

TOWARD A MOLECULAR PHYLOGENY FOR *PEROMYSCUS*: EVIDENCE FROM MITOCHONDRIAL CYTOCHROME-*b* SEQUENCES

ROBERT D. BRADLEY,* NEVIN D. DURISH, DUKE S. ROGERS, JACQUELINE R. MILLER,
MARK D. ENGSTROM, AND C. WILLIAM KILPATRICK

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA (RDB, NDD)

Museum of Texas Tech University, Lubbock, TX 79409-3191, USA (RDB)

Department of Integrative Biology and Monte L. Bean Life Science Museum, Brigham Young University,
Provo, UT 84602, USA (DSR)

Department of Natural History, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario M5S 1C3, Canada (JRM, MDE)

Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada (JRM, MDE)

Department of Biology, University of Vermont, Burlington, VT 05405-0086, USA (CWK)

One hundred DNA sequences from the mitochondrial cytochrome-*b* gene of 44 species of deer mice (*Peromyscus* (sensu stricto), 1 of *Habromys*, 1 of *Isthmomy*s, 2 of *Megadontomys*, and the monotypic genera *Neotomodon*, *Osgoodomys*, and *Podomys*) were used to develop a molecular phylogeny for *Peromyscus*. Phylogenetic analyses (maximum parsimony, maximum likelihood, and Bayesian inference) were conducted to evaluate alternative hypotheses concerning taxonomic arrangements (sensu stricto versus sensu lato) of the genus. In all analyses, monophyletic clades were obtained that corresponded to species groups proposed by previous authors; however, relationships among species groups generally were poorly resolved. The concept of the genus *Peromyscus* based on molecular data differed significantly from the most current taxonomic arrangement. Maximum-likelihood and Bayesian trees depicted strong support for a clade placing *Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, and *Podomys* within *Peromyscus*. If *Habromys*, *Megadontomys*, *Neotomodon*, *Osgoodomys*, and *Podomys* are regarded as genera, then several species groups within *Peromyscus* (sensu stricto) should be elevated to generic rank. *Isthmomy*s was associated with the genus *Reithrodontomys*; in turn this clade was sister to *Baiomys*, indicating a distant relationship of *Isthmomy*s to *Peromyscus*. A formal taxonomic revision awaits synthesis of additional sequence data from nuclear markers together with inclusion of available allozymic and karyotypic data.

Key words: cytochrome-*b* gene, *Peromyscus*, phylogeny, species group, systematics

Aside from *Mus* and *Rattus*, more is known about the biology of deer mice, genus *Peromyscus* (Neotominae—Musser and Carleton 2005), than any other group of small mammals (King 1968; Kirkland and Layne 1989). Members of the genus *Peromyscus* are model organisms for studies in ecology (Kaufman and Kaufman 1989), behavior (Wolff 1989), physiology (MacMillen and Garland 1989), reproductive and developmental biology (Millar 1989), biochemistry (Alderman et al. 1987; Dudley and Winston 1995; Zheng et al. 1993), chromosomal evolution (Committee for Standardization of

Chromosomes of *Peromyscus* 1977, 1994; Greenbaum and Baker 1978; Robbins and Baker 1981; Rogers et al. 1984; Stangl and Baker 1984), allozymes (Avisé et al. 1974; Kilpatrick and Zimmerman 1975; Rennert and Kilpatrick 1986, 1987; Rogers et al. 2005; Selander et al. 1971; Zimmerman et al. 1975, 1978), cytogenetics (Greenbaum et al. 1986a, 1986b; Greenbaum and Reed 1984; Hale 1986; Hale and Greenbaum 1988a, 1988b; McAllister and Greenbaum 1997; Sudman and Greenbaum 1990; Sudman et al. 1989), speciation (Greenbaum et al. 1978; Zimmerman et al. 1978), biogeography (Sullivan et al. 1997), and many other areas of research. In addition, members of the genus *Peromyscus* are reservoirs for rodent-borne diseases such as Lyme disease (Levine et al. 1985; Magnarelli et al. 1988; Mather et al. 1989; Rand et al. 1993), hantaviruses (Childs et al. 1994, 1995; Jay et al. 1997; Mills et al. 1997; Morzunov et al. 1998; Salazar-Bravo et al. 2004), and arenaviruses (Fulhorst

* Correspondent: robert.bradley@ttu.edu

et al. 2002). In support of the importance of *Peromyscus* to a variety of scientific disciplines, Dewey and Dawson (2001) referred to *Peromyscus* as “the *Drosophila* of North American mammalogy.” Despite, this significance and associated abundance of information, surprisingly little is known about the phylogenetic relationships within this genus. Given the importance of members of the genus *Peromyscus* as model organisms and status of the genus as one of North America’s most common and diverse groups of rodents, recovering the phylogenetic history of *Peromyscus* is crucial for many scientific disciplines.

In developing a phylogenetic hypothesis for *Peromyscus*, 2 issues must be considered and reviewed concerning taxonomic history and organization. First, the most basic question is, what is *Peromyscus*? Through several revisions and classifications (Carleton 1980, 1989; Hooper 1968; Hooper and Musser 1964; Musser and Carleton 2005; Osgood 1909), recognition of genera and subgenera has influenced the concept of *Peromyscus*. Second, are the species groups established by Osgood (1909) valid taxonomic entities?

Osgood’s (1909) revision of *Peromyscus* included 6 subgenera (*Baiomys*, *Haplomyomys*, *Megadontomys*, *Ochrotomys*, *Peromyscus*, and *Podomys*) in *Peromyscus*. Subsequently, Miller (1912) and Hooper (1958) assigned 2 of these (*Baiomys* and *Ochrotomys*) to generic status. Three additional subgenera (*Habromys*, *Isthmomys*, and *Osgoodomys*) were proposed by Hooper and Musser (1964). Hooper (1968) therefore included 7 subgenera in his classification. However, Carleton (1980) contended that 5 of these subgenera (*Habromys*, *Isthmomys*, *Megadontomys*, *Osgoodomys*, and *Podomys*) were not as closely related to the subgenera *Peromyscus* and *Haplomyomys* than were some forms of *Reithrodontomys*. Consequently, Carleton (1980) elevated these taxa to generic rank leaving *Peromyscus* and *Haplomyomys* as the remaining subgenera in *Peromyscus*. Carleton (1989) subsequently reviewed the genus and subsumed *Haplomyomys* within *Peromyscus* (hereafter referred to as *Peromyscus* (sensu stricto)), a treatment that remains the most comprehensive review of *Peromyscus* and allies to date and has served as the basis of the 2 most recent classifications (Musser and Carleton 1993, 2005) of the genus.

Two other genera, *Neotomodon* and *Nelsonia*, historically have been affiliated with *Peromyscus*. Osgood (1909) appears to have accepted Merriam’s (1898) suggestion that *Neotomodon* was aligned with *Neotoma*. However, Goldman (1910), Davis and Follansbee (1945), Hooper and Musser (1964), and Hooper (1968) hypothesized that *Neotomodon* was a close relative of *Peromyscus*; and Yates et al. (1979) and Rogers et al. (2005) presented data that suggested that it may be a congener of *Peromyscus*. Conversely, Carleton (1980, 1989) and Musser and Carleton (2005) hypothesized that *Neotomodon* was aligned closely with *Podomys* and *Habromys*. *Nelsonia* largely has been ignored in most revisions because of its scarcity in museum collections. Carleton (1980) and Musser and Carleton (2005) placed *Nelsonia* as a separate genus closely related to other neotomines (*Hodomys* and *Neotoma*); however, examination of primitive morphological characters (Hooper and Musser 1964) and karyotypic data (Engstrom and Bickham 1983, Engstrom et al. 1992) suggested an affinity to peromyscines.

Several molecular studies have generated data used to infer phylogenetic relationships among *Peromyscus* and allied genera. Cladistic analyses of protein electrophoretic (Patton et al. 1981) and chromosomal banding data (Rogers 1983; Rogers et al. 1984; Stangl and Baker 1984) were interpreted as supportive of some aspects of the hypothesis of Hooper and Musser (1964). A DNA–DNA hybridization study by Dickerman (1992) supported the phylogeny of Hooper and Musser (1964) because *Podomys* was contained within the *Peromyscus* cluster, and *Reithrodontomys* was sister to a cluster containing *Podomys*, *Peromyscus*, and *Onychomys*. Similarly, Bradley et al. (2004), Reeder and Bradley (2004, 2007), and Reeder et al. (2006) commented that in some cases *Megadontomys*, *Neotomodon*, and *Osgoodomys* were embedded within *Peromyscus* (sensu stricto). However, Engel et al. (1998) supported the contention of Carleton (1980) that some forms of *Peromyscus* were more closely related to *Reithrodontomys* than they were to *Osgoodomys* and *Isthmomys*. To date, only 1 study (Rogers et al. 2005) was designed specifically to discern among the alternative positions of Hooper (1968) and Carleton (1980). Their phylogenetic analyses of protein electrophoretic data placed all subgenera that Carleton (1980) had elevated to generic rank (*Habromys*, *Megadontomys*, *Osgoodomys*, and *Podomys*) together with *Neotomodon* into a single clade that, with the exception of *Isthmomys*, was identical to the concept of *Peromyscus* as expressed by Hooper (1968).

In addition to providing the 1st revision of *Peromyscus*, Osgood (1909) placed related species into species groups. Osgood’s (1909) recognition of 7 species groups within the subgenus *Peromyscus* (*boylei* [= *boylei*], *lepturus*, *leucopus*, *maniculatus*, *megalops*, *melanophrys*, and *truei*) was conservative because relatively few taxa were described at that time. As more taxa were described, a need arose for additional species groups to partition the discrete morphological variation evident among all taxa and to eliminate paraphyletic assemblages. Hall and Kelson (1959) added the *mexicanus* group; Hooper (1968) recognized the *crinitus* group and placed the *lepturus* group under the subgenus *Habromys*; and Carleton (1989) added the *aztecus*, *hooperi*, and *furvus* groups and recognized the *californicus* and *eremicus* groups in the subgenus *Haplomyomys*. A critical evaluation of phylogenetic relationships within and among species groups is paramount to continued usage of this nomenclatural delineation.

In terms of phylogenetic relationships among species, Carleton (1989) provided a comprehensive review of the systematic studies of *Peromyscus* conducted before 1988. Recent studies include examinations of morphology (Allard and Greenbaum 1988; Bradley and Schmidly 1987; Bradley et al. 1989, 1990, 1996a; Schmidly et al. 1988; Sullivan et al. 1990), G- and C-banded karyotypes (Greenbaum et al. 1994; Smith 1990; Smith et al. 1989), protein electrophoresis (Calhoun and Greenbaum 1991; Calhoun et al. 1988; Harris and Rogers 1999; Janecek 1990; Rogers and Engstrom 1992; Rogers et al. 2005; Sullivan and Kilpatrick 1991; Sullivan et al. 1991), restriction fragment length polymorphisms (DeWalt et al. 1993; Walpole et al. 1997), DNA–DNA hybridization (Dickerman 1992), DNA sequencing (Bradley et al. 2000, 2004; Durish

et al. 2004; Engel et al. 1998; Hogan et al. 1997; Sullivan et al. 1995, 1997; Tiemann-Boege et al. 2000), and combinations of these techniques (Bradley et al. 1996b; Hogan et al. 1993). However, most of these studies did not include an adequate sample of taxa to allow construction of a phylogeny of recognized genera and subgenera.

The objective of our study was to develop a molecular phylogenetic hypothesis, based on DNA sequences from the mitochondrial cytochrome-*b* (*Cytb*) gene, for species of *Peromyscus* (sensu lato—Hooper and Musser 1964) and use that phylogeny to begin to evaluate the monophyly and validity of species groups, subgenera, and genera. We used the concept of Hooper and Musser (1964) of *Peromyscus* as a null hypothesis because it is inclusive and readily refutable based on nonmonophyly. Also, we recognize from the onset that the *Cytb* gene is most useful in recovering phylogenetic relationships among closely related taxa and can lose resolution at deeper nodes. We include a majority of species putatively assigned to this group (51 of 72, or 70%), comprising a sample that represents all genera, subgenera, and species groups, establishing this study as a foundation for a revised and more thoroughly inclusive classification of *Peromyscus*. We propose that our study be viewed as a foundation upon which inclusion of additional taxa and DNA sequences can be added, the ultimate goal being to estimate a robust phylogeny for the genus. In the words of Emmet T. Hooper (1968:33–34), “A taxonomic classification is a tentative thing; it is not sacred. . . . It is a reasonable yet tentative framework against which new systematic data may be tried for fit.” It is in this spirit that we tackle the concept of “what is *Peromyscus*?”

MATERIALS AND METHODS

Samples.—Kimura 2-parameter genetic distances (Kimura 1980) and the neighbor-joining method of Saitou and Nei (1987) were used in a preliminary analysis of 189 *Cytb* sequences, generated in our laboratories or obtained from GenBank. In several instances, ≥ 10 DNA sequences were available for examination of a single species; consequently 100 individuals representing 44 species of *Peromyscus* (sensu Carleton 1989), 1 species of *Habromys*, 1 species of *Isthmomys*, 2 species of *Megadontomys*, and the monotypic genera *Neotomodon*, *Osgoodomys*, and *Podomys* were selected for further analysis. The rationale for the reduced data set was to examine the most genetically divergent members within each species (determined from preliminary analyses), include individuals representing geographic extremes within a species distribution, and insure that all individuals of a species were monophyletic, while maintaining the data set at a manageable size. This was accomplished by including a maximum of 3 individuals per species. If possible, individuals with complete DNA sequences were included. Specimen numbers, GenBank accession numbers, collection localities, and specimen voucher numbers are listed in Appendix I.

Sequence data.—Mitochondrial DNA was extracted from liver samples (0.1 g), either frozen or preserved in 95% ethanol and purified using the Wizard Miniprep kit (Promega,

Madison, Wisconsin) or the DNeasy Tissue Kit (Qiagen, Valencia, California). For some specimens, genomic DNA was isolated following methods of Smith and Patton (1999). Polymerase chain reaction (Saiki et al. 1988) parameters and primers, summarized in Durish et al. (2004) and Rogers et al. (2007), were used to amplify the complete *Cytb* gene (1,143 base pairs [bp]). The resulting polymerase chain reaction product was purified using the QIAquick polymerase chain reaction purification kit (Qiagen) and cycle sequencing was conducted using the ABI Big Dye version 3.0 ready reaction mix (PE Applied Biosystems, Foster City, California). Excess dye terminator was removed using Millipore Multiscreen Filter Plates for High Throughput Separations (Millipore, Billerica, Maryland) and samples were analyzed on an ABI 3100 *Avant* automated sequencer (PE Applied Biosystems). Sequencher software (versions 3.1 and 4.1.1; Gene Codes Corporation, Ann Arbor, Michigan) and Vector NTI 7.0 software (Informax, Inc., Bethesda, Maryland) were used to align and proof sequences. A small number of samples were amplified and sequenced using modified protocols. Standard phenol–chloroform extractions of frozen liver were subsequently reduced and purified by alcohol precipitation (Sambrook et al. 1989). A 2-step touchdown polymerase chain reaction thermal profile was used (an initial 2–3 min of denaturing at 94°C; 40 s at 94°C, 40 s at 56°C, 1 min 45 s at 72°C, for 15–17 cycles; 40 s at 94°C, 40 s at 50°C, 1 min 45 s at 72°C for 21–26 cycles; 5-min final extension at 72°C). Where polymerase chain reaction amplification was difficult, downward adjustments of annealing and extension temperatures were made. Amplicons were electrophoresed on a 1.5% agarose gel. Resulting bands were extracted for cycle sequencing and purified by spin column reduction. The DYNAMIC Direct Cycle Sequencing kit (GE Healthcare Bio-Sciences Inc., Baie D’Urfe, Quebec, Canada) was used for cycle sequencing, and samples were analyzed on a LICOR LongReader 4200 analyzer (LI-COR Biosciences, Lincoln, Nebraska). All sequences were edited and aligned using Sequencher version 4.1.1 (Gene Codes Corporation). Sequences generated in this study were deposited into GenBank and accession numbers are reported in Appendix I.

Data analyses.—Based on phylogenetic relationships presented in Carleton (1980), Bradley et al. (2004), and Reeder and Bradley (2004), *Oryzomys palustris*, *Sigmodon hispidus*, *Nyctomys sumichrasti*, *Tylomys nudicaudus*, and *Ototylomys phyllotis* were used as outgroup taxa. Because of the uncertain phylogenetic relationships among the tribes Baiomini, Neotomini, Ochrotomyini, and Reithrodontomyini, *Baiomys taylori*, *Neotoma mexicana*, *Onychomys arenicola*, *Ochrotomys nutalli*, *Reithrodontomys mexicanus*, and *Reithrodontomys megalotis* all were included as reference taxa. By including these taxa, all genera previously assigned to *Peromyscus* (e.g., *Baiomys* and *Ochrotomys*) were represented. Given spurious nucleotides (unreliable in that they did not match well with other *Peromyscus* sequences) in the 3' region of the *P. polius* sequence, this sequence was truncated to include only the first 700 bp. All GenBank accession numbers for outgroup and reference samples are listed in Appendix I. Likelihood, Bayesian, and parsimony models (PAUP* [Swofford 2002]

and MRBAYES 3.1.1.1 [Huelsenbeck and Ronquist 2001] were used to generate hypotheses concerning phylogenetic relationships of taxa. Variable nucleotide positions were treated as unordered, discrete characters with 5 possible states: A, C, G, T, or missing.

Some authorities advocate removal of 3rd-position information in sequence data when saturation is suspected (e.g., Ericson and Johansson 2003; Huchon et al. 2002). However, synonymous substitutions at 3rd positions can be phylogenetically informative, even in sequences that are moderately saturated (Poux and Douzery 2004; Yoder et al. 1996; Yoder and Yang 2000). The value of this information also has been demonstrated in cases where taxa are closely related (Björklund 1999; Hästad and Björklund 1998). All models employed acknowledge base position characteristics; therefore, all codon positions were included in analyses.

Unconstrained parsimony analysis (PAUP*—Swofford 2002) was conducted, using unweighted characters and excluding uninformative characters. All parsimony analyses employed a heuristic search using tree-bisection-reconnection, with random stepwise addition of taxa and 100 repetitions to obtain the most-parsimonious tree-set. Bootstrap analysis (Felsenstein 1985) with 1,000 iterations and 50 random sequence addition replicates was used to evaluate internal stability and establish nodal support.

Transition–transversion plots (subroutines in DAMBE—Xia 2000; Xia and Xie 2001) regressed against sequence divergence values were used to assess relative degrees of saturation at each codon position. These plots suggested a moderate degree of saturation with increasing distance among taxa at 3rd positions (not shown). Bias in transitions and transversions was assessed by means of index values (transition/transversion [Ts/Tv]) calculated for the overall data matrix and at each codon position using the program MEGA (Kumar et al. 1993). Data were reanalyzed under the same search options as the unconstrained parsimony, but with application of either a priori constraints (transition–transversion weighting, codon position downweighting), or a posteriori constraints (successive reweighting by rescaled consistency index [RC]) following recommendations in the literature (e.g., Barker and Lanyon 2000; Farias et al. 2001; Farris 1969; Honeycutt et al. 1995; Horovitz and Meyer 1995; Huchon et al. 2002; Irwin et al. 1991).

MODELTEST software (Posada and Crandall 1998) was used to determine the model of DNA evolution best fitting the data. The GTR+I+G model generated significantly better likelihood scores than all other models and included the following parameters: base frequencies (A = 0.3920, C = 0.3297, G = 0.0517, and T = 0.2266), rates of substitution (A–C = 0.4007, A–G = 6.7581, A–T = 0.6293, C–G = 0.4783, C–T = 7.5063, G–T = 1.00), proportion of invariable sites (I = 0.4008), and gamma distribution (G = 0.6155). Using the above parameters and maximum likelihood methods, an optimal tree(s) was generated using the heuristic search option in PAUP* (Swofford 2002).

A Bayesian model (MRBAYES—Huelsenbeck and Ronquist 2001) was used for comparison to the likelihood method and to

generate support values (clade probabilities). A GTR+I+G model with a site-specific gamma distribution and sites partitioned by codon was used with the following options: 4 Markov chains, 20 million generations, and sample frequency of every 1,000th generation. *O. palustris* was designated as the outgroup and 2 runs were conducted simultaneously. After a visual inspection of likelihood scores, convergence statistics, and potential scale-reduction factors, the first 1,000 trees were discarded and a consensus tree (50% majority rule) was constructed from remaining trees. Additionally, 4 independent runs using 2 million generations and above conditions were conducted to investigate stabilization of likelihood scores.

RESULTS

The DNA sequences obtained in this study ($n = 40$) were combined with published sequences from GenBank ($n = 60$). Seventy-eight of 100 sequences were complete (1,143 bp). Of the remaining 22 sequences, 8 were missing fewer than 100 bp, 12 were >50–75% complete, and 2 (*P. keeni* and *P. polionotus*) were approximately 30% complete. Across all taxa, nucleotide frequencies estimated from PAUP* (Swofford 2002) for the complete data set were: A = 31.7%, C = 27.4%, G = 12.7%, and T = 28.2%; and for phylogenetically informative sites only: A = 36.3%, C = 35.9%, G = 6.0%, and T = 21.8%. Nucleotide change at each codon position agreed with observations for mammalian *Cytb* in general (Honeycutt et al. 1995; Irwin et al. 1991). Ratios for transitions to transversions were: 3.5, 2.9, and 1.9 at 1st, 2nd, and 3rd positions, respectively, and 2.1 overall. For the entire gene sequence, 514 nucleotides were conserved, 629 were variable, and 509 were phylogenetically informative.

The majority of substitutions occurred at 3rd positions (58%), with 66% being transitions. Nucleotide substitutions at 1st positions accounted for the majority of remaining replacements (26%), of which most were transitions (79%). In addition, there was a slight bias toward an A–T-rich nucleotide composition (28.2% and 31.7%, respectively), accounting for approximately 60% of all substitutions. A large proportion of substitutions represented synonymous changes reflecting a modest amino acid proportion of leucine (12–15% depending on taxon). Nonsynonymous substitutions occurred relatively frequently (187 of 381 variable amino acids, of which 108 were phylogenetically informative).

Unconstrained parsimony analysis of 509 unweighted characters (informative characters) generated 4 equally parsimonious trees of 5,132 steps, with a consistency index (CI) of 0.1775, homoplasy index (HI) of 0.8225, and retention index (RI) of 0.5705 (Table 1). A bootstrap (majority-rule) consensus tree generated from the 4 most-parsimonious trees is depicted in Fig. 1. All species represented with multiple samples formed monophyletic clades, with 1 exception; 1 sample of *P. mexicanus* was sister to *P. gymnotis*. Bootstrap values showed support for a large clade uniting members of the tribes Baiomyini (*Baiomys*), Neotomini (*Neotoma*), and Peromyscini (*Peromyscus* (sensu lato), *Onychomys*, *Ochrotomys*, and *Reithrodontomys*); however, no support was present for a group

TABLE 1.—Summary of 5 weighting schemes used under a heuristic tree-searching parsimony framework for obtaining phylogenetic relationships among taxa. Weighting models are defined in the text. Sequences were added at random, with 100 random sequence addition replicates. Abbreviations are as follows: tree length (TL), tree number (TN), consistency index (CI), homoplasy index (HI), retention index (RI), rescaled consistency index (RC), and transversion (Tv). Uninformative characters are excluded. Dynamic weighting utilizes RC values of each character, in successive iterations until tree statistics and topology stabilize. In this database this required 2 iterations, with stability determined by the 3rd iteration.

Analysis	Scores					
	TL	TN	CI	HI	RI	RC
Unweighted	5,132	2	0.1775	0.8225	0.5705	0.1030
Tv = 2	6,466	25	0.1916	0.8084	0.5930	0.1136
Codon 2:3:1	6,330	5	0.1930	0.8070	0.5838	0.1127
Codon 5:10:1	10,010	4	0.2208	0.7792	0.5942	0.1312
Tv = 4:3:2	6,859	8	0.2073	0.7937	0.5937	0.1231
1st and 2nd position	1,002	>100,000	0.2555	0.7445	0.6088	0.1555
Dynamic weighting	465.13	1	0.3031	0.6969	0.6436	0.1951

that would represent a monophyletic *Peromyscus* (either sensu lato or sensu stricto). Six smaller clades united members that generally represented the *boylei*, *aztecus*, *mexicanus*, *melanophrys*, *leucopus*, and *maniculatus* species groups. Support for relationships between species group was present only for the *leucopus* and *maniculatus* species groups. Relationships among peromyscine–neotomine taxa were unresolved. In addition, a dynamically weighted analysis using the rescaled consistency index (RC) was conducted (Farris 1969) and the unconstrained, most-parsimonious tree was set as the starting iteration. Iterations were repeated until tree topology and tree statistics stabilized (3 iterations). A strict consensus of the 2 equally parsimonious trees maintained the integrity of the larger species groups, established under the unconstrained model (not shown). Although tree lengths were not readily comparable, overall tree statistics indicated a more robust evolutionary hypothesis.

Examination of transitions and transversions by codon position, both empirically and by bivariate regression against branch length under one of the models of evolution with fewest specified parameters (Jukes and Cantor 1969), indicated moderate saturation in transitions at the 3rd position. Therefore, 5 additional analyses were conducted to downweight or correct for transitional biases. First, transitions were downweighted by a factor of 2 relative to transversions (Ts/Tv = 2) to account for the overall 2:1 ratio of transitions to transversions. Second, each codon position was assessed for independent transition–transversion ratios and transitions were downweighted according to positional bias (4:1, 3:1, and 2:1 transversion penalty, respectively, for 1st, 2nd, and 3rd positions). Third, changes at codon positions occurred in roughly a 2:1:10 ratio and were inversely weighted (codon weighting = 5:10:1). Fourth, a less-intense downweighting scheme (codon weighting = 2:3:1) was employed, representing a more relaxed correction for positional biases. Fifth, an analysis in which the 3rd codon position was eliminated (1st and 2nd positions only) was used to eliminate 3rd-position biases. Topological relationships based on 1st and 2nd codon positions resolved only a few of the large species assemblages. Basic information from these analyses is depicted

in Table 1. Although relationships and nodal support among species groups, subgenera, and genera varied between analyses, topological relationships in both the dynamic transition–transversion biasing and dynamic weighting according to RC values converged upon the general phylogenetic hypothesis recovered with likelihood and Bayesian analyses (Fig. 2).

The likelihood analysis (GTR+I+G model) generated 2 trees (not shown) that were identical in topology except for placement of *P. ochraventer*. In both trees, *P. ochraventer* was affiliated with members of the *truei* species group but differed with respect to sister relationships. All taxa of *Peromyscus* (sensu lato) were contained within a single clade; however, the 2 samples of *Reithrodontomys* were included in this clade as a sister taxon to *P. polius*. As in the parsimony analysis, all conspecific taxa formed monophyletic clades. In addition, composition of species groups was similar to that obtained in parsimony and Bayesian analyses (below), although branching patterns within clades occasionally differed. No support values were calculated because of computational constraints.

Two simultaneous Bayesian analyses generated identical trees (Fig. 2). Clade probability values differed slightly between analyses; therefore if 2 support values differed at a node, both were reported. All taxa of *Peromyscus* (sensu lato) were contained within a single well-supported clade (I, value = 98) except for samples of *I. pirrensis* and *P. polius*. *I. pirrensis* was sister to *R. megalotis* but not supported by significant clade probability values (79 and 81). The sample of *P. polius* was sister to *Peromyscus* (sensu stricto) but not supported by a significant clade probability value (89). Taxa representing species groups formed well-supported monophyletic clades except for members of the *truei* and *mexicanus* groups. *P. sagax* was strongly supported as sister to samples of *H. ixtlani*. Three genera (*Habromys* plus *P. sagax*, *Neotomodon*, and *Podomys*) recognized by Carleton (1980) and Musser and Carleton (2005) were contained within a well-supported clade along with members of the *aztecus*, *boylei*, *difficilis*, and *furvus* species groups. Similarly, *Osgoodomys* was placed within a well-supported clade containing members of the *californicus*, *eremicus*, *leucopus*, *maniculatus*, *crinitus*, and *hooperi* species

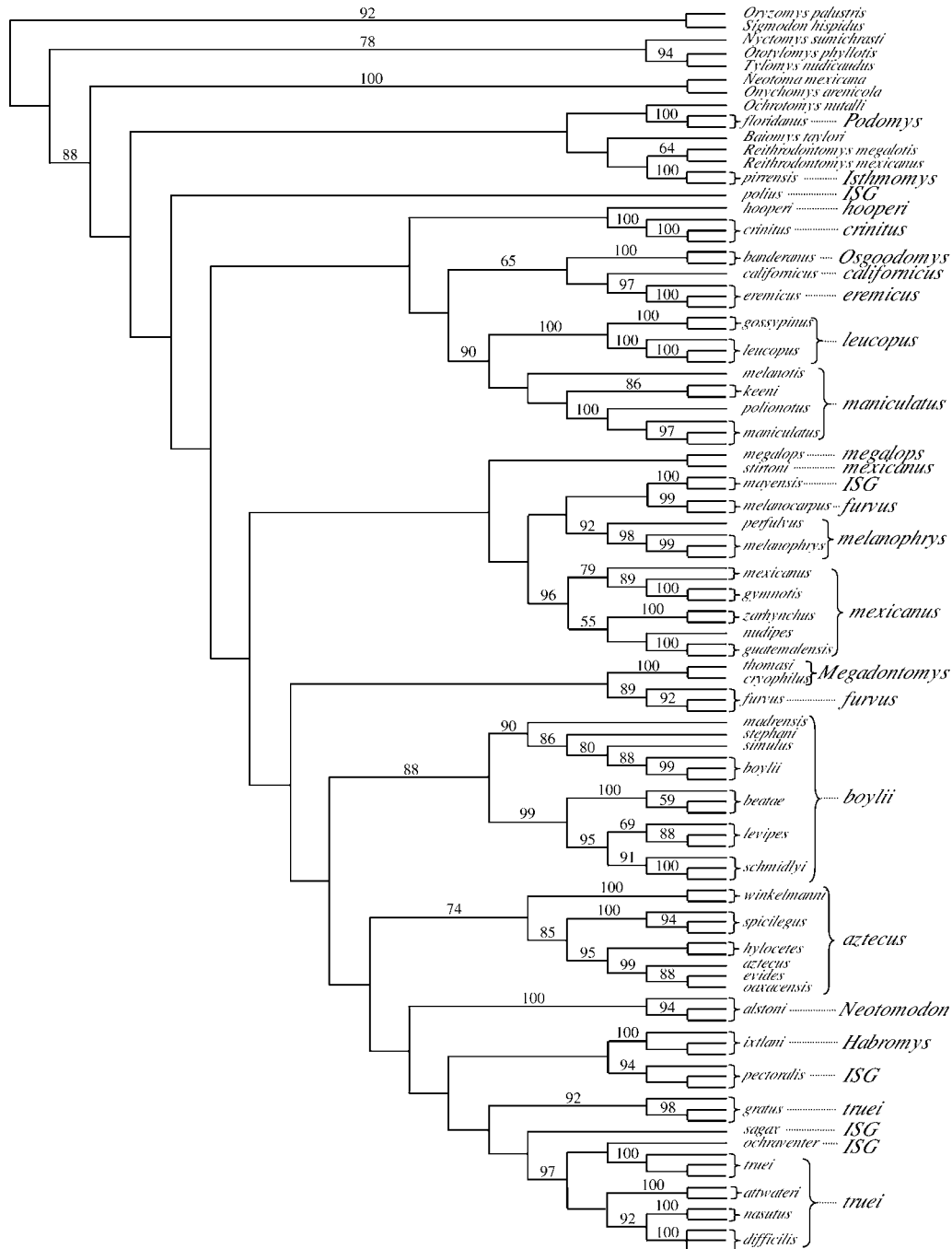


FIG. 1.—Strict consensus tree of the 4 most-parsimonious trees generated from the unweighted character analysis. Bootstrap values are shown above branches. Names to the right of dotted lines indicate species group or generic affiliation. Indeterminate species groups (ISG) as defined by Musser and Carleton (2005).

groups. *Megadontomys* was placed in the large *Peromyscus* (sensu lato) clade but its position was unresolved.

DISCUSSION

Bootstrap support and clade probability values indicated strong support (in most cases) for clades located terminally, minimal support for clades in the midregion of topologies, and strong support (for a few nodes) at the base of topologies.

Therefore, resolution and phylogenetic inference varied across the 3 analyses. The pattern of support values is not surprising given caveats and limitations associated with using a rapidly evolving gene such as *Cytb* to address relationships among genera and subgenera. Although the *Cytb* gene has proven useful in recovering phylogenetically useful information at a variety of taxonomic levels, strength of its utility can be lineage-dependent and declines with evolutionary depth (Gissi et al. 2000; Springer et al. 2001; Yoder et al. 1996; Zardoya

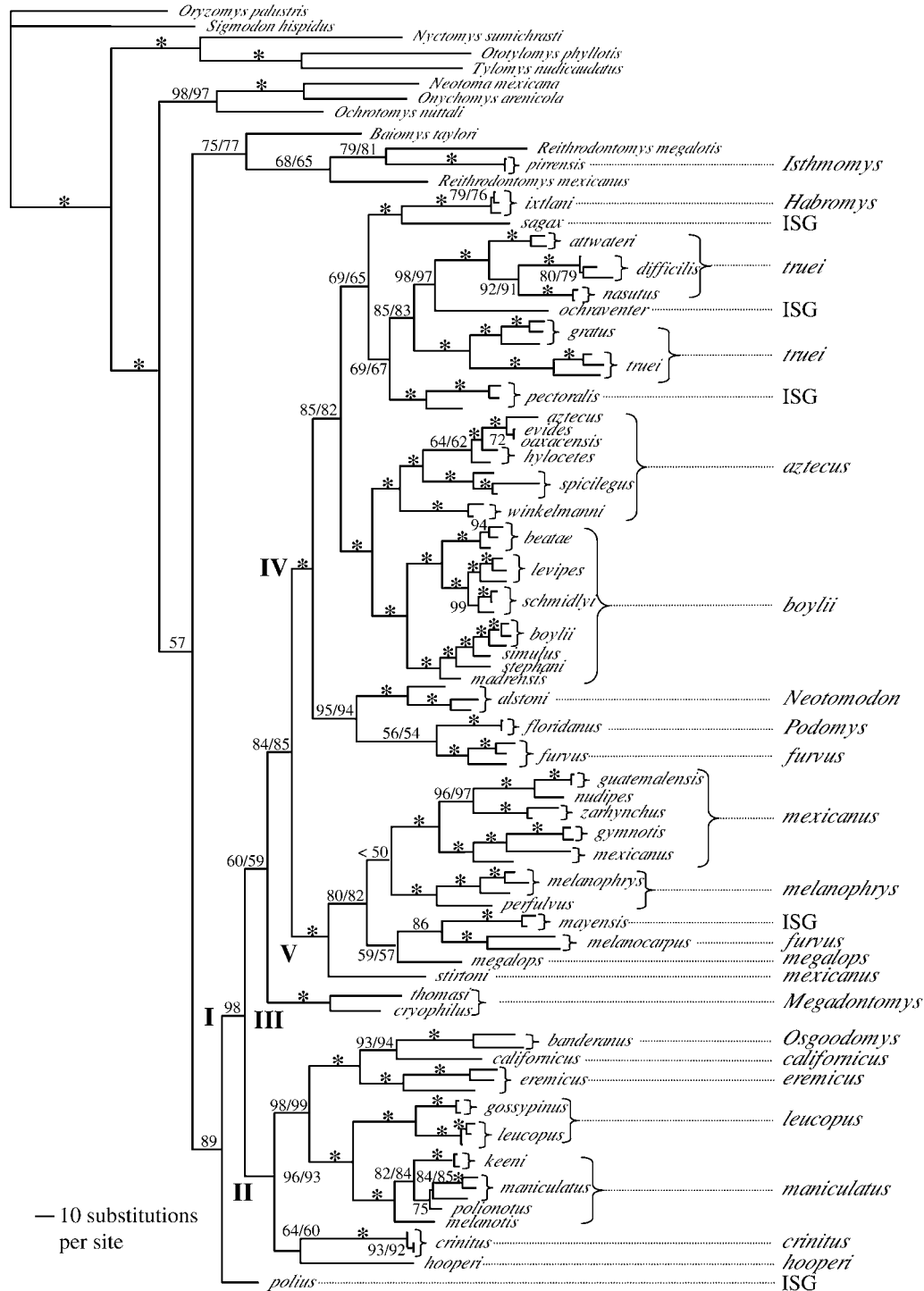


FIG. 2.—Maximum-likelihood tree calculated using Bayesian inference methods. Roman numerals refer to major clades as identified in the text. Clade probability values (depicted as percentages) are shown above branches (values to the left of slash are from the 1st run, those to the right are from the 2nd run). Asterisks indicate significant nodal support (95 or greater). Names to the right of dotted lines indicate species group or generic affiliation. Indeterminate species groups (ISG) as defined by Musser and Carleton (2005).

and Meyer 1996). At the outset we assumed that support at basal nodes would be ambiguous. This was the case for the parsimony analysis (Fig. 1), where only a single basal node possessed substantial bootstrap support. However, several basal nodes of the Bayesian tree (Fig. 2) had significant clade

probability values. Below we summarize phylogenetic relationships that were consistent across analyses, identify groups of taxa that received support (bootstrap or clade probability values), and comment on status and composition of species groups and genera recognized by previous authors.

In all analyses (maximum parsimony, maximum likelihood, and Bayesian inference), multiple samples representing conspecific taxa formed monophyletic clades with the exception of *P. mexicanus*. One sample of *P. mexicanus* was sister to the clade containing the 2 samples of *P. gymnotis*, whereas the 2nd sample of *P. mexicanus* was basal to that clade. Even if *P. gymnotis* is not a valid taxon, the amount of genetic divergence among these samples (8.3% Kimura 2-parameter) warrants additional investigation (Baker and Bradley 2006).

Phylogenetic relationships among species.—Although we were unable to include all taxa in *Peromyscus* (sensu lato), approximately 70% of the species were examined. The majority of unsampled taxa belong to the *eremicus* species group and the genus *Habromys*, where we examined only 1 of 10 species and 2 of 6 species, respectively. In addition, we were unable to include *P. sejugis* (*maniculatus* group), *P. mekisturus* (*melanophrys* group), *P. grandis* and *P. yucatanicus* (*mexicanus* group), *P. bullatus* (*truei* group), *P. slevini* (indeterminate group), *I. flavidus*, and *M. nelsoni*. Given that most taxonomic groups (genera, subgenera, and species groups) were well sampled, the phylogeny depicted in Fig. 2 can be used as a reasonable hypothesis for estimating phylogenetic relationships. To avoid a detailed description of phylogenetic relationships, we refer to Fig. 2 and clades labeled with Roman numerals.

Species groups.—Osgood's (1909) original concept of species groups within the subgenus *Peromyscus* formed the basis and provided a model for subsequent classifications as reflected in the addition of 7 species groups (*aztecus*, *californicus*, *crinitus*, *eremicus*, *furvus*, *hooperi*, and *mexicanus*) by Hall and Kelson (1959), Hooper (1968), and Carleton (1989). After the elevation of *Habromys* to the generic level (Carleton 1989) and the concomitant removal of the *lepturus* species group, Musser and Carleton (2005) recognized 13 species groups within *Peromyscus* (sensu stricto). In addition, Musser and Carleton (2005) placed 6 taxa (*melanocarpus*, *mayensis*, *ochraventer*, *pectoralis*, *sagax*, and *slevini*) as incertae sedis.

Given that some species groups are monotypic (*californicus*, *crinitus*, and *hooperi*) and others are somewhat underrepresented in our data set (*eremicus* and *megalops*), it is relatively difficult to assess their validity. However, if one compares the overall topology, branching patterns, and equivalency of clades, a pattern emerges (Fig. 2) that offers support for recognition of the 13 species groups identified by Musser and Carleton (2005). With the exception of the *furvus*, *mexicanus*, and *truei* species groups, all other species groups with 2 or more taxa are monophyletic and are well supported (clade probability and bootstrap values). The *truei* species group was split into 2 clades, the *difficilis* assemblage represented by *attwateri*, *difficilis*, *nasutus*, and *ochraventer* and the *truei* assemblage including *gratus* and *truei*. Durish et al. (2004) noted this dichotomy and suggested that the 2 assemblages may represent separate species groups.

Four of the 5 taxa (*melanocarpus*, *ochraventer*, *pectoralis*, *polius*, and *slevini*) placed as incertae sedis by Musser and Carleton (2005) also were problematic in our analyses. Only the placement of *P. ochraventer*, which received support for

being included in the *difficilis* assemblage (*attwateri*, *difficilis*, and *nasutus*), was resolved. Placement of *P. melanocarpus* was unresolved; however, its association with a clade containing members of the *furvus*, *megalops*, *melanophrys*, and *mexicanus* species groups was well supported. Although *P. pectoralis* showed some affinity with the *truei* group, this relationship was not strongly supported; consequently, *pectoralis* was placed (unresolved) in a clade with members of several species groups. *P. polius* was placed as the basal member of the *Peromyscus* (sensu lato) clade; however, the clade probability value of 89 indicated weak support for this arrangement. Placement of *P. polius* warrants some caution because it is represented by a single sample amplified from a skin clip (Tiemann-Boege et al. 2000).

Relationships among species groups were not well supported, in most cases, probably as an artifact of lack of resolution among clades in the middle regions of the tree. Exceptions included recovery of the *aztecus* and *boylei* species groups and the *leucopus* and *maniculatus* species groups as sister clades. A clade containing *californicus* and *eremicus* group members as well as *Osgoodomys* was well supported, indicating a strong affiliation among these taxa. Although there was little support for relationships among species groups, there were 3 clades that were well supported and provided phylogenetic information. The 1st clade (II) contained samples representing *Osgoodomys* and the *californicus*, *eremicus*, *leucopus*, *maniculatus*, *crinitus*, and *hooperi* species groups. The 2nd clade (IV) contained samples representing *Habromys*, *Neotomodon*, and *Podomys*; the *truei*, *boylei*, *aztecus*, and *furvus* species groups; and *ochraventer* and *pectoralis*. The 3rd clade (V) contained samples representing the *mexicanus*, *melanophrys*, *furvus*, and *megalops* species groups and *melanocarpus*.

Genera and subgenera.—Examination of the topology and support values associated with Fig. 2 provides several alternative interpretations of the status of genera and subgenera as proposed by Osgood (1909) and subsequent reviewers (Carleton 1980, 1989). First, *Baiomys* and *Ochrotomys* are basal to *Peromyscus* and are distantly removed from *Peromyscus*, as suggested in several studies (e.g., Engstrom and Bickham 1982; Reeder et al. 2006); in fact Reeder et al. (2006) and Musser and Carleton (2005) recognized *Ochrotomys* as a new tribe. Second, 5 genera (*Habromys*, *Neotomodon*, *Podomys*, *Megadontomys*, and *Osgoodomys*) and the subgenus *Haplomylomys* are embedded within *Peromyscus* (sensu stricto) and these arrangements are strongly supported. Therefore, to include all taxa in a monophyletic clade would necessitate recognition of clade I as *Peromyscus*. This also suggests a more basal position for *Isthmomyss* than previously reported (Carleton 1980; but see Rogers et al. 2005) but has the advantage of supporting the recognition of *Baiomys* and *Reithrodontomys* as genera. Another option would be to recognize strongly supported nodes (clades II–V) as equal taxonomic ranks and invoke existing generic names where appropriate. However, this would result in no fewer than 5 generic names to recognize various clades and branching patterns depicted in the phylogenetic tree. This option does not offer a realistic or desirable solution at this time.

Phylogenetic relationships and status of Peromyscus.—

Although our study is the most inclusive to date from a taxon-sampling standpoint (we examined approximately 70% of the species in *Peromyscus* (sensu lato), addition of remaining species and sequence data will impact overall phylogenetic reconstruction of the group. Moreover, in our discussion of phylogenetic relationships and status of species groups and genera we have not included any of the morphologic, allozymic, or chromosome data that are available for these taxa. Given that these complementary data are informative and necessary for testing the question of what is a *Peromyscus*, we have postponed a formal synthesis (revised classification) until more taxa can be included into a single analysis and these alternative (and potentially new) data sets are considered. However, several observations are worthy of further discussion.

Although it is premature to abandon the use of generic names, with the exception of *Isthmomys*, the concept of *Peromyscus* (sensu lato) was supported in all studies for which all genera were represented, including chromosome banding (Rogers et al. 1984; Stangl and Baker, 1984), allozymes (Rogers et al. 2005), and *Cytb* (present study). In addition, constraining taxa in our molecular data set to correspond to *Peromyscus* (sensu stricto) resulted in a significantly worse ($P < 0.02$) tree based on the test of Shimodaira and Hasegawa (1999). Second, the historical concept of species groups received strong support in our study. With a couple of minor discrepancies (placement of *mayensis* and *stirtoni* and diphyly of the *truei* group), the contents and validity of the 13 species groups of Musser and Carleton (2005) were supported by examination of the *Cytb* data. Levels of congruence among these studies are noteworthy, especially given that many of the species groups were compiled before the formal development of phylogenetic methodologies (Hennig 1966). Additionally, our study illustrates the accuracy and thoroughness of Osgood's (1909) monograph and Carleton's (1989) synthesis. Third, we provide the most comprehensive coverage of molecular phylogenetic relationships at the species level presented to date. Although the *Cytb* data contain considerable phylogenetic signal, definition of content and resolution of the phylogeny of *Peromyscus* awaits addition of taxa and sequence data, and synthesis of existing morphological, molecular, and behavioral data sets. Clearly, however, the current concept of the genus as comprising only the former subgenera *Peromyscus* and *Haplomylomys* is in need of revision.

ACKNOWLEDGMENTS

We thank B. Amman for providing some of the DNA sequences. J. W. Bickham and R. L. Honeycutt (Texas A&M University) and R. J. Baker (Museum, Texas Tech University) kindly provided tissue loans. R. R. Chambers, M. L. Haynie, J. D. Hanson, A. O. Stallings, and D. D. Henson provided helpful comments on previous versions of this manuscript. This research was supported by the National Science Foundation (DBI-0139501), Professional Development Grants, Department of Integrative Biology and the M. L. Bean Life Science Museum, Brigham Young University (to DSR), and by a grant from the National Institutes of Health (DHHS A141435-01 to RDB).

LITERATURE CITED

- ALDERMAN, J. A., T. TAKAGI, AND C. S. LIEBER. 1987. Ethanol-metabolizing pathways in deer mice. *Journal of Biological Chemistry* 262:7497–7503.
- ALLARD, M. W., AND I. F. GREENBAUM. 1988. Morphological variation and taxonomy of chromosomally differentiated *Peromyscus* from the Pacific Northwest. *Canadian Journal of Zoology* 66:2734–2739.
- AVISE, J. C., M. H. SMITH, R. K. SELANDER, T. E. LAWLOR, AND P. R. RAMSEY. 1974. Biochemical polymorphism and systematics in the genus *Peromyscus*. V. Insular and mainland species of the subgenus *Haplomylomys*. *Systematic Zoology* 23:226–238.
- BAKER, R. J., AND R. D. BRADLEY. 2006. Speciation in mammals and the genetic species concept. *Journal of Mammalogy* 87:643–662.
- BARKER, F. K., AND S. M. LANYON. 2000. The impact of parsimony weighting schemes on inferred relationships among toucans and neotropical barbets (Aves: Piciformes). *Molecular Phylogenetics and Evolution* 15:215–234.
- BJÖRKLUND, M. 1999. Are third positions really that bad? A test using vertebrate cytochrome *b*. *Cladistics* 15:191–197.
- BRADLEY, R. D., C. W. EDWARDS, D. S. CARROLL, AND C. W. KILPATRICK. 2004. Phylogenetic relationships of neotomine-peromyscine rodents: based on DNA sequences from the mitochondrial cytochrome-*b* gene. *Journal of Mammalogy* 85:389–395.
- BRADLEY, R. D., R. D. OWEN, AND D. J. SCHMIDLY. 1996a. Morphological variation in *Peromyscus spicilegus*. *Occasional Papers, The Museum, Texas Tech University* 159:1–23.
- BRADLEY, R. D., AND D. J. SCHMIDLY. 1987. The glans penes and bacula in Latin American taxa of the *Peromyscus boylii* group. *Journal of Mammalogy* 68:595–616.
- BRADLEY, R. D., D. J. SCHMIDLY, AND C. W. KILPATRICK. 1996b. The relationships of *Peromyscus sagax* to the *P. boylii* and *P. truei* species groups in Mexico based on morphometric, karyotypic, and allozymic data. Pp. 95–106 in *Contributions in mammalogy: a memorial volume honoring Dr. J. Knox Jones, Jr.* (H. H. Genoways and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock.
- BRADLEY, R. D., D. J. SCHMIDLY, AND R. D. OWEN. 1989. Variation in the glans penes and bacula among Latin American populations of the *Peromyscus boylii* species complex. *Journal of Mammalogy* 70:712–725.
- BRADLEY, R. D., D. J. SCHMIDLY, AND R. D. OWEN. 1990. Variation in the glans penes and bacula among Latin American populations of *Peromyscus aztecus*. *Occasional Papers, The Museum, Texas Tech University* 135:1–15.
- BRADLEY, R. D., I. TIEMANN-BOEGE, C. W. KILPATRICK, AND D. J. SCHMIDLY. 2000. Taxonomic status of *Peromyscus boylii sacarensis*: inferences from DNA sequences of the mitochondrial cytochrome-*b* gene. *Journal of Mammalogy* 81:875–884.
- CALHOUN, S. W., AND I. F. GREENBAUM. 1991. Evolutionary implications of genic variation among insular populations of *Peromyscus maniculatus* and *Peromyscus oreas*. *Journal of Mammalogy* 72:248–262.
- CALHOUN, S. W., I. F. GREENBAUM, AND K. P. FUXA. 1988. Biochemical and karyotypic variation in *Peromyscus maniculatus* from western North America. *Journal of Mammalogy* 69:34–45.
- CARLETON, M. D. 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muridae) and a reappraisal of the dichotomy within New World cricetinae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 157:1–146.
- CARLETON, M. D. 1989. Systematics and evolution. Pp. 7–141 in *Advances in the study of Peromyscus (Rodentia)* (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.

- CHILDS, J. E., ET AL. 1995. A household based, case-control study of environmental factors associated with hantavirus pulmonary syndrome in the southwestern United States. *American Journal of Tropical Medicine and Hygiene* 52:393–397.
- CHILDS, J. E., ET AL. 1994. Serologic and genetic identification of *Peromyscus maniculatus* as the primary rodent reservoir for a new hantavirus in the southwestern United States. *Journal of Infectious Diseases* 169:1271–1280.
- COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *PEROMYSCUS*. 1977. Standardized karyotype of deer mice, *Peromyscus* (Rodentia). *Cytogenetics and Cell Genetics* 19:38–43.
- COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *PEROMYSCUS*. 1994. Cytogenetic nomenclature of deer mice, *Peromyscus* (Rodentia): revision and review of the standard karyotype. *Cytogenetics and Cell Genetics* 66:181–195.
- DAVIS, W. B., AND A. FOLLANSBEE. 1945. The Mexican volcano mouse, *Neotomodon*. *Journal of Mammalogy* 26:401–411.
- DEWALT, T. S., E. G. ZIMMERMAN, AND J. V. PLANZ. 1993. Mitochondrial-DNA phylogeny of species of the *boylii* and *truei* groups of the genus *Peromyscus*. *Journal of Mammalogy* 74:352–362.
- DEWEY, M. J., AND W. D. DAWSON. 2001. Deer mice: “the *Drosophila*” of North American mammalogy. *Genesis* 29:105–109.
- DICKERMAN, A. W. 1992. Molecular systematics of some New World muroid rodents. Ph.D. dissertation, University of Wisconsin, Madison.
- DUDLEY, B. F., AND G. W. WINSTON. 1995. *p*-Nitrosophenol reduction by liver cytosol from ADH-positive and -negative deer mice (*Peromyscus maniculatus*). *Archival Biochemistry and Biophysics* 316:879–885.
- DURISH, N. D., K. E. HALCOMB, C. W. KILPATRICK, AND R. D. BRADLEY. 2004. Molecular systematics of the *Peromyscus truei* species group. *Journal of Mammalogy* 85:1160–1169.
- ENGEL, S. R., K. M. HOGAN, J. F. TAYLOR, AND S. K. DAVIS. 1998. Molecular systematics and paleobiogeography of the South American sigmodontine rodents. *Molecular Biology and Evolution* 15:35–49.
- ENGSTROM, M. D., AND J. W. BICKHAM. 1982. Chromosome banding and phylogenetics of the golden mouse, *Ochrotomys nuttalli*. *Genetica* 59:119–126.
- ENGSTROM, M. D., AND J. W. BICKHAM. 1983. Karyotype of *Nelsonia neotomodon*, with notes on the primitive karyotype of peromyscine rodents. *Journal of Mammalogy* 64:685–688.
- ENGSTROM, M. D., O. SÁNCHEZ-HERRERA, AND G. URBANO-VIDALES. 1992. Distribution, geographic variation, and systematic relationships within *Nelsonia* (Rodentia: Sigmodontinae). *Proceedings of the Biological Society of Washington* 105:867–881.
- ERICSON, G. P., AND U. S. JOHANSSON. 2003. Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* 29:126–138.
- FARIAS, I. P., G. ORTÍ, I. SAMPAIO, H. SCHNEIDER, AND A. MEYER. 2001. The cytochrome *b* gene as a phylogenetic marker: the limits of resolution for analyzing relationships among cichlid fishes. *Journal of Molecular Evolution* 53:89–103.
- FARRIS, J. S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* 18:374–385.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791.
- FULHORST, C. F., ET AL. 2002. Bear Canyon virus: an arenavirus naturally associated with the California mouse (*Peromyscus californicus*). *Journal of Emerging Infectious Diseases* 8:717–721.
- GISSI, C., A. REYES, G. PESOLE, AND C. SACCONI. 2000. Lineage-specific evolutionary rate in mammalian mtDNA. *Molecular Biology and Evolution* 15:1600–1611.
- GOLDMAN, E. O. 1910. Revision of the wood rats of the genus *Neotoma*. *North American Fauna* 31:1–124.
- GREENBAUM, I. F., AND R. J. BAKER. 1978. Determination of the primitive karyotype for *Peromyscus*. *Journal of Mammalogy* 59:820–834.
- GREENBAUM, I. F., R. J. BAKER, AND P. R. RAMSEY. 1978. Chromosomal evolution and the mode of speciation in three species of *Peromyscus*. *Evolution* 32:646–654.
- GREENBAUM, I. F., ET AL. 1994. Cytogenetic nomenclature of deer mice, *Peromyscus* (Rodentia): revision and review of the standardized karyotype. *Cytogenetics and Cell Genetics* 66:181–195.
- GREENBAUM, I. F., D. W. HALE, AND K. P. FUXA. 1986a. Synaptic adaptation in deer mice: a cellular mechanism for karyotypic orthoselection. *Evolution* 40:208–213.
- GREENBAUM, I. F., D. W. HALE, AND K. P. FUXA. 1986b. The mechanism of autosomal synapsis and the substaging of zygonema and pachynema from deer mouse spermatocytes. *Chromosoma* 93:203–212.
- GREENBAUM, I. F., AND M. J. REED. 1984. Evidence for heterosynaptic pairing of the inverted segment in pericentric inversion heterozygotes of the deer mouse (*Peromyscus maniculatus*). *Cytogenetics and Cell Genetics* 38:106–111.
- HAFNER, M. S., W. L. GANNON, J. SALAZAR-BRAVO, AND S. T. ALVAREZ-CASTAÑEDA. 1997. Mammal collections in the Western Hemisphere: a survey and directory of existing collections. Allen Press, Lawrence Kansas.
- HALE, D. W. 1986. Heterosynapsis and suppression of chiasmata within heterozygous pericentric inversions of the Sitka deer mouse. *Chromosoma* 94:425–432.
- HALE, D. W., AND I. F. GREENBAUM. 1988a. Chromosome pairing in deer mice heterozygous for the presence of heterochromatic short arms. *Genome* 30:44–47.
- HALE, D. W., AND I. F. GREENBAUM. 1988b. Synapsis of a chromosomal pair heterozygous for a pericentric inversion and the presence of a heterochromatic short arm. *Cytogenetics and Cell Genetics* 48:55–57.
- HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. Ronald Press Co., New York.
- HARRIS, D., AND D. S. ROGERS. 1999. Species limits and phylogenetic relationships among populations of *Peromyscus furvus*. *Journal of Mammalogy* 80:530–544.
- HÅSTAD, O., AND M. BJÖRKLUND. 1998. Nucleotide substitution models and estimation of phylogeny. *Molecular Biology and Evolution* 15:1381–1389.
- HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.
- HOGAN, K. M., S. K. DAVIS, AND I. F. GREENBAUM. 1997. Mitochondrial DNA analysis of the systematic relationships within the *Peromyscus maniculatus* species group. *Journal of Mammalogy* 78:733–743.
- HOGAN, K. M., M. C. HEDIN, H. S. KOH, S. K. DAVIS, AND I. F. GREENBAUM. 1993. Systematic and taxonomic implications of karyotypic, electrophoretic, and mitochondrial-DNA variation in *Peromyscus* from the Pacific Northwest. *Journal of Mammalogy* 74:819–831.
- HONEYCUTT, R. L., M. A. NEDBAL, R. M. ADKINS, AND L. L. JANECEK. 1995. Mammalian mitochondrial DNA evolution: a comparison of the cytochrome *b* and cytochrome *c* oxidase II genes. *Journal of Molecular Evolution* 40:260–272.

- HOOPER, E. T. 1958. The male phallus in mice of the genus *Peromyscus*. Miscellaneous Publications of the Museum of Zoology, University of Michigan 105:1–24.
- HOOPER, E. T. 1968. Classification. Pp. 27–74 in *Biology of Peromyscus (Rodentia)* (J. A. King, ed.). Special Publication 2, The American Society of Mammalogists.
- HOOPER, E. T., AND G. G. MUSSER. 1964. Notes on classification of the rodent genus *Peromyscus*. Occasional Papers of the Museum of Zoology, University of Michigan 635:1–13.
- HOROVITZ, I., AND A. MEYER. 1995. Systematics of New World monkeys (Platyrrhini, Primates) based on 16S mitochondrial DNA sequences: a comparative analysis of different weighting methods in cladistic analysis. *Molecular Phylogenetics and Evolution* 4:448–456.
- HUCHON, D., ET AL. 2002. Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. *Molecular Biology and Evolution* 19:1053–1065.
- HUELSENBECK, J. P., AND F. R. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogeny. *Biometrics* 17:754–755.
- IRWIN, D. M., T. D., KOCHER, AND A. C. WILSON. 1991. Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution* 32:128–144.
- JANECEK, L. L. 1990. Genic variation in the *Peromyscus truei* group (Rodentia: Cricetidae). *Journal of Mammalogy* 301–308.
- JAY, M., ET AL. 1997. Seroepidemiologic studies of hantavirus infection among wild rodents in California. *Emerging Infectious Diseases* 3:183–190.
- JUKES, T. H., AND C. R. CANTOR. 1969. Evolution of protein molecules. Pp. 21–132 in *Mammalian protein metabolism* (H. N. Munro, ed.). Academic Press, New York.
- KAUFMAN, D. W., AND G. A. KAUFMAN. 1989. Population biology. Pp. 233–270 in *Advances in the study of Peromyscus (Rodentia)* (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.
- KILPATRICK, C. W., AND E. G. ZIMMERMAN. 1975. Genetic variation and systematics of four species of mice of the *Peromyscus boylii* species group. *Systematic Zoology* 24:142–162.
- KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16:111–120.
- KING, J. A. (ED.). 1968. *Biology of Peromyscus (Rodentia)*. Special Publication 2, The American Society of Mammalogists.
- KIRKLAND, G. L., JR., AND J. N. LAYNE (EDS.). 1989. *Advances in the study of Peromyscus (Rodentia)*. Texas Tech University Press, Lubbock.
- KUMAR, S., K. TAMURA, AND M. NEI. 1993. MEGA: molecular evolutionary genetics analysis, version 1.02. Institute of Molecular Evolutionary Genetics, Pennsylvania State University, University Park.
- LEVINE, J. F., M. L. WILSON, AND A. SPIELMAN. 1985. Mice as reservoirs of the Lyme disease spirochete. *American Journal of Tropical Medicine and Hygiene* 34:355–360.
- MACMILLEN, R. E., AND T. GARLAND, JR. 1989. Adaptive physiology. Pp. 143–168 in *Advances in the study of Peromyscus (Rodentia)* (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.
- MAGNARELLI, L. A., J. F. ANDERSON, K. E. HYLAND, D. FISH, AND J. B. MCANINCH. 1988. Serological analysis of *Peromyscus leucopus*, a rodent reservoir for *Borrelia burgdorferi* in northeastern United States. *Journal of Clinical Microbiology* 26:1138–1141.
- MATHER, T. N., M. L. WILSON, S. I. MOORE, J. M. C. RIBEIRO, AND A. SPIELMAN. 1989. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). *American Journal of Epidemiology* 130:143–150.
- MCALLISTER, B. F., AND I. F. GREENBAUM. 1997. How common are common fragile sites: variation of aphidicolin-induced chromosome fragile sites in a population of the deer mouse (*Peromyscus maniculatus*). *Human Genetics* 100:182–188.
- MERRIAM, C. H. 1898. Descriptions of twenty new species and a new genus of *Peromyscus* from Mexico and Guatemala. *Proceedings of the Biological Society of Washington* 12:115–125.
- MILLAR, J. S. 1989. Reproduction and development. Pp. 169–232 in *Advances in the study of Peromyscus (Rodentia)* (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.
- MILLER, G. S., JR. 1912. List of North American land mammals in the United States National Museum, 1911. *Bulletin of the Natural History Museum* 79:1–455.
- MILLS, J. N., ET AL. 1997. Patterns of association with host and habitat: antibody reactive with Sin Nombre virus in small mammals in the major biotic communities of the southwestern United States. *American Journal of Tropical Medicine and Hygiene* 56:273–284.
- MORZUNOV, S. P., J. E. ROWE, T. G. KSIAZEK, C. J. PETERS, S. C. ST JEOR, AND S. T. NICHOL. 1998. Genetic analysis of the diversity and origin of hantaviruses in *Peromyscus leucopus* mice in North America. *Journal of Virology* 72:57–64.
- MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae. Pp. 501–755 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press, Washington, D.C.
- MUSSER, G. G., AND M. D. CARLETON. 2005. Superfamily Muroidea. Pp. 894–1531 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- OSGOOD, W. H. 1909. Revision of the mice of the American genus *Peromyscus*. *North American Fauna* 28:1–285.
- PATTON, J. C., R. J. BAKER, AND J. C. AVISE. 1981. Phenetic and cladistic analyses of biochemical evolution in peromyscine rodents. Pp. 288–308 in *Mammalian population genetics* (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens.
- POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- POUX, C., AND E. J. P. DOUZERY. 2004. Primate phylogeny, evolutionary rate variations, and divergence times: a contribution from the nuclear gene IRBP. *American Journal of Anthropology* 124:1–16.
- RAND, P. W., ET AL. 1993. Competence of *Peromyscus maniculatus* (Rodentia: Cricetidae) as a reservoir host for *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae) in the wild. *Journal of Medical Entomology* 30:614–618.
- REEDER, S. A., AND R. D. BRADLEY. 2004. Molecular systematics of neotomine–peromyscine rodents based on the dentin matrix protein 1 gene. *Journal of Mammalogy* 85:1194–1200.
- REEDER, S. A., AND R. D. BRADLEY. 2007. Phylogenetic relationships of neotomine–peromyscine rodents using DNA sequences from beta fibrinogen and cytochrome *b*. Pp. 883–900 in *The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson* (D. A. Kelt, E. P. Lessa, J. A. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1–981.
- REEDER, S. A., C. W. EDWARDS, D. S. CARROLL, C. W. KILPATRICK, AND R. D. BRADLEY. 2006. neotomine–peromyscine rodent systematics based on combined analyses of nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 40:251–258.
- RENNERT, P. D., AND C. W. KILPATRICK. 1986. Biochemical systematics of populations of *Peromyscus boylii*. I. Populations

- from east-central Mexico with low fundamental numbers. *Journal of Mammalogy* 67:481–488.
- RENNERT, P. D., AND C. W. KILPATRICK. 1987. Biochemical systematics of populations of *Peromyscus boylii*. II. Chromosomally variable populations from eastern and southern Mexico. *Journal of Mammalogy* 68:799–811.
- ROBBINS, L. W., AND R. J. BAKER. 1981. An assessment of the nature of chromosomal rearrangements in 18 species of *Peromyscus* (Rodentia: Cricetidae). *Cytogenetics and Cell Genetics* 31:194–202.
- ROGERS, D. S. 1983. Phylogenetic affinities of *Peromyscus* (*Megadontomys*) *thomasi*: evidence from differentially stained chromosomes. *Journal of Mammalogy* 64:617–623.
- ROGERS, D. S., AND M. D. ENGSTROM. 1992. Evolutionary implications of allozymic variation in tropical *Peromyscus* of the *mexicanus* species group. *Journal of Mammalogy* 73:55–69.
- ROGERS, D. S., M. D. ENGSTROM, AND E. ARELLANO. 2005. Phylogenetic relationships among peromyscine rodents: allozyme evidence. Pp. 437–449 in *Contribuciones mastozoológicas en homenaje a Bernardo Villa* (V. Sánchez-Cordero and R. A. Medellín, eds.). Instituto de Biología e Instituto de Ecología, UNAM, and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F.
- ROGERS, D. S., C. C. FUNK, J. R. MILLER, AND M. D. ENGSTROM. 2007. Molecular phylogenetic relationships among crested-tail mice (genus *Habromys*). *Journal of Mammalian Evolution* 14:37–55.
- ROGERS, D. S., I. F. GREENBAUM, S. J. GUNN, AND M. D. ENGSTROM. 1984. Cytosystematic value of chromosomal inversion data in the genus *Peromyscus* (Rodentia: Cricetidae). *Journal of Mammalogy* 65:457–465.
- SAIKI, R. K., ET AL. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239:487–491.
- SAITOU, N., AND M. NEI. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4:406–425.
- SALAZAR-BRAVO, J., ET AL. 2004. Serosurvey of wild rodents for hantaviruses in Panama, 2000–2002. *Journal of Wildlife Diseases* 40:103–109.
- SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. *Molecular cloning—a laboratory manual*. 2nd ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.
- SCHMIDLY, D. J., R. D. BRADLEY, AND P. S. CATO. 1988. Morphometric differentiation and taxonomy of three chromosomally characterized groups of *Peromyscus boylii* from east-central Mexico. *Journal of Mammalogy* 69:462–480.
- SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Studies in Genetics VI*. University of Texas Publication 7103:49–90.
- SHIMODAIRA, H., AND M. HASEGAWA. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16:114–116.
- SMITH, M. F., AND J. L. PATTON. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. *Journal of Mammalian Evolution* 6:89–128.
- SMITH, S. A. 1990. Cytosystematic evidence against the monophyly of the *Peromyscus boylii* species group (Rodentia: Cricetidae). *Journal of Mammalogy* 71:654–667.
- SMITH, S. A., I. F. GREENBAUM, D. J. SCHMIDLY, K. M. DAVIS, AND T. W. HOUSEAL. 1989. Additional notes on the karyotypic variation in the *Peromyscus boylii* group. *Journal of Mammalogy* 70:602–608.
- SPRINGER, M. S., ET AL. 2001. Mitochondrial versus nuclear gene sequences in deep-level mammalian phylogeny reconstruction. *Molecular Biology and Evolution* 18:132–143.
- STANGL, F. B., JR., AND R. J. BAKER. 1984. Evolutionary relationships in *Peromyscus*: congruence in chromosomal, genic, and classical data sets. *Journal of Mammalogy* 65:643–654.
- SUDMAN, P. D., AND I. F. GREENBAUM. 1990. Unequal crossing over and heterochromatin exchange in the X–Y bivalents of the deer mouse, *Peromyscus beatae*. *Chromosoma* 99:183–189.
- SUDMAN, P. D., I. F. GREENBAUM, D. W. HALE, AND S. A. SMITH. 1989. Synaptic adjustment in *Peromyscus beatae* (Rodentia: Cricetidae) heterozygous for interstitial heterochromatin. *Cytogenetics and Cell Genetics* 50:1–5.
- SULLIVAN, J., K. E. HOLSINGER, AND C. SIMON. 1995. Among-site rate variation and phylogenetic analysis of 12S rRNA data in sigmodontine rodents. *Molecular Biology and Evolution* 12:988–1001.
- SULLIVAN, J. M., AND C. W. KILPATRICK. 1991. Biochemical systematics of the *Peromyscus aztecus* assemblage. *Journal of Mammalogy* 72:681–696.
- SULLIVAN, J. M., C. W. KILPATRICK, AND P. D. RENNERT. 1991. Biochemical systematics of the *Peromyscus boylii* species group. *Journal of Mammalogy* 72:669–680.
- SULLIVAN, J., J. A. MARKERT, AND C. W. KILPATRICK. 1997. Phylogeography and molecular systematics of the *Peromyscus aztecus* species group (Rodentia: Muridae) inferred using parsimony and likelihood. *Systematic Biology* 46:426–440.
- SULLIVAN, R. M., S. W. CALHOUN, AND I. F. GREENBAUM. 1990. Geographic variation in genital morphology among insular and mainland populations of *Peromyscus maniculatus* and *Peromyscus oreas*. *Journal of Mammalogy* 71:48–58.
- SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (* and other methods), Version 4.0b10. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- TIEMANN-BOEGE, I., C. W. KILPATRICK, D. J. SCHMIDLY, AND R. D. BRADLEY. 2000. Molecular phylogenetics of the *Peromyscus boylii* species group (Rodentia: Muridae) based on mitochondrial cytochrome *b* sequences. *Molecular Phylogenetics and Evolution* 16:366–378.
- WALPOLE, D. K., S. K. DAVIS, AND I. F. GREENBAUM. 1997. Variation in mitochondrial DNA in populations of *Peromyscus eremicus* from the Chihuahuan and Sonoran deserts. *Journal of Mammalogy* 78:397–404.
- WOLFF, J. O. 1989. Social behavior. Pp. 271–291 in *Advances in the study of Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.
- YATES, T. L., R. J. BAKER, AND R. K. BARNETT. 1979. Phylogenetic analysis of karyological variation in three species of peromyscine rodents. *Systematic Zoology* 28:40–48.
- YODER, A. D., R. VILGALYS, AND M. M. RUVULA. 1996. Molecular evolutionary dynamics of cytochrome *b* in strepsirrhine primates: the phylogenetic significance of third-position transversions. *Molecular Biology and Evolution* 13:1339–1350.
- YODER, A. D., AND Z. YANG. 2000. Estimation of primate speciation dates using local molecular clocks. *Molecular Biology and Evolution* 17:1081–1090.
- XIA, X. 2000. *Data analysis in molecular biology and evolution*. Kluwer Academic Publishers, Boston, Massachusetts.
- XIA, X., AND Z. XIE. 2001. DAMBE: data analysis in molecular biology and evolution. *Journal of Heredity* 92:371–373.
- ZARDOYA, R., AND A. MEYER. 1996. Phylogenetic performance of mitochondrial protein-coding genes in resolving relationships among vertebrates. *Molecular Biology and Evolution* 13:933–942.

ZHENG, Y.-W., M. BEY, H. LIU, AND M. R. FELDER. 1993. Molecular basis of the alcohol dehydrogenase-negative deermouse: evidence for deletion of the gene for class I enzyme and identification of a possible new enzyme class. *Journal of Biological Chemistry* 268:24933–24939.

ZIMMERMAN, E. G., B. J. HART, AND C. W. KILPATRICK. 1975. Biochemical genetics of the *truei* and *boylei* groups of the genus *Peromyscus* (Rodentia). *Comparative Biochemistry and Physiology* 52:541–545.

ZIMMERMAN, E. G., C. W. KILPATRICK, AND B. J. HART. 1978. The genetics of speciation in the rodent genus *Peromyscus*. *Evolution* 32:565–579.

Submitted 9 October 2006. Accepted 5 February 2007.

Associate Editor was Carey W. Krajewski.

APPENDIX I

Specimens examined.—For each specimen examined, the collection locality is given; specimens are from the United States unless otherwise noted. Some sequences were obtained from GenBank and do not have locality data. Museum acronyms, museum catalogue numbers, and GenBank accession numbers (AF, AY, DQ, EF, U, and X) are provided in parentheses, respectively. Abbreviations for museum acronyms (in parentheses and to the left of the semicolon) follow Hafner et al. (1997): Abilene Christian University Natural History Collection (ACUNHC); Angelo State University Museum Natural History Collections (ASNHC); Colección de Mamíferos, del CEAMISH (Centro de Educación Ambiental e Investigación Sierra de Huautla), Universidad Autónoma del Estado de Morelos (CMC); Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA); Monte L. Bean Life Science Museum (BYU); The Museum of Vertebrate Zoology (MVZ); The Museum of Southwestern Biology (MSB); Museum of Texas Tech University (TTU); Royal Ontario Museum (ROM); Texas Cooperative Wildlife Collection (TCWC); United States National Museum (USNM); Universidad Nacional Autónoma de México (UNAM); University of Alaska Museum (UAM); University of Michigan Museum of Zoology (UMMZ) and Zaddock Thompson Natural History Collection (ZTNHC). If museum catalogue numbers were unavailable, specimens were referenced with the corresponding collector's numbers: CWK (personal collector number, C. William Kilpatrick), FSH (personal collector number, Charles F. Fulhorst), and KN (personal collector number, K. Nutt), or TK number (special number of the Museum of Texas Tech University).

Baiomys taylori.—Texas; Garza County, 22.5 km S, 0.6 km E Post (TTU54633, AF548469).

Habromys ixtlani.—MEXICO: Oaxaca; Distrito de Ixtlan, 28 km SW (by road) La Esperanza, 2,950 m (BYU15271, DQ861395); 2.2 km N Llano de las Flores, UTM 14-764396E-1931268N (TTU82703, DQ973099); UNAM—catalogue number unavailable, TK93160, DQ000482).

Isthmomyx pirrensis.—PANAMA: Darien; Cerro Pirre, summit, 1,570 m (ROM116308, DQ836298; ROM116309, DQ836299).

Megadontomys cryophilus.—MEXICO: Oaxaca Municipio Teotitlan, 1.5 km S Puerto de la Soledad, 18°9.742'N, 96°59.852'W, 2,600 m (BYU16076, DQ861373).

Megadontomys thomasi.—MEXICO: Guerrero; 6.4 km SSW Filo de Caballo (UNAM—catalogue number unavailable, TK93388, AY195795).

Neotoma mexicana.—New Mexico; Los Alamos County, Los Alamos (TTU79129, AF294345).

Neotomodon alstoni.—MEXICO: Michoacán; Ladera, Cerra del Burror, 3 km W Opopeo–Tacamborro (UNAM—catalogue number unavailable, TK45302, AY195796); Mexico; Nevado de Toluca (UNAM—catalogue number unavailable, TK93093, AY195797); Morelos; Lagunas de Zempoala, 3 km W Huitzilac, 19°02.020'N, 99°17.627'W, 3,018 m (BYU15513, DQ861374).

Nyctomys sumichrasti.—HONDURAS: Atlantida; Lancetilla Botanical Garden (TTU84484, AY195801).

Ochrotomys nuttalli.—Texas; Wood County, 5.6 km SE Quitman (TCWC31929, AY195798).

Onychomys arenicola.—Texas; Presidio County, Big Bend Ranch State Natural Area (TTU67559, AY195793).

Oryzomys palustris.—Texas; Galveston County, Texas City, Virginia Point (TTU82920, DQ185382).

Osgoodomys banderanus.—MEXICO: Jalisco; 6 km SE Chamela (TTU37754, AF155383); Michoacán; Coalcoman, Tehuantepec, 17.5 km WSW Coalcoman, 1,350 m, 18°42.95'N, 103°18.19'W (UNAM—catalogue number unavailable, TK45952, DQ000473).

Ototylomys phyllotis.—MEXICO: Campeche; El Remate 14 km W Tancuche (ASNHC7236, AY009789).

Peromyscus atwateri.—Oklahoma; McIntosh County, 5 km E Dustin (TTU55688, AF155384); Texas; Knox County, 4.8 km E Benjamin (ZTNHC—catalogue number unavailable, DNA27, AF155385).

Peromyscus aztecus.—MEXICO: Veracruz; 8.8 km N Huatusco (TCWC47976, U89968).

Peromyscus beatae.—MEXICO: Veracruz; Xometla (TCWC48060, AF131921); Guerrero; 6.4 km SW Filo de Caballo (TCWC45222, AF131922); HONDURAS: Francisco Morazan; 3.2 km NE El Hatillo (TCWC52288, AF131914).

Peromyscus boylii.—California; Monterey County, Hastings Natural History Reservation (MVZ—catalogue number unavailable, KN120, AF155386); Utah; Garfield County, Henry Mountains, Mt. Pennell, Sidehill Spring, 2,652 m (MSB123149, AF155392); MEXICO: Jalisco; 30 km W Huejuquilla del Alto (TTU81702, AF155388).

Peromyscus californicus.—California; San Diego County, San Onofre State Beach, 5.6 km NNE on Christmas Road (TTU81275, AF155393).

Peromyscus crinitus.—Utah; Emery County, Cottonwood Canyon, 39°16'51.8"N, 111°10'31.9"W (BYU18639, AY376413); Kane County, 59 km E, 25 km N Kanab, UTM 12-414464E-4121440N, 1,450 m (BYU18065, EF028168); 59 km E, 25 km N Kanab, UTM 12-415040E-4121500N, 1,450 m (BYU18029, DQ861378).

Peromyscus difficilis.—MEXICO: Hidalgo; 2.9 km E Jonacapa (TCWC46659, AY376419); Tlaxcala; Mt. Malinche (TCWC48071, AY376415); 18 km N, 9 km E Apizaco (TCWC13084, AY387488).

Peromyscus eremicus.—Arizona; Yavapai County, Sycamore Station, 34°23'28.2"N, 112°3'1.3"W (TTU97750, AY195799); California; Los Angeles County, Calabasas Creekside Park (TTU83249, AY322503); MEXICO: Zacatecas; 16.8 mi S Concepcion del Oro (TTU45197, DQ973100).

Peromyscus evides.—MEXICO: Oaxaca; 5.6 km S Suchxtepec (TCWC45185, U89970).

Peromyscus fuvvus.—MEXICO: Veracruz; 5 km W Naolinco de Victoria, Municipio Naolinco, 19°39'12"N, 96°55'26"W, 1,650 m (CNMA32298, AF271032); Oaxaca; 1.5 km S Puerto de la Soledad, 18°09.742'N, 96°59.852'W, 2,690 m, Municipio Teotitlán (BYU15389, AF271012); Hidalgo, 21.8 km NE Metepec (ZTNHC—catalogue number unavailable, CWK913, AF271005).

Peromyscus gossypinus.—Oklahoma; Seminole County, 5.6 km E Seminole (TTU55019, DQ973101); Texas; Cass County, White Oak

Creek Wildlife Management Area, UTM 15-350030E-3678790N (TTU80682, DQ973102).

Peromyscus gratus.—MEXICO: Durango; 6.1 km W Coyotes, Hacienda Coyotes, UTM 13-465908E-2634281N (TTU81621, AY322507); Michoacán; 4 km E Costzeo (UNAM—catalogue number unavailable, TK46354, AY376421); Puebla; 5 km SE San Antonia, UTM 14-664598E-2030332N (TTU82701, AY376422).

Peromyscus guatemalensis.—MEXICO: Chiapas; Cerro Mozotal, 15°25.866'N, 92°20.274'W, 2,930 m (CMC550, EF028171; BYU20724, EF028172).

Peromyscus gymnotis.—MEXICO: Chiapas; 21 km SE Mapastepec (TCWC—catalogue number unavailable, AK6026, EF028169; TCWC—catalogue number unavailable, AK6027, EF028170).

Peromyscus hooperi.—MEXICO: Coahuila; 24.3 km W Ocampo (TTU104425, DQ973103).

Peromyscus hylocetes.—MEXICO: Michoacán; Puerto Garnica (ZTNHC—catalogue number unavailable, CWK2035, U89976); Estacion Cerra Burror, Microodas; 3,270 m (UNAM—catalogue number unavailable, TK45309, DQ000481).

Peromyscus keeni.—Washington; Gray Harbor County, 0.8 km NE Grisdaley (ZTNHC—catalogue number unavailable, CWK2235, X89787); Alaska; Alexander Archipelago, Bushy Island, Petersburg Quad (UAM50770, AF119261).

Peromyscus leucopus.—Texas; Dickens County, 0.9 km E Afton (TTU—catalogue number unavailable, TK47506, AF131926); La Salle County, Chaparral Wildlife Management Area, UTM 14-454285E-3136441N (TTU104424, DQ973104; TTU101645, DQ000483).

Peromyscus levipes.—MEXICO: Nuevo Leon; Cola de Caballo (TCWC47956, AF131928); Mexico; 12 km S Acamby (TTU82707, AY322509); Querétaro; 13.1 km N, 2.9 km W Amealco (TCWC43468, AF155396).

Peromyscus madrensis.—MEXICO: Nayarit; Isla María Madre (USNM512599, AF155397).

Peromyscus maniculatus.—Texas; Wichita County, 6.5 km S Wichita Falls (TTU38739, DQ000484); Washington; Pierce County, Ft. Lewis, Reganberg Mount (TTU104426, DQ973111); MEXICO: Durango; 6.1 km W Coyotes Hacienda Coyotes, UTM 13-465908E-2634281N (TTU81622, AY322508).

Peromyscus mayensis.—GUATEMALA: Huetenango; Santa Eulalia, 16 km NW Santa (ROM98339, DQ836300; ROM98360, DQ836301).

Peromyscus megalops.—MEXICO: Guerrero; 6.4 km SSW Filo de Caballo (TTU82712, DQ000475).

Peromyscus melanocarpus.—MEXICO: Oaxaca; Municipio Santiago Comaltepec, La Esperanza, 11 km SW Hacienda San Isidro (CMC29192, EF028173); Municipio Tlahuitoltepec, vicinity Santa Maria Yacochi, 17°15'N, 96°00'45"W, 2,400 m (CMC136, EF028175).

Peromyscus melanophrys.—MEXICO: Durango; 2.2 km S, 2.5 km E Vicente Guerrero (TTU75509, AY322510); Jalisco; 30 km W Huejuquilla del Alto (UNAM—catalogue number unavailable, TK48638, AY376424); Zacatecas; 16.8 km S Concepcion del Oro (TTU49351, DQ973105).

Peromyscus melanotis.—MEXICO: Durango; 12 km E Ojitos, UTM 13-385011E-2775718N (UNAM—catalogue number unavailable, TK70997, AF155398).

Peromyscus mexicanus.—MEXICO: Chiapas; 14.4 km N Ocozocoautla, 15-451772E-1864243N (TTU82759, AY376425); Veracruz; 10 km SE (por carretera) Zongolica, 1,850 m, (CNMA34309, EF028174).

Peromyscus nasutus.—New Mexico; Lincoln County, 6.4 km S Carrizozo (TTU78401, AF155399); Texas; Jeff Davis County, Mt.

Livermore Preserve, UTM 13-579953E-3389871N (TTU78316, AY376426).

Peromyscus nudipes.—COSTA RICA: Heredia; 2 km NE Getze-mani, 10.04612°N, 84.10377°W (MSB61868, AY041200).

Peromyscus oaxacensis.—MEXICO: Oaxaca; 1.4 km N Llano de las Flores (TCWC45192, U89972).

Peromyscus ochraventer.—MEXICO: San Luis Potosi; 0.8 km E Las Abritas (TCWC48405, DQ973106).

Peromyscus pectoralis.—Texas; Kimble County, Walter Buck Wildlife Management Area, UTM 14-423359E-3366337N (TTU71252; AF155400); MEXICO: Durango; 2.4 km SE Los Herreras (UNAM—catalogue number unavailable, TK48519, AY322511); Jalisco; 30 km W Huejuquilla del Alto (UNAM—catalogue number unavailable, TK48642, AY376427).

Peromyscus perfulvus.—MEXICO: Michoacán; Tunel de Riego, 2 km E Cerro Colorado, 1,290 m, 19°19'22"N, 100°28'308"W (UNAM—catalogue number unavailable, TK47926, DQ000474).

Peromyscus polionotus.—Captive reared (*Peromyscus* Stock Center, Columbia, South Carolina; X89792).

Peromyscus polius.—MEXICO: Chihuahua; 4.8 km SW Santa Barbara (TCWC47255, AF155403).

Peromyscus sagax.—MEXICO: Michoacán; Puerto Garnica (ZTNHC—catalogue number unavailable, CWK2032, AF155404).

Peromyscus schmidlyi.—MEXICO: Durango; 30 km SW Ojitos (TTU81635, AY322520); 12 km E Ojitos, UTM 13-385011E-2775718N (TTU81602, AF155405); 6.1 km W Coyotes, UTM 13-465908E-2634281N (TTU81617, AY370610).

Peromyscus simulus.—MEXICO: Sinaloa; 6.4 km E Concordia, Highway 40 (TCWC45592, AF131927).

Peromyscus spicilegus.—MEXICO: Durango; San Juan de Camarones, UTM 13-356961E-2757448N (TTU81640, AY322512; UNAM—catalogue number unavailable, TK70919, DQ973107); Michoacán; km 81 carr. Ario de Rosales–La Huacana, 1,602 m, 19°10'59"N, 101°43'42"W (UNAM—catalogue number unavailable, TK47888, DQ000480).

Peromyscus stephani.—MEXICO: Sonora; Isla San Esteban (UMMZ117385, AF155411).

Peromyscus stirtoni.—NICARAGUA: Parque Nacional, Volcan Masaya (MCZ61922, DQ973108).

Peromyscus truei.—Arizona; Apache County, 35°34'51"N, 109°34'33"W (TTU104427, AY376433); California; Alameda County, Strawberry Canyon (MVZ157329, AF108703); Texas; Armstrong County, 1.2 km N, 10 km E Wayside (TTU61543, AY376428).

Peromyscus winkelmanni.—MEXICO: Michoacán; 11 km WSW Dos Aguas (TCWC45621, AF131930); Guerrero; Filo de Caballo (TCWC45175, U89983).

Peromyscus zarhynchus.—MEXICO: Chiapas; Yalentay, UTM 15-524171E-1852456N (UNAM—catalogue number unavailable, TK93297, AY195800); Municipio Chamula, Cerro Tzontehuitz, 13 km NE San Christobal de la Cases (BYU14469, EF028169).

Podomys floridanus.—Florida; Columbia County, O'leno State Park (TTU97867, DQ973109; TTU97868, DQ973110).

Reithrodontomys megalotis.—Texas; Lubbock County, Lubbock Lake Landmark State Historical Park (TTU40942, AF176248).

Reithrodontomys mexicanus.—MEXICO: Chiapas; 6 km E Rayon (ROM97843, AY859447).

Sigmodon hispidus.—Florida; Dade County, Homestead Air Force Reserve Base golf course (FSH33, AF155420).

Tylomys nudicaudatus.—GUATEMALA: Izabal, Cerro San Gil (TTU62082, AF307839).