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NEW LATE MIOCENE (LATEST CLARENDONIAN TO EARLY HEMPHILLIAN) CRICETID RODENTS FROM THE UPPER PART OF THE DOVE SPRING FORMATION, MOJAVE DESERT, CALIFORNIA

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ABSTRACT

Previous extensive biochronologic, paleomagnetic, radiometric and tephrochronologic investigations of the type Dove Spring Formation (Ricardo Group) exposed north of the El Paso Fault, Mojave Desert, California, have resulted in it being one of the most completely studied sections in North America spanning the transition from the Clarendonian to the Hemphillian North American Land Mammal Ages. The succession of numerous, superposed microfossil sites within the upper part of the Dove Spring Formation provide an unprecedented opportunity to study cricetids during this transition, an interval that is poorly sampled elsewhere in North America. Our reevaluation of the systematic paleontology of cricetid rodents has resulted in the recognition of 10 species from the upper part of the Dove Spring Formation, including the following: *Acrolophomys rhodopetros* new genus and species; *Copemys dentalis*; *Copemys* sp., cf. *C. dentalis*; *Postcopemys* sp., cf. *P. valensis*; cf. *Repomys* sp.; *Antecalomys coxae* new species; *Bensonomys* sp.; *Lindsaymys takeuchii* new genus and species; *Lindsaymys* sp., cf. *L. takeuchii*; and *Lindsaymys* sp. B. In addition, *Lindsaymys takeuchii* and *Lindsaymys* sp. A are recognized from the undifferentiated Ricardo Group exposed south of the El Paso Fault. These records document a rapid diversification and radiation of cricetids during the latest Clarendonian that continued into the earliest Hemphillian, followed by an apparent turnover of cricetid taxa during the latter part of the early Hemphillian.

INTRODUCTION

The Dove Spring Formation (DSF, formerly the Ricardo Formation) of the El Paso Basin, western Mojave Desert, California, has long been known for its vertebrate fossils (see Whistler et al., 2009, 2013). The mammalian fossil assemblage from the DSF was designated by the Wood Committee as one of the principal correlatives characterizing the Clarendonian North American Land Mammal Age (Wood et al., 1941). The most recent extensive studies on the geochronology and biostratigraphy of the DSF were presented by Whistler and Burbank (1992) and Whistler et al. (2009). Their detailed work provided one of the most complete records of superposed fossil vertebrate assemblages spanning the Clarendonian through the early Hemphillian in North America and further clarified the characterization of the Clarendonian of the West Coast, including the Cerrotejonian and Montediablan west coast provincial stages. During their research and over many years, numerous superposed samples of small mammals were recovered from the DSF by wet screen sieving of large amounts of matrix followed by heavy liquid separation of the fossils from the concentrates. Included in the specimens recovered are a number of superposed samples with cricetid rodents spanning the latest Clarendonian through much of the early Hemphillian (uppermost Member 5 through Member 6 of the DSF). This time period is critical to the late Miocene diversification of cricetid rodents because it has rarely been sampled before and never in such a complete succession. Although Whistler and Burbank (1992) and Whistler et al. (2009) provided cursory identifications of the cricetid rodents during their studies, no detailed systematic analyses were presented. The purpose of this report is to provide a detailed reevaluation of the systematic paleontology of the cricetid rodents from the upper part of the DSF that spans this critical time period.

METHODS

Small fossil vertebrates were recovered from bulk fossil-bearing matrix using under water screen sieving of samples first soaked in di-limoinene (citrus oil concentrate) to expedite clay/rock dissociation. Minimum screen openings for sieving done in the type DSF were 0.5 mm (30-mesh screening). Minimum screen openings for sieving done at the one locality

(LACM 3620) studied in the undifferentiated Ricardo Group (URG) in the southern part of the study area were much larger, 1.5 mm (window screen with 16 x18 mesh). This screen mesh size most likely created a size bias for this sample toward only the larger rodent teeth.

Measurements of specimens were taken using an optical micrometer to the nearest 0.01 mm and all teeth were measured at their greatest dimensions. Protocone and protoconid crown heights were measured from the base of the enamel to the apices of the cusps. Only M1s or m1s that are unworn or in very early wear stage were utilized for diagnostic comparisons of the relative crown heights of taxa as reflected in the ratio of their protocone height/greatest anteroposterior length or protoconid height/greatest anteroposterior length. Dental formulae follow standard usage and nomenclature for cricetids after Wood and Wilson (1936) with modifications by Lindsay (1972) and Mou (2011). We use the terms sigmodontine, democricetodontine, and galushamyine as informal references to members of the cricetid tribes Sigmodontini, Democricetodontini and Galushamyini, respectively, as recognized in the taxonomic hierarchy of Lindsay (2008). Upper teeth are designated by capital letters and lower teeth by lowercase letters. All specimens are in the vertebrate paleontology collection of the Natural History Museum of Los Angeles County and detailed locality data are on file at this repository. Subzones or subbiozones of the Clarendonian and Hemphillian North American Land Mammal Ages (e.g., Cl2, Cl3, Hh1, Hh2) follow Tedford et al. (2004).

Abbreviations are as follows: ap, greatest anteroposterior length; CV, coefficient of variation; DSF, Dove Spring Formation; L, left; Ma, megannum (one million years in the radioisotopic time scale); N, number of specimens; OR, observed range; pch, protoconid crown height; prh, protocone crown height; R, right; SD, standard deviation; tra, greatest transverse width of talon/talonid; trp, greatest transverse width of trigon/trigonid; URG, undifferentiated Ricardo Group. Institutional acronyms are as follows: LACM, Natural History Museum of Los Angeles County.

GEOLOGIC SETTING

The specimens in this study have been recovered from two geologic formations well exposed on the western slopes of the El Paso Mountains and to the southwest of the mouth of Red Rock Canyon. All but one locality is from the upper 500 m of the DSF in stratigraphy spanning approximately 9.3 to less that 8 Ma (Figure 1). The other locality, LACM 3620, is from rocks south of the El Paso Fault that we will refer to as URG (see below). The rocks of the DSF are contained within an 1800 meter succession of fluvial, lacustrine and volcanic rocks that are found in over 70 km^2 of exposures in the El Paso Mountains in the northwestern Mojave Desert, California. They and older, underlying, predominantly volcanic rocks were deposited in a depression, the El Paso Basin, that likely developed along the Garlock Fault (see below), the major structural feature in the area.

Extensive paleomagnetic, radioisotopic, tephrochronologic and biochronologic work in the DSF provides a temporal interpretation indicating an age range from 12.5 Ma to about 8 Ma (Whistler et al., 2009, 2013). The rocks of the DSF are underlain by the dominantly volcanic middle Miocene (Hemingfordian) Black Mountain Basalt and Cudahy Camp Formation (CCF). The DSF and CCF were originally included in the Rosamond Series (Baker, 1912) and subsequently the Ricardo Formation (Dibblee, 1952, 1967). The Ricardo Formation was later subdivided into two formations and elevated to group rank (Loomis et al., 1983; Loomis and Burbank, 1988). The CCF thus is composed of Members 1 and 2 of Dibblee’s (1952) Ricardo Formation and the DSF restricted to Dibblee’s Members 3-8. Dibblee (1952) considered the Black Mountain Basalt to be Quaternary but subsequent work (Cox, 1987; Loomis and Burbank, 1988) recognized that it was interbedded into the upper part of the CCF. The DSF is overlain by several episodes of Pleistocene alluvial deposition derived primarily from the emerging Sierra Nevada.

The more than 1800 m of fluviolacustrine sediments and volcanic and volcaniclastic rocks of the DSF can be broadly separated into five lithofacies: 1) fine-grained lacustrine deposits of clay, silt, reworked volcanic ash, fresh-water limestone, and bedded chert; 2) fluvial deposits of channel sandstone and channel conglomerates that weather reddish in color and regularly form prominent cliffs; 3) overbank and floodplain silts; 4) poorly sorted alluvial fan deposits, and 5) paleosol, caliche, and silicified hardpan deposits (silcretes), the latter forming prominent, light-colored exposures that are easily traceable in the upper part of the sequence. Deposition in the lower portions of the DSF resulted primarily from meandering, intermittent streams feeding into a semi-permanent lake in the center of a broad basin. The upper portions become coarser as alluvial fans prograded into the filling basin. The fossil occurrences that form the basis of this study are from the uppermost 500 m of the DSF, which is mostly composed of coarser grained fluvial sediments containing prominent paleosol and siliceous hardpan (silcrete) deposits (Figure 1).

Volcanic air-fall vitric ashes are common (Figure 1), particularly in the more basin-ward portion of the section. Eighteen of these ashes are traced throughout most of the mapped section and serve as critical marker beds for correlation of measured sections. They are the source rock of many of the radioisotopic age

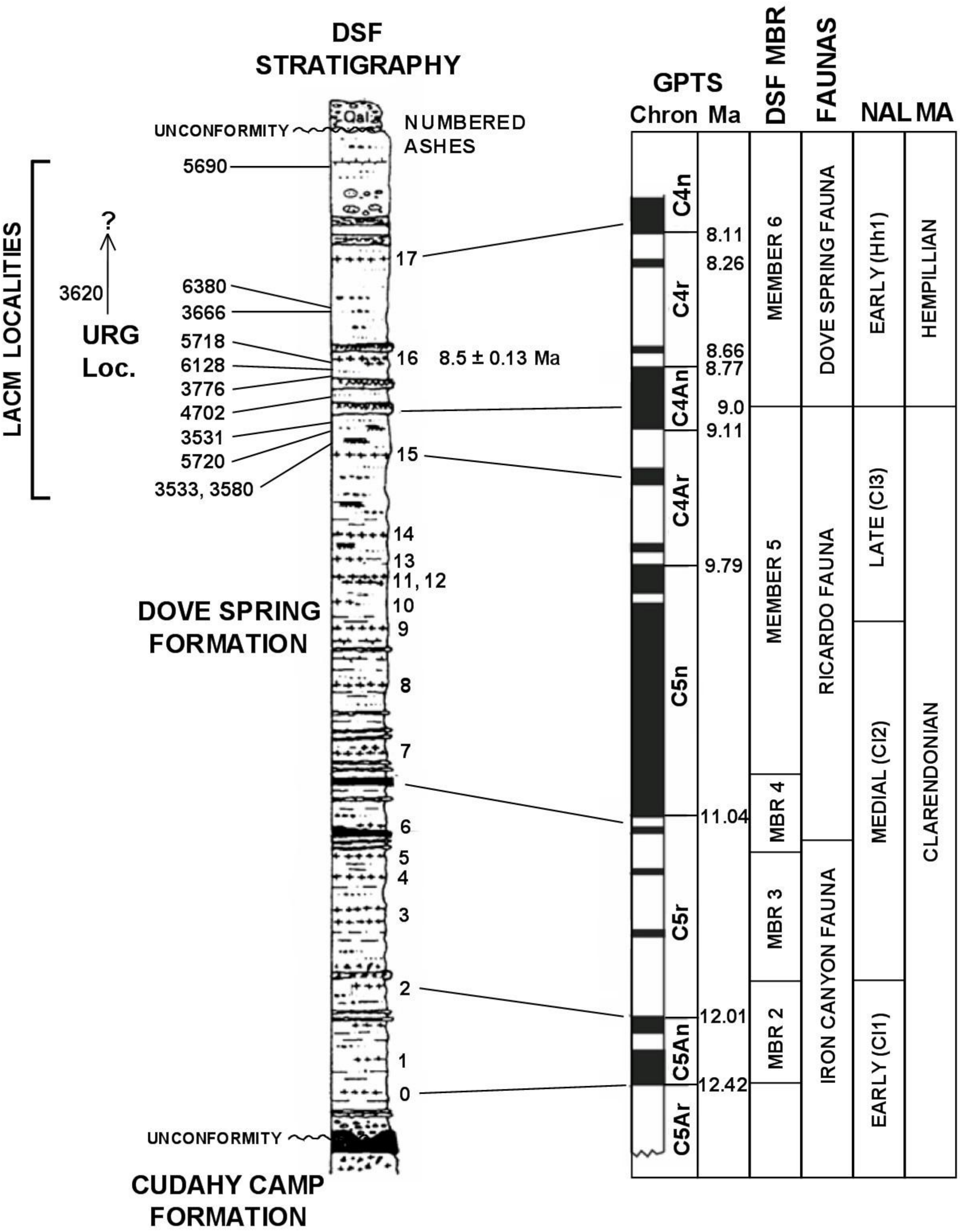

FIGURE 1. Generalized stratigraphic column of Dove Spring Formation (DSF) north of the El Paso Fault showing relative stratigraphic positions of LACM localities in upper part of formation and correlation to Global Polarity Time Scale (GPTS), members (DSF MBR), faunas, and North American Land Mammal Ages (NALMA). Stratigraphic position of locality LACM 3620 from URG south of the El Paso Fault relative those of localities in type DSF section undetermined. Modified after Whistler et al. (2009).

determinations within the DSF (Evernden et al., 1964; Cox and Diggles, 1986; Loomis and Burbank, 1988; Whistler and Burbank, 1992; Whistler et al., 2009) and many are recognized as having sources in the southern Great Basin and from the Yellowstone "Hot Spot" (Perkins et al., 1998; Perkins and Nash, 2002; Bonnichsen et al., 2008). Two prominent pink lithic tuff breccias that form cliffs in the lower part of the section can be traced along strike toward the center of the basin where they are expressed as yellow, fluvially reworked tuffaceous siltstones. The DSF also contains two basalt flow sequences that thicken to the southwest in a similar fashion to the pink tuff breccias. Each of these sequences contains a number of individual flows. The flows thin and eventually pinch out to the northeast toward the center of the depositional basin. The upper basalt sequence is the source of one of the more reliable radioisotopic dates (Whistler and Burbank, 1992).

The El Paso Mountains have been uplifted along the primarily dip-slip El Paso Fault which traverses the southern entrance of Red Rock Canyon in the southern El Paso Mountains. Rocks on both sides of the fault, mostly west and southwest of Red Rock Canyon, have been referred to the Ricardo Formation (now DSF) by most authors (Dibblee, 1952; Samsel, 1962; Castor, 1965; Dibblee, 1967; Loomis and Burbank, 1988; Whistler and Burbank, 1992). Although superficially similar to the DSF in gross outcrop exposure, closer examination of particularly the pebble and boulder content of the URG suggests a different source area than the strata of the DSF (Castor, 1965, Whistler et al., 2013). These strata are devoid of ash fall tephras that are common throughout the DSF. They are also devoid of the prominent silcrete soil horizons that dominate the upper part of the DSF where most of the specimens in this study were recovered. It has not been possible to trace or correlate a single bed from the type DSF sediments on the north across the El Paso Fault into the URG sediments to the south.

The more that 1000 m of sediments of the URG are composed predominantly of light colored, coarse grained fairly "clean," clay-poor arkosic sandstones with abundant conglomerate stringers. Darker fine to medium-grained clay-rich "dirty" sandstones occur in beds from a few centimetres to over 25 m. Reddish brown, clay-rich micaceous sandstones, likely representing paleosols, occur near the middle of the section. These are the source of most of the fossils recovered from the URG, including locality LACM 3620 that yielded some of the fossils discussed below. The URG is a totally fault-bounded block with the El Paso Fault on the north, the Cliff Canyon Fault on the west and the Garlock Fault zone on the east. In contrast to the western-dipping homoclinal structure of the type DSF, the URG is folded into four to five broad folds trending in a general east-west direction. Paleomagnetic studies (Burbank and Whistler, 1987) have demonstrated that the rocks of the DSF and URG appear to have significantly different post-deposional histories. Unfortunately, the rocks of the URG lack volcanics that would permit an independent age determination. The unpublished fossil fauna of the URG (Table 12) also contains an assemblage that differs to some extent from that of the upper DSF. All these are discussed in greater detail in Whistler, et al, (2013). It is likely that the sediments of the URG were deposited either in a separate, smaller basin developed along the Garlock Fault or in a late rejuvenation of part of the El Paso Basin. If this structural interpretation could be confirmed, the differing lithology of the URG sediments warrants a separate formational designation, a task that is beyond the scope of this study

The dominant structural feature of the El Paso Mountains area is the Garlock Fault and its major branch, the El Paso Fault. The Garlock Fault separates the mountains of the Tehachapi, Sierra Nevada and Basin and Range province on the north from the currently lower-relief Mojave province to the south. It is a major left-slip, intracontinental fault, which separates the less tectonically active Mojave Block to the south from the major crustal extensional area of the Basin and Range Province to the north (Davis and Burchfiel, 1973, Christiansen and Yeats, 1992). The CCF and DSF were deposited in elongated basin, the El Paso Basin that likely developed during early extension of the Basin and Range Province. A cumulative left-lateral displacement of 48 to 64 km has been demonstrated for the Garlock Fault zone (Smith, 1962; Chen and Moore, 1979). The El Paso Fault can be traced 6.4 km to the southwest from the southern end of the El Paso Mountains were it appears to be truncated by the Cliff Canyon Fault, a southern branch of the Sierra Front Fault (Samsel, 1962; Castor, 1965).

PALEONTOLOGY

The diverse fossil assemblages collected in the DSF over more than a hundred years contain pollen, phytolith, leaf and wood floras including the oldest published C4 grasses in North America and a diverse assemblage of at least 86 species of fossil vertebrates (Whistler, et al., 2009, 2013). Carnivores, horses, camels, antelopes and diverse microvertebrates collected from over 50 microfossil sites are well documented within the vertebrate assemblages. These fossils are described in Baker (1912), Merriam (1919), Stock and Furlong (1926), Furlong (1927), Stock (1928), Miller (1930), Osborn (1933), Frick (1937), Green (1948), Richey (1948), Tedford (1961), Estes (1963), Schultz et al. (1970), Baskin (1980), Rich (1980), MacFadden (1984), Whistler and Wright (1989), Korth and Reynolds (1994), Wang et al. (1999), Wang et al. (2005), Lander (2005), Prothero (2005), Woodburne (2007), Tedford et al. (2009), Whistler and Burbank (1992), Whistler et al. (2009, 2013) and Tseng et al. (2010).

Vertebrate fossils are broadly distributed throughout the DSF, but are most commonly recovered from finer grained sediments representing floodplain or overbank deposits. They are also commonly found in paleosols, particularly in the upper part of the section that is the source of this study, but they are rare in channel deposits. Most of the microvertebrate fossils from the lower part of the DSF were recovered from lignitic siltstones interpreted as pond or slow moving, shallow water deposits. Disarticulated fossil owl pellets in these pond deposits provide a source for much of the microvertebrate assemblage from that part of the succession. Microvertebrates from the paleosols in the upper part of the DSF appear to represent carnivore scat accumulations and/or collapsed burrow assemblages. In the cricetid samples from the upper part of the DSF, M1s are the most common tooth position represented, outnumbering m1s by about two to one.

CHRONOLOGIC FRAMEWORK

Radioisotopic dating (Evernden et al., 1964; Cox and Diggles, 1986; Whistler and Burbank, 1992), magnetostratigraphic correlation (Burbank and Whistler, 1987; Loomis and Burbank, 1988; Whistler and Burbank, 1992) and tephrochronological correlations (Perkins et al., 1998; Perkins and Nash, 2002; Whistler et al., 2009) have all been undertaken in attempts to develop a chronological framework to facilitate biochronological analyses within the DSF. The considerable radioisotopic dating within the DSF is summarized in Whistler et al. (2009:fig. 1).

A magnetostratigraphic framework was developed in the late 1980’s to early 1990’s throughout the lower 1600 m of the DSF (Burbank and Whistler, 1987; Loomis and Burbank, 1988; Whistler and Burbank, 1992) (Figure. 1). This magnetostratigraphic framework has since been reinterpreted (Whistler et al., 2009; see also Figure 1, this study). There are no radiometric or detailed magnetostratigraphic analysis for the rocks of the URG south of the El Paso Fault, thus the age estimates for these rocks are dependent on stage of evolution interpretations of the fossil assemblage.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer de Waldheim, 1817
Subfamily Cricetinae Fischer de Waldheim, 1817
Tribe Sigmodontini Wagner, 1843
Lindsaymys new genus

Type species—*Lindsaymys takeuchii*, new species.

Included species—Type species and three species left in open nomenclature.

Distribution and Age—Localities LACM 5720, 4702, 3776, 6128, 5718, 3666, 6380, upper part of DSF and LACM 3620, URG, Kern County, California. Latest Clarendonian to early Hemphillian (Cl3-Hh1, ~9.2-8.4 Ma).

Diagnosis—*Lindsaymys* is characterized by having the following suite of dental characters: 1) moderately hyposodont molars that exhibit increasing crown height through time (prh/ap ratios of older species = 0.54 to 0.65, whereas younger species = 0.70-0.73); 2) M1 usually with accessory rootlet, paracone spur usually present through early wear, protolophule II not aligned with anterior arm of hypocone, and anterocone very weakly to not bifurcated in unworn to early wear; 3) M2 with paracone spur usually present through early wear and protolophule II nearly aligned with anterior arm of hypocone; 4) M3 reduced (M3 ap = 58 - 66% of M2 ap); 5) m1 with anteroconid not bifurcated and positioned close to metaconid, metalophulid connects to protolophulid I at junction with anterolophid, entoconid spurs commonly present, and moderately deep valley between metaconid, lingual edge of anteroconid and anterolophid that forms isolated valley during early moderate to moderate wear; 6) m2 entolophulid nearly aligned with posterior arm of protoconid; and 7) m3 moderately reduced.

Comparisons—*Lindsaymys* differs from all other Clarendonian and Hemphillian sigmodontine genera (*Abelmoschomys, Antecalomys, Prosigmodon*, *Bensonomys*, *Baiomys, Symmetrodontomys, Jacobsomys*) by having an isolated valley formed on m1 between metaconid, anteroconid and anterolophid during early moderate to moderate wear (due to close positioning of lingual edges of metaconid and anteroconid, which merge with wear). *Lindsaymys* further differs from species of *Prosigmodon* by having the following: 1) relatively higher crowned molars; 2) M1-2/m1-2 primary cusps/cuspids less lophate; 3) M2 protolophule II and m2 entolophulid only slightly non-aligned relative to M2 anterior arm of hypocone and m2 posterior arm of protoconid, respectively; 4) M1-2/m1-2 with paracone/entoconid spurs (except for *P. oroscoi*, which can have M1-2 fused mesolophs that give appearance of paracone spurs); 5) M1 anterocone either not bifurcated or only slightly bifurcated in unworn through very early wear stage; 6) M2 anterior cingulum more robust; 7) m1 anteroconid not bifurcated; 8) m1 anteroconid positioned closer to metaconid; 9) m1-2 primary cusps positioned more alternately; 10) M3 more reduced relative to M2 (M3 ap = 57- 66% of M2 ap, whereas those of *Prosigmodon* = 80-84%); 11) m3 slightly more reduced relative to m2 (m3ap/m2 ap = ~85%, whereas those of *Prosigmodon* = 87-98%); and 12) M3 with a distinct, complete protolophule II that closes off the valley between the paracone and protocone posteriorly (except *P. chihuahuensis*, which can have a complete protolophule II). *Lindsaymys* further differs from *Antecalomys*, by having the following: 1) significantly higher crowned molars; 2) larger size; 3) M1-2/m1-2 with paracone/entoconid spurs commonly present; and 4) M1-2/m1-2 mesolophids almost always absent. It further differs from *Bensonomys* by having the following: 1) much higher crowned molars; 2) M1 anterocone more erect (in *Bensonomys* anterocone slanted strongly posteriorly) and very weakly bifurcated to not bifurcated (in *Bensonomys* anterocone strongly bifurcated); 3) M2/m2 protolophule II/posterior arm of protoconid more nearly aligned with anterior arm of hypocone/entolophulid, respectively; and 4) m1 anteroconid never bifurcated. *Lindsaymys* further differs from *Baiomys* by having the following: 1) larger size; 2) much higher crowned molars; and 3) m1 anteroconid not bifurcated. *Lindsaymys* further differs from *Symmetrodontomys* by having the following: 1) relatively higher crowned teeth; 2) M1 anterocone less transverse; 3) M3/m3 much more reduced; and 4) m1 anteroconid not bifurcated. *Lindsaymys* further differs from *Jacobsomys* by having the following: 1) relatively higher crowned molars; 2) M1-2/m1-2 lacking mesolophs/mesolophids; and 3) M1 anterocone weakly to not bifurcated and m1 anteroconid not bifurcated (both strongly bifurcated in *Jacobsomys*).

Etymology—*mys*, Greek for mouse, and named in honor of Everett H. Lindsay of the Department of Geosciences, University of Arizona, in recognition of his extensive contributions on fossil rodents, especially those of the Cricetidae.

Discussion—The DSF and URG samples contain several groups of specimens that, based on the presence of M1 accessory rootlets, appear to belong to the Sigmodontini. They all exhibit similar occlusal morphologies, can be easily distinguished from all other early sigmodontines by the differences listed above and, thus, are referred to the new genus *Lindsaymys*. Within the samples of *Lindsaymys*, differences in size, minor dental characters and crown heights can be recognized. Two size groups are present, one moderately large and one medium sized. All specimens of the larger sized group are indistinguishable in occlusal morphology, but do exhibit slight differences in size and significant differences in crown height through time. This clade occurs from locality LACM 5720 (latest Clarendonian, ~9.2 Ma) up to LACM 6380 north of the El Paso Fault (early Hemphillian, ~8.4 Ma) and at LACM 3620 south of the El Paso Fault (early Hemphillian). The medium sized specimens occur at different stratigraphic levels and exhibit significant differences in crown height. The teeth of the older, medium sized specimens from localities LACM 4702 and 6128 (~8.9 - 8.8 Ma) are mesodont, whereas those from locality LACM 3620 south of the El Paso Fault are significantly higher crowned. The mesodont, medium sized specimens also exhibit certain minor dental differences from the larger sized group. Based on crown height, size and certain minor dental differences (see below), the specimens of *Lindsaymys* from the DSF and URG are assigned to several different species as follows (Figures 2-3, see also species accounts below): the younger, larger sized, high crowned specimens that have prh/ap ratios of 0.70-0.73 are assigned to the new genotypic species *L. takeuchii*; the older, lower crowned, larger sized specimens are assigned to *L.* sp., cf. *L. takeuchii*; and the older, lower crowned and younger, higher crowned, medium sized specimens, which lack adequate specimens to designate as holotypes and have very small samples sizes, are assigned to different species in open nomenclature (Figures 2-3).

Early representatives of the Neotomini (e.g., *Neotoma* [*Paraneotoma*] Hibbard, 1967), also have M1 accessory rootlets commonly present (Tomida, 1987; Zakrzewski, 1991; Lindsay, 2008). Traditionally, most investigators have placed *Neotoma* along with *Galushamys* and *Repomys* in the Neotomini (e.g., Korth, 1994). However, Lindsay (2008) erected a new tribe, Galushamyini, for *Galushamys*, *Repomys* and several other subhypsodont to hypsodont genera (*Paronychomys*, *Pliotomodon*, *Goniodontomys*, and *Paramicrotoscopes*), which lack M1 accessory rootlets. Lindsay (2008) also regarded Neotomini as more closely related to Sigmodontini based primarily on the presence of M1 accessory rootlets in early forms.

Subsequently, Korth and De Blieux (2010) and Korth (2011) described two new genera, *Basirepomys* and *Miotomodon*, respectively, both of which lack M1 accessory rootlets. *Lindsaymys* differs from all galushamyines and *Basirepomys* by having M1 accessory rootlets usually present. *Lindsaymys* can be easily distinguished from *Neotoma* (*Paraneotoma*) by having the following (Hibbard, 1967; Tomida, 1987; Zakrzewski, 1991; Carranza-Castañeda and Walton, 1992; Lindsay, 2008): 1) smaller size; 2) moderately to slightly lower crowned molars; 3) molar enamel thinner; 3) molar primary cusps more distinct and less

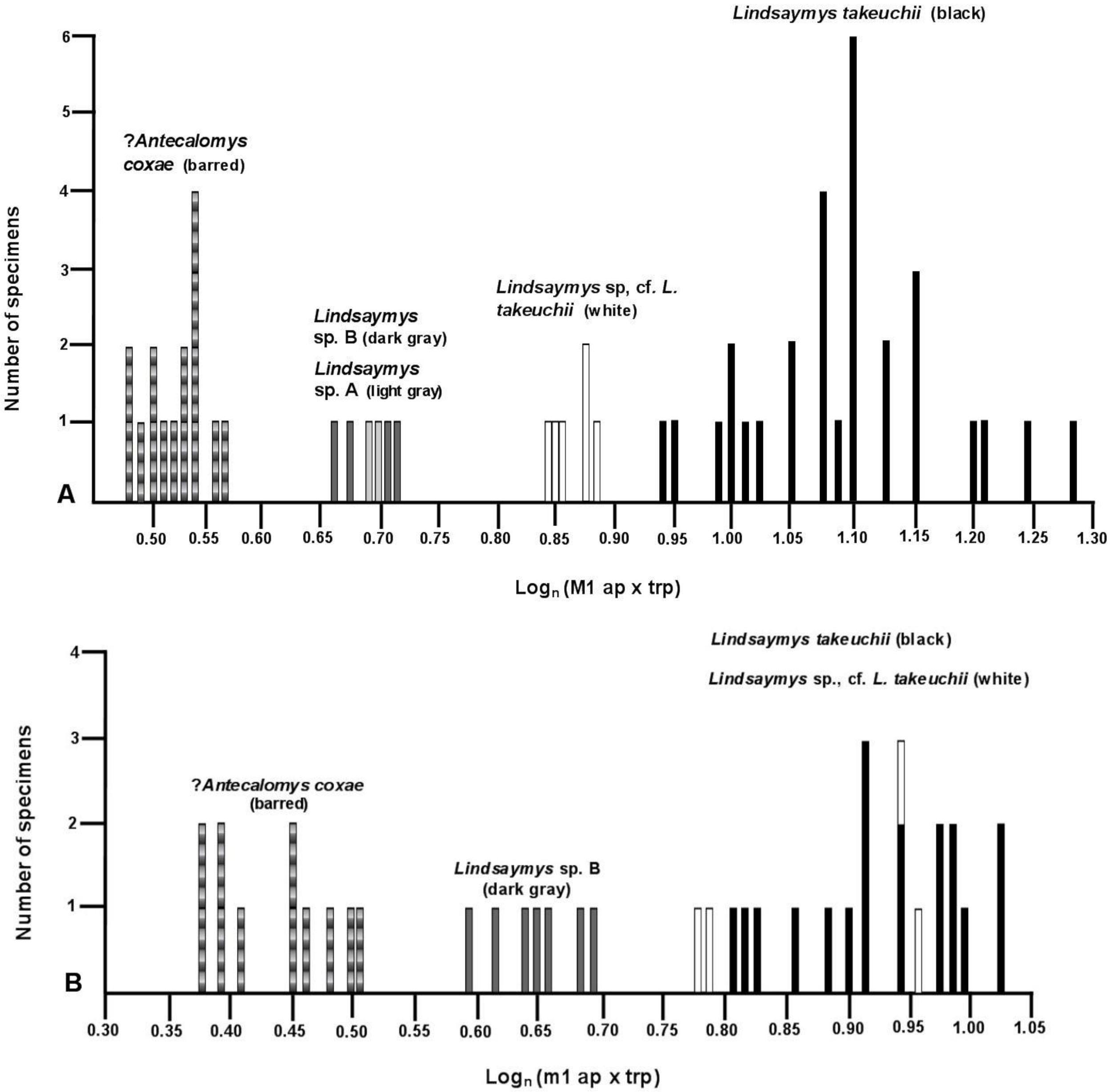

FIGURE 2. Charts plotting (A) Log_n M1 area (ap x trp) and (B) Log_n m1 area (ap x trp) versus number of specimens for proposed sigmodontine cricetid taxa from upper part of DSF and URG.

lophate with much less tendency to form a level (flat) occlusal surface with wear; 4) molar reentrants less deep and M1 reentrants do not form enamel lakes on the occlusal surface during late wear; 5) M3 with protolophule I and II present forming central isolated valley between the paracone and hypocone, and lacking the M3 transverse tri-lophid occlusal pattern typical of *Neotoma*; and 6) m1 with an isolated valley formed between metaconid, anteroconid and anterolophid during early moderate to moderate wear.

Lindsaymys takeuchii new species

Figures 2, 3, 4, 5, 6, 8; Table 1

Holotype—M1, LACM 126050.

Type Locality—LACM 3666.

Referred specimens—From locality LACM 5718: M1s, LACM 156393, 156398, 156410, 156411; M2s, LACM 156399, 156408; partial maxillae with M2-3, LACM 156397, 156401; m1s, LACM 156394, 156413; m2s, LACM 156391, 156395, 156400, 156402-156404, 156407; m3s, LACM 156396, 156405, 156406. From locality LACM 3666: M1s, LACM 126049, 150719 - 150722; M2s, LACM 150724, 150725, 150727, 150728; partial M2s, LACM 150718, 150723; partial M3s, LACM 150726, 150729; m1s, LACM 126046, 150730, 150733, 150735 - 150737; partial m1s, LACM 150731, 150734; m2s, LACM 150738, 150740; m3s, LACM 150741-150744. From locality LACM 6380: m2s, LACM 142756, 142762. From locality LACM 3620: M1s, LACM 150715, 156498 - 156505, 156520, 156529 - 156538; M2s, LACM 150714, 156512 - 156515, 156517 - 156519, 156543 - 156549, 156559; M3s, LACM 156520; m1s, LACM 156506 - 156511, 156539 - 156542; m2s, LACM 156516, 156522 - 156528, 156550 - 156558; m3s, LACM 156521, 156560, 156561.

Distribution and Age—Localities LACM 5718, 3666, 6380, upper part of DSF and LACM 3620, URG, Kern County, California. Early Hemphillian (Hh1, ~8.6-8.4 Ma).

Diagnosis—Higher crowned than other species (M1 prh/ap = 0.70-0.73, m1 pch/ap = 0.63-0.65); slightly larger than *L.* sp., cf. *L. takeuchii* and distinctly larger than *L.* sp. A and *L.* sp. B; and further differs from *L.* sp. B by having M3 slightly less reduced (M3 ap = 63-66% of M2 ap) and m2 with more robust posterior cingulid.

Etymology—Named in honor of Gary T. Takeuchi of the George C. Page Museum for his support and extensive work during the DSF research. Many of the specimens described here where recovered from his efforts in screen washing large amounts of matrix from the formation.

Description—M1 accessory rootlets are present in eight M1s from locality LACM 3620, whereas, in the remaining 11 M1s, the presence or absence of an accessory rootlet cannot be determined because the labial roots are broken off or the specimen is just a tooth cap without any roots. Of the 11 M1s from localities LACM 5718 through 3666, accessory rootlets are present in six M1s, whereas in the other five M1s this character cannot be determined for the same reasons as for those from locality LACM 3620. The accessory rootlets vary from a moderate bump to a well-developed robust projection under the paracone. The larger sample from locality LACM 3620 allows a reasonable assessment of the individual variation of M1. Accessory styles are usually absent, but a minute (five teeth) or very small mesostyle (one tooth) is present in six of the M1s. Mesolophs are lacking. However, in one tooth (LACM 156535), a minute labial projection occurs at the terminus of anterior arm of the hypocone that might be regarded as an incipient mesoloph. The M1 anterocone is either unbifurcated or very weakly bifurcated in unworn to very early wear stages, but with increasing wear any separation is obliterated. The M1 is further characterized by having the following (Figures 4A-H): 1) relatively high crowned (unworn prh/ap ratio = 0.70-0.73); 2) the M1 anterior arm of the protocone extends anteriorly and joins the anterocone just lingual of its center; 3) the protolophule II is not aligned with anterior arm of the hypocone; 4) a posteriorly directed paracone spur; 5) the reentrant valleys are deep and V-shaped in lingual and labial views; 6) the anterocone and primary cusps are relatively vertical, only slanting slightly posteriorly; 7) the anterior cingulum is weakly developed, extending almost vertically down the crown from the anterocone; and 8) the posterior cingulum is weakly to moderately developed, extending from metaloph to the posterior edge of the metacone.

TABLE 1. Dental statistics (in mm) for *L. takeuchii* new genus and species from upper part of DSF and URG.

Position/ dimension		N	Mean	SD	OR	CV
M1	ap	29	2.13	0.096	1.90-2.31	4.5
	tra	30	1.40	0.077	1.20-1.59	5.5
	trp	30	1.44	0.087	1.30-1.59	6.0
M2	ap	24	1.64	0.056	1.57-1.77	3.3
	tra	25	1.39	0.074	1.29-1.56	5.3
	trp	23	1.30	0.056	1.21-1.44	4.3
M3	ap	6	1.12	0.033	1.08-1.16	2.9
	tra	5	1.11	0.036	1.08-1.15	3.2
m1	ap	18	1.99	0.071	1.86-2.10	3.5
	tra	18	1.15	0.043	1.08-1.25	3.7
	trp	18	1.28	0.042	1.20-1.34	3.2
m2	ap	25	1.64	0.045	1.54-1.72	2.7
	tra	27	1.34	0.043	1.25-1.41	3.2
	trp	28	1.32	0.056	1.21-1.44	4.2
m3	ap	10	1.39	0.054	1.28-1.48	3.8
	tra	10	1.08	0.035	1.04-1.16	3.2
	trp	10	0.84	0.046	0.75-0.90	5.4

The larger M1s from localities LACM 4702 through 3666 and those from locality LACM 3620 cannot be separated by occlusal morphology (Figures 4 and 7). However, crown height varies relative to stratigraphic position (Figures 5A-B). Locality 4702 is the lowest locality that yielded larger M1s with prh/ap ratios for teeth in very early wear of 0.56 (unworn teeth would be slightly higher). Localities LACM 3776, 6128, 5718 are superposed localities, respectively, and occur within a relatively narrow stratigraphic interval with larger M1s from localities LACM 3776 and 6128 with prh/ap ratios for unworn teeth of 0.62-0.65. There are no complete unworn M1s from locality LACM 5718, but an unworn m1 from this locality is high crowned and compatible with those of *L. takeuchii* from locality LACM 3620 (see below). Locality LACM 3666 is significantly higher in section above the other localities with M1s with prh/ap ratios for

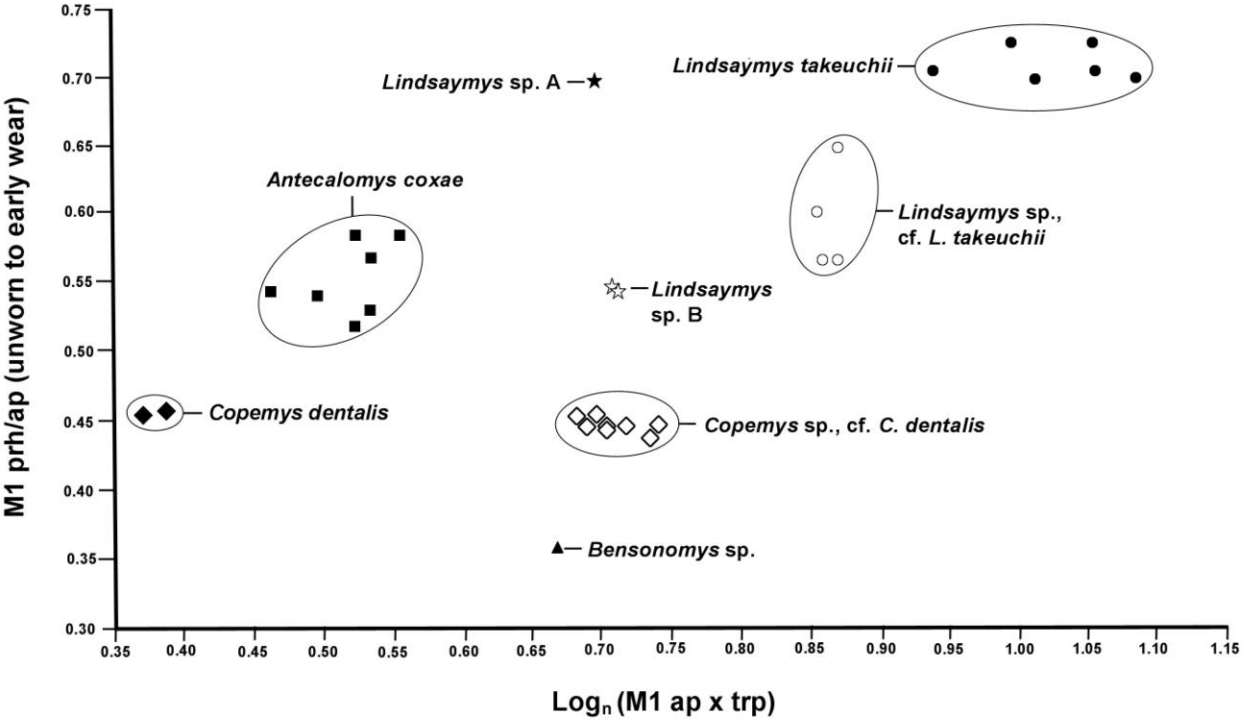

FIGURE 3. Chart plotting Log_n M1 area (ap x trp) versus M1 relative crown height (prh/ap ratio) for proposed cricetid taxa from upper part of DSF and URG. All specimens plotted are either unworn or in very early wear stage.

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unworn teeth of 0.70-0.71. Locality LACM 3620 is south of the El Paso Fault with M1s with a prh/ap ratio of 0.70-0.73. Because they all have very similar or identical occlusal morphology and crown height, all of these M1s are referred to *L. takeuchii*. Although the stratigraphic position of locality LACM 3620 is undetermined relative to the localities north of the El Paso Fault, the fact that the M1s from localities LACM 3666 and 3620 are indistinguishable in occlusal morphology and crown height suggests that these two localities may be similar in age. The larger sized, lower crowned M1s from locality LACM 6128 and lower in the section are separated from those assigned to *L. takeuchii* from higher in the section on the basis of crown height and slightly smaller size (see discussion below of *L.* sp., cf. *L. takeuchii*).

Nine larger M2s and two partial maxillae with M2-3 are present in the samples from localities LACM 5718, 3666 and 6380 (north of the El Paso Fault), whereas 16 larger M2s are present in the sample from locality LACM 3620 (south of the El Paso Fault). All of them exhibit a very similar occlusal morphology that includes the following (Figures 4I-K): 1) the anterior cingulum extends from the anterolabial corner of the paracone to about the middle of the protocone; 2) a posterior paracone spur is present (like those of the larger M1s) that is worn away after moderate wear; 3) although the paracone is not exactly aligned with the anterior arm of the hypocone, it is close to being aligned; 4) the reentrant valleys are deep and V-shaped in labial and lingual views; 5) the posterior cingulum is distinct and extends labially to about the middle of the posterior side of the metacone; and 6) high crowned. Because the larger M2s exhibit an occlusal morphology that is very similar to those of the larger M1s, but without anterocones, and they are compatible in size and crown height, they are assigned to *L. takeuchii*.

The M3s are characterized by having the following (Figure 4K): 1) M3 reduced relative to the M2 (M3 ap = 63% and 66% of M2 ap in LACM 156397 and 156401, respectively); 2) the paracone and the protocone are well developed with the paracone taller than the protocone; 3) a distinct indentation is present between the protocone and hypocone; 4) at the stage of wear that the teeth are in, the hypocone and metacone are only slightly taller than the posterior

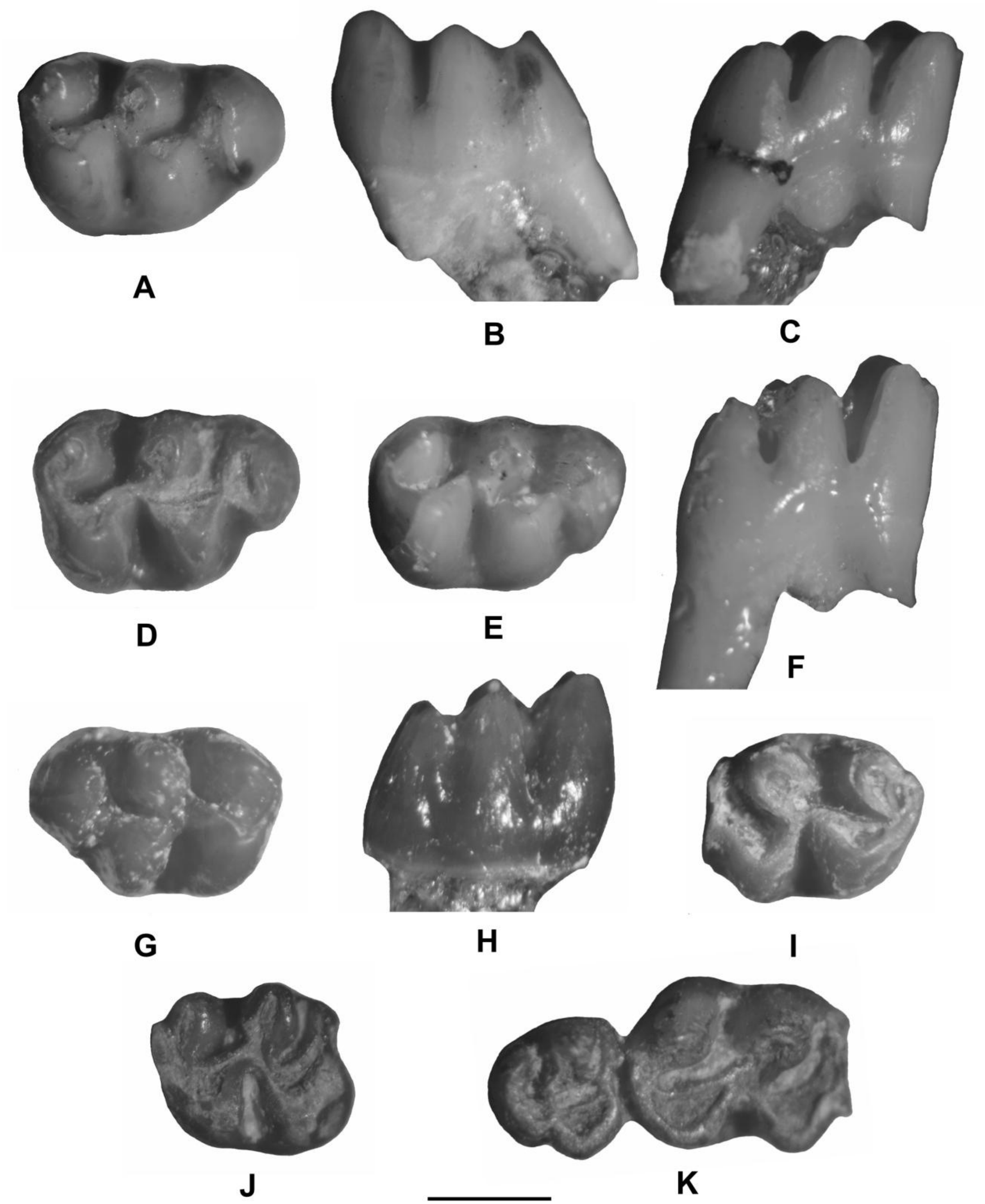

FIGURE 4. Upper molars of *Lindsaymys takeuchii* new genus and species from upper part of DSF. A-C, M1, holotype, LACM 126050. D, M1, LACM 156538. E-F, M1, LACM 150720. G-H, M1, LACM 150715. I, M2, LACM 150714. J, M2, LACM 156546. K, M2-3, LACM 156397. A, D, E, G, I, J and K, occlusal views. B and H, lingual views. C and F, labial views. Bar scale = 1 mm.

cingulum, which connects these cusps, and together, they form a continuous arc along the posterior aspect of the teeth; 5) a deep transverse valley between the paracone and the metacone that extends down to about the middle of the posterior cingulum; 6) a short anterior cingulum that extends lingually across about one-third of the width of the tooth that is separated from the paracone by a moderately deep, transverse valley; and 7) a protolophule I that extends from the anterolabial corner of the protocone to the anterolingual corner of the paracone and a protolophule II that extends from the posterolabial corner of the protocone to the posterolingual corner of the paracone that results in an isolated, moderately deep, anteroposteriorly directed valley between the paracone and protocone.

The larger m1s from the upper part of the DSF are rather consistent in their occlusal morphology (Figures 6A-E) and occur at localities LACM 5720, 4702, 6128 and 3666, and at locality LACM 3620. There is one unworn m1 (LACM 156394) from locality LACM 5718 with a pch/ap of 0.63 and one in early wear from locality LACM 3666 with a pch/ap of 0.60. The relative crown heights of these two m1s are compatible with those from locality LACM 3620 with unworn pch/ap ratios of 0.63-0.65 and an early wear pch/ap ratio of 0.59. The pch/ap ratios are lower for the larger m1s than those of the referred M1s (see above). However, it is not unusual to have the m1 pch/ap ratio slightly to moderately lower than the M1 prh/ap ratio within the same cricetid taxon or species (Korth, 2011:table 1; Kelly, 2013). The larger m1s are compatible in size, crown height and occlusal morphology to the referred M1s, strongly supporting their assignment to *L. takeuchii*.

The larger m1s from the localities stratigraphically lower in the section (below locality LACM 5718) have significantly lower pch/ap ratios as follows: the pch/ap = 0.55 for a m1 in very early wear (LACM 156419) from locality LACM 5720; the pch/ap = 0.55 for an unworn m1 (LACM 124944) from locality LACM 4702; and the pch/ap = 0.56 for an unworn m1 (LACM 156422) from locality LACM 6128 (Figures 5A-B). These data indicate that m1 crown height was lower and remained nearly equal in specimens from localities LACM 5720 through 6128, which was followed by a rapid increase in crown height of about 8% for all the m1s from the stratigraphically higher localities. The older, lower crowned m1 specimens are regarded as belonging to *L.* sp., cf. *L takeuchii*, the presumed anagenetic ancestor of *L. takeuchii* (see below).

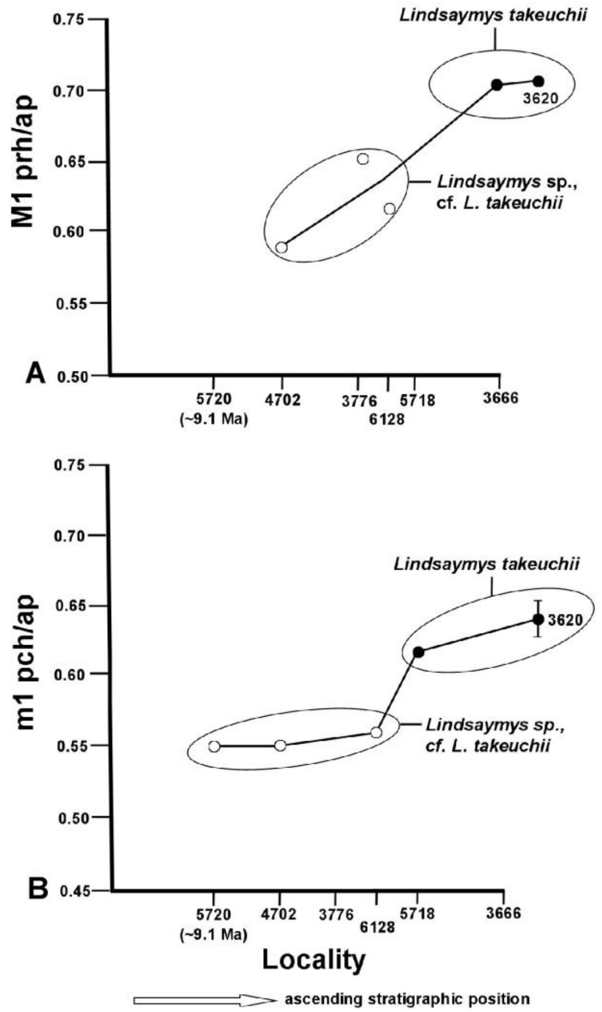

FIGURE 5. Charts plotting (A) M1 relative crown height (unworn prh/ap ratio) and (B) m1 relative crown height (unworn pch/ap ratio) of *Lindsaymys takeuchii* and *L.* sp., cf. *L. takeuchii* versus stratigraphic position of LACM localities in upper part of DSF and URG. Note increasing crown height through time of proposed anagenetic succession of species. Stratigraphic position of locality LACM 3620 in URG south of El Paso Fault relative to localities in type section north of El Paso Fault undetermined.

The m1 is further characterized by having the following (Figures 6A-E): 1) the anteroconid is centrally positioned and not bifurcated; 2) the metalophulid extends from the metaconid to join with the protolophulid I (anterior arm of the protoconid) and the anterolophid; 3) the anterolophid extends posteriorly from the anteroconid, just labial to its center, to join the metalophid; 4) the lingual edge of the metaconid is positioned close to the lingual edge of the anteroconid and a moderately deep, enclosed (isolated) valley develops between these cuspids and the anterolophid during early to moderate wear stages due to merging the lingual margins of the metaconid and anteroconid; 5) the reentrant valleys are relatively deep and V-shaped in labial and lingual views; 6) the anteroconid

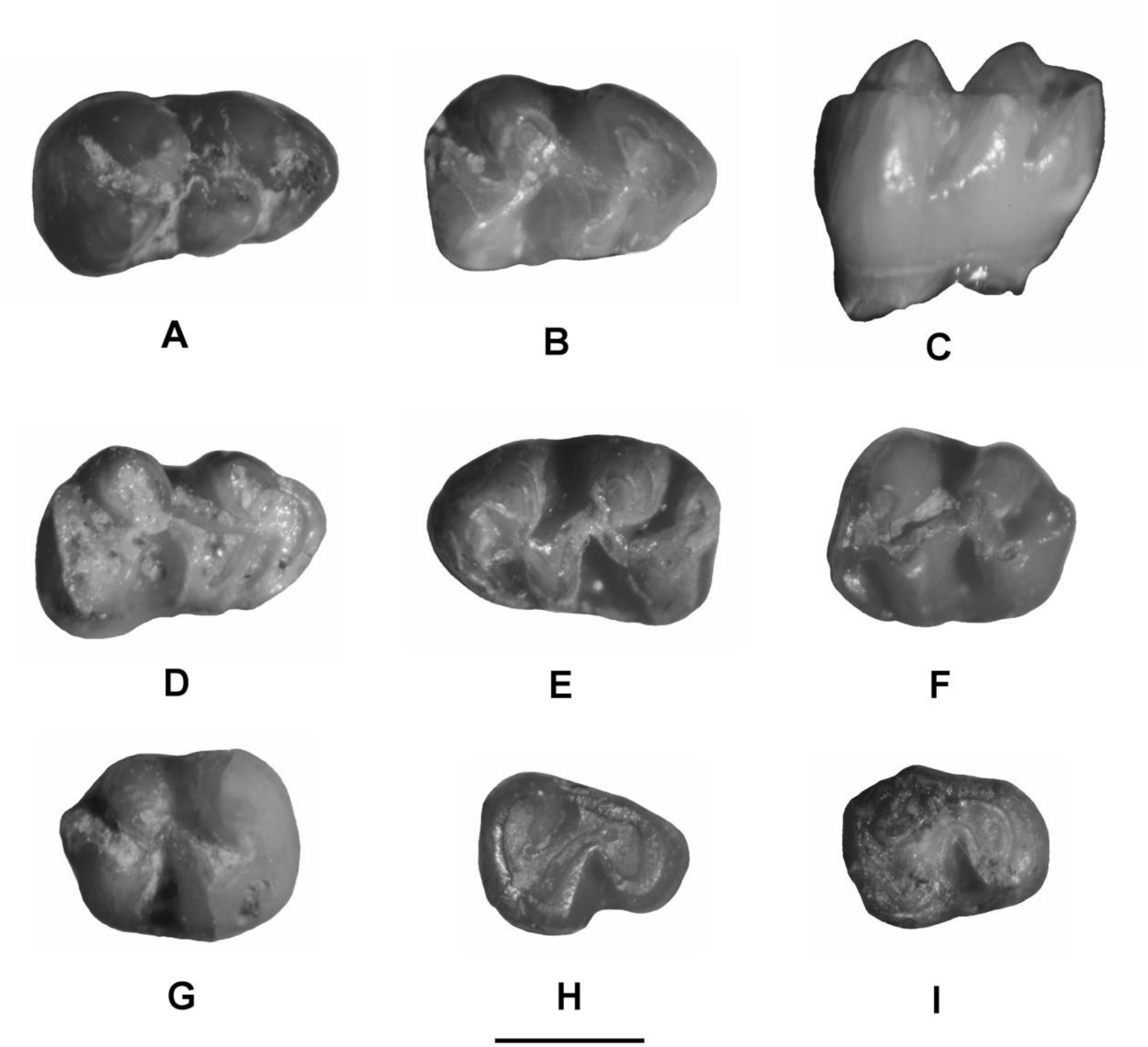

FIGURE 6. Lower molars of *Lindsaymys takeuchii* new genus and species from upper part of DSF. A, m1, LACM 156394. B-C, m1, LACM 150737. D, m1, LACM 156413. E, m1, LACM 156509. F, m2, LACM 156516. G, m2, LACM 156407. H, m3, LACM 156521. I, m3, LACM 156406. A-B, D-I, occlusal views. C, labial view. Bar scale = 1 mm.

and primary cusps are relatively vertical, only slanting slightly anteriorly; 7) the entoconid commonly has a short spur present that extends anteriorly from about the center of its anterior occlusal edge; 8) the posterior arm of the protoconid is not aligned with the entolophulid in unworn through moderate wear stages, but by late wear they take on the appearance of being nearly aligned; 9) the anterior cingulid is moderately developed and extends almost vertically downward from the anteroconid to join the protoconid; and 10) the posterior cingulid is well developed and extends from the hypoconid to the posterior base of the entoconid.

Four m2s from locality LACM 3666, six m2s from locality LACM 5718 and 17 m2s from locality LACM 3620 are compatible in size, occlusal morphology and crown height to the other larger M1-2s and m1s and are referred to *L. takeuchii*. They are characterized by having the following (Figures 6F-G): 1) a short, but robust, anterior cingulid that extends from the junction of the anterior arm of the protoconid and the metalophulid to the anterolabial corner of the protoconid; 2) the posterior arm of the protoconid extends posterolabially to join the anterior arm of the hypoconid, just anterior to the junction of entolophulid and the anterior arm of the protoconid, which results in a slight indentation giving the entoconid a slight spurred appearance; 3) although the m2s do not have full alignment of the entolophulid and the posterior arm of the protoconid, they are only slightly off, similar to the referred M2s above; 4) the primary cusps are almost vertically orientated, only being slightly slanted anteriorly; 5) the reentrant valleys are deep and V-shaped in lingual and labial views; 6) the posterior cingulid is moderately low, but robust, extending posteriorly to form a distinct bulge along the occlusal outline and is separated from the entoconid by a moderately deep and wide valley; and 7) high crowned.

Assuming that the presence of M1 accessory rootlets in *L. takeuchii* indicates that it is a sigmodontine, then the m3s of this taxon should have the S-shaped occlusal pattern that is typical of the Sigmodontini. However, it should be noted that in the early sigmodontine *Prosigmodon*, the m3 has a nearly S-shaped occlusal outline because of the presence of an entoconid that forms a small projection along the lingual edge of the occlusal outline (Lindsay and Jacobs, 1985; Carranza-Castañeda and Walton, 1992). Also, assuming the associated M2-3 specimens described above are correctly assigned to *L. takeuchii*, then one would expect the m3 to be somewhat reduced relative to m2. Ten m3s are compatible with this scenario; four from locality LACM 3666, three from locality LACM 5718, and three from locality LACM 3620. They are characterized by having the following (Figures 6H-I): 1) nearly S-shaped occlusal wear pattern; 2) a short anterior cingulid that extends from just labial of the junction of the anterior arm of the protoconid and the metalophulid to the anterolabial corner of the protoconid; 3) the posterior arm of the protoconid extends labially to join a moderately developed entoconid; 4) a small, low lophid connects the posterolingual base of the metaconid to the lingual edge of the entoconid resulting in a moderately deep valley between the posterior arm of the protoconid and the metaconid; 5) the protoconid and metaconid are the largest primary cusps; 6) a deep wide valley (labial sulcus) separates the protoconid from the hypoconid; 7) the hypoconid, posterior cingulid, and entoconid form a lobe-like talonid; and 8) relatively high crowned considering their wear stages. If correctly referred and using the referred m2s above, then the estimated mean m3 ap/mean m2 ap ratio would equal about 0.85 (or m3 ap = 85% of m2 ap). This seems a little high considering that the referred associated M2-3 specimens have a M3 ap/M2 ap ratio of 0.63 and 0.66 (or M3 ap = 63-66% of M2 ap). However, this percentage may not be representative because there are no associated m2-3s in the sample and, considering the amount of individual variation in size of the molars of other cricetids, there is no way of knowing if these m3s came from specimens with larger or smaller m2s. Moreover, in other early sigmodontines, such as *Antecalomys*, the M3 is relatively smaller than the m3, where the percentages are 69% for the M3 ap/M2 ap and 75% for the m3 ap/m2 ap. Another scenario is that these m3s actually belong with the medium sized, mesodont group of sigmodontine specimens from lower in the section, assigned here to *L.* sp. B (see below). However, this seems even more unlikely because the one specimen with an associated partial M1 and M2-3 of *L.* sp. B has the M3 even more reduced relative to the M2 (M3 ap = 58% of M2 ap). Furthermore, the vast majority of the other teeth from locality LACM 3666 represent *L. takeuchii*, so it would be expected that the few m3s from the sample would more likely also represent this taxon. A third scenario is that these m3s do not represent a sigmodontine even though they have a nearly S-shaped occlusal pattern, but are referable instead to one of the other cricetid genera from the DSF. However, most of the other m3s from the DSF have a distinct posterior cingulid present (like those of the *Copemys/Postcopemys* complex), which is lacking in these ten m3s. Of the three possible scenarios, the first appears the most reasonable and the m3s are tentatively referred to *L takeuchii*.

The measurements of the holotype M1 (LACM 126050) of *L. takeuchii* are ap = 2.13 mm, tra = 1.39 mm, and trp = 1.54. Dental statistics for *L. takeuchii* are presented in Table 1.

Discussion—*Lindsaymys takeuchii* exhibits some occlusal similarities to *Paronychomys*, *Basirepomys* and *Miotomodon*, but along with its having an isolated lake formed between the m1 anteroconid, metaconid and anterolophid, which is lacking in these taxa, it can easily be distinguished from species of these genera by its distinct suite of dental characters. In fact, most all of the teeth previously referred to *Paronychomys* spp. by Whistler and Burbank (1992) and Whistler et al. (2009, 2013) are here referred to *Lindsaymys*, and no teeth assignable to *Paronychomys* were actually identified in our study of all of the cricetid specimens from the upper part of the DSF. *L. takeuchii* further differs from *Paronychomys* by having the following: 1) M1 accessory rootlet present; 2) M1-2/m1-2 lacking labial and lingual shelf-like cingula/cingulids; 3) M1-2/m1-2 with paracone/entoconid spurs; 4) M1-2/m1-2 protolophule II and entolophulid less aligned with anterior arm of hypocone and posterior arm of protoconid, respectively; 5) m1 metalophulid connects to anterior arm of protoconid; 6) m1 anteroconid lingual margin positioned closer to metaconid lingual margin; and 7) M3 slightly more reduced. *L. takeuchi* further differs from *Basirepomys* by having the following: 1) smaller size; 2) higher crowned cheek teeth; 3) M1 accessory rootlet present; 4) M1-2/m1-2 with paracone/entoconid spurs; 5) M3 more reduced relative to M2; 6) m1 anteroconid not bifurcated (except for *B. romensis*, which also lacks a bifurcated m1 anteroconid); 7) m1 anteroconid positioned closer to metaconid; and 8) m1 metalophulid connects to anterior arm of protoconid. When Korth (1998) named *Miotomodon mayi* (a monotypic genus), he referred three M1s to his new species, but did not note whether these teeth had or lacked accessory rootlets. Of these three M1s, one is lacking an accessory rootlet, whereas in the other two this character cannot be determined (Stephen W. Edwards, pers. comm., December, 2013). Assuming that *Miotomodon* is derived from *Paronychomys* as Korth (1998) proposed and the latter is a galushamyine as Lindsay (2008) proposed, then M1 accessory rootlets should not be present. Thus, the presence of M1 accessory rootlets in *L. takeuchii* appears to be a character that is lacking in *M. mayi*. *L. takeuchii*, *Prosigmodon oroscoi* and *Miotomodon mayi* exhibit M1-2 paracone/m1-2 entoconid spurs, but differences in their development can be recognized. In *P. oroscoi* and *M. mayi*, the spurs are more transversely orientated and appear to be mesolophs/mesolophids that have fused to the paracone/entoconid, respectively. Whereas in *L. takeuchii*, the M1-2/m1-2 spurs are more anteroposteriorly orientated and a distinct indentation is present below the spurs that is just posterior to the protolophule II connection to the anterior arm of the hypocone in M1-2 and between the posterior terminus of the posterior arm of the protoconid and the junction of the entolophulid with anterior arm of the hypoconid in m1-2. *L. takeuchii* further differs from *Miotomodon mayi* by having the following; 1) M1-2/m1-2 protolophule II and entolophulid not as aligned with anterior arm of hypocone and posterior arm of protoconid, respectively; 2) M3 more reduced relative to M2; 3) M3 anterior cingulum less developed lingually; 4) m1 metalophulid connects to anterior arm of protoconid (in *Miotomodon* it connects directly to anteroconid); 6) m1 anteroconid lingual margin positioned slightly closer to metaconid lingual margin; and 7) slightly smaller size.

Lindsaymys sp., cf. L. takeuchii

Figures 2, 3, 5, 7A-E; Table 2

Referred specimens—From locality LACM 4702: M1s, LACM 125686, 125700; m1s, LACM 124932, 124944. From locality LACM 3776: M1s, LACM 125461, 125473. From locality LACM 6128: M1s, LACM 156421, 156426, 157173; M2, LACM 157172; m1, LACM 156422; m2s, LACM 156425, 156433, 157176. From locality LACM 5720: M1, LACM 156418; m1s, LACM 156419; M2, LACM 156420.

Distribution and Age—Localities LACM 5720, 4702, 3776 and 6128, upper part of DSF, Kern County, California. Latest Clarendonian to early Hemphillian (Cl3-Hh1, ~9.2-8.7 Ma).

TABLE 2. Dental measurements (in mm) of *Lindsaymys* sp., cf. *L. takeuchii* from upper part of the DSF.

LACM number	position	ap	tra	trp
125461	M1	1.90	1.10	1.26
125473	M1	1.82	1.23	1.31
125700	M1	1.90	1.10	1.24
125686	M1	1.90	1.18	1.26
156418	M1	1.85	1.16	1.25
156421	M1	-	1.23	-
156426	M1	1.87	1.13	1.24
157173	M1	-	1.18	-
156420	M2	1.49	1.14	1.15
157172	M2	1.51	1.13	1.16
156422	m1	1.80	1.10	1.21
124944	m1	1.83	1.03	1.18
124932	m1	2.05	1.16	1.28
156419	m1	2.00	1.10	1.28
156425	m2	1.52	1.21	1.16
156433	m2	1.54	1.19	1.16
157176	m2	-	-	1.21

Discussion—The larger teeth from locality LACM 6128 and lower in the section are indistinguishable in occlusal morphology from those assigned to *L. takeuchii*, but, on average are slightly smaller (Figures 7A-G, Table 2). As noted above, they also differ by having lower crown heights, with unworn M1s from localities LACM 3776 and 6128 having prh/ap ratios of 0.62-0.65 and M1s in very early wear from locality LACM 4702 having a prh/ap ratio of 0.56. If all of the larger M1s from the DSF are assigned to the same species, then there would be range of individual variation of the prh/ap of about 0.56 - 0.73. Undoubtedly, if samples were available only from high and low in the section, they would be assigned to different species of the same genus. Although it could also be argued that all the M1s are conspecific because most of the M1 prh/ap ratios for other mesodont to moderately high crowned cricetid genera from the Hemphillian (galushamyines in particular) were limited to very small sample sizes, often calculated using only one to a few unworn M1s or estimated from worn teeth (e.g., Korth, 2011), so that the range in variation for this character has not been well established. However, this scenario does not seem likely because the range of variation of the prh/ap ratios is so significant in the DSF samples. Furthermore in large samples of extant *Onychomys*, Carleton and Eshelman (1979) found that the m1 protoconid height was one of the most consistent dental characters for distinguishing between species. Although Carleton and Eshelman's (1979) study did not include upper molars, it would seem reasonable to extrapolate their results to M1 protocone height.

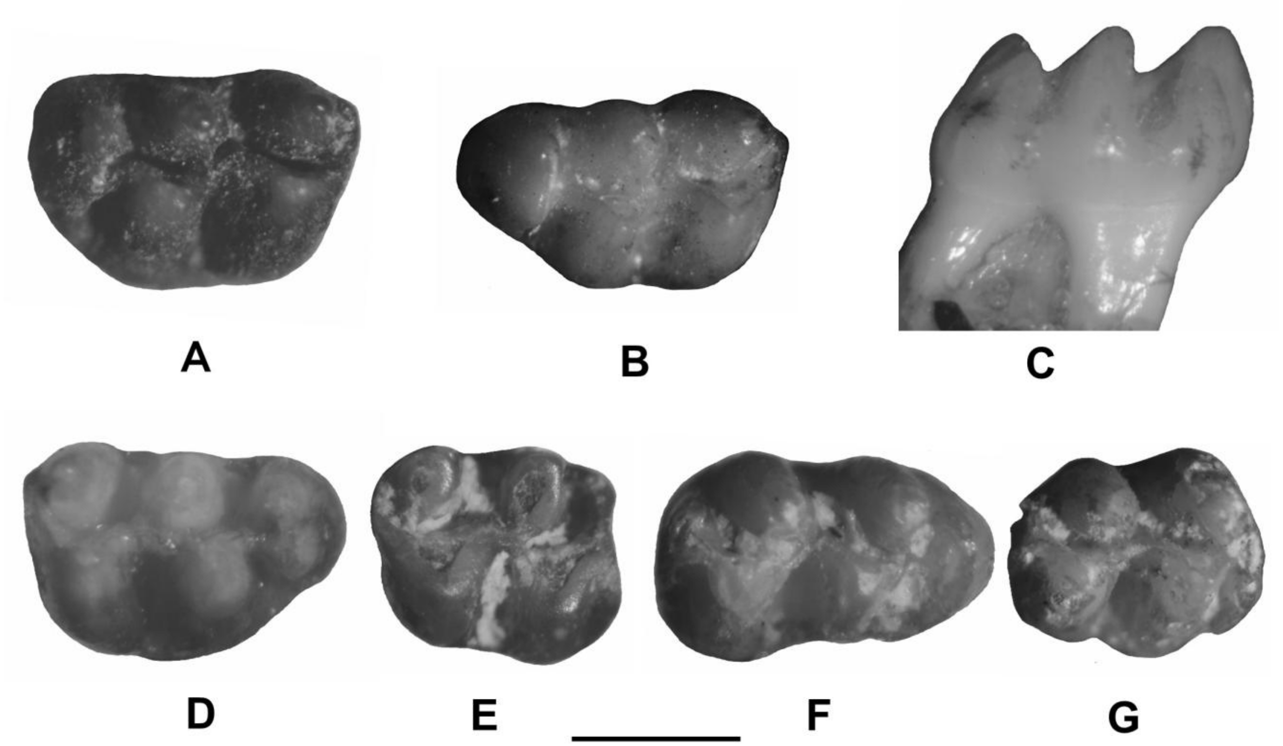

FIGURE 7. Molars of *Lindsaymys* sp., cf. *L. takeuchii* from upper part of DSF. A, M1, LACM 125461. B-C, M1, LACM 125700. D, M1, LACM 156426. E, M2, LACM 156420. F, m1, LACM 156419. G, m2, LACM 156433. A, B and D-G, occlusal views. C, lingual view. Bar scale = 1 mm.

Similar results were also found by Czaplewski (1987) for m1 metaconid height in *Sigmodon*. Thus, three scenarios are available: 1) assign all of the larger teeth to *L. takeuchii*; 2) specifically separate the older, slightly smaller sized and lower crowned samples into two species of *Lindsaymys* (one specific name for those from LACM 3776 and 6128, and another specific name for those from LACM 4702 and 5720) based primarily on relative crown height alone; or 3) interpret the older, slightly smaller sized and lower crowned specimens as representatives of a single anagenetic lineage with increasing crown height through time, ultimately resulting in *L. takeuchii*. We consider the last scenario as the most prudent and assign all of the older, lower crowned teeth to *L.* sp., cf. *L. takeuchii* to reflect its proposed ancestral relationship to *L. takeuchii*.

Lindsaymys sp. A
Figures 2, 3, 8, 9A-C; Table 3

Referred specimens—M1s, LACM 156476, 156477; M2s, LACM 156478 - 156480.

Distribution and Age—Locality LACM 3620, URG, Kern County, California. Early Hemphillian (Hh1, ~8.4 Ma?).

TABLE 3. Dental measurements (in mm) of *Lindsaymys* sp. A from URG.

LACM number	position	ap	tra	trp
156476	M1	1.72	1.18	1.16
156477	M1	1.76	1.26	1.28
156478	M2	1.34	1.08	1.13
156479	M2	1.34	1.13	1.13
156480	M2	1.23	1.05	1.10

Discussion—Two M1s and three M2s from locality LACM 3620 have very similar occlusal morphology and equal crown height (unworn M1 prh/ap = 0.73) to those of *L. takeuchii*, but are significantly smaller in size (Figures 2, 3, 8A-B, 9A-C; Table 3). The M1s are also similar in size and occlusal morphology to those of *L.* sp. B (see below) from lower in the section at localities LACM 5720 through 6128, but are much higher crowned (*L.* sp. B has unworn M1 prh/ap of 0.58 and, in the unworn M1, the paracone spur is slightly better developed). The smaller M2s are like those of the *L.* sp. B from localities LACM 4702 to 6128 and differ from those of *L. takeuchii* by having the posterior cingulum slightly less developed. The fact that these teeth cannot be easily distinguished from the those of *L. takeuchii* except primarily by size might support their inclusion in the species. However, they could also represent a

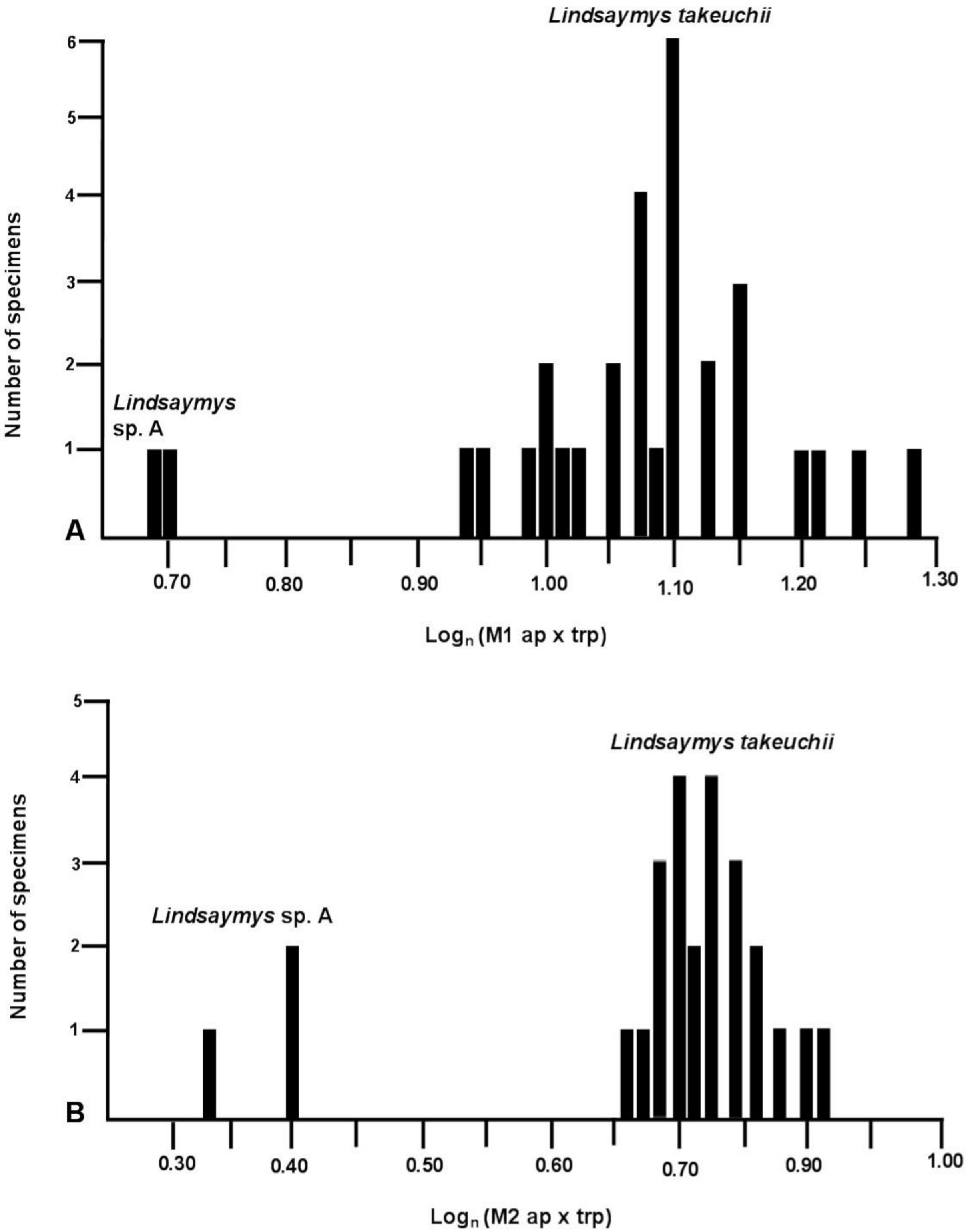

FIGURE 8. Charts plotting (A) Log_n M1 area (ap x trp) and (B) Log_n M2 area (ap x trp) versus number of specimens for *Lindsaymys takeuchii* and *L*. sp. A from upper part of DSF and URG.

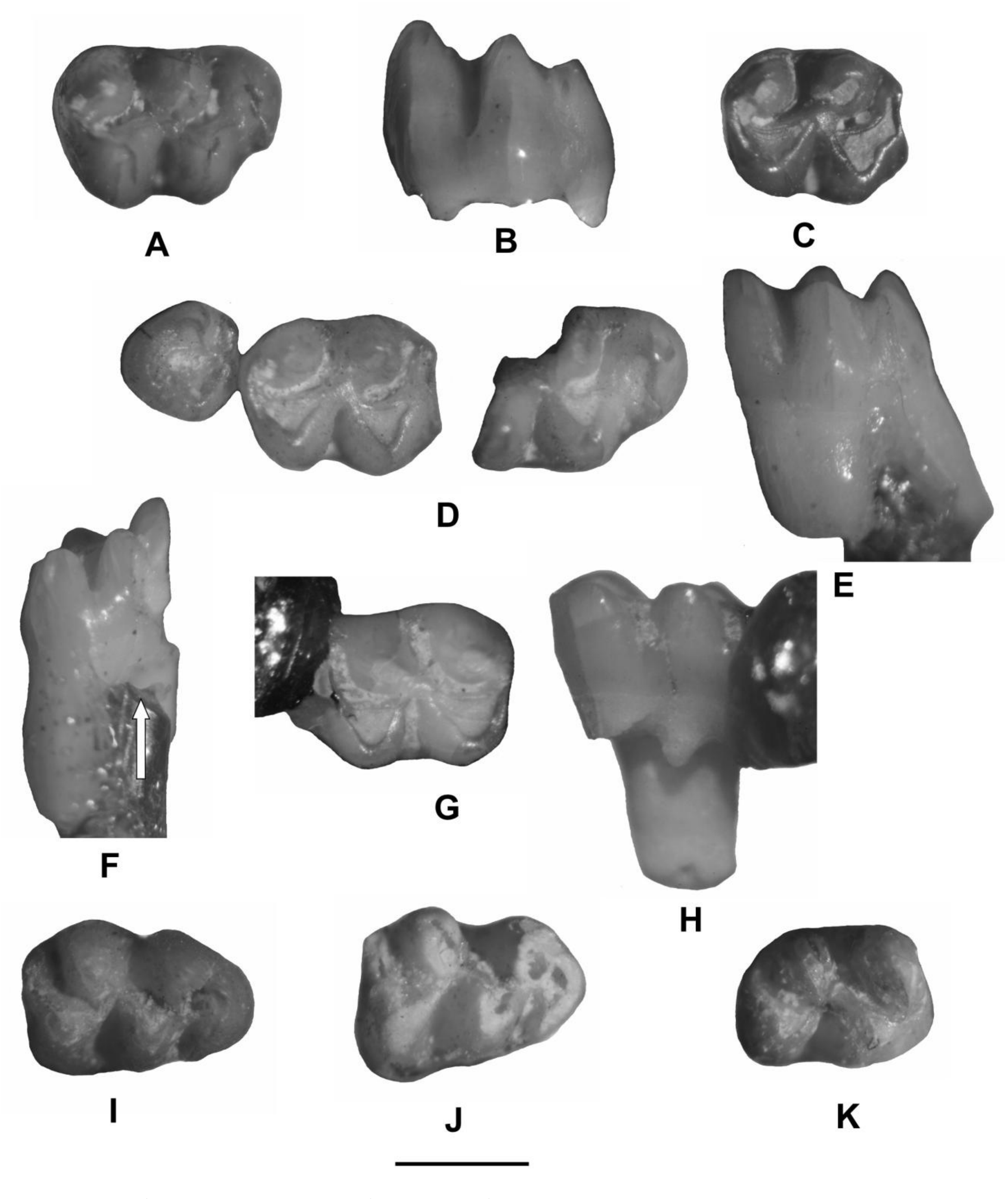

FIGURE 9. Molars of *Lindsaymys* sp. A and *L*. sp. B. from upper part of DSF. *Lindsaymys* sp. A: A-B, M1, LACM 156476; C, M2, LACM 156478. *Lindsaymys* sp. B: D-F, partial M1 and associated M2-3, LACM 125655; G-H, partial M1, LACM 125691; I, m1, LACM 124927; m1, LACM 156429; m2, LACM 156432. A, C, D, G, I-K, occlusal views. B and E, lingual views. F, anterior oblique view with white arrow showing accessory rootlet. H, labial view. Bar scale = 1 mm.

second smaller species of *Lindsaymys*. Moreover, the probability that these five smaller sized teeth just represent extremes within the sample of *L. takeuchii* seems unlikely, especially since the M1s and M2s are compatible in size and there are no teeth intermediate in size between them and the larger sized upper molars referred to *L. takeuchii*. Furthermore, many investigators have used the natural log of the molar area (anteroposterior length x transverse width) to separate closely related species that differ primarily in size (e.g., Gingerich, 1976; Carleton and Eshelman, 1979) and when the samples of M1s and M2s of *L. takeuchii* are plotted with the smaller M1s and M2s from locality LACM 3620, there appears to be two distinct groupings or species (Figures 8A-B). Therefore, these teeth are not included in the sample referred to *L. takeuchii*, but are tentatively assigned to a separate smaller species of *Lindsaymys*. However, they are not given a formal specific name because the sample size is too small to adequately define the species and are left in open nomenclature as *L*. sp. A.

Lindsaymys sp. B

Figures 2, 3, 9D-K; Table 4

Referred specimens—From locality LACM 5720: m1, LACM 157168. From locality LACM 4702: M1, LACM 125704; partial M1, LACM 125691; associated partial M1 and M2-3, LACM 125655; m1, LACM 124927. From locality 3776: M1, LACM 125475; partial M1, LACM 156362. From locality LACM 6128: M1, LACM 156427; m1s, LACM 156423, 156428, 156429; m2s, 156430, 156432, 156434.

Distribution and Age—Localities LACM 5720, 4702, 3776 and 6128, upper part of DSF, Kern County, California. Latest Clarendonian to early Hemphillian (Cl3-Hh1, ~9.2-8.7 Ma).

Description—The above referred teeth are similar in occlusal morphology to *L. takeuchii*, but differ by being smaller in size and lower crowned. The M1s and M2 are also similar in occlusal morphology and size to those of *L*. sp. A from the URG, but significantly lower crowned. LACM 125691 and 156362 are missing the anterior portion of the anterocone and, along with LACM 125475, have a distinct accessory rootlet. LACM 156427 has a small accessory rootlet, whereas LACM 125704 appears to be lacking an accessory rootlet (difficult to see under mounted tooth). The partial M1 that is associated with M2-3 (LACM 125655) has a moderately developed accessory rootlet. So it appears that M1 accessory rootlets are usually present in this group. The prh/ap ratios for LACM 125655 and 125691, which are in early moderate wear, are estimated to be ~0.53-0.54, whereas those of LACM 156427 and 125704, which are both in early wear, are 0.56. All the M1s have a paracone spur, the protolophule II not aligned with the anterior arm of the hypocone, deep reentrant valleys that are V-shaped in lingual and labial views, relatively vertically orientated primary cusps and anterocones, and lack accessory lophs and styles. Whether the anterocone was slightly bifurcated when unworn cannot be determined confidently for the M1s because they are in early to moderate wear stages, but LACM 125655 and 156427 do have a slight anterior indentation on the anterocone.

The M2 is characterized by having the following: 1) protolophule II aligned with anterior arm of hypocone; 2) posterior cingulum weakly developed; 3) anterior cingulum moderately developed labially and lingually; 4) reentrant valleys deep and V-shaped in labial and lingual views; and 5) accessory lophs or styles lacking.

The M3 is characterized by having the following: 1) significantly reduced (m3 ap = 58% of m2 ap); 2) anterior cingulum moderately developed labially and lingually; 3) hypocone reduced resulting in a round occlusal outline; 4) no metacone; and 5) single anteroposteriorly elongated oval central valley. The M3 differs from that of *L. takeuchii* by being more reduced and by having a more rounded occlusal outline due to a relatively smaller hypocone with less indentation between it and the protocone.

There are four m1s, one from locality LACM 4702 and three from locality LACM 6128, that are very similar in occlusal morphology to those of *L. takeuchii*, but are lower crowned and smaller in size. They further differ from those of *L. takeuchii* by having the entolophulid slightly closer to being aligned with the posterior arm of the protoconid and less developed entoconid spurs. They are characterized by having the following: 1) mesodont (pch/ap of unworn m1 = 0.56); 2) anteroconid lacking any bifurcation; 3) anteroconid positioned close to metaconid, wherein their lingual edges join forming an isolated valley between the anteroconid, metaconid and anterolophid in early moderate to moderate wear stages; 4) weakly-developed entoconid spurs present; 5) entolophulid almost aligned with posterior arm of protoconid; 5) metalophulid joins the anterior arm of the protoconid at the junction with the anterolophulid; 6) the anterior cingulid is moderately developed; 7) the posterior cingulid is robust extending lingually to near the lingual base of the entoconid; and 8) lacking accessory stylids (except LACM 156423 with a small ectostylid) or lophids. These m1s are compatible in size, occlusal morphology and crown height with the upper molars described above.

There are three m2s (LACM 156430, 156432, 156434) with an occlusal morphology that is similar to the those of *L. takeuchii*, but are significantly smaller in size. They further differ from those of *L. takeuchii* by having the anterior and posterior cingulids more weakly developed. In *L. takeuchii*, the m2 posterior cingulid extends posteriorly at its lingual terminus commonly forming a distinct projection on the occlusal outline. These teeth are compatible in size, crown height and occlusal morphology to the other molars referred above. No m3s have been identified for *L.* sp B. Dental measurements for *L.* sp. B are presented in Table 4.

TABLE 4. Dental measurements (in mm) of *Lindsaymys* sp. B from upper part of DSF (e = estimated).

LACM number	position	ap	tra	trp
125691	M1	1.72e	1.20	1.20
125704	M1	1.72	1.13	1.18
156427	M1	1.69	1.12	1.15
125655	M1	1.70e	1.14	-
156362	M1	-	1.13	1.14
125475	M1	1.72	1.10	1.14
125655	M2	1.47	1.15	1.13
125655	M3	0.85	0.84	-
156428	m1	1.69	1.00	1.10
156429	m1	1.64	0.99	1.10
156423	m1	1.67	1.03	1.13
124927	m1	1.71	1.00	1.13
157168	m1	1.69	0.98	1.13
156430	m2	1.44	1.10	1.03
156432	m2	1.46	1.08	1.05
156434	m2	1.48	1.04	1.00

Discussion—The group of mesodont, medium-sized teeth from localities LACM 5720, 4702, 3776 and 6128 differ from those of *L. takeuchii* by slight differences in occlusal morphology (see above), slightly greater reduction of M3, smaller size and are lower crowned. The M1-2 are equal in size to *L.* sp. A from locality LACM 3620 (Figures 2, 3; Tables 3, 4), but are significantly lower crowned. This group appears to be specifically distinct from *L. takeuchii*, *L.* sp., cf. *L. takeuchii*, and *L.* sp. A. Similar to the situation for *L.* sp. A., the sample size of this group is small and there are no adequate specimens to designate as a holotype for a new species, so it not given a formal specific name, but left in open nomenclature as *L.* sp. B. The fact that older *L.* sp. B from localities LACM 5720 through 6128 cannot be distinguished by size from younger *L.* sp. A. from locality LACM 3620 and they both exhibit similar occlusal morphology, suggests the possibility that these species may be closely related. In this scenario, *L.* sp. B could have given rise anagenetically to *L.* sp. A by increasing its crown height through time. However, specimens with intermediate crown height are unknown from the localities stratigraphically above locality LACM 6128 in the DSF, so this putative relationship remains speculative.

Genus *Antecalomys* Korth, 1998

Antecalomys coxae new species

Figures 2, 3, 10A-M, 11; Table 5

Holotype—M1, LACM 156416.

Type Locality—LACM 5720, uppermost part of Member 5, DSF (latest Clarendonian, ~9.2 Ma).

Referred specimens—From locality LACM 3580: m1s, LACM 124880, 124884. From locality LACM 3531: M2, LACM 156354; m2, 156352. From locality 5720: m1, LACM 157169; m2s, LACM 156417, 157164, 157165. From locality LACM 4702: M1s, LACM 125685, 125688, 125695, 125702; m1, LACM 124918. From locality LACM 3776: partial maxillae with M1-2, LACM 125654, 125689; M1s, LACM 125471, 125697, 156359, 156364, 156367, 157158; m1s, LACM 124870, 124871, 156370, 156371; m2s, LACM 156368, 156373 - 156376, 157156, 157157. From locality LACM 6128: M1s, LACM 156431, 157174; m1s, LACM 156436, 156437, 157175; m2s, LACM 156424, 156438. From locality LACM 5718: m2, LACM 157161. From locality LACM 3666: m2, LACM 150739. From locality LACM 6380: M1, LACM 142757; m2, LACM 142761.

Distribution and Age—DSF, type locality plus localities LACM 3580, 3531, 4702, 3776, 6128, 5718 and 6380. Latest Clarendonian to early Hemphillian (Cl3-Hh1, ~9.3-8.4 Ma).

Diagnosis—Differs from *Antecalomys phthanus* Korth, 1998, by having higher crowned molars, M1-2/m1-2 mesoloph/mesolophid often present (about 50% of the time), m1 anteroconid never weakly bifurcated, and m1 anteroconid positioned closer to metaconid.

Etymology—Named in honor of Shelley M. Cox of the Page Museum for her considerate support of the DSF field research. For 20 years, Shelly organized the Page Museum volunteers for the Memorial Day weekend search for fossils at Red Rock Canyon. This work resulted in the discovery of a number of localities (LACM 5718, 5720, 6128 and 5690) that yielded rodents, including many of those described here.

Description—There are nine M1s that have distinct accessory rootlets clearly visible (LACM 156416 [holotype], 125654, 125685, 125695, 125689, 142757, 156431, 157158, 157174). LACM 156431 is unworn with a prh/ap of 0.57. LACM 125685, 125695, 142757 and 156431 are in early wear with prh/ap ratios that range of 0.52 - 0.54. LACM 125654 and 125689 (partial maxillae with M1-2) are in moderate wear with M1 prh/ap ratios of 0.41 and 0.38, respectively. LACM 157174 is in early late wear with a M1 prh/ap

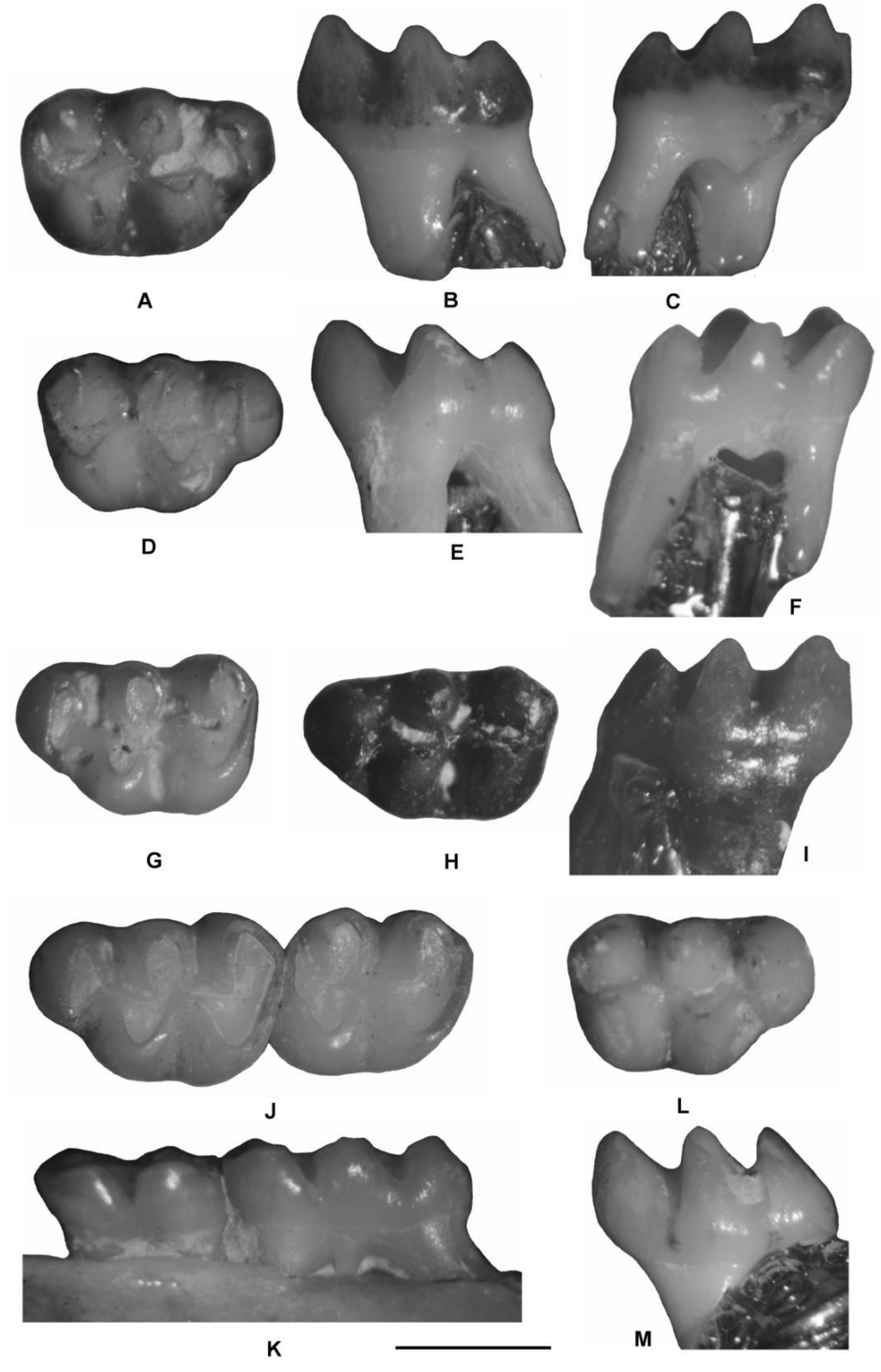

FIGURE 10. Upper molars of *Antecalomys coxae* new species from upper part of DSF. A-C, M1, holotype, LACM 156416; D-F, M1, LACM 125695; G, M1, LACM 156359; H-I, M1, LACM 156431; J-K, M1-2, LACM 125689; L-M, M1, LACM 156367. A, D, G, H, J and L, occlusal views. B, E I and K, lingual views. C, F and K, labial views showing accessory rootlets. Bar scale = 1 mm.

ratio of 0.36. In LACM 125689, the maxillary bone is intact on the labial side and exhibits a small alveolus for the accessory root (Figure 10K). All have very similar occlusal morphology and crown height, but LACM 125654, 125685, 156416 and 156431 have a short mesoloph present, whereas in the other five M1s the mesoloph is lacking. The significance of this difference is difficult to evaluate because in many other cricetid taxa that are known from large sample sizes, the presence or absence of a mesoloph within a species can be a variable character state (e.g., Hooper, 1957; James, 1963; Shotwell, 1967). Moreover, often the frequency of whether an accessory loph or style is present or absent within a cricetid species is used to distinguish it from other closely related species (e.g., Hooper, 1957; Shotwell, 1967). Seven additional M1s referred to *Antecalomys coxae*, which are discussed below, vary from having a very short mesoloph present (four teeth) to lacking a mesoloph (three teeth). Similarly, the m1s and m2s referred to *Antecalomys coxae* have a short mesolophid variably present (see below). Thus, the presence of a short M1 mesoloph is regarded as a variable character state for *Antecalomys coxae*.

There are seven other M1s (LACM 125471, 125688, 125697, 125702, 156359, 156364, 156367) from localities LACM 4702, 3776 and 3666 that are mesodont (prh/ap ratios from 0.54 -0.55 in early wear to 0.58 unworn) and their occlusal morphology and size agrees well with that of the M1s discussed above with distinct accessory rootlets. Of these seven M1s; the presence of accessory rootlets cannot be determined for LACM 125471, 125702, 156364 and 156367 because the labial roots are broken off. LACM 125697 and 156359 have a small bump under the paracone (similar to, but slightly less distinct, than that of LACM125695), whereas 125688 is lacking an accessory rootlet. In early sigmodontines, M1 accessory rootlets can be variably present, such as in *Antecalomys* and *Prosigmodon* (Korth, 1998; Lindsay, 2008). Therefore, eliminating the one tooth that lacks an accessory rootlet or the four teeth for which this character cannot be determined from *Antecalomys coxae* is not necessary, especially since they otherwise agree well morphologically and in crown height with the 11 referred M1s with accessory rootlets. Therefore, the presence of a M1 accessory rootlet is regarded as variable in *Antecalomys coxae*, ranging from absent (one M1) to a slight bump (two M1s) to a distinct rootlet (nine M1s). Furthermore, when all 16 M1s are grouped together, their dental statistics are acceptable as a single species (Table 5).

The M1 is characterized by having the following: 1) mesodont with unworn prh/ap ratio = 0.57 - 0.58; 2) accessory rootlets usually present; 3) the anterocone is very slightly bifurcated in early wear, labially positioned, moderate in size, and connected to the anteroloph slightly labial of its center; 4) the protolophule II is not aligned with the anterior arm of the hypocone; 5) a short mesoloph is variably present; 6) the anterior cingulum (= anterolingual cingulum) is reduced (not expanded lingually) resulting in a moderate indentation between the anterocone and protocone in occlusal view and vertically orientated giving the reentrant between the anterocone and protocone a narrow V-shape in lingual view; 7) the lingual cingulum is very weakly developed giving the reentrant between the protocone and hypocone a narrow V-shape in lingual view; and 8) the posterior cingulum is weakly developed.

TABLE 5. Dental statistics (in mm) for *Antecalomys coxae* from upper part of DSF.

Position/ dimension		N	Mean	OR	SD	CV
M1	ap	15	1.60	1.50-1.64	0.034	2.1
	tra	16	1.03	0.95-1.05	0.031	3.0
	trp	16	1.04	1.03-1.09	0.021	2.0
M2	ap	3	1.29	1.26-1.34	0.042	-
	tra	3	1.06	1.04-1.07	0.017	-
	trp	3	1.02	1.00-1.04	0.021	-
m1	ap	13	1.53	1.41-1.62	0.065	4.2
	tra	13	0.93	0.85-1.00	0.048	5.1
	trp	13	1.02	0.98-1.05	0.025	2.4
m2	ap	16	1.27	1.19-1.38	0.049	3.8
	tra	16	1.02	0.90-1.10	0.058	5.3
	trp	16	1.01	0.95-1.05	0.034	3.3

LACM 125689 and 125654 are partial maxillae with associated M1-2s, which allows a confident description of the M2 of *Antecalomys coxae*. Another M2 (LACM 156354) is also assigned to *A. coxae* because it is compatible in size, relative crown height and occlusal morphology with the referred associated M2s. A short mesoloph is present in LACM 125654 and 156354, but lacking in LACM 125689. The M2 is further characterized by having the following: 1) mesodont (unworn prh = 0.90 mm); 2) the protolophule II is not aligned with the anterior arm of the hypocone; 3) the anterior cingulum is moderately well developed both labially and lingually; and 5) the posterior cingulum is weakly developed.

Thirteen m1s are referred to *Antecalomys coxae* that all have very similar occlusal morphology, size and crown height. They differ only in whether a very short mesolophid is present (seven) or absent (six), similar to the frequency of their occurrence in the M1s referred above. The entolophulid and posterior arm of the protoconid are completely aligned in those lacking a mesolophid, whereas they are nearly aligned in

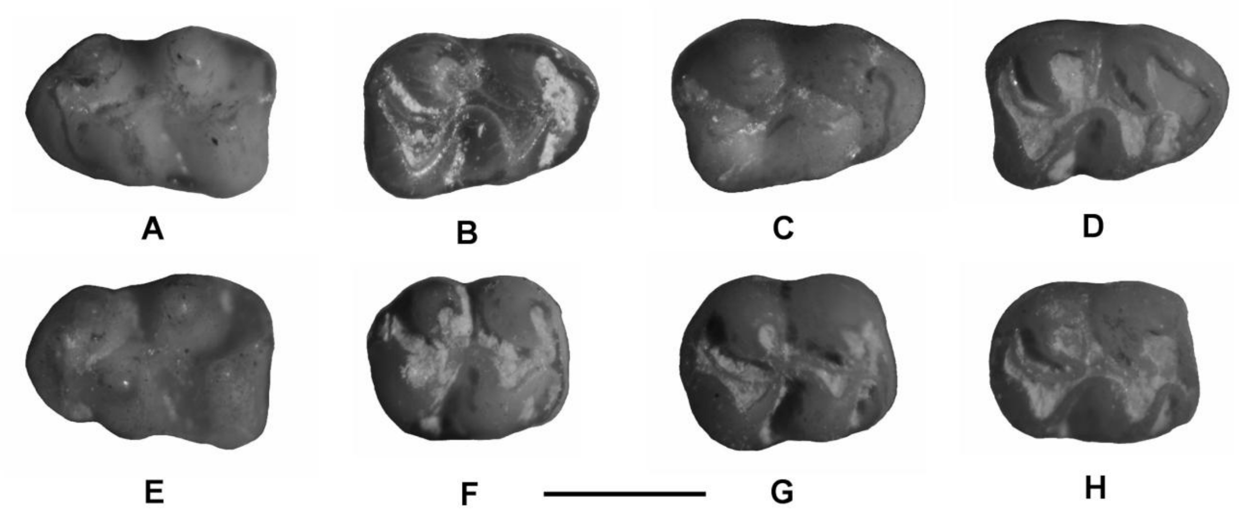

FIGURE 11. Lower molars of *Antecalomys coxae* new species from upper part of DSF. A, m1, LACM 124870. B, m1, LACM 124370. C, m1, LACM 124871. D, m1, LACM 156371. E, m1, LACM 124870. F, m2, LACM 156373. G, m2, LACM 156374. H, m2, LACM 156376. All occlusal views. Bar scale = 1 mm.

those with a mesolophid. All of these m2s are regarded as conspecific because, other than the absence or presence of a mesolophid, they are indistinguishable in all other occlusal characters and size. The m1s are further characterized by having the following: 1) mesodont (unworn pch/ap = 0.54 - 0.55); 2) the anteroconid is unbifurcated, slightly lingually positioned and connected to the metalophid by a short anterolophid; 3) the anterolingual edge of the metaconid is positioned close to the posterolingual edge of the anteroconid, only separated by a shallow notch that disappears in early wear, joining the metaconid to the anteroconid; 4) accessory stylids are lacking; 5) the anterior cingulid is moderately well developed extending posterolabially from the apex of the anteroconid to the anterolabial base of the protoconid; and 6) the posterior cingulid is moderately robust.

Sixteen m2s are referred to *Antecalomys coxae* that, except for lacking an anteroconid, are very similar in size, crown height and occlusal morphology to the referred m1s. Like the referred m1s, eight are lacking a mesolophid and eight have a very short or incipient mesolophid. The entolophulid is either aligned or nearly aligned with the posterior arm of the protoconid. They are further characterized by having the following: 1) mesodont (unworn pch = 0.98 mm); 2) well-developed anterior and posterior cingulids; and 3) accessory stylids are lacking.

No M3s or m3s have been identified for *Antecalomys coxae*. The measurements of the holotype M1 (LACM 156416) are ap = 1.64 mm, tra = 1.05 mm, and trp = 1.05 mm.

Discussion—Korth (1998) erected a new genus and species of sigmodontine, *Antecalomys phthanus*, from the late Clarendonian Ash Hollow Formation of Nebraska. The smaller, mesodont DSF sigmodontine is very similar to *A. phthanus* by having the following (Korth, 1998; Lindsay, 2008): 1) moderately small size, as compared with other sigmodontine cricetids; 2) M1 accessory rootlets variably present; 3) lacking molar accessory styles/stylids; 4) M1 anterocone weakly bifurcated in early wear; and 5) M1 protolophule II not aligned with anterior arm of hypocone, but m1-2 entolophulid aligned or nearly so with posterior arm of protoconid. Korth (1998) also listed the lack of M1-2 mesolophs and m1-2 mesolophids in *A. phthanus* as diagnostic for his new genus. Korth (1998) regarded *A. phthanus* as being intermediate in morphology between *Abelmoschomys* and *Bensonomys*. Korth (1998) also reassigned *Copemys valensis* and *C. vasquezi* to his new genus because these species are morphologically similar to *A. phthanus* and also exhibit non-alignment in M1-2, but have alignment or near-alignment in m1-2. Lindsay and Czaplewski (2011) described a new genus, *Postcopemys*, with two new species (the genotype *P. repenningi* and *P. maxumensis*). They reassigned *A. valensis* and *A. vasquezi* to *Postcopemys* because these taxa lack M1 accessory rootlets, which are present in the genotype *A. phthanus*. Like Korth (1998), they also suggested that *A. phthanus* may possibly be related to *Abelmoschomys* and other "sigmodontines," which share the development of upper molar accessory rootlets. *Abelmoschomys simpsoni* from the late Clarendonian Love Bone Bed of the Alachua Formation, Florida, was described by Baskin (1986) and is characterized by having the following: 1) small size; 2) brachydont molars; 3) accessory rootlet usually present on M1 and occasionally present on m1; 4) weakly to moderately bifurcated M1 anterocone; 5) m1 anteroconid single cusped to weakly bifurcated; 6) non alignment of M1 protolophule II with anterior arm of hypocone and non-alignment of m1 entolophulid with posterior arm of protoconid; and 7) M1 with short to medium length mesoloph present and m1 with medium length mesolophid commonly present.

The DSF smaller, mesodont sigmodontine exhibits similarity to both *Antecalomys* and *Abelmoschomys*, but is more similar to the former by having the M1 anterocone more weakly bifurcated and alignment or near-alignment of the m1 entolophulid with the posterior arm of the protoconid. It differs from the genotype *A. phthanus* by having the following: 1) higher crowned molars; 2) M1 paralophule lacking; 3) M1 anterocone more weakly bifurcated and lacking shelf-like cingulum along its anterior base; 4) m1 anteroconid never weakly bifurcated; 5) m1 anteroconid positioned closer to the metaconid; and 6) short M1-2/m1-2 mesolophs/mesolophids often present. It could be argued that these differences could justify erecting a new genus for the DSF smaller, mesodont sigmodontine. However, this argument does not appear justified considering that the presence or absence of mesolophs and mesolophids alone or higher crown height are not generally regarded as characters that require generic separation. In fact, the presence, absence or frequency of occurrence of accessory lophs and lophids are more often utilized for separation of species (e.g., Hooper, 1957; Shotwell, 1967). Because the DSF smaller, mesodont sigmodontine exhibits certain distinctive characters, but overall is most similar to the genotype *A. phthanus*, it is tentatively assigned to a new species of the genus, *Antecalomys coxae*.

Based on four isolated molars (M1, M2 and two m1s), Lindsay and Jacobs (1985) described *Copemys* near *C. valensis* from the late Hemphillian Yepómera Fauna of Chihuahua, Mexico. Subsequently, Lindsay and Czaplewski (2011) noted that *C.* near *C. valensis* from Yepómera may actually represent *Antecalomys* instead because on the one M1 referred to this taxon there is a "slight bulbous expansion" below the paracone that might represent an incipient accessory rootlet. From their description of *C.* near *C. valensis*, this speculation appears reasonable, but a meaningful comparison of the Yepómera taxon to *Antecalomys coxae* cannot be made until a much larger sample of this taxon is available. Interestingly, the single, isolated M1 referred to the Yepómera taxon is disproportionally larger (ap = 1.68 mm, tr = 1.02 mm) than the two referred m1s (ap = 1.10 mm, tr = 0.80-0.82 mm), which might indicate that these teeth are not conspecific.

Antecalomys coxae can be easily distinguished from species of *Lindsaymys* from the DSF by having the following: 1) molars slightly to considerably lower crowned; 2) smaller size; 3) M1/m1-2 mesolophs/mesolophids variably present; 4) M1/m1-2 lacking paracone/metaconid spurs; and 5) m1 lacking a moderately deep valley between metaconid, anteroconid and anterolophid, which forms a isolated lake with wear in *Lindsaymys*. *A. coxae* can also be easily distinguished from *Bensonomys* sp. from the DSF (see below) by having the following: 1) significantly higher crowned; 2) slightly smaller size; 3) M1 anterocone much more weakly bifurcated and more vertically orientated; 4) M1/m1-2 mesoloph/mesolophids shorter and variably present; 5) m1-2 entolophulid and posterior arm of protoconid aligned or nearly so; and 6) m1 anteroconid not bifurcated.

Genus *Bensonomys* Gazin, 1942
Bensonomys sp.
Figures 3, 12A-I; Table 6

Referred specimens—Partial maxillae with M1, LACM 156379, 157150; M1, 156385; partial maxilla with M2, LACM 157149; M2s, LACM 150710, 156380; m1s, LACM 156382, 156386; m2s, LACM 156388, 150711, 157151; partial dentary with m2-3, LACM 156389.

Distribution and Age—Locality LACM 5690, uppermost part of DSF, Kern County, California. Early Hemphillian (Hh1, ~8.0 Ma).

Description—This species occurs only at locality LACM 5690, the highest locality in the type section of the DSF north of the El Paso Fault, which is correlated to the lower half of Chron C4n (~8.0 Ma). Its M1s and m1s can be easily distinguished from all the other DSF cricetids and their association as a single species is confident because they are compatible in size, crown height and occlusal morphology (Figures 12A-I; Table 6). Similarly, three M2s and three m2s from LACM 5690 agree in size, crown height and occlusal morphology to the M1s and m1s, respectively, and can also be confidently assigned to this species. A partial left dentary with well worn m2-3 (LACM 156389) from LACM 5690 appears to also belong to this group because the m2 is similar to the other three m2s in size, crown height, and, even though very worn, there is a small projection along the m2 occlusal outline between

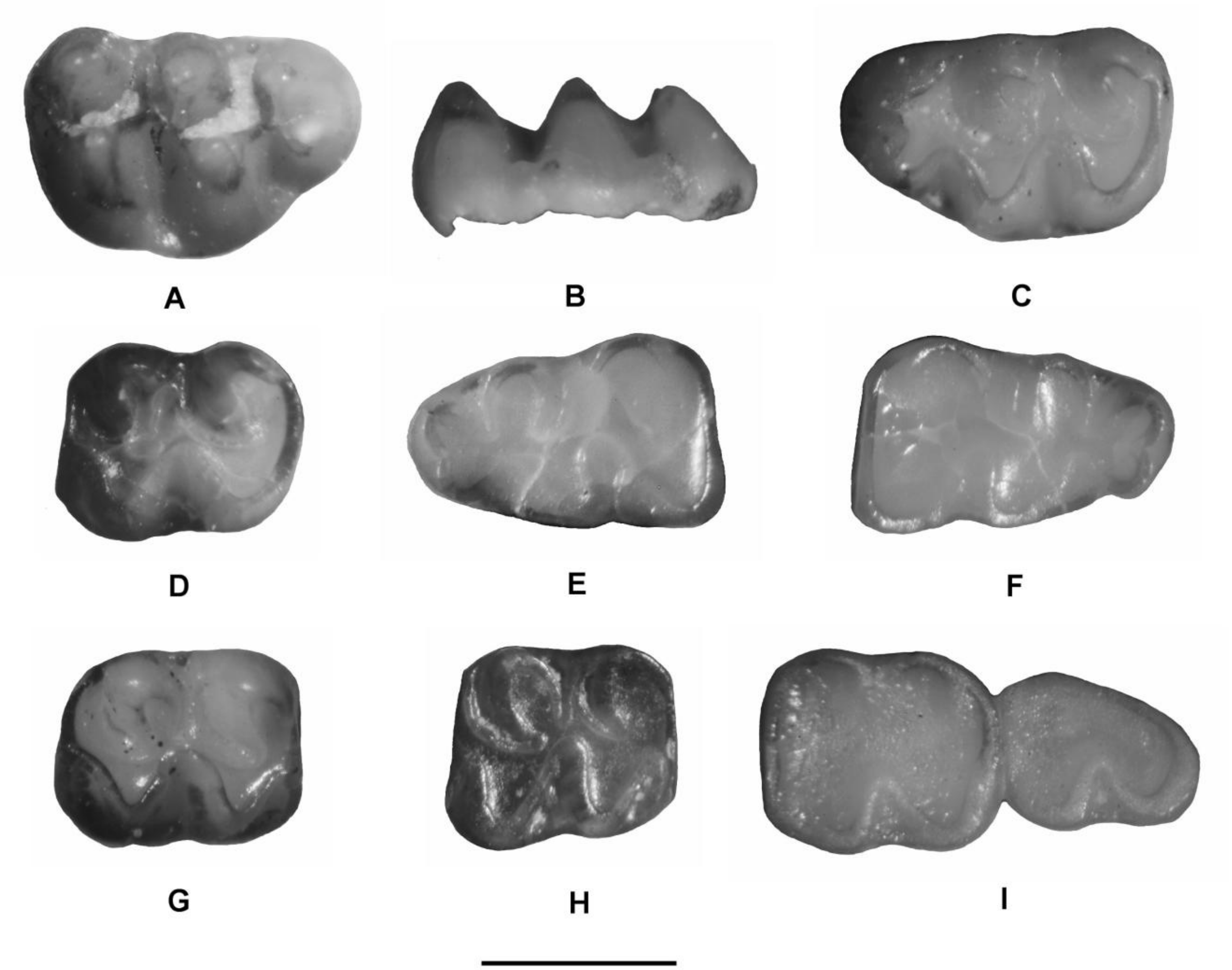

FIGURE 12. Molars of *Bensonomys* sp. from upper part of DSF. A-B, M1, LACM 156385; C, M1, LACM 156379; D, M2, LACM 150710; E, m1, LACM 156386; F, m1, LACM 156382; G, m2, LACM 156388; H, m2, LACM 150711; I, partial dentary with m2-3, LACM 156389. A and C-I, occlusal views. B, labial view. Scale bar = 1 mm.

the metaconid and entoconid that is the remnant of a mesolophid.

The M1s are characterized by the following: 1) brachydont (M1 prh/ap in unworn tooth = 0.35); 2) a strongly bifurcated M1 anterocone that is significantly slanted posteriorly, well separated from the metacone and protocone, and connected centrally to the anterolophule; 3) non-alignment of the protolophule II and the anterior arm of the hypocone; 4) a moderately long, low metaloph that extends labially to about three quarters of the way to the labial edge of the tooth; 5) a distinct parastyle; 6) a very weak, low anterior shelf (cingulum) along the anterior base of the anterocone; 7) a very weak, low anterior cingulum between the lingual lobe of the anterocone and the anterolingual base of the protocone; and 8) a moderately developed posterior cingulum. The presence of accessory rootlets cannot be determined for two of the M1s because one is a tooth cap lacking roots (LACM 156385) and in the other the lingual roots are embedded in maxillary bone and not visible (LACM 156379). However in LACM 157150, the M1 is slightly raised out of the maxillary bone and a small accessory rootlet is visible below the paracone.

The M2s are very similar in occlusal morphology to the M1s except for lacking an anterocone and are characterized by having the following: 1) brachydont; 2) non-alignment of the protolophule II and the anterior arm of the hypocone; 3) a moderately long, low mesoloph; and 4) moderately well developed anterior and posterior cingula.

The m1s are characterized by having the following: 1) brachydont; 2) a strongly bifurcated anteroconid that is well separated from the metaconid and protoconid, centrally positioned and connected centrally to the anterolophulid; 3) a parastylid present; 4) a moderately long mesolophid (even though well worn, a distinct projection can be distinguished along the occlusal outline between the metaconid and entoconid that represents a worn mesolophid); 5) the entolophulid and the posterior arm of the protoconid are not aligned; 6) a weak anterior cingulid; and 7) a moderately developed posterior cingulid.

TABLE 6. Dental measurements of *Bensonomys* sp. from upper part of DSF.

LACM number	position	ap	tra	trp
156385	M1	1.72	1.13	1.13
156379	M1	1.70	1.06	1.10
157150	M1	1.71	1.08	1.10
150710	M2	1.26	1.02	1.08
156380	M2	1.23	1.03	1.04
157149	M2	1.25	1.04	1.07
156386	m1	1.65	0.90	1.08
156382	m1	1.64	0.89	1.07
156388	m2	1.26	1.02	1.05
150711	m2	1.25	1.03	1.10
157151	m2	1.26	1.04	1.08
156389	m2	1.26	1.06	1.06
156389	m3	1.04	0.82	0.62

The m2s are similar in occlusal morphology to the M2s and are characterized by having the following: 1) brachydont; 2) non-alignment of the entolophulid and posterior arm of the protoconid; 3) a moderately long, low mesolophid; and 4) moderately well-developed anterior and posterior cingulids. If LACM 156389 is correctly referred to this species, then, even though very worn, the following characters can be distinguished for the m3: 1) brachydont; 2) a small entoconid was probably present because there is a slight bump along the occlusal outline posterior to the metaconid; 3) a distinct posterior cingulid lacking (the talonid is lobe shaped without any noticeable distortion along the posterior lingual edge of its occlusal outline that would indicate a distinct posterior cingulid was present at an earlier wear stage); and 4) moderate reduction in size relative to the m2 (m3 ap = 83% of m2 ap). Although the occlusal pattern during an earlier wear stage cannot be determined for the m3, the worn lobe-shaped talonid is compatible with the S-shaped pattern of sigmodontines and differs from those of Democricetodontini, wherein a distinct posterior cingulid is commonly present.

Discussion—The dental characters of this species are most similar to those of *Bensonomys* including the following (Figures 12A-I) : 1) very brachydont molars; 2) M1 with accessory rootlet; 3) anterocone strongly slanted posteriorly; 4) M1/m1 anterocone/anteroconid strongly bifurcated, well separated anteriorly from protoloph/metalophid, and protoloph/metalophid centrally connected to anteroloph/anterolophid; 5) M1-2 and m1-2 with non-alignment of the protolophule II with the anterior arm of the hypocone and non-alignment of the entolophulid with the posterior arm of the protoconid, respectively; 6) M1/m1 parastyle/parastylid present; 7) M1/m1 mesoloph/mesolophid present; 8) m1 with labial and lingual constriction between anteroconid and metalophid; and 9) if LACM 156389 is correctly referred, m3 moderately reduced with m3 ap = 83% of m2 ap and m3 ap = 64% of m1 ap (those of species of *Bensonomys* are m3 ap = 78-89% of m2 ap and m3 ap = 61-69% of m1 ap).

Bensonomys sp. also exhibits similarities to *Abelmoschomys simpsoni* Baskin, 1986 (a monotypic basal sigmodontine genus known only from M1/m1), by having the following: 1) M1 with strongly bifurcated anterocone and a parastyle; 2) M1/m1 brachydont with non-alignment of protolophule II and anterior arm of hypocone/non-alignment of entolophulid and posterior arm of protoconid; and 3) M1/m1 with a mesoloph/mesolophid. It differs from *A. simpsoni* by being slightly larger in size and by having the M1/m1 lacking a mesocone/mesoconid, m1 anteroconid more strongly bifurcated (more like those of *Bensonomys*), and m1 with a much less developed anterior cingulid.

The late Barstovian to Clarendonian *Copemys esmeraldensis* Clark et al., 1964, has the M1/m1 with a slightly bifurcated anterocone/anteroconid and a mesoloph/mesolophid present (Clark et al., 1964; Shotwell, 1967; Lindsay, 1972). *Bensonomys* sp. can be easily distinguished from *C. esmeraldensis* by having the following differences: 1) significantly smaller size; 2) molars significantly lower crowned (very brachydont); 3) M1 accessory rootlet present; 4) M1 anterocone strongly slanted posteriorly with much greater bifurcation (much more bilobed), relatively larger (more transverse) and extending relatively further anteriorly with a distinct lingual constriction between it and the protoloph; 5) m1 anteroconid with much greater bifurcation (much more bilobed) with lobes equal in size and it extends relatively further anteriorly from the metalophid with labial and lingual constrictions between it and the metalophid; 6) M1 with weak, shelf-like cingulum along anterior base of anterocone; and 7) M1/m1 with a much weaker anterior cingulum/anterior cingulid.

Latest Hemphillian to early Blancan *Symmetrodontomys* exhibits certain dental and mandibular similarities to *Bensonomys* and has been regarded by some investigators as being derived from *Bensonomys*. *Bensonomy*s sp. differs from *Symmetrodontomys* by having the following (Martin et al., 2002a; Kelly, 2007): 1) lower crowned molars; 2)

M1-2/m1-2 primary cusps with greater alternation; 3) m1 lacking X-shaped occlusal pattern formed with wear between anteroconid and metalophid because of the greater separation of the anteroconid and metalophid; and 4) m3 more reduced relative to m1-2 (in species of *Bensonomys*, m3 ap = 61-69% of m1ap and m3 ap = 78-89% of m2 ap; in DSF species m3 ap = 64% of m1 ap and m3 ap = 83% of m2 ap; in *Symmetrodontomys simplicidens*, mean m3 ap = 76.4% of mean m1 ap and mean m3 ap = 97.6% of mean m2 ap; and in *Symmetrodontomys dammsi*, mean m3 ap = 76.7% of mean m1 ap and mean m3 ap = 98.3% of mean m2 ap).

In summary, *Bensonomy*s sp. agrees well in occlusal morphology and crown height to other species of the genus. *Bensonomys* was previously known from the medial Hemphillian (Hh2) through the Blancan (Gidley, 1922; Hibbard, 1938, 1953, 1956; Gazin, 1942; Baskin, 1978; Dalquest, 1983; Lindsay and Jacobs, 1985; Carranza-Castañeda and Walton, 1992; Martin et al., 2002b; Kelly, 2007). The discovery of *B.* sp. at locality LACM 5690 extends the chronologic range of the genus downward into the early Hemphillian (Hh1, ~8.0 Ma).

The DSF *Bensonomys* exhibits a suite of minor dental differences from the other recognized species of the genus. It is similar in size to *Bensonomys arizonae*, *B. eliasi*, *B. meadensis*, and *B. coffeyi*, larger than *B. yatzi*, *B. gidleyi*. *B. hershkovitzi*, *B. winklerorum*, *B. lindsayi* and *B. elachys*, and smaller than *B. baskini* and *B. stirtoni*. *Bensonomys* sp. differs from all later species of *Bensonomys* by having the shelf-like cingulum along the anterior base of the M1 anterocone slightly less developed. *Bensonomys* sp. differs from *B. lindsayi* by having the M1 anterocone not quite as strongly bifurcated and a mesolophid present on M1-2/m1-2. *Bensonomys* sp. differs from *B. arizonae* by M1-2/m1-2 having a mesoloph/mesolophid present and M1 lacking a mesostyle. *Bensonomys* sp. differs from *B. baskini* by having M1-2/m1-2 with moderately long mesolophid present (except for one M2 with a short mesolophid, *B. baskini* is usually lacking M1-2/m1-2 mesolophs/mesolophids), M1-2 lacking a mesostyle, and M2 lacking a midline cuspule (anterocone?) on the anterior cingulum. *Bensonomys* sp. differs from *B. coffeyi* by having a mesolophid present on m1-2. *Bensonomys* sp. differs from *B. elachys* by having the M1 mesoloph better developed (*B. elachys* has a short M1 mesoloph) and m1-2 mesolophids present (absent in B. elachys). *Bensonomys* sp. differs from *B. hershkovitzi* by having slightly greater bifurcation of the m1 anteroconid, m1 anterior labial cingulid much less developed (in *B. hershkovitzi* it is well developed, extending from the labial lobe of the anteroconid to near the labial base of the protoconid, a character that is lacking in all other species of *Bensonomys*), and m1 mesolophid and parastylid present. *Bensonomys* sp. differs from *B. meadensis* by having m1 with a slightly stronger anterior cingulid and M1-2/m1-2 mesolophids present. *Bensonomys* sp. differs from *B. winklerorum* by having M1/m1 with a moderately long mesoloph/mesolophid (in *B. winkelerorum*, M1 mesoloph absent or short when present, m1 mesolophid absent) and m1 anteroconid strongly bifurcated (in *B. winklerorum* it is not bifurcated). *Bensonomys* sp. differs from *B. eliasi* by having m1-2 mesolophids present. *Bensonomys* sp. differs from *B. yatzi* by having M1/m1 mesoloph/mesolophid present, M1/m1 parastyle/parastylid present and a slightly less developed m1 anterior cingulid. *Bensonomys* sp. differs from *B. stirtoni* by having m1-2 mesolophid and parastylid present. *Bensonomys* sp. differs from *B. gidleyi* by having by having M1/m1 with parastyle/parastylid present, m1 with mesolophid present, and m1 anterior cingulid slightly less developed. Considering the above differences, it appears that the DSF *Bensonomys* represents a new species, but assigning a new specific name is withheld until a better sample is available, so it is referred to *Bensonomys* sp. This is the first record of the genus from the DSF.

Tribe Democricetodontini Lindsay, 1987
Genus *Copemys* Wood, 1936
Copemys dentalis (Hall, 1930)
Figures 3, 13A-B, 14A-B; Table 7

Referred specimens—From locality LACM 5718: M1, LACM 156390. From locality LACM 3533: partial dentary with m1-3, LACM 156358; m1, LACM 124889. From locality LACM 4702: M2, LACM 156360; m1s, LACM 124915, 124920. From locality LACM 3776: m1, LACM 156363. From locality LACM 3666: partial dentary with i and m1, LACM 150702. From locality LACM 6380: partial maxilla with M1, LACM 142760; M2, LACM 142758; partial dentary with m1, LACM 142759.

Distribution and Age—Localities LACM 3533, 5718, 3776, 3666 and 6380 in upper part of DSF plus also known from Members 3-5 of DSF (see Whistler et al., 2009, 2013). Early Clarendonian through early Hemphillian (Cl1-Hh1, ~11.7-8.4 Ma).

Description—Only two M1s from the upper part of the DSF are referred to *C. dentalis*. They are characterized by having the following: 1) brachydont, unworn prh/ap ratios = 0.45-0.46; 2) the anterocone is relatively large, positioned slightly labially, single cusped, and connected centrally to the anteroloph; 3) rounded, bulbous primary cusps with little alternation; 4) the protolophule II is not aligned with the anterior arm of the hypocone; 5) the lingual cingulum is moderately well developed giving the reentrant between the protocone and hypocone a U-shaped appearance in lingual view; 6) a short mesoloph; 7) a small parastyle and mesostyle; 8) the anterior cingulum is well developed and the posterior cingulum is moderately developed; and 9) relatively small as compared with other species of *Copemys*.

Two M2s from the upper part of the DSF are compatible in size, crown height, and occlusal morphology to the referred *C. dentalis* M1s. They are characterized by having the following: 1) brachydont; 2) little alternation of the primary cusps with the protolophule II not aligned with the anterior arm of the hypocone; 3) a short mesoloph present; 4) the anterior cingulum is well developed; and 5) the posterior cingulum is moderately developed.

TABLE 7. Dental measurements of *Copemys dentalis* from upper part of DSF.

LACM number	position	ap	tra	trp
142760	M1	1.46	1.01	1.00
156390	M1	1.51	0.95	0.98
142758	M2	1.21	0.89	0.93
156360	M2	1.20	0.89	0.94
142759	m1	1.41	0.84	0.99
124889	m1	1.50	0.91	1.00
124915	m1	1.46	0.87	1.00
124920	m1	1.36	0.87	0.99
156363	m1	1.46	0.93	1.00
150702	m1	1.39	0.78	0.98
156358	m1	1.48	0.87	0.95
156358	m2	1.28	0.97	0.98
156358	m3	1.03	0.87	0.62

A partial dentary with m1-3 and six other m1s are compatible in size and occlusal morphology to the referred *C. dentalis* M1s. The m1 is characterized by having the following: 1) brachydont (although no unworn m1s are known, the pch/ap ratios range from 0.36-0.45 for m1s in moderate wear to very early wear, respectively); 2) the anteroconid is moderate in size, centrally positioned, single cusped, and connected centrally to the anterolophid; 3) the metaconid is separated from the anteroconid by a moderately deep valley; 4) the entolophulid is not aligned with the posterior arm of the protoconid; 5) a short mesolophid; and 6) the anterior cingulid is moderately well developed and the posterior cingulid is well developed. Besides lacking an anteroconid and having a much more robust anterior cingulid, the m2 is nearly identical in occlusal morphology to the m1. The m2 is relatively large as compared with the m1 (m2 ap = 86% of m1 ap). The m3 is characterized by having the following: 1) oblong occlusal outline and slightly reduced (m3 ap = 80% of m2 ap); 2) the metaconid is about equal in size to the protoconid, but taller; 3) the hypoconid is reduced; 4) the entoconid is a very small cusp positioned along the posterolingual margin of the talonid; 5) a distinct, relatively high mesolophid that extends to the lingual margin of the tooth where it joins a moderately high, continuous ridge between the metaconid to the entoconid resulting in two isolated, moderately deep valleys (one between the mesolophid, metaconid and protoconid, and one between the mesolophid, entoconid and hypoconid); and 6) a moderately well-developed anterior cingulid.

Discussion—These DSF specimens are assigned to *Copemys dentalis* because they are indistinguishable in crown height, size and occlusal morphology from those of *C. dentalis* from medial Clarendonian Esmeralda Formation of Nevada and late Clarendonian Black Butte localities of Oregon (Hall, 1930; Shotwell, 1967). As reported in Whistler and Burbank, (1992;fig. 5) and Whistler et al. (2009:fig. 4, table 1), *C. dentalis* is a long ranging taxon (Cl1-Hh1) in the type area of the DSF. These specimens also confirm the identifications of Whistler and Burbank (1992) and Whistler et al. (2009), wherein they reported the uppermost occurrence of *C. dentalis* in the lower part of Member 6 of the type section of the DSF.

Copemys sp., cf. *C. dentalis* (Hall, 1930)
Figures 3, 13C-G, 14A-B; Table 8

Referred specimens—From locality LACM 3580: M1s, LACM 125446, 125448, 125450, 125452, 125453; m1, LACM 124881. From locality LACM 3531: M1s, LACM 156350, 156351, 156353. From locality LACM 3533: M1, LACM 156355; M2s, LACM 156356, 156357. From locality LACM 5720: M1s, LACM 156414, 156415, 157167, 157170; partial dentary with m1-3, LACM 150716. From locality LACM 4702: partial maxillae with M1-3, LACM 125656, 125688, 125670; partial maxillae with M1-2, LACM 125672, 125673; M1s, LACM 125678, 125683. From locality LACM 3776: partial maxilla with M1-2, LACM 125653; M1s, LACM 125729, 156365, 156366, 125463, 125464; M2s, LACM 156361, LACM 156369.

Distribution and Age—Localities LACM 3580, 3531, 3533, 5720, 4702 and 3776. Latest Clarendonian through early Hemphillian (Cl3-Hh1, ~9.3 - 8.8 Ma).

Description—There is a group of specimens from the upper part of the DSF whose M1-2 and m1-3 are indistinguishable from those referred above to *C. dentalis*, but are significantly larger in size (Figures 13C-G, Tables 7-8). They are also brachydont with unworn to very early wear M1 prh/ap ratios of 0.45-0.46 and an unworn m1 pch/ap ratio of 0.46. It could be argued that these specimens just represent large representatives of *C. dentalis*, but specimens intermediate in size are lacking in the DSF samples (Figures 14A-B). The group of larger-sized *Copemys*

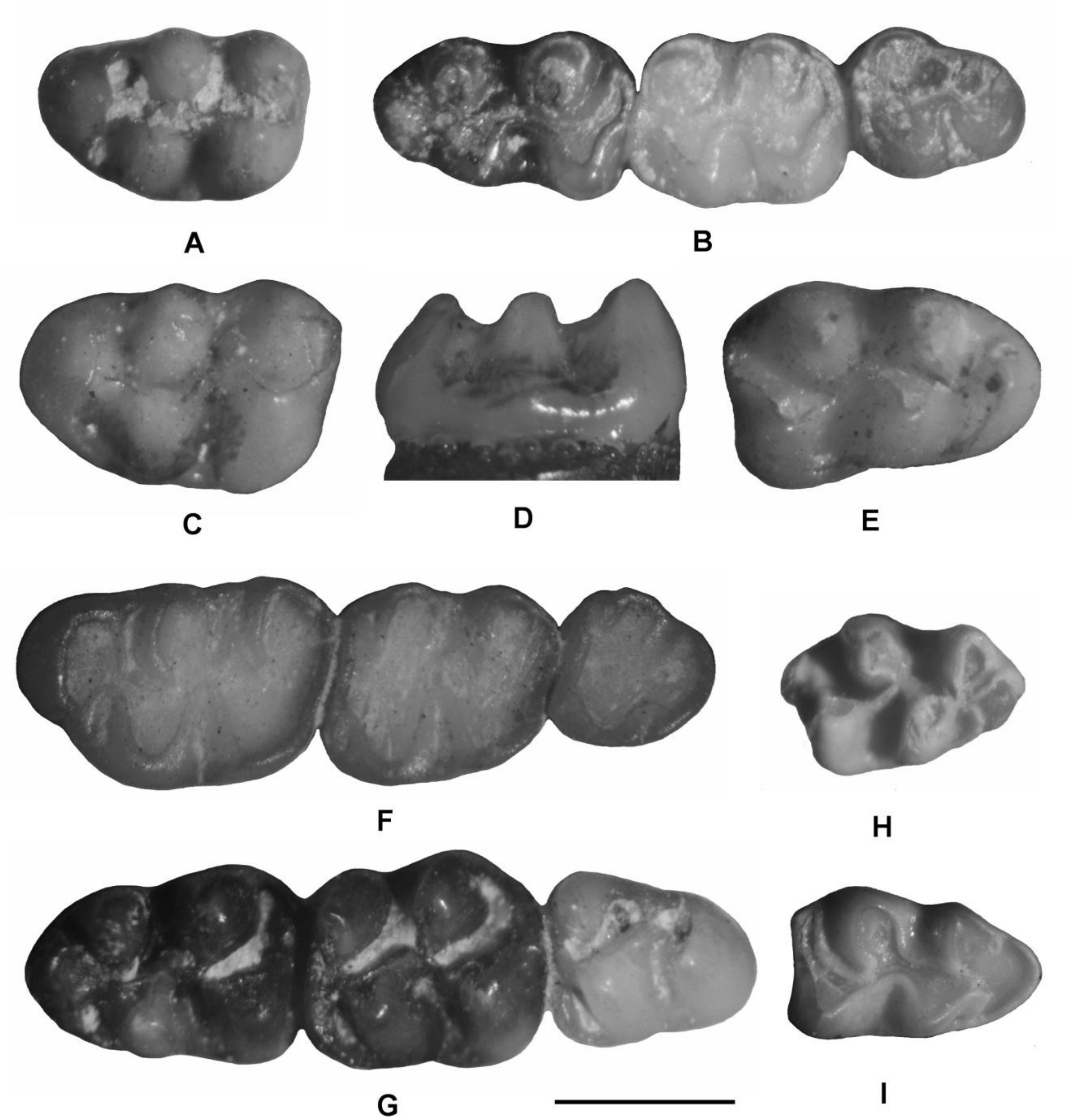

FIGURE 13. *Copemys* and *Postcopemys* from upper part of DSF. A-B, *Copemys dentalis*: A, M1, LACM 156390; B, m1-3, LACM 156358. C-G, *Copemys* sp., cf. *C. dentalis*: C-D, M1, LACM 125446; E, m1, LACM 124881; F, M1-3, LACM 125670; G, m1-3, LACM 150716. H-I, *Postcopemys* sp., cf. *P. valensis*: H, m1, LACM 156383; I, m1, LACM 156387. A-C and E-I, occlusal views. D, lingual view. Scale bar = 1 mm.

specimens are much better represented, including 15 isolated M1s and six partial maxillae with M1-3 or M1-2. The above descriptions of the M1 and m1-3 for *C. dentalis* apply also to the larger-sized group of *Copemys* with no notable differences. However, the larger sample size does allow for a better assessment of individual variation of the M1 including the following: 1) all M1s have a short mesoloph present; 2) 20% have a small parastyle present; 3) 20% have a small mesostyle present; 4) 5% have a protolophule I present; and 5) one specimen has a very small entostyle present. In the two partial dentaries with m1-3, the m3 ap =

82% of the m2 ap, which is similar to that of *C. dentalis*.

The six M2s of the larger-sized *Copemys* group are characterized by having the following: 1) little alternation of the primary cusps with the protolophule II not aligned with the anterior arm of the hypocone; 2) a short mesoloph is present in all specimens; 3) a small parastyle is present in one specimen; 4) a small mesostyle is present in two specimens; 5) a protolophule I is present in two specimens; and 6) moderately-developed anterior and posterior cingula.

All of the M3s of the larger-sized *Copemys* group are well worn, but the following characters can still be observed: 1) a suboval occlusal outline that is slightly wider than long; 2) the paracone and hypocone are the largest primary cusps, whereas the hypocone and metacone are very reduced; 3) the anterior cingulum is moderately developed, extending lingually from the anterior base of the paracone to about the middle of the hypocone; 4) remnants of a moderately deep valley are present between the anterior cingulum and paracone and a deeper valley between the paracone and metacone; 5) the posterior cingulum forms a continuous arc from the hypocone to the metacone; 6) a protolophule I and II may have been present because, in the less worn M3, a central isolated valley is present between the paracone and hypocone; and 7) moderately reduced size (M3 ap = 70-72% of M2 ap).

TABLE 8. Dental statistics (in mm) for *Copemys* sp., cf. *C. dentalis* from upper part of DSF.

Position/ dimension		N	Mean	OR	SD	CV
M1	ap	26	1.73	1.64-1.81	0.052	3.0
	tra	26	1.09	1.00-1.16	0.045	4.1
	trp	26	1.11	1.03-1.18	0.041	3.6
M2	ap	10	1.29	1.21-1.33	0.045	3.4
	tra	10	1.07	1.00-1.13	0.060	5.6
	trp	10	1.04	0.95-1.09	0.062	5.9
M3	ap	3	0.91	0.89-0.94	0.027	-
	tr	3	0.85	0.83-0.87	0.021	-
m1	ap	2	1.68	1.59-1.77	0.127	-
	tra	2	0.97	0.93-1.00	0.050	-
	trp	2	1.09	1.04-1.13	0.064	-
m2	ap	1	1.39	-	-	-
	tra	1	1.13	-	-	-
	trp	1	1.21	-	-	-
m3	ap	1	1.13	-	-	-
	tra	1	0.96	-	-	-
	trp	1	0.75	-	-	-

Discussion—A group of *Copemys* specimens in the samples from the DSF whose M1-2 and m1-3 are indistinguishable in occlusal morphology from the *C. dentalis* specimens, are significantly larger is size. They are also brachydont with unworn to very early wear stages with M1 prh/ap ratios of 0.45-0.46. It could be argued that these specimens just represent large representatives of *C. dentalis*, but specimens intermediate in size are lacking in the DSF samples (Figures 14A-B). Thus, these specimens probably represent a second species of *Copemys* in the DSF that is closely related to *C. dentalis*. However, Lindsay (2008) noted that several previously identified species of *Copemys*, including *C. dentalis*, have never been adequately differentiated, suggesting that the genus is in need of revision. Also, specimens of *Copemys* are the most abundant rodent in the entire stratigraphic extent of the DSF, with over a thousand specimens previously assigned to at least three separate species of *Copemys* (Whistler and Burbank, 1992; Whistler et al., 2009). No detailed taxonomic analysis similar to the one presented here has been undertaken of this material. It is possible that such an analysis would recognize both a greater taxonomic diversity and range extension for species described in this study. Therefore, rather than assigning a new specific name to the larger-sized group of *Copemys* from the DSF based primarily on size, we refer these specimens to *Copemys* sp., cf. *C. dentalis*.

The M1s of *Antecalomys coxae* and *Lindsaymys* sp. A are similar in size to those of *Copemys dentalis* and *C.* sp., cf. *C. dentalis*, respectively, but can be easily distinguished by having the following: 1) higher crowned; 2) M1 accessory rootlet present; 3) the lingual cingulum between the protocone and hypocone is reduced forming a more narrow V-shaped reentrant in lingual view, whereas in *Copemys* the cingulum is better developed (more shelf-like) forming a relatively wider U-shaped reentrant in lingual view; and 4) the anterior cingulum is vertically orientated and much less expanded labially, whereas in *Copemys* the cingulum is much better developed and extends in a more inclined arc from the anterocone to the anterolabial base of the protocone (compare Figures 4B-C, 9B and E and 13D). The more reduced anterior cingulum of *Lindsaymys* and *A. coxae* results also in the anterocone appearing less elongated transversely with a more defined indentation between the anterocone and the protocone in occlusal view.

Genus *Postcopemys* Lindsay and Czaplewski, 2011

Postcopemys sp., cf. *P. valensis* (Shotwell, 1967)

Figures 13H-I, Table 9

Referred Specimens—From locality LACM 5690: m1, LACM 156387; partial m1, LACM 156383. From locality 6380: partial dentary with m1, LACM 142755.

Distribution and Age—Upper to uppermost part of DSF. Early Hemphillian (Hh1, ~8.4 - 8.0 Ma).

Discussion—Three m1s from localities LACM 5690 and 6380 are significantly smaller than all of the

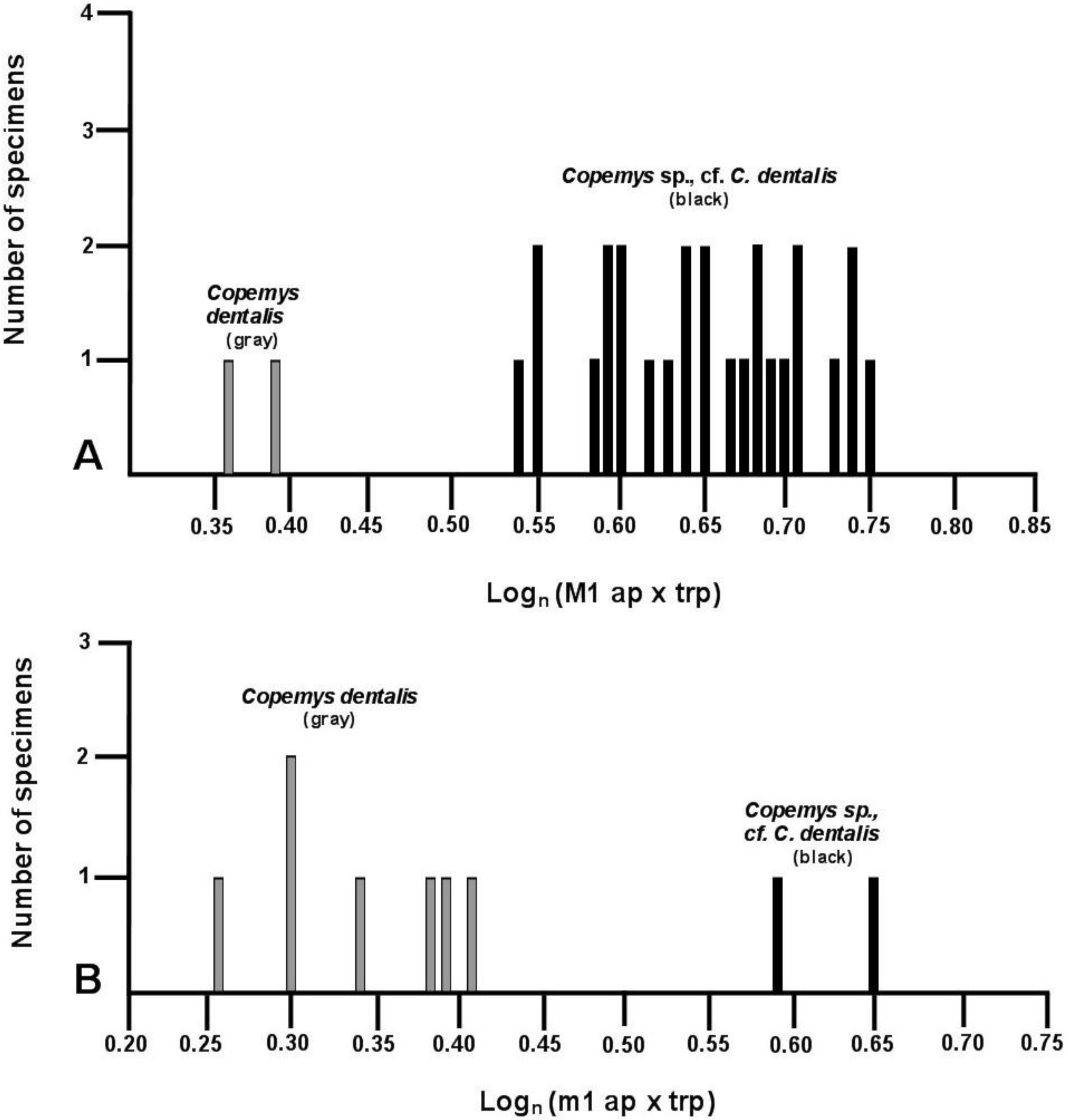

FIGURE 14. Charts plotting (A) Log_n M1 area (ap x trp) and (B) Log_n m1 area (ap x trp) versus number of specimens for *Copemys dentalis* and *Copemys* sp., cf. *C. dentalis* from upper part of DSF.

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other cricetid m1s from the DSF and have the posterior arm of the protoconid aligned with the entolophulid (Figures 13H-I), which is characteristic of *Postcopemys* and most species of *Peromyscus* (Lindsay, 1972; Lindsay and Czaplewski, 2011). These m1 specimens are further characterized by having the following: 1) brachydont (pch/ap = 0.42 for LACM 142755, 0.37 for LACM 156383 and 0.34 for LACM 156387); 2) the anteroconid positioned centrally, relatively close to the metaconid, but separated from it by a distinct, narrow valley; 3) stylids and accessory lophids are lacking (except for a small spur on the posterior side of the metaconid in one specimen, LACM 156383); 4) the anterior cingulid is well developed; and 5) the posterior cingulid is moderately robust. The m1s agree well in size and occlusal morphology to those of *Postcopemys valensis* from the late Hemphillian of Oregon and California (Shotwell, 1967; May et al., 2011). However, formal assignment of these specimens to *P. val*ensis is withheld until a more complete sample is available. This is the first record of the genus from the DSF.

TABLE 9. Dental measurements of *Postcopemys* sp., cf. *P. valensis* from upper part of DSF (e = estimated).

LACM number	position	ap	tra	trp
142755	m1	1.36	0.82	0.90
156383	m1	1.34e	0.82	0.90
156387	m1	1.38	0.78	0.90

Repomys May, 1981
cf. *Repomys* sp.
Figure 15

Referred Specimens—M2, LACM 156378.

Distribution and Age—Locality LACM 5690. Early Hemphillian (Hh1, ~8.0 Ma).

Description—A partial M2 from locality LACM 5690 has the anterolingual corner of the tooth missing, including part of the protocone and anterior cingulum. It is also cracked transversely at about the middle of the tooth with the talonid displaced slightly anterolingually. It is characterized by having the following: 1) relatively large size (broken ap = 1.90 mm, trp = 1.77 mm); 2) relatively high crowned, even though moderately well worn the pch = 1.06 mm; 3) wide, deep reentrant valleys between the paracone and metacone (metaflexus) and protocone and hypocone (hypoflexus); 4) reentrant valley between anterior cingulum and paracone (paraflexus) deep, but nearly closed off by anteriorly orientated projection from paracone and small posteriorly orientated projection from anterior cingulum (= anterostyle of May [1981]) that with slightly further wear would result an isolated lake on the occlusal surface; 5) a short posteriorly orientated projection (= parastyle of May [1981] = mesostyle of Mou [2011]) from the paracone; 6) the anterolabial portion of the anterior cingulum robust; 7) although the posterior cingulum is merged with the metacone due to wear, it appears to have been moderately developed; 8) thick enamel; and 9) three roots.

Discussion—The distinctive occlusal morphology of LACM 156378 separates it from all other cricetid taxa from the DSF. It is similar to the M2 of *Repomys* (May, 1981; Tomida, 1987; Lindsay, 2008; Mou, 2011) by having a deep, wide metaflexus and hypoflexus, a small parastyle on the anterolingual wall of the anterior cingulum, a mesostyle on the posterior wall of the paracone, a relatively flat occlusal surface, thick enamel and three roots (compare Figures 15A-B with May, 1981:figures 5A, 6A). The molars of *Repomys* are hypsodont with the M2 crown as tall as the ap length (May, 1981; Tomida, 1987; Korth, 2011; Mou, 2011). LACM 156378 appears to have been high crowned because, even though moderately well worn, its crown height is about half its length. It differs from those of *Repomys* by having the paraflexus almost closed off by a small anterostyle and an anterior projection of the paracone, which, with further wear would result in an isolated lake. One of the most diagnostic characters of *Repomys* is the reduction and distinctive occlusal pattern of the M3/m3 (Lindsay, 2008; Korth, 2011; Mou, 2011). Unfortunately, only a few cricetid third molars are known from locality LACM 5690, none of which are similar to those of *Repomys*.

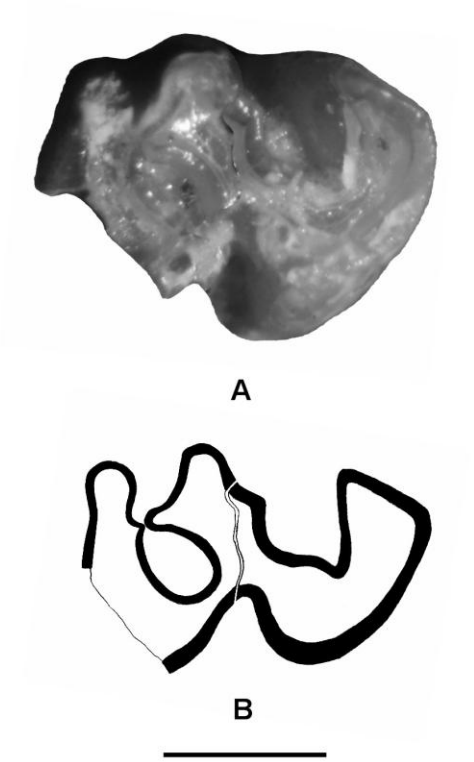

FIGURE 15. cf. *Repomys* sp. from upper part of Dove Spring Formation. A, partial M2, LACM 156378. B, partial M2, LACM 156378, line drawing of occlusal outline. All occlusal views. Scale bar = 1 mm.

Two other rare, hypsodont cricetid genera that form isolated lakes on the M2 occlusal surface are *Galushamys*, described by Jacobs (1977) from the late Hemphillian Redington Local Fauna of Arizona, and *Pliotomodon*, described by Hoffmeister (1945) from the late Hemphillian Mullholland Formation of California. *Pliotomodon* has been generally regarded as an Eurasian immigrant whose subfamilial status is uncertain (Jacobs, 1977; May, 1981; Jacobs and Lindsay, 1984; Korth, 1994). Lindsay (2008) placed *Pliotomodon* in Galushamyini, but also noted it probably represents a late Miocene immigrant from Eurasia. LACM 156378 exhibits distinct differences from the M2s of *Pliotomodon* and *Galushamys*. In *Pliotomodon*, the M2 paraflexus forms an isolated lake with wear due to a well-developed anterostyle that extends to the metacone, but lacks the anterior projection of the metacone seen the DSF species (Hoffmeister, 1945; Lindsay, 2008). In *Galushamys*, the paraflexus is narrowed between the paracone and metacone, but does not form an isolated lake (Jacobs, 1977; Lindsay, 2008). However in *Pliotomodon* and *Galushamys*, the metaflexus forms an isolated lake due a continuous ridge from the posterolabial edge of the paracone to the anterolabial edge of the metacone. In LACM 156378, the metaflexus is wide and deep, more like those of *Repomys*.

LACM 156378 appears to represent a new genus of Galushamyini, less derived than *Repomys*, *Galushamys* or *Pliotomodon*. However, it is slightly more similar morphologically to *Repomys* than the other two genera and therefore is only compared to the genus as cf. *Repomys* sp.

Acrolophomys new genus

Type and Only Species—*Acrolophomys rhodopetros*, new species.

Distribution and Age—Localities LACM 3580, 4702 and 3776. Latest Clarendonian to early Hemphillian (Cl3-Hh1, ~9.3-8.8 Ma).

Diagnosis—A moderate sized, democricetodontine cricetid rodent characterized by having the following: 1) mesodont (unworn m1 pch/ap = 0.54); 2) reentrant valleys wide, deep and open both labially and lingually; 3) accessory stylids and lophids lacking; 4) m1 anteroconid and primary cusps (especially metaconid and entoconid) narrow and tapering to relatively sharp, pointed apices; 5) m1 anteroconid well separated from metaconid and protoconid and connected to metalophid by anterolophid just labial of its center; 6) near alignment of posterior arms of m1-2 protoconids with entolophulids (primary cusps nearly in complete alternation); 7) m1-3 anterior cingulid moderately well-developed and m1-2 posterior cingulid robust; and 8) m3 moderately reduced relative to m1-2.

Comparisons—*Acrolophomys* is significantly smaller than species of *Basirepomys*, *Miotomodon*, *Pliotomodon*, and *Repomys* and lower crowned than species of *Paronychomys*, *Miotomodon*, *Pliotomodon* and *Repomys*, but higher crowned than species of *Peromyscus*, *Copemys* and *Postcopemys*. Most similar in crown height, size and occlusal morphology to species of *Onychomys*, but differs by having the following: 1) alternation of m1-2 primary cusps slightly less (posterior arms of m1-2 protoconids slightly less aligned with entolophulids); and 2) m3 significantly less reduced with much wider talonid and lacking diagnostic "key-hole" shaped occlusal outline of *Onychomys*.

Etymology—*acro*, Greek for summit, pointed, sharp; *loph*, Greek for ridge, crest; and *mys*, Greek for mouse; in reference to a mouse with sharp-crested teeth.

Acrolophomys rhodopetros new species

Figure 16, Table 10

Holotype—Lm1, LACM 124912

Type Locality—LACM 3533, upper part of Member 5, DSF.

Referred Specimens—From locality LACM 4702: partial dentary with m1-3, LACM 125052; m1, LACM 124930. From locality LACM 3776: m1s, LACM 124878, 156372.

Distribution and Age—Same as for genus.

Diagnosis—Same as for genus.

Etymology—*rhodo*, Greek for rose, red; *petros*, Greek for rocks; in reference to its occurrence in DSF exposures at Red Rock Canyon State Park.

Description—The four m1s are mesodont with an unworn pch/ap ratio of 0.54. Their increased crown height is due primarily to an increase in the length of the cusps above the crown base. The anteroconid and primary cusps are tall, slender, conical and sharp (piercing). The anteroconid is single cusped, positioned well anterior of the metalophulid and connected by the anterolophid to metalophulid just labial of its center. The metaconid is well separated from the anteroconid by a wide, deep valley. The anterior cingulid is moderately well developed and the posterior cingulid is robust. The posterior arm of the protoconid is nearly aligned with the entolophulid resulting in nearly complete alternation of the primary cusps. The labial and lingual reentrants between the primary cusps are wide, deep and open labially and lingually. Accessory lophids and stylids are lacking. There are two well developed primary roots and accessory rootlets are lacking.

LACM 125052 is a partial dentary with well worn m1-3. Small portions of the lingual edges of the m1 metaconid and entoconid are broken away. LACM

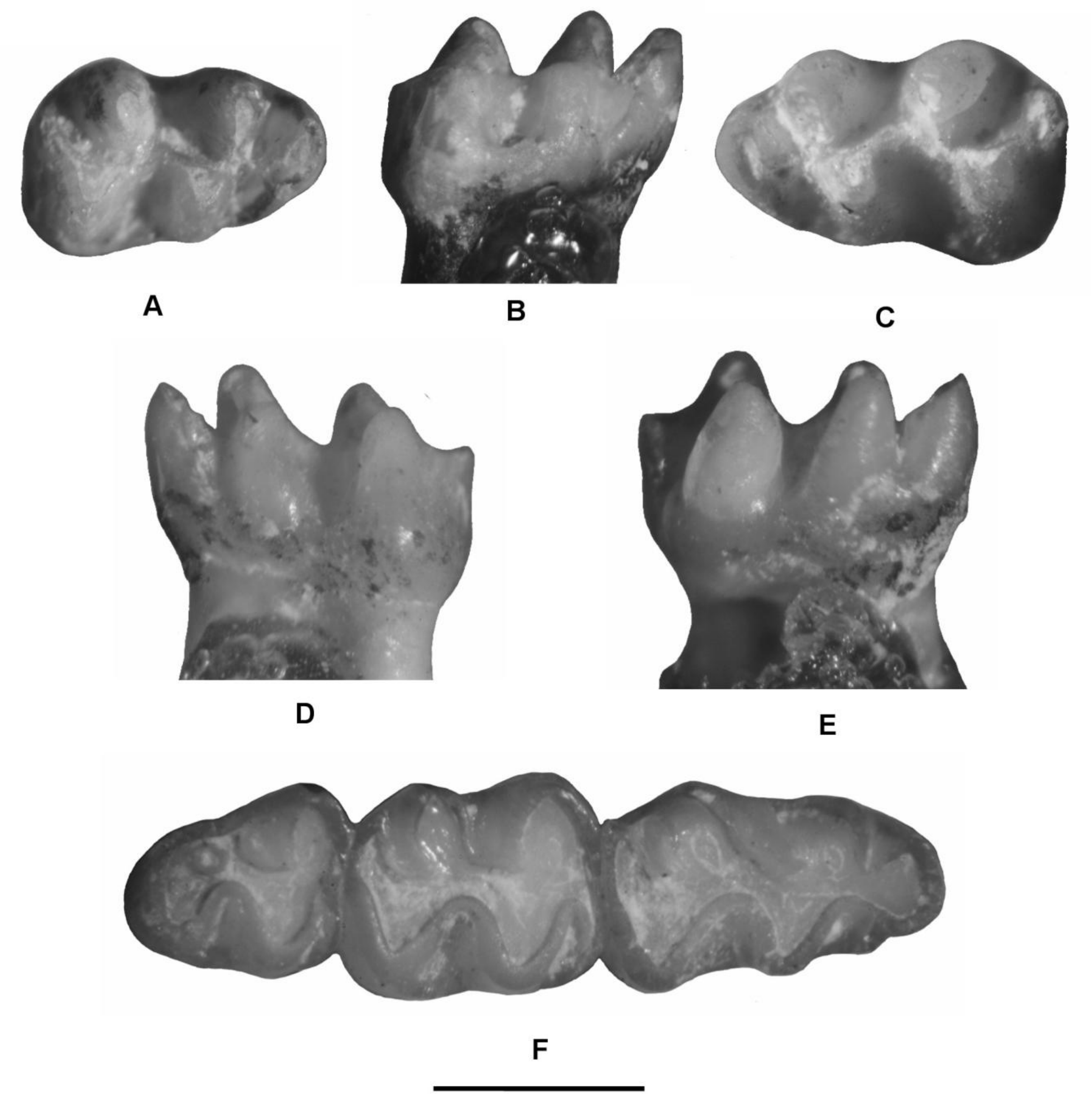

FIGURE 16. *Acrolophomys rhodopetros* new genus and species from upper part of DSF. A-B, m1, LACM 156372. C-E, m1 (Holotype), LACM 124912. E, partial m1 and m2-3, LACM 125052. A, C and E, occlusal views. B and D, labial views. E, lingual view. Scale bar = 1 mm.

125052 is assigned to this species because the m1 agrees in size with the above referred m1s and, even in its advanced stage of wear, the m1 pch = 0.58 mm, indicating it was mesodont when unworn. In addition, the following characters for the m1-2 further support its referral to the species: 1) the m1 anteroconid is well separated from the metaconid by a wide, deep valley and positioned well anterior of the metalophulid; 2) the m1-2 reentrants between the primary cusps are wide and open labially and lingually; 3) the m1-2 posterior arms of the protoconids are nearly aligned with the entolophulids; 4) the m1-2 anterior cingulids are moderately well developed and the posterior cingulids are robust; and 5) accessory stylids and lophids are lacking. The m3 is characterized by having the following: 1) moderately reduced (m3 ap = 82% of m2 ap); 2) wide reentrant valleys between the primary cusps; 3) a lingually positioned, isolated enamel lake between trigonid and talonid; and 4) a moderately developed anterior cingulid.

TABLE 10. Dental measurements of *Acrolophomys rhodopetros* new genus and species from upper part of DSF (e = estimated).

LACM number	position	ap	tra	trp
124912 (Holotype)	m1	1.62	0.90	1.01
124930	m1	1.54	0.87	0.95
124878	m1	1.50	0.85	0.95
156372	m1	1.44	0.85	0.93
125052	m1	1.63	0.85e	1.00e
125052	m2	1.26	1.05	1.05
125052	m3	1.03	0.90	0.62

Discussion—*Acrolophomys rhodopetros* is distinct from all other cricetids from the upper part of the DSF by having sharply pointed m1 anteroconids and primary cusps, and an anteroconid that is well separated from the metalophulid and positioned further anteriorly. *A. rhodopetros* further differs from *Bensonomys* sp. of the DSF by having the following: 1) significantly higher crowned; 2) lacking accessory stylids and lophids; 3) a more vertically orientated m1 anteroconid that is single cusped; and 4) greater alternation of the primary cusps with the posterior arm of the protoconid of m1-2 nearly in full alignment with the entolophulid. *A. rhodopetros* further differs from *Lindsaymys* by having the following: 1) smaller size; 2) slightly to significantly lower crowned; 3) the m1 anteroconid much better separated from the metaconid; 4) the labial cingulid between protoconid and hypoconid better developed and more U-shaped in labial view; and 5) lacking entoconid spurs. *A. rhodopetros* further differs from *Antecalomys coxae* by having the following: 1) the m1 anteroconid relatively larger and much better separated from the metaconid; 2) the m1-2 reentrant valleys relatively wider and more open; 3) the m1-2 anterior and posterior cingulids slightly more robust; and 3) mesolophids are lacking. *A. rhodopetros* further differs from *Copemys* from the DSF by having the following: 1) higher crowned; 2) the m1 anteroconid separated lingually from the metaconid by a much wider, deeper valley; 3) wider reentrant valleys between the primary cusps; 4) mesolophids lacking; and 5) the posterior arm of the protoconid of m1-2 nearly aligned with the entolophulid. *A. rhodopetros* further differs from *Postcopemys* sp., cf. *P. valensis* from the DSF by having the following: 1) higher crowned; 2) larger size; 3) the m1 anteroconid much better separated lingually from the metaconid by a much deeper, wider valley; and 4) wider reentrant valleys between the primary cusps.

Wilson (1937) described a new species of *Peromyscus*, *P. pliocenicus*, from the early Hemphillian Kern River Formation of California and noted that it differed from other species of the genus by having higher crowned molars and larger size. Subsequently, additional specimens were referred to *P.* cf. *pliocenicus* by Shotwell (1967) from the Hemphillian of Little Valley, Juniper Creek and Mackay Reservoir of Oregon and May (1981) from the late Hemphillian Pinole Local Fauna of California. Jacobs and Lindsay (1984) also referred specimens from the early Hemphillian Rome Fauna to *P. pliocenicus*. May (1981) regarded *P. pliocenicus* as ancestral to *Repomys* and Korth (1994) questioned the referral of *P. pliocenicus* to *Peromyscus*, and suggested that it should be referred to a new genus. Following May (1981), Korth (1994) regarded ?*P. pliocenicus* related to *Repomys* as a basal member of Neotomini, in which he also included *Galushamys* and *Neotoma*. Lindsay (2008) placed ?*P. pliocenicus* in the tribe Democricetodontini, allying it with *Copemys*, *Peromyscus*, *Onychomys* and certain other cricetids, whereas he separated *Paronychomys*, *Galushamys* and *Repomys* as a separate clade in his new tribe Galushamyini. Korth and De Blieux (2010) then erected a new genus *Basirepomys* with *P. pliocenicus* from the Kern River Formation (Wilson, 1937) designated as the type species and described an additional species, *B. robertsi* from the Hemphillian Sevier Formation of Utah. Most recently, Korth (2011) described a third species, *B. romensis* (= *P. pliocenicus* of Jacobs and Lindsay [1984], not Wilson [1937]) from the early Hemphillian Rome Fauna of the Drewsey Formation of Oregon. Korth (2011) also reassigned the specimens assigned by Shotwell (1967) to *P.* cf. *pliocenicus* from Juniper Creek, Oregon, to a new species of *Paronychomys*, *P. shotwelli*, and specimens assigned to *Peromyscus* cf. *pliocenicus* by May (1981) from the Pinole Local Fauna, California, to a new monotypic genus *Miotomodon*. Thus, most all of specimens previously referred to *Peromyscus pliocenicus* or *P*. cf. *pliocenicus* are now divided into three genera: *Basirepomys*, including *B. pliocenicus* (= genotype and restricted sample of "*Peromyscus*" *pliocenicus* first described by Wilson [1937] from Kern River Formation) and *B. romensis*; *Paronychomys* (*P. shotwelli*); and *Miotomodon mayi*. Korth and De Blieux (2010) did not assign *Basirepomys* to any cricetid tribe, but considered it to be intermediate between *Peromyscus* and *Repomys*, and regarded it as a basal neotomyine. Korth (2011) regarded *Miotomodon* as a probable ancestor of *Repomys*, with *Miotomodon* being derived from *Paronychomys* rather than *Peromyscus* or *Basirepomys*. Although, Lindsay (pers.

comm., May, 2014) regards *Basirepomys* more closely allied with *Copemys* and *Peromyscus* than the genera he assigned to Galushamyini, including *Repomys*, suggesting that *Basirepomys* belongs in Democricetodontini. Needless to say, the tribal affiliation of *Basirepomys* is uncertain and in need of further investigation.

Acrolophomys rhodopetros is similar in crown height to species of *Basirepomys*, but can be easily distinguished from them by having the following (Korth and De Blieux, 2010; Korth, 2011): 1) significantly smaller size; 2) the m1-2 primary cusps are narrower anteroposteriorly with more acute apices, especially the metaconid and entoconid; 3) the m1 anteroconid is narrower with a sharp apex, further separated from metalophid and not bifurcated (except *B. romensis*, whose anteroconid is unbifurcated); and 4) accessory stylids and lophids are completely lacking.

Acrolophomys rhodopetros exhibits some dental similarities to species of *Paronychomys*, but can be easily distinguished from them by having the following (Jacobs, 1977; Baskin, 1979; Martin, 2008; Korth, 2011; Kelly, 2013): 1) slightly lower crowned (unworn m1 pch/ap = 0.54, whereas those of unworn to early wear stage for species of *Paronychomys* = 0.59-0.63); 2) the m1 anteroconid is relatively larger, positioned much further anteriorly from the metaconid and separated from the metaconid by a much deeper, wider valley that persists through late wear, whereas in *Paronychomys* the anteroconid is subcircular and positioned very close to the metaconid, separated by a shallow valley that rapidly disappears in early wear joining the metaconid with the anteroconid; 3) the m1-2 primary cusps are more lingually and labially positioned, whereas in *Paronychomys*, the primary cusps of unworn m1-2 are strongly slanted inwards towards the centerlines of the teeth; 4) the m1-2 labial and lingual cingulids are less developed, whereas in *Paronychomys* they are robust and shelf-like; 5) slightly wider reentrant valleys between the m1-2 primary cusps; and 6) the m1 primary cusps and the anteroconid especially are more strongly tapered with their apices more sharply defined (pointed).

Of all other democricetodontine and galushamyine cricetid genera, the m1s of *A. rhodopetros* exhibit greatest similarity to those of *Onychomys* (Gidley, 1922; Hibbard, 1937, 1941, 1953; Hoffmeister, 1945; Carleton and Eshelman, 1979; Martin et al., 2002a, 2002b, 2003). The anteroconids and primary cusps are sharply pointed in *A. rhodopetros*, like those of *Onychomys*. This character has been correlated with the primarily insectivorous diet of extant *Onychomys* (Carleton and Eshelman, 1979; Satoh and Iwaku, 2006; Williams et al., 2009) and may indicate a similar dietary preference for the *A. rhodopetros*. In *Onychomys*, the m1-2 posterior arm of the protoconid is fully aligned with the entolophulid resulting in complete alternation of the primary cusps. In *A. rhodopetros*, the m1-2 posterior arm of the protoconid is almost aligned with the entolophulid and the primary cusps alternate, but not quite as completely as those of *Onychomys*. *Onychomys* molars also usually lack accessory stylids and lophids. The m1-2 reentrant valleys between the primary cusps of *Onychomys* are wider than those of *Copemys* and *Peromyscus* (Carleton and Eshelman, 1979; Mou, 2011), as are those of *A. rhodopetros*. The mean unworn m1 pch/ap ratios of extant *Onychomys* are 0.53-0.54 (Carleton and Eshelman, 1979), which is equal to that of the unworn m1 of *A. rhodopetros* (0.54). The m3 of *Onychomys* is significantly reduced relative to the m1-2 with a transversely narrowed talonid and distinctive "key-hole" shaped occlusal outline (Carleton and Eshelman, 1979). In the oldest recognized species of *Onychomys*, *O. gidleyi*, the mean m3 ap = 77% of mean m2 ap, whereas in extant *O. leucogaster* the mean m3 ap = 64% of mean m2 ap (Carleton and Eshelman, 1979). In *A. rhodopetros*, the m3 is less reduced, wherein the m3 ap = 82% of the m2 ap, and its talonid is relatively wider with an occlusal morphology and outline much more similar to that of *Copemys* than that of *Onychomys*.

The dental similarities of *A. rhodopetros* to those of *Onychomys* strongly suggest they are related, but its lower molars are less derived because the m1-2 primary cusps alternate slightly less (m1-2 posterior arms of the protoconids slightly less aligned with the entolophulids) and m3 is much less derived. Morphological, mitochondrial and nuclear sequences studies have placed *Onychomys* as the closest sister taxon to the peromyscines (e.g., Carleton, 1980; Reeder, 2003; Miller and Engstrom, 2008) and Jacobs and Lindsay (1984) regarded *Copemys* as most likely ancestral to *Onychomys*. When Jacobs (1977) first described *Paronychomys*, he regarded it as closely related to *Onychomys* and also derived from *Copemys* or a *Copemys*-like ancestor. However, more recent studies have shown that *Paronychomys* exhibits a suite of dental characters that appear to eliminate it as ancestral to *Onychomys* (Lindsay, 2008; Korth and De Blieux, 2010; Korth, 2011). Korth (1994) assigned *Paronychomys* along with *Copemys*, *Onychomys*, *Peromyscus*, *Reithrodontomys*, *Poamys* (= *Copemys* vide Lindsay, 2008) and *Tregomys* to the subfamily Sigmodontinae, tribe Peromyscini. Based on his new proposed phylogenetic relationships within Cricetidae, Lindsay (2008) placed *Paronychomys*, *Repomys* and *Galushamys* in a clade within the subfamily Cricetodontinae, tribe Galushamyini, separating them from a clade including *Copemys*, *Peromyscus*, *Onychomys*, *Reithrodontomys*, and *Pseudomyscus*, which he placed within the subfamily Cricetinae, tribe Democricetodontini. Lindsay (2008) assigned *Tregomys* to the subfamily Cricetinae, tribe Megacricetodontini, and regarded it as a probable middle Miocene immigrant from Eurasia that may well have given rise to the Sigmodontini. Korth (2011) described *Miotomodon* (= *Peromyscus* cf. *pliocenicus* of May, 1981 [not Wilson, 1937], misidentification) from the late Hemphillian Pinole Formation of California. He provided convincing evidence that *Miotomodon* was most likely derived from *Paronychomys* and that *Miotomodon* then gave rise to *Repomys* and possibly extant *Neotomodon*, which would suggest that *Miotomodon* belongs in Lindsay's (2008) tribe Galushamyini. Kelly (2013) described *Paronychomys jacobsi* from the medial Hemphillian of Nevada and, based on shared derived characters, questionably reassigned *Peromyscus antiquus*, first described by Kellogg (1910) from the early Hemphillian of Nevada, to *Paronychomys*. If future studies corroborate this assignment, then ?*Paronychomys antiquus* would be the oldest known species of the genus. Thus, *Onychomys* was most likely derived from *Copemys* or a *Copemys*-like ancestor. *Paronychomys* appears to have also been derived from *Copemys* or a *Copemys*-like ancestor, but as a basal member of a clade separate from that including *Onychomys*, which then gave rise to *Miotomodon* and possibly *Repomys*.

In summary, the unique suite of dental characters of *A. rhodopetros* distinguish it from any recognized cricetid genus. However, this suite includes a combination of dental characters that are either shared with or intermediate to those of *Onychomys* and *Copemys*, suggesting that *A. rhodopetros* may represent a transitional form ancestral to *Onychomys*.

BIOSTRATIGRAPHIC IMPLICATIONS

There is a long history of biostratigraphic studies within the DSF (Tedford, 1965; Tedford et al., 1987, 2004; Whistler, 1969; Whistler and Burbank, 1992, Whistler et al, 2009). Each of these studies proposed faunal subdivisions based primarily on fossil mammalian content. By biostratigraphic correlation, the fossil assemblages of the DSF were also used extensively in the characterization of the west coast mammalian provincial stages (Savage, 1955; Prothero and Tedford, 2000; Woodburne, 2006). The lower boundary of the Montediablan west coast provincial stage is defined by the first occurrence of the horse *Hipparion forcei* in the DSF (Savage, 1955; Woodburne, 2006). In his original definition, Savage (1955) defined the top of the Montediablan as at least the provincial boundary between the Clarendonian and Hemphillian, which was also supported by Woodburne (2006). We use this boundary in this study.

The current study focuses on the diverse cricetid rodents from a succession of superposed microfossil yielding localities in the upper part of the DSF in strata spanning the 9 Ma boundary between the Clarendonian and Hemphillian and extending upward to approximately 8 Ma (Figures 1, 17). The 9 Ma strata also form the boundary between the locally defined late Clarendonian (Cl3) Ricardo Fauna and the early Hemphillian (Hh1) Dove Spring Fauna. These faunas contain a diversity of both large and small vertebrate taxa (Whistler et al., 2009:fig. 4 and table 4 in part; also see Table 11 this study) most of which are not restricted to a single fauna. However, the faunas are characterized both by restricted and joint occurrences of taxa whose abundance varies stratigraphically. With one exception (the antilocaprid antelope, *Illingoceros*), all of the larger taxa reported from the Dove Spring Fauna also occur at least in the upper part of the underlying, older Ricardo Fauna. The apparent drop off of larger taxa in the lower part of the Dove Spring Fauna (Whistler et al., 2009:fig. 4) primarily represents a rapid coarsening of sediments and lack of fossils in the upper DSF, not a biostratigraphic event. Consequently, most of the larger vertebrate fossils of the Dove Spring Fauna came from the basal part of the strata yielding this fauna.

One of the localities containing an abundant sample of the new cricetids described herein, LACM 3620, is located in the undifferentiated Ricardo Group sediments south of the El Paso Fault. As discussed above, the sediments of the URG cannot be directly traced to any sediments in the type DSF area. In the absence of any other means of direct correlation (radiometrics, paleomagnetics), the biostratigraphic correlation of locality LACM 3620 in the URG (Figures 1 and 17) with its abundant samples *Lindsaymys takeuchii* and *Lindsaymys* sp. A. is based primarily on the joint occurrence of *L. takeuchii* in the two areas. The URG also contains an assemblage of other fossils from numerous sites (Table 12) that shares 20 taxa at the generic or species level with those from the Dove Spring Fauna. Although the fossils of the URG have not been studied in detail, these shared taxa lend further support of at least a biochronologic correlation of the URG with the upper part of the DSF.

Although the distribution and frequency of occurrence of cricetid taxa from each locality may be biased by the amount of matrix processed per locality or by possible differences in the taphonomic history of each locality (e.g., paleosol accumulations, carnivore scat accumulations, collapsed burrow assemblages, owl pellets, etc.), patterns can still be discerned (Table 13, Figure 17). Locality LACM 6380 occurs only 15 m above locality LACM 3666 in the DSF section and

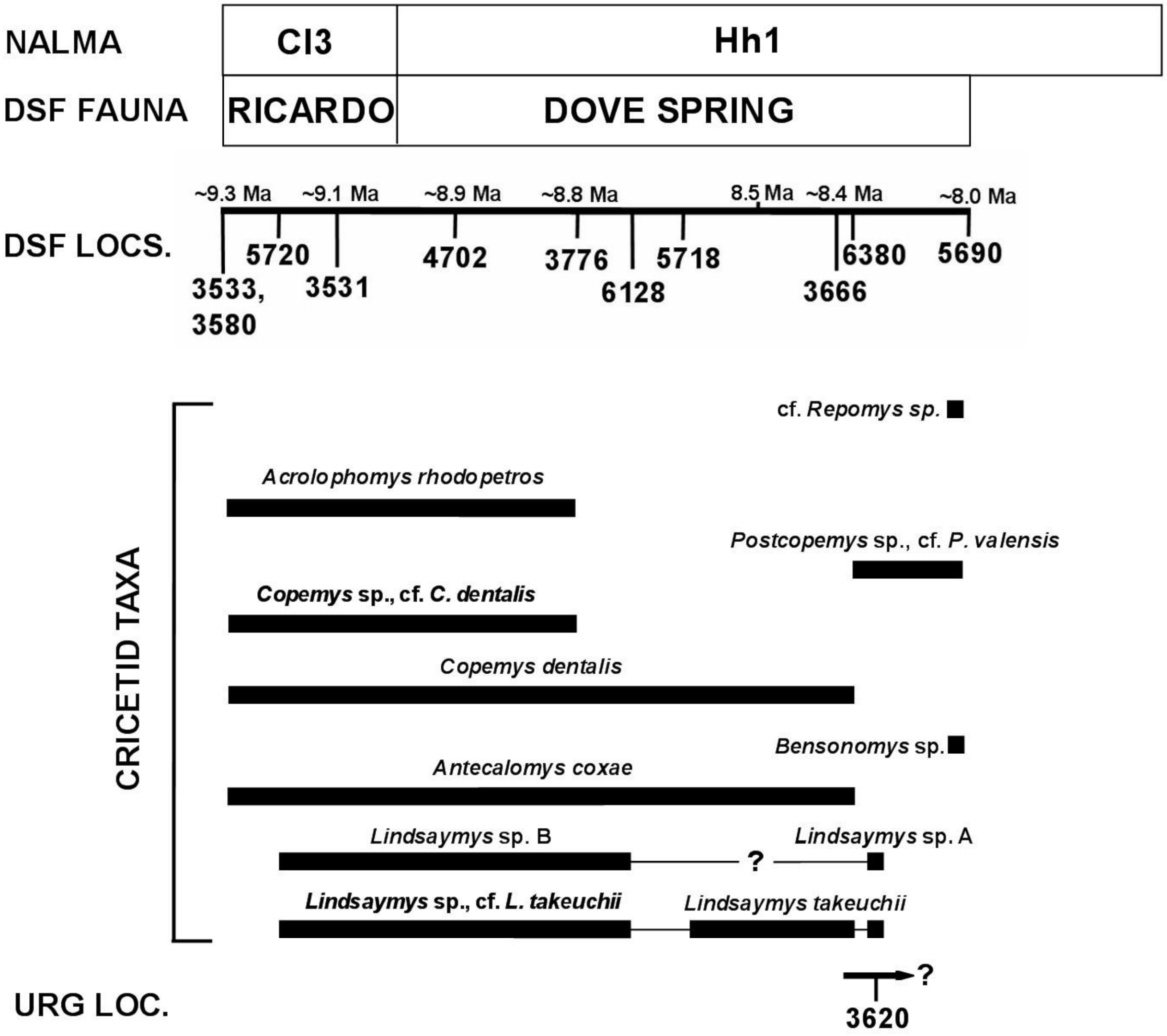

FIGURE 17. Teilzones of cricetid taxa from LACM localities in upper part of type Dove Spring Formation (DSF) from north of El Paso Fault and undifferentiated Ricardo Group (URG) from south of El Paso Fault. Note, Ricardo Fauna extends further down section in DSF (see also Whistler et al., 2009, 2013 for teilzones of other biostratigraphically pertinent DSF taxa). Stratigraphic position of locality LACM 3620 from URG uncertain relative to localities in type DSF (shared occurrence of *L. takeuchii* at localities LACM 3620 and 3666 suggests localities are similar in age, see discussion in text). Subbiozones Cl3 (late Clarendonian) and Hh1 (early Hemphillian) of North American Land Mammal Ages (NALMA) follow Tedford et al. (2004).

yielded a very small sample of cricetid teeth. Because locality LACM 6380 is only slightly younger than locality LACM 3666 and locality LACM 3666 yielded a large sample of cricetid teeth, the samples from these two localities were combined for the calculations presented in Table 13.

At about 9.3 Ma (localities LACM 3580/3533), *Copemys* is the dominant cricetid representing about 75% of the specimens followed by *Antecalomys coxae* (16.2%) and *Acrolophomys rhodopetros* (8.3%). *Copemys* continues to occur up through the DSF section, but its numbers decrease above locality LACM 3776 with only *C. dentalis* extending up to LACM 6380. *A. coxae* exhibits a general increase in its frequency of occurrence starting at about 9.2 Ma (locality LACM 5720) and reaches its highest frequency of occurrence at about 8.8 Ma (locality LACM 3776), but then shows a rapid decline thereafter and is absent from the DSF shortly after about 8.4 Ma. *A. rhodopetros* first occurs at about 9.3 Ma (locality LACM 3533) and extends up to about 8.8 Ma (locality LACM 3776), but is never common, representing about

6-8% of the cricetid specimens at the localities in which it is present. *Lindsaymys* sp. B first occurs at about 9.2 Ma (locality LACM 5720), where it represents only 9% of the cricetid specimens, and last occurs at about 8.7 Ma (locality LACM 6128), where it becomes the second most common cricetid taxon. *Lindsaymys* sp., cf. *L. takeuchii* first occurs also at about 9.2 Ma (locality LACM 5720), where it is a relatively common cricetid taxon, and extends up to about 8.7 Ma (locality LACM 6128). *Lindsaymys takeuchii*, the presumed anagenetic descendant of *L.* sp., cf. *L. takeuchii*, first occurs in the DSF at locality LACM 5718 (between ~8.7 to 8.6 Ma) and extends up through localities LACM 3666/6380 (~8.4 Ma), wherein it is the dominant cricetid taxon representing from 83-91% of the cricetid specimens. *L. takeuchii* also occurs in the URG at locality LACM 3620, wherein it is the dominant cricetid taxon representing about 90% of the cricetid specimens. *Lindsaymys* sp. A is the only other cricetid known from the URG at locality LACM 3620, where it represents less than 10% of the cricetid specimens. *Postcopemys* is a rare taxon that first occurs at locality LACM 6380 and extends up to locality LACM 5690, or from about 8.4-8.0 Ma. By about 8.0 Ma in the DSF at locality LACM 5690, two new cricetid taxa make their first appearances (*Bensonomys* sp. and cf. *Repomys* sp.), whereas, except for *Postcopemys*, all of the other DSF cricetid taxa are absent. *Bensonomys* is the most common cricetid from locality LACM 5690, representing over 76% of the cricetid specimens. As noted above, the stratigraphic position of locality LACM 3620 in the URG relative those in the DSF is difficult to determine. The co-occurrence and dominance of *L. takeuchii* at localities LACM 3666 and 3620 suggest these localities may be similar in age, whereas the absence of *L. takeuchii* and all of the other DSF cricetid taxa (except *Postcopemys*) along with the first appearances of two relatively derived cricetid taxa at locality LACM 5690 suggests that this locality is the youngest.

TABLE 11. Revised faunal lists for early Hemphillian Dove Spring Fauna from DSF (after Whistler et al., 2013; this paper).

- Chelonia
  - Testudinidae
    - *Clemeys* sp.
    - *Geochelone* sp.
    - ?*Gopherus* sp.
- Lacertilia
  - Iguanidae
    - *Sceloporus* sp.
    - *Leiocephalos* sp.
  - Xantusiidae
    - *Xantusia* sp.
  - Anguidae
    - *Elgaria* cf. *E. kingi*
  - Boidae
    - *Lichanura* sp.
  - Colubridae
    - *Paracoluber* sp.
    - *Paleoheterodon* sp.
    - *Proptychopis achoris*
- Aves
  - Acciptaridae
    - *Neophrontops ricardoensis*
- Lipotyphla
  - Soricidae
    - *Alluvisorex chasseae*
    - Soricidae, new genus and species
  - Talpidae
    - *Scapanus schultzi*
    - Scalopini, unidentified gen. and sp.
- Carnivora
  - Canidae
    - *Carpocyon webbi*
    - *Epicyon haydeni*
    - *Epicyon saevus*
    - *Metalopex macconnelli*
  - Procyonidae
    - *Bassariscus* sp., cf. *B. parvus*
  - Mustelidae
    - *Martes buwaldi*
    - *Martes* sp. B
  - Mephitidae
    - *Martinogale faulli*
  - Felidae
    - *Pseudaelurus* sp A.
  - Nimravidae
    - *Barbourofelis* sp.
- Rodentia
  - Sciuridae
    - *Spermophilus* sp.
    - *Ammospermophilus* sp.
  - Heteromyidae
    - *Cupidinimus tertius*
    - *Cupidinimus* sp., cf. *C. tertius*
    - *Perognathus furlongi*
  - Cricetidae
    - *Copemys dentalis*
    - *Copemys* sp., cf. *C. dentalis*
    - *Antecalomys coxae*
    - *Lindsaymys takeuchii*
    - *Lindsaymys* sp., cf. *L. takeuchii*
    - *Lindsaymys* sp. B
    - *Bensonomys* sp.
    - cf. *Repomys* sp.
    - *Acrolophomys rhodopetros*
- Lagomorpha
  - Leporidae
    - *Hypolagus tedfordi*
    - *Alilepus* sp., cf. *A. vagus*
  - Ochotonidae
    - *Hesperolagomys* sp.
- Proboscidea
  - Gomphotheriidae
    - *Gomphotherium* sp.
- Perissodactyla
  - Equidae
    - *Hipparion forcei*
  - Rhinocerotidae
    - *Aphelops megalodus*
- Artiodactyla
  - Camelidae
    - *Procamelus* sp.

  - *Megatylopus* sp.
  - *Aepycamelus* sp.
- Oreodontidae
  - *Merychyus major*
- Antilocapridae
  - cf. *Illingoceras* sp.
  - *Plioceros* sp.

In summary, from Member 2 through much of Member 5 of the DSF, below Tuff 15, *Copemys* is the only cricetid genus present (Whistler et al., 2009, 2013). Two species of *Copemy*s continue to occur above Tuff 15 with the last occurrence of the genus at locality LACM 6380 (~8.4 Ma). At about 9.3 Ma, two new cricetid taxa make their first appearances in the DSF, the sigmodontine *Antecalomys coxae* and democricetodontine *Acrolophomys rhodopetros*. Shortly thereafter at about 9.2 Ma, *Lindsaymys*, represented by two different species, makes its first appearance at locality LACM 5720, but thereafter only *Copemys*, *A. coxae* and *Lindsaymys* continue up to localities LACM 6380 or about 8.4 Ma. *Postcopemys*, which is more derived than *Copemys* (Lindsay and Czaplewski, 2011), makes its first appearance at about 8.4 Ma. Then at about 8.0 Ma at locality LACM 5690, two new genera make their first appearances in the DSF (*Bensonomys* and cf. *Repomys* sp.). Except for *Postcopemys*, all of the other DSF cricetids are absent from locality LACM 5690, suggesting they became locally extinct prior to 8.0 Ma. These data document a rapid increase in the diversity of cricetids (four genera, six species) in the DSF at about 9.3-9.2 Ma that continued up to about 8.8 Ma, spanning the latest Clarendonian through the earliest Hemphillian, followed by a decrease in diversity at about 8.7 Ma (three genera, three species) to slight increase in diversity at about 8.4 Ma (four genera, four species). By about 8.0 Ma in the DSF at locality LACM 5690, an apparent turnover occurred in the cricetid taxa with two new genera making their first appearances and only one taxon, *Postcopemys*, continuing from lower in the section. Several scenarios explaining this diversification and/or turnover are possible: 1) three separate immigration events occurred, the first one during in the latest Clarendonian at about 9.3-9.2 Ma followed by two others in the early Hemphillian (one at about 8.4 Ma and one at about 8.0 Ma); 2) the new genera in the DSF were derived by cladogenesis from endemic *Copemys* of the DSF; or 3) a combination of immigration and cladogenesis occurred. Of these scenarios, the immigration of new cricetid genera into the El Paso Basin is preferred because their sudden appearances in the stratigraphic record are grouped into three distinct events and no ancestral intermediate morphotypes have been indentified from lower in the DSF section. Nevertheless, whether due to immigration or cladogenesis, the record from the DSF demonstrates that a rapid diversification and radiation of cricetids occurred from the latest Clarendonian through the early Hemphillian.

TABLE 12. Faunal list of unnamed assemblage from URG (after Whistler et al. [2013]; this paper). Taxa with * found at locality LACM 3620. Taxa with + in common, or very similar to those found in Dove Spring Fauna.

- Chelonia
  - Testudinidae
    - *Clemeys* sp. * +
    - *Geochelone* sp. +
    - ?*Gopherus* sp. +
- Lacertilia
  - Iguanidae
    - *Sceloporus* sp. * +
    - *Leiocephalos* sp. * +
  - Xantusiidae
    - *Xantusia* sp. * +
  - Anguidae
    - *Elgaria* cf. *E. kingi* * +
  - Boidae
    - *Lichanura* sp. * +
- Aves
  - Galliformes , genus and sp. not determined *
- Lipotyphyla
  - Talpidae
    - *Scapanus* sp. +
- Carnivora
  - Canidae
    - *Borophagus littoralis*
    - *Vulpes* sp. +
  - Mustelidae
    - Lutrine, unidentified gen. and sp.
  - Felidae
    - *Nimravides* sp., cf. *N. thinobates*
- Rodentia
  - Sciuridae
    - *Spermophilus* sp. +
    - *Ammospermophilus* sp. +
  - Heteromyidae
    - *Perognathus* sp. +
  - Geomyidae, undetermined gen. and sp.
  - Cricetidae
    - *Lindsaymys takeuchii* * +
    - *Lindsaymys* sp. A *
- Lagomorpha
  - Leporidae
    - *Hypolagus* sp. +
- Proboscidea
  - Gomphotheriidae
    - *Gomphotherium* sp. * +
- Perissodactyla
  - Equidae
    - "*Pliohippus*" sp. *
  - Rhinocerotidae
    - ?*Aphelops* sp. +
- Artiodactyla
  - Oreodontidae
    - *Merychyus* sp. * +
  - Camelidae*
    - *Procamelus* sp. +
    - *Megatylopus* sp. +
  - Antilopcapridae
    - *Plioceros* sp. * +

TABLE 13. Percentage (%) that each taxon represents of the total number of cricetid specimens from LACM localities in DSF (in ascending stratigraphic order) and URG. Samples from localities LACM 3580 and 3533 combined because from same stratigraphic level, and LACM 3666 and 6380 combined because they are stratigraphically little separated (only 15 m).

	DSF									URG
Taxon - Percent of each taxon/ locality	3580 3533	5720	3531	4702	3776	6128	5718	6380 3666	5690	3620
A. coxae	16.2	36.4	40	24	58	33.3	4.5	5.0	-	-
L. takeuchii	-	-	-	-	-	-	91.0	82.5	-	90.4
L. sp., cf. *L. takeuchii*	-	27.2	-	16	6.4	22.2	-	-	-	-
L. sp. B	-	9	-	16	6.4	44.4	-	-	-	-
L. sp. A	-	-	-	-	-	-	-	-	-	9.6
Bensonomys sp.	-	-	-	-	-	-	-	-	76.9	-
C. dentalis	16.2	-	-	-	3.2	-	4.5	10	-	-
C. sp., cf. *C. dentalis*	58.3	27.2	60	36	19.3	-	-	-	-	-
Postcopemys sp., cf. *P. valensis*	-	-	-	-	-	-	-	2.5	15.2	-
cf. *Repomys* sp.	-	-	-	-	-	-	-	-	7.6	-
Acrolophomys rhodopetros	8.3	-	-	8	6.4	-	-	-	-	-

PHYLOGENETIC IMPLICATIONS

The development of molar accessory rootlets is one of the defining synapomorphies of Sigmodontini (Baskin, 1986; Korth, 1994, 1998; Lindsay, 2008). The oldest known North American sigmodontines are *Antecalomys phthanus* and *Abelmoschomys simpsoni*, both of which first occur in the late Clarendonian (Cl3) and have M1 accessory rootlets variably present. The next oldest known sigmodontine with M1 accessory rootlets is *Lindsaymys*, which first appears in the latest Clarendonian, followed by *Bensonomys* sp. in the latter part of the early Hemphillian (this study). Another early sigmodontine, *Prosigmodon* first appears in the late Hemphillian. *Baiomys* first appears in the late Hemphillian and is generally regarded my most paleontologists as belonging to Sigmodontini (e.g., Lindsay, 2008). However, numerous morphological and molecular studies have placed *Baiomys* in a *Baiomys-Scotinomys* clade within the tribe, Baiomyini, that is phylogenetically closer to *Neotoma* than the Sigmodontini (e.g., Carleton, 1980; Engel et al., 1998; D'Elia, 2003; Amman and Bradley, 2004; Bradley et al., 2004, 2007; Miller and Engstrom, 2008). *Neotoma* is generally regarded as more closely related to the galushamyines or democricetodontines, but Lindsay (2008) considered the fact that early representatives of *Neotoma* also have M1 accessory rootlets indicates that it should be placed near the Sigmodontini in its own tribe, Neotomini.

Baskin (1986) argued that *Abelmoschomys* was intermediate in dental morphology between *Copemys* and *Bensonomys*, and proposed that it was derived from the former. Korth (1994) noted that previous investigators have presented evidence supporting both a North American origin of Sigmodontini from *Copemys* or an origin from a later Miocene megacricetodontine immigrant from Eurasia (e.g., Jacobs and Lindsay, 1984; Slaughter and Ubelaker, 1984), but preferred the former scenario. Korth (1998) described *Antecalomys* and proposed that it may be an intermediate link between *Abelmoschomys* and *Bensonomys* and other later sigmodontines. Lindsay (2008) placed *Copemys* plus other democricetodontines as the closest sister clade to a clade including *Tregomys* (Megacricetodontini) plus the Sigmodontini. Lindsay (2008) regarded the appearance of *Tregomys* in the Barstovian as a probable immigration event from Eurasia and that *Tregomys* may well have given rise to the Sigmodontini. M1 accessory rootlets are not present in *Tregomys*. The origin of *Copemys* is still uncertain. Previous investigators have suggested that *Copemys* may have been derived from North American *Eumys* or *Leidymys* (Wood, 1936; Clark et al., 1964) or from a middle Miocene immigration event of Eurasian *Democricetodon* with some even suggesting that *Democricetodon* should only be subgenerically separated from *Copemys* (e.g., Fahlbusch, 1967; Lindsay, 1972, 2008; Freudenthal, 2006; Fejfar et al., 2011). Most recently in an ongoing study of North American Miocene cricetid rodents by Lindsay and Whistler (2013), they suggested that their new findings have increased "the likelihood that a suitable ancestor of *Copemys* might be found in North America."

Antecalomys is derived relative to other early sigmodontines by having the posterior arm of the protoconid aligned or nearly so with the entolophulid, whereas in *Abelmoschomys* and *Bensonomys* they are not aligned. *Lindsaymys* also exhibits a tendency towards alignment of these lophids. Although both *Antecalomys* and *Abelmoschomys* have the M1 anterocone weakly bifurcated (bilobed), the bifurcation in *Abelmoschomys* is slightly greater. The m1 anteroconid of *Antecalomys* is not bifurcated, whereas that of *Abelmoschomys* exhibits a tendency towards bifurcation. In *Bensonomys* and most other later sigmodontines, the M1/m1 anterocone/anteroconids are commonly well bifurcated. In *Lindsaymys*, the M1 anterocone is either not bifurcated or very weakly bifurcated and the m1 anteroconid is not bifurcated, more similar to the condition of *Antecalomys* than to that of *Abelmoschomys*. The M3/m3 of *Antecalomys*, *Lindsaymys* and *Baiomys* are more reduced than those of *Bensonomys* and most later sigmodontines (M3/m3 unknown for *Abelmoschomys*). In *Antecalomys*, M1-2/m1-2 accessory styles/stylids and lophs/lophids are lacking or their occurrence is significantly reduced, whereas in *Bensonomys* and many later sigmodontines they are commonly present. Both *Lindsaymys* and *Antecalomys coxae* are derived relative to *Abelmoschomys*, *Bensonomys*, *Baiomys* and *Antecalomys phthanus* by having increased molar crown height, especially so in *Lindsaymys*.

Although a phylogenetic analysis of the origin and radiation of Sigmodontini is beyond the scope of this paper, certain observations can be made regarding the DSF sigmodontines. *Lindsaymys* may be more closely related to *Antecalomys* than to *Abelmoschomys* and *Bensonomys* by having the following shared characters: 1) M1 anterocone, when bifurcated, only very weakly; 2) m1 anteroconid not bifurcated; 3) a progressive tendency towards alignment or near alignment of the posterior arm of the protoconid and the entolophulid; 3) reduction in accessory lophs/ lophids and styles/stylids; and 4) significant reduction of M3/m3. Although, the polarity of characters 1 and 2 are uncertain and may be sympleisomorphies if the Sigmodontini were derived from *Copemys* or *Tregomys* (Lindsay, 2008). *Lindsaymys* does not appear to have lead to any later known sigmodontine. *Bensonomys* sp. of the DSF differs most significantly from *Abelmoschomys* by having the M1/m1 anterocone/anteroconids more strongly bifurcated, but both taxa are pleisomorphic relative to *Antecalomys* and *Lindsaymys* by having complete non-alignment of the posterior arm of the protoconid and the entolophulid. *Bensonomys* sp. of the DSF appears slightly less derived than later species of the genus by having the shelf-like cingulid along the basal anterior aspect of the M1 anterocone much more weakly developed. Based on the above comparisons, the proposed relationships of the DSF sigmodontines within the phylogenetic scenario of Lindsay (2008) are presented in Figure 18.

CONCLUSIONS

We present an analysis of the abundant fossil cricetid rodents in a succession of eleven superposed microfossil sites from the upper part of the DSF and a single locality from the URG, a separate succession of sediments separated from the DSF by the El Paso Fault. Extensive geologic mapping and radiometric, paleomagnetic, tephrochronologic and biochronologic studies (Whistler et al., 2009; 2013) have established the DSF as one of the most completely documented Clarendonian and early Hemphillian successions in North America. The fossil sites examined in this study span the latest Clarendonian, (Cl3) to early Hemphillian, (Hh1), from approximately 9.3 Ma to 8 Ma (Figures 1, 17), an interval that is poorly sampled elsewhere in North America. Although there are no direct lithologic ties between the DSF and URG, they can be biochronologically correlated based on comparisons of their fossil vertebrate content including the joint occurrence of the most abundant new species recognized in this study.

Our reevaluation of the cricetid diversity has resulted in the recognition of 10 species (9 new) within 7 genera (2 new) in the upper DSF and two species (1 additional new) in a single genus in the URG, this including the largest sample of the most abundant new species from the DSF. In terms of both numbers of specimens and taxonomic diversity, Sigmodontini are the most abundant (6 species) with Democricetodontini a close second (4 species). There is a single species representing Galushamyini.

Most diverse (at the species level) and most abundant overall is the newly described moderate to large sized and higher crowned Sigmodontini genus, *Lindsaymys*. Based on size, cusp morphology and relative crown height, four species of *Lindsaymys* within two size groups are recognized, only one of which we have formally named, *L. takeuchii*. Both size groups exhibit a significant increase in crown height through time. These samples appear to represent a separate clade that is not ancestral to any later group. The other new small, mesodont species of Sigmodontini with its own distinct suite of dental characters is assigned to the new taxon *Antecalomys coxae*. *A. coxae* is a relatively long ranging species (ca 9.3 to 8.4 Ma), but does not demonstrate the size differences or increased crown height through time as seen in *Lindsaymys*. There is a small sample of specimens from the youngest locality sampled assigned to the Sigmodontini genus *Bensonomys*. This unnamed species is the oldest record of the genus at ca 8.0 Ma.

Democricetodontini is represented, in part, by two species of *Copemys*, both of which likely range to much lower in the DSF in samples not included in this study (Whistler et al., 2009; 2013). Although indistinguishable in occlusal morphology, these two species are separated by size. The smaller species, *C. dentalis*, is the longest ranging taxon in the upper DSF, last occurring at ca 8.4 Ma. The larger species, which we assign to *C.* sp., cf. *C. dentalis*, last occurs at ca 8.8 Ma. A few teeth from several localities low in the section studied are mesodont and characterized by

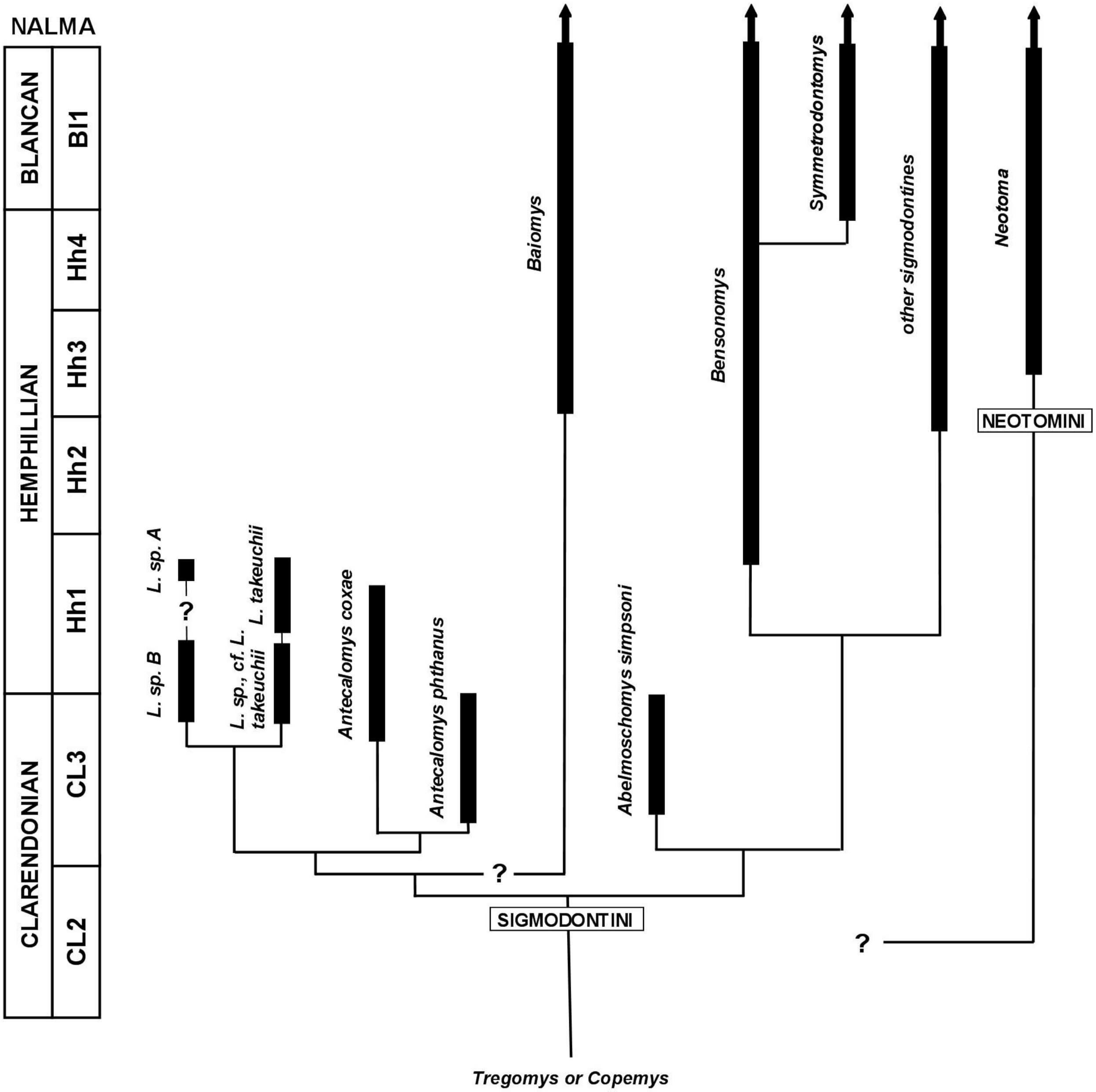

FIGURE 18. The phylogenetic scenario of Lindsay (2008) for tribe Sigmodontini with proposed relationships of DSF sigmodontines added (see text for discussion). Lindsay (2008) regarded Barstovian *Tregomys* as an Eurasian megacricetidontine immigrant and the most likely ancestor of Sigmodontini, whereas other investigators regarded endemic *Copemys* as the likely ancestor (e.g., Baskin, 1986; Korth, 1994). Thick, vertical black bars represent chronologic ranges. Arrows indicate chronologic ranges extend upward beyond early Blancan. Other sigmodontines include *Jacobsomys*, *Prosigmodon*, and *Sigmodon* from North America. North American Land Mammal Ages (NALMA) and subbiozones follow Tedford et al. (2004).

having sharply pointed m1 anteroconids and high, well separated primary cusps, similar to the morphology seen in *Onychomys*, have been assigned to the new taxon *Acrolophomys rhodopetros*. The suite of dental characters in *A. rhodopetros* suggest either an ancestral relationship to *Onychomys* or convergences related to a similar diet. Three small, brachydont m1s from the uppermost sites in the DSF with the posterior arm of the protoconid aligned with the entolophulid are assigned to *Postcopemys*. If this assignment is correct, this would be an early record for the genus.

Galushamyini are represented by a single partial tooth from the uppermost DSF locality, which probably represents a new genus that is morphologically most similar to *Repomys*. We assign this specimen to cf. *Repomys* sp. to reflect this putative relationship.

Contrary to previous analyses (Whistler and Burbank, 1992; Whistler et al., 2009; 2013), in this detailed taxonomic study we find no records of either *Prosigmodon* or *Paronychomys.* Specimens previously assigned to either *Prosigmodon* spp. or *Paronychomys* spp. are now included in the new taxa *Lindsaymys*, *Antecalomys coxae*, *Acrolophomys rhodopetros* and cf. *Repomys sp*.

An analysis of the distribution and frequency of occurrence of the cricetid taxa from each locality in the superposed succession in the upper DSF documents a rapid diversification and radiation of cricetids during the latest Clarendonian and earliest Hemphillian (Table 13). This radiation was apparently followed by a turnover during the latter part of the early Hemphillian with the successive appearance of three new genera and no carryover of the previous taxa after ca 8.4 Ma. These relationships are summarized in Figure 17.

The presence of several new taxa, particularly within Sigmodontini, provides new evidence to analyze the polarity of characters in the early evolution of this group. One such character is the development of M1 accessory rootlets, a defining synapomorphy of Sigmodontini. Both *Lindsaymys* spp. and *Antecalomys coxae*, which bear accessory rootlets, provide additional evidence supporting the importance of this character. The new records in the DSF also provide evidence regarding other characters used in defining Sigmodontini such as alignment or non-alignment of primary cusps, bifurcation of anterocone/anteroconid and reduction of M3/m3.

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LITERATURE CITED

Amman, B. R. and R. D. Bradley. 2004. Molecular evolution in *Baiomys* (Rodentia: Sigmodontinae): evidence for a genetic subdivision in *B. musculus*. Journal of Mammalogy 85:162-166.

Baker, C. L. 1912. Physiography and structure of the western border of the Mojave Desert. Carnegie Institution of Washington Publications 516:3-129.

Baskin, J. A. 1978. *Bensonomys*, *Calomys* and the origin of the phyllotine group of Neotropical cricetines (Rodentia: Cricetidae). Journal of Mammalogy, 59:125-135.

Baskin, J. A. 1979. Small mammals of the Hemphillian age White Cone Local Fauna, northeastern Arizona. Journal of Paleontology 53:695-708.

Baskin, J. A. 1980. The generic status of *Aelurodon* and *Epicyon* (Carnivora, Canidae). Journal of Paleontology 54:1349-1351.

Baskin, J. A. 1986. The late Miocene radiation of Neotropical sigmodontine rodents in North America. Contributions to Geology, University of Wyoming Special Paper 3:287-303.

Bonnichsen, B., W. P. Leeman, N. Honjo, W. C. McIntosh, and M. M. Godchaux. 2008. Miocene silicic volcanism in southwestern Idaho: geochronology, geochemistry, and evolution of the central Snake River Plain. Bulletin of Volcanology 70:315-342.

Bradley, R. D., C. W. Edwards, D. S. Carroll, and W. Kilpatrick. 2004. Phylogenetic relationships of neotomine-peromyscine rodents: based on DNA sequences from mitochondrial Cytochrome-b gene. Journal of Mammalogy 85:389-395.

Bradley, R. D., N. D. Durish, D. S. Rogers, and J. R. Miller. 2007. Toward a molecular phylogeny for *Peromyscus*: evidence from mitochondrial Cytochrome-b sequences. Journal of Mammalogy 88:1146-1159.

Burbank, D. W. and D. P. Whistler. 1987. Temporally constrained tectonic rotations derived from magnetostratigraphic data: implications for the initiation of the Garlock Fault, California. Geology 15:1172-1175.

Carleton, M. D. 1980. Phylogenetic relationships neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications, Museum of Zoology, University of Michigan 157:1-146.

Carleton, M. D. and R. E. Eshelman. 1979. A synopsis of fossil Grasshopper Mice, genus *Onychomys*, and their relationships to recent species. Papers on Paleontology No. 21, Museum of Paleontology, University of Michigan, Papers on Paleontology No. 21:1-69.

Carranza-Castañeda, O. and A. H. Walton. 1992. Cricetid rodents from the Rancho El Ocote Fauna, late Hemphillian (Pliocene), state of Guanajuato. Universidad Nacional Autónoma de México, Instituto de Geologia Revista 10:71-93.

Castor, S. B. 1965. Geology of the southwestern part of the Ricardo Formation, Kern County, California. Unpublished senior thesis, University of California, Riverside, Department of Geology.

Chen, J. H. and J. G. Moore. 1979. Late Jurassic Independence dike swarm. Geology 7:129-133.

Christiansen, R. L. and R. S. Yeats. 1992. Post-Laramide geology of the U.S. Cordilleran region, Pp. 350-357, in B. C. Burchfiel, P. W. Lipman, and M. L. C. Zoback (eds.), The Cordilleran Orogen, conterminous U.S., The Geology of North America, G-3. Geological Society of America, Boulder, Colorado.

Clark, J. B., M. R. Dawson, and A. E. Wood. 1964. Fossil mammals from the lower Pliocene of Fish Lake Valley, Nevada. Museum of Comparative Zoology Bulletin 131:27-63.

Cox, B. F. 1987. Stratigraphy, depositional environments, and paleotectonics of the Paleocene and Eocene Goler Formation, El Paso Mountains, California - geologic summary and road log, Pp. 1-29, in B. F. Cox (ed.), Basin analysis and paleontology of the Paleocene and Eocene Goler Formation, El Paso Mountains, California. Pacific Section, Society of Economic Paleontologist and Mineralogists Guidebook.

Cox, B. F. and M. R. Diggles. 1986. Geologic map of the El Paso Mountains wilderness study area, Kern County, California. U.S. Geological Survey Miscellaneous Field Studies Map Mf-1827.

Czaplewski, N. J. 1987. Sigmodont rodents (Mammlia: Muroidea; Sigmodontinae) from the Pliocene (early Blancan) of the Verde Formation, Arizona. Journal of Vertebrae Paleontology 7:183-199.

Dalquest, W. W. 1983. Mammals of the Coffee Ranch local fauna: Hemphillian of Texas. Pearce-Sellards Series, 38:1-39.

Davis, G. A. and B. C. Burchfiel. 1973. Garlock Fault: and intercontinental transform structure, southern California. Geological Society of America Bulletin 84:1407-1422.

D'Elia, G. 2003. Phylogenetics of Sigmodontinae Rodentia, Muroidea, Cricetidae, with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307-323.

Dibblee, T. W., Jr. 1952. Geology of the Saltdale quadrangle, California. California Division of Mines Bulletin 42:135-144.

Dibblee, T. W., Jr. 1967. Areal geology of the western Mojave Desert, California. U. S. Geological Survey Bulletin 1089C:141-253.

Engel, S. R., K. M. Hogan, J. F. Taylor, and S. K. Davis. 1998. Molecular systematics and paleobiogeography of the South American sigmodontine rodents. Molecular Biology and Evolution 15:35-49.

Estes, R. 1963. A new gerrhonotine lizard from the Pliocene of California. Copeia 1963:676-680.

Evernden, J. F., D. E. Savage, G. H. Curtis, and G. T. James. 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. American Journal of Science 262:154-198.

Fahlbusch, V. 1967. Die beziehungen swischen einigen Cricetiden (Mamm., Rodentia) des nordamerikanischen und europäischen Jungtertiärs. Paläontologie Zeitschrift 41:154-164.

Fejfar, O., W-D Heinrich, L. Kordos, and L. C. Maul. 2011. Microtoid cricetids and the early history of arvicolids (Mammalia, Rodentia). Palaeontologia Electronica 14:1-38.

Freudenthal, M. 2006. The status of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* (Cricetidae, Mammalia). a reply to Van der Meulen et al. (2004). Geobios 39:43-55.

Frick, C. 1937. Horned ruminants of North America. American Museum of Natural History Bulletin 69:1-669.

Furlong, E. L. 1927. The occurrence and phylogenetic status of *Merycodus* from the Mojave Desert Tertiary. University of California Publications, Department of Geological Sciences Bulletin 17:145-186.

Gazin, C. L. 1942. The late Cenozoic vertebrate faunas from the San Pedro Valley, Arizona. Proceedings of the U.S. National Museum 92:475-518.

Gidley, J. W. 1922. Preliminary report on fossil vertebrates of the San Pedro Valley, Arizona, with descriptions of new species of Rodentia and Lagomorpha. U.S. Geological Survey Professional Paper, 131-E:119-131.

Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Museum of Paleontology, University of Michigan, Papers on Paleontology No. 15:1-140.

Green, M. 1948. A new species of dog from the lower Pliocene of California. University of California Publications, Department of Geological Sciences Bulletin 28:81-90.

Hall, E. R. 1930. Rodents and lagomorphs from the later Tertiary of Fish Lake Valley, Nevada. University of California Publications in Geological Sciences 19:295-311.

Hibbard, C. W. 1937. Additional fauna of Edson Quarry of the middle Pliocene of Kansas. American Midland Naturalist 18:460-464.

Hibbard, C. W. 1938. An upper Pliocene fauna from Meade County, Kansas. Transactions of the Kansas Academy of Science, 40:239-265.

Hibbard, C. W. 1941. Mammals of the Rexroad Fauna from the upper Pliocene of southwestern Kansas. Transactions of the Kansas Academy of Science 44:265-313.

Hibbard, C. W. 1953. The Saw Rock Canyon fauna and its stratigraphic significance. Papers Michigan Academy of Science, Arts, and Letters, 38:387-411.

Hibbard, C. W. 1956. Vertebrate fossils from the Meade Formation of south-western Kansas. Papers Michigan Academy of Science, Arts, and Letters, 41:145-203.

Hibbard, C. W. 1967. New rodents from the late Cenozoic of Kansas. Papers of the Michigan Academy of Science, Arts and Letters 52:115-132.

Hoffmeister, D. F. 1945. Cricetine rodents of the middle Pliocene of the Mulholland Fauna, California. Journal of Mammalogy 26:186-191.

Hooper, E. T. 1957. Dental patterns in mice of the genus *Peromyscus*. Miscellaneous Publications, Museum of Zoology 99:1-59.

Jacobs, L. L. 1977. Rodents of the Hemphillian age Redington Local Fauna, San Pedro Valley, Arizona. Journal of Paleontology 51:505-519.

Jacobs, L. L. and E. H. Lindsay. 1984. Holarctic radiation of Neogene muroid rodents and the origin of South American cricetids. Journal of Vertebrate Paleontology 4:265-272.

James, G. T. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley Badlands, California. University of California Publications in Geological Sciences 45:1-154.

Kellogg, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. University of California Publications, Bulletin of the Department of Geology 5:411-437.

Kelly, T. S. 2007. A new species of *Bensonomys* (Rodentia, Cricetidae) from the late early Hemphillian (late Miocene), Coal Valley Formation, Smith Valley, Nevada. Paludicola 6:125-138.

Kelly, T. S. 2013. New Hemphillian (late Miocene) rodents from the Coal Valley Formation, Smith Valley, Nevada. Paludicola 9:70-96.

Korth, W. W. 1994. The Tertiary record of rodents in North America. Topics in Geobiology, Vol. 12. Plenum Press, New York.

Korth, W. W. 1998. Rodents and lagomorphs (Mammalia) from the late Clarendonian (Miocene) Ash Hollow Formation, Brown County, Nebraska. Annals of Carnegie Museum 67:299-348.

Korth, W. W. 2011. New species of cricetid rodents (Mammalia) from the late Miocene (Hemphillian) previously referred to *Peromyscus pliocenicus*. Annals of Carnegie Museum 79:137-147.

Korth, W. W. and D. D. De Blieux. 2010. Rodents and lagomorphs (Mammalia) from the Hemphillian (late Miocene) of Utah. Journal of Vertebrate Paleontology 30:226-235.

Korth, W. W. and R. E. Reynolds. 1994. A hypsodont gopher (Rodentia, Geomyidae) from the Clarendonian (Miocene) of California. San Bernardino County Museum Association Special Publication 94:91-95.

Lander, E. B. 2005. *Merychyus medius* Leidy and *M. major* Leidy (Mammalia, Artiodactyla, Oreodontidae, Techoleptinae) from strata of late early Clarendonian to earliest Hemphillian age, Dove Spring Formation, Red Rock Canyon, western Mojave Desert, Kern County, California. Western Association of Vertebrate Paleontologists 2005 Meeting Abstracts. Natural History Museum of Los Angeles County, Los Angeles, California, pp. 5-6.

Lindsay, E. H. 1972. Small mammal fossils from the Barstow Formation, California. University of California Publications in Geological Sciences 93:1-104.

Lindsay, E. H. 2008. Cricetidae, Pp. 456-479, in C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), Evolution of Tertiary Mammals of North America. Cambridge University Press, New York.

Lindsay, E. H. and N. J. Czaplewski. 2011. New rodents (Mammalia, Rodentia, Cricetidae) from the Verde Fauna of Arizona and the Maxum Fauna of California, USA, early Blancan Land Mammal age. Palaeontologia Electronica 14.3.29A:1-16.

Lindsay, E. H. and L. L. Jacobs. 1985. Pliocene small mammal fossils from Chihuahua, Mexico. Universidad Nacional Autonoma de Mexico, Paleontologia Mexicana, 51:1-42.

Lindsay, E. H. and D. P. Whistler. 2013. History of the Barstow Formation cricetid record, Pp. 71-77, in R. E. Reynolds (ed.), Raising questions in the central Mojave Desert. 2013 Desert Symposium, California State University Desert Studies Center.

Loomis, D. P. and D. W. Burbank. 1988. The stratigraphic evolution of the El Paso Basin, southern California: implications for the Miocene development of the Garlock Fault and uplift of the Sierra Nevada. Geological Society of America Bulletin 100:12-28.

Loomis, D. P., B. F. Cox and D. P. Whistler. 1983. Basin analysis of the Ricardo Formation and implications for Miocene history of the Garlock Fault. Geological Society of America, Cordilleran Section, Abstracts with Programs 15:438.

MacFadden, B. J. 1984. Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. American Museum of Natural History Bulletin 179:1-195.

Martin, J. E. 2008. Hemphillian rodents from northern Oregon and their biostratigraphic implications. Paludicola 6:155-190.

Martin, R. A., H. T. Goodwin, and J. O. Farlow. 2002a. Late Neogene (late Hemphillian) rodents from the Pipe Creek Sinkhole, Grant County, Indiana. Journal of Vertebrate Paleontology, 22:137-151.

Martin, R. A., R. T. Hurt, J. G. Honey, and P. Pleáez-Campomanes. 2003. Late Pliocene and early Pleistocene rodents from the northern Borchers Badlands (Meade County , Kansas), with comments on the Blancn-Irvingtonian boundary in the Meade Basin. Journal of Paleontology 77:985-1001.

Martin, R. A., J. G. Honey, P. Peláez-Campomanes, H. T. Goodwin, J. A. Baskin, and R. J. Zakrzewski. 2002b. Blancan lagomorphs and rodents of the Deer Park assemblages, Meade County, Kansas. Journal of Paleontology, 76:1072-1090.

May, S. R. 1981. *Repomys* (Mammalia: Rodentia Gen. Nov.) from the late Neogene of California and Nevada. Journal of Vertebrate Paleontology 2:219-230.

May, S. R., M. O. Woodburne, E. H. Lindsay, L. B. Albright, A. Sarna-Wojcicki, E. Wan, and D. B. Wahl. 2011. Geology and mammalian paleontology of the Horned Toad Hills, Mojave Desert, California, USA. Palaeontologia Electronica 14.3.28A:1-63.

Merriam, J. C. 1919. Tertiary mammalian faunas of the Mojave Desert. University of California Publications, Department of Geological Sciences Bulletin 11:437-585.

Miller, L. H. 1930. A fossil goose from the Ricardo Pliocene. The Condor 32:208-209.

Miller, J. R. and M. D. Engstrom. 2008. The relationships of major lineages within peromyscine rodents: a molecular Phylogeny hypothesis and systematic reappraisal. Journal of Mammalogy 89:1279-1295.

Mou, Y. 2011. Cricetid rodents from the Pliocene Panaca Formation, southeastern Nevada, USA. Palaeontologia Electronica 14.3.31A:1-53.

Osborn, H. F. 1933. *Serbelodon burnhami*, a new shovel-tusker from California. American Museum Novitates 639:1-5.

Perkins, M. E. and W. P. Nash. 2002. Explosive silicic volcanism of the Yellowstone hotspot: the ash fall tuff record. Geological Society of America Bulletin 114:367-381.

Perkins, M. E., F. H. Brown, W. P. Nash, W. McIntosh, and S. K. Williams. 1998. Sequence, age, and source of silicic fallout tuffs in middle to late Miocene basins of the northern Basin and Range Province. Geological Society of America Bulletin 110:344-360.

Prothero, D. R. 2005. The evolution of north american rhinoceroses. Cambridge University Press, Cambridge, United Kingdom, pp. 1-228.

Prothero, D. R. and R. H. Tedford. 2000. Magnetic stratigraphy of the type Montediablan Stage (late Miocene), Black Hawk Ranch, Contra Costa County, California: Implications for regional correlations. PaleoBios 20:1-10.

Reeder, S. A. 2003. Molecular systematics of neotomine-peromyscine rodents based on nuclear DNA sequences. Unpublished M.S. Thesis, Texas Tech University, 88 p.

Rich, P. V. 1980. New world vultures with Old World affinities, a review of fossil and recent Gypaetinae of both the old and new world, Pp. 1-115, in M. K. Hecht and F. S. Szalzy (eds.), Contributions to Vertebrate Evolution, Volume 5. S. Karger AG Basel, Switzerland.

Richey, K. A. 1948. Lower Pliocene horses from Black Hawk Ranch, Mount Diablo, California. University of California Publications, Department of Geological Sciences Bulletin 28:1-44.

Samsel, H. S. 1962. Geology of the southeast quarter of the Cross Mountain quadrangle, Kern County, California. California Division of Mines and Geology Map sheet 2.

Satoh, K. and F. Iwaku. 2006. Jaw muscle functional anatomy in Northern Grasshopper Mouse, *Onychomys leucogaster*, a carnivorous murid. Journal of Morphology 287:987-999.

Savage, D. E. 1955. Nonmarine lower Pliocene sediments in California, a geochronologic-stratigraphic classification. University of California, Publications in Geological Sciences 31:1-26.

Schultz, C. C., M. R. Schultz, and L. D. Martin. 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. University of Nebraska State Museum Bulletin 9:1-31.

Shotwell, J. A. 1967. *Peromyscus* of the late Tertiary in Oregon. Bulletin of the Museum of Natural History, University of Oregon 5:1-35.

Slaughter, B. H. and J. E. Ubelaker. 1984. Relationship of South American cricetines to rodents of North America and the Old World. Journal of Vertebrate Paleontology 4:255-264.

Smith, G. I. 1962. Large lateral displacement on Garlock Fault California, as measured from offset dike swarm. American Association of Petroleum Geologists Bulletin 46:85-104.

Stock, C. 1928. Canid and proboscidean remains from the Ricardo deposits, Mojave Desert, California. Carnegie Institution of Washington, Contributions in Paleontology 393:39-47.

Stock, C. and E. L. Furlong. 1926. New canid and rhinocerotid remains from the Ricardo Pliocene of the Mohave Desert, California. University of California Publications, Department of Geological Sciences Bulletin 16:43-60.

Tedford, R. H. 1961. Clarendonian Insectivora from the Ricardo Formation, Kern County, California. Southern California Academy of Sciences Bulletin 60:57-76.

Tedford, R. H. 1965. Clarendonian faunal succession, Ricardo Formation, Kern County, California (abs.). Geological Society of America Special Paper 87:174.

Tedford, R. H., X. Wang, and B. E. Taylor. 2009. Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 325:1-218.

Tedford, R. H., M. F. Skinner, R. W. Fields, J. M. Rensberger, T. Galusha, B. E. Taylor, J. R. Macdonald, S. D. Webb, and D. P. Whistler. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs) in North America, Pp. 153-210, in M. O. Woodburne (ed.), Cenozoic Mammals of North America. University of California Press, Berkeley, California.

Tedford, T. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr., J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs), Pp. 169-231, in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic mammals of North America. Columbia University Press, New York.

Tomida, Y. 1987. Monograph 3: small mammals fossils and correlation of Continental deposits, Safford and Duncan basins, Arizona, USA. Tokyo: National Science Museum, 141 pp.

Tseng, Z. J., G. T. Takeuchi, and X. Wang. 2010. Discovery of the upper dentition of *Barbourofelis whitfordi* (Nimravidae, Carnivora) and an evaluation of the genus in California. Journal of Vertebrate Paleontology 30:244-254.

Wang, X., R. H. Tedford, and B. Taylor. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 243:1-391.

Wang, X., D. P. Whistler, and G. T. Takeuchi. 2005. A new basal skunk *Martinogale* (Carnivora, Mephitinae) from late Miocene Dove Spring Formation, California, and origin of new world mephitines. Journal of Vertebrate Paleontology 25:936-949.

Whistler, D. P. 1969. Stratigraphy and small fossil vertebrates of the Ricardo Formation, Kern County, California, Ph.D. dissertation. University of California, Berkeley, California, 269 pp.

Whistler, D. P. and D. W. Burbank. 1992. Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California, and the characterization of the Clarendonian Land Mammal Age (late Miocene) in California. Geological Society of America Bulletin 104:644-658.

Whistler, D. P., and J. W. Wright. 1989. A late Miocene rear-fanged colubrid snake from California with comments on the phylogeny of North American Snakes. Herpetologica 45(5):350-367.

Whistler, D. P., G. T. Takeuchi, L. T. Grooves, and X. Wang. 2013. Western Mojave Desert geology and vertebrate Paleontology with special emphasis on the Dove Spring Formation. Society of Vertebrate Paleontology, Field Trip Guidebook, 73rd Annual Meeting, 76 pp.

Whistler, D. P., R. H. Tedford, G. T. Takeuchi, X. Wang, Z. J. Tseng, and M. E. Perkins. 2009. Revised Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California. In L. B. Albright, III (ed.), Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin 65:331-362.

Williams, S. H., E. Peiffer, and S. Ford. 2009. Gape and bite force in the rodents *Onychomys leucogaster* and *Peromyscus maniculatus*: does jaw-muscle anatomy predict performance. Journal of Morphology 270:1338-1347.

Wilson, R.W. 1937. New middle Pliocene rodent and lagomorph faunas from Oregon and California. Carnegie Institution of Washington Publication 487:1-19.

Wood, A. E. 1936. The cricetid rodents described by Leidy and Cope from the Tertiary of North America. American Museum Novitates 822:107.

Wood, A. E. and R. W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Journal of Paleontology 10:388-391.

Wood, H.. E. II, R. W. Chaney, J. Clark, E. D. Colbert, G. L. Jepsen, J. B. Reeside, and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of American Bulletin 52:1-48.

Woodburne, M. O. 2006. Mammal ages. Stratigraphy 3:229-261.

Woodburne, M. O. 2007. Phyletic diversification of the *Cormohipparion occidentale* complex (Mammalia; Perissodactyla, Equidae), late Miocene, North America, and the origin of the old world *Hippotherium* datum. Bulletin of the American Museum of Natural History 306:1-138.

Zakrzewski, R. J. 1991. New species of Blancan woodrat (Cricetidae) from north-central Kansas. Journal of Mammalogy 72:104-109.