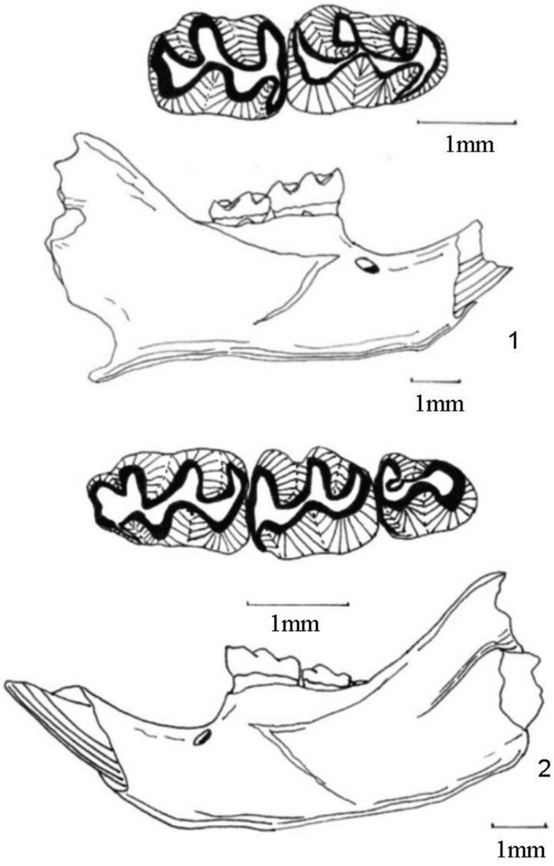

FIGURE 4. The lower molars of *Peromyscus hagermanensis* from the Panaca local fauna. 1**:** occlusal and labial views of UALP 22969, a right dentary fragment with m1-m2 from 9602. 2**:** occlusal and labial views of UALP 23015, a left dentary fragment with m1-.3 from Locality 9702.

averages 3.64 mm, and ranges from 3.45 mm to 4.10 mm.

The M1 has five distinct cusps: anterocone, protocone, hypocone, paracone, and metacone. The protocone and hypocone are located slightly anterior to the position of the paracone and metacone, respectively. The anterocone is broad, weakly bilobed, asymmetrical with a prominent labial cusp and a variably developed (small to indistinct) lingual conule. A shallow anteromedian flexus is distinct between the labial and lingual sides of the anterocone in unworn or slightly worn teeth; the flexus gets shallower with advanced wear and disappears with late wear. One specimen (UALP 22916 from Locality 9504) has a unicusped anterocone. The protocone has a long anterior arm directed toward and connecting with the anterocone and a short posterior arm directed obliquely to join the mure. The short anterior arm of the hypocone is directed toward the paracone and connects with a mesoloph and the mure. It is not in linear alignment with the paraloph. The posterior arm of hypocone joins the metaloph and continues labially as the posterior cingulum, and the posterior cingulum is distinct in unworn and moderately worn specimens but becomes indistinct in well-worn ones. The paracone and metacone are conical. Wear on lingual cusps is medial, and wear on labial cusps is posteromedial. A minute parastyle is present on 70% of M1s (Table 1), joining the paraflexus. A short anteroloph connecting the anterocone with the parastyle is present in 5% of the specimens. Sixty-three percent of M1s have a minute mesostyle, which may or may not connect with a mesoloph. Sixty-five percent of M1s present a mesoloph. One specimen from Locality 8197 (UALP 21251) has a minute protostyle. No enterostyle or enteroloph is seen on any of the M1s. Table 1 lists the frequencies of styles and lophs of M1s from each locality. Each M1 has three distinct roots (anterior, lingual, and posterior). None of the M1s developed accessory rootlets.

The M2 is smaller than M1, with four prominent cusps: protocone, hypocone, paracone, and metacone. The anterocone is lost. Instead, a broad anterior cingulum is present, joining with the long anterior arm of the protocone near or slightly lingual to the midline. The labial half of the anterior cingulum is separated from the paracone until it reaches the labial margin. The short posterior arm of the protocone joins the paraloph and central mure. The paraloph and anterior arm of the hypocone are not in alignment. A posterior arm of the hypocone is present in unworn and moderately worn specimens. The development of styles and lophs are similar to those in M1 except that four out of five M2s from Locality 9602 and two out of nine from Locality 9504 have both anterior and posterior paralophs (Figure 3.3; paralophule I and II in Lindsay 1972, figure 40). This structure is not observed in any of the M1s. Each M2 has three roots.

The M3 is well reduced relative to M1 and M2. A narrow anterior cingulum is present. The protocone and paracone are prominent, whereas the hypocone and metacone are minute or indistinct. A thin posterior cingulum is distinct on slightly worn specimens. The paracone has an anterior paraloph connecting with the anterior cingulum and a posterior paraloph that joins the posterior arm of the protocone to form a large enamel islet between the paracone and protocone. This anterior paraloph is present in all M3s. The M3s have two or three roots, with the medial and posterolabial roots fused in the teeth with two roots.

The m1 is narrow anteriorly in occlusal view. The anteroconid is broad, weakly bilobed, with the lingual conule slightly larger than the labial conule. A short anterior cingulum almost closes the protoflexid. Seven of 41 m1s (17%) have a unicuspid anteroconid, resulting in an oblique occlusal outline. The principal cusps alternate in position, with the metaconid and entoconid placed anterior to the protoconid and hypoconid, respectively. The anterior arm of the protoconid is directed anteriorly and connected to the metalophid and a short posteriorly directed anterolophid from the anteroconid slightly labial to the median plane. The long posterior arm of the protoconid is directed toward and aligned with the entolophid regardless of the wear. The metalophid and entolophid are both short and straight. The anterior arm of the hypoconid is relatively short, joining the entolophid near the midline. The posterior arm of the hypoconid is longer, directed toward the posterior midline where it joins the posterior cingulum. The posterior cingulum is prominent and relatively heavy, oriented transversely. The mesostylid is present on 14% of m1s, and a mesolophid is present on 11% of the specimens (Table 1); both are less frequent than in M1s. No metastylid is seen on the m1s. Only one specimen (22956 from Locality 9601) shows an ectostylid and a long ectolophid. Each m1 has two roots without any accessory rootlets.

The m2 has a rectangular occlusal outline. The cusps and lophids are similar to those in m1 except that the anteroconid is absent. There is a shallow but distinctive posterolabial sulcus between the hypoconid and the prominent posterior cingulum, as in m1. A mesostylid is present on 17% of the m2s (seven out of 42), and different from the other localities, Locality 9602 has 45% of m2s (five out of 11) with the mesostylid. No mesolophid is seen on any m2. Only one m2 (UALP 23010 from Locality 9602) has a distinct ectostylid, but it has no ectolophid. Each m2 has two roots.

The m3 has a prominent protoconid and metaconid, and a smaller hypoconid. The entoconid is indistinct or absent. An anterior cingulum is developed on the labial side of the tooth, anterior to the protoconid. The posterior cingulum is usually reduced, forming a thin enamel wall that joins the hypoconid and the metaconid on the lingual side of the tooth. Each m3 has two roots.

Discussion. It was noticed that a few m1s have an oblique occlusal outline and differ from the majority of m1s in this fauna. These specimens are UALP 21262 and 21265 from Locality 8197, UALP 22921 from Locality 9616, UALP 22903 from Locality 9504, UALP 22993 and 23001 from Locality 9602, and UALP 22956 from Locality 9601. Each of these teeth is narrow anteriorly with a unicuspid anteroconid. Their averaged anteroposterior length is 1.57mm, and transverse width is 0.98mm. These measurements are very close to the other m1s of *P. hagermanensis* from the fauna. They are also close to the 14 specimens of *Peromyscus hagermanensis* from the Duncan and 111 Ranch local faunas of Arizona, which have an average length of 1.58 mm and width of 0.99mm (Tomida 1987, table 20). One-third of the m1s from the 111 Ranch l.f. also have a unicuspid anteroconid. Therefore, the seven specimens from the Panaca l.f. mentioned above are here assigned to *P. hagermanensis*. *Reithrodontomys*, another brachydont cricetid, often has a unicuspid anteroconid on m1; however, members of this genus are distinctly smaller in size.

Lindsay (1972) found that the differential character of living *Peromyscus* from *Copemys* is the alignment of the paraloph-anterior arm of hypocone in the M1-M2 and entolophid-posterior arm of protoconid in the m1-m2 in *Peromyscus*. In the M1s and M2s of *P. hagermanensis* from the Panaca fauna, the paraloph and anterior arm of hypocone are apparently offset. However, this alignment does occur in the m1s and m2s. After checking the upper molars of *P. hagermanensis* from the type locality (UMMP 52739, Zakrzewski 1969) and from the Duncan and 111 Ranch faunas in Arizona (Tomida 1987), the author found that the nonalignment in upper molars is quite common in those samples. The modern species *Peromyscus eremicus* also has non-alignment of the lophs (Lindsay, personal commun., 1999). Therefore, the only character that consistently differentiates *Peromyscus* from *Copemys* is the alignment of entolophid-posterior arm of protoconid in the lower molars of the former. The alignment in lower molars and nonalignment in upper molars are also seen in two species of *Copemys*: *C. valensis* (Shotwell 1967) and *C. vasquezi* (Jacobs 1977). Korth (1994) considered them ?*Copemys* as they could be justifiably included in *Peromyscus*. As Tomida (1987) suggested, *P. hagermanensis* is closer to *Copemys* in this feature than the other species of *Peromyscus*.

Brachydont cricetids have very similar dental morphology. Tomida (1987) gave some characters to distinguish *Onychomys*, *Peromyscus*, *Calomys*

(*Bensonomys*), *Reithrodontomys*, and *Baiomys*. *Peromyscus hagermanensis* from the Panaca fauna can be differentiated from *Onychomys* by its smaller size and narrower reentrant valleys; from *Calomys* (*Bensonomys*) by its weakly bilobed anterocone, shallower anteromedian flexus, higher and steeper cusps, and lack of accessory rootlets; from *Reithrodontomys* by its larger size, and from *Baiomys* by its larger size, wider lower incisor, and weakly bilobed anterocone.

The Hemphillian *Peromyscus antiquus* has a significantly larger size compared to *P. hagermanensis*. *P. kansasensis* (Hibbard 1941) from the Blancan Rexroad fauna has a similar size, but it lacks accessory styles or lophs. *P. sawrockensis* (Hibbard 1964) from the Sawrock Canyon l.f. is larger and lacks accessory styles or lophs. *P. baumgartneri* from the Rexroad l.f. (Hibbard 1954) and *P. cragini* from the Cudahy l.f. (Hibbard 1944) are smaller and either lack styles or retain minute vestiges of them. *P. nosher* from the early Blancan White Bluffs (Gustafson 1978) l.f. has a distinctly bilobed anteroconid on m1, and a broad and smooth connection between the posterior cingulum and the hypoconid of m2. Dalquest (1978) erected a new species, *P. beckensis*, for the brachydont cricetids from the early Blancan Beck Ranch l.f. and gave the diagnosis of this species as “having m1 slender, narrowed anteriorly, m3 unreduced, mental foramen dorsal, and dentition brachydont.” Only the dorsally located mental foramen can distinguish *P. beckensis* from the other species of *Peromyscus*.

The M3s from the Panaca fauna are slightly larger than those from the Duncan and 111 Ranch faunas. No M3 of *P. hagermanensis* has been found at its type locality.

It should be noted that there are some slight differences in *Peromyscus hagermanensis* among the Panaca localities. Four M1s from Locality 9702 have no styles or lophs. Three of them are well worn, and the less worn specimen shows a distinctively bilobed anterocone with a shallow but very wide anteromedian flexus. This character is not seen in the other M1s. Four out of five M2s (18%) from Locality 9602 have two paralophs, whereas the majority of M2s from the other localities only has a posterior paraloph. Since the other molars from these two localities are very similar to those of *P. hagermanensis*, I consider these abnormalities of M1s from Locality 9702 and M2s from Locality 9602 to be intraspecific variations.

Occurrence. Rodent Ravine section: 9702, 9616, 9619; Limestone Corner section: 8197; Brown Bone Beds: 9620, 9621; Rodent Hill section: 9504, 9601, 9602, in the Fm., southeast Nevada; Duncan and 111 Ranch local faunas, Gila Conglomerate, southern Arizona; Hagerman l.f., Glenns Ferry Formation, Idaho.

Range. Blancan.

Genus ONYCHOMYS Baird, 1858
Onychomys spp.
(Table 3; Figure 5)

Material examined*.* UALP **Locality 9504:** a left maxillary with M1-M3, 22895.left m1: 22906. **Locality 9601:** right m1: 22957. **Locality 8197:** left M1: 21253. **Locality 9620:** right m2: 22927.

Description. The maxillary from Locality 9504 is moderately worn. Posterior margin of the incisive foramina extends to approximately the anterior margin of M1. The anterocone is asymmetrical with a prominent labial conule. Presence of a lingual conule cannot be determined due to the wear. Labial cusps are located across from the posterior side of lingual cusps. Three molars do not have any styles or lophs. Both M1 and M2 are distinctively larger than those of *Peromyscus hagermanensis* (Table 3) and have wider reentrant valleys; however, the M3 is the same size as that of *P. hagermanensis*. M2 and M3 have a long labial anterior cingulum.

The isolated M1 from Locality 8197 is broken at the posterior cingulum, but its overall size is comparable to the M1 of the maxillary from Locality 9504. This tooth is unworn, with a broad, slightly asymmetrically bilobed anterocone. The lingual conule is slightly lower than the labial conule. The cusps are high and steep. It has a minute parastyle. There is no mesoloph. The reentrant valleys are wide. The mure is longer and higher than that of *P. hagermanensis.*

The two isolated m1s from Locality 9504 and 9601 are larger and more robust than most m1s of *P. hagermanensis* (Table 3). The anteroconid is short, narrow, symmetrical, and unicuspid. The anteroconid is slightly smaller than the more prominent alternating cusps. The protoflexid is slightly closed due to a low anterior cingulum. The posterior cingulum is relatively short, terminating before reaching the posterior lingual corner of the tooth. Both specimens have wide reentrant valleys, high and steep cusps, and high mures. They do not have any stylids or lophids.

The m2 from Locality 9620 is larger than the m2s of *P. hagermanensis*. The cusps are alternating but not as strongly as in *P. hagermanensis*; the mure is relatively long, and the reentrant valleys

TABLE 3. Measurements (in mm) of molars of *Onychomys* from the Panaca local fauna.

Locality	Specimen		Length	Width
9504	22895	LM1-M3	4.40	
		M1	2.08	1.44
		M2	1.36	1.28
		M3	0.92	0.92
8197	21253	M1	--	1.28
9504	22906	m1	1.64	1.12
9601	22957	m1	--	1.08
9620	22927	m2	1.44	1.12

are wide. The short posterior cingulum resembles a small lingual posteroconid. It has no stylids or lophids.

Discussion. These specimens are referred to the genus *Onychomys* because of their larger sizes, steeper cusps, near absence of accessory styles and lophs, and wider reentrant valleys compared to *Peromyscus*.

There are two recent grasshopper mouse groups in North America, *O. leucogaster* and *O. torridus*, one larger than the other. The earliest known species of *Onychomys* is *O. martini* from the late Hemphillian Edson Quarry of Kansas (Hibbard 1937). The early Blancan species are *O. gidleyi* Hibbard 1941 and *O. larrabeei* Hibbard 1953. Hibbard (1953) named *O. larrabeei* from the Sawrock Canyon l.f. of Kansas based on the sizes of molars; however, Carleton and Eshelman (1979) found that the size of *O. larrabeei* fell within the range of *O. gidleyi*, and therefore, they considered *O. larrabeei* as the junior synonym of *O. gidleyi*. The diagnostic characters on the species of *Onychomys* are focused on the lower jaws, especially the reduction of m3 and the development of capsular process on the dentary.

Compared to the type specimen of *O. martini* (KU 3850, a right maxillary with M2-M3), UALP 22895 is very similar to it in occlusal view and size. The two m1s from the Panaca fauna are smaller than those of *O. gidleyi* or *O. larrabeei* but well within the range of smaller species *O. hollisteri* Carleton and Eshelman 1979 and *O. bensoni* Gidley 1922. On the other hand, the m2 from Locality 9620 is close to the m2s of *O. gidleyi* in size (Table 3). Carleton and Eshelman (1979) considered that *O. gidleyi* and *O. pedroensis* Gidley 1922 were in the same lineage giving rise to the recent species *O. leucogaster*. The size of the maxillary from Locality 9504 is very similar to those of *O. pedroensis* from the 111 Ranch l.f. of southern Arizona (Tomida 1987). Therefore, there could have been two groups of *Onychomys* living in Panaca at the early Blancan. The larger specimens may represent a species in the group of *O. martini*, *O. gidleyi*, and *O. pedroensis*, whereas the smaller one could be close to *O. hollisteri* or *O. bensoni*.

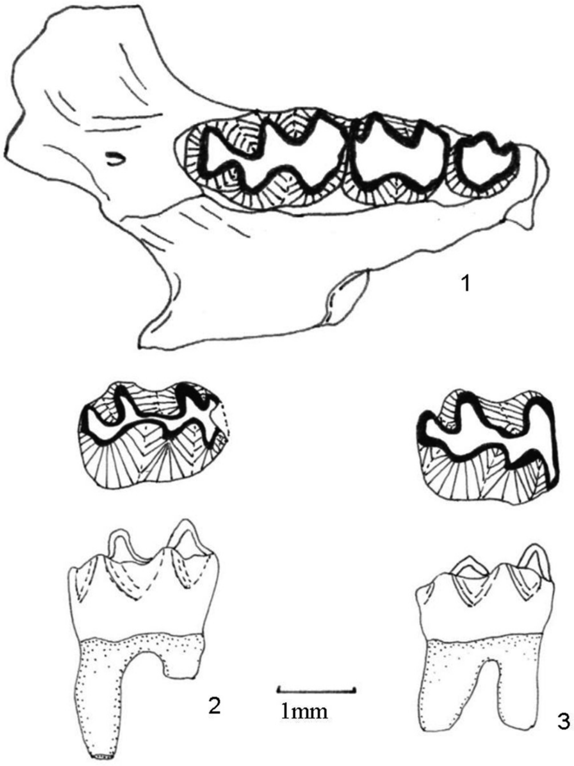

FIGURE 5. *Onychomys* from the Panaca local fauna. 1**:** occlusal view of a left maxillary fragment with M1-M3, UALP 22895 from Locality 9504. 2**:** occlusal and labial views of UALP 22957, a right m1 from Locality 9601. 3**:** occlusal and labial views of UALP 22927, a left m2 from Locality 9620.

Occurrence. Rodent Hill section: 9504, 9601, Limestone Corner section: 8197, and Brown Bone Beds: 9620, in the Fm., southeast Nevada.

Range. Early Blancan to Recent.

Tribe Neomyini Merriam, 1894
Genus REPOMYS May, 1981

Emended diagnosis. Neomyine with slender, high-crowned but rooted cheek teeth, having relatively thick enamel. There is no enamel islet on M1 or M2. M3 has two labial reentrants in an "E" shape when unworn or slightly worn, a single anterolabial reentrant in an "F" shape when moderately worn, or no reentrant but an anterior enamel islet when worn. Posterior enamel islet present or absent on M3. Keyhole-shaped m3 with an anterolingual reentrant and a short anterolabial cingulum that are lost with wear; anterior enamel islet present or absent on m3.

Discussion. The most diagnostic teeth of *Repomys* are the M3 and m3. However, when May (1981) named *R. panacaensis*, only eight specimens were available, and those were all moderately worn to well-worn teeth. No M3 was found at that time. We have found that *Repomys* is actually one of the most abundant small mammals from the Panaca l.f. With more complete specimens and much larger samples, the emendation of the diagnosis of this genus is necessary.

In the following description, the terminology of cheek teeth follows Tomida (1987) as shown in Figure 6. Since the occlusal view changes considerably at different level of wear, the degrees of wear are used for description as follows: unworn—no wear and roots not yet developed; slightly worn—wear is less than one-third of original crown, and roots are starting to develop but very short; moderately worn—crown is about one-third to half of original height, and roots are open; worn—crown is lower than half of original height, and roots are closed.

Repomys panacaensis May, 1981
(Tables 4-6; Figures 7-8)

Emended diagnosis. Size smaller than *R. gustelyi* and *R. maxumi*, close to *R. arizonensis*. the metaconid is close to the anteroconid on m1, and the anterolingual reentrant (entoflexid) is shallow. M3 has two labial reentrants at unworn or slightly worn stages, with a single anterior reentrant (paraflexus) or with an anterior enamel islet at moderately worn stage. Reentrants and enamel islet on M3 lost with advanced wear. m3 has anterolingual reentrant present at unworn or slightly worn stage, an anterior enamel islet present at slightly or moderately worn stage and lost with advanced wear.

Material examined. UALP **Locality 8197:** M2s: 21182-21184; M3s: 21185-21188; 21190, 21191; right mandible with m1-m2: 21160; m1s: 21201-21203; m2s: 21205, 21211, 21212; m3s: 21213, 21217, 21425. **Locality 9502:** M1: 21400. **Locality 9504:** partial skulls with two incisors and two complete dentitions: 21658; SBDM 1; a partial skull with two incisors and left M1-M3: 21657; maxillaries with M1-M3: 21372, 21724; maxillaries with M1-M2: 21371, 21373, 22510, 21659-21663; maxillary with M2 and alveolus of M1: 21726; M1s: 21666-21668, 21670, 21727-21730; M2s: 21671-21673, 21733-21739, 21386; M3s: 21388-21391, 21741-21745, 21675-21684; mandibles with m1-m3: 21370, 22509, 21700, 21701; mandibles with m1-m2: 21702-21707, 21725, 21746; mandible with m1 and m3: 21708; mandibles with m3 and alveoli of m1 and m2: 21710, 21711; m1s: 21685-21691, 21747, 21748, 21376-21379; m2s: 21692-21694, 21749-21755, 21380-21382, 21384; m3s: 21756-21759, 21695, 21697, 21761, 21393-21395. **Locality 9616:** M1s: 22552, 22553; M2s: 22554, 22555; M3s: 22556, 22557; m1: 22558; m2: 22559. **Locality 9619:** M1s: 22562-22564; M2s: 22565-22568; M3: 22572; m1: 22569; m2: 22570; m3: 22571. **Locality 9620:** M2: 22511; M3s: 22512-22515; left mandible with m2-m3: 22516; m2: 22517; m3: 22519. **Locality 9621:** M1s: 22526-22531; M2s: 22532-22534; M3s: 22535-22538; left mandible with m1-m2: 22539; m1s: 22540-22542; m2s: 22543, 22544; m3s: 22545, 22546. **Locality 9601:** right maxillary with M1-M3: 22573; left maxillary with M2-M3: 22586; M1s: 22574-22580, 22581-22585; M2s: 22587-22595; M3s: 22596-22603, 22640, 23375; right mandible with m1-m3: 22604; right mandible with m1-m2: 22615; m1s: 22605-22614; m2s: 22616-22628; m3s: 22629-22638. **Locality 9602:** left maxillary with M1-M3: 22647; right maxillary with M1-M2: 22651; M1s: 22652-22670; M2s: 22671-22691; M3s: 22692-22701, 22776; right mandible with m1-m3: 22649; left mandible with m1 and m3: 22650; left mandible with m2: 22648; m1s: 22702-22724, 22846; m2s: 22725-22748; m3s: 22749-22772, 22847. **Locality 9702:** right M1-M3: 23370; left M1-M2: 23371; M1s: 22780-22783, 22826, 22829-22830, 22832; M2s: 22784-22790; M3s: 22791-22794, 23353-23354; mandibles with m1-m3: 22795, 22796; mandibles with m1-m2: 22797-22799, 23372; left mandible with m1 and alveoli of m2-m3: 23355; m1s: 22800-22805, 23356-23357; m2s: 22807-22814, 23358; m3s: 22815-22823, 23359.

Description. UALP 21657 preserved two upper incisors in the partial skull. The incisors are strongly curved, and the anterior parts point downward, almost perpendicular to the premaxillary. The incisors are smooth and slender, with a width of 1.15 mm. The diastema between the incisor and M1 is 7.80 mm. Measured from SBDM 1, the width of two nasal bones at the widest points is 3.15 mm, and choana is 2.45 mm wide. The posterior border of the incisive foramina terminates at the anterior or medial part of M1 at a point slightly more posterior than the posterior border of the incisive foramen of *Neotoma*. The anterior palatine foramen is

TABLE 4. Measurements (in mm) of molars of *Repomys panacaensis* from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		**Length**					**Width**				
		N	M	SD	CV	OR	N	M	SD	CV	OR
9504	M1	17	2.01	0.077	3.86	1.88-2.16	17	1.22	0.085	6.99	1.08-1.34
	M2	23	1.70	0.044	2.57	1.64-1.78	23	1.21	0.090	7.41	1.12-1.36
	M3	24	0.95	0.074	7.84	0.85-1.10	24	0.90	0.083	9.30	0.90-1.04
	m1	16	2.05	0.055	2.68	2.00-2.20	16	1.13	0.053	4.70	1.00-1.20
	m2	19	1.72	0.035	2.03	1.66-1.78	19	1.14	0.100	8.71	0.96-1.34
	m3	11	1.14	0.064	5.67	1.06-1.22	11	1.00	0.053	5.26	0.92-1.10
9601	M1	11	2.02	0.092	4.54	1.84-2.16	9	1.28	0.107	8.30	1.16-1.48
	M2	11	1.78	0.049	2.73	1.72-1.88	11	1.26	0.075	5.92	1.16-1.40
	M3	10	1.02	0.071	6.99	0.88-1.12	10	1.01	0.075	7.44	0.88-1.12
	m1	7	2.03	0.119	5.84	1.92-2.20	7	1.17	0.075	6.40	1.08-1.28
	m2	11	1.76	0.055	3.13	1.68-1.84	11	1.15	0.060	5.18	1.00-1.24
	m3	8	1.16	0.087	7.51	1.00-1.28	8	1.02	0.048	4.68	0.96-1.08
9602	M1	17	1.97	0.060	3.02	1.88-2.04	17	1.26	0.099	7.81	1.12-1.44
	M2	21	1.77	0.074	4.21	1.68-1.96	14	1.28	0.095	7.82	1.12-1.40
	M3	12	1.05	0.056	5.36	0.96-1.12	12	1.09	0.085	7.82	0.96-1.20
	m1	16	2.09	0.054	2.59	2.00-2.16	13	1.21	0.044	3.66	1.16-1.28
	m2	22	1.75	0.052	2.97	1.64-1.84	20	1.20	0.078	6.51	1.08-1.36
	m3	14	1.18	0.084	7.11	1.04-1.32	19	1.01	0.055	5.41	0.92-1.12
9702	M1	8	2.00	0.098	4.89	1.86-2.10	8	1.24	0.135	10.56	1.08-1.48
	M2	7	1.73	0.019	1.10	1.72-1.76	7	1.26	0.011	8.93	1.12-1.48
	M3	6	1.13	0.033	2.88	1.08-1.16	6	0.99	0.035	3.55	0.92-1.02
	m1	14	2.11	0.128	6.07	1.96-2.36	13	1.16	0.090	7.80	1.00-1.32
	m2	11	1.73	0.097	5.58	1.56-1.84	11	1.22	0.082	6.77	1.08-1.30
	m3	10	1.11	0.043	3.92	1.04-1.16	10	0.99	0.063	6.42	0.88-1.08
9616	M1	2	2.06	----	----	2.04-2.08	2	1.42	----	----	1.40-1.44
	M2	2	1.94	----	----	1.92-1.96	2	1.36	----	----	1.36-1.36
	M3	2	1.22	----	----	1.20-1.24	2	1.12	----	----	1.12-1.12
	m1	1	2.20	----	----	------	1	1.32	----	----	----
	m2	1	1.80	----	----	------	1	1.40	----	------	----
	m3	0	----	----	----	------	--	--	----	----	----

6.85 mm long, and it ends between the anterior and lingual roots of M1. The posterior palatine foramen is at the position of the posterior root of M2. The averaged alveolar length of M1-M3 from eight measurements is 5.33 mm.

M1 is very high-crowned, as tall as it is long in slightly worn teeth. It has five major cusps: anterocone, protocone, paracone, hypocone and metacone. The anterocone is asymmetrically bilobed in unworn or slightly worn specimens, with the labial conule slightly larger than the lingual. The anteromedian flexus is very shallow, and it is lost at the early stage of wear (less than one-third of the original height of crown). The anterostyle on the posterior arm of the anterocone slightly constricts the paraflexus, and the mesostyle on the posterior arm of the paracone slightly constricts the metaflexus. These two small styles are obliterated at the moderately worn stage, and they never join

TABLE 5. Measurements of some characters of *Repomys panacaensis* from the Panaca local fauna. N=number of teeth with the character, M=mean of the measurement (in mm), OR=observed range.

	N	**M**	**OR**
Width of upper incisor	1	1.15	----
Alveolar length of M1-M3	8	5.33	5.20-5.50
Diastema between I and M1	2	7.65	7.50-7.80
Width of lower incisor	9	1.04	1.00-1.20
Diastema between I and m1	11	4.11	4.10-4.30
Mandibular depth below m1	15	4.16	4.05-4.35
Alveolar length of m1-m3	14	5.37	5.15-5.70

TABLE 6. The root conditions of M2, M3, and m3 of *Repomys panacaensis* from the Panaca local fauna. A/B: A--number of specimens with that character; B--sample size.

	2-rooted M2s	**3-rooted M3s**	**2 rooted M3s**	**1 rooted M3s**	**1 rooted m3s**
Rodent Ravine section:					
9619	0/3	1/1	0/1	0/1	----
9616	0/2	0/2	2/2	0/2	----
9702	0/7	2/7	5/7	0/7	1/11
Limestone Corner section:					
8197	1/2	1/8	5/8	2/8	0/2
Brown Bone Beds:					
9621	0/3	0/3	0/3	3/3	3/3
9620	0/1	0/2	0/2	2/2	0/1
Rodent Hill section:					
9602	3/17	1/11	8/11	2/11	7/20
9601	2/10	1/8	3/8	4/8	2/8
9504	0/11	0/18	17/18	1/18	5/9
Total:	5/55 (9%)	5/59(8%)	40/59(68%)	14/59(24%)	18/53(34%)

the opposing enamel to form an islet prior to the loss of metaflexus through wear.

In slightly worn specimens, the protocone is located slightly anterior to the paracone, and the hypocone is slightly anterior to the metacone. In well-worn specimens, the hypocone and metacone are nearly transversely opposed. The protocone is differentiated from the anterocone by a shallow protoflexus, and this protostria persists to just above the base of the crown. Posterior arm of the protocone may be separated from the anterior arm of the paracone in unworn specimens, but they become confluent with moderate wear. A small enterostyle is present on the posterior arm of the protocone in unworn to slightly worn specimens. A broad and deep hypoflexus separates the protocone and hypocone. Anterior arm of the hypocone is confluent with the paracone, and its posterior arm is confluent with the metacone.

The paracone is separated from the anterocone by a deep, posterolingually directed paraflexus. It is separated from the metacone by a deep

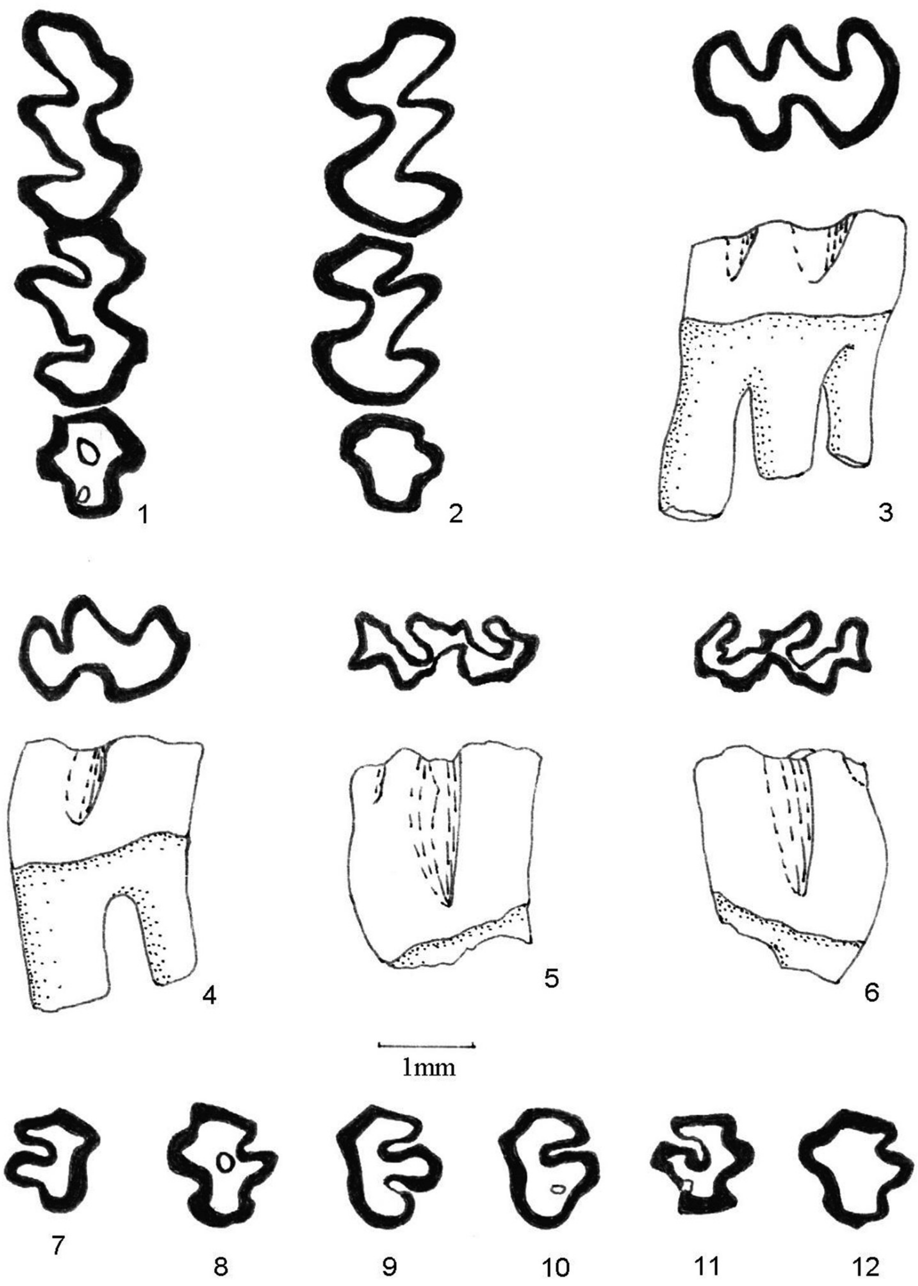

FIGURE 6. The terminology of molars of *Repomys* used in this study.

metaflexus. The metaflexus is directed posterolingually on unworn and moderately worn specimens and changes to a more transverse direction with wear. Both parastria and metastria continue to the base of the crown.

All of M1s have three well-developed roots: anterior, lingual, and posterior. They are similar in size.

M2 is similar to the M1 except for its shorter length and root condition. The shortness results from the loss of anterocone. On unworn M2s, the anterior cingulum is asymmetrically bilobed (Figures 7.5-7.6), but there is no structure homologous to the anterostyle of M1, even on young individuals. The mesostyle between the paracone and metacone is as distinct as in M1. The majority of M2s have three roots (Table 6): two anterior and

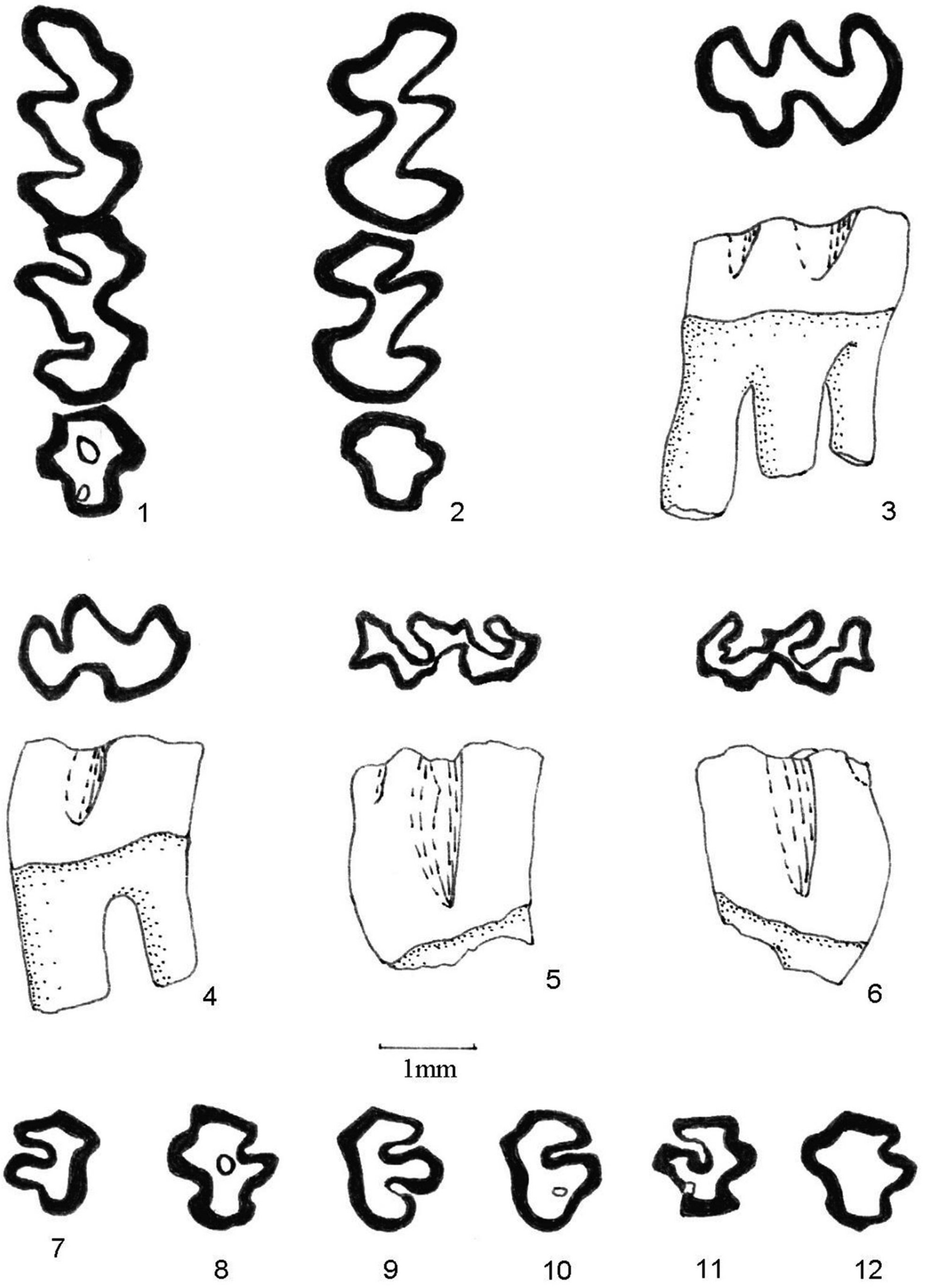

FIGURE 7. Upper molars of *Repomys panacaensis*. 1: occlusal view of right M1-M3, UALP 22573. The position of posterior border of incisive foramen is shown on the right side. 2: occlusal view of left M1-M3, UALP 21724. 3: occlusal and lingual views of a left M1, UALP 21729. 4-5: occlusal and labial views of M2s, UALP 21737, 22686, and 22683. 6-12: occlusal views of M3s, UALP 22535, 22512, 22794, 22793, 22596, and 22693.

one posterior. The anterolingual root is the strongest, and the anterolabial root is reduced. A few M2s (9%) with two roots have the two anterior ones fused, forming an L-shaped root.

M3 is well reduced, and the occlusal outline changes dramatically at different wear stages. In unworn specimens, two labial reentrants are present so that the occlusal surface is E-shaped (Fig-

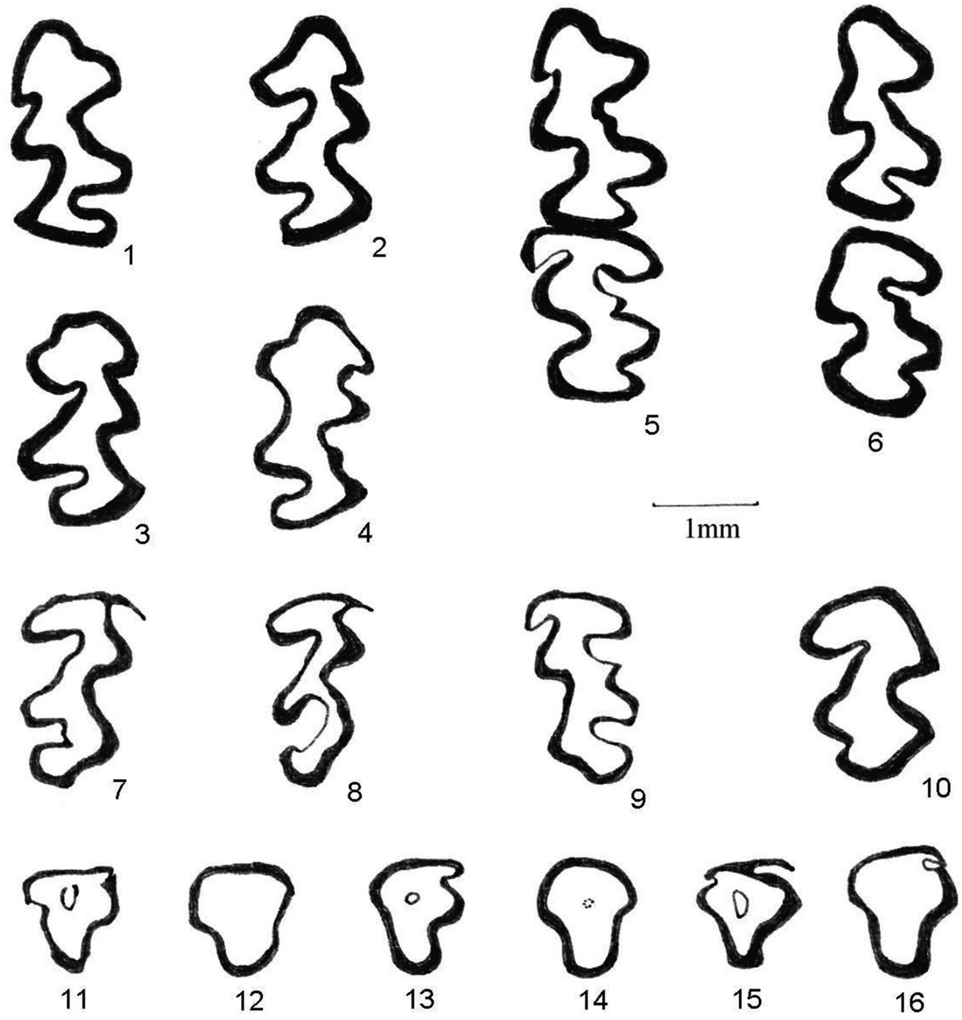

FIGURE 8. Lower molars of *Repomys panacaensis*. 1-4: occlusal views of m1s, UALP 22702, 22605, 21687, and 22718. 5-6: occlusal views of m1-m2s, UALP 22798, 22799. 7-8: occlusal views of m2s, UALP 22727, 22725, 22807, and 22809. 9-16: occlusal views of m3s, UALP 21213, 21757, 22815, 22819, 22769, and 22759.

ure 7.9). The posterior reentrant is usually shallower than the anterior reentrant. Anterior cingulum is developed. The protocone is distinct, and the paracone is large. The hypocone is smaller than the protocone but is usually distinct until moderately worn; it is separated from the protocone by a shallow hypoflexus. The metacone is indistinct or absent. In slightly worn specimens, the hypocone and posterior cingulum are reduced, forming a rounded posterior heel. With wear, the posterior cingulum connects to the paracone closing the metaflexus to form a smaller and shallow posterior enamel islet (Figure 7.10-7.11). The enamel wall of this islet is very thin, unlike that of *R. maxumi*. Also with wear, the paracone may connect to the well-developed anterior cingulum to form a large and shallow anterior enamel islet that may persist until moderate wear (Figure 7.8). Alternatively (in 14% of the M3s, nine out of 65), the opposing enamel walls of the paraflexus never connect to form an islet, and the occlusal view results in an "F" shape (Figure 7.7). With greater wear the anterior and posterior islets are lost (Figure 7.12). The root condition of M3 is highly variable: most M3s have two roots (68%), some have only one root (24%), and a few retain three roots (8%; Table 6). The bases are fused on some of the M3s with two roots. The M3s with one root have a deep groove on either the labial or lingual side.

The lower incisor is located labial to the m2 with the incisor cap placed between the coronoid process and the condyle on the labial side of the ascending ramus. The capsular process is prominent, forming a shelf that lacks a distinct knob. The masseteric crest extends anteriorly to a position beneath the anterior side of the protoconid of m1. There is a well-developed but short shelf lacking a knob at the anterior end of the masseteric crest. The mental foramen is relatively high on the dorsal-labial side of the dentary, well separated from the masseteric crest and the anterior root of m1. This position is similar to that of *Neotoma* but lower than that of *Sigmodon*, where the mental foramen is higher and located on the dorsal surface of dentary. The coronoid process of *R. panacaensis* curves posteriorly, and the condyle faces upward. The distance between the coronoid process and the condyle is 3.35 mm on a single measurable specimen (UALP 21701). The other measurements of these mandibles are included in Table 5.

The m1 is hypsodont, as tall as long in unworn specimens. It has five cusps: anteroconid, protoconid, metaconid, entoconid, and hypoconid. The anteroconid is single-cusped with an anterolabial cingulum directed posterolabially. The anterior cingulum is lost after moderate wear. The metaconid is distinct but smaller than in *R. gustelyi* and *R. maxumi*. It confluently connects to the anteroconid and protoconid. The entoflexid is shallow; its apex projects anteriorly in unworn specimens, anterolabially in slightly worn specimens, and transversely in well-worn specimens.

Anterior arm of the protoconid connects to the anteroconid, and the posterior arm is confluent with the anterior arm of the entoconid even in unworn specimens. The anterior arm of the entoconid joins a small mesostylid in unworn and slightly worn specimens, slightly constricting the apex of the entoflexid. The hypoconid and protoconid are labially separated by a broad and moderately deep hypoflexid, with the apex directed anterolingually. The anterior arm of hypoconid confluently joins the labial side of entoconid. A small ectostylid, smaller than mesostylid, projects anterolabially on the anterior arm of hypoconid in unworn and slightly worn specimens, similar to *R. arizonensis*. The protostriid is very shallow, and the hypostriid is deep but well above the base of the crown. The entostriid is slightly deeper than the posterostriid.

The lingually directed posterior cingulum is very well developed; it is broadly confluent with the hypoconid. The posteroflexid is slightly shallower and much narrower than the entoflexid. The m1 has two distinct roots: anterior and posterior. Two specimens (UALP 21687 from Locality 9504 and 22718 from Locality 9602) have a tiny rootlet between the anterior and posterior roots.

The m2 is similar to m1 except it is shorter. The anterior cingulum is relatively broad, with a short labial extension anterior to the protoconid. The entoflexid is directed anterolabially in all specimens. The posterior cingulum is longer in unworn and slightly worn specimens than in well-worn specimens. The enamel wall on the anterior side of posterior cingulum is very thin in unworn and slightly worn specimens, like that of *R. arizonensis*. The protostriid is very shallow; the hypostriid and entostriid are very deep but terminate above the base of the crown; the posterostriid is very shallow. The m2 has two distinct roots as in m1.

The m3 is reduced relative to m1 and m2. It is keyhole shaped in occlusal view in moderately worn specimens. In unworn specimens, a shallow entoflexid is present, with the apex pointing anterolingually. An anterolabial cingulum is present in slightly worn specimens and absent in moderately worn specimens. The posterior heel represents the greatly reduced hypoconid; it is deflected lingually. The posterolabial reentrant (hypoflexid) is very broad and shallow, as is the posteroflexid. The entostriid is very shallow; the posterostriid and hypostriid are deeper, with the hypostriid nearly reaching the base of the crown. More than half of m3s in this sample have two roots as in m1 or m2 (66%), some partially fused, but the others have only one root, with the anterior and posterior ones fused medially or labially.

Discussion. Three other species of *Repomys* have been reported in North America: *R. gustelyi* May 1981 from the late Hemphillian Warren l.f. of California, *R. maxumi* May 1981 from the early Blancan Maxum l.f. of California, and *R. arizonensis* Tomida 1987 from the late Blancan of 111 Ranch l.f. of Arizona. As May (1981) stated, *R. panacaensis* can be differentiated from *R. gustelyi* or *R. maxumi* by its smaller size. The M1 and M2 are very similar among these species; however, the M3s of *R. panacaensis* frequently present an anterior enamel islet, which is not seen in the other two species. The M3 of the latter two species is characterized by a deep anterior reentrant, but this reentrant never constricts to form an islet. Also, the posterior reentrant is deeper in the M3 of *R. panacaensis* compared to those of *R. gustelyi* or *R. maxumi* at the same stage of wear. In unworn or slightly worn M3s of *R. panacaensis*, this posterior reentrant forms the shape of an E in the occlusal view instead of an F that is seen in the other two species. Comparison of root condition of M3 between these three species is difficult because it is highly variable in *R. panacaensis* and only one specimen of *R. gustelyi* and four specimens of *R. maxumi* are available. Larger samples are needed to conclude if there is a trend in the root reduction on M3 from *R. gustelyi* and *R. maxumi* to *R. panacaensis*.

The apex of entoflexid in m1 is another important character to distinguish *R. panacaensis* from *R. gustelyi* or *R. maxumi* (May 1981). In *R. panacaensis*, this reentrant only points anteriorly in unworn specimens and gradually changes its direction transversely in advanced wear. However, in the latter two species, the entoflexid is deep, and the apex is directed strongly anteriorly even in worn specimens. This configuration makes the metaconid rather separated from the anteroconid in the latter two species. The anterolabial cingulum in m1 is also obliterated with moderate wear in *R. panacaensis*, whereas it continues in more advanced wear in the other two species. The m2 and m3 are similar in the three species except for their sizes. The anterior enamel islet on m3 is preserved until moderate wear in *R. panacaensis*, similar to that in *R. gustelyi* and *R. maxumi*.

When Tomida (1987) erected the species *R. arizonensis*, neither an M3 nor an m3 was found. He listed the following characters of *R. arizonensis* to differentiate it from *R. panacaensis*: 1) size is significantly larger; 2) the lingual reentrant on m1 extends further across the tooth, and the metaconid is not as close to the anteroconid; 3) posterior cingulum of m1 is better developed; 4) M2 has only two roots, with anterior and lingual roots fused, forming an L-shaped large root. It is noticed that when this comparison was made, only a small sample and moderately well worn specimens of *R. panacaensis* were available (see May 1981). With more specimens and unworn teeth available, there is only one character of those listed above that can distinguish *R. arizonensis* from *R. panacaensis*: the metaconid on m1 of *R. arizonensis* is better developed and less close to the anteroconid. The sizes of these two species are not significantly different, and on unworn or slightly worn m1s, the posterior cingulum in *R. panacaensis* is as developed as in *R. arizonensis*. The majority of M2s of *R. panacaensis* have three roots, but some of them are also reduced to two roots, and the anterior one is L-shaped. Since only one M2 of *R. arizonensis* was available for root identification (Tomida 1987), a larger sample is needed to make this character secure for differentiation.

In addition to the metaconid on m1, two other characters may be added to distinguish these two morphologically similar species: 1) the metaflexid on m1 is deeper in *R. panacaensis* than in *R. arizonensis* at the same stage of wear. This configuration makes the metaconid more distinct from the anteroconid in *R. panacaensis*; 2) the hypoflexid on m1 is broader and shallower in *R. panacaensis* than in *R. arizonensis* at the same stage of wear. The apex of this flexid in *R. panacaensis* points more transversely. This character is seen in more primitive species like *R. gustelyi*. *R. panacaensis* could give rise to *R. arizonensis*, but the discovery of M3 and m3 of *R. arizonensis* will be very important and useful to understand the phylogenetic relationship between these two species.

Repomys can by readily distinguished from two other similar hypsodont cricetines, *Galushamys* and *Pliotomodon*, by the absence of enamel islet on M1 or M2. *Pliotomodon*, as suggested by Jacobs (1977), is probably an immigrant close to European *Ruscinomys hellenicus*. *Repomys* differs from *Neotoma* or *Neotomodon* by its F-shaped M3 and keyhole-shaped m3. Based on the record of *Peromyscus* cf. *P. pliocenicus* from the early Hemphillian of Oregon, which starts to develop hypsodonty and has a single cusped anteroconid on m1, May (1981) suggested that *Repomys* was likely derived from *P. pliocenicus*. The M3 of *P. pliocenicus* has an E-shaped occlusal view, and the m3 is S-shaped with a deep posterior lingual reentrant (May 1981, figures 2c, 4). Both M3 and m3 of *Peromyscus* cf. *P. pliocenicus* have a primitive pattern compared to *Repomys*, but they are not quite reduced. Korth (1994) supported this *P. pliocenicus*-*Repomys* hypothesis, but he suggested that *P. pliocenicus* should be referred to a genus other than *Peromyscus* because its crown height is greater than any other known species of this genus.

It is noticed that *Paronychomys* from the late Hemphillian of the Redington l.f. of Arizona (Jacobs 1977) is morphologically more similar to *Repomys* than to *Peromyscus pliocenicus*. It has substantial height of crown, and the third upper and lower molars are quite reduced. *Repomys* could be derived from *Paronychomys* through the increase of height of crown. The m1 of *Paronychomys* has a bilobed anteroconid, but the anteromedian flexid is very shallow and obliterated at the early stage of wear (F:AM 3230). The M3 of *Paronychomys* is E-shaped in occlusal view at a slightly worn stage (F:AM 3249), but the posterior reentrant is lost, and the anterior reentrant formed an enamel islet

(AMNH 98592, the type specimen of *Paronychomys lemredfieldi*) as seen in *R. panacaensis*. The m3 of *Paronychomys* is S-shaped with a deep posterolabial reentrant that lasts to the base of the crown. The m3 of *Repomys* could be derived from *Paronychomys* through the reduction of this reentrant because the posterior heel of m3 in *Repomys* is deflected lingually due to this reentrant.

However, if *R. gustelyi* gave rise to *R. maxumi*, and *R. panacaensis* is on a side branch as May (1981) suggested, there is a problem for the above *Paronychomys*-*Repomys* hypothesis: *R. gustelyi* and *R. maxumi* are both greatly larger than *Paronychomys tuttlei* (larger species of *Paronychomys*) or *P. lemredfieldi*. Also, both *R. gustelyi* and *Paronychomys* are found in late Hemphillian faunas. It is possible that the small-sized group, including *R. panacaensis*, *R. minor*, n. sp., below, and *R. arizonensis* are in a different lineage from that of the large-sized group, including *R. gustelyi* and *R. maxumi*.

Occurrence*.* Rodent Ravine section: 9702, 9616, 9619; Double Butte section: 9502; Brown Bone Beds: 9620, 9621; Rodent Hill section: 9504, 9601, 9602; Limestone Corner section: 8197, in the Panaca Fm., southeast Nevada.

Range. Early Blancan.

Repomys minor sp. nov.
(Tables 7-8; Figures 9-10)

Diagnosis. Smallest known species in the genus. The entoflexid on m1 points more anteriorly, and the metaconid is more distant from the anteroconid than in *R. panacaensis*.

Holotype. UALP 21369 from Locality 9504: left mandible with incisor and m1-m3.

Etymology. *minor*, refers to small size.

Material examined. UALP **Locality 8197:** M1s: 21161-21172, 21204; M2s: 21173-21181; M3: 21189; m1s: 21192-21200, 21137; m2s: 21206-21210; m3s: 21214-21216. **Locality 9502:** M1s: 21397-21399; M2: 21401. **Locality 9504:** left maxillary with M1-M2: 21374, 21664; M1s: 21385, 21665, 21669, 21371, 21372; M2s: 21656, 21674, 21740; M3: 21392; m2: 21383; m3s: 21696, 21698, 21699, 21396, 21760. **Locality 9616:** m1: 22560; m2: 22561. **Locality 9620:** M1: 22520; M2s: 22521, 22522; M3: 22523; m1s: 22524, 22525; m2: 22518. **Locality 9621:** M1s: 22548-22550; M2: 22547; m1: 22551. **Locality 9601:** M2: 22639; m1s: 22641, 22642; m2: 22643; m3s: 22644-22646. **Locality 9602:** M2: 22773; M3s: 22774, 22775; m1s: 22777, 22778; m2: 22779; m3: 22756. **Locality 9702:** M1s: 22824-22825, 22827-22828; M2s: 22833-22835; m1s: 22806, 22836-22838; m2s: 22840-22844; m3s: 22839, 22845.

Description. *Repomys minor* is morphologically most similar to *R. panacaensis* except for its smaller size.

M1 is very high-crowned, as tall as long in slightly worn teeth. It has five major cusps: anterocone, protocone, paracone, hypocone, and metacone. The anterocone is asymmetrically bilobed in unworn or slightly worn specimens, with the labial conule slightly larger than the lingual. The anteromedian flexus is very shallow, and it is lost at the early stage of wear. The anterostyle on the posterior arm of the anterocone slightly constricts the paraflexus, and the mesostyle on the posterior arm of the paracone slightly constricts the metaflexus. These two small styles are obliterated at the moderately worn stage, and they never join the opposing enamel to form an islet prior to the loss of metaflexus through wear.

In slightly worn specimens, the protocone is located slightly anterior to the paracone, and the hypocone is slightly anterior to the metacone. In well-worn specimens, the hypocone and metacone are nearly transversely opposed. The protocone is differentiated from the anterocone by a shallow protoflexus, and this protostria persists to just above the base of the crown. The posterior arm of the protocone may be separated from the anterior arm of the paracone in unworn specimens, but they become confluent with moderate wear. A small enterostyle is present on the posterior arm of the protocone in unworn to slightly worn specimens. A broad and deep hypoflexus separates the protocone and hypocone. The anterior arm of the hypocone is confluent with the paracone, and its posterior arm is confluent with the metacone.

The paracone is separated from the anterocone by a deep, posterolingually directed paraflexus. It is separated from the metacone by a deep metaflexus. The metaflexus is directed posterolingually on unworn and moderately worn specimens and changes to a more transverse direction with wear. Both parastria and metastria continue to the base of the crown. Each M1 has three distinct roots.

M2 is similar to the M1 except for its shortness and root condition. The shortness results from the loss of the anterocone. There is no anterostyle on the posterior arm of the anterocone even on young individuals, but the mesostyle between the paracone and metacone is as distinct as in M1. Each

TABLE 7. Measurements (in mm) of molars of *Repomys minor*, n. sp., from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		Length					Width				
		N	M	SD	CV	OR	N	M	SD	CV	OR
9504	M1	4	1.70	0.030	1.77	1.68-1.74	4	0.95	0.107	11.38	0.80-1.06
	M2	4	1.50	0.023	1.54	1.48-1.52	4	0.96	0.086	9.00	0.88-1.08
	M3	1	0.68	----	----	------	1	0.68	----	------	----
	m1	5	1.83	0.043	2.39	1.80-1.88	5	1.06	0.036	3.39	1.04-1.12
	m2	4	1.52	0.034	2.25	1.48-1.56	4	1.09	0.087	8.00	0.96-1.14
	m3	7	0.94	0.087	9.26	0.80-1.02	7	0.83	0.057	6.95	0.76-0.94
9601	M2	1	1.52	----	----	------	1	1.04	----	------	----
	M3	0	----	----	----	------	0	----	----	------	----
	m1	2	1.68	----	----	1.60-1.76	2	0.96	----	------	0.92-1.00
	m2	1	1.48	----	----	------	1	1.00	----	------	----
	m3	3	0.84	0.069	8.25	0.76-0.88	3	0.75	0.061	8.18	0.68-0.80
9602	M1	0	----	----	------	----	0	------	----	------	------
	M2	1	1.44	----	----	------	1	0.84	----	------	----
	M3	2	0.90	----	----	0.88-0.92	2	0.80	----	------	0.76-0.84
	m1	2	1.76	----	----	1.76-1.76	2	0.88	----	------	0.84-0.92
	m2	1	1.40	------	------	------	1	1.00	----	------	------
	m3	1	0.80	----	----	------	1	0.68	----	------	----
9702	M1	5	1.76	0.009	0.51	1.76-1.78	5	1.00	0.003	2.99	0.96-1.04
	M2	3	1.56	0.069	4.44	1.48-1.60	3	1.11	0.083	7.52	1.04-1.20
	M3	0	----	----	----	------	0	----	----	------	----
	m1	4	1.80	0.046	2.57	1.76-1.84	4	1.00	0.025	2.50	0.98-1.04
	m2	5	1.54	0.022	1.43	1.52-1.56	5	0.99	0.052	5.26	0.96-1.08
	m3	2	0.82	----	----	0.80-0.84	2	0.75	----	------	0.74-0.76
9616	m1	1	1.80	----	----	------	1	1.00	----	------	----
	m2	1	1.44	----	----	------	1	0.96	----	------	----
8197	M1	13	1.65	0.046	2.78	1.60-1.76	13	1.02	0.117	11.53	0.80-1.16
	M2	9	1.44	0.073	5.06	1.32-1.52	9	0.98	0.095	9.73	0.80-1.12
	M3	0	----	----	----	------	0	----	----	------	----
	m1	7	1.79	0.062	3.47	1.68-1.84	7	1.00	0.061	6.11	0.92-1.10
	m2	3	1.60	0.035	2.17	1.56-1.62	3	1.17	0.136	11.67	1.06-1.32
	m3	3	0.91	0.129	14.18	0.76-1.00	3	0.73	0.115	15.75	0.60-0.80
9502	M1	2	1.70	----	----	1.68-1.72	1	1.20	----	------	----
	M2	1	1.44	----	----	------	0	----	----	------	----
9620	M1	1	1.62	----	------	------	1	1.20	----	------	------
	M2	2	1.58	----	----	1.56-1.60	2	1.02	----	------	0.92-1.12
	M3	1	0.88	----	----	------	1	0.84	----	----	------
	m1	2	1.80	----	----	1.76-1.84	2	1.02	----	------	1.02-1.04
	m2	1	1.56	------	------	------	1	1.04	----	------	------
	m3	0	----	----	----	------	0	----	----	------	----
9621	M1	2	1.70	----	----	1.60-1.80	2	0.94	----	------	0.92-0.96
	m1	1	1.76	----	----	------	1	0.92	----	------	----
	m2	1	1.52	----	----	------	1	0.92	----	------	----

TABLE 8. The stratigraphic changes of the ratio of total number of specimens of *Repomys panacaensis* and *R. minor* in the Panaca Formation. Ratio=*R. minor*/*R. panacaensis*. The ratio decreases from the lower stratigraphic level to higher stratigraphic level.

Locality	Repomys panacaensis	Repomys minor	Ratio
Rodent Hill section:			
9602	128	7	5.5%
9601	66	8	12.1%
9504	104	18	17.3%
Rodent Ravine section:-			
9619	12	0	0
9616	8	2	25%
9702	54	22	41%

M2 has three roots (18 specimens). The anterolingual root is the strongest, and the anterolabial root is reduced.

M3 is well reduced, and the occlusal outline changes dramatically at different wear stages. In unworn specimens, two labial reentrants are present so that the occlusal surface is E-shaped. The posterior reentrant is usually shallower than the anterior reentrant. The anterior cingulum is developed. The protocone is distinct, and the paracone is large. The hypocone is smaller than the protocone but is usually distinct until moderately worn. It is separated from the protocone by a shallow hypoflexus. The metacone is indistinct or absent.

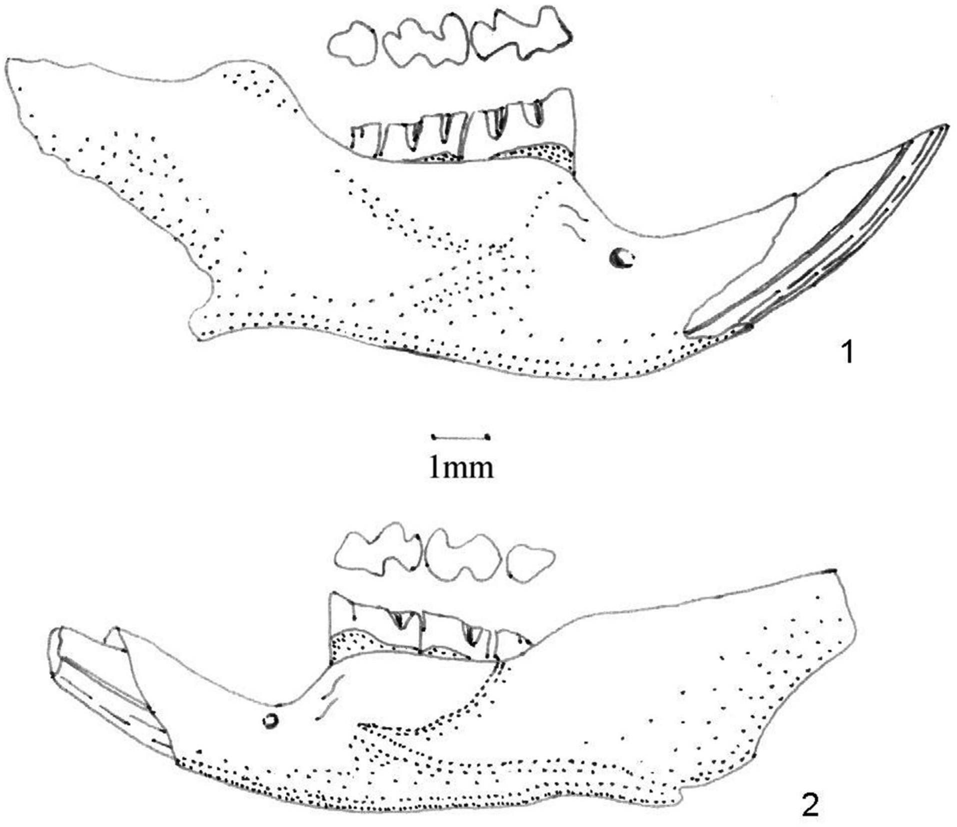

FIGURE 9. Lower jaws of *Repomys panacaensis* and *Repomys minor* n. sp. 1: *Repomys panacaensis*, UALP 21370. 2: *Repomys minor* n. sp., UALP 21369.

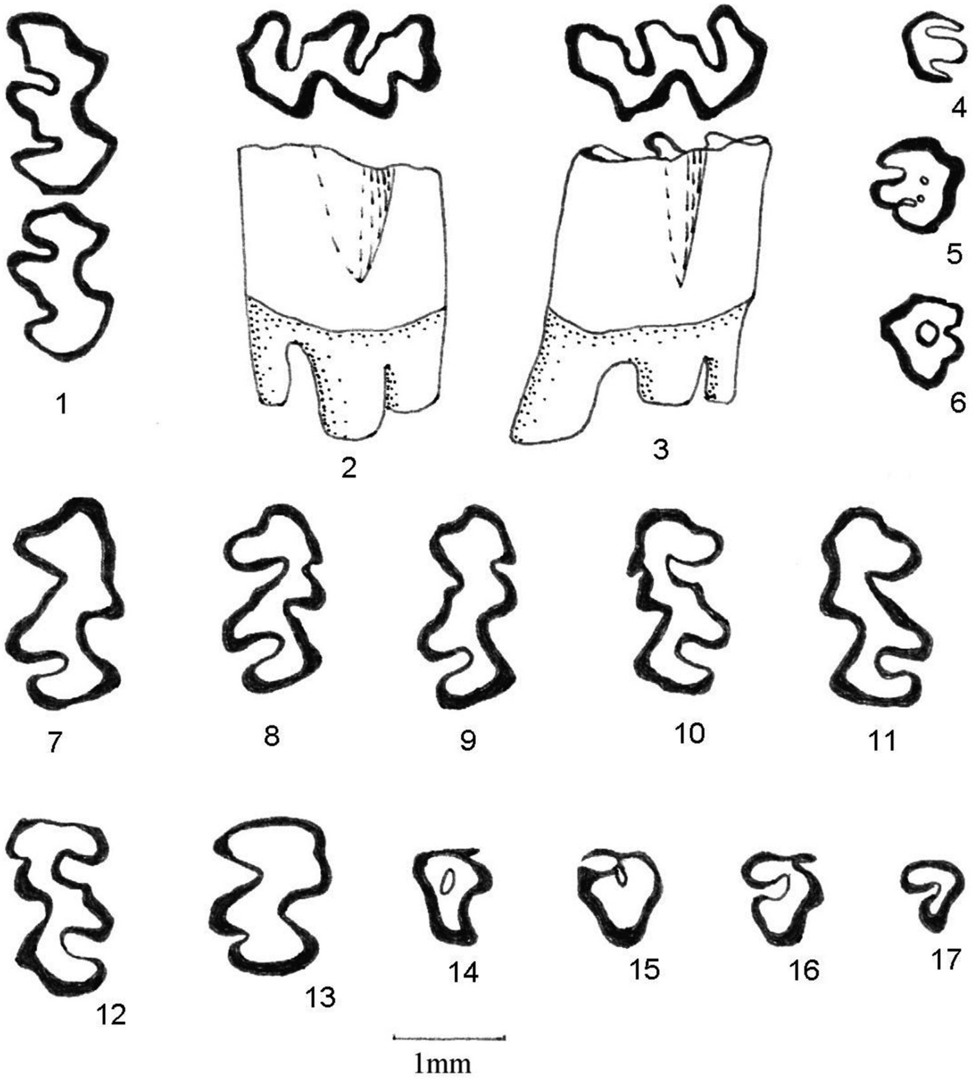

FIGURE 10. Molars of *Repomys minor*, n. sp. 1: occlusal view of right M1-M2, UALP 21664. 2-3: occlusal and labial views of M1s, UALP 21665, 22828. 4-6: occlusal views of M3s, UALP 21189, 22523, 21392. 7-11: occlusal views of m1s, UALP 22836, 21195, 22777, 22641, 22642. 12-13: occlusal views of m2s, UALP 22844, 22779. 14-17: occlusal views of m3s, UALP 21698, 22839, 22756, and 21215.

In slightly worn specimens, the hypocone and posterior cingulum are reduced, forming a rounded posterior heel. With wear, the posterior cingulum connects to the paracone closing the metaflexus to form a smaller and shallow posterior enamel islet. The enamel wall of this islet is very thin, as that of *R. panacaensis*. With wear, the paracone may connect to the well-developed anterior cingulum to form a large and shallow anterior enamel islet that may persist until moderate wear. With greater wear the anterior and posterior islets are lost. Of the four M3s, two have two roots, and two have one root.

The mandible is more slender than that of *R. panacaensis*. The diastema between the incisor and m1 is long relative to the mandible depth (Figure 9). Its ratio is 1.28, whereas it is 0.99 in *R. panacaensis*. The incisor is 0.80 mm wide, and the mandible depth below m1 is 3.20 mm. The alveolar length of m1-m3 is 4.20 mm. All of these measurements are outside the respective ranges of *R. panacaensis*. The capsular process for the recep-

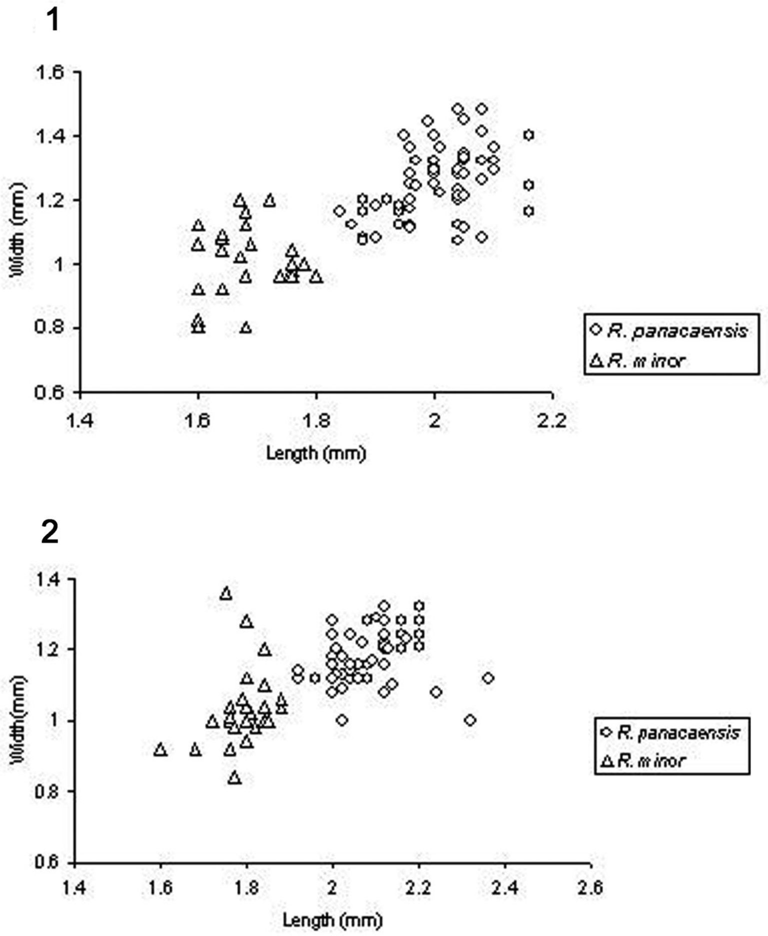

FIGURE 11. Scatter plots of M1s (above) and m1s (below) of *Repomys* from the Panaca local fauna.

tion of incisor is less prominent than in *R. panacaensis*.

The m1 is hypsodont, as tall as long in unworn specimens. It has five cusps: anteroconid, protoconid, metaconid, entoconid, and hypoconid. The anteroconid is single-cusped with an anterolabial cingulum directed posterolabially. The anterior cingulum is lost after moderate wear. The metaconid is distinct but smaller than in *R. gustelyi* and *R. maxumi*. It confluently connects to the anteroconid and protoconid. The m1 has a slightly different occlusal pattern from that of *R. panacaensis*. At the similar wear stage, the entoflexid is deeper and pointed more anteriorly in *R. minor*, which results in the metaconid being further from the anteroconid.

The anterior arm of the protoconid connects to the anteroconid, and the posterior arm is confluent with the anterior arm of the entoconid even in unworn specimens. The anterior arm of the entoconid joins a small mesostylid in unworn and slightly worn specimens, slightly constricting the apex of the entoflexid. The hypoconid and protoconid are labially separated by a broad and moderately deep hypoflexid, with the apex directing anterolingually. The anterior arm of hypoconid confluently joins the labial side of entoconid. The protostriid is very shallow, and the hypostriid is deep but well above the base of the crown. The entostriid is slightly deeper than the posterostriid.

The lingually directed posterior cingulum is very well developed and is broadly confluent with the hypoconid. The posteroflexid is slightly shallower and much narrower than the entoflexid. The m1 has two distinct roots: anterior and posterior.

The m2 is similar to m1 except it is shorter. The anterior cingulum is relatively broad, with a short labial extension anterior to the protoconid. The entoflexid is directed anterolabially in all specimens. The posterior cingulum is longer in unworn and slightly worn specimens than in well-worn specimens. The enamel wall on the anterior side of the posterior cingulum is very thin in unworn and slightly worn specimens, like that of *R. arizonensis*. The protostriid is very shallow; the hypostriid and entostriid are very deep but terminate above the base of the crown; the posterostriid is very shallow. The m2 has two distinct roots as in m1.

The m3 is reduced relative to m1 and m2. It is keyhole shaped in occlusal view in moderately worn specimens. In unworn specimens, a shallow entoflexid is present, with the apex pointing anterolingually. An anterolabial cingulum is present in slightly worn specimens and absent in moderately worn specimens. The posterior heel represents the greatly reduced hypoconid and is deflected lingually. The posterolabial reentrant (hypoflexid) is very broad and shallow, as is the posteroflexid. The entostriid is very shallow; the posterostriid and hypostriid are deeper, with the hypostriid nearly reaching the base of the crown. Of the 12 m3s, five have only one root.

Discussion. *Repomys minor* is recognized as a new species because of its significantly smaller size compared to the other species in this genus. There is no overlap with *R. panacaensis* in the observed range of the lengths of M1 and m1 (Figure 11). *R. minor* could be more primitive than *R. panacaensis*, based on the morphology of m1 as mentioned above.

Repomys minor occurs with *R. panacaensis* in the same localities in the Fm. except for Locality 9619 in Rodent Ravine section. The absence of *R. minor* from Locality 9619 is probably due to the small sample of sediments processed from this site, rather than representing the absence of this species, as *R. minor* was still found from sites at a higher stratigraphic level. Except for Locality 8197 in the Limestone Corner section and Locality 9502 in the Double Butte section, the other localities produce smaller abundance of *R. minor* than that of *R. panacaensis*, especially the three localities in the Rodent Hill section. Interestingly, in the Rodent Hill section, the ratio of specimens of *R. minor* relative to *R. panacaensis* decreases as the stratigraphic levels of sites increase. This pattern is also observed in the Rodent Ravine section and Brown Bone Beds (Table 8), which could suggest a gradual replacement of *R. minor* by *R. panacaensis* in the higher stratigraphic level. Localities 8197 (ratio of *R. minor* to *R. panacaensis* is 211%) and 9502 (ratio is 400%) are exceptions. They are relatively high stratigraphically, but *R. minor* seems more abundant than *R. panacaensis* at these sites. The ratio of specimens from Locality 9502 is probably biased by the small sample size (five specimens total, two species).

Occurrence. Rodent Ravine section: 9702, 9616; Limestone Corner section: 8197; Double Butte section: 9502; Brown Bone Beds: 9602, 9621; Rodent Hill section: 9504, 9601, 9602, in the Fm., southeast Nevada.

Range. Early Blancan.

Subfamily ARVICOLINAE Gray, 1882

Figure 12

The dental terminology follows Martin (1995, figure1) except that the alternating triangles within the anteroconid complex of m1 are called primary wings following Repenning (personal commun., 1995) and Czaplewski (1990), instead of Triangle 4 and Triangle 5. By using the term “primary wing,” we can avoid the ambiguity in the counting of triangles on m1, especially for the *Mimomys*-like arvicoline rodents. The concepts of “reentrant pit” and “shelf” follow Mou (1997): a reentrant pit refers to the depression on the anterior lingual surface or posterior surface at the base of the enamel. It usually presents a sulcus in occlusal view. A shelf refers to the swelling of enamel at the base of the crown. It is the same structure as the “cingulum” of Zakrzewski (1969). The degrees of closure between the occlusal alternating triangles or lobes also follow Mou (1997), in which four degrees are used: closed, slightly open, moderately open, and open. However, it should be noted that the degree of closure between the alternating triangles changes even on the same tooth at different degrees of wear. Only a general pattern can be extracted, and no emphasis should be placed on the exact percentages. The closure of alternating triangles is useful when we compare *Mimomys* or other advanced genera to primitive genera, like *Microtoscoptes*, which has open triangles; however, caution must be exercised when we compare the different species within *Mimomys*.

Five stages of wear were used: young—crown not worn, roots not yet developed; slightly worn—crown slightly worn, roots developed but short; moderately worn—crown worn down about halfway, roots long but not closed; worn—crown worn down more than halfway, roots closed; well worn—crown almost worn out, roots closed.

Genus MIMOMYS Forsyth Major, 1902

Mimomys panacaensis Mou, 1997

(Tables 9-10; Figures 13-16)

Material examined. UALP **Locality 9502:** M1s: 21323-21332, 21364, 22115-22118; M2s: 21338-21347, 22132-22135; M3s: 21348-21355, 22136-

TABLE 9. Measurements (in mm) of molars of *Mimomys panacaensis* from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		Length					Width				
		N	M	SD	CV	OR	N	M	SD	CV	OR
9702	M1	28	2.47	0.078	3.16	2.30-2.50	28	1.60	0.114	7.09	1.34-1.65
	M2	29	2.11	0.081	3.86	1.88-2.19	28	1.52	0.127	8.33	1.15-1.58
	M3	25	2.00	0.148	7.39	1.65-2.15	25	1.24	0.087	7.01	1.04-1.35
	m1	25	2.81	0.185	6.59	2.46-3.08	29	1.35	0.102	7.56	1.12-1.46
	m2	29	2.01	0.118	5.87	1.73-2.08	30	1.34	0.124	9.20	1.03-1.42
	m3	26	1.83	0.101	5.51	1.58-1.96	26	1.16	0.084	7.27	0.96-1.23
9619	M1	3	2.45	0.046	1.88	2.4-2.48	3	1.44	0.040	2.78	1.40-1.48
	M2	3	2.11	0.061	2.90	2.04-2.16	3	1.32	0.040	3.03	1.28-1.36
	M3	4	1.87	0.055	2.95	1.80-1.92	4	1.21	0.050	4.16	1.16-1.28
	m1	6	2.83	0.154	5.46	2.6-3.08	6	1.37	0.084	6.11	1.20-1.42
	m2	6	2.01	0.041	2.06	1.96-2.06	6	1.39	0.078	5.59	1.24-1.46
	m3	6	1.78	0.104	5.82	1.60-1.88	6	1.10	0.041	3.70	1.02-1.12
9502	M1	8	2.60	0.147	5.67	2.40-2.76	8	1.60	0.141	8.86	1.44-1.84
	M2	13	2.12	0.107	5.03	2.00-2.28	13	1.46	0.096	6.56	1.28-1.56
	M3	5	2.02	0.092	4.57	1.88-2.12	5	1.17	0.027	2.29	1.14-1.20
	m1	3	2.80	0.069	2.47	2.76-2.88	3	1.40	0.000	0.00	1.40-1.40
	m2	17	1.99	0.072	3.66	1.80-2.12	17	1.37	0.063	4.62	1.26-1.46
	m3	8	1.84	0.087	4.74	1.7-1.96	8	1.16	0.080	6.94	1.08-1.28
9601	M1	1	2.48	-------	-------	-------	1	1.48	-------	-------	-------
	M2	1	2.20	-------	-------	-------	1	1.32	------	------	------
	m1	m1	1	2.88	-------	-------	1	1.36	------	------	------
	m2	2	1.84	------	-------	1.8-1.88	2	1.12	----	----	1.08-1.16
9602	M1	1	1	2.80	1	1.76	----	------	----	----	----
	M2	2	2.26	0.085	3.75	2.2-2.32	2	1.5	0.141	1.77	1.40-1.60
	M3	2	1.96	0.170	8.66	1.84-2.08	2	1.16	0.056	4.88	1.12-1.20
	m1	2	2.72		0.113	4.16	2.64-2.8	2	1.46	0.141	9.69
	m2	1	2.08	------	------	------	1	1.32	------	------	------
	m3	3	1.81	0.167	9.18	1.68–2.00	3	1.21	0.023	1.90	1,20–1.24
9609	M3	1	1.96	----	----	------	1	1.16	----		----

22137; m1s: 21293-21300, 21363, 22125-22131; m2s: 21301-21314, 22119-22122; 21315, 21318-21320, 21322, 21323, 21316. **Locality 9619:** M1s: 21849-21854; M2s: 21855-21859; M3s: 21860-21864; m1s: 21865-21872, 21883, 21884; m2s: 21865, 21873-21877; m3s: 21873, 21878-21882. **Locality 9702:** an individual with skull and two mandibles: 22401; an individual with a partial skull and the right mandible: 23369; partial skull with right M1 and left M1-M2: 23368; palate with two dentitions: 22402, 23336-23337, 23339; palate with right M1-M3 and left M1-M2: 23338; palate with right M1-2 and left M1: 23340; maxillary with M1-M3: 22417; M1-M3: 22403; maxillary with M1-

TABLE 10. Measurements of some characters of *Mimomys panacaensis* from the Panaca local fauna. N=number of teeth with the character, ( ) =sample size, %=percentage of teeth with the character in the sample; M=mean of the measurement (in mm).

	Loc. 9702		Loc. 9619		Loc. 9502		Loc. 9602	
	N	% or M	N	% or M	N	% or M	N	% or M
Enamel islet on AC of young-moderately worn m1s	15(16)	94%	4(4)	100%	4(4)	100%	0	--
Dentine tracts on the labial side of AC	15	0.40	5	0.64	3	0.65	2	0.70
M2s with 2 roots	0(14)	0%	2(4)	50%	0(12)	0%	1(3)	33%
M3s with 2 roots	16(21)	76%	4(4)	100%	5(7)	71%	1(2)	50%
M3s with anterior islet	0(29)	0%	1(5)	20%	1(7)	14%	0	0%
M3s with posterior islet	2(29)	7%	2(5)	40%	0(7)	0%	0	0%
Width of lower incisor	9	1.29	2	1.38		--	0	--
Diastema between I and m1	9	4.30	0	--	0	11	0	--
Mandibular depth below m1	10	5.43	0	--	0	--	0	--
Alveolar length of m1-m3	11	6.85	0	--	0	--	--	--
Alveolar length of M1-M2	4	7.13	0	--	0	--	0	--
Palate width	4	3.4	0	--	0	--	0	--

M2: 22418; maxillary with M2-M3: 22436, 22440; M1s: 22420-22435, 22507; M2s: 22437-22439, 22441-22451, 22508, 23341; M3s: 22452-22463, 23342-23346; mandibles with I and m1-m3: 22404-22412, 22414, 23347; m1-m3: 22413; mandible with I and m1-m2: 22416; m1-m2s: 22415, 22464-22468, 23350; right m2-m3: 23348; m1s: 22469-22478, 22506, 23349; m2s: 22479-22489; m3s: 22490-22503. **Locality 9601:** M1: 22108; M2s: 22109-22111; m1: 22112; m3s: 22113. **Locality 9602:** M1s: 22092-22093; M2s: 22094-22096, 23351; M3s: 22097-22099; m1s: 22100-22103; m2: 22104; m3s: 22105-22107. **Locality 9609:** right M1: 23373; right M3: 23374.

Description. UALP 22401 is an owl pellet with a partial skull, two dentaries, and several post-cranial bones. This preservation allows the direct correlation of upper and lower dentition. The upper incisor is 1.60 mm wide, without any groove or depression. The diastema between the upper incisor and M1 is 8.9 mm. The width of the two nasal bones at the widest position is 3.7 mm.

The M1 has an anterior lobe and four alternating triangles (T1, T2, T3, and T4 in Figure 12). The apices of labial reentrant angles are flexed posteriorly in moderately worn and well worn specimens. No anterior shelf is present on the M1s from Locs. 9619 and 9702, but one (out of 13) from Locality 9502 and one (out of 3) from Locality 9602 have this anterior shelf. The dentine tract is weakly developed on the lingual side of Triangle 1. Each M1 has three roots, including the anterior, lingual, and posterior roots.

The M2 has an anterior lobe and three alternating triangles (T2, T3, and T4 in Figure 12). The

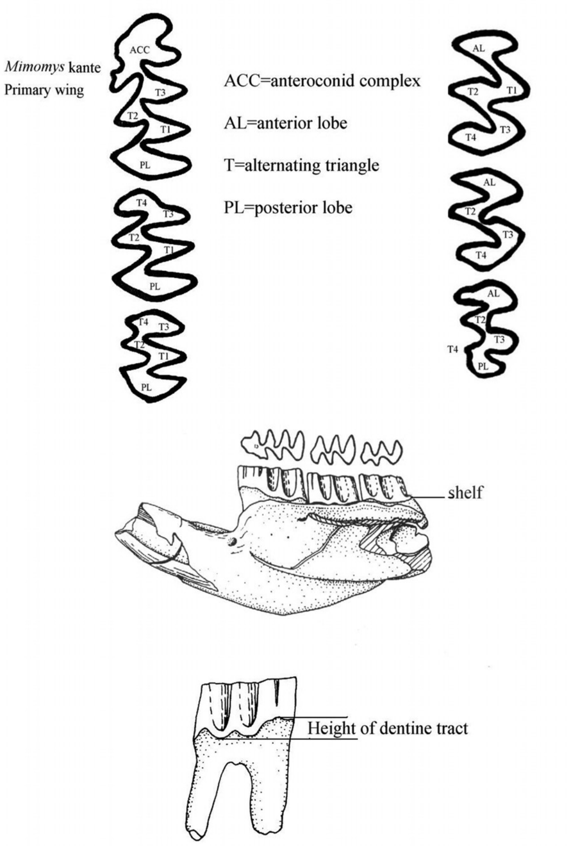

FIGURE 12. The terminology of molars of arvicoline rodents.

lingual reentrant apex is slightly curved posteriorly. No reentrant pit occurs at the base of the anterior lobe. The dentine tract is weakly developed on the lingual side of anterior lobe. The majority of M2s (91%) have three roots, two anterior and one posterior. The lingual-anterior root is wide and strong. Two M2s from Locality 9619 and one from Locality 9602 have only two roots. On these specimens, the two anterior roots are fused, forming an L-shaped root.

The M3 has an anterior lobe, three alternating triangles (T2, T3, and T4 in Figure 12), and a posterior lobe. Labial triangles are much smaller than the lingual triangles. In moderately well worn M3s, the anterior lobe is open to Triangle 2. The majority of M3s do not develop either anterior or posterior islet (see Table 10 for details), even at worn stages. About two-thirds of M3s (76%) have only two roots, but the others still preserve three roots (Table 10).

The posterior part of the dentaries of this individual is lost, but UALP 22406 from the same locality (Locality 9702) has an almost complete dentary. It is an adult with three molars. The lower incisor passes underneath the m2 and labial relative to the m3. It ends at the labial side of the dentary between the coronoid process and condyle, forming a prominent capsular process. The mental foramen in the lower jaw is anterior to the first root of m1 on the dorsolateral surface of the dentary, slightly anterior relative to the anterior end of the masseteric crest. This position is fairly consistent in all individuals. For the measurements of lower incisor, depth of dentary, and alveolar length of m1-m3, see Table 10.

The m1 has a posterior lobe, three alternating triangles, and an anteroconid complex (ACC). Labial triangles are slightly smaller than lingual triangles. The enamel is uniform in thickness. The degree of closure between the posterior lobe and the first triangle is usually slightly open; it is moderately open to open between the first and second triangles, moderately open between the second and third triangles, and slightly to moderately open between the third triangle and ACC. The apex of the second lingual reentrant is constricted and curved anteriorly. An enamel islet is usually present on unworn, slightly or moderately worn m1s. In younger specimens, the islet is larger and its shape is oval, whereas in older ones, the islet is smaller and circular. This islet disappears at the worn stage. Two m1s at the worn stage from Locality 9502 and one from Locality 9602 still preserve this islet. The "*Mimomys* kante" is present in all specimens except the well-worn ones. The enamel folds on the anterior-labial enamel wall only extend halfway down the crown so that the anterior ACC is quite smooth on moderately and well-worn m1s. The dentine tract on the labial side of the ACC is incipient .

The m2 has a posterior lobe and four alternating triangles. Labial triangles are slightly smaller than lingual triangles. The degree of closure between alternating triangles is moderately open. The dentine tract is absent labially.

The m3 has a posterior lobe and four alternating triangles, with labial triangles slightly smaller than lingual triangles. Triangle 4 is reduced and confluent with Triangle 3. The apices of lingual reentrant angles are wide. No posterior shelf is present on the m3s from Locs. 9619 and 9702. One m3 (out of five) from Locality 9502 has a posterior shelf.

Seven molars were chosen to examine their schmelzmuster by SEM, including four from Locality 9702, two from Locality 9502, and one from Locality 9602. All of them have the same schmelz-

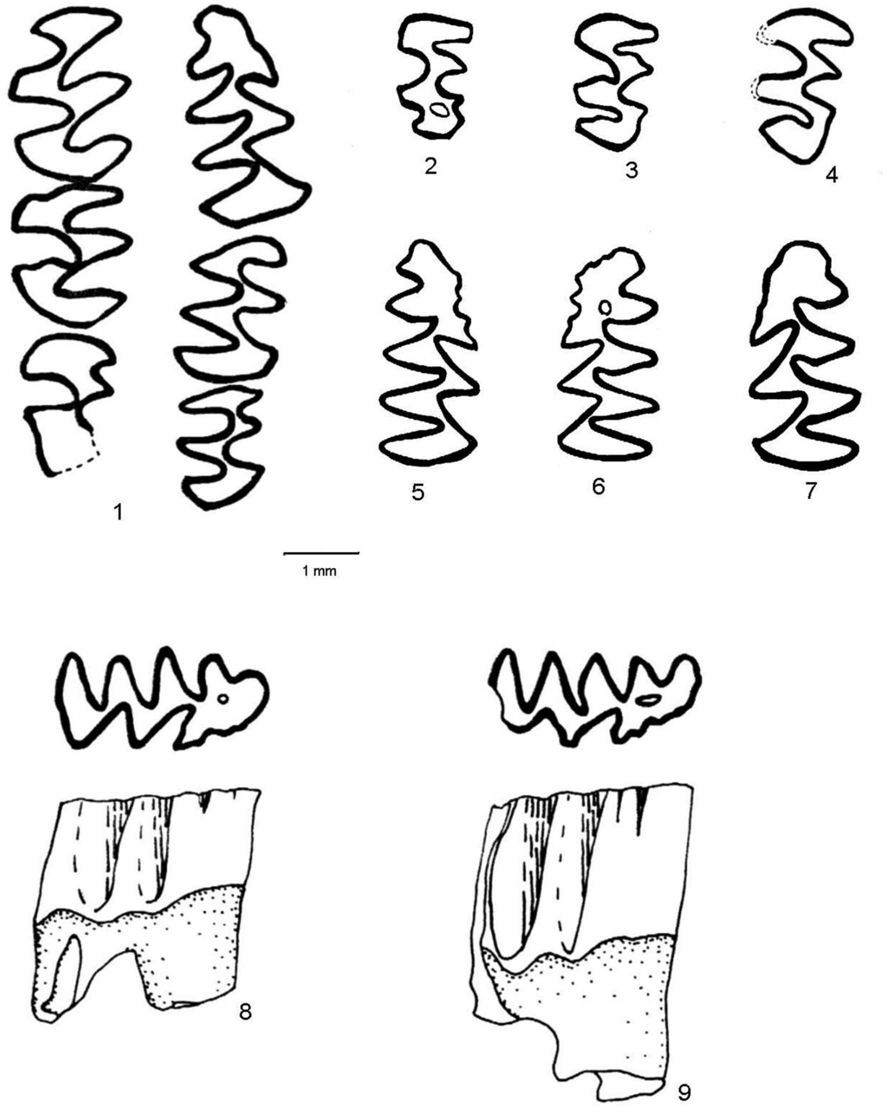

FIGURE 13. *Mimomys panacaensis* from the Panaca local fauna. 1: UALP 22401, occlusal views of left M1-M3 and right m1-m3 of one individual from Locality 9702. 2: UALP 22454, occlusal view of left M3 from Locality 9702. 3: UALP 21348, occlusal view of left M3 from Locality 9502. 4: UALP 22455, occlusal view of left M3 from Locality 9702. 6-7: occlusal views of m1s from Locality 9502, UALP 22125, 21299, 21298. 8-9: occlusal and labial views of m1s, UALP 22469, 22475.

muster on the leading and trailing edges of alternating triangles. The leading edge of ACC of m1s presents discrete lamellar enamel inside and radial enamel outside (Figure 15). The leading edges on alternating triangles present two radial enamel layers, and the trailing edges show radial enamel inside and primitive tangential enamel outside (Figure 16). The specimens from the above localities demonstrate similar schmelzmuster as that of specimens from the type locality, with the following slight differences among the specimens: 1) primitive tangential enamel sometimes is not present on the trailing edges of lingual alternating triangles (22474 from Locality 9702; 21297 from Locality 9502); 2) discrete lamellar enamel sometimes is absent on the apices of lingual alternating triangles (the same two specimens). Since the primitive tangential enamel and discrete lamellar enamel are poorly developed on the lingual alternating triangles of the other specimens, I consider these two differences as intraspecific variation.

Discussion. The size of teeth from these localities is similar to that of *M. panacaensis* from the type locality (Locality 8197). The following characters

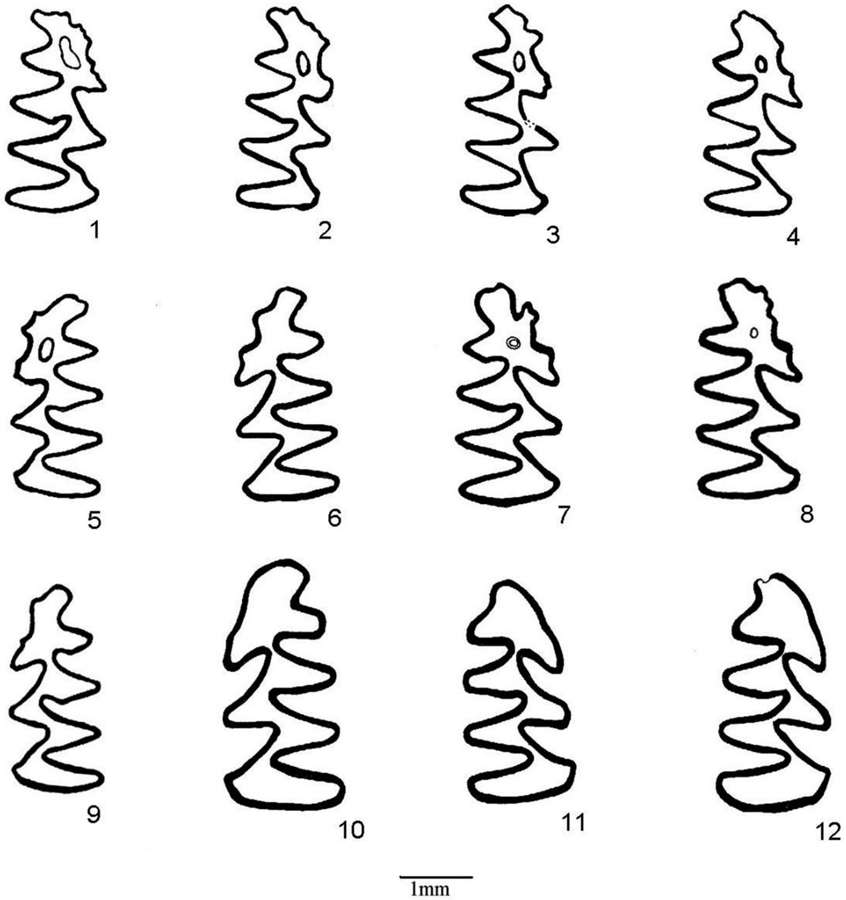

FIGURE 14. The first lower molars of *Mimomys panacaensis* from the Panaca local fauna. 1-12: occlusal views of m1s from Locality 9702. UALP 22470, 22473, 22472, 22455, 22471, 22405, 22466, 22404, 22467, 22412, 22408, and 22413.

indicate that these populations represent *M. panacaensis*: 1) the frequent occurrence of enamel islet on ACC of m1; 2) this islet on ACC extends to about halfway of the crown, persisting until the tooth is more than moderately worn; 3) the majority of M2s have three roots; 4) about two-thirds of M3s have two roots; 5) occasional occurrence of anterior or posterior islet on M3; 6) schmelzmuster of enamel band is like that of *M. panacaensis* from the type locality.

Notice that *M. panacaensis* from these localities, especially the population from Locality 9619, has a higher percentage of M3s with two roots than the one from the type locality which has 57% of two-rooted M3s (Mou 1997). The ancestor of *Mimomys*, *Promimomys*, has three-rooted M3s; it is likely that there will be some fluctuations on the percentages of root condition of M3 in different populations of *M. panacaensis*. Higher percentages are not surprising due to the smaller samples from the above localities. Locality 9619 has only four M2s that preserved roots. Although all four M2s have two roots, which is the same percentage as that of *M.* (*Ophiomys*) *mcknighti* from the White Bluffs l.f. of Washington (Gustafson 1978), it is noticed that this population has a significant portion of M3s with enamel islets. An enamel islet was not seen in any of the six known M3s of *M. (Ophiomys) mcknighti*. Therefore, I refer the arvicolines from Locality 9619 to *M. panacaensis*.

The finding of a partial skull with incisors make it possible to verify the absence of a groove on the upper incisor of *M. panacaensis*. This character can help us differentiate *M. panacaensis* from *M.* (*Ogmodontomys*) *sawrockensis* from the Saw Rock Canyon l.f. of Kansas, which has a groove on the upper incisor (Hibbard 1941). Other morphological differences occur in the enamel islet on m1, root condition on M3, and schmelzmuster (Mou 1997). In the dentary of *M. panacaensis*, the cap-

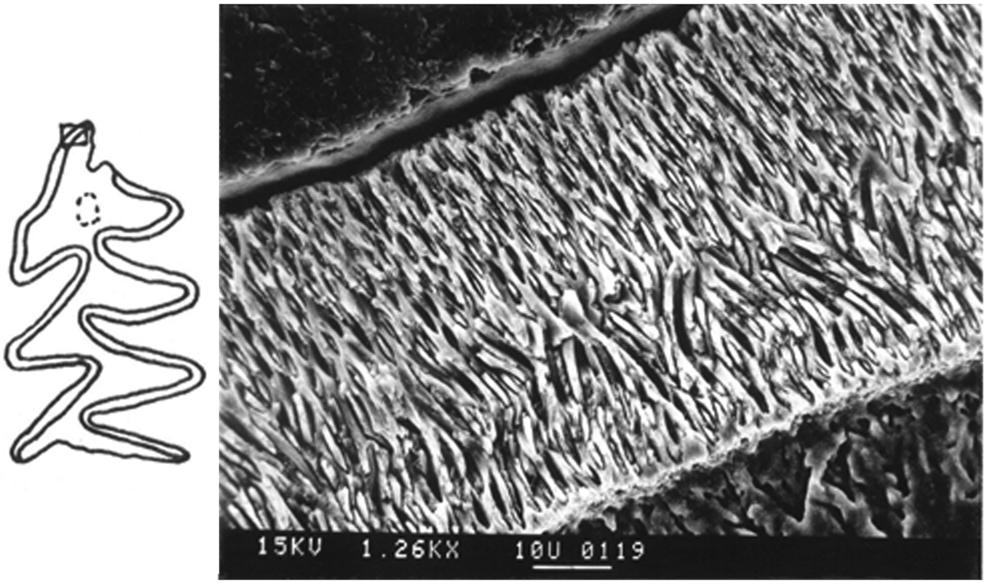

FIGURE 15. Schmelzmuster of *Mimomy panacaensis* on the leading edge of ACC of a left m1 (UALP 22506). Close to dentine (below right) is a layer of discrete lamellar enamel, and outside is a layer of radial enamel.

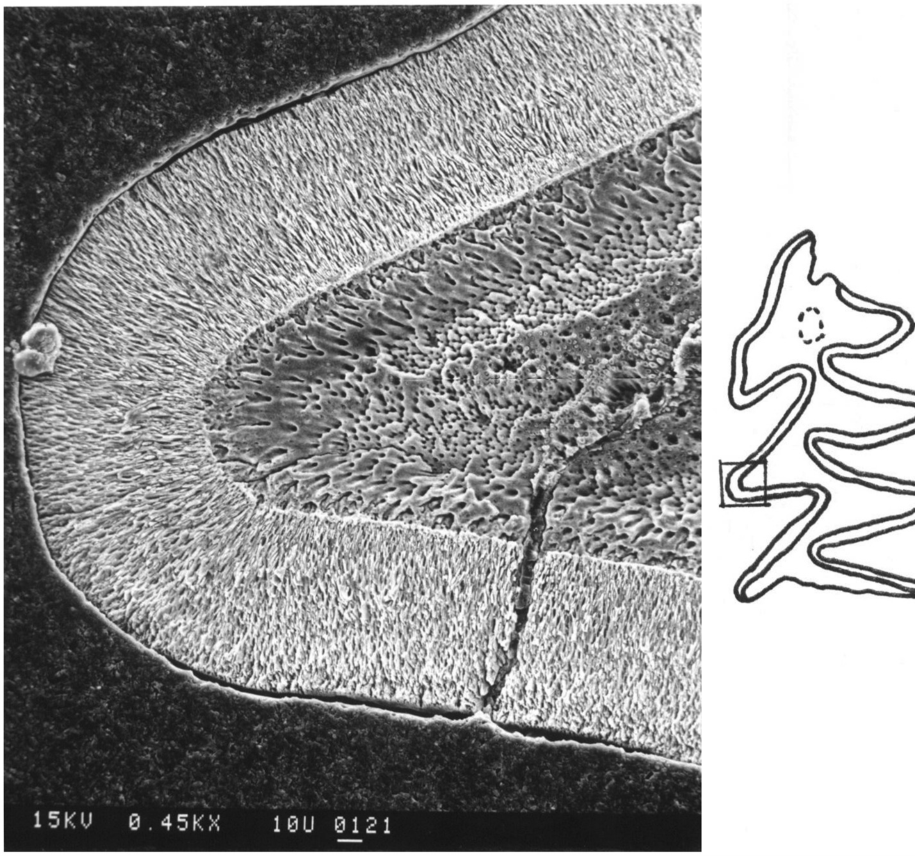

FIGURE 16. Schmelzmuster of *Mimomys panacaensis* on the alternating Triangle 2 of the same specimen as Figure 15. The leading edge is composed of a radial enamel layer and a discrete lamellar enamel layer. The trailing edge is composed of a radial enamel layer and a primitive tangential enamel layer.

sular process for the reception of the lower incisor is prominent, similar to that of *M.* (*Cosomys*) *primus*. However, several characters, including the number of roots on M3, the shape of ACC on m1, and the schmelzmuster, can readily differentiate *M. panacaensis* from *M.* (*Cosomys*) *primus* (Mou 1997, 1998).

M. panacaensis is recorded in the lowest level of the Rodent Ravine section and continued to the highest level in the Rodent Hill section.

Occurrence. Rodent Ravine section: 9702, 9619; Double Butte section: 9502; Rodent Hill section: 9601, 9602, 9609; Limestone Corner section: 8197, in the Fm., southeast Nevada.

Range. Early Blancan.

Subfamily PROMETHEOMYINAE Kretzoi, 1955
Genus NEVADOMYS gen. nov.

Diagnosis. Hypsodont, rooted, prismatic cheek teeth, lacking cement in reentrant angles. The three alternating triangles on m1 have labial triangles distinctly smaller than lingual triangles. An enamel islet on ACC is only present on very young individuals and disappears in early stage of wear. The enamel folds on the anterior margin of ACC are well developed and persist into late wear. Dentine tract on the labial side of molars is very low. M3 has a large posterior islet. An anterior islet is present or absent on M3. Primitive radial enamel is present on both leading and trailing edges of alternating triangles.

Differential diagnosis. The cheek teeth of *Nevadomys* can be distinguished from those of *Promimomys* by their larger size, higher dentine tract, and much less frequent retention of enamel islet on ACC of m1. *Nevadomys* differs from *Mimomys* by reduction of an islet on ACC of m1 and the much more frequent occurrence of large posterior enamel islet on M3. It is distinguished from *Pliopotamys* and *Pliophenacomys* by its smaller size, having three rather than five alternating triangles on m1, and usually having the posterior islet on M3.

Genotype. *Nevadomys fejfari*.

Etymology. *Nevad*, for the state of Nevada where the species ocurrs, plus *mys*, for mouse.

Nevadomys fejfari gen. et sp. nov.
(Tables 11-12; Figures 17-20)

Diagnosis. Size of cheek teeth is slightly larger than *Mimomys panacaensis*, similar to *M.* (*Ogmodontomys*) *sawrockensis*. "*Mimomys* kante" is present or absent on ACC of m1. One-third of M3s has a small anterior islet. M3 has two roots. Hypsodont, rooted, prismatic cheek teeth with no cement in reentrant angles, very low dentine tract on the labial side of molars. Of the alternating triangles on m1 labial triangles are distinctly smaller than lingual triangles. An enamel islet on ACC is only present on very young individuals and disappears in early wear. The enamel folds on the anterior margin of ACC are well developed and persisting into late wear. M3 has a large posterior islet. Primitive radial enamel is present on both leading and trailing edges of alternating triangles.

Holotype*.* UALP 21358, left mandible with m1-m2.

Type locality. UALP Locality 9504, in the Rodent Hill section.

Etymology*. fejfari*, in appreciation for Dr. Oldrich Fejfar who found the type locality of this species, and for his great achievements on European arvicoline rodents.

Material examined. UALP **Locality 9504:** partial palate with right M1-M2 and left M1-M2: 21637, 21638; partial palate with right M1-M3 and left M1: SBDM 1; partial palate with right M1-M2 and left M1: 21639; partial palate with right M2 and left M1-M2: 21641; partial palates with M1-M2: SBDM 16, 19; partial palate with left M2-M3: 21640; maxillaries with M1-M3: 21634-21636, SBDM 14; maxillaries with M1-M2: 21601, 21642, 22505, SBDM 15, 18, 20; left M2-M3: SBDM 8; maxillary with M1 alveolus: 21714; M1s: 21602—21607, 21713, SBDM 11, 17; M2s: 21608, 21609, SBDM 17, 21, 22; M3s: 21610-21616, 21600, 21362, 21715-21716, SBDM 9, 10, 12, 13; mandibles with m1-m3: 21356, 21643, 21644, 21646, SBDM 4, 23; mandibles with m1-m2: 21357, 21358, 21647-21650, 21651-21653, SBDM 5, 24-26, 30-32; mandibles with m2-m3s: 21712, 21645; mandible with m1: SBDM 6; mandible with m3: 21655; left m2-m3: 21617; m1s: 21618-21622, 21599, 21718-21720, SBDM 28, 29; m2s: 21623-21625, 21721, 21359, 21365, SBDM 27; m3s: 21360, 21361, 21626-21633, 21722, 21723, SBDM 33.

Description. The M1 has an anterior lobe and four alternating triangles. The apex of the second labial reentrant angle is slightly flexed posteriorly in moderately and well-worn specimens. The closure of alternating triangles is as follows: slightly open between the anterior lobe and Triangle 1, moderately open between Triangle 1 and Triangle 2; slightly or moderately open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. The anterior shelf is absent on M1. One slightly worn specimen (UALP 22505) has thinner enamel on the posterior surface, but the rest of enamel band has the same thickness. This thin-

TABLE 11. Measurements (in mm) of molars of *Nevadomys* n. gen. from the Panaca local fauna. N=number of specimens, M=mean, SD=standard deviation, CV=coefficient of variation, OR=observed range.

Locality		**Length**					**Width**				
		OR	N	M	SD	CV	OR	N	M	SD	CV
Nevadomys fejfari, n. sp.:											
9504	M1	22	2.60	0.112	4.33	2.44-2.76	22	1.63	0.091	5.57	1.52-1.73
	M2	22	2.20	0.082	3.75	2.12-2.40	22	1.51	0.097	6.44	1.36-1.67
	M3	14	1.94	0.079	4.05	1.78-1.90	14	1.24	0.044	3.51	1.16-1.27
	m1	12	2.94	0.180	6.12	2.64-3.28	12	1.37	0.072	5.27	1.20-1.44
	m2	22	2.06	0.080	3.91	1.92-2.44	22	1.36	0.095	7.00	1.20-1.48
	m3	11	1.77	0.102	5.75	1.52-1.89	11	1.04	0.052	4.97	0.96-1.10
Nevadomys cf. *N. fejfari*:											
9620	M1	13	2.49	0.084	3.38	2.40-2.60	13	1.60	0.071	4.45	1.44-1.68
	M2	10	2.16	0.080	3.72	2.04-2.32	10	1.46	0.091	6.23	1.32-1.60
	M3	14	1.94	0.063	3.27	1.80-2.04	14	1.23	0.087	7.05	1.00-1.32
	m1	9	2.95	0.125	4.24	2.76-3.16	9	1.39	0.057	4.08	1.32-1.48
	m2	15	2.01	0.036	1.78	1.96-2.08	15	1.43	0.042	2.98	1.34-1.48
	m3	16	1.76	0.095	5.39	1.64-1.96	16	1.18	0.053	4.51	1.04-1.26
Nevadomys downsi, n. sp.:											
9621	M1	8	2.63	0.107	4.07	2.48-2.76	8	1.60	0.124	7.76	1.44-1.80
	M2	7	2.20	0.077	3.49	2.08-2.32	7	1.46	0.089	6.09	1.32-1.60
	M3	13	2.02	0.055	2.74	1.92-2.08	13	1.25	0.066	5.28	1.08-1.36
	m1	4	2.96	0.139	4.68	2.76-3.08	4	1.36	0.033	2.40	1.32-1.40
	m2	10	2.03	0.076	3.72	1.96-2.20	10	1.39	0.041	2.97	1.32-1.44
	m3	10	1.86	0.055	2.98	1.76-1.92	10	1.18	0.054	4.56	1.08-1.24
Nevadomys lindsayi, n. sp.:											
9616	M1	7	2.84	0.083	2.93	2.72-2.92	7	1.73	0.056	3.26	1.68-1.80

ning is not observed in the other specimens. Each M1 has three roots, including the anterior, lingual, and posterior roots.

The M2 has an anterior lobe and three alternating triangles. The lingual and second labial reentrant apices are slightly flexed posteriorly. Closure between alternating triangles as follows: slightly open between the anterior lobe and Triangle 2, slightly or moderately open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. The reentrant pit is absent on the lingual side of anterior lobe. Enamel bands have the same thickness on the occlusal surface. A dentine tract is weakly developed on the lingual side of anterior lobe. Each M2 has three roots (Table 11), two anterior and one posterior. The lingual-anterior root is wide and strong.

The M3 has an anterior lobe, three alternating triangles, and a posterior lobe. Labial reentrants and triangles are much smaller than lingual reentrants and triangles. This molar is very distinctive by possessing a large enamel islet on the posterior lobe, even in young individuals. Thirty percent of M3s have a small anterior islet between the anterior lobe and the first labial reentrant. The majority of M3s (94%, see Table 12) have only two roots.

The palatal groove is as deep as that of *M.* (*Ogmodontomys*) *sawrockensis*, deeper than that of *M. panacaensis*. The mental foramen in the lower jaw is anterior to the root of m1 on the lateral surface of the dentary, about the same height as

TABLE 12. Measurements of some characters of *Nevadomys* from the Panaca local fauna. N=number of teeth with the character, ( ) =sample size, %=percentage of teeth with the character in the sample; M=mean of the measurement (in mm).

	N. fejfari Loc. 9504		**N. cf. N. fejfari Loc. 9620**		**N. downsi Loc. 9621**		***N. lindsayi*| Loc. 9616**	
	N	% or M	**N**	% or M	**N**	% or M	**N**	% or M
Enamel islet on AC of young-moderately worn m1s	3(8)	38%	1(4)	25%	2(7)	29%	3(10)	30%
Young-worn m1s without *Mimomys kante* on AC	4(13)	31%	9(14)	64%	12(12)	100%	13(13)	100%
M2s with 2 roots	0(11)	0%	0(9)	0%	0(17)	0%	0(12)	0%
M3s with 2 roots	16(17)	94%	17(17)	100%	14(16)	88%	2(16)	13%
M3s with anterior islet	6(20)	30%	3(16)	19%	1(19)	5%	1(17)	6%
M3s with posterior islet	20(20)	100%	14(16)	88%	15(19)	79%	17(17)	100%
Dentine tracts on the labial side of AC	6	0.63	10	0.53	4	0.84	7	0.77
Width of lower incisor	6	1.39	0	--	1	1.40	0	--
Diastema between I and m1	10	4.92	0	--	0	--	0	--
Mandibular depth below m1	11	6.05	0	--	0	--	0	--
Alveolar length of m1-m3	12	7.56	0	--	0	--	2	8.40
Palate width	4	3.03	0	--	0	--	0	
Alveolar length of M1-M3	3	7.28	0	--	0	--		

the apex of the masseteric crest. Its position is consistent in young and old individuals. The incisor passed laterally under m3, ending on the labial side of the ramus between the coronoid process and the condyle. In young individuals (UALP 21358), the capsular process is only an indistinct swelling, but in old individuals (UALP 21646), the process is prominent.

The m1 has a posterior lobe, three alternating triangles, and an ACC. Labial triangles are much smaller than lingual triangles. The degree of closure between the alternating triangles is the same as that of *M. panacaensis*: slightly open between the posterior lobe and Triangle1, moderately open between Triangle 1 and Triangle 2, slightly or moderately open between Triangle 2 and Triangle 3, and slightly or moderately open between Triangle 3 and ACC. The apex of the second lingual reentrant angle curves anteriorly. "*Mimomys* kante" is absent on two-thirds of m1s (Table 12). The enamel folds on the anterior-labial surface of ACC are well developed and extend quite low in depth, close to the base of the enamel (Figure 17.4-17.6). The enamel islet is much reduced compared to that of *M. panacaensis*. There is no islet on any moderately or well-worn specimens. Only young individuals show this structure, and it disappears after a slight wear (Table 12). The islet is small and circular. The dentine tract on the labial side of ACC is incipient, comparable to that of *M. panacaensis* (Table 12).

The m2 has a posterior lobe and four alternating triangles. Labial triangles are slightly smaller than lingual triangles. The degree of closure between alternating triangles is moderately open. The dentine tract is absent labially. In young individuals, enamel is thinner on the anterior surface of Triangle 4 (Figure 17.7), but the rest of enamel band is uniform in thickness. The posterior shelf is absent on m2.

The m3 has a posterior lobe and four alternating triangles, with two deep lingual reentrants and two shallow and broad labial reentrants. Labial triangles are slightly smaller than lingual triangles. Triangle 4 is reduced and confluent with Triangle 3. As in the m2s, enamel is thinner on the anterior surface of Triangle 4 of unworn or slightly worn specimens. The posterior shelf is absent on m3.

Four molars, including two m1s, one M1, and one M3 were chosen for examination of their schmelzmuster of enamel bands. These molars differ from *M. panacaensis* in that, the leading edge of ACC of m1 is occupied completely by primitive radial enamel, and no discrete lamellar enamel is seen anywhere even at the apex of alternating triangles (Figure 19.1). The leading edges of alternating triangles of all specimens have two radial enamel bands with about the same thickness,

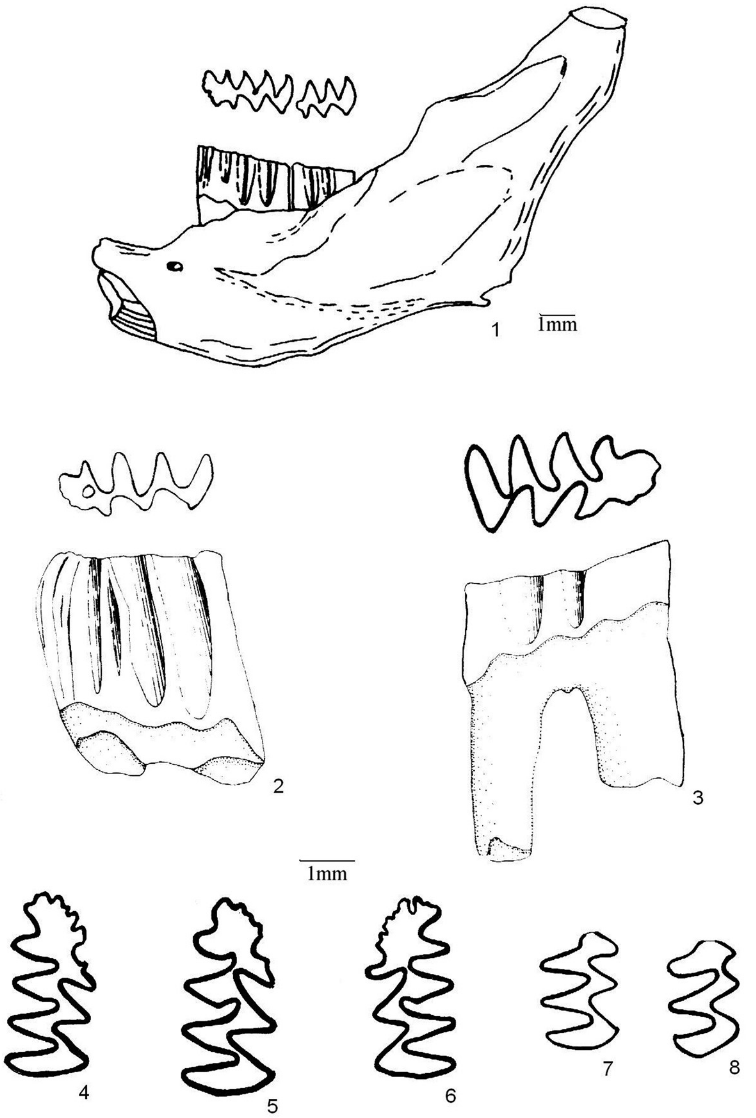

FIGURE 17. Lower molars of *Nevadomys fejfari* n. gen. and sp. from Locality 9504. 1: UALP 21358, occlusal and labial views of a left dentary with m1-m2 (Holotype). 2-3: occlusal and labial views of m1s, UALP 21620, 21619. 4-6: occlusal views of m1s, SBCM 5 and 6, UALP 21357. 7: occlusal view of a right m2, UALP 21623. 8: occlusal view of a right m3, UALP 21629.

which is similar to that of *M. panacaensis*. The inner radial enamel (close to dentine) is more compressed than the outer radial enamel (Figure 20). However, the trailing edges of alternating triangles are also composed of two radial enamel bands, similar to the schmelzmuster of the leading edges. Primitive tangential enamel is only present on the trailing edge of the posterior lobe of m1 (Figure 19.2) and the anterior lobe of upper molars. Some primitive tangential enamel can also be observed on the trailing edges of Triangle 2 of m1s.

Discussion. *Nevadomys fejfari* can be easily distinguished from North American arvicoline rodents by the shape of ACC on m1 and the large posterior enamel islet on M3. Enamel folds on the anterolabial side of ACC are well developed and extend down close to the base of the enamel. Enamel islet on ACC is much reduced, and the disappearance of this islet occurs at an earlier stage of wear than that of *M. panacaensis*, *M.* (*Cosomys*) *primus*, or species of *M.* (*Ophiomys*), in which the islet persists until the tooth is moderately worn. Reduction

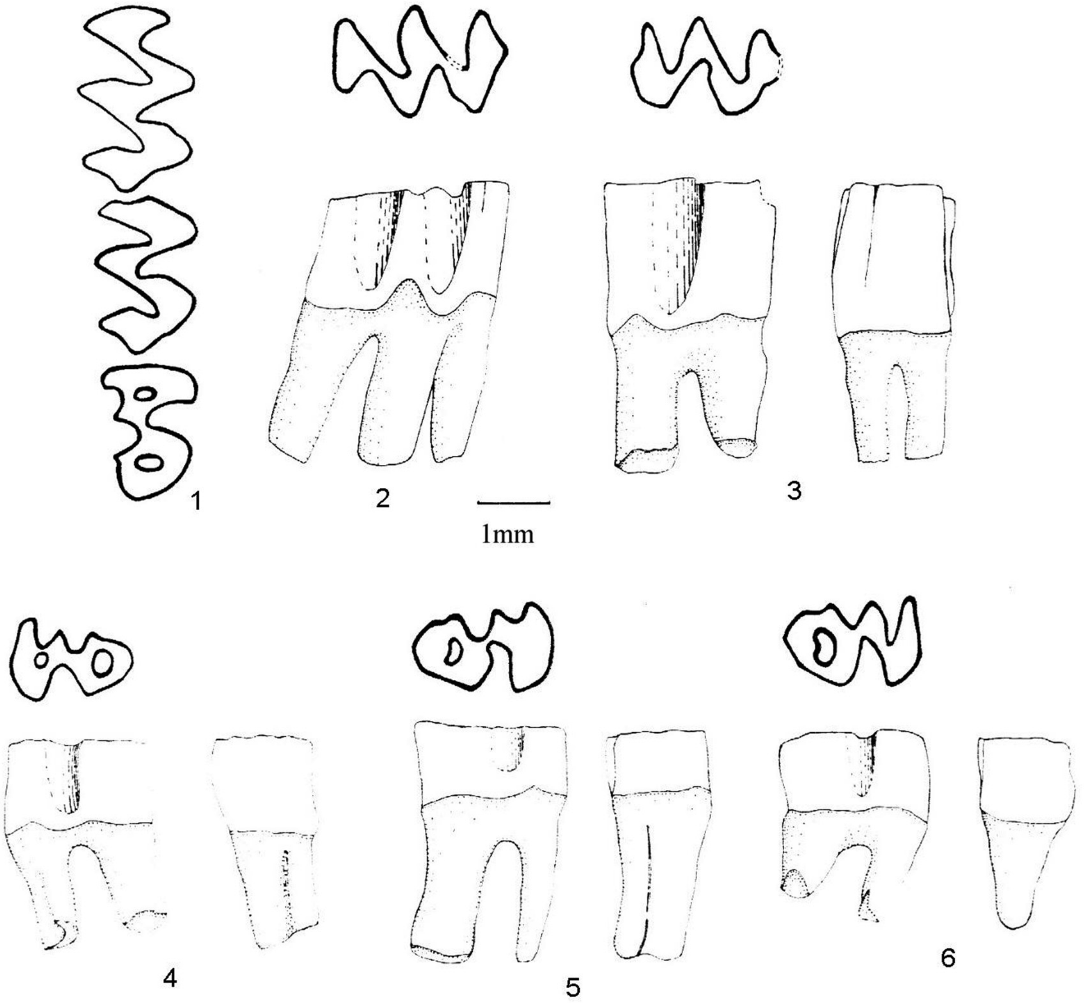

FIGURE 18. Upper molars of *Nevadomys fejfari* n. gen. and sp. from Locality 9504. 1: occlusal view of the right M1-M3, UALP 21636. 2: occlusal and labial views of a left M1, UALP 21602. 3: occlusal, labial, and anterior views of a left M2, UALP 21608. 4-6: occlusal, lingual, and anterior views of M3s, UALP 21611, 21610, and 21715.

of the enamel islet is also seen in the species of *M.* (*Ogmodontomys*) (Zakrzewski 1967) and *Pliophenacomys*, but *N. fejfari* can be readily distinguished from *M.* (*Ogmodontomys*) by the presence of enamel folds on its ACC and its distinctive M3. *Pliophenacomys* has five alternating triangles on m1, and the enamel folds on ACC are better developed on the labial side. The posterior islet on M3 in *Pliophenacomys* is absent. *Nevadomys fejfari* has a higher dentine tract on the labial side of ACC than *Promimomys* or *Microtoscoptes*; its dentine tract is comparable to *M. panacaensis* and *M.* (*Ophiomys*) *mcknighti*.

Compared to *M. panacaensis*, on one hand, *N. fejfari* has dental characters more derived in (1) reduction of enamel islet on ACC and (2) reduction of root numbers on M3; on the other hand, *N. fejfari* has some characters more primitive in the schmelzmuster of enamel bands and the enamel islet on M3. The thinner enamel on the anterior surface of m2 and m3, and on the posterior surface of upper molars that is characteristic of *N. fejfari* is not observed in *M. panacaensis*. However, this enamel thinning differs from the concept of enamel differentiation that we observe in advanced arvicolines, as the leading edges and trailing edges in these molars of *N. fejfari* have the same thickness. *N. fejfari* is less complex and probably more primitive than that of *M. panacaensis*. It has no traces of lamellar or discrete lamellar enamel anywhere in

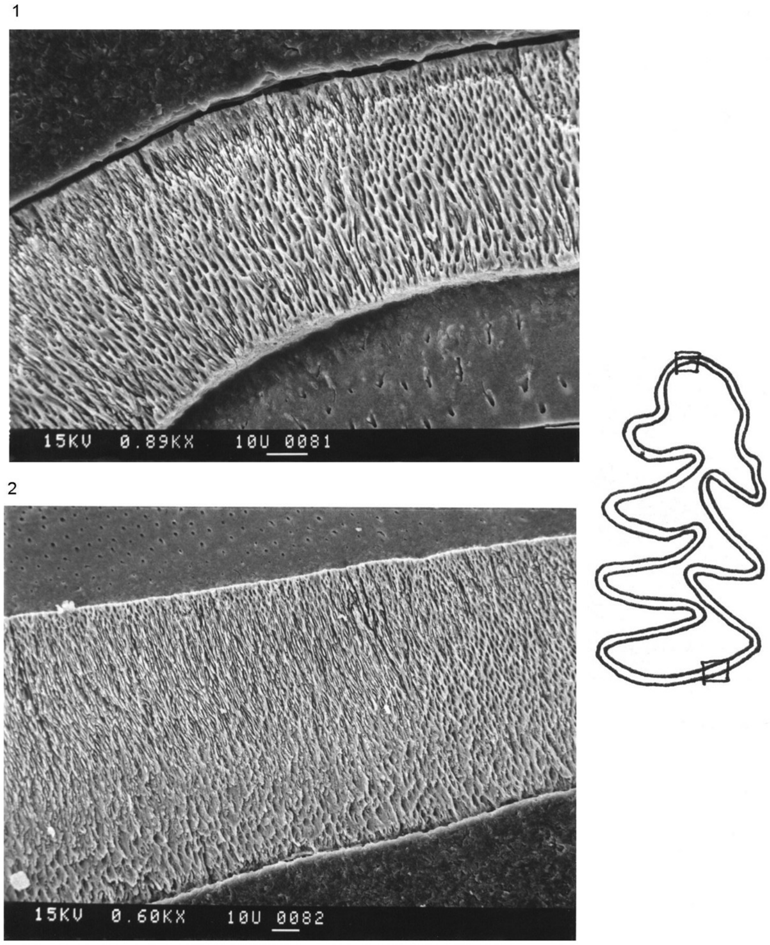

FIGURE 19. Schmelzmuster of *Nevadomys fejfari* n. gen. and sp. on the ACC and posterior lobe of m1. 1: the leading edge of ACC of a right m1 (21619) from Locality 9504, completely comprising radial enamel. 2: the trailing edge of posterior lobe of the same specimen. A primitive tangential enamel layer is developed on the outside (below right), about one-third of the enamel band. The other part is occupied by radial enamel.

the enamel band. The leading and trailing edges of alternating triangles are composed of radial enamel. The primitive tangential enamel on the posterior lobe of m1 and the anterior lobes of M1 and M3 is not developed as well as that in *M. panacaensis*.

This population has some characters similar to European *Mimomys vandermeuleni* (Fejfar et al., 1990): 1) There are deep and well-developed fine enamel folds on the anterior margin of ACC. 2) The M3 has a large posterior islet, and the anterior islet is also frequently present. 3) The M3 has two roots. 4) Size is similar. 5) Dentine tract on the labial side of ACC has similar height. However, *M. vandermeuleni* has a deep and large enamel islet on ACC of m1. Its descendant in Europe, *M. davakosi*, retains this character. Since *N. fejfari* has so many distinctive characters compared to *M. panacaensis* as well as the other known *Mimomys*, I consider it a new genus, and it is probably native to North America. For a phylogenetic discussion, please see the section "Remarks on *Nevadomys*" below

Occurrence. Rodent Hill section: 9504, in the Fm., southeast Nevada.

Range. Early Blancan.

Nevadomys cf. *N. fejfari*
(Tables 11-12; Figures 21-22)

Material examined. UALP

Locality 9620: maxillaries with M1-M2: 21887, 21888, 21895; M1s: 21885, 21886, 21889-21894, 21896-21900, 21902-21904; M2s: 21901, 21905-21915, 21972; M3s: 21916-21935; right mandible with m1-m3: 21936; mandibles with m1-m2: 21937-21939; left m2-m3: 21962; m1s: 21940-

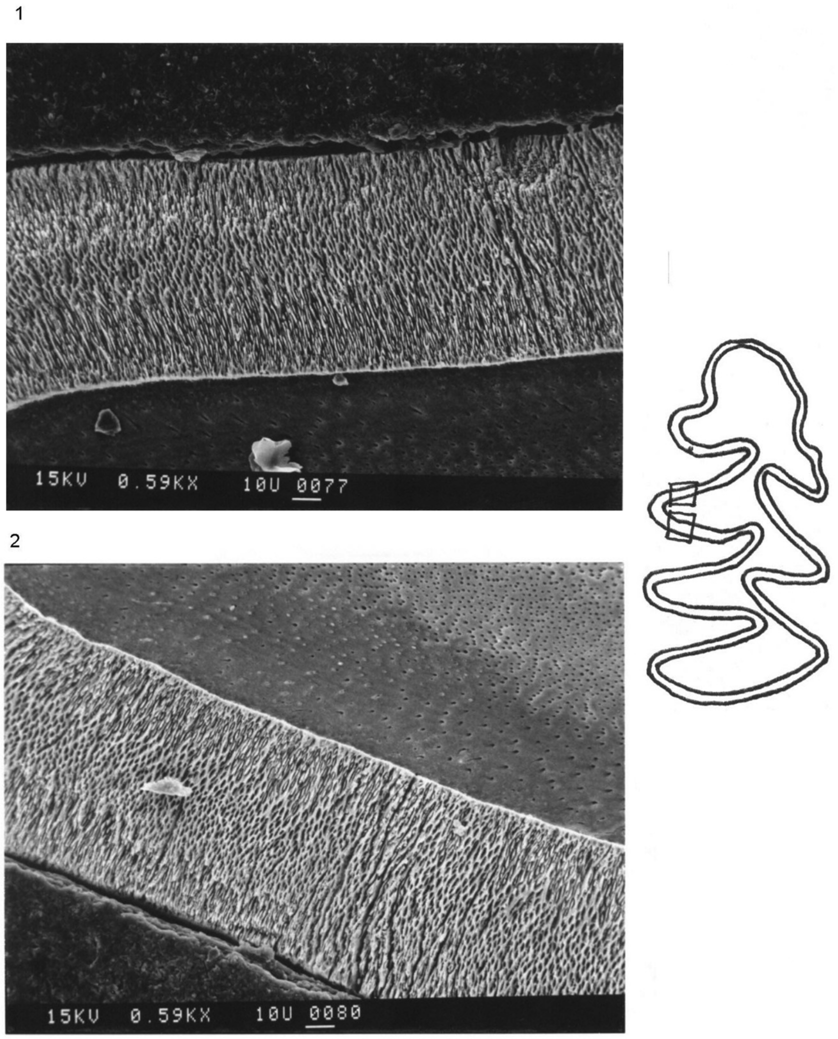

FIGURE 20. Schmelzmuster of *Nevadomys fejfari* n. gen. and sp. on the alternating Triangle 3 of m1. 1: the leading edge of Triangle 3 of the same tooth as Figure 5.5. Two radial enamel layers are present: the inner layer (close to dentine, below) is more compressed than the outer layer (up). 2: the trailing edge of Triangle 3 of the same tooth, with the same pattern as the leading edge.

21961; m2s: 21963-21971; 21973-21977; 21978-21995.

Description. The M1 has an anterior lobe, three alternating triangles, and a posterior lobe. An anterior shelf is present on 18% (3 out of 17) of the observable specimens. One M1 has an enamel interruption on the posterior surface of Triangle 4 (UALP 21894). The M2s are similar to those of *N. fejfari* from the type locality. Each M2 has three roots.

As seen on the M3s of *N. fejfari* from the type locality, the majority of M3s (88%) from Locality 9620 have a large posterior enamel islet, and each tooth has only two roots. The teeth that do not have a posterior enamel islet have the Triangle 3 bending posteriorly. This bending is not seen in any M3 of *M. panacaensis*.

The m1 has a posterior lobe, three alternating triangles, and an ACC. As in the m1s from the type locality of *N. fejfari*, the enamel islet is only present on young individuals (Table 12; Figure 21.1-21.4), and fine enamel folds are well developed on the anterior and anterolabial surfaces of ACC. The degree of closure between alternating triangles is similar to that of *N. fejfari* from the type locality. The m2s and m3s are similar to *N. fejfari*, respectively. The enamel on the anterior surface of Triangle 4 is thinner than the rest of the enamel band on unworn or slightly worn m2s and m3s, but in more

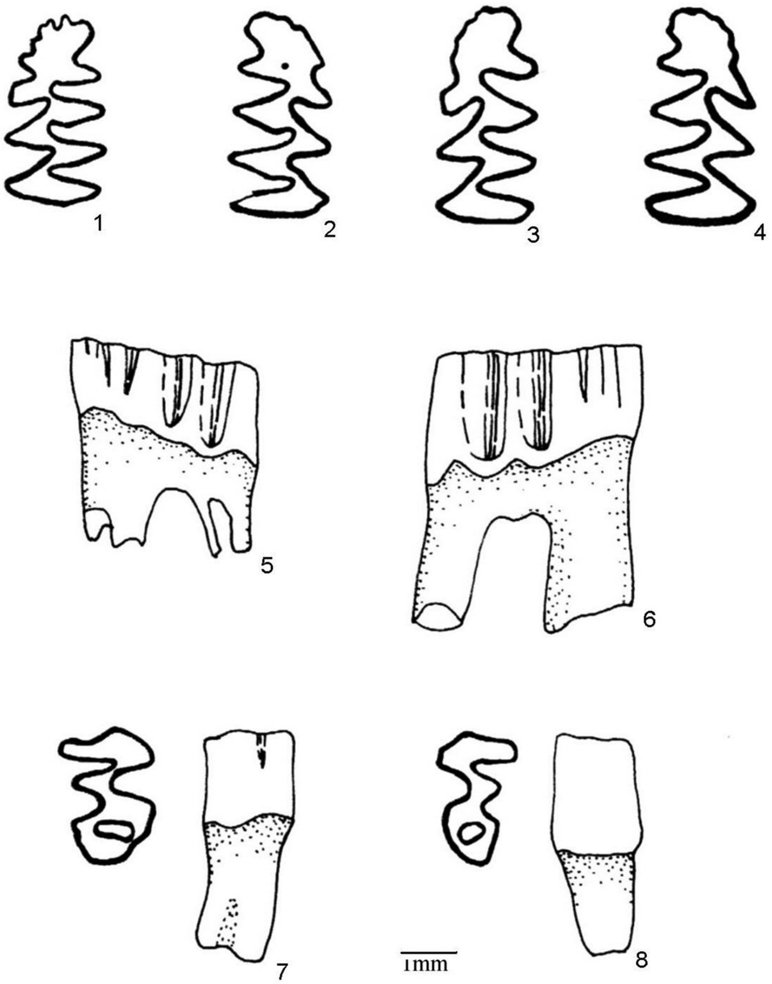

FIGURE 21. *Nevadomys* cf. *N. fejfari* n. gen and sp. from Locality 9620. 1-4: occlusal views of m1s, UALP 21947, 21940, 21944, and 21943. 5: labial view of 1(21947). 6: labial view of 2 (21940). 7-8: occlusal and anterior views of M3s, UALP 21921 and 21916.

worn specimens, the enamel thinning is absent. The posterior shelf is absent in all m2s and m3s.

Moderately worn dentary UALP 21936 may represent an aberrant *N. fejfari* in that its mental foramen is situated on the labial side of the mandible, slightly lower than the apex of masseteric crest (Figure 22). This position is lower than the mental foramen of most specimens of *N. fejfari*, but a similar low position is also seen on specimens of *Nevadomys* n. sp. from Locality 9621 (UALP 22047 and 22048). The m1 on UALP 21936 has a posterior lobe, three alternating triangles, and an ACC. No enamel islet is present on the ACC. A “*Mimomys* kante” is well developed on the primary wing.

Two m1s and one M1 are investigated for schmelzmuster. On one m1, a well developed, thick lamellar enamel layer is present on the leading edge of ACC (Figure 23.1), but on the other m1, a thick discrete lamellar enamel layer is observed. The leading edges of alternating triangles are composed of two radial enamel layers, similar to those of *N. fejfari* from the type locality, and the trailing edges have the same schmelzmuster as the leading edges with the exception that primitive tangential enamel is observed on the trailing edges of the posterior lobe of m1s and anterior lobe of the M1 (Figure 23.2).

Discussion. Except for the schmelzmuster on the ACC, other characters are very similar to those of *Nevadomys fejfari* from the type locality. The schmelzmuster on the ACC of m1 from this population is more derived than that of *N. fejfari* and comparable to that of *M. panacaensis*. However, the schmelzmuster on the rest of the enamel bands is

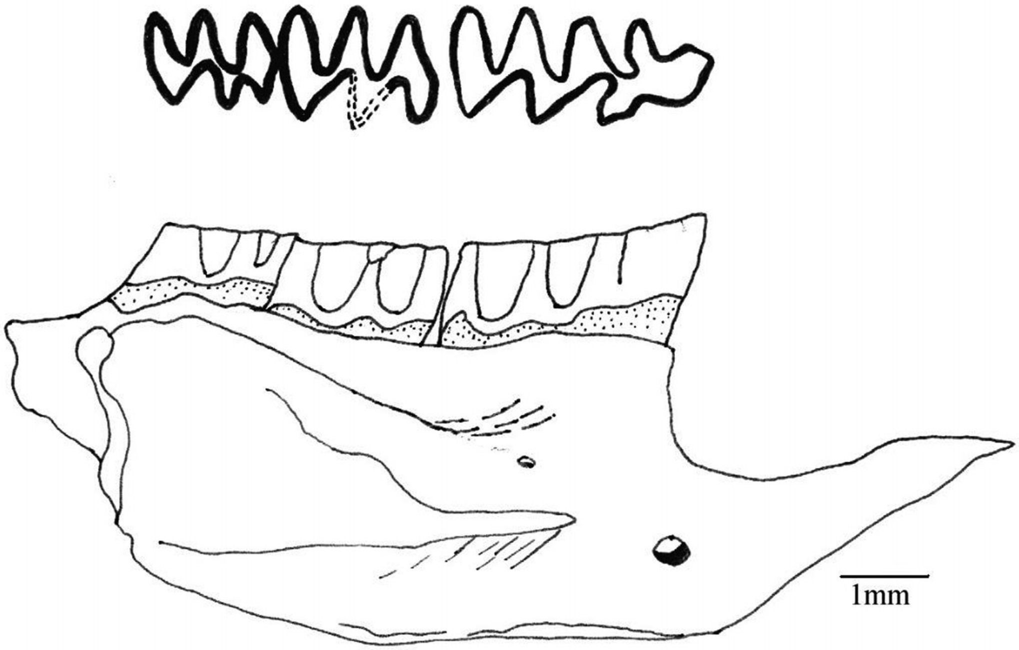

FIGURE 22. A lower jaw of *Nevadomys* cf. *N. fejfari* n. gen and sp. from Locality 9620.

comparable to that of *N. fejfari* but more primitive than that of *M. panacaensis*. The characters of M3s in this population are distinctive from *M. panacaensis* in that M3s of *N. fejfari* have two roots and well-developed large posterior enamel islet.

Occurrence. Brown Bone Beds: 9620, in the Panaca Fm., southeast Nevada.

Range. Early Blancan.

Nevadomys lindsayi gen. et sp. nov.
(Tables 11-12; Figures 24-28)

Diagnosis. Largest species of *Nevadomys*. It has no "*Mimomys* kante" and ACC is simple, without extra triangles. Majority (87%) of M3s have three roots, having the anterior-lingual root thin and largely reduced.

Holotype. UALP 21809: an old adult with left and right mandibles with m1-m3.

Type locality. UALP Locality 9616, in the Rodent Ravine section.

Etymology. *lindsayi*, named for Dr. Everett H. Lindsay for his outstanding contributions to the research of North American rodents.

Material examined. UALP **Locality 9616:** M1s: 21762-21776; M2s: 21777-21789; M3s: 21790-21808; m1s: 21810-21824; m2s: 21825-21839; m3s: 21840-21848.

Description. The M1 has an anterior lobe and four alternating triangles. The apices of labial reentrant angles are flexed posteriorly in moderately well worn specimens. The degree of closure between the anterior lobe and Triangle 1 is slightly open, open between Triangle 1 and Triangle 2, slightly open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. The enamel is thinner on the posterior surface of Triangle 4 on a slightly worn specimen (UALP 21771). Other enamel bands have the same thickness. No anterior shelf is seen on the M1s. Each M1 has three roots, including the anterior, lingual, and posterior.

The M2 has an anterior lobe and three alternating triangles. The lingual reentrant apex is slightly curved posteriorly. The degree of closure between the anterior lobe and Triangle 1 is slightly open, slightly to moderately open between Triangle 1 and Triangle 2, and open between Triangle 2 and Triangle 3. The dentine tract is weakly developed on the lingual side of anterior lobe. No reentrant pit is seen on the M2s. Each M2 has three roots (Table 11), two anterior and one posterior. The lingual-anterior root is wide and strong.

The M3 has an anterior lobe, three alternating triangles, and a posterior lobe. Labial triangles are much smaller than lingual ones. Each M3 has a large posterior islet. As in the type population of *N. fejfari*, this islet occurs at unworn stage and lasts

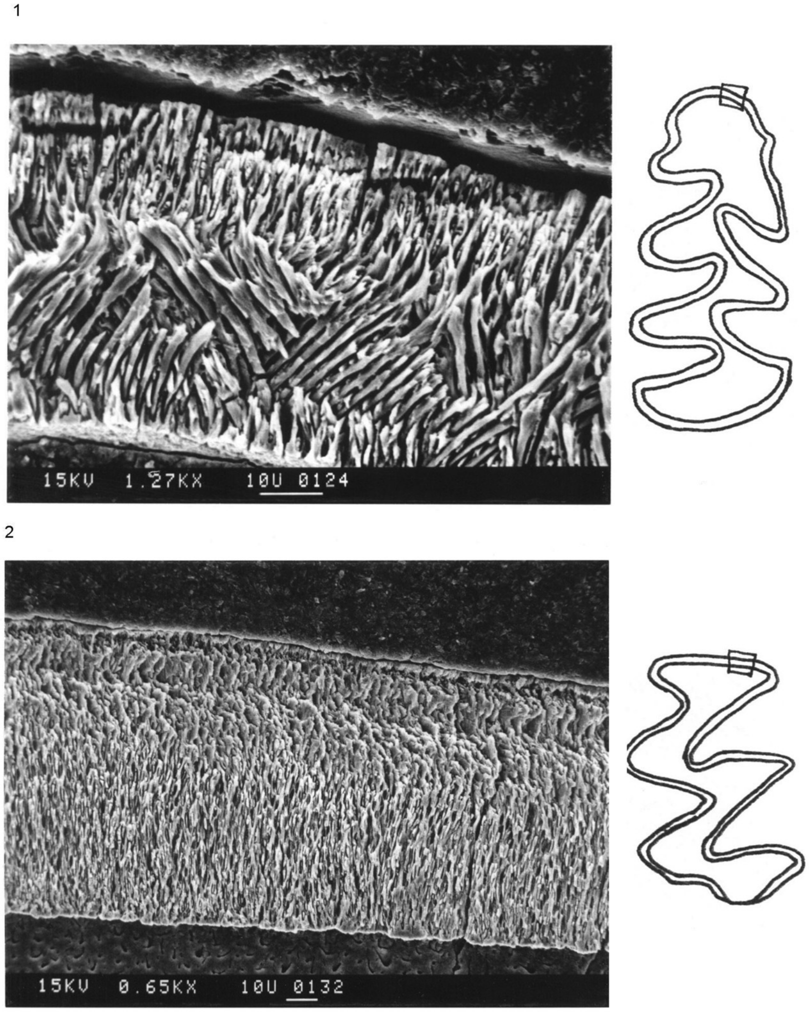

FIGURE 23. Schmelzmuster of *Nevadomys* cf. *N. fejfari* n. gen and sp. of the ACC of m1 and the trailing edge of M1. A: the leading edge of ACC of a right m1 (21945) from Locality 9620. A true lamellar layer is on the inside (below), occupying two-thirds of the enamel band. Outside is a thin radial enamel layer. B: the trailing edge of anterior lobe of a left M1 (21894) from Locality 9620. A primitive tangential enamel layer is present on the outside (up), occupying one-third of the enamel band.

until well-worn. An anterior islet is occasionally present (1 out of 17, 6%). The majority of M3s have three roots (14 out of 16, 88%), two anterior and one posterior. The anterior root at the lingual side is much reduced and the thinnest of the three roots (Figures 25.5-25.6). On the two M3s with only two roots, the two anterior roots are fused with a groove (Figure 25.7).

The m1 has a posterior lobe, three alternating triangles, and an anteroconid complex. Its size is significantly larger than *N. fejfari* or *N. downsi.* Only on two juvenile m1s is there an enamel islet on ACC. The islet is small and circular, like those of *N. fejfari*. The degree of closure between alternating triangles is slightly open to moderately open. The apex of the second lingual reentrant is curved forward. "*Mimomys* kante" is absent on each m1. The fine enamel folds are well developed on the anterior margin of ACC, and they disappear at the worn stage. The dentine tract on the labial side of ACC is incipient, similar to that of *N. fejfari* (Table 12).

The m2 has a posterior lobe and four alternating triangles. Labial triangles are slightly smaller than lingual triangles. The degree of closure between the posterior lobe and Triangle 1 is slightly open or moderately open, open between Triangle 1 and Triangle 2, slightly or moderately open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. The dentine

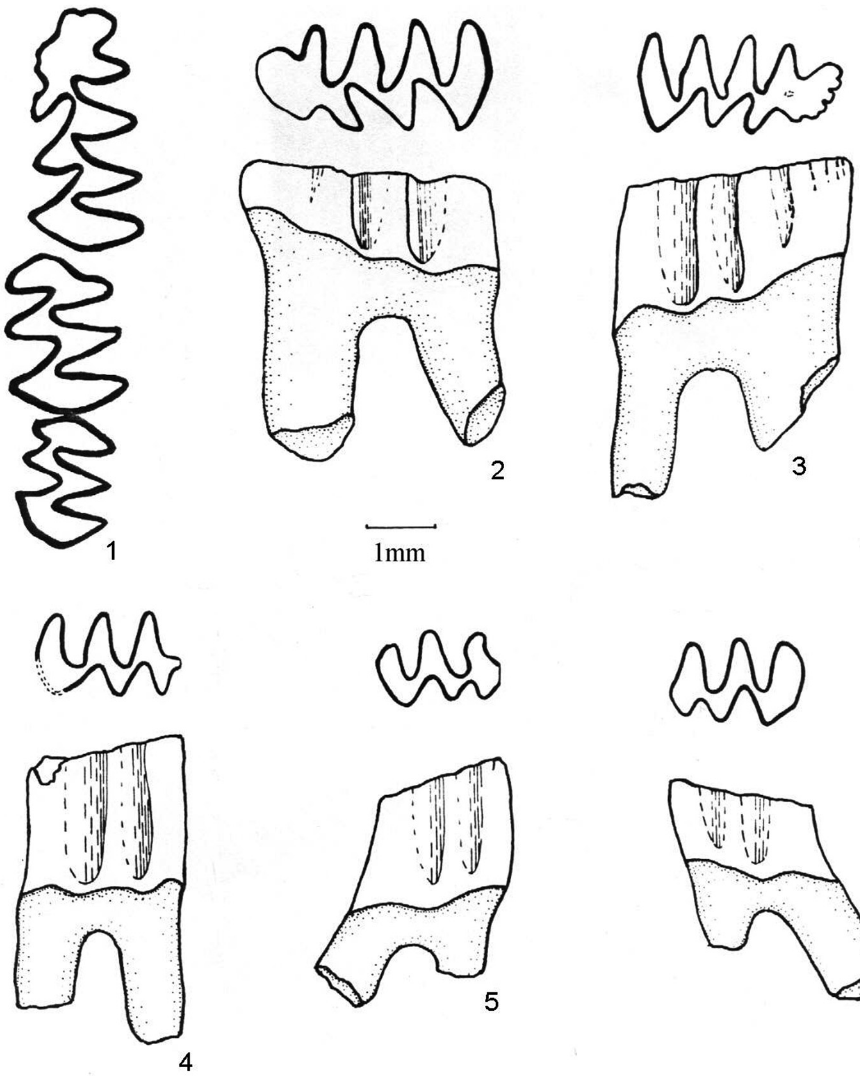

FIGURE 24. Lower molars of *Nevadomys lindsayi* n. gen. and sp. 1. occlusal view of a left m1-m3, UALP 21809. 2-3: occlusal and labial views of m1a, UALP 21810 and 21811. 4: occlusal and labial views of a right m2, UALP 21829. 5-6: occlusal and labial views of m3s, UALP 21840 and 21841.

tract is absent labially. As in *N. fejfari*, thinner enamel is present on the anterior surface of Triangle 4 in unworn or slightly worn specimens (Figure 24.4), but other enamel bands are uniform in thickness. No posterior shelf is present on any m2.

The m3 has a posterior lobe and four alternating triangles, with labial triangles distinctly smaller than lingual triangles. The degree of closure between the posterior lobe and Triangle 1 is slightly open or moderately open, open between Triangle 1 and Triangle 2, slightly or moderately open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. As in the m2s, thinner enamel is present on the anterior surface of slightly worn specimens (Figure 24.5). The posterior shelf is absent on m3.

Four teeth, including two m1s, one M1, and one M3, are subjected to schmelzmuster examination. As in *N. fejfari*, the leading edge of ACC is composed totally of radial enamel (Figure 26.1). The leading and trailing edges both show two radial enamel bands, with the inner one more compressed (Figure 27). Some primitive tangential enamel can be seen on the trailing edges of the labial alternating triangles. The trailing edge of the posterior lobe presents a tangential enamel layer (Figure 28.2) better developed than that of *N. fejfari*.

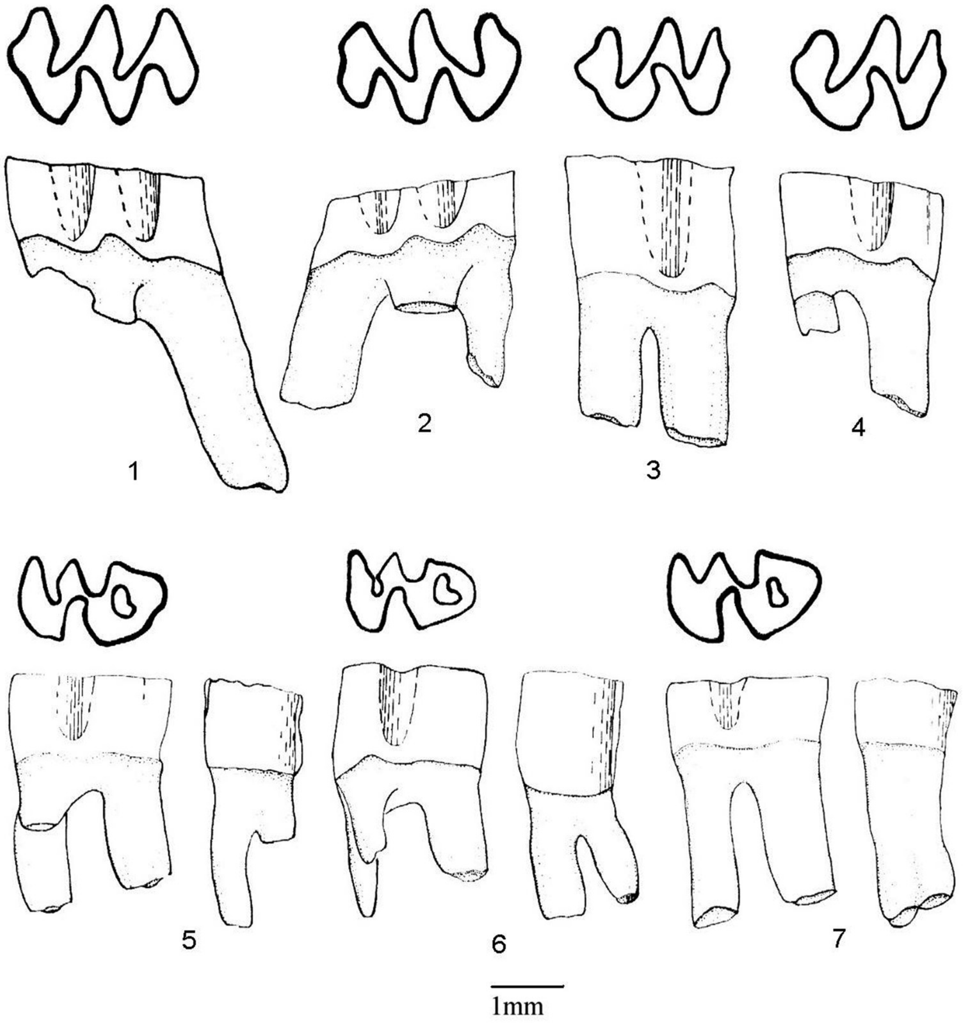

FIGURE 25. Upper molars of *Nevadomys lindsayi* n. gen. and sp. 1-2: occlusal and lingual views of M1s, UALP 21762 and 21763. 3-4: occlusal and lingual views of M2s, UALP 21777 and 21779. 5-7: occlusal, lingual, and anterior views of M3s, UALP 21791, 21790, and 21792.

Since one of the differences of *Nevadomys lindsayi* from *N. fejfari* is the three-rooted M3s, UALP 21794 was chosen to represent M3 schmelzmuster. It presents the same pattern as that of *N. fejfari*. One-third of the enamel thickness of primitive tangential enamel is present on the trailing edge of the anterior lobe. The leading and trailing edges of alternating triangles are composed of radial enamel.

Discussion. The well-developed enamel folds on the anterior margin of ACC of m1, the reduction of enamel islet on ACC, and the presence of large posterior islet on each M3, strongly indicate that the population from Locality 9616 is a species within the genus *Nevadomys*. Two distinctive characters of this population can be used to differentiate it from *N. fejfari*: 1) significantly larger size and 2) the majority of M3s developing three roots (88%, 14 out of 16). *N. fejfari* has only has 6% (1 out of 17) M3s with three roots.

The schmelzmuster of *Nevadomys lindsayi* is primitive in that no trace of discrete or true lamellar enamel is seen on any part of the enamel band, and primitive tangential enamel is poorly developed. This pattern is very similar to that of *N. fejfari*. A slight difference from *N. fejfari* is that *N. lindsayi* has true tangential enamel on the trailing edge of posterior lobe of m1s.

Locality 9504, where *Nevadomys fejfari* came from, is stratigraphically higher than Locality 9616. *N. fejfari* could be derived from *N. lindsayi* by the fusion of two anterior roots on M3 and decreasing in overall size.

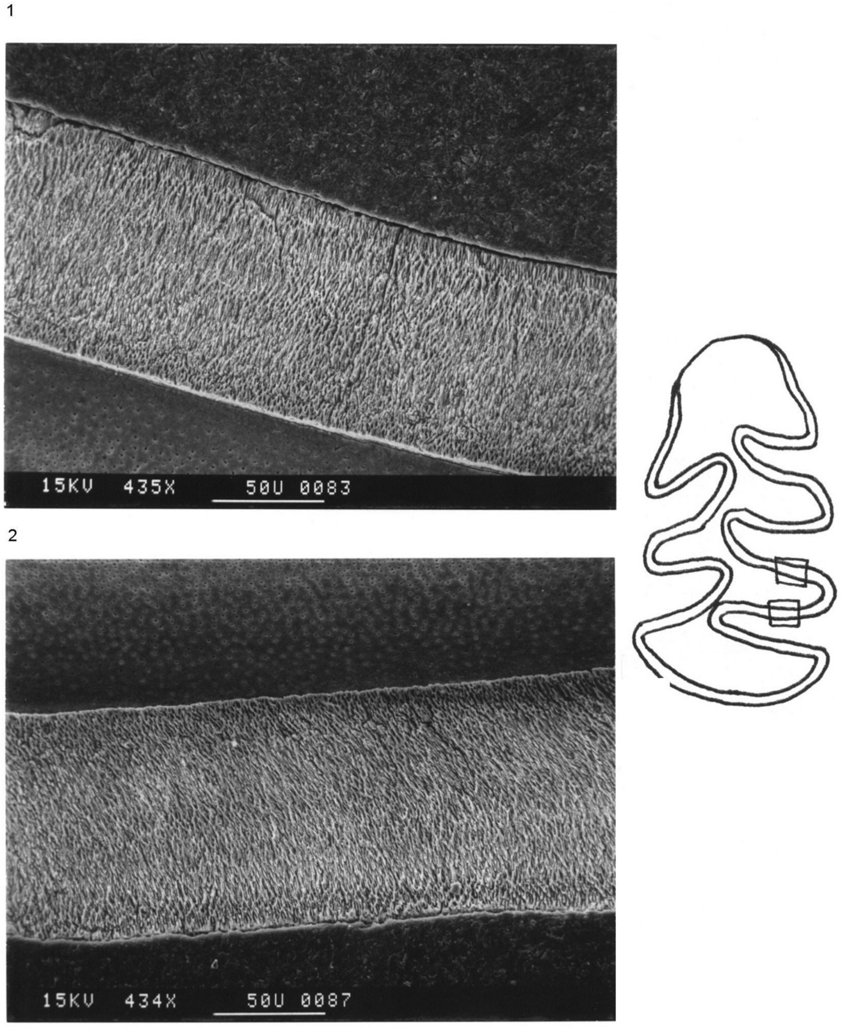

FIGURE 26. Schmelzmuster of *Nevadomys lindsayi* n. gen. and sp. on the ACC of m1 and the trailing edge of M1. 1: the leading edge of ACC of a right m1 (21816) from Locality 9616, occupied by radial enamel. 2: the trailing edge of a left M1 (21765) from Locality 9616. Traces of primitive tangential enamel are observed close to the apex.

Occurrence. Rodent Ravine section: 9616, in the Panaca Fm., southeast Nevada.

Range. Early Blancan.

Nevadomys downsi gen. et sp. nov.

(Tables 11-12; Figure 29-31)

Diagnosis. Size similar to *Nevadomys fejfari*. ACC of m1 is four-lobed with a deep prism fold on the anterior and lingual surfaces. "*Mimomys* kante" is absent on ACC of m1. Majority of M3s have a large posterior islet. M3 has two roots.

Holotype. UALP 22054, a left m1.

Type locality. UALP Locality 9621, in the Brown Bone Beds section.

Etymology. *downsi*, in appreciation for the late William R. Downs who found several localities in the Fm.

Material examined. UALP

Locality 9621: right maxillary with M1-M2: 22091; right M2-M3: 22028; M1s: 21996-22010; M2s: 22011-22027; M3s: 22029-22046; right mandible with m1-m2: 22047; right mandible with m1: 22048; left m1-m2: 22049; m1s: 22050-22064; 22065-22076; m3s: 22077-22090.

Description. The M1 has an anterior lobe and four alternating triangles. Lingual triangles are distinctly smaller than labial triangles. The apices of labial reentrant angles are flexed slightly posteriorly in moderately and well-worn specimens. The degree of closure between the alternating triangles is

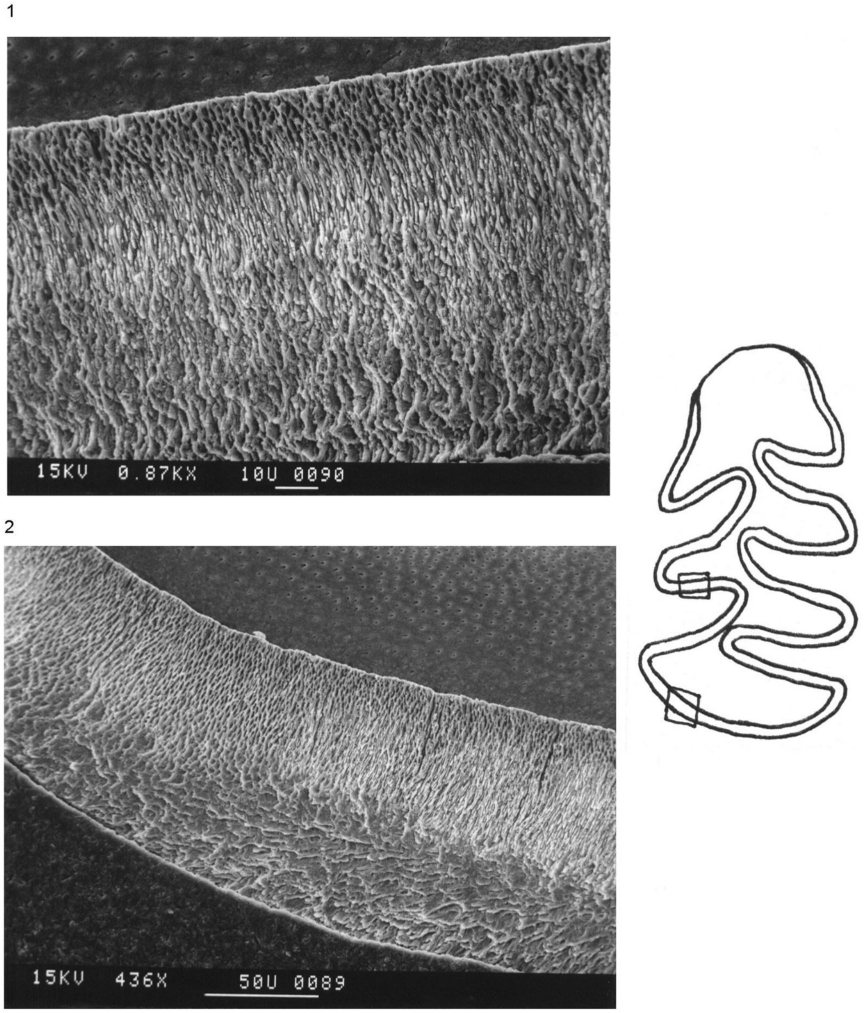

FIGURE 27. Schmelzmuster of *Nevadomys lindsayi* n. gen. and sp. on the alternating triangles of m1. 1: the leading edge of Triangle 1 of a left m1 (21817) from Locality 9616, totally composed of radial enamel. 2: the trailing edge of Triangle 1 of the same tooth, with the same pattern as the leading edge.

slightly open between the anterior lobe and Triangle1, moderately open between Triangle 1 and Triangle 2, closed or slightly open between Triangle 2 and Triangle 3, and moderately open between Triangle 3 and Triangle 4. Enamel is thinner on the posterior surface of Triangle 4 on a slightly worn specimen (UALP 21997). Otherwise, enamel bands have the same thickness. Interestingly, on 40% (4 out of 10) of the specimens, an anterior-directed enamel prism is developed from the base of the crown on the anterior surface (Figure 29.11). Two of them are very distinct, and the other two are low ridges. An anterior shelf is absent on the M1s. Each M1 has three roots, including the anterior, lingual, and posterior ones.

The M2 has an anterior lobe and three alternating triangles. Lingual triangles are slightly smaller than labial triangles. The lingual reentrant apex is slightly curved posteriorly. The degree of closure between the anterior lobe and Triangle 2 is slightly open; it is slightly open between Triangle 2 and Triangle 3, and moderately open between Triangle 3 and Triangle 4. The dentine tract is incipiently developed on the lingual side of anterior lobe. No enamel prism is observed on the anterior surface of M2. Each M2 has three roots (Table 11), two anterior and one posterior. The lingual-anterior root is wide and strong.

The M3 has an anterior lobe, three alternating triangles, and a posterior lobe. Labial triangles and reentrants are much smaller than lingual ones. Seventy-nine percent of M3s have the posterior islet. Three specimens (UALP 22033, 22037, and 22038) have the islet incompletely closed by hav-

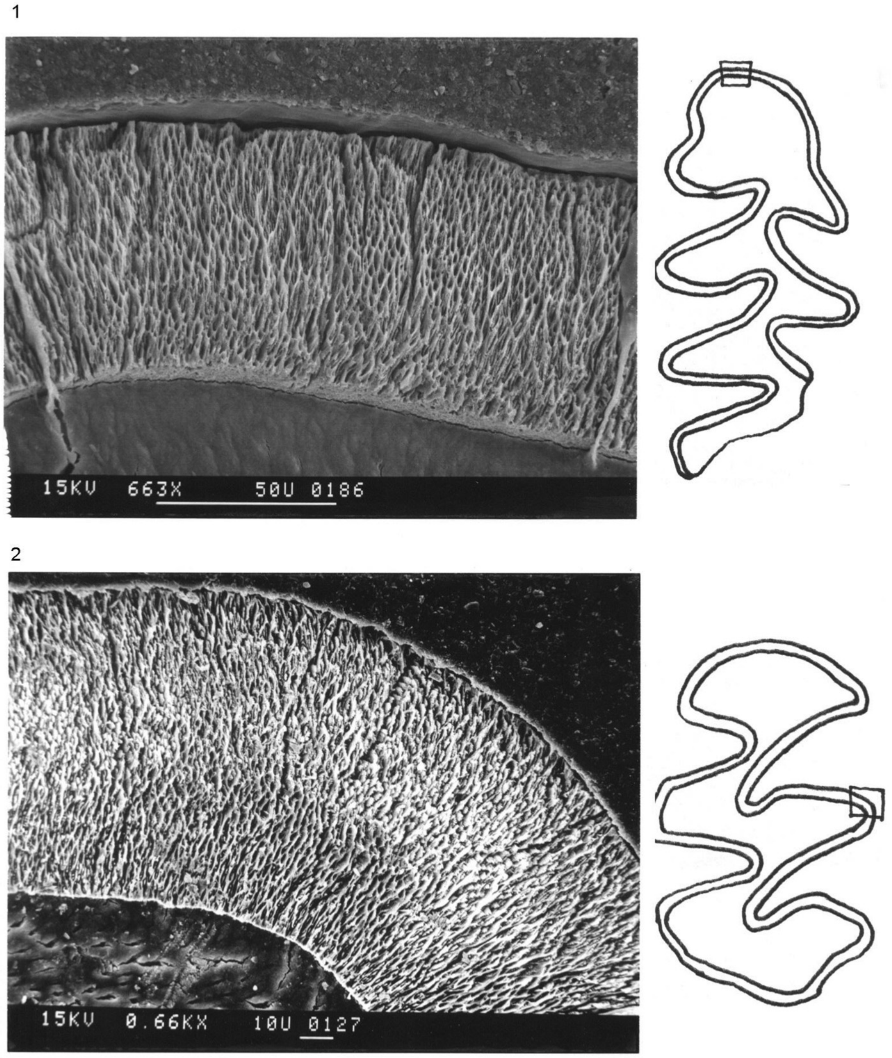

FIGURE 28. Schmelzmuster of *Nevadomys lindsayi* n. gen. and sp. on the trailing edge of m1. 1: the trailing edge of Triangle 2 of the same tooth of Figure 26. A primitive tangential enamel layer can be recognized outside (below); radial enamel layer is inside (up). 2: the trailing edge on the labial side of posterior lobe of the same tooth; tangential enamel layer (below left) occupies about half of the enamel band. The other half is radial enamel layer.

ing the posterior lingual reentrant slightly open. The islet will be formed with further wear. Four specimens (UALP 22031, 22032, 22034, and 22035) lack the posterior islet and have the posterior lingual reentrant open until late wear. Within these four specimens, three have a posteriorly bent Triangle 3 (Figure 29.12), as some M3s of *Nevadomys* cf. *N. fejfari* from Locality 9620. One (UALP 22032) out of 19 specimens has a small anterior islet. As in *N. fejfari*, the majority of M3s (88%) have only two roots.

The m1 from this site has a posterior lobe, three alternating triangles, and the ACC. Labial triangles are distinctly smaller than lingual triangles. The enamel folds are well developed on the anterior margin of ACC, but they disappear at the moderately worn stage. After the crown is slightly worn, a single narrow but deep fold is preserved on the anterior margin of ACC. A labial fold persists on the ACC until moderate wear. The ACC do not have "*Mimomys* kante." An enamel islet is present only on very young individuals. The degree of closure between the posterior lobe and Triangle 1 is slightly open; it is open between Triangle 1 and Triangle 2, moderately open between Triangle 2 and Triangle 3, and slightly to moderately open between Triangle 3 and the ACC. The dentine tract is gently rounded, slightly higher than *N. fejfari* from Locality 9504 and 9620 (Table 12).

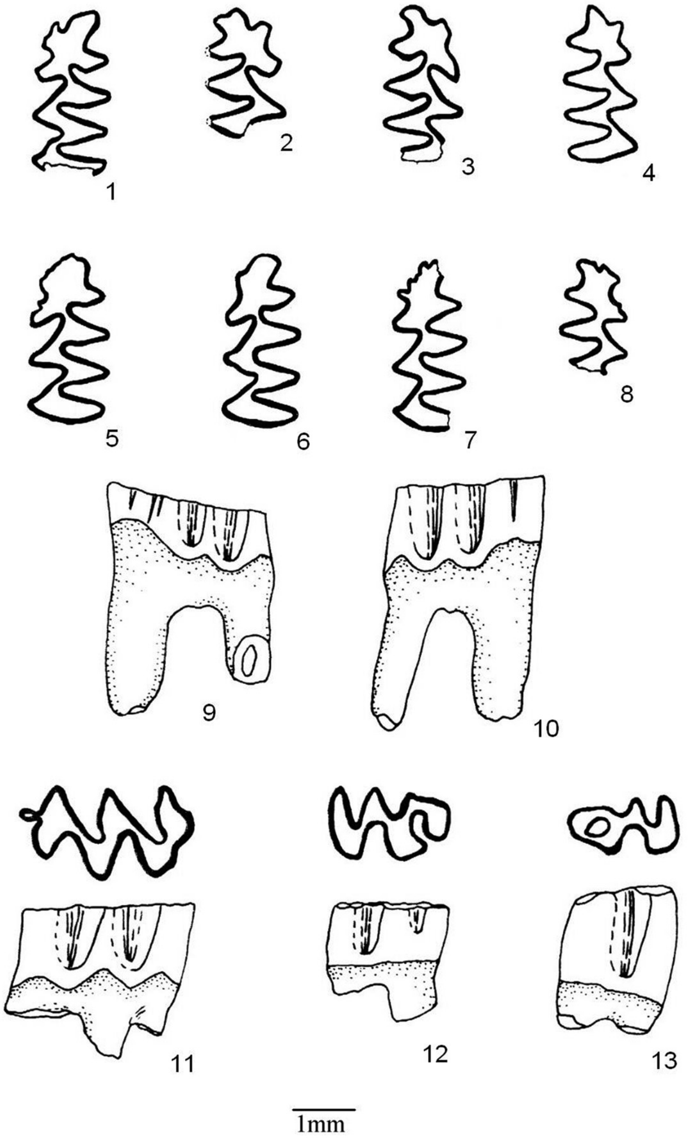

FIGURE 29. *Nevadomys downsi* n. gen. and sp. from Locality 9621. 1-8: occlusal views of m1s, UALP 22.54, 22060, 22053, 22051 (used for schmelzmuster), 22050, 22049, 22052, 22055. 9: labial view of E (22050). 10: labial view of D (22051). 11: occlusal and lingual views of a left M1, UALP 22001. 12-13: occlusal and lingual views of M3s, UALP 22033, 22036.

The m2 has a posterior lobe and four alternating triangles. Labial triangles are much smaller than lingual triangles. The degree of closure between alternating triangles is slightly open between the posterior lobe and Triangle 1, moderately open between Triangle 1 and Triangle 2, slightly open between Triangle 2 and Triangle 3, open between Triangle 3 and Triangle 4. The dentine tract is incipient labially. As in *N. fejfari*, thinner enamel is present on the anterior surface of Triangle 4 in unworn or slightly worn specimens, but the rest of the enamel band are uniform in thickness. No posterior shelf is present on any m2.

The m3 has a posterior lobe and four alternating triangles, with labial triangles much smaller than lingual triangles. The degree of closure between alternating triangles is slightly open between the posterior lobe and Triangle 1, moderately open between Triangle 1 and Triangle 2, slightly open between Triangle 2 and Triangle 3, and open between Triangle 3 and Triangle 4. As in the m2s, thinner enamel is present on the anterior surface of unworn or slightly worn specimens. No posterior shelf is present on any m3.

Two m1s and one M1 were examined under SEM for their schmelzmuster. The leading edge on

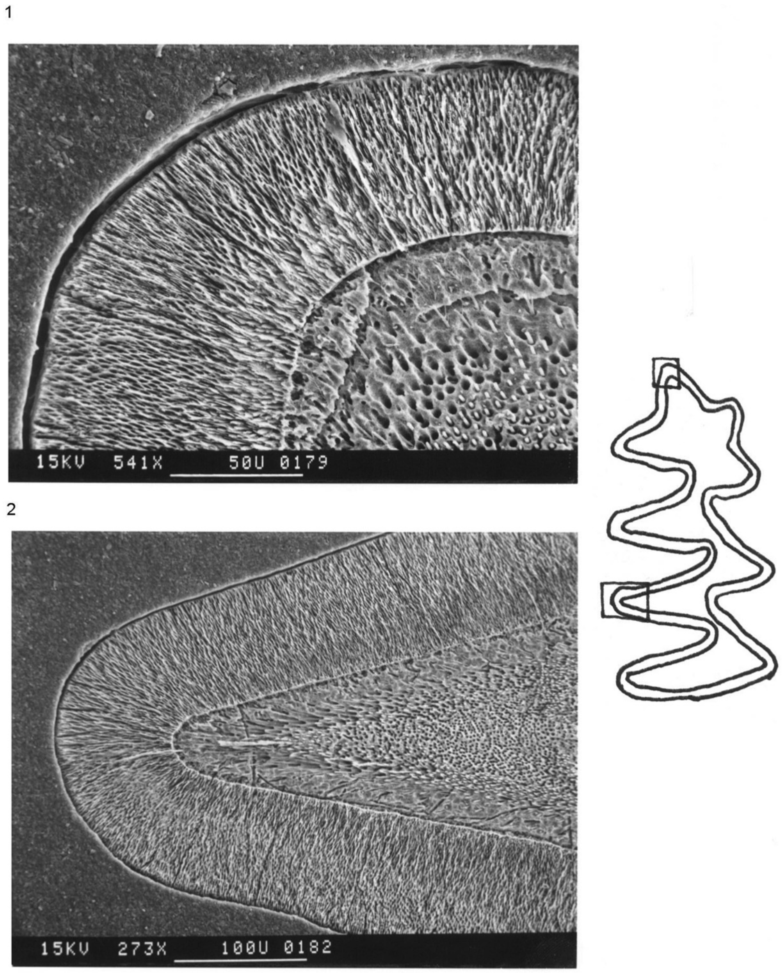

FIGURE 30. Schmelzmuster of *Nevadomys downsi* n. gen. and sp. on the ACC and alternating triangle of m1. 1: the leading edge of ACC of a right m1 (22051) from Locality 9621. A few enamel prisms rise out toward the occlusal surface at the apex close to dentine (below right), forming a trace of discrete lamellar enamel. The other part of the enamel band is occupied by radial enamel. 2: Triangle 1 of the same tooth; both leading and trailing edges are composed of two radial enamel layers.

ACC of two m1s is composed of radial enamel. A few prisms close to the dentine at the apices of the lobes on ACC may extend toward the occlusal surface, forming a trace of discrete lamellar enamel (Figure 30.1). The leading edges and trailing edges have the same pattern, and both are composed of two radial enamel bands. The inner layer is more compressed than the outer layer (Figure 30). Primitive tangential enamel is observed on the trailing edge of the posterior lobe of m1. No discrete lamellar enamel is seen on the apices of the alternating triangles.

A moderately worn M1 (UALP 21999) with a distinct enamel "prism" on the anterior surface was chosen for examination. Traces of primitive tangential enamel are seen on the trailing edge of the anterior lobe, and the enamel "prism" on the anterior surface is composed totally of radial enamel (Figure 31).

Discussion. This population has the following characters similar to *Nevadomys fejfari*: 1) size; 2) enamel folds on the anterior margin of m1; 3) reduction of enamel islet on m1; 4) two-rooted M3; 5) majority of M3s with the posterior islet; and 6) primitive radial enamel. However, it also has several characters that are different from *N. fejfari*: 1) the four-lobed ACC that is caused by a deep prism fold on the anterior and lingual surfaces; 2) absence of "*Mimomys* kante" on majority of m1s; 3) slightly higher dentine tract on the labial side of ACC; 4) a strong but narrow enamel prism may be present on the anterior surface of M1; and 5)

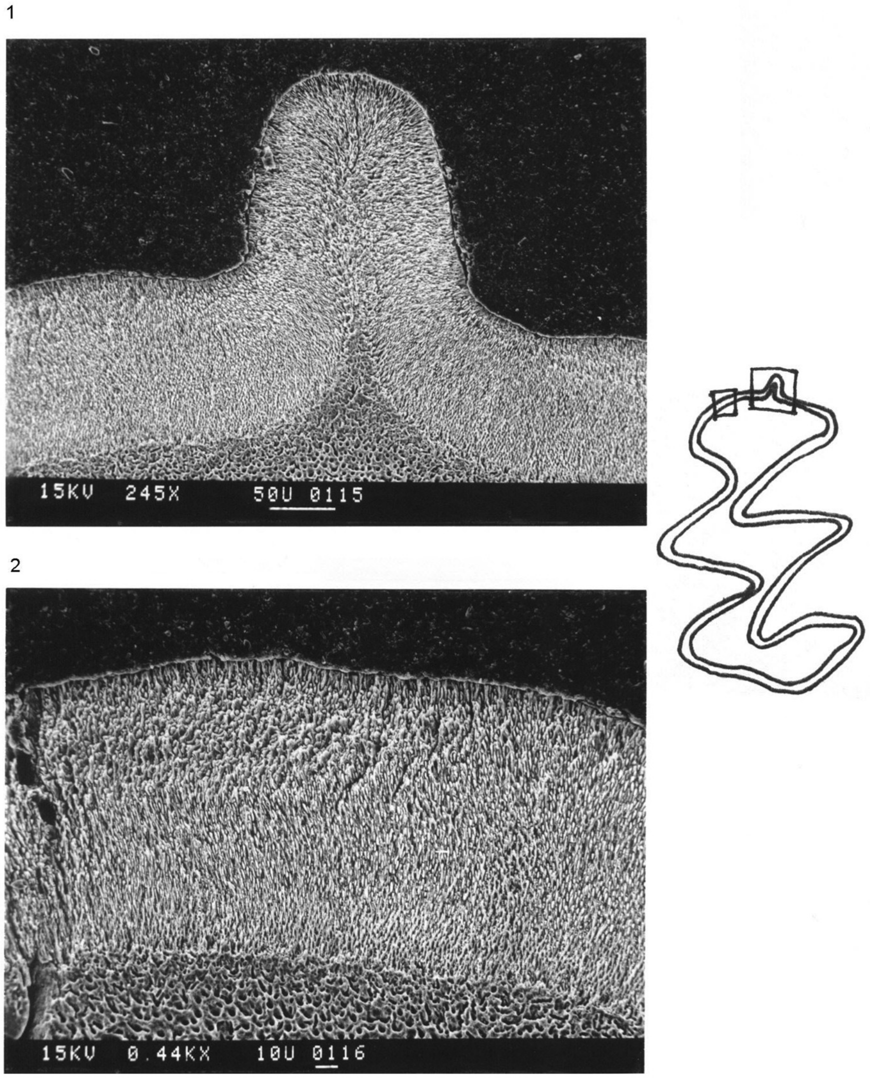

FIGURE 31. Schmelzmuster of *Nevadomys downsi* n. gen. and sp. on the trailing edge of the anterior lobe of M1. 1: the prism on the anterior lobe of a left M1 (21999) from Locality 9621, composed of radial enamel. 2: the trailing edge on the anterior lobe of the same tooth. A trace of primitive tangential enamel is present (top).

incomplete closure of the posterolingual reentrant in M3 of some specimens.

Locality 9621 is only 2 m higher than Locality 9620 in the same section (Brown Bone Bed section). The latter produced a population identified as close to *Nevadomys fejfari*. These two species probably evolved from their ancestor somewhere else in North America and immigrated to Panaca at about the same time. They represent a similar evolutionary stage of development in the *Nevadomys* lineage.

The four-lobed ACC on m1 is also seen in some European arvicolines: *Germanomys*, *Stachomys*, and *Ungaromys* (Fejfar et al. 1998). *Stachomys* and *Ungaromys* are distinctive from *Nevadomys* in their m2, m3, and M3 (Fejfar et al. 1998, plate 7). *Germanomys* (Fejfar and Repenning 1998) is more similar to *Nevadomys* in the following characters: 1) well-developed fine enamel folds on the anterior of ACC of m1; with further wear, the ACC is four-lobed; 2) reduction of enamel islet on ACC; 3) comparable low dentine tract on the labial side of ACC; and 4) the Triangle 3 on M3 bent posteriorly, as in some M3s of *Nevadomys fejfari* and *N. downsi* (percentages or root condition is not published). However, the closure degree between Triangle 3 and ACC is more open than that of *N. downsi*, and there is a distinct reentrant on Triangle 4 of m2 that is not seen in the m2 of *N. downsi*. A shallow depression, instead of a distinct enamel prism, is present on the anterior surface of M1. Based on these differences, I tentatively consider that the population from Locality 9621 is a species of *Nevadomys* rather than *Germanomys*.

Occurrence. Brown Bone Beds: 9621; in the Fm., southeast Nevada.

Range. Early Blancan.

Remarks on *Nevadomys*. To summarize the differences of *Nevadomys* and *Mimomys panacaensis*, the genotype *N. fejfari* is chosen to compare with *M. panacaensis* as the following:

Nevadomys fejfari	*Mimomys panacaensis*
Enamel islet on m1 reduced (derived)	not reduced (primitive)
"*Mimomys* kante" absent/present	present
Enamel folds on ACC well developed	lost at early worn stage
Posterior enamel isleton M3 majority(>80%) (primitive)	few(<10%) (derived)
Roots on M3 majority (>90%) with 2 roots (derived)	half with 3 roots (primitive)
Schmelzmuster radial enamel (primitive)	discrete lamellar or lamellar on CC (derived)

N. fejfari have some more advanced as well as more primitive characters relative to *M. panacaensis*. Therefore, it is not likely that the two genera share the most recent ancestor. *M. panacaensis* is probably an immigrant from Europe, whereas *Nevadomys* is most likely endemic to North America.

The earliest known species that have prismatic, high-crowned cheek teeth in North America are *Goniodontomys* and *Microtoscoptes* from the Hemphillian NALMA. *Microtoscoptes* was first reported from Ertemte, Inner Mongolia of China based on one m1 and M1 (this tooth was actually an M2, Fahlbusch 1987). The genotype is *M. praetermissus*. Its diagnosis was summarized by Gromov and Polyakov (1977) as the following: lingual triangle of M2 and M3 about half the size of the labial one; only one lingual reentrant on M2, and correspondingly, only two lingual triangles on the tooth; M3 shorter than M2; posterior lobe of M3 simple. *Goniodontomys* was erected by Wilson (1937) based on two lower jaws from Oregon. Wilson (1937) named the genotype species *Goniodontomys disjunctus*, with its diagnosis that the triangles are opposite rather than alternating. Hibbard (1959) studied similar specimens from Wyoming and Idaho, and he changed *Goniodontomys disjunctus* into *Microtoscoptes disjunctus*, considering that *Goniodontomys* is the junior synonymy of *Microtoscoptes*. This opinion was followed by Repenning (1968), Hibbard (1972), and Shotwell (1970), but was not followed by Gromov and Polyakov (1977) and Fahlbusch (1987). Comparing the Eurasian and North American specimens, Gromov and Polyakov (1977) gave a diagnosis of *Goniodontomys* as the following: lingual triangle of M2 and M3 the same size as the labial one, facing oppositely; two lingual reentrants on M2, and correspondingly, three lingual triangles on the tooth; M3 longer than M2; a deep reentrant on the posterior lobe of M3.

Martin (1975) studied some Hemphillian arvicoline rodents from the upper portion of the Ogallala Group in Nebraska. He identified some specimens as *Microtoscoptes disjunctus*, but he recognized *Microtoscoptes disjunctus* of Shotwell (1970) and some other specimens from Nebraska as a new genus, *Paramicrotoscoptes*, with the new species designated as *Paramicrotoscoptes hibbardi* (genotype of *Paramicrotoscoptes*). This species is also characterized by its opposite triangles; its M2 has only one broad lingual reentrant, which is similar to that of *Microtoscoptes praetermissus* but different from that of *Goniodontomys disjunctus*. However, its M3 differs from that of *M. praetermissus* in its larger size and the presence of a posterior enamel islet.

In his review, Repenning (1987) made the following changes informally: 1) *Microtoscoptes disjunctus* was changed back into *Goniodontomys disjunctus*, following Gromov and Polyakov (1977); 2) *Paramicrotoscoptes* was considered the junior synonymy of *Microtoscoptes*; the species *Paramicrotoscoptes hibbardi* was changed to *Microtoscoptes hibbardi*, which was the only species of *Microtoscoptes* in North America. This classification was later followed by Korth (1994) in his review of North American Tertiary rodents.

However, almost at the same time, Fahlbusch (1987) studied a much larger sample of *Microtoscoptes praetermissus* (about 150 specimens) from Ertemte, the topotypic locality and described the morphology of the whole dentitions of this species. He concluded that *Microtoscoptes* and *Goniodontomys* are two distinct genera, with the major differences on the morphology of M2, M3, and m3. *Paramicrotoscoptes* is different from *Microtoscoptes*, but closer to *Microtoscoptes* than to *Goniodontomys*. Along with this paper (Fahlbusch 1987), Koenigswald (1987) described the enamel microstructure of molars of the three genera. He found that *Microtoscoptes* and *Goniodontomys* have similar schmelzmuster, whereas *Paramicrotoscoptes* has a different schmelzmuster.

Based on the above reviews and examination of Martin's (1975) illustration, I agree with Gromov and Polyakov (1977) and Fahlbusch (1987) that *Microtoscoptes*, *Goniodontomys*, and *Paramicrotoscoptes* are three distinct genera. So far, *Microtoscoptes* has not been found in North America, whereas *Goniodontomys* and *Paramicrotoscoptes* have not been found in Europe.

Repenning (1987) derived *Pliophenacomys* from "*Propliophenacomys,*" and further suggested that *Paramicrotoscoptes* gave rise to "*Propliophenacomys*" (Repenning *et al*. 1990). However, the intermediate genus in this lineage, "*Propliophenacomys,*" is very poorly documented as pointed out by Korth (1994).

Compared to the taxa *Goniodontomys disjunctus*, *Paramicrotoscoptes hibbardi*, and "*Propliophenacomys*" *parkeri*, *Nevadomys* seems more closely related to *Paramicrotoscoptes hibbardi*. In the m1s of *P. hibbardi*, the ACC is four-lobed with a deep anterior enamel fold, which is similar to that of *Nevadomys downsi*. The enamel islets only exist on unworn or slightly worn m1s in *P. hibbardi*, and *Nevadomys* is derived by further reduction of this islet. A large posterior enamel islet is present on the M3 of *P. hibbardi*; *Nevadomys* still retains this character, but the M3 is more derived by its reduction (as in *N. lindsayi*) or even fusion (as in *N. fejfari* and *N. downsi*) of the anterolingual roots.

Following the phylogeny of *Pliophenacomys* proposed by Repenning (1987), Korth (1994) placed this genus in the same subfamily as *Paramicrotoscoptes* and *Goniodontomys*, which is Prometheomyinae. For the reasons discussed above, *Nevadomys* was likely derived from *Paramicrotoscoptes*, and is therefore placed in the subfamily Prometheomyinae.

The *Paramicrotoscoptes*-*Nevadomys* relationship is not only supported by the dental morphology discussed above but also by the enamel microstructure of molars. According to Koenigswald (1980, 1987), the leading and trailing edges of opposite triangles of *Paramicrotoscoptes hibbardi* has the same schmelzmuster, which is composed of two radial enamel layers, each occupying half of the width of enamel band. *Microtoscoptes* and *Goniodontomys*, which also have opposite triangles on their molars, display a different schmelzmuster from that of *Paramicrotoscoptes*. These two genera have the schmelzmuster composed of two radial enamel layers and a thin tangential enamel layer in the middle. Schmelzmuster of *Nevadomys* does not have the thin tangential enamel in the middle. Both of its leading and trailing edges of the enamel bands are composed of two radial enamel layers. It is comparable to that of *Paramicrotoscoptes*, but quite different from that of *Microtoscoptes* or *Goniodontomys*.

SUMMARY

The Pliocene Panaca Fm. in southeast Nevada has yielded abundant small mammal fossils. Including the cricetids and other small mammals, more than 20 species were identified in the Panaca l.f. from Meadow Valley. The cricetids, dominated by *Mimomys panacaensis*, *Nevadomys* n.gen., and *Repomys*, suggest the very early Blancan NALMA for the Panaca l.f..

Cricetids are the major group of rodents in the Panaca l.f., including the subfamilies Sigmodontinae, Arvicolinae, and Prometheomyinae. The low-crowned cricetids are represented by *Peromyscus hagermanensis* and a species in the genus *Onychomys*. The high-crowned cricetid in sigmodontine cricetids is *Repomys*, including *R. panacaensis* and a new species, *R. minor* n. sp. The two species are morphologically similar to each other, with different sizes and the occlusal outline of the first lower molar. *R. minor* is significantly smaller than *R. panacaensis*. With a large sample of *R. panacaensis*, especially the last upper and lower molars, the diagnoses of the genus *Repomys* and the species *R. panacaensis* are emended.

Arvicolines are abundant in the Panaca l.f.. *Mimomys panacaensis* was recognized from three other localities in the Fm. in addition to its type locality. A new genus, *Nevadomys*, is erected for the arvicoline-like rodents from four localities in Meadow Valley. This new genus is distinctive from *Mimomys* by its combination of the reduction of enamel islet on the first lower molar and a large posterior enamel islet on the last upper molar. Different from *M. panacaensis*, *Nevadomys* was considered endemic to North America. A phylogeny of *Paramicrotoscoptes*-*Nevadomys* was suggested, and *Nevadomys* was placed in the same subfamily as *Paramicrotoscoptes*. *Nevadomys* includes three species, *N. fejfari*, *N. lindsayi*, and *N. downsi*. *N. fejfari* is characterized by its two-rooted condition on the last upper molar. *N. lindsayi* is distinctive on its large size and three-rooted condition on the last upper molar. *N. downsi* is characterized by its four-lobed anteroconid complex on the first lower molar. *N. fejfari* was probably derived from *N. lindsayi* through decreasing size and fusion of the two anterior roots on the last upper molar.

The enamel microstructures at the level of schmelzmuster are examined under the SEM for *Mimomys panacaensis* and three species of *Nevadomys*. *M. panacaensis* from Locality 9702 presents very similar schmelzmuster to that of *M. panacaensis* from the type locality, indicating that there is no significant difference in the schmelzmuster among different populations of this species. *Nevadomys* has a more primitive schmelzmuster than *M. panacaensis*, with only radial enamel on the leading and trailing edges of alternating triangles. In *N. fejfari* and *N. lindsayi*, the leading edge of anteroconid complex of the first lower molar is entirely occupied by radial enamel, whereas in *N. downsi*, traces of discrete lamellar enamel were seen close to the dentine on this leading edge.

The presence of derived horse *Equus* and a primitive arvicoline rodent *Mimomys panacaensis* indicate that the Panaca l.f. represents the early Blancan land mammal age. The evolutionary stage of *Nevadomys* supports this inference.

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