Journal of Mammalogy, 103(5):1221–1236, 2022
https://doi.org/10.1093/jmammal/gyac031
Published online April 14, 2022

Reevaluation of the phylogenetic relationships among Neotomini rodents (*Hodomys*, *Neotoma*, and *Xenomys*) and comments on the woodrat classification

Robert D. Bradley,[1,2,*] Cody W. Edwards,[3] Laramie L. Lindsey,[1,6] Joanna R. Bateman,[1] Maria N.B. Cajimat,[4] Mary L. Milazzo,[4] Charles F. Fulhorst,[4] Marjorie D. Matocq,[5] and Matthew R. Mauldin[1,2]

[1]*Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409-3131, USA*
[2]*Natural Science Research Laboratory, Museum of Texas Tech University, Lubbock, Texas 79409-3191, USA*
[3]*Smithsonian-Mason School of Conservation (SMSC), George Mason University, Front Royal, Virginia 22030, USA*
[4]*Department of Pathology, University of Texas Medical Branch, Galveston, Texas 77555-0609, USA*
[5]*Department of Natural Resources and Environmental Science, University of Nevada, Reno, Nevada 89557, USA*
[6]*Present address: Department of Veterinary and Biomedical Sciences, University of Minnesota, Saint Paul, Minnesota 55108-0609, USA*

**To whom correspondence should be addressed: robert.bradley@ttu.edu*

The woodrats or packrats of the genus *Neotoma* have been the subject of a wide array of research including paleoecology, physiology, morphological evolution, systematics, speciation, and hybridization. In recent years, much work has been done to elucidate evolutionary relationships within and between closely related species of the genus; in particular the addition of newly collected specimens from critical geographic regions has provided new opportunities for taxonomic assessment. Given these new data and their potential, parsimony (PARS), maximum likelihood (ML), and Bayesian inference (BI) analyses were conducted on DNA sequences obtained from nine individual genes (four mitochondrial loci: *12S*, *16S*, *CoII*, and *Cytb*; five nuclear loci: *AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Myh6*) to estimate the phylogenetic relationships among 23 species of *Neotoma*. Results of these analyses depicted a wide array of phylogenetic relationships among taxa; with substantial nodal support recovered in both the ML and PARS analyses at some mid-level and terminal positions. Several individual genes, particularly *12S*, *AdhI2*, *BfibI7*, *CoII*, and *Cytb*, provided support at several basal positions; however, phylogenetic resolution was limited in the other genes. A final BI analysis where the nine genes were concatenated into a single data set produced several supported clades that corresponded to previously recognized species groups (*floridana*, *micropus*, *mexicana*, and *lepida*) and the subgenus *Homodontomys*. Levels of genetic divergence for within-species comparisons (estimated from the *Cytb* data set) ranged from 0.88% (*N. magister*) to 6.82% (*N. fuscipes*); for between sister species comparisons ranged from 4.68% (*N. devia* and *N. lepida*) to 12.70% (*N. angustapalata* and *N. nelsoni*); and for members within closely related clades ranged from 8.70% (*N. bryanti* and *N. lepida*) to 12.57% (*N. goldmani* and *N. magister*). Evaluations of generic, subgeneric, and species group boundaries were explored using phylogenetic principles on the DNA sequence data presented herein, as well as morphological findings from previous studies. Results obtained suggest that the most conservative taxonomic interpretation involves the abandonment of subgeneric delineations and relies on the recognition of eight species groups (*cinerea*, *floridana*, *fuscipes*, *lepida*, *mexicana*, *micropus, phenax*, and *stephensi*) as the backbone of the woodrat classification.

Key words: genetic species, mitochondrial genes, *Neotoma*, nuclear genes, phylogenetics, systematics

Las ratas cambalacheras del género *Neotoma* han sido estudiadas en varios tipos de investigaciones incluyendo paleoecología, fisiología, evolución morfológica, sistemática, especiación e hibridación. Recientemente, se

han realizado numerosos estudios para elucidar las relaciones evolutivas dentro del género y entre especies cercanamente relacionadas al mismo; en particular la inclusión de nuevos especímenes provenientes de regiones geográficas críticas han brindado nuevas oportunidades para evaluaciones taxonómicas. A partir de estos nuevos datos se realizaron análisis de parsimonia (PARS), Máxima Verosimilitud (MV), e Inferencia Bayesiana (IB) en secuencias de ADN provenientes de nueve genes individuales (cuatro loci mitocondriales: 12S, 16S, *Co*II, y *Cyt*b; cinco loci nucleares: *Adh*-I2, *Bfib*-I7, *En*2, *Mlr*, and *Myh*6) para determinar la relación filogenética de 23 especies de *Neotoma*. Los resultados de estos análisis presentan una amplia gama de relaciones filogenéticas entre taxa con un soporte nodal importante en los análisis de MV y PARS en algunas posiciones terminales de nivel medio. Varios genes individuales, en particular 12S, *Adh*-I2, *Bfib*-I7, *Co*II, and *Cyt*b, ofrecieron soporte en varias posiciones basales; sin embargo, la resolución filogenética fue reducida en los demás genes. El último análisis de IB, en donde nueve genes se concatenaron en un solo conjunto de datos, produjo soporte en varios clados que correspondieron a especies de grupos previamente reconocidos (*floridana*, *micropus*, *mexicana*, y *lepida*) y el sub-género *Homodontomys*. Los niveles de divergencia genética para comparaciones intraespecíficas fluctuaron entre 0.88% (*N. magister*) y 6.82% (*N. fuscipes*); para especies hermanas (4.68%—*N. devia* y *N. lepida* hasta 12.70%—*N. angustapalata* y *N. nelsoni*); y para los miembros de clados cercanos (8.70%—*N. bryanti* y *N. lepida* hasta 12.57%—*N. goldmani* y *N. magister*). Las evaluaciones de los limites genéricos, subgenéricos y de grupos de especies fueron explorados usando principios filogenéticos en las secuencias de ADN de este trabajo, y también se basaron en las conclusiones morfológicas de estudios previos. Los resultados obtenidos sugieren que la interpretación taxonómica más conservadora incluye el abandono de las delineaciones subgenéricas y se depende en el reconocimiento de ocho grupos de especies (*cinerea*, *floridana*, *fuscipes*, *lepida*, *mexicana*, *micropus, phenax*, y *stephensi*) como el pilar central de la clasificación de las ratas cambalacheras.

Palabras claves: especies genéticas, filogenética, genes mitocondriales, genes nucleares, *Neotoma*, sistemática

Woodrats or packrats (genus *Neotoma*) are members of the New World subfamily Neotominae (Musser and Carleton 2005). Their relatively large body size (for North American rodents), propensity for constructing middens (stick houses), and tendency to collect shiny objects for decoration of middens have made woodrats one of the most easily recognizable rodents in North America. Woodrats are adapted to a variety of habitats and ecological regions and occur throughout southern Canada, most of the continental United States, Mexico, and northern portions of Central America (see Hall 1981). Twenty-three extant species currently are recognized (Musser and Carleton 2005; Patton et al. 2007; Ordóñez-Garza et al. 2014; Bradley and Mauldin 2016; Pardiñas et al. 2017) and three species are presumed to have been extirpated in recent years (Mellink 1992; Smith et al. 1993; Cortés-Calva et al. 2001).

Early alpha-level taxonomic studies (Merriam 1892, 1894; Goldman 1904, 1905, 1909, 1915, 1932; Hall and Genoways 1970; and many others) utilizing morphological data resulted in the description of several species and subspecies. Goldman (1910), in his revision of *Neotoma*, provided not only a comprehensive synopsis of the taxonomy and systematics for the genus, but formulated a rudimentary organization of relationships through his recognition of subgenera and species groups. Following several decades of morphometric, allozymic, and chromosomal investigations (see citations in Edwards and Bradley 2002b) the first DNA sequence-based phylogeny was developed for the genus *Neotoma* (Edwards and Bradley 2002b). Although the phylogenetic and taxonomic results presented in Edwards and Bradley (2002b) resulted solely from DNA sequences obtained from the mitochondrial cytochrome-*b* gene (*Cytb*) and was limited to 13 species that were available for study at that time, they were able to develop phylogenetic hypotheses concerning the relationships of species within *Neotoma*, determine the validity and composition of species groups, status of subgenera, and to ascertain the taxonomic status of *Hodomys* and *Xenomys* relative to *Neotoma*.

In an attempt to expand phylogeny reconstruction beyond mitochondrial DNA data, Longhofer and Bradley (2006) used DNA sequences obtained from intron 2 of the nuclear gene alcohol dehydrogenase (*Adh1-I2*) and a subset of the individuals reported in Edwards and Bradley (2002b). Their findings supported the phylogenetic relationships and topology based on examination and analysis of *Cytb* sequences (Edwards and Bradley 2002b). Although not a primary focus of their research, phylogenetic analysis of a multigene data set (and morphologic data) by Matocq et al. (2007) further enhanced our knowledge of the phylogenetic relationships of woodrats by: (i) expanding the data set of Edwards and Bradley (2002b) to include additional individuals per taxon, (ii) increasing the number of sequenced genes (three mitochondrial and four nuclear), (iii) expanded the taxonomic coverage by including a newly recognized taxon, *N. macrotis* (Matocq 2002), and (iv) adding morphologic characters associated with the male genitalia. The topology presented in Matocq et al. (2007), for the most part, was in agreement with the findings of the earlier studies by Edwards and Bradley (2002b) and Longhofer and Bradley (2006) and provided support (posterior probabilities) at additional nodes. In addition, Matocq et al. (2007) provided increased resolution for: (i) composition and interrelationships among species groups and (ii) interpretation and recognition of subgenera.

Several recent taxonomic changes warrant a reevaluation of phylogenetic relationships within *Neotoma* as well as a reassessment of the overall classification of *Neotoma* and its allies

(*Hodomys* and *Xenomys*). First, Patton et al. (2007) provided a much-needed revision of the *N. lepida* complex. Their findings revealed that four species should be recognized (*N. bryanti*, *N. devia*, *N. insularis*, and *N. lepida*) and that *N. anthonyi*, *N. bunkeri*, and *N. martinensis* should be subsumed into *N. bryanti*. Second, Rogers et al. (2011) suggested that although *N. angustapalata* genetically was indistinguishable from *N. leucodon*, sufficient morphological differentiation existed to retain *N. angustapalata* as a species. Third, Edwards and Bradley (2002a) and Ordóñez-Garza et al. (2014) reevaluated the taxonomy of the *N. mexicana* complex and applied a senior synonym (*N. ferrunginea*) to woodrats in southern Mexico and portions of northern Central America; resulting in the placement of *N. isthmica* into synonymy with *N. ferrunginea*. In addition, Hernández-Canchola et al. (2021) subsumed two additional subspecies of *N. mexicana* (*tropicalis* and *solitaria*) into *N. ferrunginea* further solidifying the status of that taxon. Fourth, Fernández (2014) reevaluated the status of *N. nelsoni* and suggested it was no more than a subspecies of *N. leucodon*. Fifth, Bradley and Mauldin (2016) recognized *N. melanura* as a species distinct from *N. albigula*. Together, these revisions indicate that 23 species reside in *Neotoma* (see Pardiñas et al. (2017) for a list).

Therefore, our goals were to: (i) develop a molecular phylogeny based on DNA sequences that encompasses numerous individuals per species and that includes a reasonable subsampling of the geographic distribution of each species to determine an approximation of within- and between-species genetic variation, (ii) augment the multigene data set of Matocq et al. (2007) based on recent taxonomic changes, newly available samples, and additional genetic data to examine the phylogenetic relationships within *Neotoma*, and (iii) produce a classification that addresses the validity of previously described species groups (Goldman 1910; Burt and Barkalow 1942; Birney 1976; Planz et al. 1996; Edwards and Bradley 2002b) and subgenera (Gray 1843; Merriam 1894, 1903; Goldman 1910; Burt and Barkalow 1942; Edwards and Bradley 2002b). To accomplish this task, DNA sequences from five mitochondrial and four nuclear genes were examined as described below.

Materials and Methods

Samples.—The sampling scheme involved two stages relative to the goals outlined herein. First, DNA sequences from the entire mitochondrial cytochrome-*b* gene (*Cytb*—1,143 bp) were obtained from 691 individuals representing 21 of the 23 recognized species of *Neotoma* (see Appendix I) and examined to investigate intraspecific variation and to establish broad hypothesized species delineations. Second, DNA sequences were obtained from three additional mitochondrial (small subunit rRNA, *12S*—531 bp; large subunit rRNA, *16S*—566 bp; and cytochrome-*c* oxidase subunit II, *CoII*—633 bp) and five nuclear loci (intron 2 of alcohol dehydrogenase, *Adh1-I2*—577 bp; intron 7 of B-fibrinogen, *BfibI7*—668 bp; exon 3 of engrailed 2, *En2*—146 bp; exon 3 of mineralocorticoid receptor, *Mlr*—205 bp; and exon 35 and intron 35 of myosin heavy polypeptide 6α, *Myh6*—238 bp) as presented in Matocq et al. (2007) and Longhofer and Bradley (2006). For the second data set, one to two individuals per species were examined for the 21 *Neotoma* species. Following Edwards and Bradley (2002b), samples of *Xenomys nelsoni* and *Hodomys alleni* were included to establish a genetic benchmark for evaluating generic (*Xenomys* and *Hodomys*) and subgeneric (*Homodontomys*, *Neotoma*, *Teonoma*, and *Teonopus*) level relationships relative to *Neotoma*.

DNA isolation, polymerase chain reaction, and sequence methods.—For most specimens, genomic DNA was isolated from approximately 0.1 g of frozen liver tissue using the DNeasy kit (Qiagen, Valencia, California). The four mitochondrial loci (*12S*, *16S*, *CoII*, and *Cytb*) and five nuclear loci (*AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Myh6*) were amplified using the polymerase chain reaction (PCR) method (Saiki et al. 1988) following Matocq et al. (2007) and Longhofer and Bradley (2006); specific primers and thermal profiles are listed in Table 1. PCR products were purified with a QIAquick PCR Purification Kit or QIAquick Gel Extraction Kit (Qiagen, Valencia, California). Purified products were sequenced with an ABI 3100-Avant automated sequencer and ABI Prism Big Dye version 3.1 terminator technology (Applied Biosystems, Foster City, California). Resulting sequences were aligned and checked by eye using Sequencher 4.10 software (Gene Codes, Ann Arbor, Michigan); chromatograms were examined to verify all base changes. All sequences obtained in this study were deposited in GenBank and museum specimen catalog numbers are listed in Table 2.

To expand taxonomic coverage, skin clips were obtained from *N. phenax*. Small pieces of skin, approximately 2 mm × 2 mm in size, were obtained from the ventral suture of museum voucher specimens. Skin clips were rinsed, and DNA extracted following protocols outlined in Fulton et al. (2012) and Campos and Gilbert (2012). PCRs for skin clips used Phire II Hot Start DNA polymerase (Finnzymes Thermo Scientific, Rockford, Illinois), and the thermal profiles listed in Table 1. PCR products were purified, sequenced, aligned, and proofed as above. All DNA extractions and PCR methods were performed in a separate laboratory from the general PCR laboratory to minimize the risk of contamination; standard positive and negative controls were included at all stages to further reduce the possibility of contamination.

Phylogenetic and genetic divergence analyses.—DNA sequence data were analyzed using four approaches. First, the 691 *Cytb* sequences were used to construct a robust phylogeny that could be used to (i) establish a global view of nucleotide diversity within *Neotoma* and its allies, (ii) denote genetically divergent taxa and delineate species boundaries, and (iii) based on the rapid genetic divergence associated with this gene, serve as the primary data set for identifying nodal support for more terminal taxa. Second, each of the nine individual genes (four mitochondrial loci—*12S*, *16S*, *CoII*, and *Cytb*; five nuclear loci—*AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Myh6*) were analyzed independently so that the contribution of each gene could be visualized relative to the overall phylogeny. Third, the DNA sequences from the nine genes were concatenated into a single data set and analyzed jointly, with each gene analyzed under its own priors. Fourth, genetic distances were estimated for DNA

Table 1.—Information for specific loci examined in this study: locus being investigated, size of polymerase chain reaction (PCR) amplicons, primers used in PCR and sequencing methods, and thermal profiles for PCR reactions (all profiles included an initial 2–10 min denaturation cycle). Abbreviations for genes are as follows: small subunit rRNA, *12S*; large subunit rRNA, *16S*; intron 2 of alcohol dehydrogenase, *Adh1-I2*; intron 7 of B-fibrinogen, *Bfib*; cytochrome-*c* oxidase subunit II, *CoII*; cytochrome-*b*, *Cytb*; exon 3 of engrailed 2, *En2*; exon 3 of mineralocorticoid receptor, *Mlr*; and exon 35 and intron 35 of myosin heavy polypeptide 6α, *Myh6*. References for methods are listed in parentheses. The annealing temperature for the *Adh1-I2* reaction was ramped from 53°C to 48°C to −53°C to 73°C at a rate of 0.6°C per second.

Locus	Size	Primers	Thermal profile			
			Cycles	Denaturation	Annealing	Extension
12S	531 bp	12Sa (Matocq et al. 2007) 12Sb (Matocq et al. 2007)	33	94°C, 1 min	62°C, 1 min	72°C, 1 min
16S	571 bp	16Sa (Matocq et al. 2007) 16Sb (Matocq et al. 2007)	33	94°C, 1 min	45°C, 1 min	72°C, 1 min
Adh1-I2	583 bp	EXONII-F (Amman et al. 2006) EXONIII-R (Amman et al. 2006)	30	95°C, 30 s	53°C to 73°C*	73°C, 4 min
Bfib	777 bp	β17-mammL (Matocq et al. 2007) βfib-mammU (Matocq et al. 2007)	33	94°C, 1 min	60°C, 1 min	72°C, 1 min
CoII	633 bp	COIIa (Atkins and Honeycutt 1994) COIIb (Atkins and Honeycutt 1994)	33	94°C, 1 min	51°C, 1 min	72°C, 1 min
Cytb	1,143 bp	LGL765 (Bickham et al. 1995) LGL766 (Bickham et al. 2004) 700H (Peppers and Bradley 2000) 400F (Edwards et al. 2001)	33	94°C, 40 s	51°C, 45 s	73°C, 1 min 20 s
En2	146 bp	EN2f (Lyons et al. 1997) EN2r (Lyons et al. 1997)	33	94°C, 1 min	57°C, 1 min	72°C, 1 min
Mlr	205 bp	MLRf (Lyons et al. 1997) MLRr (Lyons et al. 1997)	33	94°C, 1 min	56°C, 1 min	72°C, 1 min
Myh6	236 bp	MYH2f (Lyons et al. 1997) MYH2r (Lyons et al. 1997)	33	94°C, 1 min	62°C, 1 min	72°C, 1 min

sequences obtained from the *Cytb* gene and used to examine the magnitude of genetic divergence between taxa.

In two of the analytical approaches (nine individual genes and concatenated), sequence data were analyzed using Bayesian inference (BI; MrBayes v3.2.6; Huelsenbeck and Ronquist 2001; Ronquist et al. 2012), maximum likelihood (ML; RAxML Version 8.2.12, Stamatakis 2014), and parsimony methods (PARS, PAUP* Version 4.0a167; Swofford 2002); only the BI and ML methods were used to analyze the *Cytb* data set. In all analyses, *Ototylomys phyllotis* and *Tylomys nudicaudus* were used as outgroups to set character polarity.

For the BI and ML analyses, 88 likelihood models were evaluated using jModelTest-2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012) and the Akaike information criterion with a correction for finite sample sizes (AICc; Hurvich and Tsai 1989; Burnham and Anderson 2004) was used to identify the most appropriate model of evolution for each data set. The "best-fit models" predicted for each gene are shown (Table 3); however, the GTR model of evolution (and +I +G when appropriate) was used because RAxML only uses the GTR model. The most appropriate nucleotide substitution model and the following parameters were used: two independent runs with four Markov chains (one cold and three heated; MCMCMC), 10^6 generations, and sample frequency of every 1,000 generations from the last 9 million generated. A visual inspection of likelihood scores resulted in the first 2,000,000 trees being discarded (10% burn-in) and a consensus tree (50% majority rule) constructed from the remaining trees. Clade probability values (CPV) ≥ 0.95 were used to designate nodal support (Huelsenbeck et al. 2002) in BI analyses and bootstrap values (BS; ≥ 70) based on 1,000 iterations (Felsenstein 1985) were used to designate nodal support in the ML analyses.

In the parsimony analysis (PAUP* Version 4.0a167; Swofford 2002), characters were assigned equal weight and variable nucleotide positions were treated as unordered, discrete characters with four possible states; A, C, G, and T. Phylogenetically uninformative characters were removed from the analysis. The most parsimonious trees were estimated using the heuristic search and tree bisection–reconnection option. A strict consensus tree from the resulting pool of most parsimonious trees and bootstrap values (BS; ≥ 70) based on 1,000 iterations (Felsenstein 1985) were used to designate nodal support.

The Kimura 2-parameter model of evolution (Kimura 1980) was used to estimate genetic distances (Table 4). Comparisons were based on sequences generated herein, as well as sequences obtained from other studies (Edwards et al. 2001) and Edwards and Bradley (2002b), Ordóñez-Garza et al. (2014), and GenBank. These values were then used to assess levels of genetic divergence among species of *Neotoma* following the criteria for the Genetic Species Concept as outlined in Bradley and Baker (2001) and Baker and Bradley (2006).

Results

A total of 691 DNA sequences, obtained from the mitochondrial *Cytb* gene, were examined under ML and BI frameworks in order to ascertain the phylogenetic relationships, delineate species boundaries, and identify genetically diverse taxa (Fig. 1) between and within the 21 species of *Neotoma* included in this study. For all species, a monophyletic arrangement was

Table 2.—List of museum catalog and GenBank accession numbers for taxa examined in this study. No sequence data were obtained for *N. chrysomelas* and *N. palatina*. Abbreviations for genes are as follows: small subunit rRNA, *12S*; large subunit rRNA, *16S*; cytochrome-*c* oxidase subunit II, *CoII*; cytochrome-*b*, *Cytb*; exon 3 of mineralocorticoid receptor, *Mlr*; exon 35 and intron 35 of myosin heavy polypeptide 6α, *Myh6*; exon 3 of engrailed 2, *En2*; intron 7 of B-fibrinogen, *Bfib*; and intron 2 of alcohol dehydrogenase, *Adh1-I2*. An N/A indicates that no sequence data were available. Abbreviations for museum catalog numbers follow Hafner et al. (1997) are: University of Kansas, Natural History Museum and Biodiversity Research Center (KU), Louisiana State University Museum of Natural Science (LSUMZ), Brigham Young University, Monte L. Bean Life Science Museum (BYU), University of New Mexico, Museum of Southwestern Biology (MSB), Museum of Texas Tech University (TTU), University of California-Berkeley, Museum of Vertebrate Zoology (MVZ), and University of California, Los Angeles, Dickey Collection (UCLA). A TK number (reference number used by the TTU Robert J. Baker Genetic Resources Collection) was used when museum catalog numbers were unavailable.

	Catalog #	*12S*	*16S*	*CoII*	*Cytb*	*Mlr*	*Myh6*	*En2*	*Bfib*	*Adh1-I2*
H. alleni	TK45042	DQ179660	DQ179710	DQ179760	AF186801	DQ179860	DQ179910	DQ179960	DQ180010	AY817627
X. nelsoni	TTU37790	DQ179663	DQ179713	DQ179763	AF307838	DQ179863	DQ179913	DQ179963	DQ180013	AY817628
N. albigula	TTU78451	DQ179666	DQ179716	DQ179766	AF376477	DQ179866	DQ179916	DQ179966	DQ180016	AY817648
N. albigula	MSB60812	DQ179708	DQ179758	DQ179808	AF186804	DQ179908	DQ179958	DQ180008	DQ180058	AY817651
N. albigula	MSB77371	DQ179707	DQ179757	DQ179807	AF186808	DQ179907	DQ179957	DQ180007	DQ180057	AY817650
N. albigula	TTU76474	DQ179667	DQ179717	DQ179767	AF186803	DQ179867	DQ179917	DQ179967	DQ180017	AY817649
N. angustapalata	BYU27733	N/A	N/A	N/A	HM989966	N/A	N/A	N/A	N/A	N/A
N. angustapalata	KU37062	N/A	N/A	N/A	HM989965	N/A	N/A	N/A	N/A	N/A
N. bryanti	TTU79131	DQ179680	DQ179730	DQ179780	AF307835	DQ179880	DQ179930	DQ179980	DQ180030	AY817633
N. bryanti	TTU79134	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	AY817634
N. bryanti	MVZ159790	DQ179685	DQ179735	DQ179785	DQ179835	DQ179885	DQ179935	DQ179985	DQ180035	N/A
N. cinerea	MSB74610	DQ179705	DQ179755	DQ179805	AF186800	DQ179905	DQ179955	DQ180005	DQ180055	AY817636
N. cinerea	MSB121427	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	AY817635
N. cinerea	BYU17790	DQ179709	DQ179759	DQ179809	DQ179859	DQ179909	DQ179959	DQ180009	DQ180059	N/A
N. devia	MVZ202447	DQ179682	DQ179732	DQ179782	DQ179832	DQ179882	DQ179932	DQ179982	DQ180032	MZ064564
N. devia	MVZ197094	DQ179686	DQ179736	DQ179786	DQ179836	DQ179886	DQ179936	DQ179986	DQ180036	N/A
N. ferruginea	TTU82666	DQ179679	DQ179729	DQ179779	AF305567	DQ179879	DQ179929	DQ179979	DQ180029	AY817631
N. ferruginea	TTU82665	DQ179678	DQ179728	DQ179778	AF329079	DQ179878	DQ179928	DQ179978	DQ180028	AY817630
N. floridana	TTU75413	DQ179669	DQ179719	DQ179769	AF186819	DQ179869	DQ179919	DQ179969	DQ180019	AY817638
N. floridana	TK27751	DQ179670	DQ179720	DQ179770	AF294341	DQ179870	DQ179920	DQ179970	DQ180020	AY817639
N. floridana	TK28244	DQ179671	DQ179721	DQ179771	AF186818	DQ179871	DQ179921	DQ179971	DQ180021	AY817640
N. floridana	MSB74955	DQ179704	DQ179754	DQ179804	AF294335	DQ179904	DQ179954	DQ180004	DQ180054	AY817637
N. fuscipes	MVZ196405	DQ179672	DQ179722	DQ179772	DQ179822	DQ179872	DQ179922	DQ179972	DQ180022	MZ064565
N. fuscipes	MVZ196371	DQ179675	DQ179725	DQ179775	DQ179825	DQ179875	DQ179925	DQ179975	DQ180025	MZ064566
N. goldmani	TTU45227	DQ179677	DQ179727	DQ179777	AF186829	DQ179877	DQ179927	DQ179977	DQ180027	AY817656
N. insularis	UCLA19911	N/A	N/A	N/A	DQ781161	N/A	N/A	N/A	N/A	N/A
N. lepida	MSB77775	DQ179703	DQ179753	DQ179803	AF307833	DQ179903	DQ179953	DQ180003	DQ180053	N/A
N. lepida	MVZ197126	DQ179688	DQ179738	DQ179788	DQ179838	DQ179888	DQ179938	DQ179988	DQ180038	MZ064567
N. leucodon	TTU75440	DQ179689	DQ179739	DQ179789	AF186809	DQ179889	DQ179939	DQ179989	DQ180039	AY817644
N. leucodon	TTU71198	DQ179665	DQ179715	DQ179765	AF186806	DQ179865	DQ179915	DQ179965	DQ180015	AY817643
N. macrotis	TTU81391	DQ179694	DQ179744	DQ179794	AF376479	DQ179894	DQ179944	DQ179994	DQ180044	AY817632
N. macrotis	TTU79134	DQ179693	DQ179743	DQ179793	AF307836	DQ179893	DQ179943	DQ179993	DQ180043	N/A
N. magister	MSB74952	DQ179706	DQ179756	DQ179806	AF294336	DQ179906	DQ179956	DQ180006	DQ180056	AY817641
N. melanura	TTU110072	N/A	N/A	N/A	KM488358	N/A	MZ147829	N/A	N/A	N/A
N. melanura	MVZ147661	MZ027647	MZ020779	MZ064558	AF337750	MZ064571	N/A	MZ064569	MZ064573	MZ064568
N. mexicana	TTU79129	DQ179697	DQ179747	DQ179797	AF294345	DQ179897	DQ179947	DQ179997	DQ180047	AY817646
N. mexicana	TK51346	DQ179696	DQ179746	DQ179796	AF186821	DQ179896	DQ179946	DQ179996	DQ180046	AY817647
N. micropus	TK31643	DQ179698	DQ179748	DQ179798	AF186822	DQ179898	DQ179948	DQ179998	DQ180048	AY817652
N. micropus	TTU80856	DQ179690	DQ179740	DQ179790	AF186827	DQ179890	DQ179940	DQ179990	DQ180040	AY817655
N. nelsoni	LSUMZ36663	KC758853	KC758852	N/A	KC758854	N/A	N/A	N/A	N/A	N/A
N. phenax	TTU6947	N/A	MZ020780 N/A	MK202784	MZ064572	N/A	MZ064570	N/A	N/A	
N. picta	TK93390	DQ179701	DQ179751	DQ179801	AF305569	DQ179901	DQ179951	DQ180001	DQ180051	AY817629
N. stephensi	TTU78505	DQ179702	DQ179752	DQ179802	AF308867	DQ179902	DQ179952	DQ180002	DQ180052	AY817642
O. phyllotis	TTU84371	DQ179664	DQ179714	DQ179764	DQ179814	DQ179864	DQ179914	DQ179964	DQ180014	AY817624
T. nudicaudus	TTU62082	DQ179662	DQ179712	DQ179762	N/A	DQ179862	DQ179912	DQ179962	DQ180012	AY817625
T. nudicaudus	TTU77530	N/A	N/A	N/A	AF307839	N/A	N/A	N/A	N/A	N/A

Table 3.—Summary of best-fit evolutionary models as determined by the programs jModelTest-2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012) and the Akaike information criterion with a correction for finite sample sizes (AICc; Hurvich and Tsai 1989; Burnham and Anderson 2004). Columns depict: locus name for each gene examined; best-fit evolutionary model; and appropriate GTR model used in the program RAxML for maximum likelihood analysis.

Locus	Best-fit evolutionary model	RAxML model
12S	GTR+I+G	GTR+I+G
16S	TIM2+I+G	GTR+I+G
Adh	HKY+G	GTR+G
Bfib	TIM2+G	GTR+G
CoII	TIM2+I+G	GTR+I+G
Cytb	GTR+I+G	GTR+I+G
En2	HKY	GTR
Mlr	HKY+G	GTR+G
Myh6	TrN+I+G	GTR+I+G

recovered with the exceptions of a clade containing samples of *N. leucodon*, *N. angustapalata*, and *N. nelsoni*. In most cases, sister species and other closely related taxa exhibited substantial nodal support (CPV ≥ 0.95 and BS ≥ 70) at the terminal positions of the topology; however, little support was recovered for clades located at middle-level positions (Fig. 1) and no support was recovered for clades located at basal positions.

Results of the PARS, ML, and BI analyses of the nine individual genes (four mitochondrial loci: *12S*, *16S*, *CoII*, and *Cytb*; five nuclear loci: *AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Myh6*) depicted a wide array of phylogenetic relationships among taxa. A synthesis of each analysis is provided in Fig. 2. Not only was substantial nodal support recovered in both the ML and PARS analyses at the mid-level and terminal position; several individual genes, particularly A, C–E, and I, provided support at the basal positions; however, phylogenetic resolution was limited in most genes.

The final BI analysis was based on concatenation of the nine genes into a single data set (Fig. 2). Several supported clades (CPV ≥ 0.95) were evident and are shown by an asterisk (*) above the node and to the left of the slash (/). Most of the supported clades corresponded to previously recognized species groups (*floridana*, *micropus*, *mexicana*, and *lepida*) and the subgenus *Homodontomys*. In general, CPV obtained from the concatenated analysis depicted support at the terminal and basal positions of the topology; however, little support was recovered for clades located at middle-level positions (i.e., species group relationships).

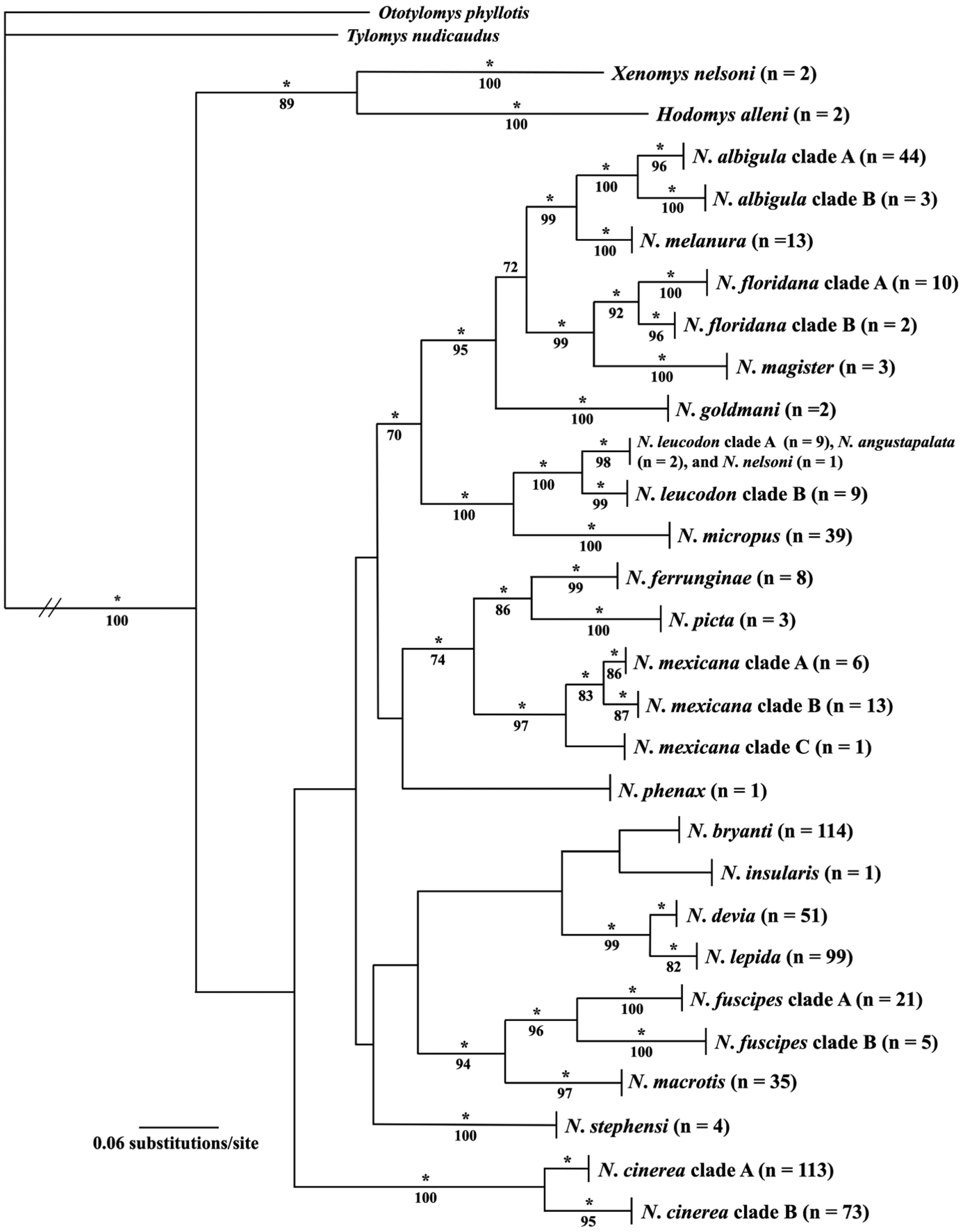
Genetic distances (Kimura 2-parameter; Kimura 1980) were estimated for DNA sequences obtained from the *Cytb* gene (Table 4) and used to examine the magnitude of genetic divergence between sister taxa and selected members of closely related clades. Values for within-species variation ranged from 0.88% (*N. magister*) to 6.82% (*N. fuscipes*). Between sister species values ranged from 4.68% (*N. devia* and *N. lepida*) to 12.70% (*N. angustapalata* and *N. nelsoni*); whereas members within closely related clades ranged from 8.70% (*N. bryanti* and *N. lepida*) to 12.57% (*N. goldmani* and *N. magister*).

Discussion

The first goal of this study was to use DNA sequence data from the *Cytb* gene (obtained from 691 individuals) to determine the magnitude of genetic variation within and between species and to develop a molecular phylogeny that could serve as a test of monophyly for taxonomic boundaries (Fig. 1). Within-species variation was relatively low compared to other species of rodents with most values < 3% and ranging from 0.88% for individuals of *N. magister* to 6.82% for individuals of *N. fuscipes* (Table 4). Given that sister species values obtained herein ranged from 4.68% (*N. devia* and *N. lepida*) to 12.70% (*N. angustapalata* and *N. nelsoni*) only *N. magister* seemed to approach those observed for other sister species of woodrats (see Hayes and Harrison 1992; Hayes and Richmond 1993; Edwards and Bradley 2001 for a synopsis of the relationship of *N. magister* to *N. floridana*). The intraspecific genetic variation identified within *N. fuscipes* (6.82%) primarily was due to the two genetically divergent groups (8.81% divergent at the *Cytb* locus) of *N. fuscipes* first noted by Matocq (2002). These groups exhibit divergence on the higher end of the between-species average for rodents (see Bradley and Baker 2001; Baker and Bradley 2006). Matocq (2002) referred to these groups as the "northern" and "west central" groups and estimated they may have diverged 1.8 mya. Recent genome-wide, single-nucleotide polymorphism data coupled with demographic modeling support this estimate of the timing and magnitude of divergence between the major lineages of *N. fuscipes* (Boria et al. 2021), and work is ongoing to reevaluate morphological variation across the group.

Table 4.—Genetic distances, estimated from mitochondrial cytochrome-*b* sequences using the Kimura 2-parameter model (Kimura 1980), for sister taxa and closely related (supported) species. Within-species distance values are in parentheses.

Pairwise comparison	Genetic distance
N. albigula (2.57%) vs. *N. melanura* (2.19%)	7.51%
N. albigula (2.57%) vs. *N. floridana* (2.26%)	9.98%
N. albigula (2.57%) vs. *N. magister* (0.88%)	11.61%
N. albigula (2.57%) vs. *N. goldmani* (1.06%)	10.73%
N. floridana (2.26%) vs. *N. magister* (0.88%)	8.01%
N. floridana (2.26%) vs. *N. melanura* (2.19%)	9.61%
N. floridana (2.26%) vs. *N. goldmani* (1.06%)	11.06%
N. magister (0.88%) vs. *N. melanura* (2.19%)	10.38%
N. magister (0.88%) vs. *N. goldmani* (1.06%)	12.57%
N. melanura (0.88%) vs. *N. goldmani* (1.06%)	10.14%
N. leucodon (4.20%) vs. *N. nelsoni* (NA)	13.00%
N. leucodon (4.20%) vs. *N. angustapalata* (NA)	3.78%
N. leucodon (4.20%) vs. *N. micropus* (0.83%)	9.87%
N. nelsoni (NA) vs. *N. angustapalata* (NA)	12.70%
N. nelsoni (NA) vs. *N. micropus* (0.83%)	16.89%
N. angustapalata (NA) vs. *N. micropus* (0.83%)	9.42%
N. ferruginea (2.21%) vs. *N. picta* (1.04%)	7.84%
N. ferruginea (2.21%) vs. *N. mexicana* (2.98%)	9.52%
N. picta (1.04%) vs. *N. mexicana* (2.98%)	9.86%
N. bryanti (2.88%) vs. *N. devia* (2.11%)	8.34%
N. bryanti (2.88%) vs. *N. lepida* (2.71%)	8.70%
N. bryanti (2.88%) vs. *N. insularis* (NA)	6.28%
N. devia (2.11%) vs. *N. lepida* (2.71%)	4.68%
N. devia (2.11%) vs. *N. insularis* (NA)	8.31%
N. lepida (2.71%) vs. *N. insularis* (NA)	8.68%
N. fuscipes (6.82%) vs. *N. macrotis* (2.74%)	8.52%


Ototylomys phyllotis
Tylomys nudicaudus
Xenomys nelsoni (n = 2)
Hodomys alleni (n = 2)
N. albigula clade A (n = 44)
N. albigula clade B (n = 3)
N. melanura (n =13)
N. floridana clade A (n = 10)
N. floridana clade B (n = 2)
N. magister (n = 3)
N. goldmani (n =2)
N. leucodon clade A (n = 9), N. angustapalata (n = 2), and N. nelsoni (n = 1)
N. leucodon clade B (n = 9)
N. micropus (n = 39)
N. ferrunginae (n = 8)
N. picta (n = 3)
N. mexicana clade A (n = 6)
N. mexicana clade B (n = 13)
N. mexicana clade C (n = 1)
N. phenax (n = 1)
N. bryanti (n = 114)
N. insularis (n = 1)
N. devia (n = 51)
N. lepida (n = 99)
N. fuscipes clade A (n = 21)
N. fuscipes clade B (n = 5)
N. macrotis (n = 35)
N. stephensi (n = 4)
N. cinerea clade A (n = 113)
N. cinerea clade B (n = 73)
0.06 substitutions/site

The second goal of this study was to determine if the phylogenetic relationships obtained from the expanded multigene data set added resolution to previous topologies generated for *Neotoma* and its allies. The topology obtained from the phylogenetic analysis of the 691 *Cytb* sequences (Fig. 1) was similar to that obtained in the concatenated analyses (Fig. 2, ML and BI), especially for terminal and mid-level clades. In no cases were clades based solely on *Cytb* sequences incongruent with supported clades (CPV ≥ 0.90; BS ≥ 70) obtained from the concatenated analyses, although the concatenated analyses provided superior support for basal and some mid-level arrangements. In addition, topologies and support values obtained from the ML, BI, and PARS were similar across most nodes.

Although the three molecular-based studies by Edwards and Bradley (2002b), Longhofer and Bradley (2006), and Matocq et al. (2007) supported similar interpretations of the phylogenetic relationships of *Neotoma* and its allies; Matocq et al. (2007) was the most inclusive in terms of taxonomic and character coverage. Consequently, the topology presented in Matocq et al. (2007) served as the primary comparison and point of discussion for the topology obtained from the concatenated analyses (Fig. 2). Given that the current study contained additional taxa not examined by Matocq et al. (2007), there were instances where the topologies could not be compared directly. To simplify the comparison of topologies (current study and Matocq et al. 2007) and to initiate a discussion of phylogenetic relationships that was used as the basis of developing a classification (Table 5), clades were described in relation to species-group assignment (Fig. 2) following that presented by Edwards and Bradley (2002b), Matocq et al. (2007), and modified herein.

A sister relationship between *Xenomys* and *Hodomys* was recovered (to the exclusion of a monophyletic *Neotoma*—remaining 21 species examined); this relationship agreed with that discussed by Matocq et al. (2007). This finding supports: (i) the interpretation that *Hodomys* should be recognized as a separate genus (Goldman 1910; Carleton 1980; Edwards and Bradley 2002b; Musser and Carleton 2005) and not as a subgenus within *Neotoma* (Burt and Barkalow 1942; Hall 1981) and (ii) *Neotoma* is monophyletic (Edwards and Bradley 2002b; Musser and Carleton 2005).

Four well-supported clades (Fig. 2) were recovered that corresponded to the *floridana* (*albigula*, *floridana*, *goldmani*, *magister*, and *melanura*), *lepida* (*bryanti*, *devia*, *insularis*, and *lepida*), *mexicana* (*ferrunginae*, *mexicana*, and *picta*), and *micropus* (*angustapalata*, *leucodon*, *micropus*, and *nelsoni*) species groups as described in Edwards and Bradley (2002b) and Matocq et al. (2007). These species groups were identified based on support as defined by BS (> 70) and CPV (> 0.95) and are indicated by letters A–I (corresponding to the nine mitochondrial and nuclear markers, respectively) and superimposed on Fig. 2, where appropriate.

Two species (*phenax* and *stephensi*) were not associated within any species group because of lack of nodal support values (Fig. 2). However, both species were included within the traditional subgenus *Neotoma* (Fig. 2) as defined by data from *AdhI2* and *CoII* markers. Three additional species (*macrotis*, *fuscipes*, and *cinerea*) formed a clade based on data from the *AdhI2* gene. Within this clade, *macrotis* and *fuscipes* were sister taxa as defined by the *12S*, *AdhI2*, *BfibI7*, *CoII*, *Mlr*, and *Cytb* genes; the taxonomic ramifications of this clade are discussed in the classification section.

The four mitochondrial genes (*12S*, *16S*, *CoII*, and *Cytb*) provided support at 7, 11, 10, and 23 nodes, respectively, whereas the five nuclear markers (*AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Mlr*) provided support at 18, 10, 5, 3, and 2 nodes, respectively. The distribution and contribution of nodal support for each marker is provided (Fig. 2).

The final goal of this study was to produce a classification for *Neotoma* and its allies based on DNA sequences obtained from single-gene analyses and from analyses of nine concatenated mitochondrial and nuclear genes. To accomplish this task, monophyletic groups obtained from analyses were evaluated for: (i) levels of support (BS > 70 and CPV > 0.95) and (ii) congruence to previous classifications and taxonomic arrangements. For this exercise, we used the arrangements presented in Goldman (1910), Hall (1981), Edwards and Bradley (2002b), and Musser and Carleton (2005) knowing that these studies differed in the types of data sets used and number of taxa recognized. In several cases, we drew upon information presented in more narrowly focused taxonomic studies (Patton et al. 2007; Rogers et al. 2011; Fernández 2014; Ordóñez-Garza et al. 2014; Bradley and Mauldin 2016). The proposed classification (Table 5) and below we provide a synopsis highlighting the differences and similarities between the five classification schemes.

Recognition of genera.—Essentially all analyses (single or concatenated) depicted a sister relationship between *Xenomys* and *Hodomys* and all remaining ingroup taxa contained within a monophyletic *Neotoma*. The recognition of *Xenomys* as a separate genus is supported by all other classifications discussed herein. Support for the recognition of *Hodomys* as a separate genus is supported in all other classifications except that of Hall (1981) where *Hodomys* was treated as a subgenus of *Neotoma* and, by extension *H. alleni* was assigned to *N. alleni*. Recognition of a traditional *Neotoma* assemblage (Musser and Carleton 2005) was supported by the concatenated data set and five single-gene data sets (Fig. 2). Recognition of *Teanopus* (*T. phenax*, Goldman 1910) was not supported by the sequence data analyzed herein because *N. phenax* was included in a clade containing 13 other species of *Neotoma* (although this support was weak; Fig. 2). To recognize *Teanopus* as a genus would require a major reorganization of the genus *Neotoma* and given the limited data we were able to assemble for *N. phenax*, any restructuring at that level would be premature.

Fig. 1.—Phylogenetic tree generated using Bayesian methods (MrBayes; Huelsenbeck and Ronquist 2001), the GTR+I+G model of evolution, and 691 DNA sequences obtained from the mitochondrial *Cytb* gene for the 23 species of *Neotoma* and allies examined in this study. Clade probability values (≥ 0.95) are indicated by an asterisk and are depicted above branches and bootstrap support values (≥ 70) obtained from the maximum likelihood analysis (RaxML Version 8.2.12, Stamatakis 2014) of the same data set are depicted below the branches.

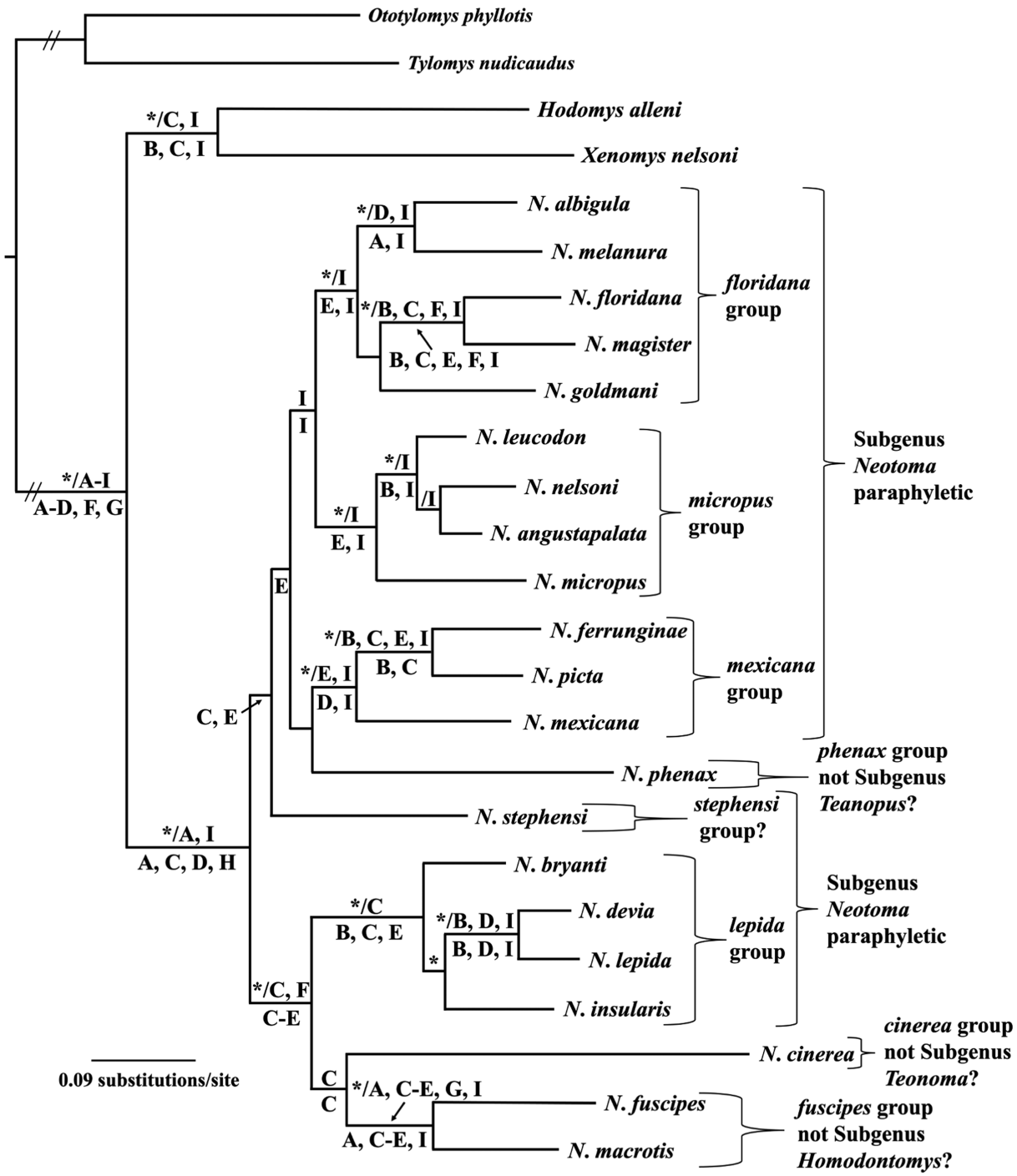


Fig. 2.—Phylogenetic tree generated using Bayesian methods (MrBayes; Huelsenbeck and Ronquist 2001), the GTR+I+G model of evolution, and a single data set represented by concatenated DNA sequences obtained from nine individual genes (four mitochondrial loci: *12S*, *16S*, *CoII*, and *Cytb* - denoted by A, B, E, and I, respectively; five nuclear loci: *AdhI2*, *BfibI7*, *En2*, *Mlr*, and *Myh6* - denoted by C, D, F, G, and H, respectively) for the 23 species of *Neotoma* examined in this study. Clade probability values (≥ 0.95) are placed above branches and depicted by an asterisk (*) to the left of the slash (/). Results of the maximum likelihood (ML; RaxML Version 8.2.12, Stamatakis 2014) and parsimony analysis (PARS, PAUP* Version 4.0a167; Swofford 2002) of individual genes (A–I) were superimposed on the Bayesian inference topology. Bootstrap support values (≥ 70) obtained from the ML analysis of individual genes (A–I) were placed above branches and to the right of the slash (/). Bootstrap support values (≥ 70) obtained from the PARS analysis of individual genes (A–I) were placed below branches.

Recognition of subgenera.—Historically, five subgenera (*Hodomys*, *Homodontomys*, *Neotoma*, *Teanopus*, and *Teonoma*) have been recognized (see Edwards and Bradley 2002b; Matocq et al. 2007; Table 5 for a discussion of the historical perspectives). In short, the subgenus *Neotoma* contained all recognized species except: *alleni* which previously was assigned to subgenus *Hodomys*; *macrotis* and *fuscipes* were assigned to subgenus *Homodontomys*; *cinerea* assigned to subgenus

Table 5.—Classification of *Neotoma* and allies (following Edwards and Bradley 2002; Musser and Carleton 2005; Matocq et al 2007). *Neotoma anthonyi*, *N. bunkeri*, and *N. martinensis* are included as either subspecies of, or synonyms of, *N. bryanti* following Patton et al. (2007). *Neotoma palatina* and *N. chrysomelas* were not examined in this study; however, they were placed into the classification based on the most current synopsis of the literature. Letter representations are as follows: X = no sequences available for examination, did not evaluate, or taxon was not recognized at time of study; A = agreement of previous taxonomy with that proposed herein; D = disagreement of previous taxonomy with proposed herein; Y = agreement of previous classifications (Goldman 1910; Hall 1981; Edwards and Bradley 2002; Musser and Carleton 2005) with that proposed herein; N = disagreement of previous classification with proposed herein; and NSG = no species-group assignment. Explanations relative to disagreements in taxonomy or classification between previous and current studies are placed in parentheses.

Proposed classification	Goldman (1910)	Hall (1981)	Edwards and Bradley (2002)	Musser and Carleton (2005)
Genus *Hodomys*				
H. alleni Merriam, 1894	A, Y	D (*N. alleni*), N (subgenus *Hodomys*)	A, Y	A, Y
Genus *Xenomys*				
X. nelsoni Merriam, 1892	A, Y	A, Y	A, Y	A, Y
Genus *Neotoma*	A, N (subgenus *Neotoma*)	A, N (subgenus *Neotoma*)	A, N (subgenus *Neotoma*)	A, N (subgenus *Neotoma*)
Species group *floridana*				
N. albigula Hartley, 1894	A, N (*albigula* group)	A, NSG	A, Y	A, Y
N. floridana (Ord, 1818)	A, Y	A, NSG	A, Y	A, Y
N. magister Baird, 1858	A, N (*pennsylvanica* group)	D (*N. fl. magister*), NSG	A, Y	A, Y
N. melanura Merriam, 1894	D (*N. a. melanura*), N	D (*N. a. melanura*), NSG	X	D (*N. a. melanura*), Y (*floridana* group)
N. goldmani Merriam, 1903	A, N (*desertorum* group)	A, NSG	A, Y	A, Y
Species group *lepida*				
N. bryanti Merriam, 1887	A, N (*intermedia* group)	A, NSG	X, X	A, Y
N. devia Goldman, 1927	X, X	D (*N. l. devia*), NSG	A, Y	A, Y
N. insularis Townsend, 1912	X, X	D (*N. l. insularis*), NSG	X, X	D (*N. l. insularis*), Y
N. lepida Thomas, 1893	A, N (*desertorum* group)	A, NSG	A, Y	A, Y
Species group *mexicana*				
N. chrysomelas J. A. Allen, 1908	A, Y	A, NSG	X, X	A, Y
N. ferruginea Tomes, 1862	D (*N. fe. ferruginea*), Y	D (*N. fe. ferruginea*), NSG	X, X	D (*N. me. ferruginea*), Y
N. mexicana Baird, 1855	A, Y	A, NSG	A, Y	A, Y
N. picta Goldman, 1904	D (*N. fe. picta*), Y	D (*N. fe. picta*), NSG	A, Y	D (*N. me. picta*), Y
Species group *micropus*				
N. angustapalata Baker, 1951	X, X	A, NSG	X, X	A, N (*mexicana* group)
N. leucodon Merriam, 1894	D (*N. a. leucodon*), N (*albigula* group)	D (*N. a. leucodon*), NSG	A, Y	A, Y
N. micropus Baird, 1855	A, Y	A, NSG	A, Y	A, Y
N. nelsoni Goldman, 1905	A, N (*albigula* group)	A, NSG	X, X	A, Y
N. palatina Goldman, 1905	A, N (*albigula* group)	A, NSG	X, X	A, Y
Species group *stephensi*				
N. stephensi Goldman, 1905	D (*N. l. stephensi*), N (*desertorum* group)	A, NSG	A, N (*lepida* group)	A, N (*lepida* group)
Species group *fuscipes*				
N. fuscipes Baird, 1858	A, N (*Homodontomys*)	A, NSG	A, N (*lepida* group)	A, N (*lepida* group)
N. macrotis Thomas, 1893	D (*N. fu. macrotis*), N (*fuscipes* group)	D, (*N. fu. macrotis*), NSG	X, X	A, N (*lepida* group)
Species group *phenax*				
N. phenax (Merriam, 1903)	D (*T. phenax*), N (genus *Teanopus*)	A, N (subgenus *Teanopus*)	X, X	A, N (subgenus *Teanopus*)
Species group *Teonoma*				
N. cinerea (Ord, 1815)	A, N (subgenus *Teanoma*)	A, N (subgenus *Teanoma*)	A, NSG	A, N (subgenus *Teanoma*)

Teonoma; and *phenax* was assigned to subgenus *Teanopus*. Recognition of subgenera historically was based on sound morphological interpretations; and one could argue for the use of subgenera based on those data; however, given the lack of statistical support provided by the phylogenetic analysis of the DNA sequence data presented herein, there appears to be no justification for the continued recognition of subgenera. First, although *Hodomys* represents a monophyletic assemblage, it was statistically supported as sister to *Xenomys* and outside of *Neotoma*; consequently, *Hodomys* was so different from other species of *Neotoma* that we follow Goldman (1910), Edwards and Bradley (2002b), Musser and Carleton (2005), and Matocq et al. (2007) in considering it distinct at the generic level.

Second, recognition of the remaining four subgenera (*Homodontomys*, *Neotoma*, *Teanopus*, and *Teonoma*) would require several major reorganizations of the remaining 22 species. For example: (A) the subgenus *Neotoma* is not monophyletic because *bryanti*, *devia*, *insularis*, and *lepida* are sister to a clade containing *cinerea* (subgenus *Teonoma*), *fuscipes* and *macrotis* (subgenus *Homodontomys*) resulting in a need to reorganize the subgenus *Neotoma* by splitting it into at least two clades (one poorly supported clade representing 14 species formerly comprising the subgenus *Neotoma* and the second being a strongly supported but unnamed subgenus containing (*bryanti*, *devia*, *insularis*, and *lepida*)); (B) *Teonoma* and *Homodontomys* are each monophyletic and represent distinct clades that could be recognized at the subgeneric level, but doing so would require a reevaluation of many species groups within the former subgenus *Neotoma* which appears to have evolved prior to the divergence of the *Teonoma* and *Homodontomys* clades; (C) alternatively, given that *Teonoma* and *Homodontomys* are sister groups they could be combined into a single subgenus, with *Teonoma* having taxonomic priority; and (D) similarly, to recognize *Teanopus* as a subgenus would require a major reorganization of the subgenus *Neotoma* and as discussed above, is premature. Based on the data presented herein, it seems prudent to abandon the use of subgenera.

Recognition of species groups.—Edwards and Bradley (2002b), Musser and Carleton (2005), Matocq et al. (2007), and Patton et al. (2007) placed most *Neotoma* species into four basic species groups (Table 5; *floridana*, *lepida*, *mexicana*, and *micropus*). Herein, we use information obtained from the inclusion of additional sequence data and increased taxon sampling to expand on these earlier premises, by further refining the species groups; as well as suggesting the formation of four new species groups. This refinement necessitates five taxonomic interpretations: (i) the *lepida* species group should be restricted to *bryanti*, *devia*, *insularis*, and *lepida* (recently extinct taxa from the Baja California region could be added following the synopsis provided by Patton et al. 2007); (ii) *stephensi* should be removed from the *lepida* species group as tentatively suggested by Edwards and Bradley (2002b) and recognized as its own species group (*stephensi* species group); (iii) given its level of genetic and morphologic distinction (summarized by Matocq et al. 2007) *cinerea* should be recognized as its own species group (*cinerea* species group) unless it is combined into a larger species group with *fuscipes* and *macrotis* with *cinerea* species group having priority; (iv) *fuscipes* and *macrotis* should be recognized in a separate species group (*fuscipes* species group) unless it is combined into a larger species group with *cinerea* as mentioned above; and (v) although little DNA sequence data were available for analyses, it appears that *phenax* should be recognized as its own species group (*phenax* species group) unless it is combined into a larger species group with members of the *mexicana* species group with the *mexicana* species group having priority. Conservatively, this interpretation results in the recognition of eight species groups (*cinerea*, *floridana*, *fuscipes*, *lepida*, *mexicana*, *micropus, phenax*, and *stephensi*).

At this juncture, the use of additional species groups to partition and define monophyletic groupings over the historical implementation of subgenera and a limited number of species groups seems to be a reasonable and superior approach given that: (i) six of the eight species (as defined herein) are monophyletic and are defined by statistical support; only *phenax* and *stephensi* received no support as species groups but given their exclusion from any species group predicates their independent evolutionary trajectory compared with other species groups that were defined by statistical support, and (ii) this simplifies the controversies in trying to invoke the subgenera concepts onto the phylogenetic results.

Recognition of species.—Description of woodrat species has taken place over two major time intervals, loosely defined here as the morphology/natural history era (circa pre-1970) and the molecular data era (circa post-1970). Our intent is not to justify one method over the other but simply to reflect the efforts of alpha- and beta-taxonomists as different research methods were employed; however, it is interesting that although several subspecific names have been elevated to species rank, no novel species name has been proposed since *N. angustapalata* (Baker 1951) and no new subspecies name has been proposed since *N. albigula subsolana* (Alvarez 1962; now *N. leucodon subsolana* - Edwards et al. 2001). A detailed list of species names and the authorities is provided in Table 5.

For species described prior to the utilization of molecular data in taxonomic decision-making, data presented herein unequivocally support the initial species recognition of Hartley (*albigula*, 1894), Merriam (*bryanti*, 1887), Ord (*cinerea*, 1818), J. A. Allen (*chrysomelas*, 1908), Ord (*floridana*,1815), Baird (*fuscipes*, 1858), Merriam (*goldmani*, 1903), Thomas (*lepida*, 1893), Baird (*mexicana* and *micropus*, 1855), Goldman (*palatina*, 1905), Merriam (*phenax*, 1903), and Goldman (*stephensi*, 1905). Recognition of two additional species (*angustapalata* - Baker 1951 and *nelsoni* Goldman 1905), described during the morphology/natural history era, is less certain; as these taxa were either embedded within the *N. leucodon* clade (*Cytb* data set) or were poorly supported as distinct taxa (concatenated data set). The only *Cytb* sequence available to this study (GenBank accession number KC758854) differs from other *Neotoma* sequences near the 3′ end. Elimination of the last ~230 bp of the sequence reduces the genetic divergence estimate between *angustapalata* and *nelsoni* from 12.7% to 7.6% and between *angustapalata* and *leucodon* from 12.7% to 8.8%, respectively; indicating a closer genetic relationship than originally implied. However, until additional samples of these two taxa can be examined, we take a

conservative approach and retain both as species—agreeing with the findings of Rogers et al. (2011) but disagreeing with Fernández (2014). In defense of Fernández (2014), whose position was based on a single specimen, the *leucodon* clade is more complex than depicted herein and additional studies are needed to determine the taxonomic status of populations in Mexico relative to those in the United States. During the molecular data era, two taxa originally described as subspecies were elevated to species status (*devia* - Goldman 1927, see Patton et al. 2007 and *melanura* - Merriam 1894, see Bradley and Mauldin 2016) and six taxa originally described as species but eventually relegated to subspecies, were reelevated to species status (*ferruginea* - Tomes 1862, see Ordóñez-Garza et al. 2014; *insularis* - Townsend 1912, see Patton et al. 2007; *leucodon* - Merriam 1894, see Edwards et al. 2002; *macrotis* - Thomas 1893, see Matocq 2002; *magister* - Baird 1858, see Edwards et al. 2001; and *picta* - Goldman 1904, see Edwards and Bradley 2002b). The elevation of these eight species was strongly supported by the data presented herein.

Epilogue.—Clearly, a more complete sequence data set and multiple samples would enhance the analyses and ultimately the interpretation of this taxonomic group. However, the combination of data (sequence and morphometric) and concepts discussed in Edwards and Bradley (2002b), Musser and Carleton (2005), Matocq et al. (2007), Patton et al. (2007), and this study act as a hypothesis for now. Samples of *N. chrysomelas* and *N. palatina* are needed to complete the complement of species. In addition, our understanding of phylogenetic relationships within *Neotoma* will be enhanced by examination of whole genomes; for example, the genomes of *N. lepida*, *N. bryanti*, *N. fuscipes*, and *N. macrotis* currently are being completed (M.D. Matocq and M.D. Dearing, pers. comm.). Genome-wide data coupled with morphological analyses and field collections targeted to represent the full scope of within- and between-species variation will be needed to further elucidate the evolutionary history of *Neotoma* and its allies.

Acknowledgments

This manuscript is dedicated to the late Dr. Charles (Chuck) F. Fulhorst who talked us into working on woodrat systematics in 1997. Inclusion of Dr. Fulhorst as an author is warranted, as Chuck was involved in data acquisition, conceptual design, funding, and overall direction of the manuscript until his untimely death. We thank E. K. Roberts, E. A. Wright, S. C. Vrla, M. A. Krishnamoorthy, S. Castañeda-Rico, and M. Becker for comments on earlier versions of the manuscript. We thank H. Garner and K. MacDonald (Museum of Texas Tech University) for assisting tissue loans from the Natural Science Research Laboratory. Portions of this project were funded by grants from the National Institutes of Health (DHHS A141435-01 to RDB) and by the State of Texas line-item through the Biological Database Project.

Literature Cited

Adkins R.M., Honeycutt R.L. 1994. Evolution of the primate cytochrome *c* oxidase subunit II gene. Journal of Molecular Evolution 38:215–231.

Alvarez T. 1962. A new subspecies of wood rat (*Neotoma*) from northeastern Mexico. University of Kansas Publications, Museum of Natural History 14:139–143.

Amman B.R., Hanson J.D., Longhofer L.K., Hoofer S.R., Bradley R.D. 2006. Intron 2 of the alcohol dehydrogenase gene (ADH1-I2): a nuclear DNA marker for mammalian systematics. Occasional Papers, Museum of Texas Tech University 256:1–16.

Baker R.J., Bradley R.D. 2006. Speciation in mammals and the genetic species concept. Journal of Mammalogy 87:643–662.

Bickham J.W., Patton J.C., Schlitter D.A., Rautenbach I.L., Honeycutt R.L. 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). Molecular Phylogenetics and Evolution 33:333–338.

Bickham J.W., Wood C.C., Patton J.C. 1995. Biogeographic implications of cytochrome b sequences and allozymes in sockeye (*Oncorhynchus nerka*). Journal of Heredity 86:140–144.

Birney E.C. 1976. An assessment of relationships and effects of interbreeding among woodrats of the *Neotoma floridana* species-group. Journal of Mammalogy 57:103–132.

Boria R.A., Brown S.K., Matocq M.D., Blois J.L. 2021. Genome-wide genetic variation coupled with demographic and ecological niche modeling of the dusky-footed woodrat (*Neotoma fuscipes*) reveal patterns of deep divergence and widespread Holocene expansion across northern California. Heredity 126:521–536.

Bradley R.D., Baker R.J. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Bradley R.D., Mauldin M.R. 2016. Molecular data indicate a cryptic species in *Neotoma albigula* (Cricetidae: Neotominae) from northwestern México. Journal of Mammalogy 97:187–199.

Burnham K.P., Anderson D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Burt W.H., Barkalow F.S., Jr. 1942. A comparative study of the baculum of woodrats (subfamily Neotominae). Journal of Mammalogy 23:287–297.

Campos P.F., Gilbert T.M. 2012. DNA extraction from keratin and chitin. In: Shapiro B., Hofreiter M., editors. Ancient DNA: methods and protocols. Humana Press, New York, USA; p. 43–49.

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

Cortès-Calva P., Alvarez-Castañeda S.T, Yenssen E. 2001. *Neotoma anthonyi*. Mammalian Species 663:1–3.

Darriba D., Taboada L.G.L., Doallo R., Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772.

Edwards C.W., Bradley R.D. 2001. Molecular phylogenetics of the *Neotoma floridana* species group. Journal of Mammalogy 82:791–798.

Edwards C.W., Bradley R.D. 2002a. Molecular systematics and the historical phylobiogeography of the *Neotoma mexicana* species group. Journal of Mammalogy 83:20–30.

Edwards C.W., Bradley R.D. 2002b. Molecular systematics of the genus *Neotoma*. Molecular Phylogenetics and Evolution 25:489–500.

Edwards C.W., Fulhorst C.F, Bradley R.D. 2001. Molecular phylogenetics of the *Neotoma albigula* species group: further evidence of a paraphyletic assemblage. Journal of Mammalogy 82:267–279.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Fernàndez J.A. 2014. Mitochondrial phylogenetics of a rare Mexican endemic: Nelson's woodrat, *Neotoma nelsoni* (Rodentia: Cricetidae), with comments on its biogeographic history. The Southwestern Naturalists 59:81–90.

Fulton T.L., Wagner S.M, Shapiro B. 2012. Case study: recovery of ancient nuclear DNA from toe pads of the extinct passenger pigeon. Methods in Molecular Biology 840:29–35.

Goldman E.A. 1904. Description of five new mammals from Mexico. Proceedings of the Biological Survey of Washington 17:79–82.

Goldman E.A. 1905. Twelve new wood rats of the genus *Neotoma*. Proceedings of the Biological Survey of Washington 18:27–34.

Goldman E.A. 1909. Five new woodrats of the genus *Neotoma*. Proceedings of the Biological Survey of Washington 22:139–142.

Goldman E.A. 1910. Revision of the wood rats of the genus *Neotoma*. North American Fauna 31:1–124.

Goldman E.A. 1915. Five new mammals from México and Arizona. Proceedings of the Biological Survey of Washington 31:133–137.

Goldman E.A. 1932. Review of the woodrats of *Neotoma lepida* group. Journal of Mammalogy 13:59–67.

Gray J.E. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum of Natural History Publication, London, United Kingdom.

Guindon S., Gascuel O. 2003. A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52:696–704.

Hafner M.S., Gannon W.L., Salazar-Bravo J., Alvarez-Castañeda S.T. 1997. Mammal collections in the western hemisphere: a survey and directory of existing collections. Allen Press, Lawrence, Kansas, USA.

Hall E.R. 1981. The mammals of North America. 2nd ed. John Wiley & Sons, Inc., New York, USA.

Hall E.R., Genoways H.H. 1970. Taxonomy of the *Neotoma albigula*-group of woodrats in central México. Journal of Mammalogy 51:504–516.

Hayes J.P., Harrison R.G. 1992. Variation in mitochondrial DNA and the biogeographic history of woodrats (*Neotoma*) in the eastern United States. Systematic Biology 41:331–344.

Hayes J.P., Richmond M.E. 1993. Clinal variation and the morphology of woodrats (*Neotoma*) of the eastern United States. Journal of Mammalogy 74:204–216.

Hernández-Canchola G., Léon-Panagua L., Esselstyn J. 2021. Mitochondrial DNA indicates paraphyletic relationships of disjunct populations in the *Neotoma mexicana* species group. Therya 12:163–169.

Huelsenbeck J.P., Larget B., Miller R.E., Ronquist F.R. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Systematic Biology 51:673–688.

Huelsenbeck J.P., Ronquist F.R. 2001. MrBayes: Bayesian inference for phylogeny. Biometrics 17:754–756.

Hurvich C.M., Tsai C.-L. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Kimura M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111–120.

Longhofer L.K., Bradley R.D. 2006. Molecular systematics of the genus *Neotoma* based on DNA sequences from intron 2 of the alcohol dehydrogenase gene. Journal of Mammalogy 87:961–970.

Lyons L.A., Laughlin T.F., Copeland N.G., Jenkins N.A., Womack J.E., O'Brien S.J. 1997. Comparative anchor tagged sequences (CATS) for integrative mapping of mammalian genomes. Nature Genetics 15:47–56.

Matocq M.D. 2002. Morphological and molecular analysis of a contact zone in the *Neotoma fuscipes* species complex. Journal of Mammalogy 83:866–883.

Matocq M.D., Shurtliff Q.R., Feldman C.R. 2007. Phylogenetics of the woodrat genus *Neotoma* (Rodentia: Muridae): implications for the evolution of phenotypic variation in male external genitalia. Molecular Phylogenetics and Evolution 42:637–652.

Mellink E. 1992. The status of *Neotoma anthonyi* (Rodentia; Muridae, Cricetinae) of Todos Santos Islands, Baja California, Mexico. Bulletin of the California Academy of Sciences 9:137–140.

Merriam C.H. 1892. Description of nine new, Mexico mammals collected by E. W. Nelson in the states of Colima and Jalisco. Proceedings of the Biological Society of Washington 7:164–174.

Merriam C.H. 1894. Abstract of a study of the American wood rats, with descriptions of fourteen new species and subspecies of the genus *Neotoma*. Proceedings of the Biological Survey of Washington 9:117–128.

Merriam C.H. 1903. Two new wood rats (genus *Neotoma*) from the state of Coahuila, Mexico. Proceedings of the Biological Survey of Washington 16:47–48.

Musser G.G., Carleton M. D. 2005. Superfamily Muroidea. In: Wilson D.E., Reeder D.M., editors. Mammal species of the World: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland, USA; p. 894–1531.

Ordóñez-Garza N., Thompson C.W., Unkefer M., Edwards C.W., Owen J.G., Bradley R.D. 2014. Systematics of the *Neotoma mexicana* species group (Mammalia: Rodentia: Cricetidae) in Mesoamerica: new molecular evidence on the status and relationships of *N. ferruginea* Tomes, 1862. Proceedings of the Biological Society of Washington 127:518–532.

Pardiñas U., Myers P., León-Paniagua L., Ordóñez Garza N., Cook J.A., Kryštufek B., Haslauer R., Bradley R.D., Shenbrot G., Patton J.L. 2017. Cricetidae (true hamsters, voles, lemmings, and New World rats and mice). In: Wilson D.E., Lacher T.E., Jr., Mittermeier R.A., editors. Handbook of the mammals of the world, volume 7. Rodents II. Lynx Editions in association with Conservation International and ICUN, Barcelona, Spain; p. 355–396.

Patton J.L., Huckaby D.G., Alvarez-Castañeda S.T. 2007. The evolutionary history and a systematic revision of the *Neotoma lepida* group. University of California Publications in Zoology 135:1–411.

Peppers L.L., Bradley R.D. 2000. Cryptic species in *Sigmodon hispidus*: evidence from DNA sequences. Journal of Mammalogy 81:332–343.

Planz J.V., Zimmermann E.G., Spradling T.A., Akins D.R. 1996. Molecular phylogeny of the *Neotoma floridana* species group. Journal of Mammalogy 77:519–535.

Rogers D.S., Leite R.N., Reed R.J. 2011. Molecular phylogenetics of an endangered species: the Tamaulipan woodrat (*Neotoma angustapalata*). Conservation Genetics 12:1035–1048.

Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M., Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542

Saiki R.K., Gelfand D.H., Stoffel S., Scharf S.J., Horn G.T., Mullis K.B., Erlich H.A. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science 239:487–491.

Smith F.A., Bestelmeyer B.T., Strong M. 1993. Anthrogenic extinction of the endemic woodrat *Neotoma bunkeri* Burt. Biodiversity Letters 1:149–155.

Stamatakis A. 2014. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Swofford D.L. 2002. PAUP* phylogenetic analysis using parsimony (*and other methods). Version 4.0a (build 169). Sinauer Associates, Sunderland, Massachusetts, USA.

Submitted 15 May 2021. Accepted 12 March 2022.

Associate Editor was Jacob Esselstyn.

Appendix I

Specimens for which cytochrome-*b* sequences were either generated herein or obtained from GenBank. For each specimen, museum catalog numbers (abbreviations for museum acronyms follow Hafner et al. 1997) are provided to the left of the slash (/) and GenBank accession numbers are provided to the right of the slash. Abbreviations are as follows: Centro de Investigaciones Biológicas del Noroeste (CIB), Cornell University Museum of Vertebrates (CUMV), Denver Museum of Nature and Science (DMNS), Louisiana State University, Museum of Natural Science (LSUMZ), Midwestern State University (MWSU), Monte L. Bean Life Science Museum (BYU), New Mexico Museum of Natural History (NMMNH); Recent Collection of Mammals, Museum of Texas Tech University (TTU), Royal Alberta Museum (RAM), Royal British Columbia Museum (RBCM), Royal Ontario Museum (ROM), United States National Museum of Natural History (USNM), Universidad Autónoma de Morelos (CMC), University of Alaska Museum (UAM), University of California, Berkeley, Museum of Vertebrate Zoology (MVZ), University of California Los Angeles, Dickey Collection (UCLA), University of Colorado, Museum of Natural History (UCM), University of Kansas, Natural History Museum and Biodiversity Research Center (KU), University of New Mexico, Museum of Southwestern Biology (MSB), University of Utah, Natural History Museum of Utah (UMNH), and University of Washington, Thomas Burke Memorial Washington State Museum (UWBM). If museum catalog numbers were unavailable, specimens were referenced with a corresponding collector or other special number (CR, Camp Roberts collection by Marjorie D. Matocq; JLP, James L. Patton; JO, James G. Owen, collector number; MDM, Majorie D. Matocq collector number; MDMNCN, Majorie D. Matocq no collector number; OK, Scott J. Steppan, collector number; OSR, Clinton Epps, collector number; SP, special number of the Carnegie Museum of Natural History; and TK, number special number of the Museum of Texas Tech University).

Ototylomys phyllotis.—TTU84371/AY009789.

Tylomys nudicaudus.—TTU62082/AF307839.

Xenomys nelsoni.—TTU37790/AF307838; TTU28546/KY754179.

Hodomys alleni.—TK45042/AF186801; TK45043/AF186802.

Neotoma albigula.—MSB77708/AF186811; MSB77331/AF186810; NMMNH3795/KM488335; NMMNH4891/KM488336; MSB82999/EU141962; TTU99846/EU141960; TTU99895/EU141964; MSB60812/AF186804; MSB60818/KF267873; TTU78448/AF186816; TTU106657/EU141959; TTU89870/KM488337; TTU97573/KF733991; TTU106915/KM488340; TTU99958/KM488341; TTU97577/KM488339; TTU97812/KF733995; TTU97811/KF733994; TTU97692/KF733990; TTU97776/KF733993; TTU106768/KM488338; TTU106619/KM488347; TTU97139/KF733989; TTU116582/KC250463; TTU76476/AF376472; TTU97148/EU141961; TTU88387/EU141963; TTU97657/KM488342; TTU88153/MZ064559; TTU99878/MZ064560; TTU97156/KF733996; TTU76474/AF186803; MSB77977/AF186807; MSB77371/AF186808; MSB83932/KM488343; MSB41715/AF186814; MSB83827/KM488346; MSB42599/KM488345; NMMNH5325/KM488344; TTU78447/AF186817; TTU78450/AF376476; TTU78451/AF376477; CIB14472/HQ328520; CIB1572/HQ328519; CIB15474/HQ328518; CIB4551/HQ328516; CIB14458/HQ328515; CIB14445/HQ328514; CIB4546/HQ328513; CIB14444/HQ328512; CIB14443/HQ328511; CIB4542/HQ328510; CIB4539/HQ328509; CIB14432/HQ328508; CIB4558/HQ328507; CIB4536/HQ328506; CIB14467/HQ328517.

Neotoma angustapalata.—KU37062/HM989965; BYU27733/HM989966.

Neotoma bryanti.—MSB42979/AF307832; TTU41898/AF376467; TTU83326/KF267875; TTU79131/AF307835; TTU119510/MZ064560; TTU119509/MZ064561; TTU119508/KF267874; MVZ186296/DQ781160; MVZ197380/DQ781135; MVZ195972/KY754056; MVZ186295/DQ781159; MVZ195981/DQ781158; MVZ198589/DQ781157; MVZ198588/DQ781156; MVZ198585/DQ781155; MVZ198584/DQ781154; MVZ195968/DQ781153; MVZ195967/DQ781152; MVZ195963/DQ781151; MVZ195962/DQ781150; MVZ196769/DQ781149; MVZ196098/DQ781148; MVZ196097/DQ781147; MVZ195977/DQ781146; MVZ195976/DQ781145; MVZ198580/DQ781144; MVZ198583/DQ781143; MVZ198582/DQ781142; MVZ196756/DQ781141; MVZ196755/DQ781140; USNM137201/DQ781138; USNM137173/DQ781137; MVZ197381/DQ781136; MVZ197376/DQ781134; MVZ197375/DQ781133; MVZ197175/DQ781132; MVZ197174/DQ781131; MVZ195244/DQ781130; MVZ195243/DQ781129; MVZ196146/DQ781128; MVZ196145/DQ781127; MVZ196144/DQ781126; MVZ196140/DQ781125; MVZ196138/DQ781124; MVZ202544/DQ781123; MVZ202543/DQ781122; MVZ198658/DQ781121; MVZ198657/DQ781120; MVZ196103/DQ781119; MVZ196101/DQ781118; MVZ202539/DQ781117; MVZ199807/DQ781116; MVZ199806/DQ781115; MVZ195325/DQ781114; MVZ195323/DQ781113; MVZ198577/DQ781112; MVZ196120/DQ781111; MVZ196119/DQ781110; MVZ196133/DQ781109; MVZ196132/DQ781108; MVZ198678/DQ781107; CIB7577/DQ781106; CIB7576/DQ781105; CIB7580/DQ781104; CIB7579/DQ781103; CIB7584/DQ781102; CIB7583/DQ781101; CIB2781/DQ781100; CIB2785/DQ781099; UCLA19720/DQ781098; CIB11575/DQ781097; CIB11574/DQ781096; CIB11572/DQ781095; CIB11579/DQ781094; CIB11595/DQ781093; CIB9840/DQ781092; CIB9844/DQ781091; CIB9842/DQ781090; CIB7590/DQ781089; CIB9835/DQ781088; CIB9246/DQ781087; CIB10908/DQ781086; CIB10907/DQ781085; CIB10909/DQ781084; CIB8659/DQ781083; CIB8657/DQ781082; CIB865/DQ781081; CIB8654/DQ781080; CIB7594/DQ781079; CIB2798/DQ781078; CIB7707/DQ781077; CIB7706/DQ781076; CIB7595/DQ781075; CIB5158/DQ781074; CIB7591/DQ781073; CIB7589/DQ781072; CIB8651/DQ781071; CIB7586/DQ781070; CIB8650/DQ781069; CIB7585/DQ781068; CIB3396/DQ781067; CIB2788/DQ781066; CIB7709/DQ781065; CIB7708/DQ781064; USNM139030/DQ781139.

Neotoma cinerea.—MDM148/AF337751; MSB121427/AF186799; MSB121427/AF186799; MSB74610/AF186800; BYU17790/DQ179859; MSB149469/JN593138; RAM04121/JQ241228; UWBM78604/JQ241243; RBCM0207/JN593210; UAM35116/JN593213; MVZ223394/JN593165; MVZ201915/JN593152; MVZ223440/JN593189; MVZ223425/JN593181; MVZ223445/JN593193; MVZ223443/JN593192; MVZ223435/JN593187; MSB140843/JN593136; MVZ207659/KY754057; UWBM76808/JQ241242; UWBM72137/JQ241241; UWBM72108/JQ241240; UWBM72106/JQ241239; UMNH32654/JQ241238; UMNH32653/JQ241237; UMNH32187/JQ241236; UMNH31874/JQ241235; UMNH3187/JQ241234; UAM50132/JQ241233; UAM35118/JQ241232; UAM35117/JQ241231; UAM24567/JQ241230; UAM2456/JQ241229; RAM0183/JQ241227; MVZ223462/JQ241226; MVZ223461/JQ241225; MVZ223460/JQ241224; MVZ223459/JQ241223; MVZ223458/JQ241222; MVZ223455/JQ241221; MVZ223448/JQ241220; MVZ223447/JQ241219; MVZ223446/JQ241218; MVZ223444/JQ241217; MVZ223439/JQ241216; MVZ223437/JQ241215; MVZ223436/JQ241214; MVZ223432/JQ241213; MVZ223429/JQ241212; MVZ223427/JQ241211; MVZ223426/JQ241210; MVZ223421/JQ241209; MVZ223420/

JQ241208; MVZ223419/JQ241207; MVZ223418/JQ241206; MVZ223417/JQ241205; MVZ223415/JQ241204; MVZ223412/JQ241203; MVZ223411/JQ241202; MVZ223410/JQ241201; MVZ223409/JQ241200; MVZ223408/JQ241199; MVZ223402/JQ241198; MVZ223400/JQ241197; MVZ223399/JQ241196; MVZ223396/JQ241195; MVZ220747/JQ241194; MVZ218379/JQ241193; MVZ201916/JQ241192; MSB92136/JQ241191; MSB76967/JQ241190; MSB76527/JQ241189; MSB76526/JQ241188; MSB74646/JQ241187; MSB74611/JQ241186; MSB74609/JQ241185; MSB152693/JQ241184; MSB152633/JQ241183; DMNS11517/JQ241182; UWBM79658/JN593237; UWBM79495/JN593236; UWBM78852/JN593235; UWBM78606/JN593234; UWBM78139/JN593233; UWBM78001/JN593232; UWBM76813/JN593231; UWBM76811/JN593230; UWBM76799/JN593229; UWBM76697/JN593228; UWBM75217/JN593227; UWBM73810/JN593226; UWBM49066/JN593225; UMNH32655/JN593224; UMNH32468/JN593223; UMNH32202/JN593222; UMNH31875/JN593221; UMNH31172/JN593220; UMNH29794/JN593219; UCM18902/JN593218; UAM71646/JN593217; UAM54423/JN593216; UAM49980/JN593215; UAM35134/JN593214; UAM35063/JN593212; UAM35061/JN593211; RBCM20000/JN593209; RAM953034/JN593208; RAM03132/JN593207; RAM03131/JN593206; OSU/JN593205; NMMNH614/JN593204; NMMNH1006/JN593203; MVZ223463/JN593202; MVZ223457/JN593201; MVZ223456/JN593200; MVZ223454/JN593199; MVZ223453/JN593198; MVZ223452/JN593197; MVZ223451/JN593196; MVZ223450/JN593195; MVZ223449/JN593194; MVZ223442/JN593191; MVZ223441/JN593190; MVZ223438/JN593188; MVZ223434/JN593186; MVZ223433/JN593185; MVZ223431/JN593184; MVZ223430/JN593183; MVZ223428/JN593182; MVZ223424/JN593180; MVZ223423/JN593179; MVZ223422/JN593178; MVZ223416/JN593177; MVZ223414/JN593176; MVZ223413/JN593175; MVZ223407/JN593174; MVZ223406/JN593173; MVZ223405/JN593172; MVZ223404/JN593171; MVZ223403/JN593170; MVZ223401/JN593169; MVZ223398/JN593168; MVZ223397/JN593167; MVZ223395/JN593166; MVZ222572/JN593164; MVZ220748/JN593163; MVZ220746/JN593162; MVZ220623/JN593161; MVZ220570/JN593160; MVZ220134/JN593159; MVZ219951/JN593158; MVZ219950/JN593157; MVZ218378/JN593156; MVZ216409/JN593155; MVZ215473/JN593154; MVZ206431/JN593153; MVZ199348/JN593151; MVZ197092/JN593150; MSB99135/JN593149; MSB92141/JN593148; MSB92140/JN593147; MSB92137/JN593146; MSB90783/JN593145; MSB86004/JN593144; MSB76968/JN593143; MSB74612/JN593142; MSB73684/JN593141; MSB70026/JN593140; MSB152695/JN593139; MSB141113/JN593137; MDM148/JN593135; LSUMZ452/JN593134; DMNS11518/JN593133; DMNS11383/JN593132; CUMV20269/JN593131; BYU18998/JN593130; BYU18997/JN593129; BYU16618/JN593128; BYU16617/JN593127; BYU14868/JN593126; BYU13888/JN593125; BYU13887/JN593124; BYU13886/JN593123; MDMNCN 182/JN593122; MDMNCN 137/JN593121; DMNS11178/JN593120.

Neotoma devia.—MSB41675/AF307829; MSB41678/AF307830; MVZ200714/DQ781302; MVZ195239/DQ781288; MVZ197123/DQ781283; BYU18948/DQ781290; MVZ197117/KY754058; MVZ200713/DQ781301; MVZ199819/DQ781300; MVZ200712/DQ781299; MVZ200711/DQ781298; MVZ200710/DQ781297; MVZ200709/DQ781296; MVZ202447/DQ781295; MVZ200708/DQ781294; MVZ200707/DQ781293; MVZ200706/DQ781292; MVZ200705/DQ781291; MVZ195240/DQ781289; MVZ195238/DQ781287; MVZ195237/DQ781286; MVZ195236/DQ781285; MVZ199818/DQ781284; MVZ197122/DQ781282; MVZ197121/DQ781281; MVZ197120/DQ781280; MVZ197119/DQ781279; MVZ197118/DQ781278; MVZ197117/DQ781277; MVZ197116/DQ781276; MVZ197115/DQ781275; MVZ197097/DQ781274; MVZ197096/DQ781273; MVZ197095/DQ781272; MVZ197093/DQ781271; BYU18947/DQ781270; MVZ199820/DQ781269; MVZ199384/DQ781268; MVZ199381/DQ781267; MVZ199380/DQ781266; MVZ199378/DQ781265; MVZ197112/DQ781264; MVZ197107/DQ781263;l MVZ197106/DQ781262; MVZ197105/DQ781261; MVZ197104/DQ781260; MVZ197103/DQ781259; MVZ197114/DQ781258; MVZ197113/DQ781257.

Neotoma ferrunginae.—TTU104897/MZ064574; JO9027/KF772873; TTU36179/AF298840; TTU82666/AF305567; TTU82665/AF329079; USNM569657/KF772874; USNM569672/KF772875; USNM569553/KF772876.

Neotoma floridana.—TTU75413/AF186819; TTU71587/AF294343; TTU75402/AF294344; MSB74955/AF294335; TK28244/AF186818; TK27751/AF294341; TTU54731/AF294340; MWSU15766/AF294342; MSB84770/AF294333; TTU54717/AF294339; MSB81532/AF294334; OK107/KY754059.

Neotoma fuscipes.—MVZ195212/DQ781303; MVZ196356/DQ179826; MVZ196405/DQ179822; CRS697/KP129298; CR3356/KP129297; CRS514/KP129296; CRS492/KP129295; CRS374/KP129294; CR758/KP129293; CR3696/KP129292; CR3600/KP129291; CR3560/KP129290; CRS129/KP129289; CRS358/KP129288; CRS573/KP129287; CRS521/KP129286; MDM662/AF337767; MDM495/AF337766; MDM656/AF337765; MDM314/AF337764; MDM764/AF337763; MDM433/AF337762; MDM299/AF337761; MDM356/AF337760; MDM273/AF337759; MDM1824/AF337758; MDM415/AF337757; MDM1912/AF337756; MDM259/AF337755; MDM351/AF337754; JLP17478/AF337753; MDM313/AF337752; MVZ196371/DQ179825; MVZ196394/DQ179824; MVZ196386/DQ179823.

Neotoma goldmani.—TTU45227/AF186829; TTU45228/AF186830.

Neotoma insularis.—UCLA19911/DQ781161.

Neotoma lepida.—JLP16824/AF337749; BYU18153/DQ781256; BYU18300/DQ781254; BYU15035/DQ781234; MSB77775/AF307833; MSB56401/AF307831; TTU137769/KC250464; BYU18154/DQ781255; MVZ199397/DQ781253; MVZ199396/DQ781252; MVZ199395/DQ781251; MVZ199393/DQ781250; MVZ199392/DQ781249; MVZ199391/DQ781248; MVZ199404/DQ781247; MVZ199400/DQ781246; MVZ199399/DQ781245; MVZ199389/DQ781244; MVZ199373/DQ781243; MVZ199370/DQ781242; MVZ199369/DQ781241; MVZ197154/DQ781240; MVZ199376/DQ781239; MVZ197152/DQ781238; MVZ197151/DQ781237; MVZ197148/DQ781236; BYU15034/DQ781233; MVZ197158/DQ781232; MVZ197157/DQ781231; MVZ197156/DQ781230; MVZ197155/DQ781229; MVZ199359/DQ781228; MVZ199358/DQ781227; MVZ199356/DQ781226; MVZ199355/DQ781225; MVZ199354/DQ781224; MVZ199353/DQ781223; MVZ199352/DQ781222; MVZ202485/DQ781221; MVZ197167/DQ781220; MVZ197130/DQ781219; MVZ197165/DQ781218; MVZ197126/DQ781217; MVZ199366/DQ781216; MVZ199364/DQ781215; MVZ199362/DQ781214; MVZ199361/DQ781213; MVZ195261/DQ781212; MVZ195311/DQ781211; MVZ198670/DQ781210; MVZ198914/DQ781209; MVZ195912/DQ781208; MVZ198668/DQ781207; MVZ198662/DQ781206; MVZ195923/DQ781205; MVZ202461/DQ781204; MVZ202459/DQ781203; MVZ195282/DQ781202; MVZ195277/DQ781201; MVZ195266/DQ781200; MVZ197161/DQ781199; MVZ197159/DQ781198; MVZ195934/DQ781197; MVZ198578/DQ781196; MVZ195931/

DQ781195; MVZ195930/DQ781194; MVZ195919/DQ781193; MVZ195917/DQ781192; MVZ199803/DQ781191; MVZ199817/DQ781190; MVZ199772/DQ781189; MVZ199816/DQ781188; MVZ199349/DQ781187; MVZ199776/DQ781186; MVZ202511/DQ781185; MVZ195926/DQ781184; MVZ202497/DQ781183; MVZ202495/DQ781182; MVZ192240/DQ781181; MVZ199787/DQ781180; MVZ199786/DQ781179; MVZ199798/DQ781178; MVZ202486/DQ781177; MVZ202540/DQ781176; MVZ198665/DQ781175; MVZ202527/DQ781174; MVZ195319/DQ781173; MVZ202524/DQ781172; MVZ199809/DQ781171; MVZ199808/DQ781170; MVZ199805/DQ781169; MVZ199804/DQ781168; MVZ202502/DQ781167; MVZ199800/DQ781166; MVZ199814/DQ781165; MVZ199813/DQ781164; MVZ199812/DQ781163; MVZ195324/DQ781162; TTU119266/KY754060; MVZ197094/DQ179836; MVZ159790/DQ179835; MVZ195223/DQ179834; MVZ197379/DQ179833; MVZ202447/DQ179832; MVZ197142/DQ179831; TTU79131/DQ179830.

Neotoma leucodon.—TTU71198/AF186806' TTU77530/AF186828; TTU75440/AF186809; MSB48164/AF186812; TTU44923/AF186805; TTU35381/AF186813; TTU43294/AF186815; TTU111780/KM488349; TTU111790/KM488350; TTU111791/MZ099558; TTU109269/GU220381; TTU83378/KF733992; MSB58295/KM488348; TTU119729/MK253559; TTU138867/MK253561; TTU135171/MK253560; TTU120435/MK253564; TTU138862/MK253565.

Neotoma macrotis.—TTU81391/AF376479; MDM800/DQ179841; TTU79134/AF307836; TTU79132/AF307837; TTU79133/AF376475; TTU83037/FJ744107; MVZ198597/DQ781304; TTU83010/KC250457; TTU83358/KC250456; TTU83629/KC250459; TTU83033/KC250458; TTU83026/KC250460; TTU107307/KC250461; TTU115841/KC250462; TTU83017/KF267876; TTU107272/KF860897; TTU83019/KF860898; MDM1824/AF337758; CRS367/KP129305; CRS67/KP129304; CRS266/KP129302; CRS439/KP129301; CRS344/KP129300; CRS477/KP129299; MVZ196550/KY754061; MVZ196585/DQ179842.

Neotoma magister.—MSB74952/AF294336; SP799/AF294338; SP798/AF294337.

Neotoma melanura.—MVZ147661/AF337750; MVZ147667/AF108704; MSB55524/KM488355; MSB140889/KM488352; NMMNH2750/KM488360; NMMNH5132/KM488354; TTU110072/KM488358; TTU110074/KM488359; TTU110070/KM488357; NMMNH4947/KM488351; NMMNH4934/KM488361; MSB53951/KM488362; MSB55037/KM488353.

Neotoma mexicana.—TTU104970/KF801364; TTU104969/KF801365; MSB121363/AF298841; TTU101643/AF294346; TK45631/AF298842; TTU100791/FJ716222; DMNS8577AF186821; TTU79129/AF294345; TTU79128/AF298849; MSB74280/AF298848; MSB82309/AF298846; MSB74277/AF298847; TTU81714/AF376478; TTU107426/FJ716223; TTU110066/KF772877; TK47774/AF298843; TTU110064/KM488363; TTU122944/KY754062; CMC1204/MK803421; TTU137443/MZ064563.

Neotoma micropus.—TK31643/AF186822; TTU79086/AF376473; TTU79096/AF376474; TTU79078/KC153474; TTU79095/KC153473; TTU78977/KC153475; TTU79069/KC153472; TTU77529/AF298844; TTU136394/AF298845; TTU81033AF186825; TTU80855/AF186826; TTU80856/AF186827; TTU75113/AF376469; TTU81029/FJ716221; TTU80957/KC153488; TTU80915/FJ716220; TTU100185/KC153485; TTU115428/KC153482; TTU115413/KC153483; TTU115412/KC153484; TTU115427/KC153481; TTU115424/KC153480; TTU115410/KC153486; TTU115411/KC153487; TTU119505/KC153477; TTU109272/KC153476; TTU130662/KC153479; TTU115759/KC153478; TTU43296/FJ716217; TTU43297/KC812730; TTU35383/AF186824; TTU70894/DQ179818; ROM114902/EF989952; ROM114903/EF989953; TTU116487/MK253562; TTU116475/MK253563; TTU138864/MK253566; TTU42833/EU286808; TTU116316/KY754063.

Neotoma nelsoni.—LSUMZ36663/KC758854.

Neotoma phenax.—TTU6947/MK202784.

Neotoma picta.—TTU82667/AF305568; TK93390/AF305569; 1118.27/AB618728.

Neotoma stephensi.—MSB72986/AF307834; TTU78505/AF308867; MVZ197170/DQ781305; MVZ197173/KY754064.