New rodents (Mammalia, Rodentia, Cricetidae) from the Verde Fauna of Arizona and the Maxum Fauna of California, USA, early Blancan Land Mammal Age

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ABSTRACT

The cricetid rodent *Postcopemys repenningi*, new genus and new species, is described from the Verde fauna in Arizona and the Maxum fauna in California. Two other rodents, *Postcopemys maxumensis*, new species, and *Jacobsomys dailyi* are reported herein from the Maxum fauna. *Jacobsomys dailyi* is described and *Postcopemys valensis* is reported (May et al. 2011) from the Warren fauna in southern California. *Jacobsomys verdensis* had been reported from the Verde fauna by Czaplewski (1987a). These three faunas (the Warren and Maxum faunas in California and the Verde fauna in Arizona) are considered close to the Blancan/Hemphillian boundary, and the two genera *Postcopemys* and *Jacobsomys* are important small mammal taxa whose stage of evolution should prove useful for demonstrating the morphologic transition between *Copemys* and extant *Peromyscus* via *Postcopemys*, and between *Bensonomys* and extant *Oryzomys* via *Jacobsomys*, as well as for ordering mammalian faunas relative to the Blancan/Hemphillian boundary.

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INTRODUCTION

The last 50 years have seen an explosive increase of small mammal fossils recorded from late Cretaceous and Cenozoic deposits, especially in North America. Two important factors contributed to this explosive increase: development and refinement of screenwashing methods of fossil collection initially advocated by Hibbard (1949), and a virtual army of eager young students to apply those collection methods. We both shared, with C. A. Repenning, numerous experiences and frustrations in the development of these fossil records, and this contribution is a small dividend from among numerous shared experiences.

Vertebrate fossils were initially reported from the Verde Formation (Fm.) of Arizona, USA, by Twenter (1962) and by Twenter and Metzger (1963). Nations et al. (1981) studied the paleoecologic-stratigraphic framework of the Verde Fm., establishing that it represents deposition in a late Cenozoic lake basin. About 1980 NJC initiated serious collecting of small mammal fossils from the Verde Fm., culminating in graduate training and the following publications (Czaplewski 1987a, 1987b, 1987c, and 1990). Czaplewski (1987b) reported six vertebrate localities from the Verde Fm.; these include MNA loc. 181 from the upper part of the Verde Fm which represents the Clarkdale local fauna (l.f.). The Clarkdale l.f. includes the rodents ?*Marmota, Spermophilus, Perognathus, Geomys, Peromyscus, Reithrodontomys, Bensonomys, Sigmodon, Repomys, Neotoma (Paraneotoma),* and *Pliopotamys* (Czaplewski 1987c); it is assigned to the middle Blancan interval of the North American Land Mammal Ages (NALMA).

Czaplewski (1987a) described sigmodont rodents from two of the Verde localities curated in the Museum of Northern Arizona (MNA 318 and MNA 319) that include the bulk of the Verde small mammals, which he characterized as the Verde l.f. MNA locs. 318 and 319 occur south of House Mountain, east of Cornville; they are separated geographically by about 1 km, and MNA loc. 318 is about 35 m stratigraphically and about 55 m in elevation above MNA loc. 319. The Verde l.f. includes the rodent genera *Perognathus, Prodipodomys, Geomys, Bensonomys, Prosigmodon, Sigmodon, Jacobsomys, Reithrodontomys, Onychomys, Neotoma (Paraneotoma),* the arvicoline *Ogmodontomys,* and another indeterminate arvicoline; it is interpreted as an early Blancan fauna. Assignment to Blancan NALMA is based primarily on presence of the arvicolines in the Verde l.f. Bressler and Butler (1978) produced a magnetic polarity sequence for part of the Verde l.f., allowing the age of the local fauna to be placed in the vicinity of 4.5 to 4.9 Ma. On the basis of the above references, along with current calibration of the Geomagnetic Polarity Time Scale (Gradstein et al. 2004), MNA loc. 318 occurs in the upper part of chron C3n.1r (~4.2 Ma), and MNA loc. 319 occurs in the top of chron C3n.3r (~4.6 Ma), both securely placed in early Blancan (NALMA). Czaplewski (1990) formally defined the Verde l.f. and characterized it with stratigraphic, radiometric, and paleomagnetic data, as well as a comprehensive faunal list.

Collections made by Czaplewski during the 1980s also produced a taxon listed as *Copemys* sp. (Czaplewski 1990) from three of the Verde sites (MNA loc. 701, 698, and 319). This taxon is described below as *Postcopemys repenningi,* new genus and new species. Most (22 of the 27 specimens) of the hypodigm for *Postcopemys repenningi* are from MNA loc. 701, with only three specimens from MNA loc. 698 and two specimens from MNA loc. 319. MNA loc. 701 is located in Buckboard Wash, a dry tributary of the Verde River northeast of Clarkdale; the site was discovered by Twenter (1962), designated his locality no. 6. The fossils come from a brown, highly calcareous mudstone with fragments of the gastropod *Lymnaea elodes* exposed near the bottom of the wash. MNA site 701 is shown in Figure 1. In addition to the taxon identified as *Postcopemys repenningi,* this site produced a cleithrum of a catfish (Ictaluridae), an unidentified salamander (rib and tooth-bearing jaw fragment), a partial upper molar of a small bat (?*Myotis*), several isolated teeth of a rabbit (*Hypolagus* sp.), an isolated tooth of a geomyoid rodent (cf. *Prodipodomys*), four isolated teeth of a cotton rat (*Sigmodon holocuspis)*, and molar fragments of a woodrat (*Neotoma (Paraneotoma) sp.*). The best represented taxon from MNA loc. 701 is *Postcopemys repenningi* described below.

The paucity of other taxa represented in the Verde l.f. from MNA loc.701, along with the near absence of *Postcopemys repenningi* from MNA loc. 319 and its absence from MNA loc. 318, suggests that MNA loc. 701 is probably significantly older than MNA locs. 318 and 319 in the Verde Fm. Unfortunately, there is no precise correlation for the stratigraphic level of MNA loc. 701. For convenience (or we should say, ignorance) we continue to recognize MNA loc. 701 as part of the Verde l.f., but realize that if at some later time MNA loc. 701 can be confidently assigned to late Hemphillian LMA it must be removed from the Verde l.f. All of the specimens discussed above are curated in the collections of the Museum of Northern Arizona (MNA), in Flagstaff, Arizona.

The Maxum local fauna from University of California Museum of Paleontology (UCMP) locality V-6889, was collected from the backyard of Dr. B. J. Maxum at 291 Barrett Circle in Danville, California. Dr. Maxum reported the fossil site to paleontologists at the UCMP and the United States Geological Survey (USGS), Menlo Park. The fossils were collected in 1968 when real estate development was active in and around Danville. The fossil assemblage was initially identified by C.A. Repenning (we believe) who noted the presence of an arvicolid rodent [*Mimomys (Cosomys) sawrock-*

FIGURE 1. View of MNA locality 701 in the left bank of Buckboard Wash near Clarkdale, Arizona, as it appeared in September 2007.

ensis], and abundant high-crowned cricetid rodents described as *Repomys maxumi*, new species, by S. May (May 1981). The arvicolid rodent, along with the large size of the *Repomys,* convinced Repenning that the Maxum site fits within the early Blancan NALMA. The site, now covered by grass and construction, is from interbedded olive clay and gritty gray-green clay sediments now assigned to the Tassajera Formation; D. Whistler (a graduate student at the University of California, Berkeley at that time, who helped collect the site in 1968) noted that the sediments dip about 45º to the northeast at the collecting site. The geology of that area is rather complex, with several faults crossing the area. The Lawlor Tuff, dated 4.83 ± 0.02 Ma (Sarna-Wojcicki et al. 2005) is recorded from the Tassajera Fm. but the relationship between the Lawlor Tuff and the Maxum fossil site is indeterminate because exposures in the vicinity of the fossil site are now covered by widespread residential development. Repenning's initial age assignment of the site as early Blancan is unquestioned relative to subsequent knowledge and the additional fossils described below.

The important and undescribed rodents from the Maxum site were "discovered" during a visit to the UCMP by E. Lindsay and M. Woodburne in August 2006, to evaluate fossils from the Warren local fauna in the Mojave Desert. At that time, we discovered that the rodent genus *Jacobsomys* Czaplewski, described from the Verde fauna, is also recorded from the Maxum and Warren faunas. The *Jacobsomys* material from the Warren fauna is described by May et al. (2011) in this volume; we recognize it as the same species, *Jacobsomys dailyi* new species, that we describe from the Maxum fauna below. The Verde and Maxum faunas are considered early Blancan NALMA, whereas the Warren fauna is considered late Hemphillian NALMA. These faunas all appear close to the boundary of the Hemphillian and Blancan NALMAs.

There had been considerable effort by a former graduate student at UC Berkeley (or by C.A. Repenning) to identify the Maxum rodents prior to our "discovery." We tried to locate the person who made these identifications with the help of Dr. P. Holroyd, now in charge of the UCMP mammal collection. None of the obvious leads proved fruitful, so we assume these identifications were made by C.A. Repenning when he was still working at the USGS in Menlo Park during the 1970s and 1980s,

and who provided the *Repomys* fossils for S. May to describe. There are several clues to the paleontologist who initially studied these fossils, including several felt-tip pen marks on the cork associated with each specimen that presumably indicate some morphological attribute of the specimen. Also, long insect pins were used as a base for gluing the specimens. Some specimens were glued parallel to the shaft of the pin, and others were glued to the tip of the pin whose head had been cut off. Virtually all of the pins to which specimens were glued are very long, which makes it difficult to avoid bumping the vial and knocking the glued specimen from the pin when removing the protective vial from the cork into which the pin is embedded. We know that some of these curatorial practices were used by C.A. Repenning, so he is our prime candidate for the researcher who initially studied and identified these fossils. Tooth cusp terminology for specimens described below is from Lindsay (1972).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Rochebrune, 1883
Postcopemys, new genus

1967 *Peromyscus valensis* Shotwell, p. 9; fig. 5

1977 ?*Copemys vasquezi* Jacobs, p. 512; Text-fig. 2 a-c

1979 *Copemys* sp. Baskin, p. 703

1985 *Copemys* near *C. valensis* Lindsay and Jacobs, p.19; fig. 8 a-b

1987 *Copemys twenteri* Czaplewski, p. 86; fig. 8

1994 ?*Copemys* Korth, p. 233

Type species. *Postcopemys repenningi,* new genus and new species

Referred species. *Postcopemys valensis* (Shotwell 1967), *Postcopemys vasquezi* (Jacobs 1977), and *Postcopemys maxumensis,* new species.

Distribution. Late Hemphillian and early Blancan of the North American Land Mammal Ages, including the Verde, Redington faunas, and possibly the White Cone fauna in Arizona; the Little Valley, McKay Reservoir, and Bartlett Mountain faunas in Oregon; and possibly the Yepómera fauna in Chihuahua.

Diagnosis. Small, brachydont cricetid rodents having protolophule II not aligned with the anterior arm of the hypocone in upper molars, but with the entolophulid aligned with the anterior arm of the protoconid in lower molars. Protolophule I is absent in M1, it is usually present but weakly developed in M2 and is strongly developed in M3. The hypocone of M3 is reduced. Upper cheek teeth have three prominent roots and lack accessory rootlets; lower cheek teeth have two prominent roots and lack accessory rootlets.

Discussion. In his emended diagnosis of the genus *Copemys*, Lindsay (1972:75) included the condition wherein the "metalophule on M^{1-2} [is] weakly developed, not aligned with anterior arm of hypocone," and in his differential diagnosis, he distinguished the genus *Copemys* from the genus *Peromyscus* in having "nonalignment of metalophule-anterior arm of hypocone [in upper molars] and entolophulid-posterior arm of protoconid" [in lower molars]. However, from his cusp terminology diagram (Lindsay 1972, figure 40), the protolophule II is clearly the name of the intended loph where the term "metalophule" was used in the text (see also Jacobs 1977, Baskin 1979). Therefore, *Copemys* is distinguished from its descendant, *Peromyscus* on the basis of not having alignment of protolophule II with the anterior arm of the hypocone in upper molars, and not having alignment of the entolophulid with the posterior arm of the protoconid in lower molars. In the genus *Peromyscus* these lophules and cusps are aligned, or nearly so.

The genus *Antecalomys* Korth 1998 is somewhat intermediate with respect to these features in that lophs and cusps in upper molars are not aligned (as in *Copemys*), but lophs and cusps in lower molars are aligned as in *Peromyscus*. When Korth (1998) created this intermediate step by naming and describing *Antecalomys* he had in mind a transition between *Abelmoschomys* Baskin (1986) and *Bensonomys* Gazin (referred to *Calomys* Waterhouse by Baskin), placing *Antecalomys* between *Abelmoschomys* and *Calomys (Bensonomys)*, in a lineage of putative sigmodontine rodents.

Baskin (1986) had previously described *Abelmoschomys*, suggesting it as a likely ancestor of *Calomys (Bensonomys)* and other sigmodont rodents. One of the other prime features that Baskin (1986) noted in *Abelmoschomys* is the development of accessory rootlets, especially in the M1, noting that *Abelmoschomys* shares this feature with *Sigmodon* Say and Ord and with *Calomys* Waterhouse, as well as some other sigmodontines. Korth (1998) also noted presence of an accessory rootlet in M1 of the genotype of *Antecalomys*, *A. phthanus*, from the Pratt Quarry in Nebraska.

Pardiñas et al. (2002) monographed our knowledge of the fossil and living South American

and fossil North American Cricetidae including sigmodontines and presumed sigmodontines. These authors cogently argued that the North American fossils that are often referred to as Sigmodontinae have never actually been demonstrated monophyletic in a phylogenetic analysis that includes all of the extinct and extant South American genera. Numerous molecular phylogenetic analyses conducted in recent years show South American sigmodontines as monophyletic and separate from neotomine-peromyscine cricetids (e.g., Almeida et al. 2007; Jansa and Weksler 2004; Miller and Engstrom 2008; Reeder et al. 2006). On the other hand, there is no known ancestor in South America for the Sigmodontinae of South America, and the record of alleged Sigmodontinae in North America have a long and robust record that is older than any known record of a South American Sigmodontinae. We must admit there is a great deal of uncertainty regarding the evolutionary relationships among the New World cricetids (Musser and Carleton 2005:p. 1048; D'Elia 2000), and this uncertainty is likely to persist for a long time. We offer the present contribution as a tiny step toward resolution of that problem. In the mean time, it is prudent to consider the North American fossils as neotomine-peromyscines, or possibly sigmodontines, and we suggest use of the generic name *Bensonomys* Gazin for the North American taxon rather than *Calomys (Bensonomys)* Waterhouse, at least until more phylogenetic studies are completed.

Korth (1998) also referred two species to *Antecalomys*: *Copemys valensis*, orginally described by Shotwell (1967) from Hemphillian faunas in Oregon, and ?*Copemys vasquezi*, described by Jacobs (1977) from the Hemphillian Redington fauna in Arizona. Korth based his referral on the the fact that in all this material the protolophule II is not aligned with the anterior arm of the hypocone in upper molars but the entolophulid is aligned with the posterior arm of the protoconid in lower molars. However, alignment of the entolophulid with the posterior arm of the protoconid that occurs in *Copemys valensis* and ?*Copemys vasquezi* may have little or nothing to do with the genus *Antecalomys* and the "sigmodontine" cricetids. As a general rule, accessory rootlets are never common in either *Copemys* Wood or *Peromyscus* Gloger. Also, unfortunately, roots and rootlets are rarely described for small rodents. To our knowledge, this feature, development of accessory rootlets is not commonly seen in any of the other Pliocene species of North American cricetid rodent although it developed in the late Miocene genus *Abelmo*

schomys. Yet it separates the type species of *Antecalomys*, *A. phthanus*, from all the other Pliocene species of North American cricetid rodent that develop loph-cusp alignment in lower molars, such as *Copemys valensis,* ?*Copemys vasquezi,* and *Copemys twenteri* from the Verde fauna (Czaplewski 1987b). We assign these last three named species to the new genus *Postcopemys* along with the new species *Postcopemys maxumensis* from the Maxum fauna that we describe below. We suggest that the only species that should be assigned to *Antecalomys* is the type, *A. phthanus*, based on the presence of accessory rootlets on M1.

Two other poorly known Hemphillian cricetids [*Copemys* sp. from the White Cone fauna, Arizona (Baskin 1979) and *Copemys* near *C. valensis* from the Yepómera fauna, Chihuahua (Lindsay and Jacobs 1985)] resemble *Antecalomys* and *Postcopemys*. They also tend to align the entolophulid with the posterior arm of the hypoconid in the lower molars although alignment (which is gradational) is less well developed, and upper molars of these taxa lack alignment of protolophule II with the anterior arm of the hypocone, as seen in *Copemys.* We discuss these taxa in comparisons of *Postcopemys repenningi.* We consider *Postcopemys* to be a member of the neotomine-peromyscine radiation of Cricetidae, along with *Copemys* and *Peromyscus*.

Postcopemys repenningi new genus and new species
Figures 2-4

1987 *Copemys twenteri*, new species Czaplewski, p. 86; fig. 8.
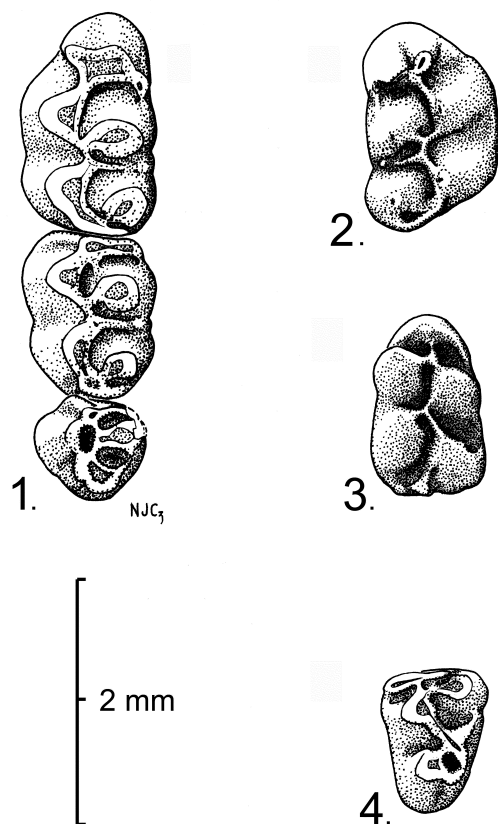
Holotype. MNA V4996, left M1-2

Type locality. MNA locality 701, Buckboard Wash, Verde Fm., Yavapai County, Arizona

Hypodigm. Holotype plus MNA nos. V5003, associated right and left M1s and right m1; V5004, associated right and left M1s and right m1; V5000, left M1; V5001-5002, V5014, M1s; V4999, V5015-5016, V5022, M2s; V4997, V5008-5009, M3s; V5007, V5011-5013, m1s; V5017, right m2; V4998, V5006, V5010, m3s from MNA loc. 701.

Material from other Verde sites: V5018, left M1; V5019-5020, left m1s from MNA loc. 698. V5005, left M2; V5021, left m1 from MNA loc. 319.

Material from Maxum site: 35 isolated cheek teeth: UCMP 87472, 87473, 87477, 87478, 87481, 87483, 87487, 87496, 87519, 87525, 87535, 87537, 87542, 87543, 87545, 87552, 87557, 87558, 87559, 87561, 87565, 87897, 87899,

FIGURE 2. *Postcopemys repenningi*, gen. and sp. nov. from the Verde Formation, Arizona; occlusal views of molars. 1, left M1-2 (holotype, MNA V4996) and M3 (MNA V4997). 2, right M1 (MNA V5003). 3, right m1 (MNA V5003). 4, left m3 (MNA V4998). Anterior is at top of figure.

FIGURE 3. *Postcopemys repenningi*, gen. and sp. nov. from the Maxum fossil site, Tassajera Formation, California; occlusal views of upper molars: 1, right M1 (UCMP 87535). 2, left M1 (UCMP 87958). 3, right M2 (UCMP 87950). 4, right M2 (UCMP 87543). 5, left M3 (UCMP 87525). 6, left M3 (UCMP 87496).
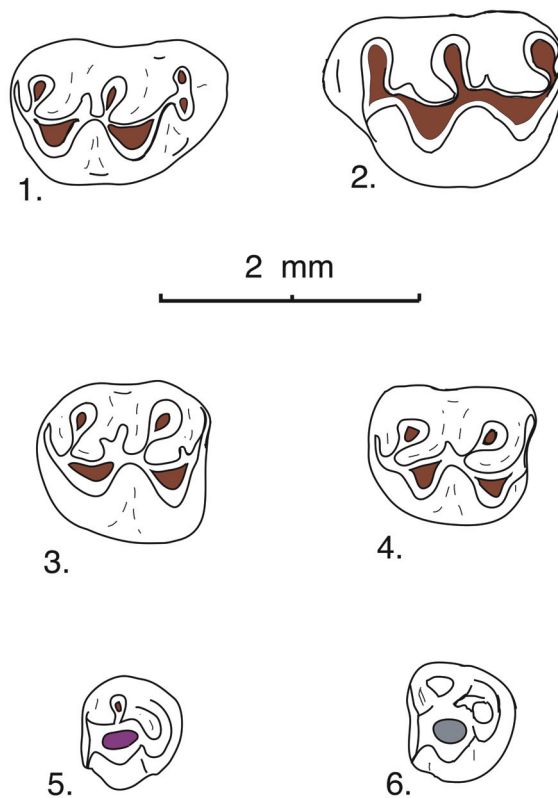
87901, 87905, 87921, 87924, 87925, 87926, 87928, 87943, 87950, 87958, 87963, and 87965 from UCMP locality V6869.

Distribution: Buckboard Wash, MNA loc. 701; Anderson Butte, MNA loc. 698; and North of Beaverhead Flat, MNA loc. 319, Verde Fm., Arizona; and Maxum fauna, UCMP loc. V6869, Tassajera Fm., California.

Age. Early Blancan and possibly latest Hemphillian NALMA.

Etymology. Named for Charles A. Repenning, a weathered, spirited, decorated, kind, and always helpful gentleman paleontologist.

Diagnosis. As in the generic diagnosis of *Postcopemys* above; also, *P. repenningi* differs from other species of *Postcopemys* in having smaller size than *P. maxumensis* and larger size than *P. valensis* and *P. vasquezi*. In addition, *P. repenningi*

has a short- to medium-length mesoloph in M1 and M2; mesolophids are absent in m1 and m2.

Description. The molars are low crowned and have thick enamel. Main cusp positions are slightly alternate with lingual cusps anteriorly situated relative to labial cusps.

M1. The anterocone is asymmetrical. Four of six specimens are slightly concave on the anterior slope of the anterocone, which thus appears "squarish" with wear. Two of six specimens have the anterocone asymmetrically bilobed. Anterior cingulum is reduced or absent. A parastyle is connected to the posterolabial portion of the anterocone. Protolophule I is absent. Protolophule II is not aligned with the anterior arm of the hypocone. A very short mesoloph is present that does not reach the mesostyle. Three roots are present, and accessory rootlets are absent.

M2. The anterior cingulum is reduced in its lingual portion. A weak protolophule I is present connect-
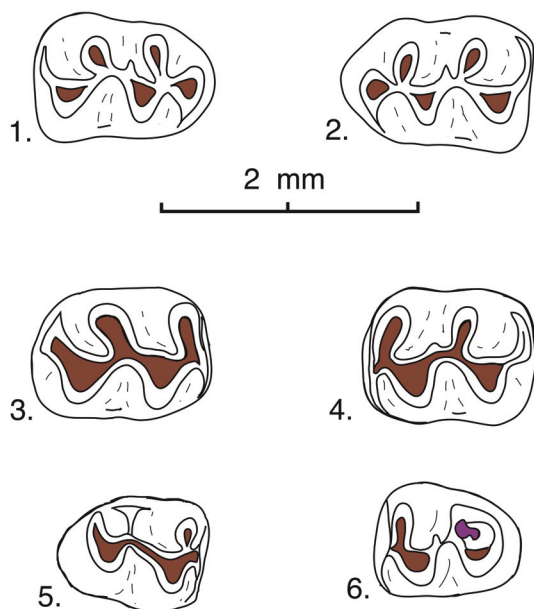
FIGURE 4. *Postcopemys repenningi*, gen. and sp. nov. from the Maxum fossil site, Tassajera Formation, California; occlusal views of lower molars: 1, right m1 (UCMP 87897). 2, left m1 (UCMP 87901). 3, right m2 (UCMP 87559). 4, left m2 (UCMP 87921). 5, right m3 (UCMP 87924). 6, left m3 (UCMP 87905).

ing the paracone with the anterior arm of the protocone. A strong protolophule II connects the paracone to the posterior arm of the protocone. Protolophule II is not aligned with the anterior arm of the hypocone. The mesoloph is of short- or medium length and does not reach the mesostyle. Three roots are present, and accessory rootlets are absent.

M3. This tooth is small, and its occlusal outline is subcircular, wider than long. Strong protolophules I and II unite the protocone and paracone. The hypocone is reduced.

m1. Occlusal outline is relatively long, narrow, and rounded anteriorly. Five distinct cusps are present but the metaconid is situated close to the anteroconid so that the intervening valley is quite shallow. The anteroconid is relatively short, broad, conical, and symmetrical in most specimens. In two of eight specimens the anteroconid is weakly bilobed. A strong anterior cingulum is present. Lophulids connecting cusps are weak. Mesolophid and mesostylid are absent. The entolophulid is aligned with the posterior arm of the protoconid. The posterior cingulum is shortened. Accessory rootlets are unknown.

m2. Occlusal outline is longer than wide. Mesolophid and mesostylid are absent. The entolophulid is aligned with the posterior arm of the protoconid. The posterior cingulum is well developed. Accessory rootlets are unknown.

m3. Occlusal outline is subtriangular, longer than wide. The hypoconid is reduced. The entoconid is indistinct. The posterior cingulum extends from the posterolingual side of the hypoconid to the posterior side of the entoconid, enclosing a deep pit. A broad short mesolophid(?) or lingual cingulum extends anterolingually from the entoconid.

Comparisons. *Postcopemys repenningi,* new genus and species, is slightly larger than *P. vasquezi* and *P. valensis* (see scatter plot of m1 teeth in Figure 5) although size range of these three species overlap so they cannot be distinguished by size alone. Also, *P. repenningi* differs from *P. valensis* in having a short and persistent mesoloph in M1 and M2. Shotwell (1967) described *P. valensis* having a mesoloph, mesostyle, and ectostylid in 15-20 percent of his specimens. He also illustrated two specimens (UO 26939, an isolated m1 [figure 5 b], and UO 25648, an isolated M1 [figure 5g]; Shotwell 1967) with a long and narrow mesoloph(id). Other than those illustrated specimens we have never seen specimens of *P. valensis* from Oregon with a mesoloph(id). Jacobs (1977) described ?*Copemys vasquezi* as having the mesoloph and mesostyle present but never prominent on M1, mesoloph short on M2, plus mesolophid and mesostylid absent on m1 and m2.

P. repenningi is also similar in size to the unnamed species of *Copemys* from the White Cone l.f. of Arizona described by Baskin (1979) and the *Copemys* near *C. valensis* from Yepómera described by Lindsay and Jacobs (1985), both of which have protolophule II non-aligned with the anterior arm of the hypocone in upper teeth and alignment (more or less) of the entolophulid with the posterior arm of the protocone in lower molars. One M1 of *Copemys* near *C. valensis* has a slight bulbous expansion below the paracone, suggesting possible incipient development of an accessory rootlet as in *Antecalomys phthanus*. It is likely that the *Copemys* material from the White Cone and Yepómera faunas will be assigned to a species of *Antecalomys* or *Postcopemys* when those samples have been enlarged.

Discussion. Before leaving this topic we should also point out that at least one extant species of the common North American genus *Peromyscus*,
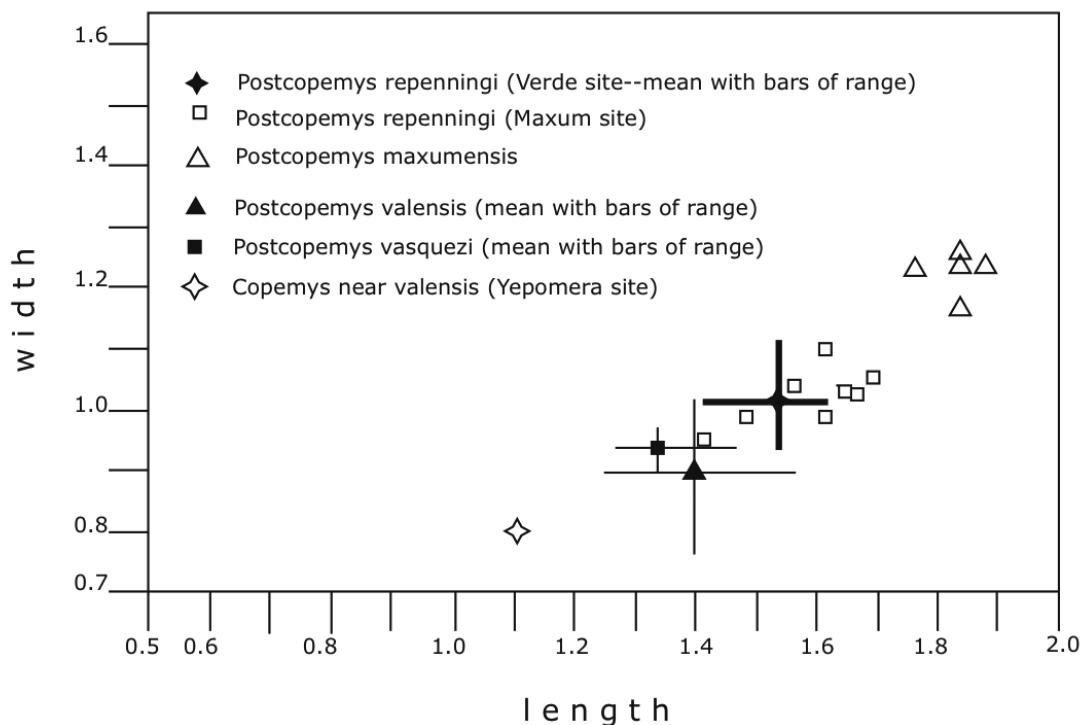
FIGURE 5. Scatter diagram of *Postcopemys* species m1s. Units are in mm.

namely *Peromyscus eremicus*, should probably also be assigned to the genus *Postcopemys* based on dental morphology. An important study of dental variation in *Peromyscus* was published by Hooper (1957) in which variation in loph attachment and development of the mesoloph (id) and stylar cusps were reviewed and tabulated in 17 extant species of *Peromyscus*, including M1-2 and m1-2 of *P. eremicus* (Hooper 1957). Hooper's study stimulated EHL who in 1965 was struggling to identify fossil rodents collected from the Miocene Barstow Formation in southern California. Lindsay wanted to compare dental variation in modern species of *Peromyscus*—especially in large samples in which sex of the specimens had been recorded—in order to assess dental variation in fossil material that had been assigned by previous authors to *Peromyscus*. A prime goal was to see if some of the dental variation ascribed to *Peromyscus* by Hooper might be related to sexual dimorphism. Fortunately, large collections of *Peromyscus* species had been curated as skins and skulls in the Museum of Vertebrate Zoology at Berkeley, collected by Joseph Grinnell and his colleagues over several years, and sex of the preserved specimens had been recorded along with other important information. Some of the results of that study were summarized by Lindsay (1972, pp. 71-74) in his publication of the Barstow study. In summary, Lindsay found no dental variation that could be correlated with sexual dimorphism of the extant specimens, but after spending several days measuring and recording dental variation in extant *Peromyscus*, Lindsay realized that he could distinguish the dentition of extant *Peromyscus* from the dentition of fossils that had been assigned to *Peromyscus*. The difference was seen in the occlusal wear of the specimens. Extant *Peromyscus* species had developed alignment of protolophule II with the posterior arm of the hypocone to form an oblique ridge in upper teeth that would occlude against an oblique ridge (oriented at an angle of ~60-80 degrees) in lower molars formed by the entolophulid aligning with the posterior arm of the protoconid. None of the Miocene specimens assigned to *Peromyscus* exhibited that type of efficient grinding because the lophs and cusps were not properly aligned to enable such occlusion.

Realizing that Miocene cricetids from Barstow can, and should be, distinguished from extant *Peromyscus*, Lindsay looked for another genus to which the Miocene cricetids could be assigned.

Hoffmeister (1959) had described *Miochomys nio-brariensis* from the Niobrara Formation in Nebraska, with the holotype located in the UCMP collection, readily available to Lindsay. So, Lindsay compared *Miochomys niobrariensis* with the cricetids from the Barstow Fm., finding them generically identical; when he completed his study of the Barstow small mammals Lindsay assigned all of the fossil cricetids to the genus *Miochomys* Hoffmeister. Later Lindsay presented the results of his Barstow small mammal study at an annual meeting of the Society of Vertebrate Paleontology held at Yale University, assigning the Barstow cricetid rodents to *Miochomys* Hoffmeister. Immediately after his presentation Repenning introduced Lindsay to V. Fahlbusch (in the restroom of the Peabody Museum), who had borrowed the type of *Copemys loxodon*, described by Wood (1936), wherein Fahlbusch informed Lindsay that features ascribed to *Copemys loxodon* were in error, and that most North American cricetids should be assigned to the genus *Copemys* Wood. Fahlbusch produced the type specimen of *Copemys loxodon* and upon examination Lindsay agreed with Fahlbusch's interpretation.

Revisiting the study of dental variation in *Peromyscus* by Hooper (1957), Hooper illustrated M1-2 and m1-2 for 6 of the 17 species that he used: *Peromyscus eremicus,* figure 3; *Peromyscus melanophrys*, figure 9; *Peromyscus oaxacensis* (presently considered a synonym and tentative subspecies of *P. aztecus*; Musser and Carleton 2005, p. 1063), figure 15; *Peromyscus mexicanus*, figure 16; *Peromyscus nuttalli* (now = *Ochrotomys nuttalli*), figure 18; and *Peromyscus nudipes* (now considered a synonym of P. mexicanus; Musser and Carleton 2005, p. 1074), figure 19. In all of the lower teeth of his illustrated taxa the entolophulid is aligned with the posterior arm of the protoconid. In the upper teeth of some taxa (e.g., *P. eremicus* and *P. oaxacensis* [= *P. aztecus*]) protolophule II is not aligned with the anterior arm of the hypocone, and in some taxa (e.g., *P. melanophrys* and *Ochrotomys nuttalli*) alignment of protolophule II with the anterior arm of the hypocone is incomplete, reaching alignment only after moderate wear; in still other taxa (e.g., *P. mexicanus* including specimens formerly called *P. nudipes*) alignment of protolophule II with the anterior arm of the hypocone is complete with little or no wear. It is *P. eremicus* and *P. oaxacensis* (= *P. aztecus*) that show non-alignment of protolophule II with the anterior arm of the hypocone in M1 and M2; these are the features seen in *Postcopemys*, suggesting that at least

these two species might be evolutionarily related and should probably be assigned to *Postcopemys*, as *P. eremicus* and *P. aztecus*. On the other hand, it would be inappropriate to reassign these species to another genus without a thorough review of all North American species of *Peromyscus*, which is beyond the scope of this study. We leave this task to interested students of evolution.

When he examined the extant species of *Peromyscus* in the collection of the Museum of Vertebrate Zoology many years ago, Lindsay did not realize that *Peromyscus eremicus* lacked alignment of protolophule II with the anterior arm of the hypocone; he confined his study at the MVZ to samples with 20 males and 20 females of the same species, which did not include *P. eremicus*. Later, when Lindsay moved to southern Arizona where *P. eremicus* is the dominant cricetid rodent in the local fauna, he became acquainted with *P. eremicus* and realized the distinctiveness of its dental morphology relative to his previous interpretation. The present paper is the first time he reviewed and addressed its taxonomic relationships.

In subsequent years much additional morphological and molecular genetic research on the systematics of extant cricetids has been accomplished. *Ochrotomys nuttalli* is widely considered a distinct monotypic genus and an early lineage of Neotominae separate from *Peromyscus* (Musser and Carleton 2005:p. 1061). Two subgenera of *Peromyscus*, *P. (Peromyscus)* and *P. (Haplomylomys)*, which may or may not represent phyletic lineages, are presently recognized. Of these, *P. (Haplomylomys)* contains the *P. eremicus* and *P. californicus* groups of species, and *P. (Peromyscus)* contains all other extant species (Musser and Carleton 2005, p. 1062).

Postcopemys maxumensis, new species
Figures 6 and 7

Holotype. UCMP 87890, isolated left m1.

Type locality. UCMP locality V6869.

Hypodigm. Holotype and 24 isolated cheek teeth: UCMP 87891, 87892, 87893, 87895, 87896, 87898, 87909, 87910, 87912, 87914, 87918, 87920, 87923, 87927, 87929, 87930, 87937, 87939, 87942, 87947, 87951, 87952, 87954, and 87973.

Age. Early Blancan

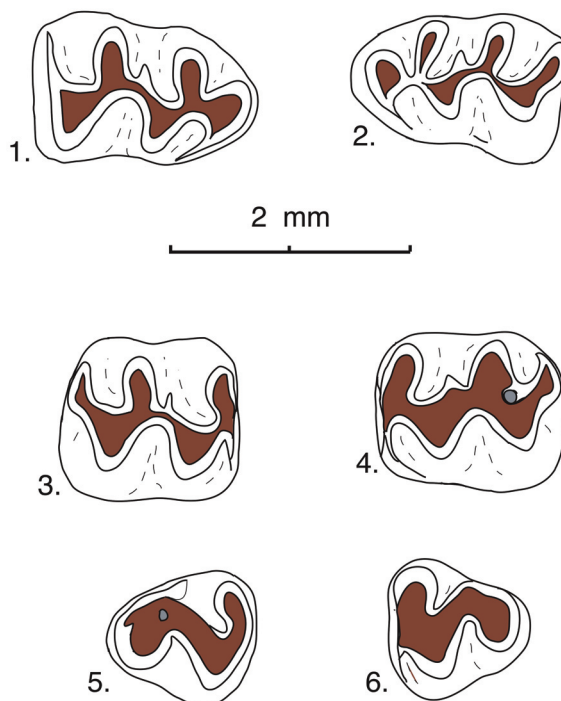**Etymology.** ensis, for occurrence in the Maxum local fauna.

Diagnosis. Larger size than *P. repenningi* and with a smaller bilobed anterocone on M1. Similar to *P.*
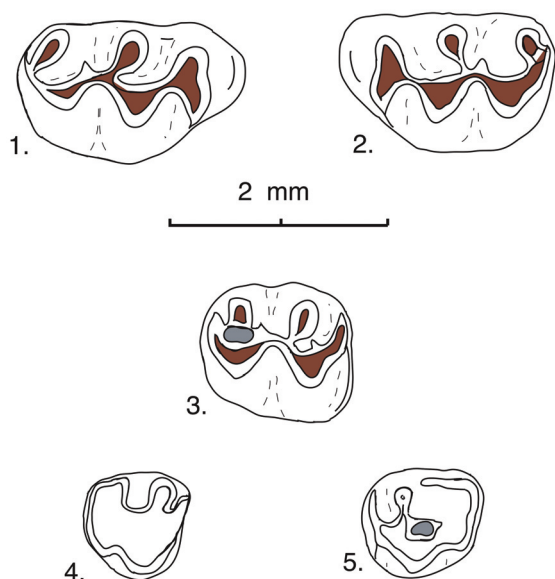
FIGURE 6. *Postcopemys maxumensis* sp. nov., from the Maxum fossil site, Tassajera Formation, California; occlusal views of upper molars: 1, right M1 (UCMP 87942). 2, left M1 (UCMP 87891). 3, right M2 (UCMP 87918). 4, right M3 (UCMP 87973). 5, left M3 (UCMP 87951).

FIGURE 7. *Postcopemys maxumensis* sp. nov., from the Maxum fossil site, Tassajera Formation, California; occlusal views of lower molars: 1, right m1 (UCMP 87892). 2, left m1 (holotype, UCMP 87890). 3, right m2 (UCMP 87898). 4, left m2 (UCMP 87910). 5, right m3 (UCMP 87927). 6, left m3 (UCMP 87923).

repenningi in that the upper molars lack alignment of protolophule II with the anterior arm of the hypocone, and the lower molars have the entolophulid aligned (or nearly aligned when unworn) with the posterior arm of the protoconid; also similar to *P. repenningi* in having a short- to medium-length mesoloph and a minute mesolophid. Anterocone of M1 bilobed with lingual cusp slightly smaller than labial cusp. Anteroconid of m1 single-cusped and slightly asymmetrical.

Description. A medium-sized, brachydont rodent with slightly alternating cusps, labial cusps placed opposite the posterior side of lingual cusps in upper molars, and lingual cusps placed opposite the anterior side of labial cusps in lower molars; anterior arm of hypocone is not aligned with protolophule II in upper M1-2 but posterior arm of protoconid is aligned—or becoming aligned in early wear—with the entolophulid in lower molars. The posterior arm of the hypocone (id) is long; it is flexed labially in M1-2 to become a posterior cingulum that terminates short of the labial tooth margin; it is flexed lingually in m1-2 to become a posterior cingulum that usually terminates short of the lingual tooth margin. A short but broad mesoloph is usually present in M1-2; a minute mesolophid occasionally occurs in m1-2. A posterolabial sulcus is occasionally developed in lower molars,

especially m2. Three prominent roots (1 lingual and 2 labial) are developed in upper teeth, two prominent roots (anterior and posterior) are developed in lower teeth; accessory rootlets are absent or unknown in all teeth.

M1. Occlusal outline is rounded oval, longer than wide; the anterocone is bilobed with the lingual lobe smaller than the labial lobe. Anterior arm of the protocone is long, joining the anterocone centrally near the midline; posterior arm of the protocone is short, joining protolophule II and the short anterior arm of the hypocone near the midline. Anterior arm of the hypocone is short, not aligned with protolophule II; metalophule II is directed lingually or posteriorly from the metacone to join the posterior cingulum labial to the midline. An anterior cingulum is low but persistent anterior to the anterocone; the lingual anterior cingulum descends from the lingual lobe of the anterocone, continuing to the base of the enamel. The anterior arm of the hypocone weakly reaches the labial side of the metacone in all specimens; metalophule II is well

developed, directed posteriorly to join the posterior cingulum labial to the midline.

M2. Occlusal outline is a rounded rectangle, longer than wide; anterior arm of the protocone is short, joining the anterior cingulum high on the midline; posterior arm of the protocone is long, joining protolophule II near the midline, and more posteriorly joining the anterior arm of the hypocone slightly labial to the midline; posterior arm of the hypocone joins metalophule II. A slight remnant of protolophule I is directed labially from the anterior side of the protocone, barely reaching the base of the paracone; protolophule II is prominent. The anterior cingulum is high and long labial to the midline, and separate from the paracone; it descends gradually lingual to the midline and is flexed posteriorly to terminate at the anterior base of the protocone.

M3. Occlusal outline is well rounded, with two small cusps (protocone and paracone) plus a minute hypocone; the metacone is indistinct or absent. Protolophule I and II join the anterior and posterior sides, respectively, of the protocone, enclosing a small central basin. A mesoloph is indistinct or absent. The anterior cingulum is high labial to the midline, descending rapidly lingual to the midline; the posterior cingulum is directed labially from the minute hypocone, terminating at the posterolabial corner of the tooth; a labial cingulum is low or indistinct.

m1. Occlusal outline is subrectangular, longer than wide, narrow and rounded anteriorly. The anteroconid is single cusped, relatively narrow and slightly asymmetrical. Short anterior arm of the protoconid joins the metalophulid and short anterolophid centrally; posterior arm of the protoconid is relatively long, joining a labially-directed entolophulid and more posteriorly joining the anterior arm of the hypoconid labial to the midline; entolophulid is short, weakly joining the posterior side of the metaconid in 2 of 4 specimens. Anterior arm of the hypoconid broadly joins the entolophulid on the midline; posterior arm of the hypoconid is directed labially, becoming the posterior cingulum. The anterior cingulum is high on the labial side of the anteroconid, descending posteriorly; on the lingual side of the anteroconid the anterior cingulum is indistinct in 3 specimens, short in 2 specimens; a posterior cingulum is directed lingually, and slightly expanded posteriorly in 2 of 3 specimens; a low labial cingulum partially closes the labial sinus.

m2. Occlusal outline is a rounded rectangle, longer than wide. Short anterior arm of the protoconid joins metalophulid I and the anterior cingulum high on the midline; long posterior arm of the protoconid joins the short anterior arm of the hypoconid and entolophulid lingual to the midline; long posterior arm of the hypoconid is flexed lingually and slightly expanded posteriorly as the posterior cingulum. A minute mesolophid is directed lingually from the posterior arm of the protoconid in 2 of 5 specimens, terminating short of the metaconid; the entolophulid is short, directed posteriorly from the entoconid and weakly joining the posterior side of the hypoconid in 2 of 4 specimens. The anterior cingulum is high on the midline, gradually descending labially, and flexed posteriorly to terminate at the anterior base of the protoconid; the anterior cingulum is absent or indistinct lingual to the midline; a low cingulum partially closes the labial sinus.

m3. Occlusal outline is a rounded triangle, narrow posteriorly. Three cusps (protoconid, small metaconid, and smaller hypoconid) are distinct, and the entoconid is indistinct or absent. The short anterior arm of the protoconid and metalophulid I join near the anterior tooth margin lingual to the midline; the long posterior arm of the protoconid joins the anterior arm of the hypoconid lingual to the midline, and apparently continues lingually (? as a mesolophid) to terminate short of the lingual tooth margin. The metaconid and hypoconid are too worn to show significant features. All of the specimens are well worn, and the anterior cingulum is preserved only labial to the midline where it is restricted to the anterolabial corner of the tooth. A lingual cingulum is high in the position of the entoconid, and continues posteriorly to merge with the posterior cingulum and the hypoconid; anterior to the position of the entoconid the lingual cingulum descends slightly, to close a deep, narrow basin posterior to the metaconid.

Comparisons and Discussion

Postcopemys maxumensis new species, is larger than known species of *Postcopemys*, e.g., *P. repenningi, P. valensis, and P. vasquezi*; in addition, the anterocone on M1 of *P. maxumensis* is more elongate, with a low anterior cingulum. The m1 anteroconid is single cusped and slightly asymmetrical; the M3 is relatively large, with a minute hypocone; and m3 is relatively short and wide, compared to *P. repenningi,* its closest analogue. *P. maxumensis* differs from *Antecalomys phthanus* in lacking accessory rootlets. *P. maxumensis is* assigned to *Postcopemys* because the upper molars lack alignment of protolophule II with the anterior arm of the hypocone, and the lower molars

2 mm
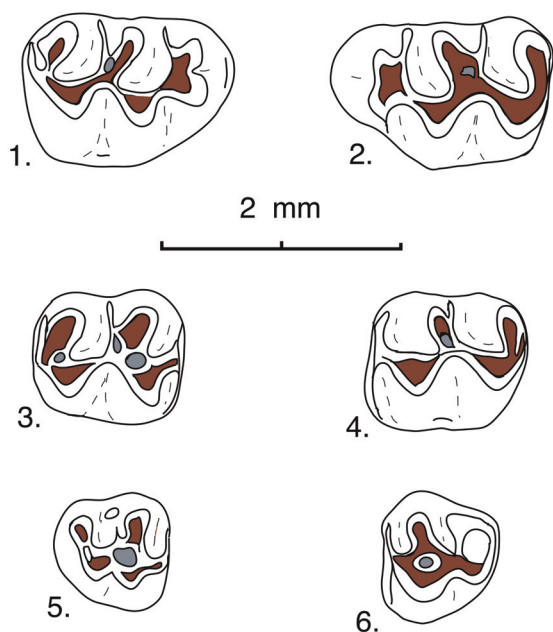
FIGURE 8. *Jacobsomys dailyi* sp. nov. from the Maxum fossil site, Tassajera Formation, California; occlusal views of upper molars: 1, right M1 (UCMP 87485). 2, left M1 (UCMP 87498). 3, right M2 (UCMP 87500). 4, left M2 (UCMP 87566). 5, right M3 (UCMP 87523). 6, left M3 (UCMP 87967).

2 mm

FIGURE 9. *Jacobsomys dailyi* sp. nov. from the Maxum fossil site, Tassajera Formation, California; occlusal views of lower molars: 1, right m1 (UCMP 87507). 2, left m1 (UCMP 87528). 3, right m1-m2 (UCMP 87567). 4, left m2 (UCMP 87541). 5, right m3 (UCMP 87536). 6, left m3 (UCMP 87915).

have the entolophulid aligned (or nearly aligned when unworn) with the posterior arm of the proto-conid.
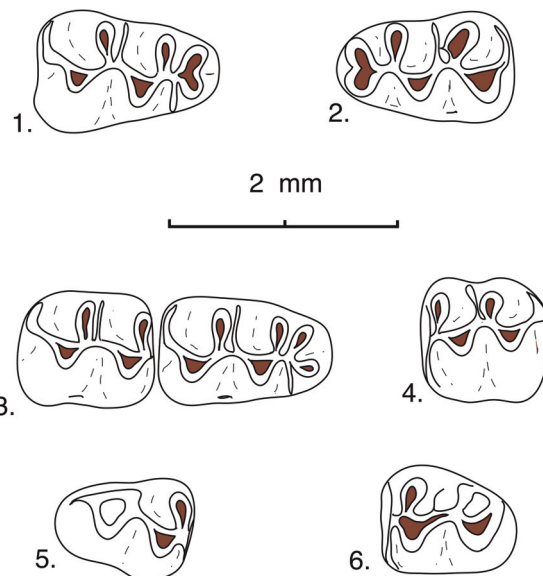
Jacobsomys dailyi May, Woodburne, Lindsay, Albright, and Sarna-Wojcicki, 2011 Figures 8 and 9

Material. 51 isolated cheek teeth: UCMP 87470, 87476, 87479, 87482, 87485, 87486, 87489, 87490, 87491, 87493, 87498, 87499, 87500, 87503, 87504, 87507, 87518, 87520, 87522, 87523, 87526, 87527, 87528, 87529, 87530, 87531, 87532, 87533, 87534, 87536, 87539, 87540, 87541, 87547, 87548, 87551, 87553, 87556, 87560, 87566, 87567, 87906, 87908, 87915, 87938, 87940, 87941, 87955, 87967, 87975, and 99800.

Localities. UCMP localities RV-7702, Warren local fauna; RV-8103, upper Horned Toad Hills local fauna; and V-6869, Maxum local fauna, all in California.

Age. Late Hemphillian and early Blancan.

Description. *Jacobsomys dailyi* is a medium-sized, brachydont cricetid rodent with a large bilobed anterocone on M1 and a large bilobed anteroconid on m1. In addition, labial cusps are placed opposite the posterior side of lingual cusps in upper molars, and lingual cusps are placed opposite the anterior side of labial cusps in lower molars; a long, thin mesoloph and mesolophid are usually present in upper and lower molars, and a thin, labial anteroloph is often present in M1, along with a long, thin, labial anterolophid in m1. These lophs are always situated anteriorly, tending to merge with the anterior lingual cusp in upper molars; in lower molars the anterolophid is situated anteriorly, tending to merge with the labial lobe of the anteroconid, whereas the mesolophid is situated posteriorly, tending to merge with the lingual entoconid; all of these lophs and lophids tending to fuse (with wear) to the base of the adjacent main cusp. Protolophule II, metalophule II, and entolophulid tend to bifurcate toward their base with the medial branch joining the mure near the midline, and the lateral branch joining the loph or lophid directed away from the mure. Thus, these teeth tend to develop three lophate transverse ridges in M1 (anteroloph, mesoloph, and posterior cingulum) and in m1 (anterolophid, mesolophid and posterior cingulum [with the metaconid of m2]). There are only two lophate ridges on M2 and m2. The enamel is worn quickly near the base of these ridges, especially at the posterior base of labial cusps in M1-2 and the anterior base of lingual cusps in m1-2, presumably the result of a strong

power stroke in mastication. Also, a posterolabial sulcus is developed between the robust posterior cingulum and the hypoconid in m1 and m2. Roots, where known, are well developed, lacking accessory rootlets; upper molars tend to elongate the lingual root anteroposteriorly, extending beneath the hypocone in M1; lower roots tend to develop a thin bony wall medially (in m1), or increase the width of the posterior root (in m2).

The dentary has a broad, prominent masseteric crest whose anterior termination is blunt, below the anterior root of m1; the masseteric crest swells posterior to its anterior termination, becoming more ridge-like. The mental foramen is exposed slightly anterior to the masseteric crest, on the posterolateral side of the diastema, slightly below the level of the anterior termination of the masseteric crest.

M1. Occlusal outline is oval, longer than wide; the anterior arm of the protocone usually (9 of 11 specimens) joins the lingual lobe of the anterocone; an anteroloph is present in 10 of 12 specimens, weakly joining the posterior side of the labial anterocone lobe. Protolophule II is bifurcated in 8 of 12 specimens with the anterior branch joining the posterior arm of the protocone near the midline and the posterior branch (if present) joining the middle of the mesoloph; metalophule II is short, bifurcating in 6 of 10 specimens with the anterior branch joining the posterior cingulum at its junction with the posterior arm of the hypocone and the posterior branch (if present) weakly joining the end of the posterior cingulum. The mesoloph joins the posterior side of the paracone in 9 of 13 specimens.

M2. Occlusal outline is subrectangular, longer than wide, with a straight and steep anterior side. Protolophule I is distinct in 4 of 5 specimens, joining the anterior arm of the protocone (3 specimens), or the labial side of the anterior cingulum (1 specimen); protolophule II is present in 4 of 5 specimens, bifurcating in 3 specimens with the anterior branch joining the posterior arm of the protocone and the posterior branch (if present) joining the middle of the mesoloph; metalophule II is present in 5 specimens, bifurcating in 4 of those with the lingual branch joining the posterior arm of the hypocone where it joins the posterior cingulum and the labial branch weakly joining the labial end of the posterior cingulum. The anterior cingulum is high labially, separate from the paracone, and descends rapidly lingual to the midline.

M3. Occlusal outline is subcircular, with a straight anterior side. The protocone and paracone are well developed although small relative to cusps on anterior teeth; the hypocone is small and the metacone is indistinct (9 specimens) as a swelling on the labial cingulum or minute (2 specimens). The anterior cingulum is long and prominent, joining the anterior arm of the protocone and the anterolabial paracone; a high, narrow loph (?protolophule I) is present in 9 of 11 specimens, joining the anterior arm of the protocone (5 specimens) or the anterior cingulum (4 specimens); another loph (?protolophule II) is directed posterolingually from the paracone, joining the anterior side of the hypocone to enclose a deep, central basin; another short loph is directed labially from the hypocone toward the posterior cingulum, terminating at a swelling (?metacone) on the cingulum, to enclose (with the posterior cingulum and ?protolophule II) a shallow posterior basin.

m1. Occlusal outline is an elongated rectangle, narrow anteriorly. The long anterior arm of the protoconid joins the short metalophid I on the midline and continues anteriorly to join centrally the lobes of the anteroconid; a low and thin anterolophid is usually directed labially (8 of 9 specimens) from the junction of the arm of the protoconid with the anteroconid, terminating at the labial tooth margin; the long posterior arm of the protoconid joins the base of the long, thin mesolophid and the short entolophulid near the midline. The short anterior arm of the hypoconid joins the posterior base of the entolophulid; posterior arm of the hypoconid is directed posteriorly and gently flexed lingually to continue as a prominent posterior cingulum that terminates short of the lingual tooth margin. Metalophulid I is bifurcated in only 2 of 9 specimens; entolophulid is bifurcated in 7 of 9 specimens, with the posterior branch joining the protoconid on the midline and the anterior branch joining the middle of the mesolophid. There is no distinct anterior cingulum descending from the lobes of the anteroconid, although low cingula partially close anterior sinuses on the labial and lingual sides of teeth.

m2. Occlusal outline is subrectangular, longer than wide. The short anterior arm of the protoconid joins the short metalophulid I and continues to join the anterior cingulum high on the midline; the long posterior arm of the protoconid joins the base of the mesolophid and continues posteriorly to join the entolophulid. The short anterior arm of the hypoconid joins the posterior base of the entolophulid near the midline; the long posterior arm of the hypoconid is directed posteriorly and flexed lin-

gually to continue as a prominent posterior cingulum that descends and terminates at the posterior base of the entoconid. Metalophulid I is bifurcated in 3 of 8 specimens; entolophulid is bifurcated in all 8 specimens. The anterior cingulum is close to (and obscured by) the metaconid lingual to the midline, it descends labially and is gently flexed posteriorly to terminate at the base of the protoconid; low labial cingula partly close the labial sinus, the lingual sinus is partly closed by the mesostylid, if present.

m3. Occlusal outline is elongate oval, longer than wide and narrow posteriorly; three cusps are prominent with the protoconid and metaconid larger and slightly higher than the hypoconid; an entoconid is indistinct or absent. The short anterior arm of the protoconid joins a short metalophid I and continues anteriorly to join the anterior cingulum high near the midline; the long posterior arm of the protoconid joins the anterior arm of the hypoconid (with a smooth flexure) lingual to the midline, anterior to a broad juncture with a short loph (?entolophulid or mesolophid). The robust posterior arm of the hypoconid is directed lingually and continues around the posterior margin of the tooth as a narrow lingual cingulum that descends anteriorly to join a short loph (?entolophid or mesolophid). An anterior cingulum is high at the midline, merging with the base of the metaconid lingual to the midline, and descending labially very steeply to terminate short of the labial tooth margin; the labial sinus is partially closed by a low labial cingulum.

Discussion. *Jacobsomys dailyi* is significantly smaller than *Jacobsomys verdensis*, the only other known species of this genus. When Czaplewski (1987a) described *Jacobsomys verdensis* he compared it to the living rice rat *Oryzomys*. Examination of modern rice rats indicates that they share many dental features with *Jacobsomys*; these two genera differ dentally primarily in that the m1 of *Jacobsomys* has a well-developed bilobed anteroconid, and the m1 of *Oryzomys* has a prominent single-cusped anteroconid. Both genera appear to share development of the anteroloph (and anterolophid) plus the mesoloph (and mesolophid) with bifurcating protolophules and metalophules in M1-2 as well as having a bifurcating entolophulid in m1-2, along with the wear pattern described above to characterize *Jacobsomys*. In addition, they share a long, thin anteroloph in M1, a long, thin mesoloph that bonds to the posterior side of the paracone in M1 and M2; a long, thin anterolophid in m1, and a long, thin mesolophid that bonds to the anterior side of the entoconid in m1-2.

Jacobsomys and *Oryzomys* have developed a distinctive mastication reflecting unusual wear on the side of cusps on both upper and lower teeth that occlude with one another. For example, *Oryzomys fulvescens* develop, in upper molars, prominent sloping well-honed wear facets on the posterior side of labial cusps resulting from bifurcation of the protolophule and to some extent the metalophule; in lower molars they develop prominent, sloping, well-honed wear facets on the anterior side of lingual cusps, resulting from bifurcation or possible bifurcation of the metalophulid and entolophulid. These same features appear on *Oryzomys palustris,* in addition to lateral expansion of the anteroloph, mesoloph and posterior cingulum in upper teeth to enclose and expand a well-worn grinding surface. Occlusal wear on the side of prominent cusps seems characteristic of *Oryzomys* and *Jacobsomys* but wear also occurs at the tip of cusps. These rodents have developed a unique and efficient method of grinding favorite foods that initially appeared in *Jacobsomys*.

Several fossil records have been assigned to *Oryzomys* in the literature. These include ?*Oryzomys pliocaenicus* from the Hemphillian Edson Quarry fauna, Kansas (Hibbard, 1937), ?*Oryzomys* from the Hemphillian Bartlett Mountain fauna in Oregon (Shotwell 1970), and cf. *Oryzomys* from the Truth or Consequences fauna Mexico (Repenning and May 1986); it now appears that these records should be checked for possible assignment to *Jacobsomys* rather than *Oryzomys* or ?*Oryzomys*. In summary, there is a strong similarity between *Jacobsomys* and *Oryzomys,* suggesting a possible ancestral-descendant relationship between these genera.

ACKNOWLEDGMENTS

whether his work in the Horned Toad should be published. The answer was a strong YES, resulting in this and May's paper in this volume. We thank May for his diligence, enthusiasm, and help in preparing this paper. Last but not least we thank the editors of this volume for their patience and for the opportunity to contribute to this volume.

C.A. Repenning touched and encouraged many graduate students in vertebrate paleontology during his life (including NJC). We all knew him as a tireless worker and an honest, sincere mentor. Once he knew you, he would never let go of you. This and his outstanding record as a decorated soldier in World War II, enable us to characterize him as a warrior. We never knew a tougher and more relentless warrior than our friend and colleague Rep.

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