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Morphology and genetics of grasshopper mice revisited in a paleontological framework: reinstatement of Onychomyini (Rodentia, Cricetidae)

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Grasshopper mice of the genus *Onychomys*, represented by three living species in North America, have a long and controversial taxonomic history. Usually allocated to either the cricetine or neotomine cricetids, they also have been considered to represent a distinct tribe. Since the discovery and description of the extinct grasshopper mouse relative *Acrolophomys rhodopetros* from the late Miocene of the upper Dove Spring Formation of California, dated at 9.3–8.8 Ma, it has become apparent that the grasshopper mouse clade has a long, distinct evolutionary history. Using a combination of morphological (including paleontological material) and molecular data, we reassessed the phylogenetic position of grasshopper mice. A morphological phylogenetic analysis was done on fossil and modern specimens of all recognized neotomine tribes, including craniodental, phallic, and soft tissue characters. A DNA-based matrix was constructed including 72 species representing all known living genera of Neotominae and 13 outgroup taxa belonging mostly to cricetid subfamilies. DNA sampling covered the mitochondrial protein-coding gene cytochrome-b (*Cytb*), and seven nuclear loci. The morphological analysis yielded a single most parsimonious tree of 42 steps, placing *Ochrotomys* (Ochrotomyini), *Baiomys* (Baiomyini), *Reithrodontomys* (Reithrodontomyini), and an *Onychomys–Acrolophomys* clade as successive sister clades to a *Peromyscus* clade, respectively. The molecular phylogenetic analyses recovered seven major clades: (1) a clade including *Habromys*, *Megadontomys*, *Neotomodon, Osgoodomys, Podomys*, and a paraphyletic *Peromyscus* clade, sister to (2) a second clade containing extant *Onychomys* species, (3) a *Reithrodontomys* clade, (4) an *Isthmomys* clade, (5) a clade including *Baiomys* and *Scotinomys*, (6) an *Ochrotomys* clade, and (7) a well-supported clade containing *Hodomys*, *Neotoma*, and *Xenomys*. A Bayesian combined morphological and molecular analysis recovered the same major phylogenetic associations as the molecular analyses. The sum of molecular markers and morphological traits expressed by *Acrolophomys* and *Onychomys* leads to a phylogenetic position supporting their recognition as a distinct tribe.

Key words: *Acrolophomys*, late Miocene, Neotominae, *Onychomys*, Peromyscini, Reithrodontomyini
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Grasshopper mice, genus *Onychomys* Baird, 1857, are widely distributed in desert and prairie habitats throughout the Great Plains, deserts of the southwestern United States, and northern Mexico. *Onychomys* includes three extant species, the northern grasshopper mouse (type species) *O. leucogaster* (Wied, 1841), the southern grasshopper mouse *O. torridus* (Coues, 1874), and

Mearns' grasshopper mouse *O. arenicola* Mearns, 1896, plus a number of fossil forms (Carleton and Eshelman 1979; Musser and Carleton 2005; Bradley et al. 2017). As the common name implies, these stocky little rodents are almost exclusively carnivorous, and will eat virtually any animals they encounter, including those more than double their size. Vernon Bailey's (1929) account of his encounters with this group makes up most of the apocryphal information repeated in the later literature. Bailey (1929) reported that both *O. leucogaster* and *O. torridus* vocalized at night, much as a wolf, by sitting up on their hindquarters, throwing their head back with mouth agape, and releasing their shrill cries. In addition to eating insects and arachnids, individuals of both species consumed other rodents caught in Bailey's traplines. This author also reported that grasshopper mice were distributed in a patchy, unpredictable pattern, and although they could be locally abundant, were generally encountered less frequently than other small rodents. Subsequent studies have confirmed much of Bailey's observations (Egoscue 1960; Hildebrand 1961; Ruffer 1968; Flake 1973; McCarty 1978; Hafner and Hafner 1979; Pasch et al. 2017). Grasshopper mice are highly aggressive and will kill other members of their species if placed in near proximity, for example, in captivity. Their home range is larger than herbivorous rodents at equal body size. Additionally, Rowe and Rowe (2008) and Rowe et al. (2013) demonstrated that *O. torridus* has a physiological response protecting it from the venom of the bark scorpion, one of its preferred dietary items.

Being so differentiated in morphology and habits from other closely related genera, the phylogenetic relationships of grasshopper mice have been controversial (e.g., Thomas 1888; Hollister 1914; Carleton and Musser 1984). Although most often allocated to the cricetine or neotomine cricetids (e.g., Musser and Carleton 2005; Lindsay 2008; Ronez et al. 2021), *Onychomys* occasionally have been considered as a more unique taxonomic group, including a separate tribe (Vorontsov 1959).

In order to further clarify the phylogenetic relationships of grasshopper mice, in this study we provide a reassessment of the morphology, genetics, and paleontology of *Onychomys* and its relatives, with special attention to the late Miocene fossil genus *Acrolophomys* Kelly and Whistler (2014).

Materials and Methods

Studied specimens and anatomical concepts.—Extant and extinct neotomine genera representing the recognized tribes (i.e., Baiomyini, Ochrotomyini, Neotomini, and Peromyscini plus several taxa corresponding to fossil forms) were directly inspected through specimens housed largely in American collections. Main anatomical concepts employed here follow Vorontsov (1967, 1982), Carleton (1980, 1989), and Carleton and Musser (1984). Dental nomenclature follows Martin et al. (2020) with modifications by Kelly et al. (2020). In addition, a topological analysis of molar occlusal structures based on the concepts developed by Barbière et al. (2019) was conducted on both *Acrolophomys* and *Onychomys*. Supplementary Data SD1 illustrates the differences in nomenclature between traditional and ICAMER (Iteration of Cuspal Area with Mirror Effect and Rotation; Barbière et al. 2019) concepts. Dental formulae follow standard usage with upper teeth designated by capital letters and lower teeth by lowercase letters.

Morphological phylogenetic analysis.—A morphological phylogenetic analysis of fossil and modern specimens—including dental, mandibular, phallic, and soft tissue characters—was performed using the TNT program of the Willi Hennig Society (Goloboff and Catalano 2016; see also Goloboff et al. 2008) with implicit enumeration and all character states unordered (nonadditive). It included *Onychomys* and *Acrolophomys*, the latter an extinct genus proposed as ancestral to *Onychomys* (Kelly and Whistler 2014), along with other extant members of Neotominae (*Ochrotomys*, *Baiomys*, *Reithrodontomys*, *Peromyscus*) that have been previously identified by a number of molecular studies as more closely related to *Onychomys* than other Neotominae, specifically Neotomini (e.g., Reeder et al. 2006; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Steppan and Schenk 2017). *Copemys loxodon*, the type species and one of the best-known species of *Copemys* (Ronez et al. 2020), was the outgroup. *Copemys* first occurs in North America during the late Hemingfordian North American Land Mammal Age at about 16.3 Ma (Lindsay 1995) and is generally accepted as a Eurasian immigrant related to Old World *Democricetodon* (Falbush 1967; Lindsay 1972, 1995, 2008; Vianey-Liaud 1974; Engesser 1979; Maridet et al. 2011; Ronez et al. 2020). *Copemys* as currently recognized comprises a complex of nine Miocene species, probably not all congeneric (Martin and Zakrzewski 2019; Kelly et al. 2020; Ronez et al. 2020). Later North American Miocene Neotominae and possibly Sigmodontinae may have been derived from various members of the *Copemys* species complex (Lindsay 2008; Ronez et al. 2020, 2021). Representative examples of the molars of taxa included in the morphological analysis are presented in Figs. 1–3. Taxa, characters states, character state matrix, and specimens used in the morphological and molecular analyses are presented in Appendices I–IV.

Molecular phylogenetic analysis.—The DNA-based matrix included 72 species representing all known living genera of Neotominae and 13 outgroup taxa belonging mostly to Cricetidae subfamilies. All nucleotide sequences were obtained from GenBank (Supplementary Data SD2). DNA sampling covered the mitochondrial protein-coding gene cytochrome-b (*Cytb*), and seven nuclear loci: intron 2 and parts of exons 2 and 3 of acid phosphatase type V (*Acp5*), intron 2 of the alcohol dehydrogenase gene (*Adh1-I2*), exon 6 of the protein-coding dentin matrix protein 1 gene (*Dmp1*), intron 7 of the beta-fibrinogen gene (*Fgb-I7*), exon 10 of the growth hormone receptor (*GHR*), single exon of the recombination activation 1 gene (*RAG1*), and the first exon of the nuclear gene interphotoreceptor retinoid-binding protein (*Rbp3*). Our selection of genes was based on their extensive use in rodent systematics (e.g., *Cytb*, *Rbp3*), and their availability for Neotominae (e.g., Reeder and Bradley 2004; Bradley et al. 2007; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Steppan and Schenk 2017).

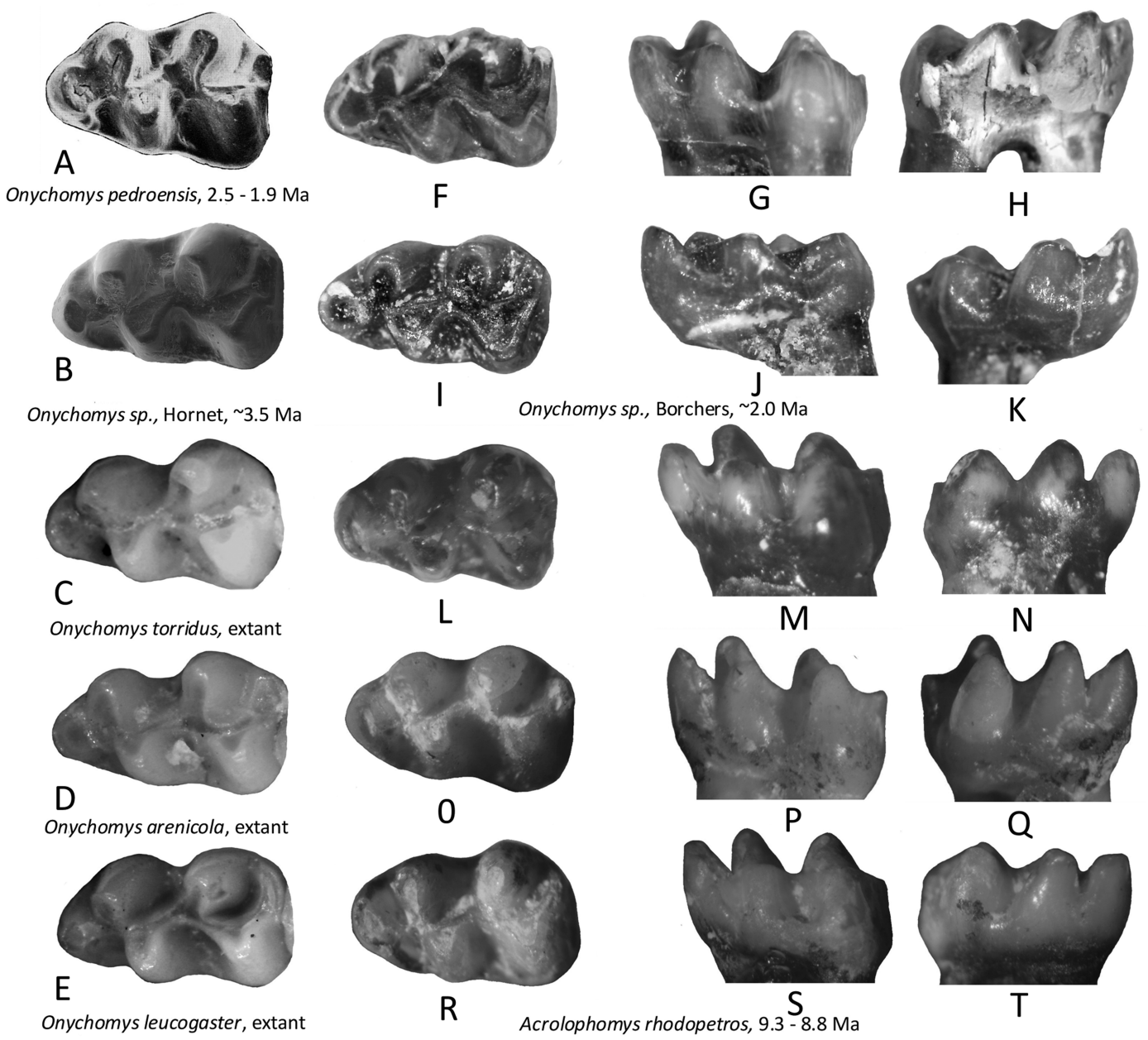

Fig. 1.—First lower molars of *Onychomys* and *Acrolophomys*. *Onychomys*: A—Lm1, UALP 13963, 111 Ranch, Arizona, Blancan (from Tomida, 1985); B—Rm1, FHSM VP-19867, reversed, Hornet, Meade Basin, Kansas, Blancan, photo by P. Peláez-Campomanes; C—Lm1, USNM 525590; D—Lm1, USNM 017881; E—Lm1, USNM 272116; F–H—Rm1, FHSM VP-19868, reversed, Borchers, Meade Basin, Kansas, Blancan; I–K—Lm1, FHSM VP-19869, Borchers, Meade Basin, Kansas. *Acrolophomys*: L–N—Rm1, reversed, LACM 124878; O–Q—Lm1, LACM 124912; R–T—Rm1, reversed, LACM 156372, Dove Springs, California, latest Hemphillian–earliest Blancan, from Kelly and Whistler (2014). Occlusal views, A–F, I, L, O, and R. Labial views, G, J, M, P, and S. Lingual views, H, K, N, Q. All m1s adjusted to equal length.

Multiple sequences alignment was carried out independently for each locus with ClustalX (Larkin et al. 2007; Supplementary Data SD3). To determine the divergence levels between Neotominae genera and the current tribal arrangements, we calculated genetic distance values using the Kimura 2-parameter correction model (K2P) with MEGAX (Kumar et al. 2018). The K2P model was chosen in order to allow comparisons between our genetic divergence values of Cytb with those obtained in the most recent study focused on *Peromyscus* and Neotominae (Platt et al. 2015). Phylogenetic analyses were conducted on the concatenated matrix using maximum parsimony (MP; Kluge and Farris 1969; Farris 1982), maximum likelihood (ML; Felsenstein 1981), and Bayesian inference (BI; Huelsenbeck et al. 2001) approaches. MP analyses were carried out in PAUP*4 (Swofford 2000) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection reconnection (TBR) branch swapping. The nodal support was calculated through 1,000 bootstrap replicates (BT) with five replicates of sequence

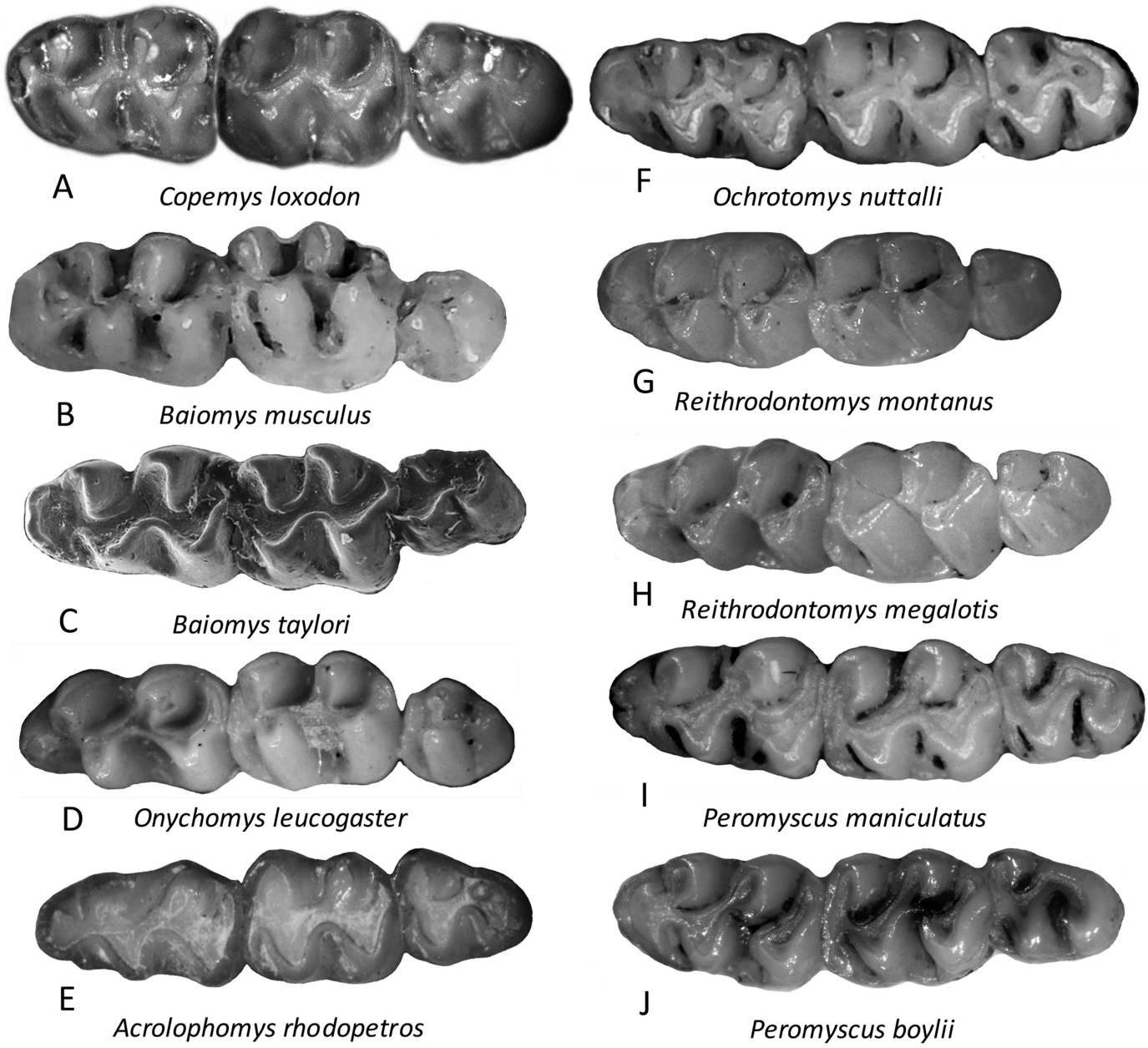

Fig. 2.—Examples of lower molars of species included in the morphological cladistic analysis. A—Rm1–3, reversed, UCMP 317546, from Ronez et al. (2020). B—Rm1–3, reversed, MVZ 105624, photo by A. Pacheco-Castro. C—Rm1–3, reversed, MNCN-275, photo by P. Peláez-Compomanes. D—Rm1–3, reversed, USNM 27211. E—Rm1–3, reversed, LACM 125052, from Kelly and Whistler (2014). F—Lm1–3, FMNH 230688, photo by C. Ronez. G—Lm1–3, UNSM 272173, photo by R. Martin. H—Rm1–3, reversed, MVZ 219614. I—Lm1–3, MVZ 225121. J—Lm1–3, MVZ 219161. Photos H, I, and J by Jessica L. Blois, UC Merced. All occlusal views. Not to scale, all m1s adjusted to equal length.

addition each. ML analysis was carried out with the IQ-TREE version 1.6 software (Nguyen et al. 2015) using the default settings, with 1,000 iterations of ultrafast bootstrap (Hoang et al. 2018) as a measure of node support. BI analysis was conducted with MrBayes 3.2 (Ronquist et al. 2012). Two independent runs, each with three heated and one cold Markov chains, were allowed to proceed for 10 million generations and were sampled every 1,000. We verified that each run had stabilized by plotting the log-likelihood values against generation time for each run in Tracer v1.7.1 (Rambaut et al. 2018) later discarding the nonstabilized regions as burn-in. The saved trees were used to construct a majority-rule consensus tree and obtain the support values for each clade as posterior probabilities. Following Abadi et al. (2019), use of a model of molecular evolution richer in parameters leads to similar inferences to the model obtained by most currently used model selection strategies (e.g., Akaike's criterion, jModeltest, PartitionFinder). For this reason, the GTR+I+Γ model was applied in both ML and BI analyses, where each locus was considered as a distinct partition. Additionally, we

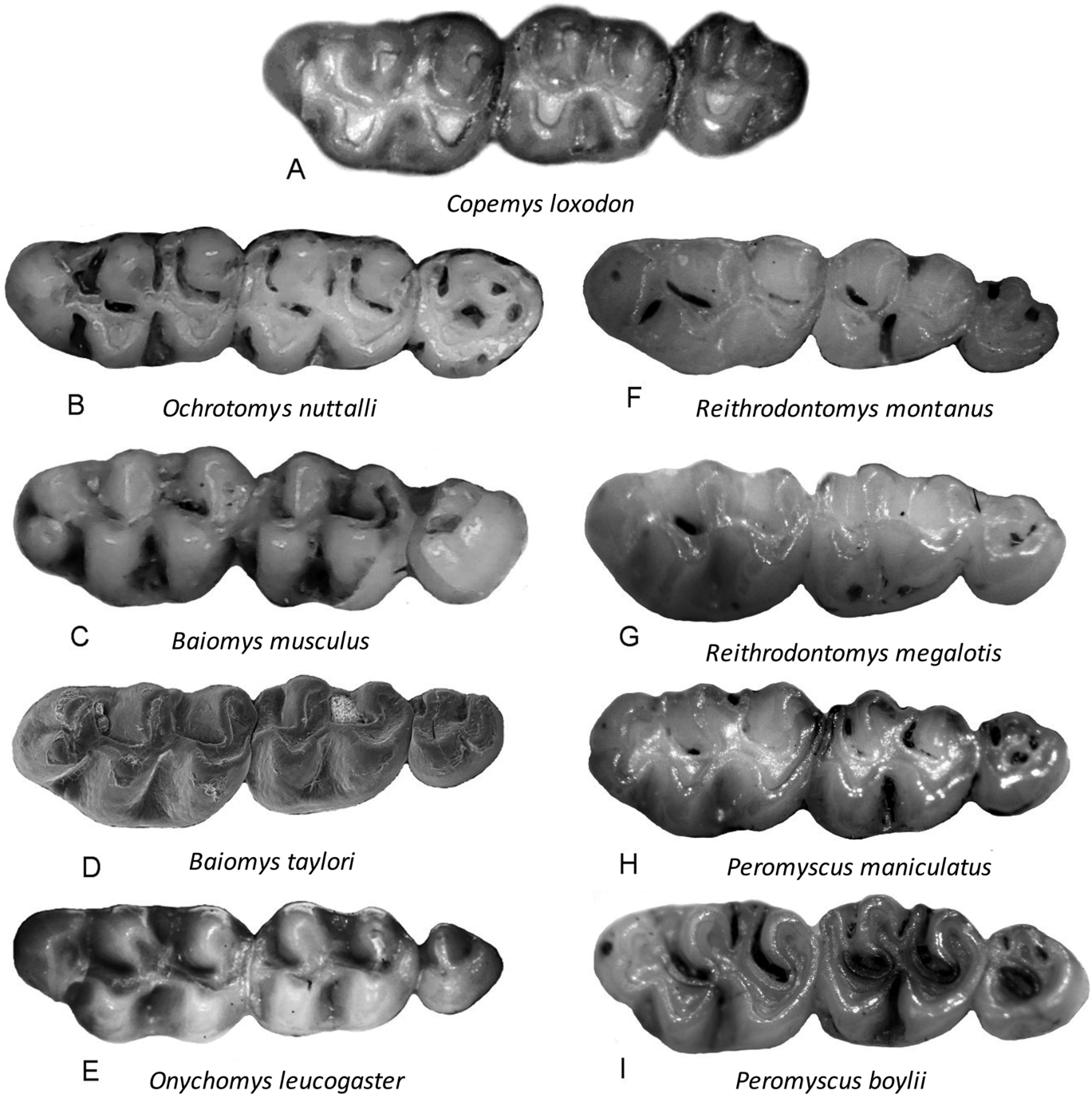

Fig. 3.—Examples of upper molars of species included in the morphological cladistic analysis, upper molars unknown for *Acrolophomys*. A—LM1–3, UCMP 317400, from Ronez et al. (2020). B—RM1–3, reversed, FMNH 230688, photo by C. Ronez. C—LM1–3, MVZ 105624, photo by A. Pacheco-Castro. D—LM1–3, MNCN-275, photo by P. Peláz-Campomanes. E—LM1–3, USNM 272116, photo by R. Martin. F—LM1–3, USNM 272176, photo by R. Martin. G—RM1–3, reversed, MVZ 219614. H—RM1–3, reversed, MVZ 225121. I—RM1–3, reversed, MVZ 219161. Photos G, H, and I by Jessica L. Blois, UC Merced. All occlusal views. Not to scale, all M1s adjusted to equal lengths.

implemented a Bayesian analysis on the combined data set. We used two-character partitions, morphology and DNA. We ran the standard partition using the Mk model, set by default in MrBayes software for morphological characters, which assumes no constant characters are present (Mkv model; Lewis 2001). This was done using the standard model for unordered characters with a standard gamma distribution to accommodate the rate variation across sites. The DNA partition was run using the same evolution model and parameters described above for the multilocus matrix. Both for the concatenated matrix of the eight loci, and for the combined analysis of the morphological and molecular characters, we added ambiguous character states or missing data for those taxa that lack information on one or more evidence sources.

Molecular dating.—In order to estimate divergence times for the sampled Neotominae taxa, a Bayesian analysis in BEAST v2.6.5 (Bouckaert et al. 2019) using the full molecular dataset was performed. Partitions and nucleotide substitution models were as in the ML and BI phylogenetic analyses. A Yule speciation process using an initial random tree and other priors set as default were used. Runs were performed under an uncorrelated lognormal relaxed-clock model previously determined based on Bayes factor comparisons. Four independent runs of 10 million generations, sampled every 1,000 generations were performed. Likelihood scores convergence and stability were checked in Tracer v 1.7.1 (Rambaut et al. 2018), obtaining an effective sample size (ESS) greater than 200 for all parameters. Log and tree files were combined using LogCombiner v.2.6.6 and compiled into a maximum clade credibility tree using TreeAnnotator to display mean node ages and highest posterior density (HPD) intervals (95% upper and lower) for each node (BEAST package; Bouckaert et al. 2019).

Fossil calibrations constraints were employed as lognormal prior distribution. We used the following fossil records as calibration points: (1) the crown group of *Baiomys* based on the first appearance of *B. kolbhi* at ~5.1 Ma (Y3 at Yepómera; Jacobs and Lindsay 1984; Lindsay et al. 2006); (2) the stem group of Neotomini tribe based on *Lindsaymys takeuchii* at ~9.2 Ma (Dove Spring Formation; Kelly and Whistler 2014; Martin and Zakrezewski 2019); (3) the crown group of *Onychomys* based on *O.* sp. record at ~5.3 Ma (Mailbox; Martin 2019:appendix 1); (4) the stem group of the Peromyscini tribe based on the first appearance of *Peromyscus* sp. at ~4.85 Ma (Horn Toad Hills; May et al. 2011); and (5) the crown clade of *Reithrodontomys* based on the first appearance of *R. wetmorei* at ~4.5 Ma (Fox Canyon; Martin 2019:appendix 1).

Abbreviations.—L, left; Ma, megannum (1 million years in the radioisotopic time scale); R, right.

North American Land Mammal ages (e.g., Clarendonian, Hemphillian, Blancan, and Rancholabrean) follow Tedford et al. (2004), Lindsay et al. (2002), and Martin et al. (2008).

Results

Morphological phylogenetic analysis.—The morphological analysis yielded a single most parsimonious tree of 42 steps with a consistency index (CI) of 0.850 and retention index (RI) of 0.920. The tree typology (Fig. 4) matches that in a number of recent molecular studies (e.g., Reeder et al. 2006; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Steppan and Schenk 2017), placing *Ochrotomys* (Ochrotomyini), *Baiomys* (Baiomyini), *Reithrodontomys* (Reithrodontomyini), and *Onychomys* (= *Onychomys–Acrolophomys* clade, this study) as successive sister clades to a *Peromyscus* clade, respectively. Our phylogenetic analysis supports the recognition of an *Acrolophomys–Onychomys* clade that diverged from the *Copemys* species complex during the late Miocene, which is close to the estimated molecular divergence date of the *Onychomys* clade in Sullivan et al. (1995) and in the maximum clade credibility tree of Keith (2015).

Molecular phylogenetic analysis.—Molecular-based phylogenies recovered a monophyletic Neotominae and produced similar well-resolved topologies (Figs. 5–7; see also Supplementary Data SD4 for outgroup topologies). The main relationships were mostly congruent with recent multilocus phylogenies (e.g., Miller and Engstrom 2008; Platt et al. 2015; Steppan and Schenk 2017). We recovered seven major clades: (1) a first clade composed of *Habromys*, *Megadontomys*, *Osgoodomys*, *Podomys*, and a paraphyletic *Peromyscus*, sister to (2) a second clade containing the three *Onychomys* species, followed by (3) a *Reithrodontomys* clade, and (4) *Isthmomys* as the most closely aligned taxon to this large group. The phylogenetic position of *Isthmomys* differed from the previous studies, where it was placed as the sister taxon of *Reithrodontomys*. Here, we recovered it with strong support at the base of all genera mentioned above. The successive three clades involved (5) *Baiomys* and *Scotinomys*, (6) *Ochrotomys*, and (7) a well-supported clade containing *Hodomys*, *Neotoma*, and *Xenomys* genera. With the exception of the *Peromyscus*-plus-allied-genera clade, the relationships between the species of the remaining groups were mostly stable between phylogenetic analyses. *Neotoma* and *Reithrodontomys*, the two most diverse genera after *Peromyscus*, exhibited two strongly supported subclades. The variable and weakly supported phylogenetic relationships obtained for some *Peromyscus* species, and therefore the uncertainty of relationships to allied taxa, hindered a complete understanding of this group. Solving the taxonomy of a paraphyletic *Peromyscus*-plus-allied-genera clade exceeds the scope of this study. Some authors have suggested a more rigorous review of these associations and proposed taxonomic changes to avoid the *Peromyscus* paraphyly, reconciling morphological and genetic variation to identify monophyletic groups (Bradley et al. 2007; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Sullivan et al. 2017). Regarding *Onychomys*, there was no doubt about the well-supported position of *O. arenicola* as sister species to *O. leucogaster*, with *O. torridus* as their closest sister clade. This phylogenetic relationship was also found by Riddle and Honeycutt (1990) in their analysis using mitochondrial DNA haplotypes.

Bayesian morphological and molecular combined analysis recovered the same major phylogenetic associations and confirm placement of the extinct taxa *Acrolophomys rhodopetros* in Neotominae (Fig. 8). Although *Acrolophomys* was placed in the *Onychomys* clade, its position with respect to the three extant species of *Onychomys* was not clear. The polytomy (probably a soft polytomy) involved the subclade of *O. arenicola* plus *O. leucogaster*, *O. torridus*, and *A. rhodopetros*. The phylogenetic position of *C. loxodon* was uncertain because it was recovered as one of the five main cricetid lineages that form a basal polytomy (i.e., Neotominae, *C. loxodon*, Arvicolinae plus Cricetinae, Tylomyinae, and Sigmodontinae; Figs. 8 and 9). The unresolved position makes sense considering *Copemys* and certain closely related extinct genera likely represent a Miocene basal North American clade that gave rise to Neotominae and possibly Sigmodontinae (Lindsay 2008; Kelly et al. 2020; Martin et al. 2020; Ronez et al. 2020, 2021). Nevertheless, further assessment of its phylogenetic position will require a comprehensive morphological analysis including *Copemys* along with all North American middle Miocene to Pliocene non-arvicoline cricetid genera.

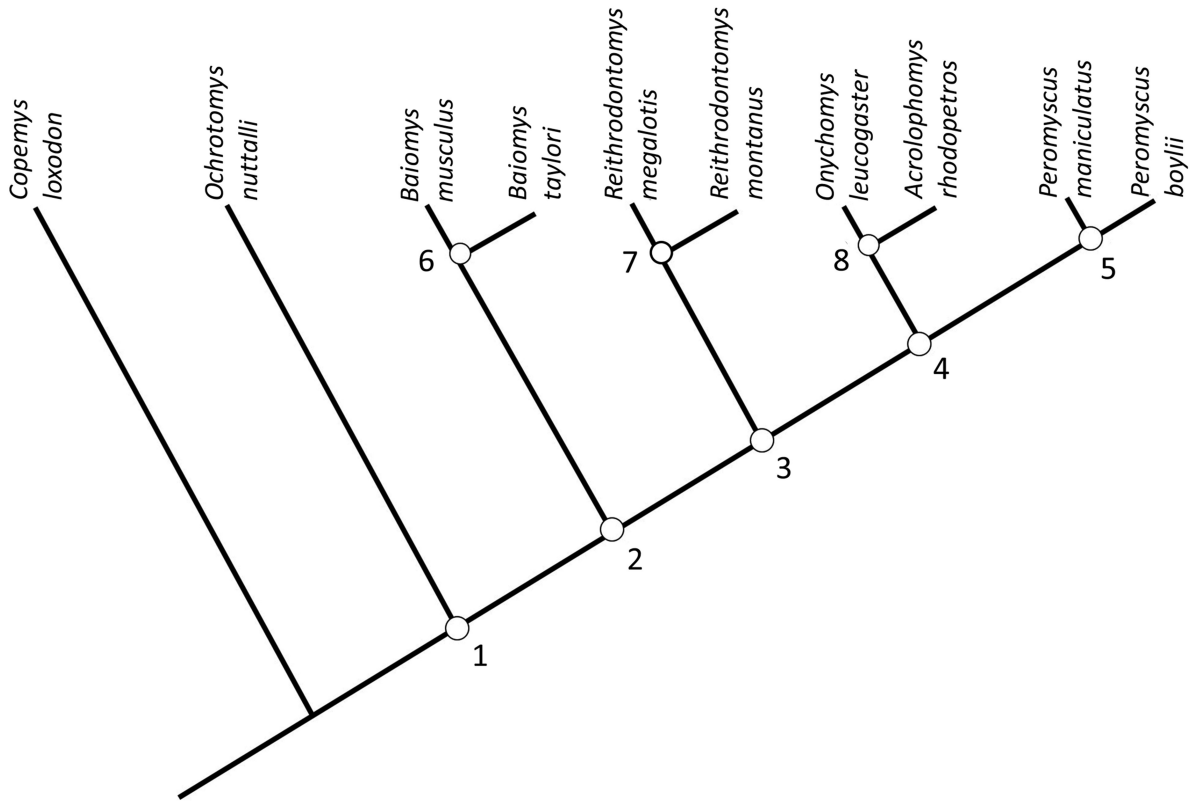

Fig. 4.—Single most parsimonious tree, 42 steps, consistency index (CI) = 0.857, retention index (RI) = 0.926. The cladogram is supported by the following list of hypothesized ancestral synapomorphies (number to left of period denotes character number and to right of period character state). Node 1, 6.1, 13.1, 17.1; Node 2, 5.2, 7.1, 11.2, 15.1, 18.1, 25.1; Node 3, 20.1, 21.1, 24.1; Node 4, 3.1, 16.1, 17.2, 23.2; Node 5, 5.1, 11.1; Node 6, 1.1, 16.2; Node 7, 12.2, 14.1; Node 8, 2.1, 4.1, 7.1, 8.1, 9.1, 10.1. Additional apomorphies for terminal taxa are: *B. taylori*, 5.2; *R. montanus*, 15.2; and *O. leucogaster*, 12.1, 14.1, 15.2.

The magnitude of the divergence values at the *Cytb* gene are mostly consistent with those reported by Platt et al. (2015). K2P distances within the Neotominae genera oscillate between 4.8% within *Megadontomys* and 14.3% within *Reithrodontomys* (Supplementary Data SD5). The three most diverse genera (*Neotoma*, *Peromyscus*, and *Reithrodontomys*) reach intrageneric divergence values > 13%. Generic comparisons with highest levels of genetic divergence were attained by Neotomini (*Hodomys*, *Neotoma*, and *Xenomys*) and all other genera, while the lowest values (12–14%) were obtained inside the *Peromyscus*-plus-allied-genera clade. Values obtained from comparisons of *Onychomys* and remaining taxa fluctuated between 16.5% for *Onychomys*/*Megadontomys*, and 23.5% for *Onychomys*/*Hodomys*. The tribal contrast ranged from 17.4% to 21.8% for Peromyscini/Reithrodontomyini and Baiomyini/Neotomini, respectively. Onychomyini K2P values fluctuate between 18% to 20.1%, which is equivalent to the observed divergence ranges seen between the other neotomine tribes.

Molecular dating.—Although Neotominae arose in the middle Miocene, most of the diversification events responsible for the current diversity of the group occurred during the Pliocene and early Pleistocene. Even though the divergence time estimates obtained by León-Paniagua et al. (2007), Keith (2015), Platt et al. (2015), Schenk et al. (2013), Steppan and Schenk (2017), León-Tapia and Cervantes (2021), and ours differ slightly, all date the main Neotominae diversification events during the same periods. Divergence dates estimates (Fig. 10) suggest that the split of our ingroup and non-neotomine taxa began approximately 11.48 Ma (95% HPD = 10.66–12.69), placing the Neotominae origin approximately ~10 Ma (95% HPD = 10.28–10.32). Molecular clock analysis estimated the following ages for the crown groups of each recognized tribe: Baiomyini 7.47 Ma (95% HPD = 6.35–8.6), Neotomini 5.12 Ma (95% HPD = 3.27–9.4), Peromyscini 5.3 Ma (95% HPD = 4.23–9.2), and Reithrodontomyini 4.5 Ma (95% HPD = 4.48–4.52). Ochrotomyini is a unique lineage composed of a single species and a specimen in this analysis, whose split from the ((((Peromyscini Onychomyini) Reithrodontomyini) *Isthmomys*) Baiomyini) clade (= stem group) began approximately 9.81 Ma (95% HPD = 8.64–10.27). For Onychomyini, the tribe is represented only by three living *Onychomys* species in this analysis, and the age for their stem group was approximately 5.98 Ma (95% HPD = 5.77–8.85), while their crown group was estimated to occur approximately 5.3 Ma (95% HPD = 5.28–5.32; Fig. 10).

ICAMER topological analysis.—The topology of the molars of *Onychomys* and *Acrolophomys* is presented in Fig. 11. Although differences occur between the species

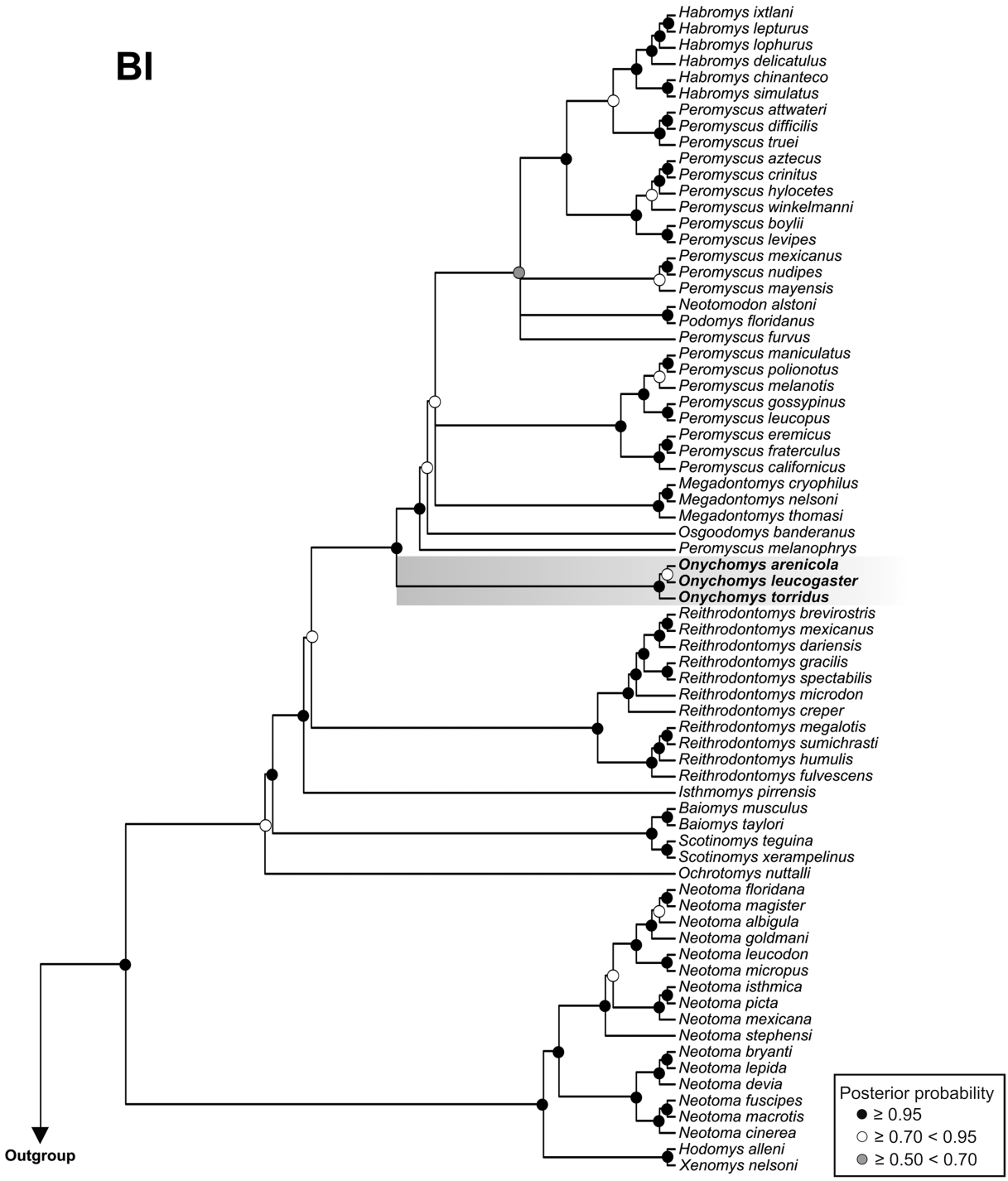

Fig. 5.—Phylogenetic consensus tree obtained from Bayesian inference (BI) analysis of the concatenated mitochondrial and nuclear independent loci. Posterior probabilities support are indicated in grayscale circles for each node. Terminal in bold indicates the Onychomyini species.

of *Onychomys*, general traits can be recognized. First, the connection between the protoconid and the procingulum is made across the metaconid, which connects either to the lingual conulid in *O. leucogaster* due to a single conulid, or to the labial conulid in *O. torridus* and *O. arenicola* when two conulids are present. The same occurs with the entoconid, which is always involved in the union between protoconid and hypoconid. In the case of *O. arenicola*, a mesolophid complex is present and formed by the mesolophulid of both the protoconid and entoconid. A posterior cingulid is well defined in all species. In upper molars, the protocone connects with the labial conule in both *O. leucogaster* and *O. torridus*. In *O. arenicola*, it connects to both conules, which is not the case in *O. torridus* even when a lingual conule is present. The paracone is always involved in the protocone–hypocone union, connecting the

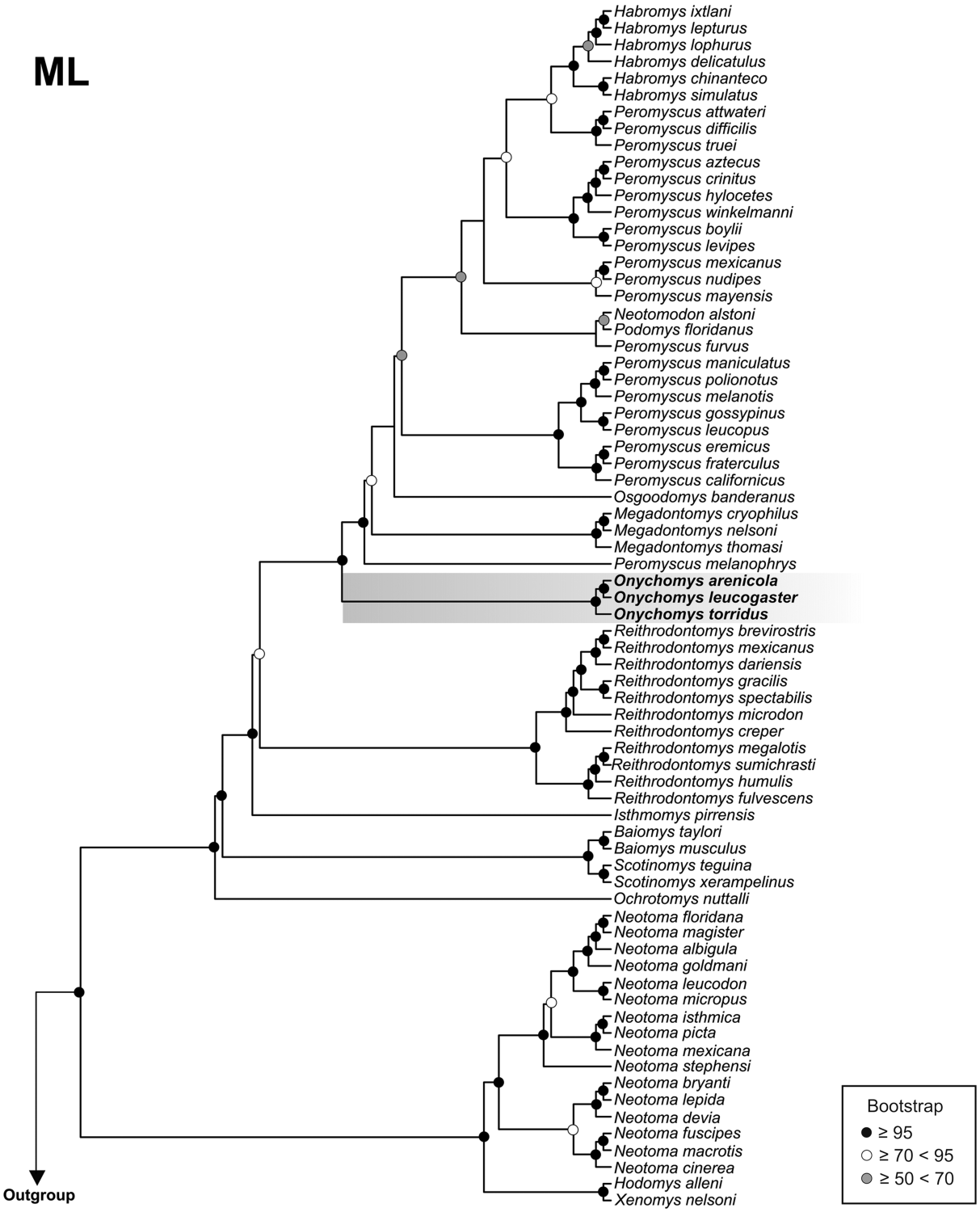

Fig. 6.—Phylogenetic consensus tree obtained from maximum likelihood (ML) analysis of the concatenated mitochondrial and nuclear independent loci. Bootstrap support is indicated in grayscale circles for each node. Terminal in bold indicates the Onychomyini species.

hypo-mesolophule in *O. leucogaster* (hypo-anterolophule in the remaining species). A mesoloph complex is always present and involves a variably developed hypo-mesolophule, para-mesolophule, and posterior arm of the paracone. In *O. arenicola* a mesostyle completes this structure and a parastyle is present in all species of *Onychomys*. The topology of *Acrolophomys* shows similarities with extant *Onychomys* species, such as (1) the presence of a sole conulid as well as (2) a small but developed proto-mesolophulid, and (3) a connection between protoconid and hypoconid involving part of the entoconid cuspal area. No upper molars are known for *Acrolophomys*, so comparison to those of *Onychomys*

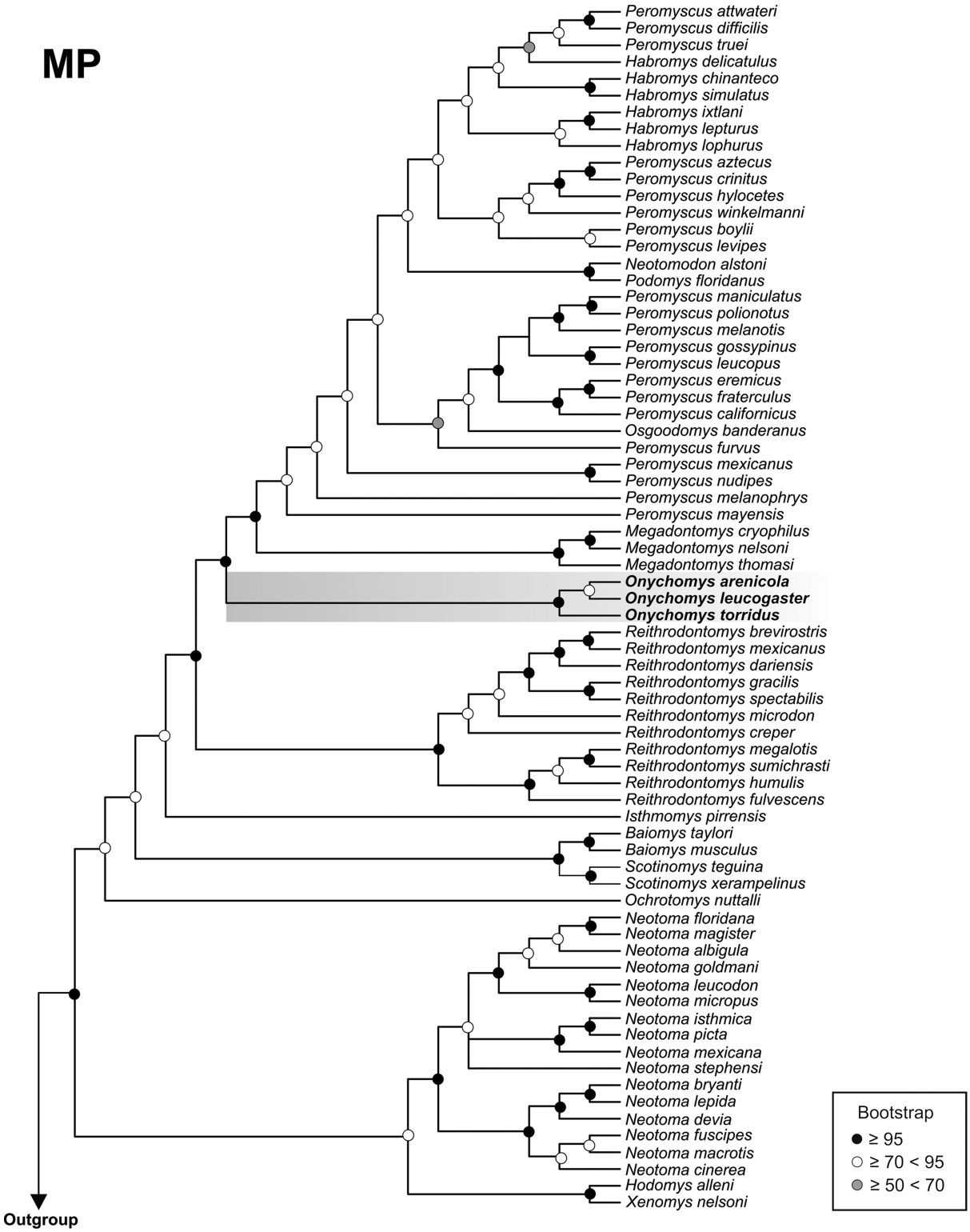

Fig. 7.—Phylogenetic consensus tree obtained from maximum parsimony (MP) analysis of the concatenated mitochondrial and nuclear independent loci. MP analysis yielded a single most parsimonious tree of 14,471 steps (consistency index [CI] = 0.399, retention index [RI] = 0.546). Bootstrap support is indicated in grayscale circles for each node. Terminal in bold indicates the Onychomyini species.

cannot be made. In any case, the topology of *Acrolophomys* m1s is in accordance with m1s of extant *Onychomys* species, consistent with a common ancestry of *Onychomys* through *Acrolophomys*. However, it should also be noted that the ICAMER topology described above is not unique for *Onychomys* and *Acrolophomys*. Indeed, among Neotominae the participation of the paracone in the protocone–hypocone connection is recurrent (e.g., *Reithrodontomys*, *Podomys*,

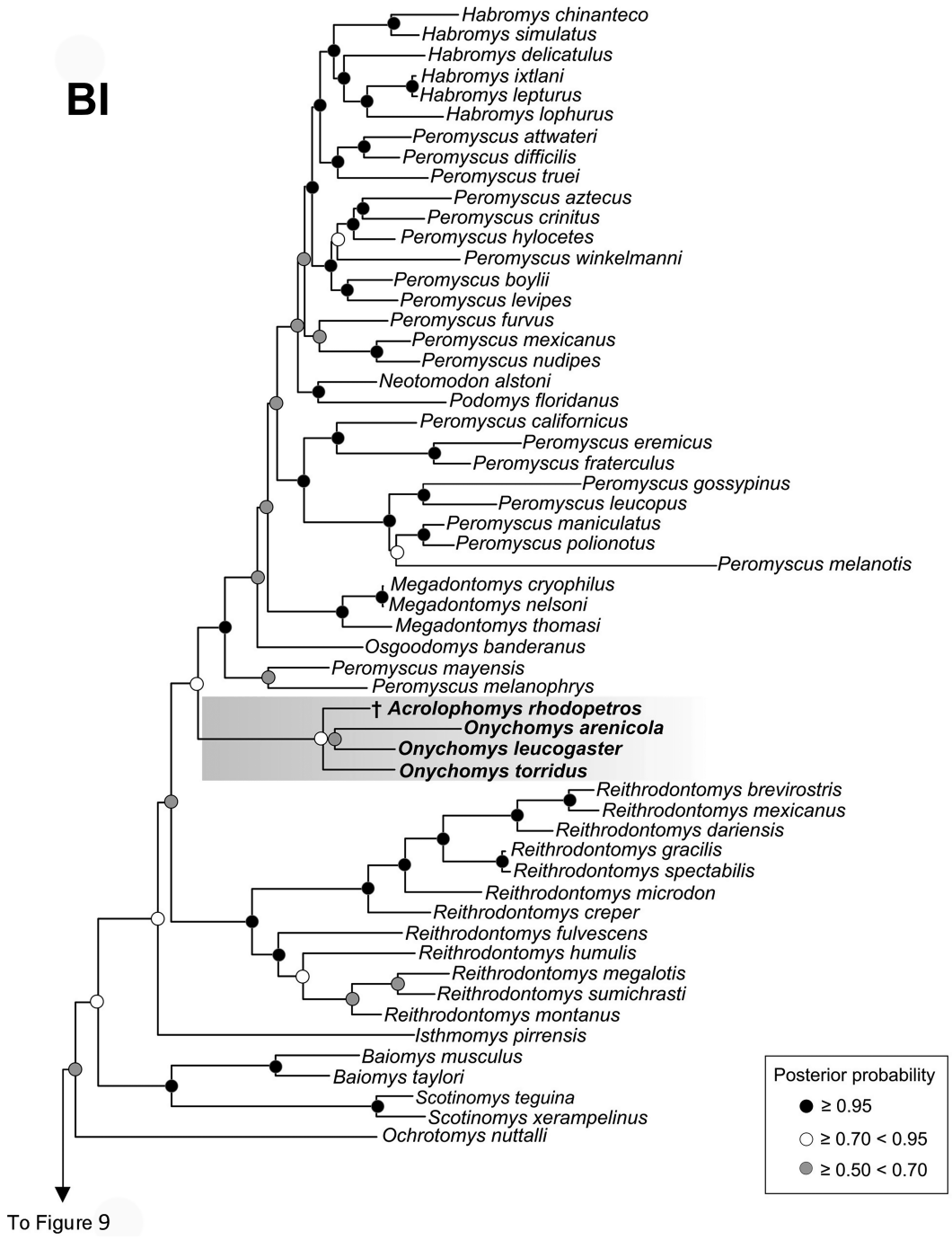

Fig. 8.—Majority-rule consensus tree obtained from Bayesian inference analysis of combined morphological and molecular data sets, in part. Details of the consensus tree corresponding to the ingroup taxa less the Neotomini tribe and outgroups. See Fig. 9 for part of the consensus tree corresponding to Neotominae and non-neotomine outgroup taxa. Posterior probabilities values are indicated in grayscale circles for each node. Terminals in bold indicate the Onychomyini and fossil species (†, extinct).

some *Peromyscus*) but is sometimes incomplete (e.g., *Megadontomys*, some *Peromyscus*). The connection between the protocone and procingulum in upper molars is also variable among the *Peromyscus*-plus-allied-genera clade, even when both conules are present. In the lower molars, the same situation occurs, except for the lack of an ectolophid complex that is usually present in the *Peromyscus*-plus-allied-genera clade, but absent in *Onychomys* and *Acrolophomys*.

Discussion

Morphological evidence.—A number of external, craniodental, and soft tissue specializations in *Onychomys* have been recognized in the literature that differentiate this genus from members of the molecular-identified *Peromyscus*-plus-allied-genera clade as well as other tribes recognized within neotomines. Although not necessarily exhaustive, the selection

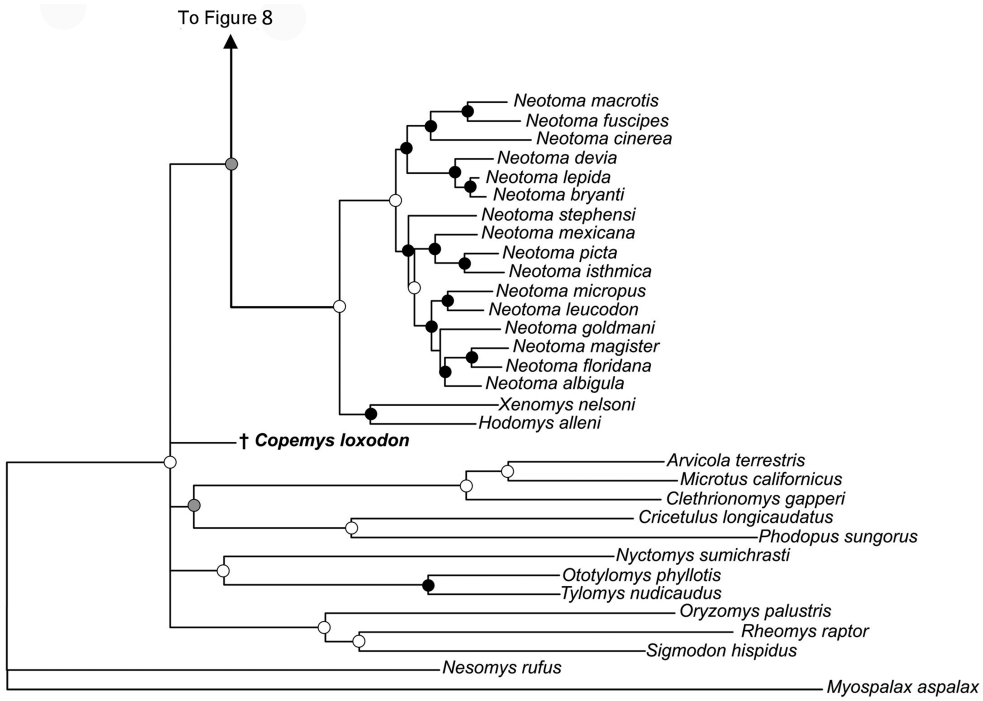

Fig. 9.—Majority-rule consensus tree obtained from Bayesian inference analysis of combined morphological and molecular data sets continued. Part of the consensus tree corresponding to Neotominae and non-neotomine outgroup taxa. Posterior probabilities values are indicated in gray-scale circles for each node. Terminal in bold indicates fossil species (†, extinct).

discussed here highlights the uniqueness of grasshopper mice and provides basic elements to rework its diagnosis.

Hypsodonty in *Onychomys* is somewhat unique in comparison with other neotomines. *Onychomys* has often been cited as expressing a classic example of tubercular hypsodonty, where cusp height is increased relative to the other parts of the tooth and the cusps taper rapidly to sharp apices (Fig. 12A). Following Koenigswald (2011, 2020), a tooth is divided into four components; cusped surface, sidewall, dentin surface, and differentiated roots. Using Koenigswald's criteria, we classified the genera of Neotominae (Fig. 13) and recognized three types of incremental proportions for crown height. First is the development of the sidewall relative to the other components, characteristic of extant Neotomini. Second is a subequal development of each part, with comparable proportions of the dentin surface, sidewall, and cusped surface. This is the most common condition observed in Neotominae, being present in Ochrotomyini, Baiomyini, and Reithrodontomyini sensu stricto (i.e., as restricted after the present study, including *Reithrodontomys* plus *Isthmomys*). Third, in the remaining Neotominae the cusped surface is the most developed portion of the crown, and this condition is exaggerated in both *Acrolophomys* and *Onychomys.*

Onychomys has four plantar pads (thenar and hypothenar missing), whereas *Ochrotomys*, *Baiomys*, *Reithrodontomys*, *Isthmomys*, *Peromyscus*-plus-allied-genera (*Habromys*, *Megadontomys*, *Podomys*, *Neotomodon*, *Osgoodomys*), and Neotomini (*Neotoma*, *Hodomys*, *Nelsonia*) have six plantar pads (Ellerman 1941; Carleton 1980, 2002; Carleton et al. 2002). In addition, the plantar fur is dense to the first interdigital pad in *Onychomys* versus naked or only lightly furred in the other genera (Carleton 1980). The shortness of the tail (consisting of 17–22 caudal vertebrae according to Carleton 1989), especially when it is judged against the head and body length, is an external feature recognized early by Thomas (1888:133) which distinguishes grasshopper mice from members of the other tribes. The tail is also thick, well furred and usually bicolored with a white tip (Bailey 1929).

The skull of *Onychomys* differs from those of *Ochrotomys*, *Baiomys*, *Reithrodontomys*, *Isthmomys*, and *Peromyscus*-plus-allied-genera by having the anterodorsal portions of the frontals inflated and nasals that are more tapered posteriorly, forming a wedge-shaped pattern (Fig. 12E). Carleton (1980) noted that *Onychomys* possesses two complete (diastemic) and four incomplete (interdental) palatal ridges, which differs from that of Neotomini (*Neotoma*, *Nelsonia*, *Xenomys*, *Hodomys*), *Ochrotomys*, *Peromyscus*, *Osgoodomys*, *Habromys*, *Podomys*, and *Megadontomys*, which have three complete and four incomplete; and *Neotomodon*, *Baiomys*, *Scotinomys*, and *Reithrodontomys*, which have two complete and five incomplete. The mandibular coronoid process of *Onychomys* is large and posteriorly elongated with a sword or scimitar-like shape that terminates well posterior of the incisor capsule, providing a large insertion for the temporal muscle (Fig. 11C). In *Ochrotomys*, *Baiomys*, *Reithrodontomys*, *Isthmomys*, and *Peromyscus*-plus-allied-genera, the coronoid process is significantly less developed, either extending anterior to or slightly posterior of the incisor capsule.

Sprague (1941) determined that the hyoid apparatus of *Onychomys* exhibits certain unique characters. A

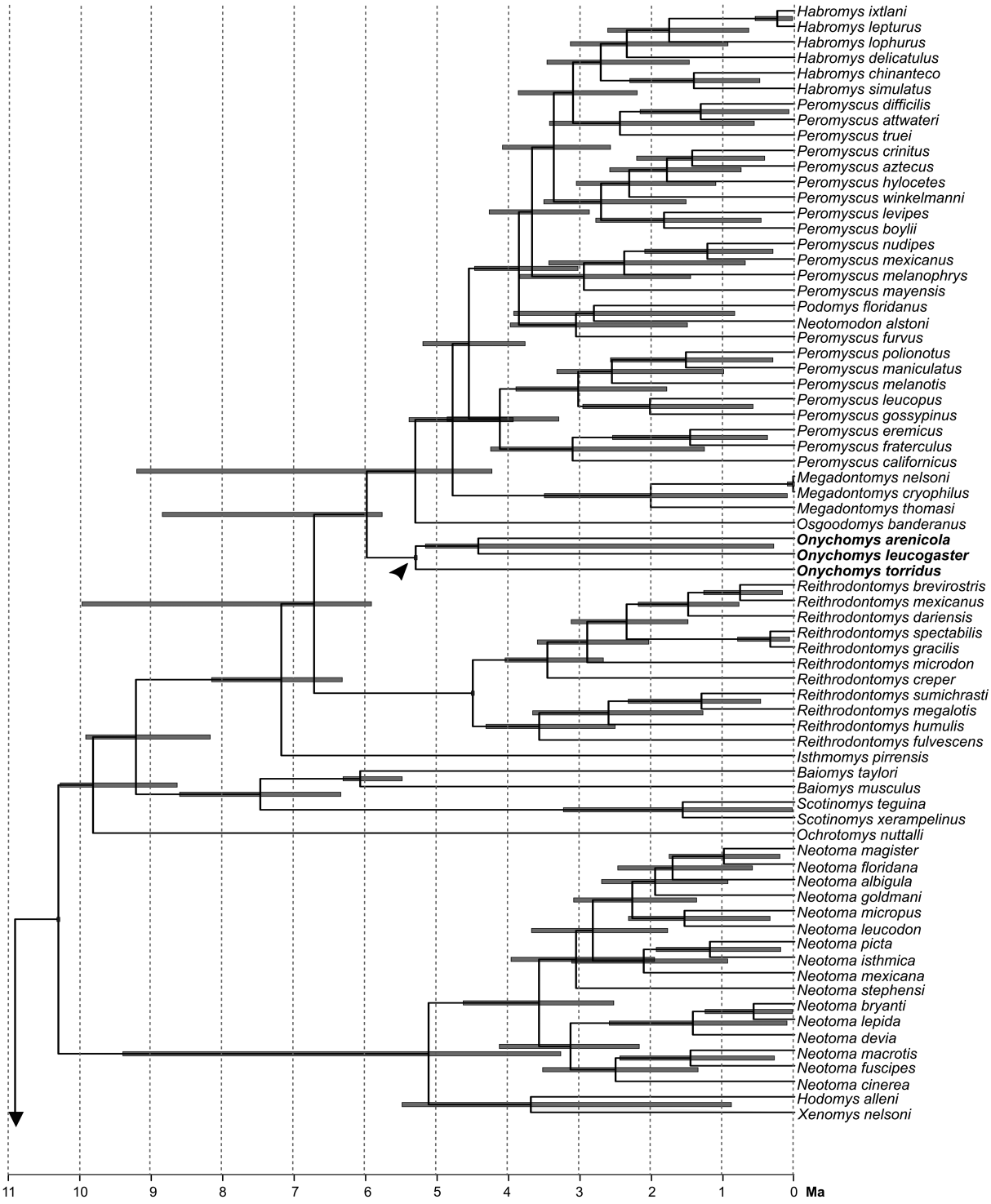

Fig. 10.—Divergence times tree for Neotominae subfamily based on a concatenated analysis of the mitochondrial protein-coding gene cytochrome-b, and intron 2 and parts of exons 2 and 3 of acid phosphatase type V, intron 2 of the alcohol dehydrogenase gene, exon 6 of the protein-coding dentin matrix protein 1 gene, intron 7 of the beta-fibrinogen gene, exon 10 of the growth hormone receptor, single exon of the recombination activation 1 gene, and the first exon of the nuclear gene interphotoreceptor retinoid-binding protein. Divergence date estimates are indicated in millions of years. Bars indicate the minimum and maximum date at the 95% highest posterior density for node height (95% HPD).

ligament that extends posteriorly and cranially from the ceratohyal through the stylomastoid foramen is calcified in *Onychomys*, whereas in other Neotominae it forms a styliform piece of cartilage. The hyoid of *Onychomys* is usually larger and the ratio of the ceratohyal length to that of the thyrohyal is greater than that of *Peromyscus*. The basihyal is lacking an arch and the entoglossal process is weakly developed.

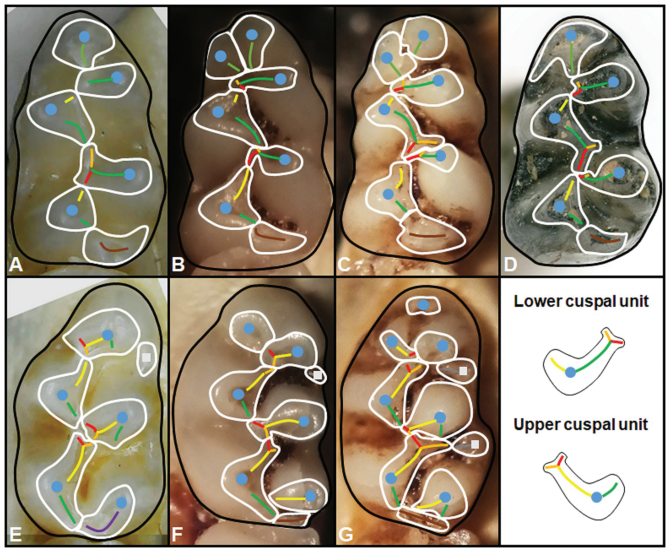

Fig. 11.—ICAMER (Iteration of Cuspal Area with Mirror Effect and Rotation) topology analysis of the m1 and M1 of: (A, E) *Onychomys leucogaster* (MVZ 76624); (B, F) *O. torridus* (CNMA 3345); (C, G) *O. arenicola* (CNMA 46447); (D) *Acrolophomys rhodopetros* (LACM 124878). See Barbière et al (2019) and Supplementary Data SD1 for ICAMER nomenclature and color coding. All scaled to the same size.

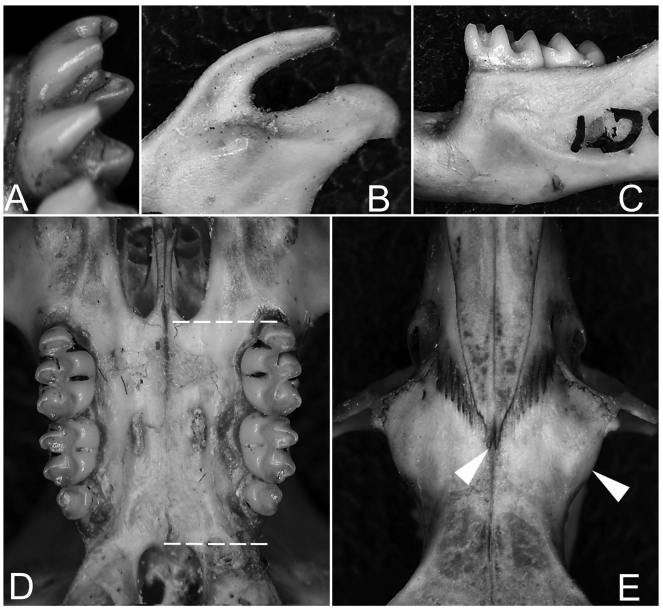

Fig. 12.—Selected dental, mandibular, and cranial characters of *Onychomys*: (A) oblique occlusal view of m1 showing tubercular hypsodonty of procingulid and primary cusps that taper to sharp apices; (B) lateral view of sword or scimitar-like, elongated coronoid process of mandible that extends well posterior of incisor capsule; (C) lateral view of mandible showing dorsoventrally narrowed masseteric scar that terminates anteriorly under anterior root of m1 and dorsal of mental foramen; (D) ventral view of palate showing positions of posterior borders of incisive foramina relative anterior border of M1 and anterior border of posterior nares relative to posterior border of M3; (E) dorsal view of skull showing posteriorly tapered nasals with wedge-shaped termination, and anterior inflation of frontals (arrows). (A–C) *O leucogaster*, MACN 13433. (D–E) *O. torridus*, CNP 6482.

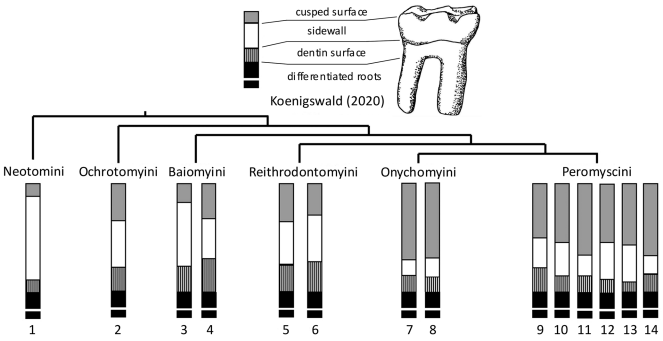

Fig. 13.—Relative proportions of crown divisions in extant genera of tribes of Neotominae following the interpretation of Koenigswald (2020). Relative lengths of differentiated roots of some taxa not available due to breakage or buried in alveolus. Numbers correspond to the following genera: 1, *Neotoma*; 2, *Ochrotomys*; 3, *Scotinomys*; 4, *Baiomys*; 5, *Isthmomys*; 6, *Reithrodontomys*; 7, *Onychomys*; 8, *Acrolophomys*; 9, *Habromys*; 10, *Megadontomys*; 11, *Neotomodon;* 12, *Osgoodomys*; 13, *Peromyscus*; 14, *Podomys*.

The gross stomach morphology of *Onychomys* shows a unique configuration by having a reduction in the glandular area where this kind of epithelium is confined to a well-developed "pouch" or "glandular diverticulum" in the fundic area. This "pouch" is connected to the main cavity of the organ by a small (1–2 mm) orifice (orificium diverticulum; Horner et al. 1965; Vorontsov 1967; Carleton 1973). Of 39 species of *Peromyscus* studied, Carleton (1973) reported that only six (15.4%) have a distinct, almost completely closed glandular pouch (e.g., *P. mexicanus* and *P.* [= *Isthmomys*, this paper] *pirrensis*), but it is less developed and significantly smaller in size relative to the size of the stomach than that of *Onychomys* (Horner et al 1965; Linzey and Packard 1977; Vornotsov 1982). Horner et al. (1965) attributed this derived state to the more carnivorous diet of *Onychomys*, but later investigators have questioned this assumption (Vorontsov 1967; Carleton 1973). Although the stomach configuration displayed by *Onychomys* was largely equated to that of the sigmodontine *Oxymycterus* (Vorontsov 1967; Carleton 1973), also having an animalivorous diet, they represent examples of convergence (Pardiñas et al. 2020). In *Ochrotomys*, *Baiomys*, and *Reithrodontomys*, a glandular "pouch" is absent (Horner et al. 1965; Carleton 1973; Linzey and Packard 1977; Vorontsov 1982).

The length of the intestines differs in *Onychomys*, being five times greater than the body length, whereas those of *Ochrotomys*, *Baiomys*, *Reithrodontomys*, and *Peromyscus* range from 2.5 to 3.6 times the length of the body (Vorontsov 1982). This is due to an increase in the length of the small intestine, which is three times longer than the colon and cecum (Vorontsov 1982). The cecum of *Onychomys*, a simple sac, also differs from the *Peromyscus*-plus-allied-genera clade by being significantly shorter relative to the length of the intestines (Vorontsov 1967; Carleton 1980). Ampullae are present at the intersection of the colon and cecum in *Onychomys* and *Peromyscus*, but lacking in *Ochrotomys*, *Baiomys*, and *Reithrodontomys* (Vorontsov 1982:figs. 254, 261).

Although *Onychomys* and *Peromyscus*-plus-allied-genera clade share a derived, very simple glans penis architecture with urethral lappets absent or vestigial plus a rounded baculum base, the glans of *Onychomys* differs by its vase shape, and the baculum is relatively thicker with a blade-like (dorsoventrally compressed) shaft (Blair 1942; Hooper 1958; Burt 1960; Hooper and Musser 1964a, 1964b; Carleton 1980; Bradley and Schmidly 1987). *Onychomys* also possesses a unique reduction of the accessory male reproductive glands, with the ampullary, vesicular, and anterior prostate glands absent, whereas these glands are present in *Ochrotomys*, *Baiomys*, *Reithrodontomys*, and *Peromyscus* (Arata 1964; Carleton et al. 1975).

The internal architecture and origin-insertion sites of jaw muscles in *Onychomys leucogaster* differ significantly from those of *Peromyscus maniculatus* (Satoh and Iwaku 2006). *Onychomys leucogaster* shows a reduction of some aponeuroses within the masseter deep layer, wherein "the anterior and posterior portions of the masseter deep layer are more anterodorsally inclined, so that the line of action of the masseter lies further from the jaw joint than in *Peromyscus*" (Satoh and Iwaku 2006:987). Williams et al. (2009) found that even though *O. leucogaster* has an absolutely longer jaw, the maximum passive gape is similar to that of *P. maniculatus*. However, they also found that both the absolute and relative bite forces of *O. leucogaster* are significantly greater than those of *P. maniculatus*. In both studies, the modifications of the masticatory muscle architecture and their effect on the resulting muscle stretch, and increased bite force appear to be derived characters for *Onychomys* relating to its more "carnivorous" diet.

The karyotype of *Onychomys* is distinct, characterized by having short biarms with the heterochromatin restricted to the centromere on chromosome numbers 1, 9, 19, 22, and 23 along with numerous heterochromatic short-arm additions resulting in high fundamental numbers ranging from 72 to 92 (Baker et al. 1979; Carleton 1989).

Paleontological evidence.—Kelly and Whistler (2014) described the extinct *A. rhodopetros* from the late Miocene of the upper Dove Spring Formation of California, dated at 9.3–8.8 Ma. *Acrolophomys* exhibits a suite of dental characters shared with *Onychomys* (Figs. 1 and 2), including (1) mesodont molars (unworn m1 protocone height/length = 0.54) due to a tubercular increase in height of the primary cusps and the m1 anteroconid above the crown base resulting in the cusps being narrow and tapering to relative sharp, pointed apices; (2) alignment or near alignment of the posterior arms of the m1–2 protoconids with the entolophids; (3) molar accessory stylids and lophids usually lacking; (4) m1 anteroconid well-separated from metaconid and protoconid; and (5) reentrant valleys between the primary cusps wide and open. The primary difference between *Acrolophomys* and *Onychomys* is the occlusal morphology of the m3. In *Acrolophomys* the m3 is unreduced with the occlusal outline forming an S-shaped wear pattern, the plesiomorphic state for Neotominae and *Copemys*, whereas in *Onychomys* the m3 is significantly reduced relative to the m1–2 with the entoconid and hypoconid reduced forming a "keyhole"-shaped occlusal outline with wear, a derived state. If only m1–2s were known for *Acrolophomys*, they would surely be identified as a species of *Onychomys* (Fig. 1). Because of the above derived, shared characters of *Acrolophomys* and *Onychomys*, Kelly and Whistler (2014) proposed *Acrolophomys* as ancestral to *Onychomys*. Carleton and Eshelman (1979) provided a synopsis of fossil *Onychomys* and their relationships to recent species. They divided *Onychomys* into two species groups, the *O. leucogaster* group and *O. torridus* group, with an incertae sedis species group allocation for *O. martini*, the latter being poorly known but possibly conspecific with *O. bensoni*. Extinct species included in the *O. leucogaster* group are *O. gidleyi* (synonym *O. larrabeei*) and *O. pedroensis* (synonyms *O. fossilis* and *O. jinglebobensis*), and in the *O. torridus* group, *O. bensoni* and *O. hollisteri*. The oldest geologic record of *Onychomys* is *Onychomys* sp. from the Mailbox locality, Nebraska, dated at ~5.3 Ma within the Eastern United States (EUS) Rodent Zone 3 of Martin (2019).

Systematics

The sum of traits exhibited by *Acrolophomys* and *Onychomys*, in addition to its phylogenetic position as revealed by molecular and morphological markers, favors their placement in a distinct tribe. Therefore, a new tribal group to contain these genera is established here, as follows:

Order Rodentia Bowdich, 1821

Family Cricetidae Fisher de Waldheim, 1817

Subfamily Neotominae Merriam, 1894

Onychomyini new tribe

Type genus, by present designation.—*Onychomys* Baird, 1857

Morphological diagnosis.—A tribe of the subfamily Neotominae characterized by the following suite of morphological traits. Molars mesodont (m1 protoconid height/m1 ap = 0.53–0.54) and tubercular with sharply tapered cusps. Lower molars: m1–3 two rooted; m1–3 molar accessory stylids and lophids usually lacking, but a reduced, transient mesolophid complex usually present in *O. arenicola* and *Acrolophomys* in initial wear that rapidly disappears with further wear; m1 procingulid and m1–2 primary cusps tapered to sharp apices (sectorial); m1–2 reentrant valleys wide and open; m1–2 protolophid 2 and entolophid aligned or nearly aligned (*Acrolophomys* m1 mean angle of entolophid/entoconid to long axis of tooth = 60.0 degrees and generic mean for *Onychomys* = 61.5 degrees); m1 procingulid single-cusped (*O. leucogaster*, *Acrolophomys*) to commonly bilobed in initial wear by addition of labial conulid (*O. torridus*, *O. arenicola*), labially positioned, well-separated from metaconid and protoconid, and indirectly connected to protoconid; m3 S-shaped occlusal wear pattern and slightly reduced relative to m1–2 in earliest representative to "keyhole"-shaped pattern and very reduced in later species. Upper molars (undetermined for *Acrolophomys*): M1–2 three rooted; M1–2 reentrant valleys between primary cusps wide and open; M1 procingulum usually single-cusped (*O. leucogaster*) to commonly bilobed in early wear by addition of lingual conulid (*O. torridus*, *O. arenicola*), well-separated from paracone and protocone, and usually directly connected to protocone centrally; M1 anteroloph absent to occasionally present;

M1 mesostyle usually absent; M1 mesoloph absent (*O. leucogaster*) to present as minute lophid, transient (disappears) with wear (*O. torridus*) or a moderately short lophid, transient with wear (*O. arenicola*); M1–2 paraloph aligned or nearly aligned with hypoloph 1 (generic m1 mean angle of *Onychomys* = 55.9 degrees); M3 reduced relative to M1–2 (15–19% of M1–3 ap); M3 paraflexus and hypoflexus vestigial, resulting in a C-shaped occlusal pattern with wear; M3 with one to two roots. Mandibular (undetermined for *Acrolophomys*): coronoid process large and elongated with scimitar-like shape extending well posterior of incisor capsule; masseteric scar <60 degrees, terminating anteriorly under anterior root of m1 and above mental foramen (Fig. 12C). Cranial (undetermined for *Acrolophomys*): two complete (diastemic) and four incomplete (interdental) palatal ridges; nasals taper posteriorly (wedge-shaped); anterior portions of frontals inflated; posterior borders of incisive foramina extend to level of anterior border of M1 procingulum or slightly farther; anterior border of posterior nares positioned well posterior of M3 posterior borders (Fig. 12D). Additional anatomical and external (undetermined for *Acrolophomys*): five palmar pads (three interdigital, thenar, and hypothenar), four plantar pads (lacking thenar and hypothenar); large palmar claws; plantar fur dense to first interdigital pad; body stout, distinctly bicolor with underparts white; tail usually bicolored with white tip, thick and short relative to head, and body length (usually near half the length with 17–22 vertebrae); masseter muscle anterior and posterior portions of deep layer anterodorsally inclined resulting in increased bite force; stomach unilocular–discoglandular with the glandular epithelium restricted into a "pocket" communicated only through a small aperture with the main lumen of the stomach; total intestine length five times greater than body length due to increase in small intestine length; cecum significantly short relative to total intestinal length with cecum ampulla present; baculum shaft moderately thick (ratio of mid-shaft diameter/length = 0.075) and dorsoventrally compressed; glans penis vase-shaped, simple in structure, lacking urethral lappets, protractile tip present, well-developed spines on body, and length about 2× width and two-fifths the hind-foot length; ampullary, vesicular and anterior prostrate (accessory male reproductive glands) absent; mammae 2 pectoral plus 4 inguinal; hyoid relatively large, ligament between ceratohyal and stylomastoid foramen calcified, basihyal arch lacking (after Baird 1857; Thomas 1888; Hollister 1914; Bailey 1929; Sprague 1941; Hooper 1958; Burt 1960; Arata 1964; Horner et al. 1965; Vorontsov 1967, 1982; Carleton 1973, 1980, 1989; this paper).

Content.—Acrolophomys Kelly and Whistler, 2014 and *Onychomys* Baird, 1857.

Age and geographic distribution.—Acrolophomys, latest Clarendonian to earliest Hemphillian North American Land Mammal Age (9.3–8.8 Ma), Mojave Desert, California, United States (Kelly and Whistler 2014). Pre-Holocene *Onychomys* species, latest Hemphillian (~5.3 Ma) to Rancholabrean, central and southwestern United States (Carleton and Eshelman 1979; Martin 2019). Holocene to extant *Onychomys* range across North America from southern Canada to northern Mexico (Musser and Carleton 2005; Bradley et al. 2017).

Remarks.—Vorontsov (1959:136) first listed the tribal name Onychomyini followed by *Onychomys* in parentheses as the sole member of the tribe, but did not provide a diagnosis or a prior reference for the tribe. In later papers, Vorontsov (1967, 1982) provided detailed discussions of the morphology of *Onychomys*, but did not refer to the Onychomyini. The International Congress of Zoological Nomenclature (ICZN) requires under Article 13.1 that names published after 1930 meet the following requirements; "Article 13.1.1, be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon," or "Article 13.1.2, be accompanied by a bibliographic reference to such a published statement, even if in a work published before 1758, or in one that is not consistently binominal, or in one that has been suppressed by the Commission..." In order for a family-group name to be available under Article 13.2.1 of the ICZN, it states "a family-group name first published after 1930 and before 1961 which does not satisfy the provisions of Article 13.1 is available from its original publication only if it was used as valid before 2000, and also was not rejected by an author who, after 1960 and before 2000, expressly applied Article 13 of the then current code." Vorontsov's (1959) Onychomyini does not meet the requirements of Articles 13.1.1, 13.1.2, or the exemption of Article 13.2.1, and therefore is a nomen nudum.

Musser and Carleton (2005) considered Vorontsov's (1959) conclusion about *Onychomys*, stating "While Voronstsov (1959) arranged *Onychomys* as sole member of its own tribe, apart from *Reithrodontomys*, a robust body of data now supports its close phyletic affinity with *Peromyscus* and related genera (Hooper and Musser 1964b; Carleton 1980; Stangl and Baker 1984; Allard and Honeycutt 1991; Sullivan et al. 1995), in particular *Osgoodomys* (Engel et al. 1998), and recommends the synonymy of these two family-group taxa (Reithrodontomyini have line priority)." Depending on the study, the phylogenetic position of *Onychomys* relative to other members of Neotominae varies, but a consensus of these studies has emerged.

In order to better understand some of the taxonomic treatments presented below, it should be noted the tribe Peromyscini was first proposed by Cockerell et al. (1914:359) based on the comparative morphology of the auditory ossicles in rodents, where they defined the tribe as having "cephalic pedicles with an abrupt bend." Subsequently, based on the comparative morphology of the glans penis, Hershkovitz (1966:747) suggested Peromyscini as an available subfamily name in the following statement; "should North American simple penis-type cricetines be regarded as tribally distinct, the name Peromyscini is available." Since then, a number of investigators have used the tribe Reithrodontomyini to include *Reithrodontomys* and *Peromyscus*-plus-allied-genera rather than Peromyscini. However, Cazzaniga et al. (2019) recognized that if *Peromyscus* and *Reithrodontomys* are included in the same tribe, then Reithrodontomyini Vorontsov, 1959, is a junior synonym of Peromyscini Cockerell et al., 1914. This synonymy would apply to some of the other molecular phylogenetic scenarios provided below that include *Peromyscus* and *Reithrodontomys* in the same tribe.

Based on a morphological analysis with 72 characters, Carleton (1980) questionably placed *Onychomys* as the closest

sister taxon to a *Neotomodon–Podomys–Habromys* clade plus a *Reithrodontomys–Peromyscus* clade with *Osgoodomys* as the closest sister taxon to *Onychomys*. However, Carleton (1980:122) stated that "in addition to lacking definition based on many derived states, the various quantitative phylogenetic techniques disclosed inconsistent, conflicting statements of relationships for certain members of this group [Peromyscini], particularly for *Onychomys* and *Ochrotomys*. For these reasons, their allocation here is considered provisional."

Based on an analysis of the cytoplasmic RNA subunits 18S and 28S, Allard and Honeycutt (1991) recognized a *Reithrodontomys–Peromyscus* clade and an *Onychomys* clade with *Mus* as the outgroup. They discussed the methods used at the time for estimating divergence dates, but noted (Allard and Honeycutt 1991:82) that they are equivocal and recommended "studies on rodent rRNA variation be conducted at the nucleotide sequence level and be confined to the variable regions mapped to the 28S gene or, possibly, to the ITS region."

Sullivan et al. (1995) provided an analysis based on the mitochondrial RNA subunit 12S where they recognized *Sigmodon* (two species), *Neotoma* (two species), and *Onychomys* (three species) as successive sister clades to *Peromyscus* (six species) using *Mus* and *Rattus* as outgroup taxa. In their equally weighted parsimony and ML analyses, *Onychomys* never nested within the *Peromyscus* clade. Their estimated divergence date for the *Onychomys* and *Peromyscus* clades was 7.5 Ma.

The molecular study by Engel et al. (1998), which was based on three subunits of the nicotinamide adenine dinucleotide dehydrogenase gene (*ND3*, *ND4*, *ND4L*) and arginine tRNA, resulted in two proposed phylogenies. In both scenarios, *Onychomys* was well nested within a *Peromyscus*-plus-allied-genera clade (*Habromys*, *Osgoodomys*, *Peromyscus*, *Podomys*), with *Onychomys* as the closest sister taxon to an *Osgoodomys–Peromyscus eremicus* clade.

D'Elía (2003) provided a phylogenetic analysis based on *Cytb* and *Rbp3*, which concentrated primarily on South American sigmodontine rodents, but also included a few North American cricetids. Their analysis resulted in *Tylomys*, a *Baiomys–Scotinomys* clade, *Onychomys*, and *Reithrodontomys* as successive sister taxa or clades to a *Peromyscus* clade.

In a molecular study of *Dmp1*, Reeder and Bradley (2004) recognized four tribes; Tylomyini (*Tylomys*, *Ototylomys*), Neotomini (*Neotoma*, *Hodomys*, *Xenomys*), Baiomyini (*Baiomys*, *Scotinomys*), and Peromyscini, the latter including an *Ochrotomys* clade, *Reithrodontomys* clade, *Onychomys* clade, and *Peromyscus*-plus-allied-genera clade (*Peromyscus*, *Osgoodomys*, *Neotomodon*).

Based on an analysis of *Cytb*, Bradley et al. (2004) placed *Onychomys* within Neotomini as the closest sister clade to a *Hodomys–Xenomys–Neotomodon* clade, with Neotomini as the closest sister group to Peromyscini, the latter included a *Reithrodontomys–Ochrotomys* clade and a *Peromyscus*-plus-allied-genera clade (*Megadontomys*, *Neotomodon*, *Osgoodomys*, *Peromyscus*).

In a molecular study of *Dmp1* and *Fgb-I7*, Reeder et al. (2006) placed Tylomyini (*Tylomys–Ototylomys* clade), Neotomini (*Neotoma* clade and *Xenomys–Hodomys* clade), Ochrotomyini (*Ochrotomys* clade), and Baiomyini (*Baiomys–Scotinomys* clade) as successive sister clades to Peromyscini. Their analysis placed *Reithrodontomys* and *Onychomys* within Peromyscini as successive sister taxa to an *Osgoodomys–Peromyscus–Neotomodon* clade. All of these clades were included in the subfamily Sigmodontinae.

Reeder and Bradley (2007) performed a molecular analysis using *Cytb* and *Fgb-17*, which placed *Ochrotomys* as the closest sister clade to Neotomini (*Neotoma*, *Xenomys*, *Hodomys*), and a *Baiomys–Scotinomys* clade and a *Reithrodontomys–Onychomys* clade as the closest successive sister clades to a *Peromyscus*-plus-allied-genera clade (*Neotomodon*, *Osgoodomys*, *Peromyscus*). They recognized the following four tribes with the tribal position of *Ochrotomys* as uncertain; Tylomyini (*Ototylomys*, *Tylomys*, *Nyctomys*), Neotomini (*Neotoma*, *Hodomys*, *Xenomys*), Baiomyini (*Baiomys*, *Scotinomys*), and Peromyscini (*Neotomodon*, *Onychomys*, *Osgoodomys*, *Peromyscus*, *Reithrodontomys*). They noted (Reeder and Bradley 2007:894) that the uncertainty of the phylogenetic position of *Ochrotomys* may be due to "a paucity of synapomorphies (3) supporting *Ochrotomys* as sister to Neotomini." and that "Carroll and Bradley (2005) found a similar lack of synapomorphies when using Fgb-17."

In a comprehensive molecular study of 100 DNA sequences of the *Cytb* gene in 44 species of deer mice plus other cricetids, Bradley et al.'s (2007) ML tree placed *Onychomys* and *Neotoma* in a clade with *Ochrotomys* as its closest sister clade, and together these clades were considered the closest sister clade to two additional major clades, one consisting of *Baiomys* and a *Reithrodontomys–Isthmomys* clade, and another consisting of a *Peromyscus*-plus-allied-genera clade (*Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, *Peromyscus*, *Podomys*). In their analysis, *Onychomys* is far removed from *Osgoodomys*. Bradley et al. (2007:1150) state; "*Osgoodomys* was placed within a well-supported clade containing members of the [*Peromyscus*] *californicus*, *eremicus*, *leucopus*, *maniculatus*, *crinitus*, and *hooperi* species groups."

Miller and Engstrom (2008) provided a molecular analysis based on *Cytb* and two nuclear genes (*GHR* and *Rbp3*). Their analysis placed Neotomini, Ochrotomyini, a *Baiomys–Scotinomys* clade, a *Reithrodontomys–Isthmomys* clade, and *Onychomys* as the successive sister taxa or clades to a *Peromyscus*-plus-allied-genera clade (*Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, *Peromyscus*, *Podomys*).

Keith (2015) provided a comprehensive molecular analysis based on *Cytb* and up to five nuclear markers (*Adh1-I2*, *Fgb-I7*, *Dmp1*, *GHR*, and *Rbp3*) that placed *Neotoma–Hodomys–Xenomys*, *Ochrotomys*, *Baiomys–Scotinomys*, *Reithrodontomys–Isthmonys*, and *Onychomys* as successive sister clades to a *Peromyscus*-plus-allied-genera clade (*Megadontomys*, *Neotomodon*, *Osgoodomys*, *Habromys*, *Peromyscus*, *Podomys*). She recognized five tribes in Neotominae; Neotomini (*Neotoma*, *Hodomys*, *Xenomys*), Ochrotomyini (*Ochrotomys*), Baiomyini (*Baiomys*, *Scotinomys*), Reithrodontomyini (*Reithrodontomys*, *Isthmomys*), and Peromyscini (*Habromys*, *Onychomys*, *Osgoodomys*, *Megadontomys*, *Neotomodon*, *Peromyscus*, *Podomys*). Her analysis demonstrated convincingly that

Peromyscini as recognized is paraphyletic and in need of revision. She separated Ochrotomyini, Baiomyini, Reithrodontomyini because they are the closest successive sister clades to Peromyscini, but *Onychomys* also stood out as a monophyletic successive sister clade to the larger, paraphyletic *Peromyscus*-plus-allied-genera clade. If one recognizes all other monophyletic successive sister clades to the *Peromyscus*-plus-allied-genera clade as deserving tribal rank, then it seems reasonable to follow the same logic and recognize the *Onychomys* clade at the tribal level. Moreover, excluding *Onychomys* from tribal rank would provide an argument that Ochrotomyini, Reithrodontomyini, and Baiomyini should also be combined within Peromyscini. The separation of *Onychomys* also reduces the paraphyly of Peromyscini and is further supported by a number of derived morphological distinctions listed above that are absent in all the other tribes, including the *Peromyscus*-plus-allied-genera clade.

In a paper on the relationships of *Peromyscus* and allied genera, Platt et al. (2015) provided a molecular analysis that was very similar to that of Keith (2015), including the same 34 ingroup taxa and outgroup taxon (*Neotoma mexicana* Baird, 1855). It differed from Keith (2015) by using only up to three nuclear loci (*ADHL12*, *Fgb-17*, *Rbp3*) instead of up to five. Platt et al. (2015) also differed in that they did not recognize Peromyscini, instead transferring all of Keith's (2015) Peromyscini taxa to the Reithrodontomyini, which the latter does not have priority (Cazzaniga et al. 2019). They estimated the split of the *Isthmonys–Reithrodontomys* clade and the *Onychomys* clade at ~7.93 Ma and the split of the Baiomyini and Reithrodontomyini clades at ~9.56 Ma.

Based on a monumental analysis of more than 900 muroid rodent species using *Cytb* and up to five nuclear genes (*BRCA1* [breast cancer 1 gene], *GHR*, *Rbp3*, *RAG1*, and *Acp5*), Steppan and Schenk (2017) provided the molecular relationships of Neotominae. Neotomini (*Neotoma*, *Hodomys*, *Xenomys*, *Nelsonia*) was placed as the sister clade to all other Neotominae and *Ochrotomys* was placed as the sister clade to all remaining Neotominae, followed by a *Baiomys–Scotinomys* clade, *Reithrodontomys–Isthmomys* clade, and *Onychomys* clade that are successive sister clades to a *Peromyscus*-plus-allied-genera clade (*Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, *Neotomodon*, *Podomys*). The *Peromyscus*-plus-allied-genera clade was further divided into at least six additional clades, indicating that it represents a paraphyletic assemblage.

Schematic cladograms showing the proposed inferences for the phylogenetic position of *Onychomys* in the morphological and molecular analyses discussed above are presented in Supplementary Data SD6.

Although Musser and Carleton (2005) cite Engel et al. (1998) as strong support for a close relationship of *Onychomys* to *Osgoodomys*, including this conclusion as one of the primary reasons they regarded Onychomyini as a synonym of the Reithrodontomyini, the consensus of subsequent molecular analyses contradict this proposal and place *Osgoodomys* as phylogenetically related and nested within either two or three of the *Peromyscus* species groups. In most all analyses, *Reithrodontomys* (plus *Isthmomys* when included) and *Onychomys* are placed as successive, closest sister clades to a series of successive sister clades within a larger *Peromyscus*-plus-allied-genera clade. Except for Engel et al. (1998), some prior and all subsequent molecular analyses (Allard and Honeycutt 1991; Sullivan et al. 1995; D'Elía 2003; Bradley et al. 2004, 2007; Reeder and Bradley 2004; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Steppan and Schenk 2017) including our analyses presented above, *Onychomys* does not nest within the *Peromyscus*-plus-allied-genera clade (*Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, *Peromyscus*, *Podomys*). Based on these observations and contrary to Musser and Carleton (2005), *Onychomys* is not closely related to *Osgoodomys*.

The reinstatement of Onychomyini leads to the recognition of Peromyscini and Reithrodontomyini as separate clades, as first proposed by Keith (2015), raising the number of tribal arrangements within Neotominae. Therefore, our phylogenetic scenario distinguishes Neotomini (*Hodomys*, *Nelsonia*, *Neotoma*, and *Xenomys*), Baiomyini (*Baiomys* and *Scotinomys*), Ochrotomyini (*Ochrotomys*), Reithrodontomyini (*Isthmomys* and *Reithrodontomys*), Onychomyini (*Onychomys* and *Acrolophomys*), and Peromyscini (*Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, *Peromyscus*, and *Podomys*), with the caveat that Peromyscini is a paraphyletic grouping in need of revision and the phylogenetic position of *Isthmomys* relative to *Reithrodontomys* requires further evaluation. Although *Nelsonia* was not included in our analysis, prior morphological and molecular analyses have placed it in the Neotomini subtribe Galushamyina as the sister taxon to the subtribe Neotomina (Martin and Zakrzewski 2019; León-Tapia and Cervantes 2021). Our progress is far from solving and understanding the phylogenetic relationships of the entire subfamily including possible related extinct species. Numerous authors have suggested that integrative revision is required to properly recognize diversity and limits, primarily within the *Peromyscus*-plus-allied-genera clade (Reeder and Bradley 2004; Miller and Engstrom 2008; Keith 2015; Platt et al. 2015; Steppan and Schenk 2017; Sullivan et al. 2017; Castañeda-Rico et al. 2020). Although recognition of the tribe Onychomyini might be interpreted as taxonomic inflation (Padial and de la Riva 2006; Dubois 2008; Zachos et al. 2013), its morphological uniqueness, recurrent isolated molecular phylogenetic position, and levels of genetic divergence similar to that observed in the other tribes provide robust evidence to justify its separation. The paleontological evidence also strongly supports tribal recognition of Onychomyini consisting of an *Onychomys–Acrolophomys* clade that diverged from other basal Neotominae or the *Copemys* species complex during the late Miocene at ~9 Ma. A classification and generic content of the extant subtribes of Neotominae with the inclusion of extinct *Acrolophomys* is presented in Table 1. The phylogenetic position of *C. loxodon* was not conclusive because it was included in a basal polytomy that involved several lineages. However, the available evidence suggests that *Copemys* may have been the ancestral lineage from which neotomines (and probably sigmodontines) evolved (Lindsay 2008; Ronez et al. 2020, 2021), so one of the possible solutions to the recovered polytomy is the one where *Copemys* is the sister group of Neotominae.

Table 1.—Classification and generic content of extant subtribes of Neotominae as recognized in this paper with the inclusion of extinct (†) *Acrolophomys* (alphabetically ordered). *Isthmomys* is provisionally included in Reithrodontomyini based on a consensus of prior molecular studies, but with the caveat that its tribal affiliation requires further evaluation.

Content of Neotominae
Tribe Baiomyini Musser and Carleton, 2005
Baiomys True, 1894
Scotinomys Thomas, 1913
Tribe Neotomini Merriam, 1894
Subtribe Galushamyina Lindsay, 2008
Nelsonia Merriam, 1897
Subtribe Neotomina Merriam, 1894
Hodomys Merriam, 1894
Neotoma Say and Ord, 1825
Xenomys Merriam, 1892
Tribe Ochrotomyini Musser and Carleton, 2005
Ochrotomys Osgood, 1909
Tribe Onychomyini, this study
†*Acrolophomys* Kelly and Whistler, 2014
Onychomys Baird, 1857
Tribe Peromyscini Cockerell, Miller and Printz, 1914
Habromys Hooper and Musser, 1964a
Megadontomys Merriam, 1898a
Neotomodon Merriam, 1898b
Osgoodomys Hooper and Musser, 1964a
Peromyscus Golger, 1841
Podomys Osgood, 1909
Tribe Reithrodontomyini Vorontsov, 1959
Isthmomys Hooper and Musser, 1964a
Reithrodontomys Giglioli, 1874

While the divergence time estimates obtained by Keith (2015), Platt et al. (2015), Schenk et al. (2013), Steppan and Schenk (2017), and ours differ slightly, all date the main Neotominae diversification events during the Pliocene to early Pleistocene.

Conclusions

A consensus of the molecular, morphological, and paleontological evidence supports *Onychomys* as a distinct North American Neotominae cricetid genus originating at least by 5 Ma near the Hemphillian–Blancan boundary. Moreover, the paleontological evidence strongly supports a monophyletic *Acrolophomys–Onychomys* clade that diverged from other Neotominae clades during the late Miocene at about 9 Ma, near the Clarendonian–Hemphillian boundary. These results reinforce elevation of the *Acrolophomys–Onychomys* clade to tribal rank as the Onychomyini, separate from the Peromyscini.

Contrary to taxonomic assignments presented in certain molecular phylogenies, when *Reithrodontomys* and *Peromyscus* are included in the same tribe, Peromyscini has priority (Cazzaniga et al. 2019). A consensus of the published molecular phylogenies supports a clade composed of *Reithrodontomys* and *Isthmomys* as the tribe Reithrodontomyini, separate from the Peromyscini. However, defining the boundaries of Reithrodontomyini is a challenge. In particular, the phylogenetic position of *Isthmomys* in our analyses suggests it represents an independent Central American lineage, and this possibility should be considered in subsequent studies.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Traditional dental nomenclature used in the morphological cladistic analysis (from Kelly et al. 2020) and ICAMER (Iteration of Cuspal Area with Mirror Effect and Rotation) terminology used for the study of the topology of *Onychomys* and *Acrolophomys* (from Barbière et al. 2019).

Supplementary Data SD2.—GenBank accession numbers for nucleotide sequences used in this study. *Cytb*—cytochrome-b, *Acp5*—intron 2 and parts of exons 2 and 3 of acid phosphatase type V, *Adh1-I2*—intron 2 of the alcohol dehydrogenase gene, *Dmp1*—exon 6 of the protein-coding dentin matrix protein 1 gene, *Adh1-I2*—intron 7 of the beta-fibrinogen gene, *GHR*—exon 10 of the growth hormone receptor, *RAG1*—single exon of the recombination activation 1 gene, and *Rbp3*—first exon of the nuclear gene interphotoreceptor retinoid-binding protein.

Supplementary Data SD3.—Aligned sequences for the eight loci used in this study (*Cytb*, *Acp5*, *Adh1-I2*, *Dmp1*, *Fgb-I7*, *GHR*, *RAG1*, and *Rbp3*).

Supplementary Data SD4.—Phylogenetic consensus trees obtained for outgroup from Bayesian inference (BI), maximum likelihood (ML), and maximum parsimony (MP) of the concatenated mitochondrial and nuclear independent loci. Bootstrap and posterior probabilities support are indicated in grayscale circles for each node.

Supplementary Data SD5.—Kimura 2-parameters genetic divergence at *Cytb* gene within and between the Neotominae genera, and their tribal arrangements.

Supplementary Data SD6.—Schematic cladograms showing the proposed inferences for the phylogenetic position of *Onychomys* (red) in prior morphological and molecular analyses. Abbreviations are: BI = Bayesian inference; ML = maximum likelihood; NJ = neighborhood joining. (A) Carleton (1980:fig. 42), morphological analysis of 72 characters; (B) Allard and Honeycutt (1991:fig. 3), strict consensus; (C) Sullivan et al. (1995:fig. 3C), strict consensus; (D) Engel et al. (1998:fig. 5), NJ; (E) D'Elía (2003), strict consensus; (F) Reeder and Bradley (2004:fig. 2), BI; (G) Bradley et al. (2004:fig. 2), ML; (H) Reeder et al. (2006:fig. 4), ML; (I) Reeder and Bradley (2007:fig. 3), BI; (J) Bradley et al. (2007:fig. 2), ML; (K) Miller and Engstrom (2008:fig. 1), BI; (L) Keith (2015:fig. 3.4), ML; (M) Platt et al. (2015:fig. 1), ML; (N) Steppan and Schenk (2017:fig. 4, section E), ML.

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Associate Editor was Jacob Esselstyn.

APPENDIX I

Taxa included in the morphological cladistic analysis (†, extinct).

†*Copemys loxodon* (Cope, 1874)—type species (outgroup)
†*Acrolophomys rhodopetros* Kelly and Whistler, 2014—type species
Onychomys leucogaster (Wied, 1841)—type species
Ochrotomys nuttalli (Harlan, 1832)—type species
Baiomys musculus (Merriam, 1892)
Baiomys taylori (Thomas, 1887)—type species
Reithrodontomys megalotis (Baird, 1857)—type species by designation Howell (1914) *Reithrodontomys montanus* (Baird, 1855)
Peromyscus maniculatus (Wagner, 1845)
Peromyscus boylii (Baird, 1855)

APPENDIX II

Characters for morphological cladistic analysis.

1. Size, based on m1 ap: 0, medium sized (m1 ap ≥1.25 mm); 1, very small (m1 ap <1.15 mm).
2. m1–2 relative crown height: 0, brachydont; 1, mesodont (unworn m1 protoconid height/m1 length = 0.53–0.54) due to tubercular increase in height.
3. m1–2 alignment of protolophid 2 and entolophid: 0, not aligned; 1, aligned or nearly aligned.
4. m1 procinglulid and primary cusps tapered to a sharp, pointed apices (sectorial) in unworn to early wear: 0, absent; 1, present.
5. m1 mesolophid: 0, mesolophid long, separated from metaconid and entoconid, lingually directed and originating from protolophid 2; 1, mesolophid short to long, usually fused to entolophid; 2, usually absent or vestigial (small transient, disappears after initial wear).
6. m1 procingulid bilobed with addition of second conulid (anterolabial conulid): 0, usually always absent; 1, variable, absent to moderately developed, anteromedian flexid moderately shallow when present.
7. m1 relative position of procingulid in occlusal view to long axis of tooth: 0, slightly lingually; 1, centrally; 2, labially.
8. m1 orientation and width of connection of protolophid 1/metalophid and procingulid: 0, relatively straight, narrow; 1, anterolabially directed, narrow.
9. m1 protoflexid: 0, relative narrow, provergent; 1, wide, provergent.

10. m1 hypoflexid: 0, relatively narrow, provergent; 1, wide, provergent.
11. m2 mesolophid: 0, mesolophid long, labially directed, isolated from paracone and metacone, origin protolophid; 1, mesolophid short to long, usually fused to entolophulid; 2. absent or vestigial.
12. m3 occlusal outline pattern with wear: 0, S-shaped; 1, keyhole-shaped; 2, C-shaped.
13. m3 posteroflexid: 0, present; 1, absent or greatly reduced.
14. Relative size of m3 talonid to trigonid: 0, moderately smaller; 1, much smaller.
15. Relative size of m3 ap to m1–3 ap (character 6 of): 0, unreduced, greater than 30% of m1–3 ap; 1, moderately reduced, 29–24% of m1–3 ap; 2, very reduced, <23% of m1–3 ap.
16. M1 procingulum bilobed: 0, absent; 1, weakly to moderately from unworn to early moderate wear with weak anteromedian flexus; 2, strongly with well-developed anteromedian flexus.
17. M1 relative anterior obliquity (mean angle for genus) of paraloph to mid-long axis of tooth: 0, slightly oblique, angle = >80 degrees; 1, moderately oblique, angle = 70–80 degrees; 2, very oblique, angle = <60 degrees.
18. Relative size of M3 ap to M1–3 ap: 0, unreduced, ≥23% of M1–3 ap; 1, reduced, 15–20% of M1–3 ap.
19. Baculum shaft diameter relative to length (ratio of mid-shaft diameter/length): 0, shaft very thick (>0.084); 1, moderately thick (0.075); 2, medium slender (0.050); 3, very slender (<0.030).
20. Baculum base shape: 0, distinct spade shape; 1, rounded, globular shape.
21. Glans penis complexity: 0, moderately simple, urethral lappets well-developed (robust) or urethral meatus surrounded by corrugated rim of tissue, protractile tip absent; 1, very simple, urethral lappets absent or vestigial, protractile tip present.
22. Glans penis shape: 0, vase-shaped; 1, urn-shaped; 2, slender, elongated cylindrical shape.
23. Stomach gross morphology: 0, hemiglandular; 1, intermediate between hemiglandular and discoglandular; 2, discoglandular.
24. Cecum ampulla (ampulla ceci): 0, absent; 1, present.
25. Angle of masseteric scar (after Vorontsov, 1982:136, fig. 61): 0, >60 degrees; 1, <60 degrees.

Appendix III

Character state matrix used in morphological cladistic analysis.

	Character number																								
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Copemys loxodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0
Onychomys leucogaster	0	1	1	1	2	0	2	1	1	1	2	1	1	1	2	1	2	1	1	1	1	0	2	1	1
Acrolophomys rhodopetros	0	1	1	1	2	0	2	1	1	1	2	0	1	0	1	?	?	?	?	?	?	?	?	?	?
Baiomys taylori	1	0	0	0	2	1	1	0	0	0	2	0	1	0	2	2	1	1	2	0	0	1	0	0	1
Baiomys musculus	1	0	0	0	2	1	1	0	0	0	2	0	1	0	1	2	1	1	2	0	0	1	0	0	1
Reithrodontomys megalotis	0	0	0	0	2	0	1	0	0	0	2	2	1	1	1	0	1	1	3	1	1	2	0	1	1
Reithrodontomys montanus	0	0	0	0	2	1	1	0	0	0	2	2	1	1	2	0	1	1	3	1	1	2	0	1	1
Peromyscus maniculatus	0	0	1	0	1	1	1	0	0	0	1	0	1	0	1	1	2	1	3	1	1	2	2	1	1
Peromyscus boylii	0	0	1	0	1	1	1	0	0	0	1	0	1	0	1	1	2	1	3	1	1	2	2	1	1
Ochrotomys nuttalli	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0

Appendix IV

Specimens used for morphological and molecular analyses.

Institutional acronyms associated with specimens.—

Angelo State Natural History Collection, Texas, United States (ASNHC); Brigham Young University, Provo, Utah, United States (BYU); Colección Nacional de Mamíferos, Instituto de Biología de la Universidad Autónoma de México, Ciudad de México, Ciudad de México, México (CNMA); Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States (CM); Fort Hays Sternberg Museum, Hays, Kansas, United States (FHSM); Field Museum of Natural History, Chicago, Illinois, United States (FMNH); University of Kansas Natural History Museum, Lawrence, Kansas, United States (KU); Natural History Museum of Los Angeles County, Los Angeles, California, United States (LACM); Louisiana State University Museum of Natural History, Baton Rouge, Louisiana, United States (LSUMZ); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Museo Nacional de Ciencias Naturales, Madrid, España (MNCN); Museum of Southwestern Biology, Albuquerque, New Mexico, United States (MSB); Museum of Vertebrate Zoology, University of California, Berkeley, California, United States (MVZ); Colección de Mamíferos del Museo de Zoología "Alfonso L. Herrera," Universidad Autónoma de México, Ciudad de México, México (MZFCM); Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, United States (OMNHN); Royal Ontario Museum, Toronto, Ontario, Canada (ROM); Texas Cooperative Wildlife Collection, Texas A&M University, College Station, Texas, United States (TCWC); Museum of Texas Tech University, Lubbock, Texas, United States (TTU); University of Arizona Laboratory of Paleontology, Tucson, Arizona, United States (UALP); University of California Museum of Paleontology, Berkeley, California, United States (UCMP); University of Michigan Museum of Zoology, Ann Arbor, Michigan, United States (UMMZ); University of South Carolina *Peromyscus* Genetic Stock Center, Columbia, South Carolina, United States (USC-PGSC), United States National Museum, Smithsonian Institute, Washington, District of Columbia, United States (USNM).

Specimens used for morphological analysis.—

Copemys loxodon specimens: UCMP 31726, 317569, 317673, 317558, 317543, 317567, 317511, 317394, 317400, 316365,

317467, 317496. *Acrolophomys rhodopetros* specimens: LACM 124912, 125052, 124930, 124878, 156372. *Onychomys leucogastor* specimens: USNM 272116; MVZ 76624, 87519, 105624; MACN 13433. *Onychomys torridus* specimens: CNMA 3345; MVZ 50695. *Onychomys arenicola*: CNMA 125, 46447. *Ochrotomys nuttalli*: FMNH 230688. *Onychomys* sp.: UALP 13963; FHSM VP-19867, -19868, -19869. *Baiomys taylori*: MNCN-275; USNM 27211. *Baiomys musculus*: FMNH 230688; MVZ 105624. *Reithrodontomys megalotis*: CNMA 45040; UNSM 272173; MVZ 113604, 219614. *Reithrodontomys montanus*: CNMA 36102; UNSM 272173, 272176. *Peromyscus maniculatus*: MVZ 70400, 219614, 225121. *Peromyscus boylii*: MVZ 219161, 222960.

Specimens used for molecular analysis.—

Museum catalog number/GenBank accession numbers of the sequences from that specimen. Museum catalog vouchers that were unavailable, unknown, or untraceable in GenBank or source publication are indicated with "?" or referenced with the corresponding tissue collection numbers (i.e., CN for the Royal Ontario Museum, LAF for Natural History Museum of Los Angeles County, OK for Sam Noble Oklahoma Museum of Natural History, NK for the Museum of Southwestern Biology, and TK for the Museum of Texas Tech University).

Ingroup.—

Baiomys musculus: TK 93194/AF548481; ?/KC953245; ?/KC953245; ?/KC953360. *Baiomys taylori*: ASNHC 11056/EF989740; MSB 46296/MF110330; NK3696/AY277408; TTU 54633/AY269983, AY274213; TTU 75580/AF548477; TTU 82642/AY994205. *Habromys chinanteco*: KU 124131/DQ861380. *Habromys delicatulus*: LAF 1801/DQ861399. *Habromys ixtlani*: CNMA 29849/EF989832, EF989842, EF989941; TK 93160/AY994239; TTU 82703/FJ214701. *Habromys lepturus:* CNMA 29970/EF989841; LSUMZ 29849/KC953506, KC953265; ROM 29849/MF110379; TTU 82703/MN057731; ?/KY753995. *Habromys lophurus*: ROM 98342/EF989745, EF989845, EF989944. *Habromys simulatus*: BYU 15052/DQ861404; ?/KF885928. *Hodomys alleni*: TK 45042/AY269968, AY817627, DQ179810, DQ180010, KT950894; ?/MF097739; ?/MF097862; ?/MF110384. *Isthmomys pirrensis*: LSUMZ 25441/KY754007, MF074888, MF097746, MF110395; TTU 39162/FJ214668, FJ214692, MK862084. *Megadontomys cryophilus*: BYU 16076/DQ861373. *Megadontomys nelsoni*: BYU 15286/HQ538496. *Megadontomys thomasi*: CNMA 29188/EF989750, EF989850; TK 93388/AY195795, AY994208, FJ214693, MK970569. *Neotoma albigula*: NK 1330/AF186814; NK 17583/AY817651, DQ180058; MVZ 197066/MF074905, MF097770, MF110441; TTU 76474/MK764759. *Neotoma bryanti*: MVZ 195972/KC953288, KC953408, KC953532, KY754056, MF110442. *Neotoma cinerea*: MSB 121427/AY269970, AY817635; MVZ 207659/KY754057, KC953409, KC953533; NK 56291/DQ180055. *Neotoma devia*: MVZ 197117/KC953410, KC953534, KY754058, MF110443. *Neotoma floridana*: OK 107/AY294959, KC953411, KY754059, MF110444; NK 64089/AY817637; TK 25389/KF861006. *Neotoma fuscipes*: MVZ 196386/DQ179823, DQ180026; TTU 81391/AY817632. *Neotoma goldmani*: TK 28315/AY817656, DQ179827, DQ180027. *Neotoma isthmica*: TK 93257/DQ179828; TK 93296/AY817631, DQ180029. *Neotoma lepida*: NK 54420/DQ180053; TTU 79134/AY817634; TTU 119266/KY754060, MF074906, MF097771, MF097896, MF110445. *Neotoma leucodon*: TK 48594/AY817644, DQ179839; ?/AY274198; ?/AY269969. *Neotoma macrotis*: MVZ 196550/KY754061, MF110446; TTU 81391/DQ180044. *Neotoma magister*: NK 64158/DQ179856, AY817641. *Neotoma mexicana*: TTU 79129/AY269971, AY274200, AY817646; TTU 122944/KY754062, MF074907, MF097772, MF097897, MF110447. *Neotoma micropus*: TTU 80855/DQ180050; TTU 80856/AY817655; TTU 116316/KY754063, MF074908, MF097773, MF097898, MF110448. *Neotoma picta*: TK 93390/AY817629, DQ179851, DQ180051. *Neotoma stephensi*: MVZ 197173/KY754064, MF097899, MF110449; TTU 78505/AY817642, DQ180052. *Neotomodon alstoni*: MSB 418171/KC953289, KC953535, KC953412, KY754065, MF110450; TK 45309/AY269973, AY274202, AY994210. *Ochrotomys nuttalli*: CM 106431/MF110463; CM 106809/KC953297, KC953422, KC953543; MSB 53299/KY754075; TCWC 31929/AY269974, AY274203, JX910114. *Onychomys arenicola*: TTU 67559/AY195793, AY269975, AY274204, JX910115; ROM 114904/EF989755, EF989856. *Onychomys leucogaster*: TK 31075/AY195794, AY269976, KT318183; TTU 60605/AY274205; ROM 017/KC953303, KC953550; ROM 114892/EF989860. *Onychomys torridus*: ASNHC 4066/EF989861, KY754082; MVZ 206851/MF110472; ROM 11491/EF989767. *Osgoodomys banderanus*: ASNHC 2664/EF989857; MZFCM 16203/MH495969; TK 45401/AY269977; TK 45952/AY994209, FJ214694. *Peromyscus attwateri*: OMNHN 33377/KY754098, MF074919, MF097784, MF097918, MF110487; TTU 55688/AY269978, AY274207, AY994220. *Peromyscus aztecus*: LSUMZ 25106/MF110488; MVZ 223195/KC953308, KC953434, KC953556; ROM 101489/EF989968; TK 45255/FJ214669, FJ214695; TTU 82696/MK970558. *Peromyscus boylii*: MVZ 216481/MF110489; TTU 81702/AY274208; TTU 82688/AY994227; ?/AF155386; ?/AY269979; ?/KC953309; ?/KC953435; ?/KC953557. *Peromyscus californicus*: MVZ 199654/KY754099, MF110490; USC-PGSC 1590/EF989772, EF989873; TTU 83292/AY994211, FJ214697, MK862086. *Peromyscus crinitus*: MVZ 217321/KY754102, MF110491, KC953310, KC953436, KC953558; TTU 108167/FJ214698, MN057725; ?/AY994213. *Peromyscus difficilis*: LSUMZ 36247/KY754103, MF074920, MF097919, MF110492; TTU 82690/AY994219; ?/AY269980; ?/AY274209. *Peromyscus eremicus*: BYU 18684/EF989877; LSUMZ 34364/KY754104, MF074921, MF097920, MF110493; TTU 81850/AY994212; TTU 83249/FJ214699, MN057726. *Peromyscus fraterculus*: USNM 569216/KC953311, KC953437, KC953559, KY754105, MF110494. *Peromyscus furvus*: ?/AF271027; ?/GQ176065; ?/JX910116; ?/MK970559. *Peromyscus gossypinus*: LSUMZ 26782/MF097921, MF110495; TTU 80682/DQ973102, FJ214671, FJ214702, MN057727. *Peromyscus hylocetes*: LSUMZ 25106/KY754100; TK 45309/AY994235, FJ214705. *Peromyscus leucopus*: OK 14/AY294927, KY754106, MF097922, MF110496; ROM 101861/EF989880; TTU 75694/AY994240; TTU 101645/FJ214706, MK970571. *Peromyscus levipes*: MVZ 159526/KY754107, MF110497; ROM 97624/EF989882; ROM 98294/EF989782; TK 47819/AY994224, MK970561; TTU 105150/FJ214707. *Peromyscus maniculatus*: MVZ 200760/KY754108, MF097923; ROM 98941/EF989783; TTU 97830/AY994242, FJ214708, MK970562; UMMZ 165752/AY163630. *Peromyscus mayensis*: ROM 98360/EF989787, EF989888, EF989987. *Peromyscus melanophrys*: TTU 49351/DQ973105; TTU 75509/AY994216, FJ214710, MN057729; USC-PGSC 1073/EF989890. *Peromyscus melanotis*: CNMA 44355/MN546877; TK 70997/FJ214673, FJ214711; USC-PGSC 25/EF989790; ?/MK970563. *Peromyscus mexicanus*: ROM 113237/EF989793, EF989894; TTU 82759/AY269981, AY274210; TTU 97013/AY994236; ?/EF028174. *Peromyscus nudipes*: NK 209245/KX998929; ROM 113216/EF989792, EF989893; TTU 96972/AY994238, FJ214713, MK970568. *Peromyscus polionotus*: USC-PGSC 11033/EF989795, EF989896, EF989995. *Peromyscus truei*: MVZ 157329/

AY277413; MVZ 197293/KY754109, MF110498; TTU 74991/MK907225; TTU 92732/FJ214677. *Peromyscus winkelmanni*: ?/AF131930; ?/FJ214678; ?/FJ214721. *Podomys floridanus*: TTU 97867/AY994214, EF989778, EF989879, FJ214723; TTU 97868/DQ973110, MN057732. *Reithrodontomys brevirostris*: ROM 116864/EF989817, EF989918, EF990017. *Reithrodontomys creper*: BYU 15244/AY859429; ROM 113346/MF110519; ?/KC953322; ?/KC953450; ?/KC953570. *Reithrodontomys dariensis*: ROM 116311/EF989815, EF989916, EF990015. *Reithrodontomys fulvescens*: OK 325/AY294928, AY294958; OK 326/KY754134, MF110520; ROM 114901/EF989904; TTU 54898/AY269982, AY274211, AY994207. *Reithrodontomys gracilis*: ROM 95890/AY859432, EF989905; ROM 116845/EF989807; ?/KC953571; ?/MF110521. *Reithrodontomys humulis*: OMNHN 36692/KY754135, MF074925, MF097791, MF097933, MF110522. *Reithrodontomys megalotis*: ASNHC 2136/KY754136; MVZ 148519/AY277414; TTU 40942/KJ697790, KJ697789, MK970570; ?/HQ269526; ?/KC953323; ?/KC953572. *Reithrodontomys mexicanus*: ROM 97308/EF989805, EF989906; TTU 85234/KJ697791; ?/HQ269527; ?/HQ269796; ?/KY754137. *Reithrodontomys microdon*: ROM 98300/KY754138, MF110523; ROM 98382/EF989814, EF989915. *Reithrodontomys spectabilis*: ASNHC 2140/AY859462; ROM 97733/EF989822, EF989923; ?/MF110524. *Reithrodontomys sumichrasti*: ROM 98383/EF989924; ROM 98384/EF989824, KY754139, MF097934, MF110525; TTU 549527/AY274212, JX910117, MK970566. *Scotinomys teguina*: TTU 104355/KT361509; UMMZ 3373/AF108705; ?/AY269984; ?/AY274214; ?/KC953328; ?/KC953578; ?/MF097799; ?/MF110540. *Scotinomys xerampelinus*: LSUMZ 25166/MF097942, MF110541; ROM 97311/EF989831, EF989932, KY754149. *Xenomys nelsoni*: TTU 28546/KY754179, MF097814, MF097958, MF110570; TTU 37790/AY269972, AY817628, DQ180013; ?/KC953343.

Outgroup.—

Arvicola terrestris: MVZ 155884/AY275106, AY277407; ?/AM392380. *Clethrionomys gapperi*: FMNH 145956/AY294952, MF074902; MVZ 179108/MF110430; UMMZ 162467/AY326080; ?/AY309431. *Cricetulus longicaudatus*: USNM 449102/AY326082; USNM 449106/MG685560, MG685601; ?/MG793226. *Microtus californicus*: MVZ 207423/KC953277, KC953401, KC953523, MF110415; MVZ 216595/EF506105. *Myospalax aspalax*: MSB 100533/KC953281, KC953525, MF110431; MSB 100576/AY326097; ?/AF326272. *Nesomys rufus*: FMNH 151915/AY326099, GQ405385; USNM 448955/KC953539, MF110454; ?/AF160592; ?/KF811250. *Nyctomys sumichrasti*: MSB 45815/KC953296, KC953421, MF097905; TTU 84484/AY195801, KT361510; TTU 88186/AY274215. *Oryzomys palustris*: MSB 64071/KC953304, KC953551; MSB 74956/MF110474; TTU 49415/AY269988, AY274219; TTU 75311/AY163623, GU126539; ?/GQ178279. *Ototylomys phyllotis*: ASNHC 7236/AY817624; ROM 35529/KC953429, KC953553; ROM 95675/EF989763; ?/AY009789; ?/AY269985; ?/AY274216; ?/MF110475. *Phodopus sungorus*: ?/AF540640; ?/AJ973390, ?/AY294954, ?/KC953439. *Rheomys raptor*: KU 159017/AY163635, KJ921706, MF097935, MF110528. *Sigmodon hispidus*: CN 42415/KR088999; NK 27055/AY277479; TTU 79181/EU652896, TTU 80626/AF425227; TTU 80759/AY269989, KT318181, KT964999; ?/AY241465. *Tylomys nudicaudus*: TTU 62082/DQ179812; TTU 67347/AY269986, AY274217; TTU 77530/AY817625; ROM 103590/AY163643, AY294933, KC953593; USNM 464885/MF110567.