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On the ancestry of woodrats

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We evaluated the fossil record of extinct and extant woodrats, and generated a comprehensive phylogenetic hypothesis of woodrat origins and relationships based on these data. The galushamyinin cricetines are redefined and reclassified as a subtribe of the Neotomini, including *Repomys, Miotomodon, Galushamys*, *Nelsonia,* and a new extinct genus with two new species. The geographic distribution of *Nelsonia*, restricted to montane coniferous forests of western Mexico, suggests that this subtribe was mostly confined to western coniferous ecosystems or similar ecosystems at lower elevation during glacial advances. A second subtribe of the Neotomini includes a new archaic genus and species, *Neotoma*, *Hodomys*, and *Xenomys*. *Lindsaymys*, a possible neotominin from the late Clarendonian (late Miocene) of California, demonstrates an occlusal morphology consistent with ancestry for the Neotomini, but the presence of a fourth root on M1 is problematic and may preclude the known populations from filling that role. Molars identified as *Neotoma* sp. from the Hemphillian (latest Miocene or early Pliocene) Rancho el Ocote assemblage of Guanajuato, Mexico, may represent the earliest *Xenomys*. Extant *Neotoma* species with a bilobed m3 appear to have originated subsequent to about 2.0 Ma, whereas *Hodomys alleni* and *Xenomys nelsoni* likely originated earlier from one or more extinct ancestors with an S-shaped m3.

Key words: Cenozoic, mammal, neotomine, rodent, woodrat

Woodrats currently range from the Yukon and New England through Nicaragua. Based on detailed morphological, biochemical, and genetic characters, *Neotoma* and related genera *Xenomys* and *Hodomys* are currently regarded as the tribe Neotomini within the neotomine cricetids (Bradley et al. 2004). The neotomines also include such diverse genera as *Baiomys*, *Ochrotomys*, *Peromyscus, Reithrodontomys*, and *Onychomys*, arranged in various tribes (Miller and Engstrom 2008). Hooper and Musser (1964) were agnostic on the relationships of *Nelsonia*, but Carleton's (1980) analysis linked *Nelsonia* with the woodrats. In the context of modern genetic studies, the origin of neotomines was estimated by Steppan et al. (2004) to have occurred approximately 9.8–11.0 Ma.

Woodrats are among a series of North American late Cenozoic small rodents characterized by the development of hypsodonty, additionally including the hypsodont arvicoline and sigmodontine cricetids, and the extinct galushamyinin cricetids. In his review of the Tertiary rodents of North America, Korth (1994) classified *Repomys* within the Neotomini, but Lindsay (2008) assigned *Repomys* to his new cricetodontine tribe Galushamyini. The fossil record of North American arvicolines and hypsodont sigmodontines is reasonably well characterized (Peláez-Campomanes and Martin 2005; Martin 2008), but ancestry of the Neotomini is uncertain. This study will concentrate on developing a theory of neotominin origins based on dental characters in extant Neotomini and late Cenozoic fossil taxa. A potential relationship of extant woodrats with Lindsay's (2008) Galushamyini is explored, and a phylogenetic hypothesis linking both clades is proposed.

Fossil woodrats are notoriously rare in North American late Neogene deposits. The oldest record is *Neotoma minutus* from Coffee Ranch of Texas, underlying a tuff dated at 6.6 Ma (Dalquest 1983). Zakrzewski (1993) and Lindsay (2008) voiced concerns about the two specimens allocated to *N. minutus*, and as discussed below, the holotype specimen is indeed not from a woodrat. *Neotoma sawrockensis* (Hibbard 1967) was reported by Voorhies (1990) from the early Blancan (late Miocene or early Pliocene) Mailbox assemblage of north-central Nebraska, but this material was examined by Zakrzewski and is not a neotominin. *Neotoma sawrockensis* was also tentatively identified from the late Hemphillian Rancho el Ocote assemblage of Guanajuato, Mexico (Carranza-Castañeda and Walton 1992), and another neotominin was listed by Carranza-Castañeda and Walton (1992) as *Neotoma* sp. *Neotoma* and

Repomys of undetermined species were also reported from the late Hemphillian (?late Miocene) Gray Fossil Site in Tennessee (Samuels et al. 2018). *Neotoma sawrockensis* from the Saw Rock Canyon assemblage of the Meade Basin in southwestern Kansas (Hibbard 1967; Martin and Peláez-Campomanes 2014) represents the earliest woodrat recovered in a long stratigraphic context at about 4.7 Ma (Table 1).

Additional extinct *Neotoma* species were described from Pliocene and Pleistocene localities (*N. ozarkensis* Brown, 1908; *N. fossilis* Gidley, 1922; *N. spelaea* Gidley and Gazin, 1933; *N. quadriplicata* Hibbard, 1941; *N. magnodonta* Alvarez, 1966; *N. taylori* Hibbard, 1967; *N. findleyi* Harris, 1984; *N. pygmaea* Harris, 1984; *N. amplidonta* Zakrzewski, 1985; *N. vaughani* Czaplewski, 1990; *N. leucopetrica* Zakrzewski, 1991) and will be discussed only to the extent that they reveal information contributing to our understanding of neotominin origins and dental evolution.

The earliest potential woodrat, *Pliotomodon primitivus* Hoffmeister, 1945, is from the Mulholland assemblage of California, currently considered to be Hemphillian. With nothing similar in the known fossil record for comparison, Hoffmeister reasonably concluded that the hypsodont and planed dentition of *P. primitivus* showed some similarities to the extant woodrats and the more brachydont extant *Neotomodon alstoni* Merriam, 1898. Hibbard (1967) concluded that *Pliotomodon* branched off from an ancestral stock that also gave rise to *Neotoma*. Hooper (1972) suggested that *Pliotomodon* might be near the ancestry of the singing mice, *Scotinomys*. Jacobs (1977) described another hypsodont cricetid, *Galushamys redingtonensis* Jacobs, 1977, from the Hemphillian Old Cabin Quarry of Arizona. Jacobs (1977) decided that *Galushamys* was too specialized to be closely related to either the extant *Neotomodon* or Hoffmeister's (1945) *Pliotomodon*. May (1981) advanced our understanding of early hypsodont cricetids with his description of *Repomys* species from localities in California and Nevada. May (1981) concluded that *Repomys* originated from a North American species such as *Peromyscus* cf. *pliocaenicus* that Shotwell (1967) had earlier described from Juniper Creek in Oregon. May (1981) also agreed with Jacobs (1977) that the presence of enamel atolls on M1 and M2 of *Pliotomodon* and *Galushamys* eliminated close relationship of those genera with either *Repomys* or extant woodrats. Jacobs (1977) and May (1981) surmised that *Galushamys* evolved from an unknown North American Clarendonian ancestor, whereas *Pliotomodon* evolved from an Asian immigrant such as *Byzantinia*. May (1981) also suggested that *Repomys* was ancestral to the living *Nelsonia neotomodon* Merriam, 1897. Modern genetic research links *Scotinomys* with *Baiomys* in the neotomine tribe Baiomyini (Miller and Engstrom 2008). Although no assessment of *Pliotomodon* has been published, we examined photos of the holotype of *P. primitivus* sent by P. Holroyd (University of California, Berkeley) and tentatively conclude that *P. primitivus* is unrelated to either the woodrats or *Scotinomys*. *Pliotomodon* and *Scotinomys* molars will be considered further in this study only to illustrate evolutionary processes resulting in certain observed occlusal patterns and to justify suggested taxonomic conclusions.

The situation remained static until considerably later, when two cricetid species were described from Hemphillian sediments in the Sevier River Formation (Fm) of Utah (Korth and De Blieux 2010). The first taxon, *Paronychomys lemredfieldi* Jacobs, 1977, was originally described from the Redington rodent assemblage of Arizona, also the source of *Galushamys*. The second taxon was the new genus and species *Basirepomys robertsi* Korth and De Blieux, 2010. Korth and De Blieux (2010) used *Peromyscus pliocaenicus* Wilson, 1937, as the type species of *Basirepomys*. In a subsequent paper, Korth (2011) clarified his position regarding Wilson's (1937) *P. pliocaenicus* and the specimens Shotwell (1967) had referred to as *Peromyscus* cf. *pliocaenicus*, in the process naming three additional species assigned to two genera. The first species was a brachydont cricetid allocated to *Basirepomys*, *B. romensis* Korth, 2011, from the Hemphillian Rome assemblage of Oregon. Thus, *Basirepomys* included three species, *B. pliocaenicus* (= *Peromyscus pliocaenicus* Wilson, 1937), *B. robertsi* Korth, 2011, and *B. romensis* Korth, 2011. In part because of the bifid anterocone on M1 and anteroconid on m1, none of the species of *Basirepomys* appear to be closely related to *Repomys*. Korth (2011) then assigned the specimens referred to as *Peromyscus* cf. *pliocaenicus* from Juniper Creek, Oregon by Shotwell (1967) to the new species *Paronychomys shotwelli* Korth, 2011. Finally, Korth (2011) assigned specimens from the Pinole Fm of California listed by May (1981) as *Peromyscus* cf. *pliocaenicus* to the new genus and species *Miotomodon mayi* Korth, 2011. May's (1981) conclusion regarding a possible

Table 1.—Temporal distribution of some Miocene through early Pleistocene neotominins. Fm = formation.

Species	Location	Age	Reference
Neotoma taylori	Borchers, KS	2.11 Ma (ash just beneath quarry)	Martin and Peláez Campomanes (2014)
Repomys arizonensis	111 Ranch, AZ	~2.48 Ma (Gauss/Matuyama boundary just above quarry)	Tomida (1987)
Neotoma fossilis	San Timoteo, CA	~2.58–~1.70 (pmag)	Albright (1999)
Neotoma sawrockensis	Saw Rock Canyon, KS	~4.70 (biostratigraphy)	Martin and Peláez-Campomanes (2014)
Repomys panacaensis	Panaca Fm, NV	4.96 Ma (pumice just beneath quarry)	Mou (2011)
Protorepomys mckayensis	McKay Reservoir, OR	~5.5–5.0 Ma (biostratigraphy)	Martin (2010)
Miotomodon mayi	Pinole, CA	5.5 Ma (ash just above quarry)	Tedford et al. (2004)
Repomys gustelyi	Horned Toad Fm, CA	~ 6.5–5.5 Ma (biostratigraphy)	Tedford et al. (2004)
Galushamys redingtonensis	Quiburis Fm, AZ	6.25–5.21 Ma (ashes in Quiburis Fm)	Jacobs (1977)
Neotoma sp. (unconfirmed)	Coffee Ranch, TX	6.6 Ma (ash above quarry)	Dalquest (1983)
Tsaphanomys shotwelli	Juniper Creek, OR	~ 7.0 Ma (biostratigraphy)	Janis et al. (2008)
Protorepomys bartlettensis	Bartlett Mountain, OR	~7.2 Ma (beneath ash dated at 7.1 Ma)	Tedford et al. (2004)
Lindsaymys takeuchii	Dove Springs Fm, CA	9.2–8.4 Ma (quarries above and beneath 8.5 Ma ash)	Kelly and Whistler (2014)

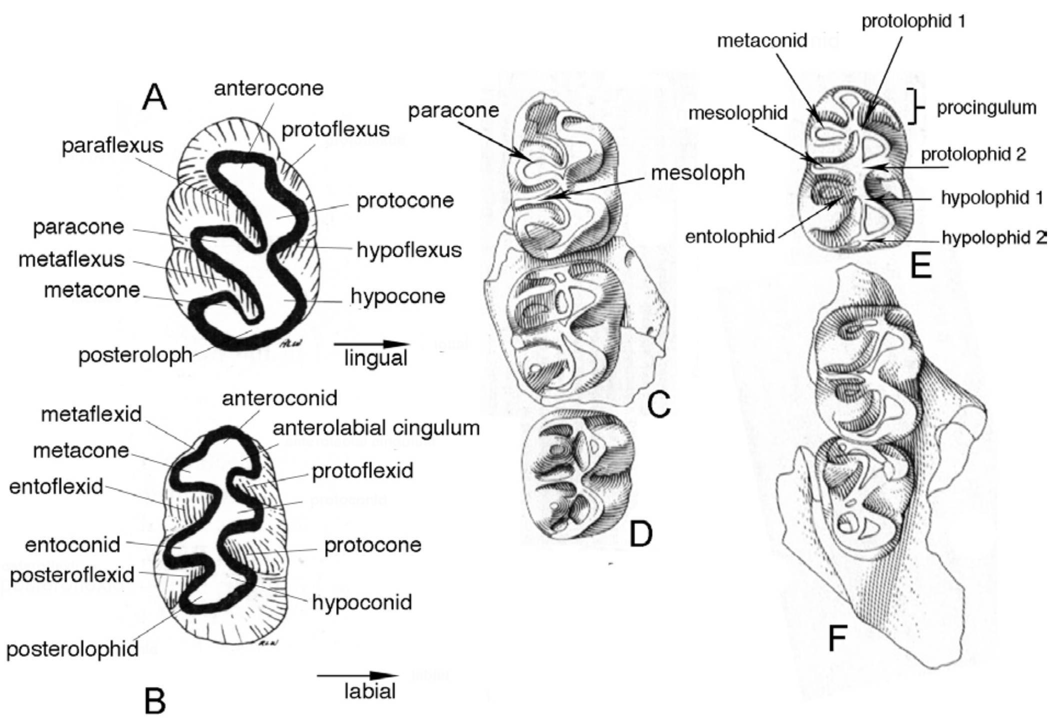

Fig. 1.—Neotominan dental terminology and outgroup for phylogenetic analysis. *Neotoma taylori* Hibbard (from Hibbard 1967); A) UMMP 53814, right M1; B) UMMP 53844, right m1. Molars of outgroup *Copemys russelli* James (from Lindsay 1972); C) UCMP 74551, left maxillary fragment with M1-2 (reversed); D) UCMP 74544, left M2 (reversed); E) UCMP 74574, right m1; F) UCMP 74546, right dentary fragment with m2–3. Protolophid 1 and 2, hypolophid 1 and 2 = anterior and posterior arms, respectively, of the protoconid and hypoconid of other authors. Note wide confluency of the metaconid, anteroconid, and anterolabial cingulum on m1 in *N. taylori* after light wear. Illustrations not to scale.

ancestry of *Peromyscus pliocaenicus* for *Repomys* was based on comparisons of *Repomys* with the Juniper Creek *P*. cf. *pliocaenicus*, which May (1981) illustrated in his fig. 4. The final contribution to this developing scenario is a recent study by Kelly and Whistler (2014) describing cricetids from the latest Clarendonian–early Hemphillian Dove Spring Fm of the Mojave Desert, California, in which they named the cricetid *Lindsaymys takeuchii* Kelly and Whistler, 2014, and reported possibly the earliest record of *Repomys*.

This study is initiated by defining dental characters of extant Neotomini. Examination of late Cenozoic cricetids for these features results in a phylogenetic hypothesis in which three species allocated to late Hemphillian *Peromyscus* are suggested as reasonable proxies for the common ancestors of two subclades of the Neotomini, one of which was not previously considered to be a neotominin. A new classification of the Neotomini is provided, supported by a phylogenetic analysis based on dental characters (Fig. 1). More specifically, this study proposes the following: 1) the occlusal morphology of *Lindsaymys takeuchii* is consistent with a common ancestor for the Neotomini, 2) the Neotomina, a new subtribe of the Neotomini, includes *Neotoma*, *Hodomys*, *Xenomys*, and a new genus, the latter replacing the generic name *Paronychomys* associated with *Paronychomys shotwelli* Korth, 2011, and 3) *Repomys*, *Miotomodon*, *Galushamys*, *Nelsonia*, and a second new genus (Fig. 2) form the Galushamyina Lindsay, 2008 nov. comb., another subtribe of the Neotomini. To avoid confusion, from this point the Neotomina will be referred to

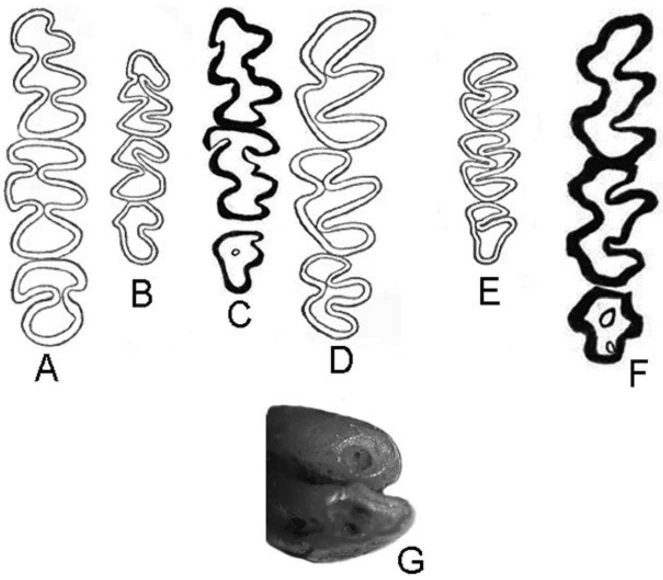

Fig. 2.—Dentition of extant *Nelsonia neotomodon, Neotoma lepida, Repomys panacaensis,* and the holotype of *Neotoma minutus.* A and D) Lower and upper left dentition of extant *Neotoma lepida* (from Merriam 1894); B and E) lower and upper left dentition of extant *Nelsonia neotomodon* (from Hooper 1954); C) UALP 22798, Lm1-m2 and UALP 22815, Lm3 of *Repomys panacaensis*; F) UALP 22573, RM1-M3 (reversed) of *Repomys panacaensis* (from Mou 2011); G) TMM 41261–68, holotype of *Neotoma minutus* Dalquest, showing geomyoid-like (p4?) features. Illustrations not to scale. Photo of *N. minutus* by C. Sagebiel.

colloquially as the neotominans and the Galushamyina as the galushamyinans.

MATERIALS AND METHODS

This investigation is based primarily on new interpretations and definitions of published information. Fortunately, there are many drawings and photographs of fossil and modern specimens revealing the salient characters used in this study. Sources are cited as the specimens are evaluated and in the Acknowledgments. We also examined casts of Hemphillian *Paronychomys lemredfieldi*, *P. tuttlei*, and *P. alticuspis* described by Jacobs (1977) and Baskin (1978), fossil specimens of Pleistocene *Neotoma floridana* from Florida and New Trout Cave, West Virginia (Holman and Grady 1987; Semken et al. 2010), and owl pellet specimens of modern *N. micropus* Baird, 1855, from Meade County, Kansas. Through the years, we have collected and examined many specimens of fossil *Neotoma* from the late Pliocene Meade Basin of Kansas and elsewhere. K. Tate and S. Hopkins (University of Oregon) provided photographs and root counts for some of Shotwell's (1967) specimens from the Miocene of Oregon.

Occlusal dental terminology basically follows that of Reig (1977) with allowances for the specialized dentition of the Neotomini (Fig. 1). Upper and lower molars are abbreviated by upper and lower case letters (M, m) and are numbered consecutively; L and R designate left and right when combined with molar designations. Otherwise, L connotes length. Enamel rings with hollow centers are termed "atolls," equal to the "fossettes," "islands," or "pits" of other authors. The procingulum of M1 and m1 may be single or divided into two cusps (bilobed). A single cusp (= conule or conulid) on the procingulum may be referred to as the anterocone (M1) or anteroconid (m1). Small enamel protuberances with or without dentine cores extending from the lingual enamel ridge between the protoconid and entoconid on m1 and the labial enamel ridge between paracone and metacone on M1 (ridges sometimes referred to as median mures) may be vestigial structures, remnants of the mesolophs, or mesolophids of ancestral cricetids that became reduced in size and irregular in placement before becoming lost entirely in various lineages. They are here referred to as mesolophules or mesolophulids. However, in another evolutionary scenario, poorly developed mesolophules or mesolophulids could be novel structures, not homologous to the ancestral mesoloph or mesolophid, which later became lost in one clade of the Neotomini and better developed in the other.

The term "lophodont" is somewhat ambiguous because the term does not refer to the presence of accessory structures such as the mesoloph or mesolophid, or other similar structures. In his exhaustive treatment of cricetid dentitions, Hershkovitz (1962) described cricetine molars as being either "pentalophodont" or "tetralophodont." Although not explicitly stated, the "lophs" Hershkovitz (1962) recognized refer to the combination of enamel borders of cusps and accessory protuberances such as mesolophs and mesolophids plus their central dentine channels that become observable after light wear. To Hershkovitz, lophs were not merely crests or ridges, as can be seen in his fig. 13 (Hershkovitz 1962: 85), where the dentine channel from each cusp is long and connects with the dentine channels of other cusps and structures. The term "lophodont" as used here refers to the tendency of dentine channels within occlusal structures to be relatively long, parallel-sided by enamel borders, and confluent with other structures after light wear. Lophodont patterns are characteristic of cricetines such as *Neotoma*, *Sigmodon*, *Phyllotis*, and the extinct *Repomys* with coronal hypsodonty and planed molars (see definitions below).

Cricetid molars display a number of crown height and occlusal conditions. The following are used throughout the text. Example genera are provided in parentheses:

Crown features.—

- brachydont: low-crowned (*Bensonomys*).
- mesodont: intermediate between brachydont and hypsodont (*Paronychomys*).
- hypsodont: high-crowned (hypsodonty is determined as the ratio of crown height [H] divided by anterior–posterior length [L] of a given tooth):
  - coronal hypsodonty: entire crown raised; dentition often planed and lophodont (*Sigmodon*).
  - tubercular hypsodonty: cusps high and relatively sectorial (blade-like; *Onychomys*).
- confluent: dentine channels connect cusps and cingula (*Neotoma*).
- Occlusal pattern
  - terraced: protocone or protoconid and hypocone or hypoconid wear flat; opposing cusps wear obliquely (*Peromyscus*, *Lindsaymys*).
  - planed: all cusps wear flat. Characteristic of mesodont and hypsodont taxa with lophodont patterns (*Sigmodon*, *Neotoma*).
  - lophodont: dentine channels developed throughout occlusal surface in early wear (*Neotoma*, *Repomys*).

*Enamel infoldings.—*Reig (1977) defined the major enamel infoldings, or re-entrant folds, as flexi or flexids (Fig. 1). We follow his terminology except for omitting the mesoflexid; the re-entrant between the metaconid and entoconid is considered here as the entoflexid. Additional terms define the direction of flexi or flexids relative to the anterior–posterior (a–p) tooth axis:

- provergent: oriented anteriorly.
- horizontal: oriented perpendicular to the a–p tooth axis.
- postvergent: oriented posteriorly.

Relative hypsodonty, a comparison of greatest crown height/greatest crown length (H/L), differs between teeth and in this study was limited to the M1. Hypsodonty measurements were mostly taken from the literature or calculated from measurements on drawings or photographs of relatively unworn teeth in the literature (estimated measurement error 10%). Hypsodonty was measured as the height of the protocone on M1, from the base of the enamel to the cusp apex. By far, the most significant influence on hypsodonty is wear. Unless comparisons are made between the same stages of wear, the resulting values may vary widely (Table 2). Although measurements from illustrations were taken from unworn or minimally worn M1s, values of hypsodonty provided in this study, especially based on single specimens, should be considered only as general indications of species hypsodonty. For descriptive purposes, H/L ≤ 0.50 = brachydont, H/L 0.50–0.75 = mesodont, and H/L > 0.75 = hypsodont.

The postincisor dentition of neotomine rodents is composed of three upper and three lower molars. As with arvicolines, the m1 is the most diagnostic tooth at all taxonomic levels, whereas the M2 and m2 tend to be the most conservative. Although developmentally unconstrained, the M1 is also anatomically conservative, usually representing a larger version of M2. The M3–m3 pair tends to become reduced in size in neotomine evolution, and especially the M3 may express considerable variation. Nevertheless, the morphology of M3 and m3 provides important phylogenetic information.

The terms Clarendonian, Hemphillian, and Blancan are North America Land Mammal Ages (NALMAs). Chronology of these NALMAs follows Lindsay et al. (2002), Tedford et al. (2004), Lindsay (2008, fig. 27.3), and Martin et al. (2008): Clarendonian (12.6–9.0 Ma), Hemphillian (9.0–5.0 Ma), and Blancan (5.0–2.0 Ma).

Institutional abbreviations associated with specimens are as follows: LACM = Natural History Museum of Los Angeles County; UO = University of Oregon; TMM = Texas Memorial Museum, University of Texas, Austin; MCZ = Museum of Comparative Zoology, Harvard University; UALP = University of Arizona; and AMNH = American Museum of Natural History.

Phylogenetic analysis was performed with MacClade 4.06 (Maddison and Maddison 2001) and the characters and character matrix are provided as Appendix I. *Copemys russelli* (James 1963) served as a generalized representative of *Copemys*, and was treated as the outgroup.

RESULTS

Dental characters of modern woodrats.—The following represents a summary of molar features characterizing extant *Neotoma*, *Hodomys*, and *Xenomys*.

General: 1) ancestral species mesodont, descendant species hypsodont, all with coronal hypsodonty; 2) molars planed and lophodont; 3) enamel thick (relative to other neotomines) and undifferentiated; 4) accessory structures (lophs, lophids; styles, stylids) rare or absent; 5) M1, m1 with single conule, conulid; and 6) molars small to medium size.

m1 characters: 1) metaconid widely confluent with anteroconid; 2) anterolabial cingulum widely confluent with anteroconid; 3) metaflexid shallow or absent in ancestral species, may secondarily deepen (e.g., *Neotoma cinerea* (Ord, 1815), *Hodomys alleni*); 4) hypoconid widely confluent with posterolophid; 5) protoflexid horizontal or provergent; 6) entoflexid deep and predominantly provergent, rarely horizontal or postvergent; and 7) posteroflexid and hypoflexid usually opposite or slightly alternate.

M1 characters: 1) protoflexus present or absent; 2) internal enamel borders of paraflexus and hypoflexus usually opposite (alternate in *Xenomys alstoni* and *Hodomys alleni*); 3) paraflexus and metaflexus deep and postvergent; 4) anterocone widely confluent with protocone; 5) hypocone widely confluent with posteroloph; and 6) with three or four (only *Hodomys alleni*) roots on M1.

m3 characters: The m3 is reduced in size relative to m2. The m3 varies from an S-shape, with alternating posteroflexid and hypoflexid (*Hodomys alleni*, *Xenomys alstoni*) to dumbbell (bilobed) shape, with posteroflexid and hypoflexid opposite to slightly alternate (extant *Neotoma* species).

M3 characters: The M3 displays the same basic pattern as M2 except the posterior part of the tooth, with the hypocone, posteroloph, and metacone, is significantly reduced in size.

Ancestral Cenozoic neotominins.—The salient expected features of ancestral Neotomini are first seen, in incipient form, in *Lindsaymys takeuchii* (Fig. 3) from the Dove Spring Fm, Mojave Desert, Kern County, California (Kelly and Whistler 2014). *Lindsaymys takeuchii* has a temporal range during the latest Clarendonian–early Hemphillian of ~9.2–8.4 Ma. Kelly and Whistler (2014) suggested at least one or two additional *Lindsaymys* species (their "species A" and "B") occur with *L. takeuchii*. With the exception of occasional diminutive lophules or lophulids extending from the paracone of M1 and entoconid of m1 in a few teeth (referred to by Kelly and Whistler [2014] as "spurs"), accessory occlusal structures are absent. Hypsodonty indices range between 0.56 and 0.73 for unworn and minimally worn M1s (Table 2). The anteroconid of m1 is single and closely associated with the metaconid, the latter opens widely into the anteroconid in LACM 150737 (Kelly and Whistler 2014, fig. 6B). Labial cusps are elevated, displaying a terraced wear pattern. Borders of lingual cusps flatten after light wear and an incipient lophodont pattern, with thick, undifferentiated enamel, appears (Fig. 3). M3 is reduced and similar in shape to the M3 of modern Neotomini. The m3 is unreduced and S-shaped, as in most extinct *Neotoma* species. The M1 commonly has an accessory root under the paracone and is developed to the extent that an alveolus is present (T. Kelly, LACM November 2017). In its terraced rather than planed wear surface, *L. takeuchii* retains an ancestral cricetid

Table 2.—Hypsodonty (H/L) of the M1 in a stem neotominin, *Lindsaymys takeuchii*. Wear categories: 1 = unworn, 8 = heavily worn; *SD* = standard deviation. Data provided by T. Kelly.

Wear category	*n*	Mean	Observed range	*SD*
1	6	0.72	0.70–0.73	0.02
2	2	0.58	0.56–0.59	
3	5	0.60	0.52–0.65	0.05
4	3	0.45	0.40–0.50	0.06
5	1	0.50		
6	2	0.40	0.40-0.40	
7	2	0.35	0.30–0.40	
8	2	0.27	0.24–0.29	

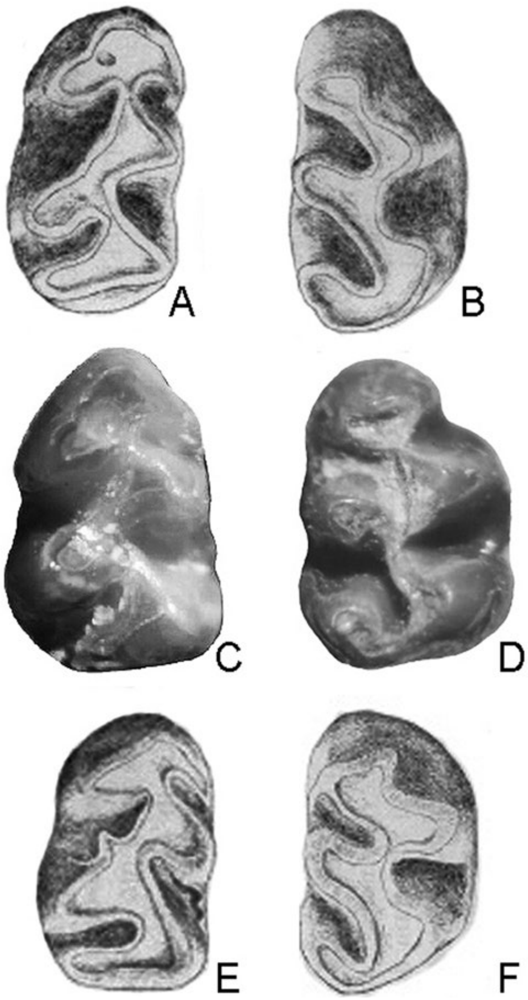

Fig. 3.—Upper and lower first molars of early neotominins. *Tsaphanomys shotwelli*: A) (UO 21719 Lm1, reversed); B) (UO 21728 RM1) (from Shotwell 1967). *Lindsaymys takeuchii*: C) (LACM 150737 Lm1); D) (LACM 156538 RM1) (from Kelly and Whistler 2014), *Protorepomys mckayensis*: E) (UO 24603 holotype Lm1, reversed) (from Shotwell, 1967); F) (UO 24588 RM1) (from Shotwell 1967). Illustrations not to scale.

condition, which it shares with other small cricetines with generalized dentitions such as *Copemys* and *Peromyscus*. Also as in the latter genera, cusps remain distinct and alternate, and dentine channels connecting them are not developed into elongated lophs or lophids. Another cricetid from the Dove Spring Fm, *Antecalomys coxae*, displays some similarity to *Lindsaymys*. Although smaller and less hypsodont, the metaconid on m1 fuses with the anteroconid after light wear (Kelly and Whistler 2014, fig. 11). Accessory structures such as mesolophs or mesolophids are developed in about 50% of the specimens. An accessory root is present on M1 in 11 of 12 specimens examined.

The next stage in Neotomini evolution is represented by *Peromyscus* cf. *pliocaenicus* from Juniper Creek, Oregon (Shotwell 1967). As noted above, this fossil sample was subsequently referred to the new species *Paronychomys shotwelli* (Korth 2011). However, the dental characters of the Juniper Creek sample do not conform to those of *Paronychomys* as described by Jacobs (1977). Instead, they define a new genus within a restructured classification of the Neotomini. Additional species from the Miocene of Oregon referred by Shotwell (1967) to *Peromyscus* will also be renamed and allocated below to the Neotomini, but placed within a newly described subtribe.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer de Waldheim, 1817
Subfamily Neotominae Merriam, 1894
Tribe Neotomini Merriam, 1894
Subtribe Neotomina Merriam, 1894 nov. rank

Type genus.—Neotoma Say and Ord, 1825.

Included genera.—Tsaphanomys nov. genus, *Neotoma*, *Hodomys*, *Xenomys.*—General: 1) ancestral species brachydont to mesodont, descendant species hypsodont, all with coronal hypsodonty; 2) molars tend towards lophodonty after light wear in ancestral taxa, highly lophodont in derived taxa; 3) accessory structures (lophs, lophids; styles, stylids) rarely present; 4) M1, m1 with single anterocone, anteroconid; and 5) molars small to medium size.

m1 characters: 1) metaconid widely confluent with anteroconid; 2) anterolabial cingulum widely confluent with anteroconid; 3) metaflexid shallow or absent in ancestral species, may secondarily deepen (e.g., *Neotoma cinerea*, *Hodomys alleni*); 4) hypoconid widely confluent with posterolophid; 5) protoflexid horizontal or provergent; 6) entoflexid deep and predominantly provergent, rarely horizontal or postvergent; and 7) posteroflexid and hypoflexid usually opposite or slightly alternate.

M1 characters: 1) protoflexus present or absent; 2) internal enamel borders of paraflexus and hypoflexus usually opposite (alternate in *Hodomys alleni*); 3) paraflexus and metaflexus deep and postvergent in derived taxa; 4) anterocone widely confluent with protocone; and 5) hypocone widely confluent with posteroloph.

m3 characters: The m3 is reduced in size relative to m2. The m3 varies from an S-shape, with alternating posteroflexid and hypoflexid (*Tsaphanomys* nov. genus, some Blancan and Irvingtonian *Neotoma* species, *Hodomys alleni*, *Xenomys alstoni*) to dumbbell (bilobed) shape, with posteroflexid and hypoflexid opposite to slightly alternate (*N. amplidonta* and modern *Neotoma* species).

M3 characters: The M3 displays the same basic pattern as M2 except the posterior part of the tooth, with the hypocone, posteroloph, and metacone, is significantly reduced in size.

Tsaphanomys nov. genus

Type species.—Paronychomys shotwelli Korth, 2011.

Diagnosis.—Molars terraced and significantly smaller than in extant species of *Neotoma*; molars incipiently lophodont after light wear; mesolophules and mesolophids absent in adult molars; hypoflexid and entoflexid opposite on m1; hypoflexid wide and horizontal on m1; wide dentine channel connects protoconid and entoconid and hypoconid and posterolophid on m1 after light wear; M1 mesodont (Table 3); paraflexus and hypoflexus opposite on M1; anterolabial cingulum on M2 relatively unreduced; M1 with three roots.

Etymology.—From the ancient Hebrew tsaphan, meaning to hoard, or "treasure up," referring to the packrat behavior of woodrats.

Comparisons.—There is a superficial resemblance of *Tsaphanomys* to *Paronychomys* (Fig. 4); both display mesodont molars and in *Paronychomys* the metaconid on m1 may be close to the anteroconid. However, the occlusal pattern in the type species *Paronychomys lemredfieldi* Jacobs, 1977, differs from that of *Tsaphanomys* in the following ways: 1) metaconid not highly confluent with anteroconid of m1; 2) anterolabial cingulum separate from the anteroconid of m1 in *Paronychomys* and *Onychomys*; 3) the metaconid and entoconid on m1–m2 are smaller and directed more horizontal than in *Tsaphanomys*, in which these cusps and associated dentine channels are more obliquely directed, in part due to deep and provergent penetrance of the entoflexid; 4) the m1 of *Paronychomys* has a bilobed procingulum, whereas the procingulum is single in *Tsaphanomys*; and 5) molars of *Paronychomys* display a tubercular hypsodont and semi-sectorial rather than coronal hypsodont mastication surface. The occlusal pattern of *Paronychomys* m1–m2 appears as a mesodont version of those molars in extant *Onychomys*, whereas the occlusal pattern of *Tsaphanomys* appears as a mesodont version of those molars in extant *Neotoma*.

Paronychomys woodburnei Martin, 2008, from the late Hemphillian Ordnance locality of northern Oregon, is also likely an early neotominan, distinct from *Paronychomys*. However, as we have not examined the specimens referred to *P. woodburnei* and as illustrations in J. Martin (2008) are not adequate for detailed examination, we refrain from further comment at this time.

Table 3.—Hypsodonty (H/L) of M1 in select extinct and extant cricetids. H = crown height M1, L = crown length M1. N = number of specimens. Mean, observed range and standard deviation (*s*) provided for *L. takeuchii*. Measurements taken from juvenile or lightly worn specimens unless otherwise noted.

Taxon	*n*	H/L
Lindsaymys takeuchii[a]	8	0.68 (0.56–0.73), *SD* = 0.07
Tsaphanomys shotwelli[b]	1	0.72
Miotomodon mayi[c]	1	0.75
Repomys gustelyi[b]	1	0.83
Repomys minor[b]	1	0.85
Neotoma vaughani[b]	1	0.88
Neotoma fossilis[b]	1	0.64
Neotoma taylori[b]	1	0.90
Neotoma micropus[d]	2	0.66, 0.72

[a] Calculated from data provided by T. Kelly (pers. comm.).

[b] From measurements made on the following illustrations: *T. shotwelli* (Shotwell 1967, fig. 10F), *R. gustelyi* (May 1981, fig. 6D), *R. minor* (Mou 2011, fig. 10–3), *N. vaughani* (Czaplewski 1990, fig. 9C), *N. fossilis* (Tomida 1987, fig. 19C; moderately worn), *N. taylori* (Tomida 1987, fig. 19K).

[c] From photograph provided by W. Korth and T. Kelly.

[d] From modern owl pellets; Meade County, KS.

Tsaphanomys shotwelli (Korth, 2011)

(*Figs. 2A and 2B; 3B; 4E and 4F*)

Peromyscus cf. *pliocaenicus*: Shotwell, 1967:27. Not *Peromyscus pliocaenicus* Wilson, 1937.

Paronychomy shotwelli Korth, 2011:140.

Holotype.—UO 21716 LM1.

Paratypes.—UO 21717 Lm2, UO 21719 Lm1, UO 21720 rm3, UO 21721 LM2, UO 21723 LM1, UO 21728 RM1.

Referred specimens.—UO 25667 Rm2–m3, UO 25666 RM2; from UO Loc. 2516, Little Valley. Korth (2011) also listed UO 41167 M2 and UO 41170 mandible without molars as referred specimens. Neither were described or figured and they are only tentatively listed here.

Type locality and age.—UO Loc. 2469, Juniper Creek Canyon, Malheur Co., Oregon; Grassy Mountain Fm; Late Miocene (Hemphillian; possibly Hh2, ~ 7.0 Ma).

Description.—Shotwell (1967, p. 27–29, figs. 10–11, table 1) and Korth (2011, p. 140–142, fig. 2, table 3) provide excellent descriptions of these specimens that need not be repeated here.

Comments.—Shotwell (1967) identified fossil cricetine samples from three Hemphillian localities in southeastern Oregon as *Peromyscus* cf. *pliocaenicus*: Juniper Creek, Little Valley, and McKay Reservoir. Because of small sample size and inconsistent morphology, the McKay Reservoir specimens are not included in this analysis.

Relationships.—The dentition of *Tsaphanomys* is more lophodont than in *Lindsaymys* and shares with *Lindsaymys* the important Neotomini synapomorphy of a highly confluent

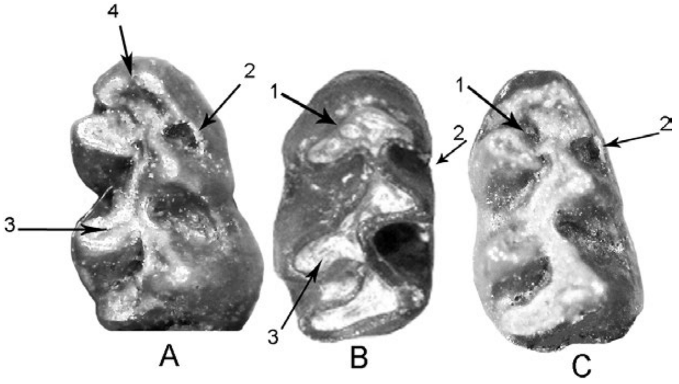

Fig. 4.—Comparison of *Tsaphanomys shotwelli* and *Paronychomys lemredfieldi* m1s. A) *P. lemredfieldi*, cast of Rm1 from AMNH 3249; B) *T. shotwelli*, Rm1 UO 21719 (reversed) (from Korth 2011); C) *P. lemredfieldi*, slightly rotated view of cast of AMNH 3249. 1 = near closure of metaflexid in *T. shotwelli*, remaining open and deep in *P. redfieldi*; 2 = distinct high, labial cingulum in *P. redfieldi*, absent in *T. shotwelli*; 3 = narrow dentine channels in *P. redfieldi*, lophodont pattern in *T. shotwelli* with wide dentine channels; 4 = bilobed procingulum in *Paronychomys*, single in *Tsaphanomys*. Note dentine extension into anterolabial cingulum of *T. shotwelli*, absent in *P. redfieldi*. Illustrations not to scale.

metaconid, anterolabial cingulum, and anteroconid on m1, coupled with obliquely oriented dentine channels connecting major cusps. These characters are also found in two samples of another late Miocene small cricetid from Oregon, described by Shotwell (1967, figs. 8, 9) as *Peromyscus* cf. *esmeraldensis* from McKay Reservoir and Bartlett Mountain (hereafter referred to as Bartlett). A third sample, from the Clarendonian Black Butte assemblage, was also referred to *P*. cf. *esmeraldensis* by Shotwell (1967) but its morphology is distinct and it will not be considered further here.

"*Peromyscus*" *esmeraldensis* was originally described by Clark et al. (1964) from the Fish Lake Valley beds of the Esmeralda Fm of western Nevada, dated at 11.73 Ma (Tedford et al. 2004; Kuiper et al. 2008) as *Copemys esmeraldensis*, but this species is likely neither a *Peromyscus* nor a *Copemys* and may represent a new genus. Although the m1 from the type lower jaw (MCZ 7644) is well worn, an unworn paratype Rm1 MCZ 7645 can be evaluated (Fig. 5D). In modern *Peromyscus*, the posterior arm of the protoconid (protolophid 2 in our terminology) and the entolophid (= the entolophulid of Lindsay and Czaplewski 2011) are aligned such that in moderate wear dentine channels of both cusps connect, whereas they do not join in *Copemys*. In this regard, *C. esmeraldensis* conforms to *Copemys*. However, in neither *Peromyscus* nor *Copemys* is a long labial anterolophid (well-developed lophid between the anteroconid and protoconid) present. Coupled with an asymmetrical anteroconid and well-developed mesolophid and ectolophid, the m1 of *C. esmeraldensis* displays a unique character combination for Cenozoic cricetids.

All of the characters defining the McKay and Bartlett *P*. cf. *esmeraldensis* as Neotomini preclude them from membership in *Peromyscus*, the latter which expresses a cuspate and terraced morphology with narrow dentine channels in all species (Fig. 5). Other distinctions are identified in Fig. 5. Ironically, none of the species identified as *Peromyscus* in Shotwell's (1967) monograph belong to that genus. In addition to features shared with *Tsaphanomys shotwelli*, the m1s of the McKay and Bartlett *P*. cf. *esmeraldensis* display well-developed mesolophulids on the three m1s illustrated by Shotwell (fig. 8A; fig. 9A, C). A small ridge possibly representing a remnant mesolophulid on the m1 of *Tsaphanomys shotwelli* likely indicates a relationship of *Tsaphanomys* with the McKay and Bartlett *P*. cf. *esmeraldensis*. In all probability, *T. shotwelli* and the McKay and Bartlett species would have appeared in the late Miocene as similar species, perhaps bearing the same relationship as any two species of *Peromyscus* have with each other today. However, the regular presence of a mesolophulid on m1 suggests an ancestral relationship of the McKay and Bartlett *P*. cf. *esmeraldensis* with *Repomys*, a hypsodont genus described by May (1981), represented by five species ranging in time from late Miocene (early Blancan) through late Pliocene time, and requires a taxonomic distinction from *Tsaphanomys* that may have phylogenetic implications.

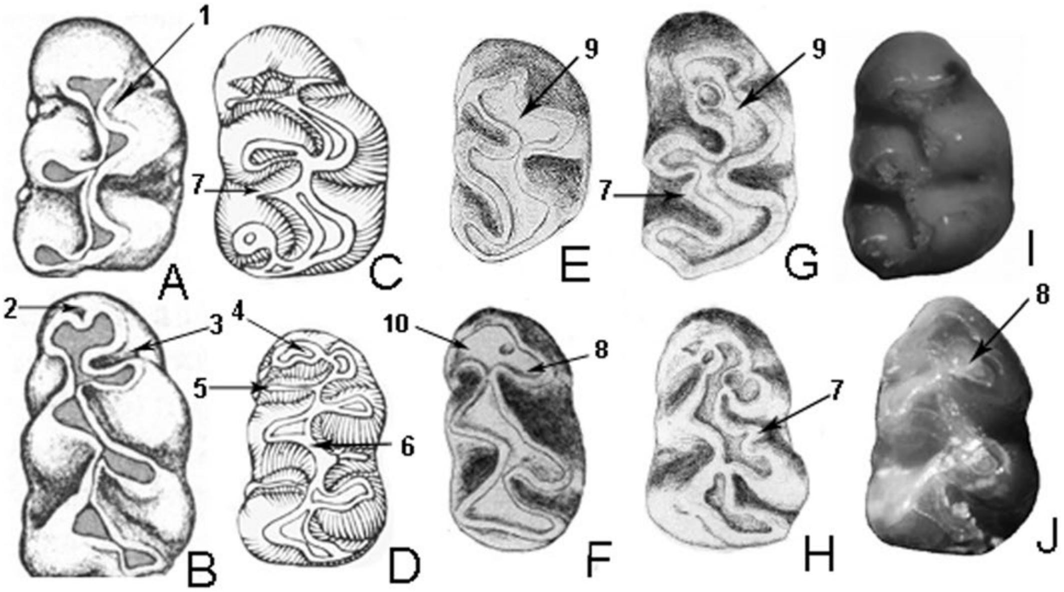

Fig. 5.—Comparison of M1s and m1s among various extant and extinct cricetids (M1s above, m1s below). A and B) (reversed), *Peromyscus eremicus* (extant, no data, from Hooper 1957); C and D) *Copemys esmeraldensis* (Fish Lake Valley, NV) (from Clark et al. 1964) (C, MCZ 7647 RM1, reversed), (D, MCZ 7645 Rm1); E and F) *Tsaphanomys shotwelli* (see Fig. 3; m1 reversed); G and H) *Protorepomys bartlettensis* (Bartlett Mountain, OR) (G, UO 24957 LM1, reversed) (from Shotwell 1967), (H, UO 25591 Lm1); I and J) *Lindsaymys takeuchii* (see Fig. 3). 1 = protoflexus deep in *Peromyscus, Copemys, Lindsaymys*; 2 = tendency for bifid anteroconid in most *Peromyscus* and *C. esmeraldensis*; 3) = metaflexid deep in *Peromyscus* and *Copemys*; 4) = unique anteroconid morphology of *C. esmeraldensis*; 5) = labial anterolophid present only in *C. esmeraldensis*; 6) = posterior arm of protoconid (protolophid 2) not aligned with entolophid in *Copemys*; 7) = mesolophule/id present in *Protorepomys*; 8) = metaconid widely connected with anteroconid in *Tsaphanomys*, *Protorepomys* and *Lindsaymys*; 9) = protoloph 1 connects widely to anterocone in *Tsaphanomys* and *Protorepomys*; 10) = anterolabial cingulum connected by dentine channel to anteroconid in *Tsaphanomys* and *Protorepomys* after modest wear. Illustrations not to scale.

Subtribe Galushamyina Lindsay, 2008 nov. rank

Type genus.—Galushamys Jacobs, 1977.

Included genera.—Protorepomys nov. genus, *Repomys*, *Miotomodon*, *Galushamys*, *Nelsonia*.

Diagnosis.—Archaic species with terraced mastication surface, derived species with planed surface; consistent mesolophulid on m1 in archaic species, absent in *Nelsonia*; mesolophule on M1 usually present (absent in *Protorepomys* mckayensis nov. species, *Nelsonia*); taxa with (*Galushamys*) or without (*Protorepomys* nov. genus, *Repomys*, *Miotomodon*, *Nelsonia*) enamel atolls developed on M1 from isolation of the enamel borders of paraflexus and metaflexus; M1 with three roots; m3 simple shield shape, with shallow or no protoflexid in most taxa (*Repomys*, *Nelsonia*); M3 usually reduced to single dentine field without flexi, occasionally with vestigial paraflexus (*Repomys*, *Nelsonia*). The primary differences between the Neotomina and Galushamyina are the persistent mesolophulid on m1 in ancestral galushamyinans and reduced, simplified M3–m3 morphology in derived taxa of the Galushamyina.

Protorepomys nov. genus

Peromyscus cf. *esmeraldensis* of Shotwell (1967); not Clark et al. 1964.

Type species.—Protorepomys mckayensis nov. species.

Diagnosis.—Molars terraced and significantly smaller than in living species of *Neotoma*; molars moderately lophodont after light wear; protoflexid and entoflexid opposite on m1; M1 with or without mesolophule; m1 with mesolophulid; hypoflexid on m1 narrow and provergent, internal enamel border almost closing protoconid from hypoconid; m1 mesodont (H/L = 0.56, UO 25591 Lm1; H/L = 0.65, UO 24603 Lm1); paraflexus and hypoflexus opposite on M1; anterolabial cingulum on M2 relatively unreduced.

Etymology.—Protorepomys, from "proto," meaning first or first in time, and the likely relationship of *Protorepomys* with *Repomys*.

Relationships.—Protorepomys, *Repomys*, and additional relatives form a distinctive clade, the Galushamyina, representing a sister group to the neotominans. *Tsaphanomys* and *Protorepomys* represent the morphological transition between *Lindsaymys* and *Neotoma* and *Repomys*. In *Lindsaymys*, the ancestral cuspate, or tubercular, pattern is retained, as well as a more primitive alternation of cusps and the dentine channels that connect them. In *Tsaphanomys* and *Protorepomys*, the dentition remains terraced rather than planed as in *Repomys* and *Neotoma*, but the lophate pattern of *Tsaphanomys* and *Protorepomys* is more evident than in *Lindsaymys*. The combination of a tendency to develop a hypsodont, lophate occlusal morphology and simple M3 and m3 pattern, identifies a character complex defining *Repomys* (May 1981). In most regards, the dentition of *Protorepomys* fits the criteria one would expect for a *Repomys* ancestor. *Tsaphanomys* shares much of the same suite of characters, but mesolophules and mesolophulids are absent. No extinct or extant species of *Neotoma* possess mesolophules or mesolophulids. Major lophs and lophids associated with cusps tend to be wider and more obliquely oriented in *Tsaphanomys*, *Neotoma*, and *Repomys* than in *Lindsaymys* and *Protorepomys*. In regards to dentine channel width, *Tsaphanomys* appears to be somewhat more advanced than *Protorepomys*. However, sample sizes of both *Tsaphanomys* and *Protorepomys* are small, and it is possible that some of the apparent difference in confluency of dentine channels is due to differential wear. In any case, in this treatment the fixed and well-developed mesolophulid on m1 in *Protorepomys* is considered a synapomorphy linking *Protorepomys* with *Repomys*, whereas the absence of this definitive character in *Tsaphanomys* suggests alliance of *Tsaphanomys* with *Neotoma*.

Protorepomys mckayensis nov. species

(*Figs. 3E and 3F*)

Peromyscus cf. *esmeraldensis*: Shotwell, 1967:22. Not *Peromyscus esmeraldensis* Clark et al., 1964.

Holotype.—UO 24603 Lm1.

Paratypes.—UO 24916 Lm1, UO 24602 Lm2, UO 26941 Lm3, UO 24588 RM1, UO 26942 RM2.

Locality and age.—McKay Reservoir (UO Loc. 2222), Shutler Fm, Northern Great Basin, Umatilla Co., Oregon. Hemphillian (late Miocene; ~ 5.5–5.0 Ma).

Etymology.—for the McKay fossil localities.

Diagnosis.—Anterolabial cingulum and metaconid confluent with anteroconid on m1; M1 without enamel atoll and lacking protolophule and mesolophule; m1 with mesolophulid; m3 S-shaped, with well-developed mesolophulid but lacking anterior atoll and posteroflexid; m2–m3 with well-developed anterolabial cingulum.

Description.—See Shotwell (1967, p. 22–26, fig. 9, table 1) for general molar descriptions and measurements.

m1: The metaconid and labial cingulum are closely associated with the anteroconid and open widely into the dentine field of the anteroconid. A mesolophulid is well-developed, extending anterio-lingually from the base of the entoconid. The mesoflexid and hypoflexid are deep and provergent, and all cusps are connected by dentine fields. Both metalophid and entolophid are directed obliquely anteriorly.

m2: The m2 is relatively simple and typical for cricetids in general. Accessory structures are absent. As in m3, the hypoflexid is wide and horizontal, with a wide internal enamel border, and the entoflexid is deep and provergent.

m3: Relatively large, the anterior half of m3 resembles that of m2. The posterior half is somewhat reduced, and the posteroflexid is absent except for a slight indentation in the lingual tooth border. Atolls are absent, and a mesolophulid is well-developed.

M1: The M1 is devoid of atolls and lacks a mesolophule. The procingulum is wide, simple, and its dentine field is highly confluent with that of the protocone. In M1 UO 24588, the paraflexus and hypoflexus are deep and opposite, separating the dentine fields of the protocone and paracone.

M2: The lightly worn M2 displays deep and postvergent paraflexus and metaflexus. The hypoflexus is wide and horizontal. The paracone is relatively narrow and its paraloph is directed obliquely and posteriorly and is aligned with hypoloph 1. A cingulum runs along the anterior tooth border.

Protorepomys bartlettensis nov. species

(*Figs. 5G and 5H*)

Peromyscus cf. *esmeraldensis*: Shotwell, 1967:22. Not *Peromyscus esmeraldensis* Clark et al., 1964.

Holotype.—UO 25591 Lm1.

Paratypes.—UO 26940 Lm3; UO 25078 LM3; UO 24957 LM1. Other specimens listed by Shotwell (1967, table 9) as paratypes but not examined by us are also provisionally included in *P. bartlettensis.*

Locality and age.—Bartlett Mountain (UO Loc. 2517), underlying an ash dated at 7.1 ± 1.09 Ma at top of Drewsey Fm. Middle Hemphillian (late Miocene).

Etymology.—for the Bartlett Mountain fossil localities.

Diagnosis.—M1 with paralophule and mesolophule; fusion of paralophule with procingulum produces an atoll at base of procingulum; m1 with enamel atoll in anteroconid; m1 with small mesolophulid; m3 with anterior enamel atoll, entoflexid and posteroflexid but lacking anterolabial cingulum.

Description.—See Shotwell (1967, p. 22–26, fig. 8, table 1) for general molar descriptions and measurements.

m1: The metaconid and labial cingulum are closely associated with the anteroconid and would open widely into the dentine field of the anteroconid with minimal wear. A mesolophulid is well-developed but other accessory structures are absent. The mesoflexid and hypoflexid are deep and provergent, and all cusps are connected by dentine fields after light wear. Both metalophid and entolophid are directed obliquely anteriorly.

m3: The lower third molar is large, as is typical for other Miocene cricetids. An atoll is developed in the dentine field between the protoconid and metaconid. The mesoflexid is well-developed and provergent; the posteroflexid is horizontal. The hypoflexid is deep and horizontal to slightly postvergent. Dentine fields connect all cusps after light wear.

M1: The M1 displays a simple procingulum, with a single, wide dentine field. A protolophule extends labially from the anterolabial base of protoloph 1. The protolophule fuses with the procingulum, producing an atoll at the labial base of the procingulum. The protoflexus and hypoflexus are horizontal. The paraflexus and hypoflexus are relatively deep and postvergent.

M3: The single, lightly worn M3 is reduced in size relative to M2. An anterior cingulum is well-developed and runs across the full anterior surface of M3. The paracone and protocone are well-developed. The paraflexus and metaflexus are deep; the protoflexus and hypoflexus are shallow and horizontal. A small posteroflexus is present.

Protorepomys mckayensis differs from *P. bartlettensis* by the presence of an anterolophule, mesolophule, and atoll on M1 and an atoll on M3 in the former.

Justification and Relationships of the Galushamyina

The characters allying *Tsaphanomys*, *Protorepomys*, and *Repomys* imply that *Repomys* and its relatives should be considered a sister group of *Neotoma* and its close relatives. In addition to characters of the Neotomini shared by *Protorepomys* and *Repomys*, supporting evidence can be seen in a comparison of juvenile M1s of *Neotoma* sp. from late Pleistocene sediments in New Trout Cave, West Virginia, with adult molars of *Repomys arizonensis* from the 111 Ranch early Blancan site of Arizona (Fig. 6). This level of morphological similarity is not likely the result of evolutionary convergence. Additionally, despite reduction of most M3s to a simple shield shape, occasional M3 variants of *Repomys* species display morphologies similar to those of *Neotoma* and a presumed, more general, morphology as evidenced by *Lindsaymys takeuchii* (Fig. 7).

Following a classification of cricetid rodents used mostly by paleontologists, Lindsay (2008) defined a new tribe of cricetodontine cricetids, the Galushamyini, including the extinct *Galushamys*, *Paronychomys*, *Repomys*, *Pliotomodon*, *Goniodontomys*, and *Paramicrotoscoptes*. We expressed the opinion above that *Paronychomys* is unrelated to *Tsaphanomys* (= *Paronychomys shotwelli* of Korth 2011) and thus unrelated to the Neotomini. Although there is certainly a general similarity of *Paronychomys* to *Repomys* in the sense that *Paronychomys* displays mesodont molars and thus an incipient tendency towards hypsodonty, that is where the similarity ends.

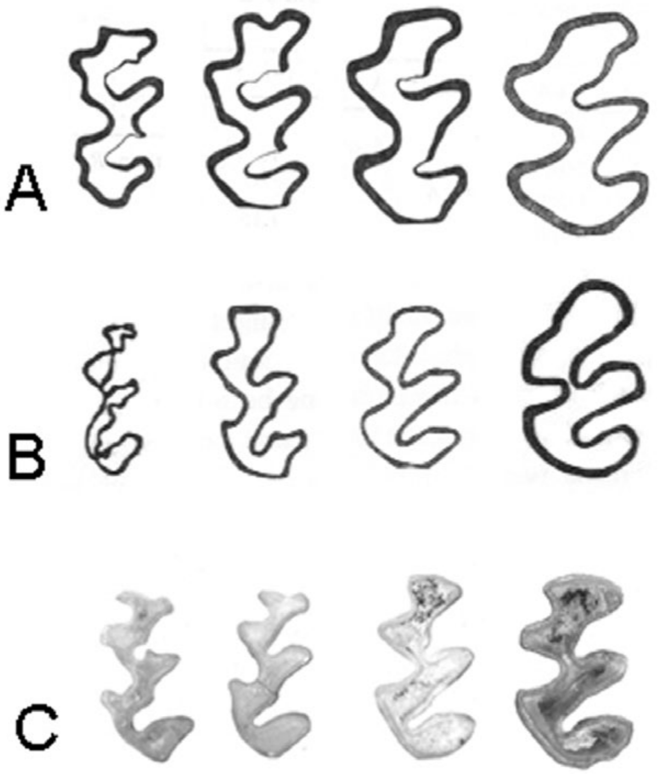

Fig. 6.—Comparison of M1 morphology in *Neotoma* and *Repomys*. Depth of wear (little worn through well worn) proceeds from left to right. A) *Repomys arizonensis,* 111 Ranch, AZ (from Tomida 1987, fig. 21); B) *Neotoma taylori* (little worn through well worn), 111 Ranch, AZ (from Tomida 1987, fig. 19); C) *Neotoma floridana* (little worn through intermediate wear), uncatalogued specimens, New Trout Cave, WV (R. A. Martin collection). *N. floridana* specimens from New Trout Cave produced consistent AMS ^{14}C dates around 50,000 radiocarbon years B. P. (Semken et al 2010). Illustrations not to scale.

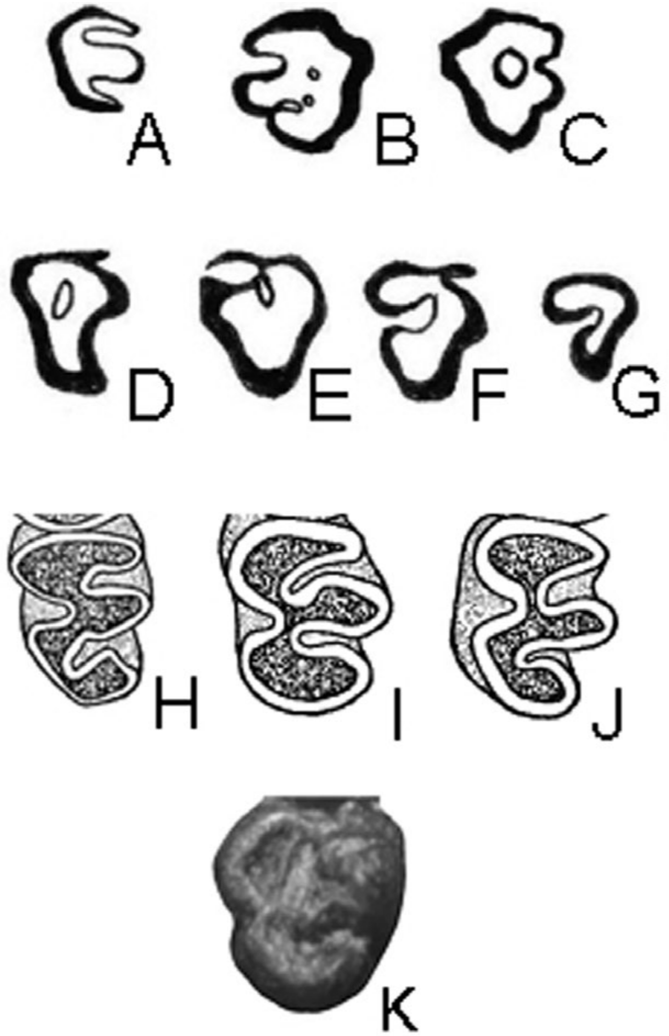

Fig. 7.—Variation in *Repomys minor* M3s (top row) and m3s (second row) and M3s of extant *Neotoma stephensi* (H), *N. lepida* (I), *N. albigula* (J), and *Lindsaymys takeuchii* (K; reversed). *Repomys* from Mou (2011), *Neotoma* from Hoffmeister and de la Torre (1960), *Lindsaymys* from Kelly and Whistler (2014). The *Lindsaymys* morphology is considered roughly ancestral. Illustrations not to scale.

In other regards, *Paronychomys* Jacobs, 1977 is more like its brachydont namesake *Onychomys* than it is like *Repomys* or the Neotomina. Actually, by the dental terminology used here, *Onychomys* displays tubercular hypsodonty rather than the coronal hypsodonty characterizing most Neotomini. *Paronychomys lemredfieldi*, the type species of *Paronychomys*, displays a dental pattern very similar to that of extant *Onychomys*, albeit more hypsodont (Fig. 4).

Goniodontomys and *Paramicrotoscoptes*, once thought to be ancient arvicolines, are now considered to be arvicoline-like cricetids descended from the Old World *Microtoscoptes* and in their own subfamily, the Microtoscoptinae (Fejfar et al. 2011). Their dental pattern, as in the rejected relationship of *Paronychomys* to *Tsaphanomys*, is similar to *Repomys* and other galushamyinans only in the sense that microtoscoptines have hypsodont, lophodont molars.

The M1s and M3s of galushamyinans as well as *Scotinomys* are illustrated in Fig. 8. Homologous structures are indicated by numbers. An anterior atoll in *Pliotomodon* and *Scotinomys* is considered homologous to the paraflexus of galushamyinans. The posterior atoll of *Galushamys*, *Pliotomodon*, and *Scotinomys* is considered homologous to the metaflexus. Despite similarities among the M1s in Fig. 8, the bilobed anterocone of *Pliotomodon* and *Scotinomys* is a character unobserved in other taxa considered here. A slight tendency in this direction is seen in little-worn molars of *Repomys* and *Neotoma* (Fig. 6), but is lost with light wear. Without an intermediate between *Protorepomys* and *Pliotomodon* demonstrating the development of a bifid anterocone, the origin of *Pliotomodon* remains obscure, raising the likelihood that, as Jacobs (1977), May (1981), and Lindsay (2008) suggested, *Pliotomodon* was an Asian immigrant. The upper dentition of *Pliotomodon* is compared with that of the Miocene Old World genus *Byzantinia* in Fig. 9.

With its single anterocone on M1 and similarity of the m1 to that of *Repomys panacaensis* (Fig. 10), *Galushamys* is tentatively considered to be descended from *Protorepomys*. The extant diminutive *Nelsonia neotomodon* and *N. goldmani* make up the final addition to the galushamyinans and their geographic distribution and ecology provide a hypothesis explaining the Cenozoic distribution of the group. In honor of his contributions to fossil rodent history and in reference to the genus *Repomys*, named for the late Charles Repenning, *Repomys* and its clade relatives are colloquially referred to as reprats.

Phylogenetic Analysis and Dental Evolutionary Trends Among Neotominins

The most parsimonious cladogram (21 steps; consistency index 0.81) for the character matrix in Appendix I is presented in Fig. 11. Based on the chronology indicated in Table 1 and Fig. 12, an estimate of about 10 Ma for the origin of at least the Neotomini component of the New World neotomine radiation proposed by Steppan et al. (2004) based on molecular characters is not unreasonable. All Neotomini are characterized by incipient lophodonty, in which the crown, even if terraced in unworn or little-worn molars, appears somewhat flat with cusps connected by dentine channels after modest wear. Simultaneously, dentine channels connect the anterolabial cingulum and metaconid with the anteroconid on m1. The common ancestor for the Neotomini, represented in this study by the proxy *Copemys russelli* for generalized *Copemys* (Figs. 1D–F) possessed a well-developed mesoloph and mesolophid on M1 and m1, respectively, which was reduced to a mesolophule and mesolophulid or lost in the Neotomini.

In our final review of dental characters, we noted that the presence of a small labial accessory root on M1 in *Lindsaymys* Kelly and Whistler, 2014 could present an issue in our phylogenetic scenario. The presence of this root leads to the conclusion that, despite a number of shared occlusal characters, the known populations of *Lindsaymys takeuchii* cannot be ancestral to *Tsaphanomys*, *Protorepomys*, or *Repomys*, and perhaps not to *Neotoma*, as samples of the former genera and

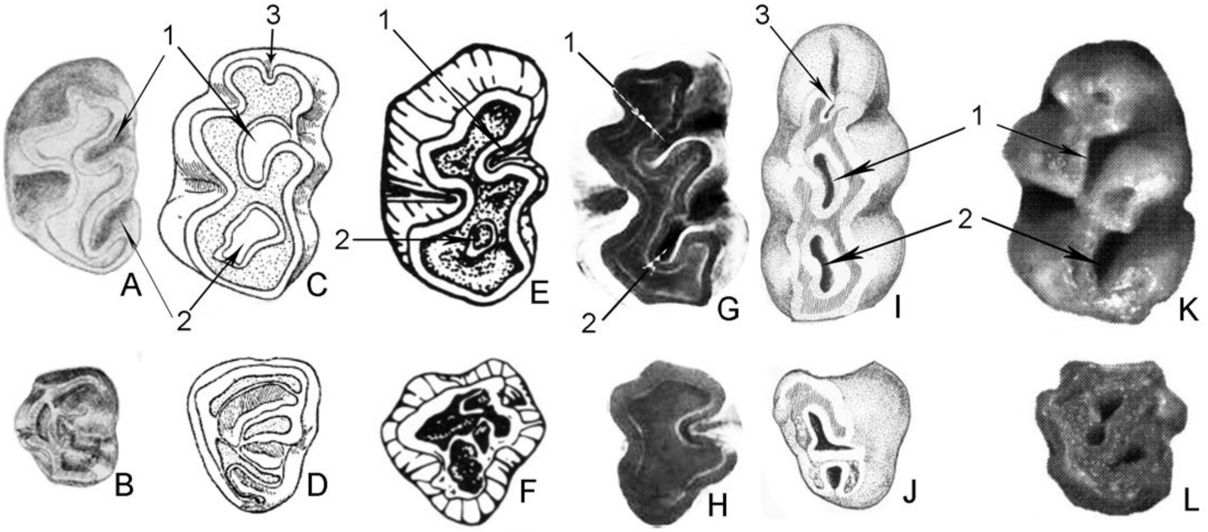

Fig. 8.—Comparison of M1s (upper row) and M3s (lower row) in some hypsodont cricetids showing presumed homologous dental structures in M1. A) (reversed) *Protorepomys mckayensis* (from Shotwell 1967); B) *Protorepomys bartlettensis* (from Shotwell 1967); C and D) *Pliotomodon primitivus* from Hoffmeister 1945); E (reversed) and F) *Galushamys redingtonensis* (from Jacobs 1977); G (reversed) and H) *Repomys gustelyi* (from May 1981); I and J) *Scotinomys xerampelinus* (from Hooper 1972); K (reversed) and L) *Miotomodon mayi* (from Korth 2011) 1 = paraflexus and anterior enamel atoll; 2 = metaflexus and posterior enamel atoll; 3 = anteromedian groove. Illustrations not to scale.

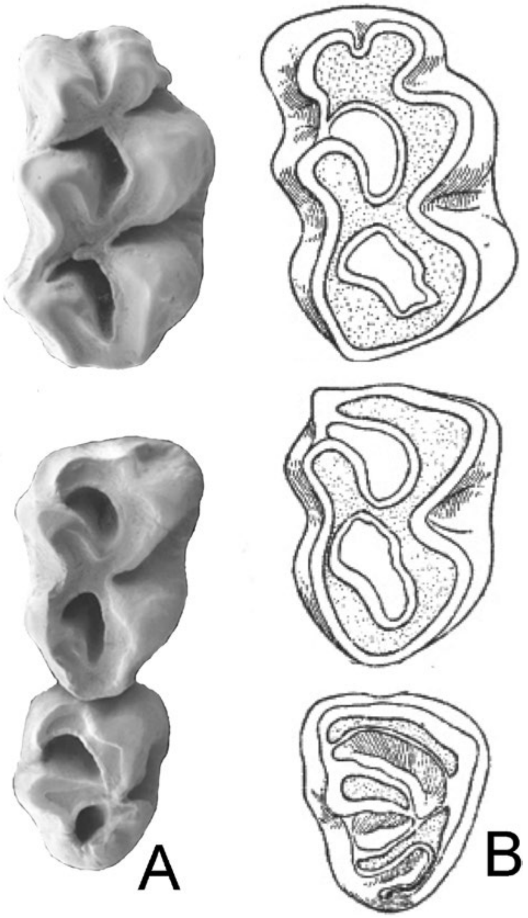

Fig. 9.—Upper dentition of *Byzantinia pikermiensis* (A) from late Miocene of Turkey (from Ünay et al. 2006) compared with that of *Pliotomodon primitivus* (B) from the late Miocene of North America (from Hoffmeister 1945). Illustrations not to scale.

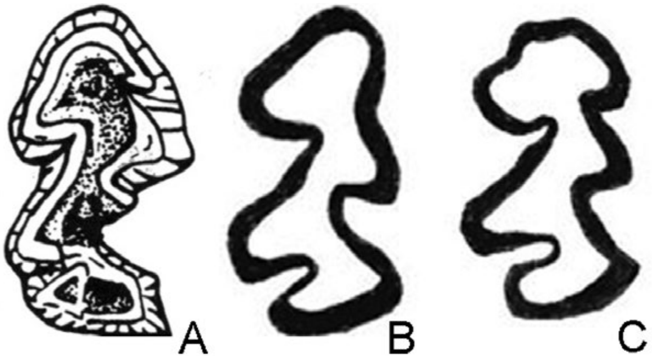

Fig. 10.—Comparison of *Galushamys* and *Repomys* m1. A) *Galushamys redingtonensis* UALP 6021, Rm1 (from Jacobs 1977); B) *Repomys panacaensis* UALP 22798 Lm1 (reversed)(from Mou 2011), C) *R. panacaensis* UALP 21687 Rm1 (from Mou 2011). Illustrations not to scale.

most extant *Neotoma* have three roots on M1 (Repenning 2004). The exceptions are Kansas Blancan *N. quadriplicata*, *N. leucopetrica*, and *N. taylori*, where a small fourth root is encountered with the following frequency (*n* four roots/*n* total; this study): White Rock (*N. leucopetrica*; 2/4), Rexroad 3A (*N. quadriplicata*: 24/30), Deer Park B (*N. quadriplicata*; 4/5), and Borchers (*N. taylori*; 2/9). Among extant woodrats, only *Hodomys alleni* demonstrates four well-developed roots on M1. Despite differences in root count, the temporal position and occlusal morphology of *Lindsaymys* are particularly suited for neotominin ancestry, and we suspect that the Neotomini are descended from a clade of archaic cricetids including *Lindsaymys*, but more likely with three rather than four roots on M1. The accessory root is tiny in *L. takeuchii*, and other populations of the same species might not have expressed

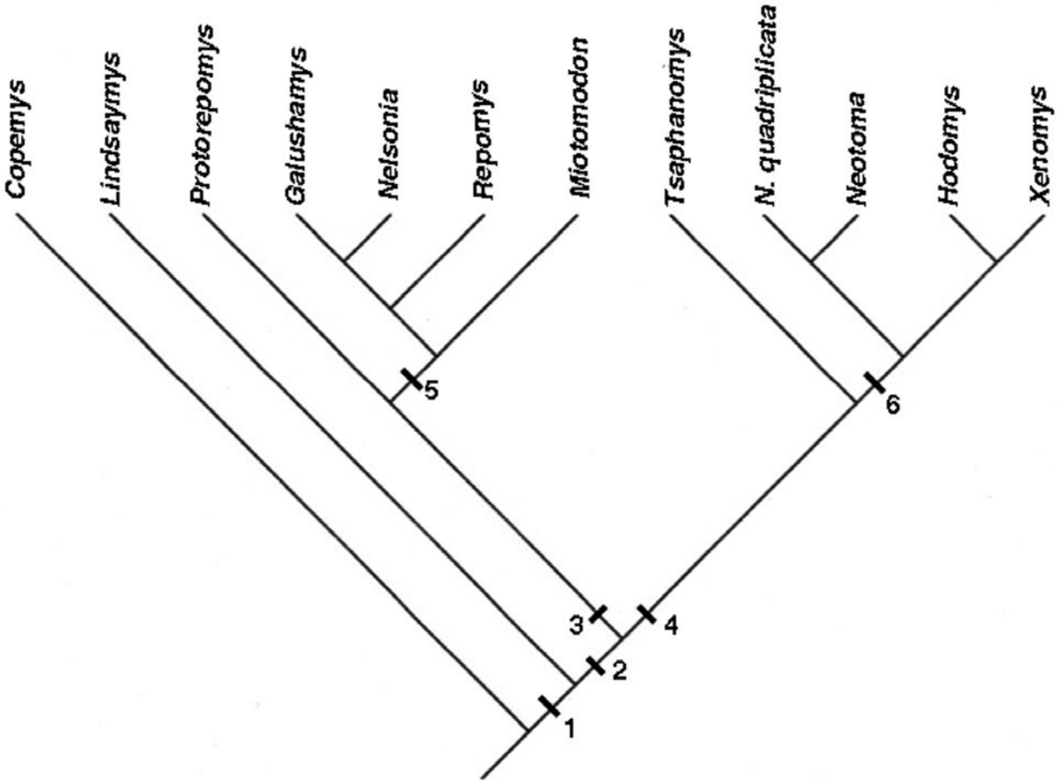

Fig. 11.—Cladogram for neotominins based on character matrix in Appendix I. *Neotoma quadriplicata* is considered as a proxy for *N. quadriplicata, N. leucopetrica* and *N. taylori*, all Blancan woodrats with varying proportions of M1s with a fourth rootlet, a condition that may have evolved independently, and more robustly, in *Hodomys alleni*. Some salient character states indicated by numbers, as follows: 1) crown height at least mesodont, loss of mesoloph/id; 2) mastication surface somewhat planed after light wear; 3) mesolophulid present on m1 in ancestral species; 4) mesolophule/id absent; 5) m3 simple shield shape, 6) M3 complex (E-shaped).

this root. Large Pliocene and Pleistocene *Neotoma* with relatively modern dentitions, four roots on M1, and an S-shaped m3 probably represent a clade separate from modern *Neotoma* with three roots on M1 and a bilobed m3. In this scenario, *Hodomys alleni* could either be descended from a species such as *N. quadriplicata* with four roots on M1 or (perhaps with *X. nelsoni*) from a different extinct species with three roots on M1, in which case the additional roots of *H. alleni* were gained independently of those in *N. quadriplicata*, *N. leucopetrica*, and *N. taylori*.

Both neotominans and galushamyinans display evolutionary trends towards hypsodonty, but a significant size increase, indicated by mean lengths of m1, occurred only in the hypsodont neotominans (Table 4). Dental measurements are not available for *Nelsonia*, but from Hooper's (1954) comparison of the postcranial skeleton, *Nelsonia* is considerably smaller than extant *Neotoma*, just larger than the *Peromyscus* species Hooper examined. The M3 and m3 pair, small to begin with relative to M2 and m2, became a modified simple shield-shape in the galushamyinans, whereas in the neotominans these molars retained more of their ancestral configuration, becoming proportionately longer in some extant *Neotoma* (e.g., *N. albigula*) than in contemporaneous and ancestral species.

Cusp alternation with little dentine connection, combined with relatively deep flexi and flexids, is common in the ancestors of both the neotominans and galushamyinans. As the molars became more lophodont, dentine connections between cusps became more prevalent. Dentine channels widely connect cusps in *Neotoma*, *Hodomys*, *Repomys*, and *Galushamys*. Extant genera in both clades (*Xenomys* and *Nelsonia*) have developed deep penetrance of flexi and flexids, defining a prismatic pattern reminiscent of arvicolines. The m1s referred to *Neotoma* sp. from the Hemphillian Rancho el Ocote assemblage of Mexico (Carranza-Castañeda and Walton 1992) demonstrate alternating cusp patterns, but as the authors noted these molars were from juveniles, and it is not known if the patterns would have opened into confluent lophids with wear. Nevertheless, the Rancho el Ocote *Neotoma* sp. may be the earliest record of *Xenomys*.

Discussion

Hibbard (1967) erected the subgenus *Paraneotoma* for those extinct *Neotoma* species, such as *N. quadriplicata*, with less hypsodont molars than extant species and an S-shaped m3 pattern. Tomida (1987) added a number of characters. However, as discussed by Zakrzewski (1993), the characters listed by Hibbard (1967) and Tomida (1987) are either plesiomorphic or individually variable in a mosaic fashion in *Neotoma* except for the m3 pattern, being either bilobed or S-shaped. The S-shaped m3 is also present in the species *Neotoma spelaea* that Gidley and Gazin (1933) described from the early Pleistocene Cumberland

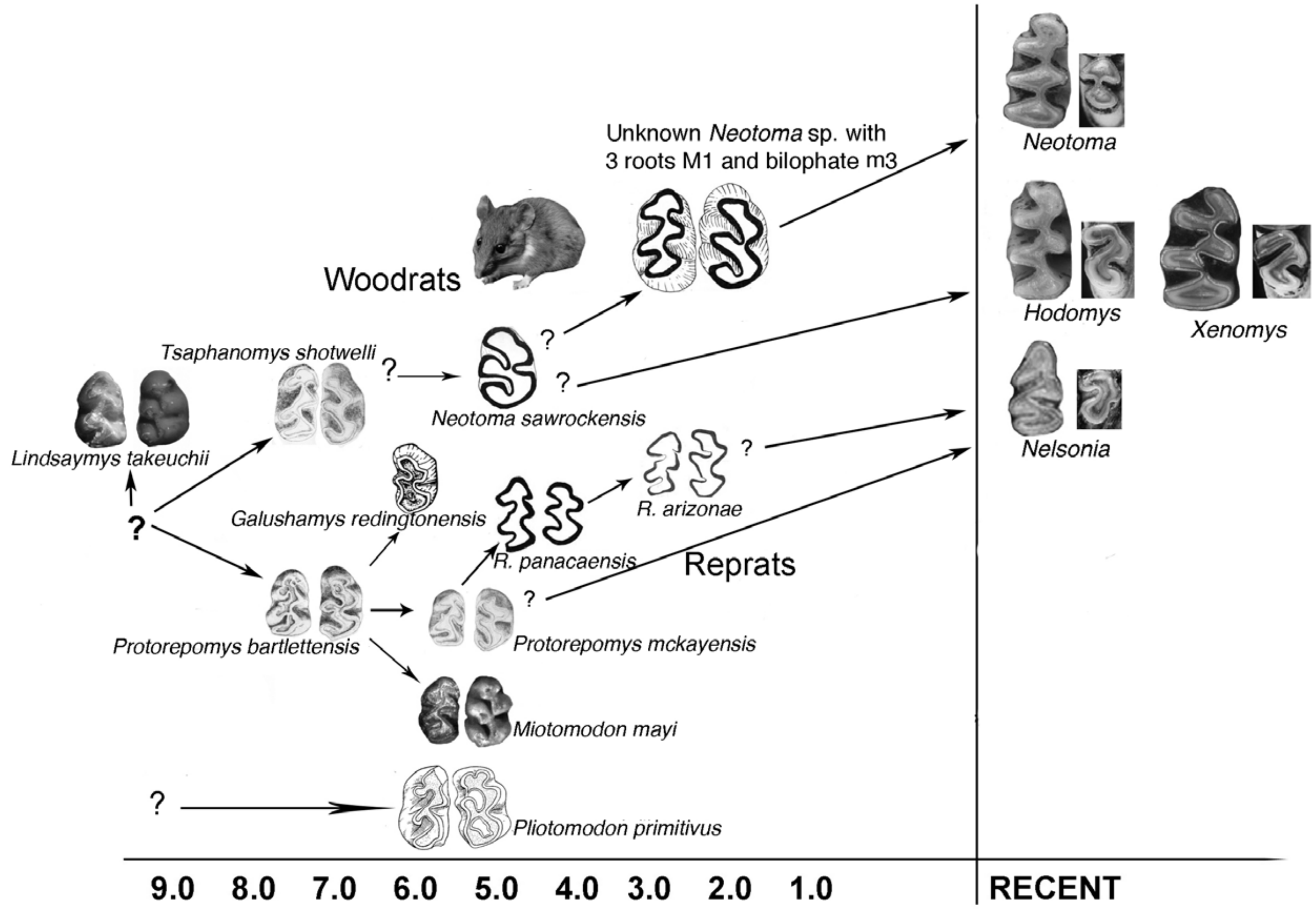

Fig. 12.—Hypothetical phylogeny of neotominin cricetids. Origin and relationships of *Pliotomodon* is uncertain. *R.* = *Repomys*.

Table 4.—Mean and observed range of m1 lengths (in mm) of fossil neotominins. NALMA = North American Land Mammal Age, Fm = formation, E = early, M = middle, L = late, N = number of specimens, O. R. = observed range.

Taxon	Locality	NALMA	*n*	Mean (O.R.)
Neotomina				
[a]*Lindsaymys takeuchii*	Dove Spring Fm	Clarendonian	18	1.99 (1.86–2.10)
[b]*Tsaphanomys shotwelli*	Juniper Creek	L. Hemphillian	1	2.26
[c]*Neotoma* cf *sawrockensis*	Rancho el Ocote	L. Hemphillian	3	2.64 (2.56–2.76)
[d]*N. quadriplicata*	Rexroad Loc. 3	M. Blancan	30	3.39 (2.96–3.80)
[d]*N. leucopetrica*	White Rock	L. Blancan	8	3.82 (3.39–4.13)
[d]*N. taylori*	Borchers	L. Blancan	10	3.32 (3.03–3.64)
[e]*N. fossilis*	San Timoteo	L. Blancan-E. Irv.	5	3.03 (2.85–3.09)
[f]*N. amplidonta*	Java	E. Irvingtonian	2	4.7 (4.5–4.8)
Galushamyina				
[b]*Protorepomys bartlettensis*	Bartlett Mountain	Clarendonian	2	1.65 (1.64–1.66)
[b]*P. mckayensis*	McKay Reservoir	L. Hemphillian	9	1.73 (1.61–1.90)
[g]*Galushamys redingtonensis*	Redington	L. Hemphillian	1	2.23
[h]*Miotomodon mayi*	Pinole	L. Hemphillian	2	2.50 (2.50, 2.50)
[i]*Repomys gustelyi*	Horned Toad Fm	?L. Hemphillian	9	2.45 (2.31–2.53)
[j]*R. minor*	Panaca	E. Blancan	22	*1.77 (1.60–1.88)
[j]*R. panacaensis*	Panaca	E. Blancan	53	**2.07 (1.92–2.36)
[i]*R. maxumi*	Maxum	?M. Blancan	4	2.78 (2.63–2.99)
[k]*R. arizonensis*	111 Ranch	L. Blancan	4	2.16 (2.08–2.28)

*Mean of 6 means, **Mean of 4 means.

[a]Kelly and Whistler (2014), [b]Shotwell (1967), [c]Carranza-Castañeda and Walton (1992), [d]Zakrzewski (1991), [e]Albright (1999), [f]Zakrzewski (1985), [g]Jacobs (1977), [h]Korth (2013), [i]May (1981), [j]Mou (2011), [k]Tomida (1987).

Cave, Maryland. Gidley and Gazin (1933) assigned *N. spelaea* to their new genus *Parahodomys*, but as noted by Hibbard (1967), despite retaining the S-shaped m3 *N. spelaea* displays more of the derived characters of modern *Neotoma* than of earlier species such as *N. quadriplicata*. Whereas a revision of fossil and modern woodrats is beyond the scope of this study, it is recommended that both *Paraneotoma* and *Parahodomys* be abandoned, as they were based on an older evolutionary grade taxonomic concept. If *Hodomys* continues to be considered a genus distinct from *Neotoma*, it may be that extinct *Neotoma* species with the S-shaped m3 plus the modern *H. alleni* and *X. nelsoni* should be combined within *Hodomys*. However, the bilobed m3 might have evolved multiple times from different ancestors with S-shaped m3s.

Nelsonia is an extant genus that has perplexed researchers for years. Hooper (1954) compared *N. neotomodon* with *Peromyscus*, *Neotomodon*, and *Neotoma*, concluding that *N. neotomodon* was a "diminutive woodrat." There is considerable resemblance between the dentition of *N. neotomodon* and that of *Neotoma* (Fig. 2), but also some derived characters in *Nelsonia*, including: 1) flexi and flexids alternate rather than opposite, and 2) simplification of M3 and m3. As in *Neotoma*, *Nelsonia* does not display the characteristic mesolophule and mesolphulid as is seen in *Repomys* and its relatives. However, the M3 and m3 morphology of *Nelsonia* is so similar to *Repomys* that despite the absence of the mesolophule and mesolophulid, *Nelsonia* is considered here to be a highly derived galushamyinan as suggested by May (1981).

In his review of Hemphillian mammals from the Coffee Ranch assemblage of Texas, Dalquest (1983) described a new woodrat, *Neotoma minutus*. The holotype TMM 41261-48 (Fig. 2E) was identified as a juvenile m3 and a paratype, TMM 41262-47, was considered an M2. The holotype is not a woodrat m3, as can be seen by the double columnar form with two sub-circular cusps. This morphology is most closely matched by p4s from an early member of the Geomyoidea (Russell 1968), in which an additional reentrant fold can also be seen part way down the tooth. Consequently, we consider the name *N. minutus* a nomen dubium. The second specimen, TMM 41262-47, was identified by Dalquest as an M2, but appears to be the M3 of a woodrat. Recent photographs of the specimen provided by C. Sagabiel (University of Texas) were consistent with the drawing provided by Dalquest (1983, fig. 11A) and will not be presented here. As an M3, measurements of this tooth are not particularly small, and are similar to those of the M3 of *N. vaughani* from the Verde Fm of Arizona (Czaplewski 1990). We are hesitant to name a new species based on the M3 or to refer the molar to a known species because the tooth is quite advanced in morphology, mimicking the M3 of a number of Pliocene through modern species of the genus *Neotoma*. Until additional material from the type Coffee Ranch quarry demonstrates that contamination from a more recent stratigraphic level has not occurred, we prefer to view TMM 41262-47 as an unsubstantiated record of *Neotoma*.

Our evolutionary scenario for the Neotomini suggests that hypsodont taxa such as *Repomys* and *Neotoma* evolved from brachydont or mesodont ancestors such as *Tsaphanomys* and *Protorepomys* subsequent to about 7 Ma, the earliest record for either of these genera in Oregon. However, Kelly and Whistler (2014) reported a single broken molar with moderate wear they interpreted as an M2 of " cf. *Repomys* sp." from locality 5690 in sediments of the type Dove Spring Fm of the Mojave Desert, southern California. They estimated the level with locality 5690 to be around 8 Ma, although they suggested the specimen, LACM 156378, "… appears to represent a new genus of Galushamyini, less derived than *Repomys*" (Kelly and Whistler 2014: 32). Locality 5690 also includes the first appearance of *Bensonomys*. All of the more ancient cricetids such as *Lindsaymys*, *Copemys*, *Acrolophomys*, and *Antecalomys* common in lower sediments were absent from locality 5690. Clearly, some sort of differentiation, either temporal or environmental, separates locality 5690 from lower rodent assemblages in the Dove Spring Fm. We accept the Kelly and Whistler (2014) assessment of LACM 156378 and, if the specimen is from a galushamyinan, it may be the earliest record of this subtribe in North America, perhaps a species of *Protorepomys*.

The limited number of advanced neotominans prior to the record of *Neotoma sawrockensis* at about 4.7 Ma is probably not a function of collecting bias. Hypsodont *Neotoma* are regularly encountered in assemblages from the early Pliocene through latest Pleistocene in North America. Modern taxa are present in Central America. However, with the possible exception of the Gray Fossil Site in Tennessee (Samuels et al. 2018), galushamyinans are absent east of the Mississippi River or south of the United States border. The Meade Basin of southwestern Kansas has been a semi-arid prairie for most of the late Cenozoic (Martin and Peláez-Campomanes 2014) but galushamyinans have not been reported from rodent assemblages in the basin. Because of their western distribution, it is tempting to suggest that galushamyinans were confined to arid ecosystems, but their absence from the Meade Basin and the ecology of *Nelsonia neotomodon* and its rare relative *N. goldmani* suggests an alternative. Both *Nelsonia* species are found at high elevations in the pine and fir forests of mountainous western Mexico. Consequently, ancestral galushamyinans might have been confined to ecosystems dominated by arid- or cold-adapted conifers, either at high elevations or lower elevations during glacial advances. This hypothesis would explain their fossil distribution, primarily confined to the Basin and Range Province of western North America. The ancestors of *Nelsonia* likely followed the Rocky Mountains south into the Sierra Madre Occidentale of western Mexico, and thus *Nelsonia* represents the last survivor of the mostly extinct Galushamyina. In the phylogeny of Fig. 12, an alternate hypothesis is presented for the ancestry of *Nelsonia*. Assuming the simplified M3 and m3 pattern of *Nelsonia* is not a convergent character with galushamyinans from a neotominan ancestor, *Nelsonia* could be descended from an earlier galushamyinan such as *Protorepomys* rather than from a more hypsodont ancestor such as *Repomys*. This remains a possibility for the following reasons: 1) *Nelsonia* apparently evolved in a geographic region separate from known species of

Repomys, 2) intermediates between *Repomys* and *Nelsonia* are unrecognized, and 3) the hypoflexid on m1 of *Protorepomys mckayensis* is relatively deep and provergent. A continuing trend towards closure of lophs, greater hypsodonty and simplification of the M3 and m3 could have theoretically produced a *Nelsonia*-like dentition from *P. mackayensis.*

The origin of modern woodrats is obscure. All Blancan and some Irvingtonian *Neotoma* and the extant *Hodomys alleni* and *Xenomys nelsoni* have an S-shaped m3, whereas all extant *Neotoma* species have a bilobed m3. The oldest fossil woodrat sample with a bilobed m3 is *Neotoma amplidonta* from the Java assemblage of South Dakota (Zakrzewski 1985). Based on a variety of taxonomic assessments, including the presence of the archaic vole *Microtus pliocaenicus*, Java is considered to have been deposited between 2.0–1.35 Ma in Great Plains rodent zone 13 (Martin 2003). The next oldest record of the bilobed m3 is *Neotoma* cf. *fuscipes* from Shutt Ranch, an Irvingtonian site in the San Timoteo Badlands of southern California assigned an age of about 0.9 Ma (Albright 1999). Around the Matuyma–Gauss boundary (~0.78 Ma), five modern *Neotoma* species are recorded from stratified deposits in Porcupine Cave, Colorado (Repenning 2004). Based on these considerations, it appears likely that the modern *H. alleni* and *X. nelsoni* originated earlier than extant *Neotoma* species from one or more ancestral woodrat species with an S-shaped m3. This is consistent with the potential record of *Xenomys* from Rancho el Ocote discussed above. Modern woodrats appear to have evolved subsequent to about 2.0 Ma from a *Neotoma* species with three roots on M1 and a bilobed m3.

In conclusion, the Neotomini comprises two subtribes, the Neotomina (woodrats), including *Tsaphanomys*, *Neotoma*, *Hodomys*, and *Xenomys* and the Galushamyina (reprats), including *Protorepomys*, *Repomys*, *Miotomodon*, *Galushamys*, and *Nelsonia*. *Galushamys* is considered a North American endemic, possibly descended from *Protorepomys*. Although its occlusal morphology possibly qualifies *Lindsaymys* as an early member of the Neotomini, four roots on M1 may preclude *Lindsaymys* from occupying an ancestral position to either later neotominans or galushamyinans. During the late Cenozoic galushamyinans were mostly confined to the Basin and Range Province of western North America, and are survived by two species of *Nelsonia* at high elevation in western Mexico. Extant *Neotoma* species with a bilobed m3 appear to have originated subsequent to about 2.0 Ma, whereas *Hodomys alleni* and *Xenomys nelsoni* likely originated earlier from one or more extinct neotominan ancestors with an S-shaped m3.

We recognize there are gaps in the fossil record of the Neotomini that leave open a number of alternative scenarios to our hypothesis of woodrat origins and relationships. The taxonomic position of *Lindsaymys* and associated cricetids from the Dove Spring Fm of California is certainly debatable. Despite results of the phylogenetic analysis, the distinction between *Tsaphanomys* and *Protorepomys* and their suggested ancestral positions to later neotominins is difficult to substantiate despite morphological similarities and the associated logical argument. We feel more secure about the phylogenetic ties of reprats and woodrats, and this has driven our search for ancestral taxa among late Miocene cricetids, especially in western North America. We hope this comprehensive hypothesis of woodrat ancestry will serve as the basis for further research and, especially, of further collection of late Miocene cricetids.

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APPENDIX I

Character matrix and characters used in phylogenetic analysis of the neotominins.

	Acd	CH	MS	Loph	Acs	Metfld	Mflx	m3	M3	rM1
Copemys russelli	0	0	0	0	0	0	0	0	0	0
Lindsaymys	1	1	0	1	2	0	0	0	0	1
Tsaphanomys	1	1	1	2	2	1	0	0	0	0
Protorepomys	1	1	1	2	1	1	0	0	0	0
Repomys	1	1	2	2	1	1	0	1	2	0
Miotomodon	1	1	1	2	1	1	0	?	2	0
Galushamys	1	1	2	2	2	1	1	?	2	0
Neotoma	1	1	2	2	2	1	0	3	1	0
N. quadriplicata	1	1	2	2	2	1	0	2	1	1
Hodomys	1	1	2	2	2	2	0	2	1	1
Xenomys	1	1	2	2	2	2	0	2	1	0
Nelsonia	1	1	2	2	2	1	0	1	2	?

Characters:
Anteroconid connections m1 (Acd): 0 = metaconid distinctly separate from anteroconid, anterolabial cingulum not highly confluent with anteroconid, 1) = metaconid, anteroconid, and anterolabial cingulum of m1 confluent after light wear (irreversible).
Crown height (CH): 0 = brachydont, 1 = mesodont or hypsodont (irreversible).
Mastication surface (MS): 0 = terraced, 1 = terraced/planed, 2 = planed (irreversible).
Lophodonty (Loph): 0 = absent, 1 = incipient, 2 = moderately developed, 3 = highly developed (irreversible).
Accessory structures (Acs): 0 = mesoloph/id present, 1= mesolophule/id present, 2 = accessory structures absent (unordered).
Protoconid/entoconid confluency (PrEnt): 0 = alternate, 1= alternate/confluent, 2 = confluent, 3 = secondarily alternate (ordered).
Metaflexid m1 (Metfld): 0 = deep, 1 = shallow or absent after light wear, 2 = secondarily deep (unordered).
Metaflexus M1 (Mflx): 0 = open, 1 = closed (irreversible).
m3 form (m3): 0 = primitive S-shaped, 1= simple shield shape, with one or no flexids, 2 = terraced S-shaped, 3 = bilophate (unordered).
M3 form (M3): 0 = not E-shaped, not reduced version of M2; 1 = E shaped, reduced version of M2; 2 = simple shape, with only paraflexus (unordered).
Roots M1 (rM1): 0 = 3, 1 = 4 (unordered).