
TEXAS TECH UNIVERSITY
Natural Science Research Laboratory

Occasional Papers

Museum of Texas Tech University Number 306 21 December 2011

Molecular Evidence for Paraphyly in *Nyctomys sumichrasti*: Support for a New Genus of Vesper Mice?

Megan S. Corley, Nicté Ordóñez-Garza, Duke S. Rogers, and Robert D. Bradley

Abstract

DNA sequences were obtained from the mitochondrial cytochrome-*b* gene of nine specimens of *Nyctomys sumichrasti* collected in Mexico and Central America. Phylogenetic analysis (Bayesian Inference) of these sequences document heretofore unrecognized patterns in genetic diversity among phylogroups that: 1) indicated substantial levels of genetic divergence among phylogroups; 2) resulted in paraphyly of taxa currently recognized as *N. sumichrasti*; and 3) argued for a re-assessment of the current taxonomy of *Nyctomys* and perhaps recognition of a new genus.

Key words: cytochrome-*b* gene, *Nyctomys sumichrasti*, phylogenetics, Sumichrast's vesper rat

Introduction

Nyctomys sumichrasti (Sumichrast's vesper rat; De Saussure 1860) is an arboreal rodent (Cricetidae, Tylomyinae, Musser and Carleton 2005) distributed from Jalisco, Mexico, to Panama (Hall 1981; Reid 2009). It inhabits evergreen lowlands and lower montane regions including cloud, secondary, riparian, and semi-deciduous forests (Hall 1981; Sánchez-Hernández et al. 1999; Cervantes et al. 2004; Hunt et al. 2004). Typically, *N. sumichrasti* prefers middle and upper level forest strata, rarely descending to the ground (Emmons 1997; Timm and LaVal 2000; Hunt et al. 2004). Given its arboreal to semi-arboreal behavior, specimens of *N. sumichrasti* are relatively rare in most museum collections and consequently a paucity of information is available concerning its ecology, genetic and morphologic variation, and systematics.

Nine subspecies of Sumichrast's vesper rat are recognized (*colimensis*, *costaricensis*, *decolorus*, *florencei*, *nitellinus*, *pallidulus*, *salvini*, *sumichrasti*, and *venustulus*; Hall 1981), however the majority of information is restricted to the original description of each taxon and little has been reported concerning the taxonomy, geographic and genetic variation, or relationships among subspecies. Musser and Carleton (2005) noted that specimens in the United States National Museum could be separated into two groups based on variation in the carotid circulatory pattern (complete versus derived) and molar-root number (three versus four). Their groups corresponded to populations occurring north and west of the Isthmus of Tehuantepec (*pallidulus* and *sumichrasti*) versus those to the south and east (*costaricensis*, *decolorus*, *florencei*, *nitellinus*,

and *venustulus*). No comments were made concerning *colimensis* and *salvini*. Karyotype data have been reported for two subspecies, with *N. s. colimensis* being polymorphic (2n = 50–52, FN = 52–54; Lee and Elder 1977; Haiduk et al. 1988) and *N. s. florencei* possessing a 2n = 50 and FN = 52 karyotype (Bradley and Ensink 1987).

Herein we assess genetic variation among nine specimens representing five of the nine subspecies (Fig. 1) of *N. sumichrasti*. To accomplish this, DNA sequences from the mitochondrial cytochrome-*b* gene (*Cyt*b) were obtained and then evaluated in a phylogenetic context.

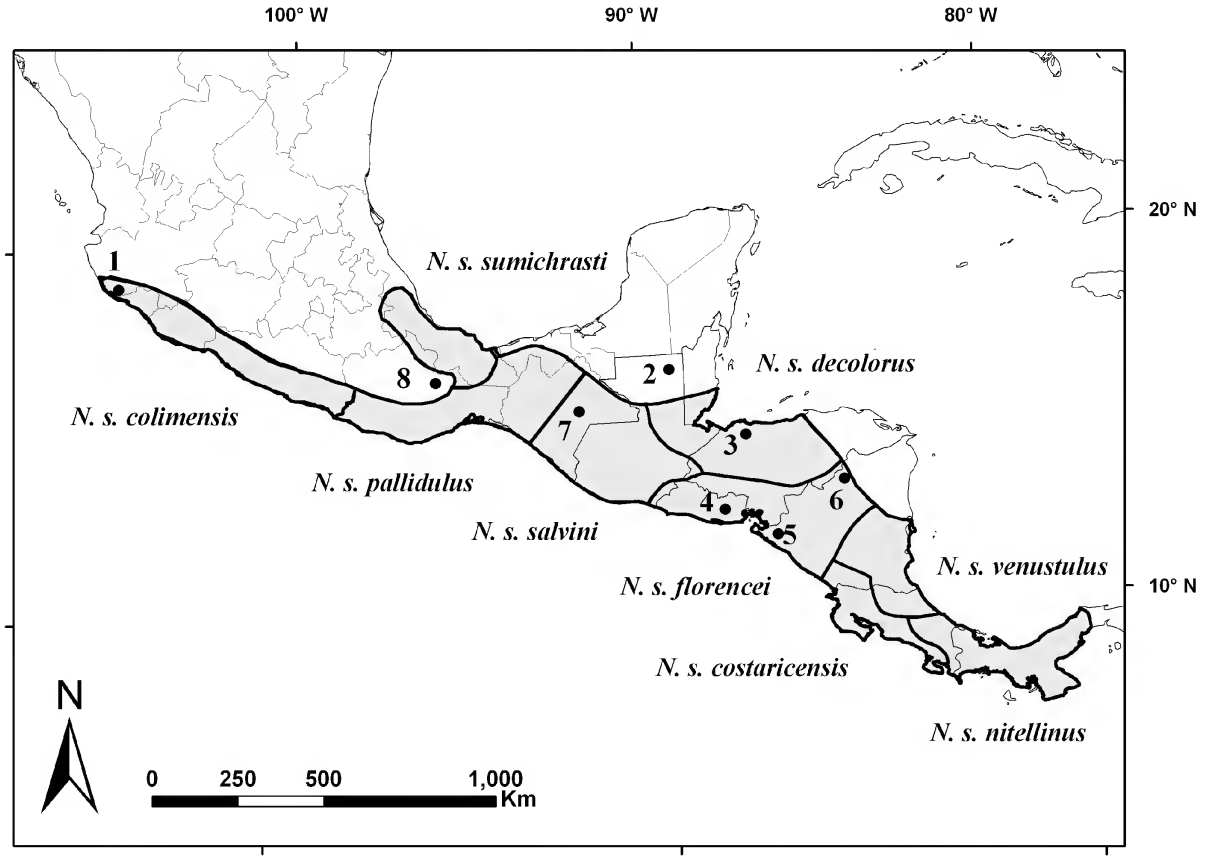


Figure 1. Map depicting collecting localities for samples examined in this study. Subspecies and distributions are recognized following Hall (1981). Numbers indicate localities as referred to in the Appendix.

METHODS

DNA sequences.—Mitochondrial DNA was isolated from approximately 0.1 g of frozen liver tissue using the Gentra Puregene Cell and Tissue Kit (Gentra Systems, Minneapolis, Minnesota) or from 0.1 g of liver preserved in 95% ethanol using the Qiagen DNeasy™ Tissue Kit (Qiagen Inc., Valencia, California). For most specimens, the entire *Cyt*b gene (1,143 bp) was amplified by polymerase chain reaction (PCR, Saiki et al. 1988) using the following primers: MVZ05 (Smith and Patton 1993) and PERO3' (Tiemann-Boege et al. 2000), or with primer pairs as follows: L14724 (Irwin et al. 1991) with CB3H (Palumbi 1996), and F1 (Whiting et al. 2003) with MVZ14 (Smith and Patton 1993). For other specimens, an approximately 400 bp fragment (at the 5' end) was amplified using primers MVZ05 and 400R (Peppers and Bradley 2000). The thermal profile for PCR reactions was as follows: initial denaturation at 95°C for 2 min, followed by 35 cycles of denatur-

ation at 95°C for 1 min, annealing at 51°C for 1 min, and extension at 72°C for 2 min, with a final extension at 72°C for 7 min. PCR products were purified using ExoSAP-IT (USB Products, Cleveland, Ohio). Primers used to cycle sequence the products consisted of MVZ05 and MVZ14 (Smith and Patton 1993), PERO3' (Tiemann-Boege et al. 2000), 870R (Peppers et al. 2002), F1 (Whiting et al. 2003), H15149, and L14841 (Irwin et al. 1991). Cycle sequencing reactions were purified using isopropanol cleanup protocols. Purified products were sequenced with an ABI 3100-Avant automated sequencer or with an ABI 377 automated sequencer using ABI Prism Big Dye version 3.1 terminator technology (Applied Biosystems, Foster City, California). Resulting sequences were subsequently assembled and proofed using Sequencher 4.9 software (Gene Codes, Ann Arbor, Michigan); chromatograms were examined to verify all base changes. The resulting DNA sequences were deposited in GenBank and the accession numbers are listed in the Appendix.

Data analyses.—Two approaches were used for data analysis. First, representatives of all tribes contained in the Neotominae (Bradley et al. 2004; Reeder and Bradley 2004, 2007; Musser and Carleton 2005; Reeder et al. 2006; Miller and Engstrom 2008) were included to test for monophyly of the subfamily Tylomyinae (Musser and Carleton 2005). The taxonomic sampling for this analysis included three members of the Neotomini (*Hodomys alleni*, *Neotoma mexicana*, and *Xenomys nelsoni*), one member of the Ochrotomyini (*Ochrotomys nutalli*), two members of the Baiomyini (*Baiomys taylori* and *Scotinomys teguina*), two members of the Reithrodontomyini (*Isthmomys pirrensis* and *Reithrodontomys fulvescens*), and eight members of the Peromyscini (*Habromys lepturus*, *Megadontomys thomasi*, *Neotomodon alstoni*, *Onychomys arenicola*, *Osgoodomys banderanus*, *Peromyscus californicus*, *Peromyscus maniculatus*, and *Podomys floridanus*). For these taxa, sequences were obtained from GenBank (accession numbers are provided in the Appendix). Two members of the subfamily Sigmodontinae (*Oryzomys palustris* and *Sigmodon hispidus*) were used as outgroup taxa for this analysis.

In the second analysis, and based on results from the first analysis, the dataset was reduced to include only members of the Tylomyinae (*Nyctomys*, n = 9; *Otonyctomys*, n = 1; *Ototylomys*, n = 1; and *Tylomys*, n = 1). Given that *Ototylomys* and *Tylomys* were sister taxa in the first analysis, *Tylomys* was selected for the outgroup taxon. Sequences were deposited in GenBank (accession numbers are provided in the Appendix). Locality information for the specimens of *Nyctomys* is provided in the Appendix.

The GTR+I+G model was identified by the Akaike information criterion in MODELTEST (Posada and Crandall 1998) as the most appropriate model of DNA evolution for both datasets. A Bayesian model (MrBayes; Huelsenbeck and Ronquist 2001) was used to obtain a phylogenetic tree and to generate support values (clade probabilities). The GTR+I+G model parameters included: a site-specific gamma distribution, four Markov-chains, 10 million generations, and sample frequency = every 1,000th generation. After a visual inspection of likelihood scores, the first 1,000 trees were discarded and a consensus tree (50% majority rule) was constructed from the remaining trees. The Kimura two-parameter model of evolution (Kimura 1980) was used to obtain genetic distances and estimate divergence times between taxa.

RESULTS

The first Bayesian analysis produced a tree (not shown) depicting a monophyletic Tylomyinae (*Nyctomys*, *Otonyctomys*, *Ototylomys*, and *Tylomys*) and Neotominae (15 genera), with each clade being supported with probability values = 1.00. Based on these results, a second Bayesian analysis (Fig. 2) was conducted using *Tylomys* as the outgroup taxon (as explained in the Methods) in order to better assign character polarity to the various sequences of *Nyctomys*. This analysis produced two major clades (I and II) and six minor clades (A–F) that were supported with probability values = 1.00. Clade I was comprised of two groups: *Otonyctomys hatti,* and seven of the nine samples of *Nyctomys*. Clade II consisted of the remaining two samples of *N. sumichrasti*.

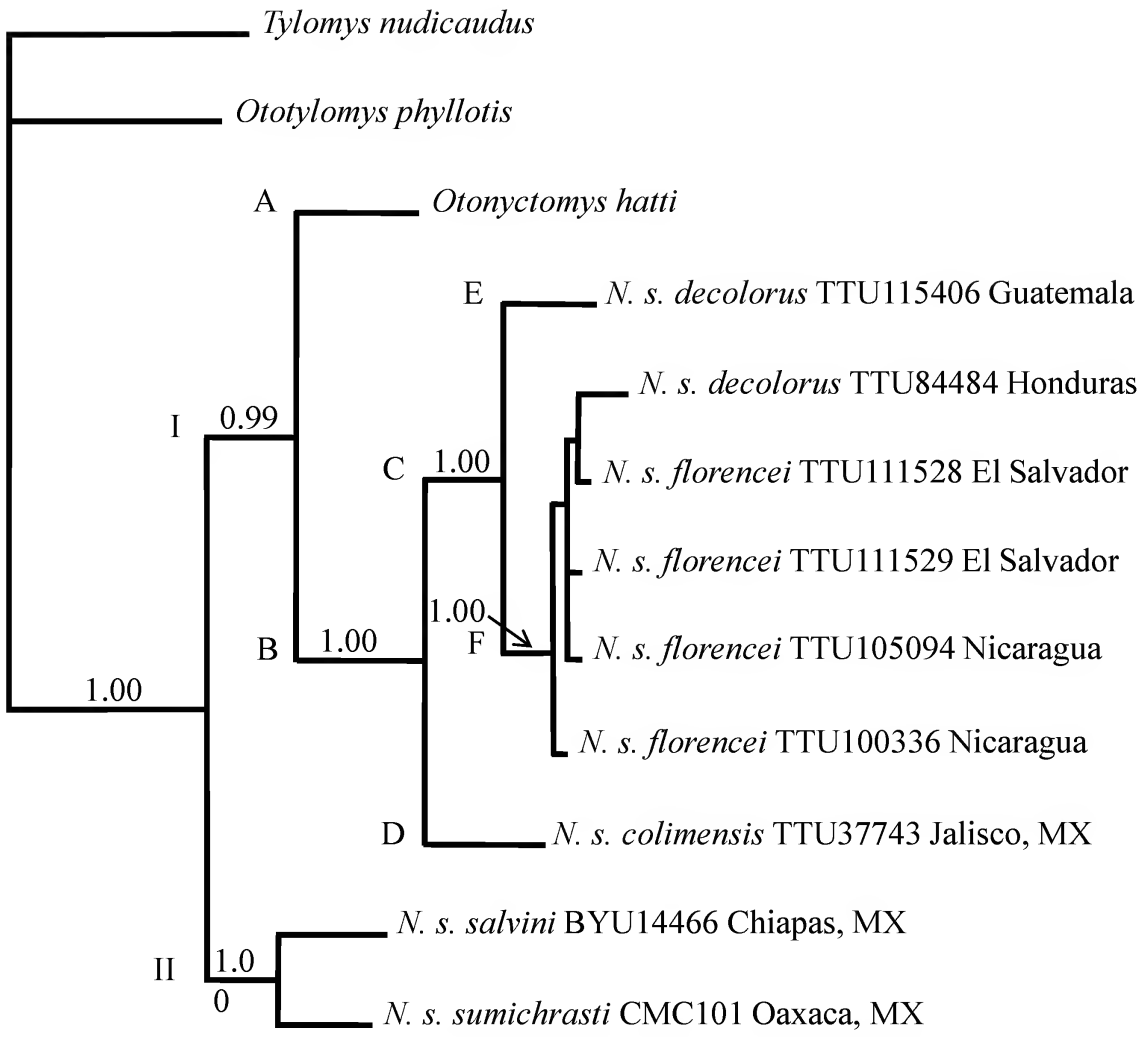


Figure 2. Phylogenetic tree obtained from the Bayesian analysis of mitochondrial cytochrome-*b* gene sequences. Values above branches indicate clade probability support values (only values ≥ 0.95 are shown).

Kimura two-parameter distance values (Kimura 1980) were obtained for comparisons among samples of *Nyctomys*, samples of *Nyctomys* versus *Otonyctomys*, and between other sister genera within the Tylomyinae and Neotominae (Table 1). Genetic distances obtained from within clade comparisons of samples of *Nyctomys* ranged from 1.5% (clade F) to 10.2% (clade II), whereas comparisons between clades containing samples of *Nyctomys* ranged from 8.4% (clades E and F) to 20.0% (clades I and II). Using a sequence divergence estimate of 3.5% per million years for *Cyt*b sequences (Arbogast and Slowinski 1998), divergence times and confidence intervals (obtained using the "POISSCI" function in MATLAB® version 6.5, The MathWorks, Inc. 2006) within clades ranged from 0.4 ± 0.34 mya (clade F) to 2.9 ± 0.58 mya (clade II) and between clades from 2.4 ± 0.54 mya (clades E and F) to 5.7 ± 0.86 mya (clades I and II) (Table 1).

Table 1. Genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of Nyctomys *and other members of the Tylomyinae and Neotominae.*

Comparison	Genetic Distance	Time Since Divergence
Within Clades containing *Nyctomys*		
Clade I	9.3%	2.7 mya ± 0.56 mya
Clade II	10.2%	2.9 mya ± 0.58 mya
Clade B	6.5%	1.9 mya ± 0.49 mya
Clade C	3.8%	1.1 mya ± 0.41 mya
Clade F	1.5%	0.4 mya ± 0.34 mya
Between Clades containing *Nyctomys*		
Clades I and II	20.0%	5.7 mya ± 0.86 mya
Clades A and B	17.7%	5.1 mya ± 0.80 mya
Clades C and D	13.3%	3.8 mya ± 0.67 mya
Clades D and E	14.4%	4.1 mya ± 0.70 mya
Clades D and F	13.1%	3.7 mya ± 0.66 mya
Clades E and F	8.4%	2.4 mya ± 0.54 mya
Between other genera		
Tylomys and *Ototylomys*	21.3%	6.1 mya ± 0.90 mya
Xenomys and *Hodomys*	16.1%	4.6 mya ± 0.75 mya
Baiomys and *Scotinomys*	17.2%	4.9 mya ± 0.78 mya
Reithrodontomys and *Isthmomys*	18.0%	5.1 mya ± 0.80 mya

DISCUSSION

Phylogenetic analysis of *Cyt*b sequences arranged samples of *N. sumichrasti* into two major clades (Fig. 2). The first clade (I) contained samples of *N. sumichrasti* from western Mexico and Central America together with the sample of *Otonyctomys hatti*. The second clade (II) contained the two samples of *N. sumichrasti* from southern Mexico. The inclusion of the sample of *O. hatti* with the nine samples of *N. sumichrasti* produced a paraphyletic arrangement and inferred a heretofore unrecognized set of relationships among the samples of *Nyctomys*. In addition, levels of genetic divergence, as reflected by the genetic distance data (Table 1), document an unusually high level of differentiation among clades. Together, these data suggest that a reassessment of the taxonomy of *Nyctomys* relative to *Otonyctomys* is necessary. Although the geneology we recovered represents a gene tree and our sample size and geographic coverage is inadequate for a formal revision, several comments are appropriate.

Morphologically, specimens of *Nyctomys* are easily distinguishable from the monotypic *Otonyctomys*. *Otonyctomys* is smaller in the majority of cranial measurements, has much larger auditory bullae and a smaller maxillary toothrow (Anthony 1932; Genoways et al. 2005); therefore, placing *Otonyctomys* as a junior synonym of *Nyctomys* is inappropriate. On the other hand, the magnitude of genetic differentiation (Table 1) between the clades containing samples of *Nyctomys* and *Otonyctomys*, relative to other closely related genera of cricetid rodents, would support recognition of three genera: *Nyctomys* (members of clade II), *Otonyctomys*, and an unnamed genus (members of clade B). For example, levels of genetic divergence for comparisons of clades I and II (20.0%) and clades A and B (17.7%) were comparable for pair-wise values obtained from *Xenomys*/*Hodomys*, *Baiomys*/*Scotinomys*, *Reithrodontomys*/*Isthmomys*, and *Tylomys*/*Ototylomys* (ranged from 16.1% to 21.3%). Conversion of these distance

values into time since divergence estimates would place the origin of the unnamed genus in the late Miocene (~5.7 ± 0.86 mya), a date comparable to those of other Neotomine and Tylomyine genera (Table 1).

Regardless of generic relationships among clades representing *Nyctomys* and *Otonyctomys,* multiple species likely are included in what currently is recognized as *N. sumichrasti*. Depending on the species concept that is invoked (phylogenetic - Cracraft 1983; genetic - reviewed by Baker and Bradley 2006), it is possible to argue for the recognition of multiple species (perhaps as many as five) within the samples included in this study. Below, we follow the postulation of Baker and Bradley (2006) that genetic distance values > 5% (within the *Cytb* gene) exceed the average value for sister species of mammals, and as such, should be further evaluated in the context that they may represent separate species.

Clade I is comprised of three minor clades (D, E, and F) whose pair-wise distance values range from 8.4% to 14.4% (Table 1). The sample from Jalisco, Mexico (*N. s. colimensis*, clade D), occurs near sea level in tropical deciduous forests, is disjunct geographically from the remaining samples comprising clades E (Guatemala) and F (El Salvador, Honduras, and Nicaragua), and differs from them by 14.4% and 13.1%, respectively. Samples in clades E (*N. s. decolorus*) and F (*N. s. decolorus* and *N. s. florencei*) differ by 8.4%. This split between low elevation samples of *Nyctomys* is similar to the pattern recovered for *Alouatta* and *Marmosa mexicana* (Baumgarten and Williamson 2007; Gutiérrez et al. 2010) and likely involved the Maya highlands as a barrier to dispersal between taxa located in the Yucatan Peninsula and those found further south. Clade II is comprised of samples from Chiapas, Mexico (*N. s. salvini*) and Oaxaca, Mexico (*N. s. sumichrasti*), that differ by 10.2%. Both samples are from cloud forests, separated by the Isthmus of Tehuantepec. The Isthmus has been recognized as an effective vicariant barrier for other mid- to high-elevation rodent taxa (Sullivan et al. 1997, 2000; Carleton et al. 2002; Edwards and Bradley 2002; Arellano et al. 2005; León-Paniagua 2007; Rogers et al. 2007).

Given the complex geography of southern Mexico and Central America (see Almendra and Rogers 2012 for a recent summary), it is possible that multiple lowland and highland forms exist, especially given the influence of the many isolated mountain ranges. Also, given the history of the Isthmus of Tehuantepec that included climatic changes coupled with marine incursions (Beard et al. 1982; Toledo 1982), it is possible that multiple invasions (from north to south, or the reciprocal) have taken place. Resolving these issues will require thorough geographic sampling and should include the addition of samples representing a more thorough geographic coverage. In addition, inclusion of unrepresented subspecies, ideally material from type localities, is essential for determining the priority of available names in cases where taxa should be elevated to species.

ACKNOWLEDGMENTS

Fieldwork was funded in part by J. Sowell through the Natural Science Research Laboratory, Museum of Texas Tech University, and the Monte L. Bean Life Science Museum and the Office of Research and Creative Activities, Brigham Young University. Collecting permits were provided by the Consejo Nacional de Áreas Protegidas (CONAP), Guatemala, to N. Ordóñez-Garza. Permits for fieldwork in Mexico were issued by the Secretaria de Medio Ambiente, Recursos Naturales y Pesca (SEMARNAP) to F. X. González-Cózatl and F. A. Cervantes. We thank A. Almendra-Villalba, E. Arellano, A. Ferguson, F. X. González-Cózatl, R. Mercado, L. Siles for assisting with field work, as well as H. Garner, K. McDonald, R. J. Baker, and the staff at the NSRL for tissue loans. We also thank C. W. Thompson, E. K. Roberts, H. R. Huynh, and M. R. Mauldin for comments on earlier versions of this manuscript.

LITERATURE CITED

Almendra, A. L., and D. S. Rogers. 2012. Biogeography of Central American mammals: Patterns and processes. Pp. 203-229 in Bones, Clones and Biomes: The History and Geography of Recent Neotropical Mammals (B. D. Patterson and L. P. Costa, eds.). University of Chicago Press, Illinois.

Anthony, H. E. 1932. A new genus of rodents from Yucatán. American Museum Novitates 586:1-3.

Arbogast, B. S., and J. B. Slowinski. 1998. Pleistocene speciation and the mitochondrial DNA clock. Science 282:1955a.

Arellano E., F. X. González-Cozátl, and D. S. Rogers. 2005. Molecular systematics of Middle American harvest mice *Reithrodontomys* (Muridae), estimated from mitochondrial Cytochrome *b* gene sequences. Molecular Phylogenetics and Evolution 37:52-540.

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

Baumgarten, A., and G. B. Williamson. 2007. The distributions of howling monkeys (*Alouatta pigra* and *A. palliata*) in southeastern Mexico and Central America. Primates 48:310-315.

Beard, J. H., J. B. Sangree, and L. A. Smith. 1982. Quaternary chronology, paleoclimate, depositional sequences, and eustatic cycles. American Association of Petroleum Geologists Bulletin 66:158-169.

Bradley, R. D., and J. Ensink. 1987. Karyotypes of five cricetid rodents from Honduras. Texas Journal of Science 39:171-175.

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.

Carleton, M. D., O. Sánchez, and G. Urbano-Vidales. 2002. A new species of *Habromys* (Muroidea: Noetominae) from México, with generic review of species definitions and remarks on diversity patterns among Mesoamerican small mammals restricted to humid montane forests. Proceedings of the Biological Society of Washington 115:488-533.

Cervantes, F. A., J. Nahú Ramírez-Vite, S. Ramírez-Vite, and C. Ballesteros. 2004. New records of mammals from Hidalgo and Guerrero, Mexico. The Southwestern Naturalist 49:122-124.

Cracraft, J. 1983. Species concepts and speciation analyses. Pp. 159-187 in Current Ornithology (R. F. Johnston, ed.). Vol. 1. Plenum Press, New York.

De Saussure, M. H. 1860. Note sur quelques mammiferes du Mexique par M. H. De Saussure. Revue Et Magasin de Zoologie Pure Et Appliquee. Series 2 Volume 12: 97-110.

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

Emmons, L. H. 1997. Neotropical rainforest mammals: A field guide. University of Chicago Press, Illinois.

Genoways, H. H., R. M. Timm, and M. D. Engstrom. 2005. Natural history and karyology of the Yucatán vesper mouse, *Otonyctomys hatti*. Pp. 213-218 in Contribuciones Mastozoológicas en Homenaje a Bernardo Villa-R (V. Sánchez-Cordero and R. A. Medellín, eds.). Instituto de Biología e Instituto de Ecología, UNAM; CONABIO, México.

Gutiérrez, E. E., S. A. Jansa, and R. S. Voss. 2010. Molecular systematics of mouse opossums (Didelphidae: Marmosa): Assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. American Museum Novitates 3692:1-22.

Haiduk, M. W., C. Sanchez-Hernandez, and R. J. Baker. 1988. Phylogenetic relationships of *Nyctomys* and *Xenomys* to other cricetine genera from G-banded chromosomes. The Southwestern Naturalist 33:397-403.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York.

Huelsenbeck, J. P., and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17:754-755.

Hunt, J. L., J. E. Morris, and T. L. Best. 2004. Nyctomys sumichrasti. Mammalian Species 754:1-6.

Irwin, D. M., T. D. Kocher, and A. C. Wilson. 1991. Evolution of the cytochrome *b* gene in mammals. Journal of Molecular Evolution 2:37-55.

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.

Lee, M. R., and F. F. B. Elder. 1977. Karyotypes of eight species of Mexican rodents (Muridae). Journal of Mammalogy 58:479-487.

León-Paniagua, L., G. Navarro-Sigüenza, B. E. Hernández-Baños, and J. C. Morales. 2007. Diversification of the arboreal mice of the genus *Habromys* (Rodentia: Cricetidae: Neotominae) in the Mesoamerican highlands. Molecular Phylogenetics and Evolution 42:653-664.

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

Musser, G. M., 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.). Third edition. The Johns Hopkins University Press, Baltimore, Maryland.

Palumbi, S. R. 1996. Nucleic acids I: The polymerase chain reaction. Pp. 205-247 in Molecular Systematics (D. M. Hillis, C. Moritz, and B. K. Mable, eds.). Second edition. Sinauer, Sunderland, Massachusetts.

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

Peppers, L. L., D. S. Carroll, and R. D. Bradley. 2002. Molecular systematics of the genus *Sigmodon* (Rodentia: Muridae): Evidence from the mitochondrial cytochrome *b* gene. Journal of Mammalogy 83:396-407.

Posada, D., and K. A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14:817-818.

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., D. S. Carroll, C. W. Edwards, 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.

Reeder, S. A., and R. D. Bradley. 2007. Phylogenetic relationships of neotomine-peromyscine rodents using DNA sequences from intron 7 of the beta fibrinogen gene. 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, Berkeley.

Reid, F. A. 2009. A field guide to the mammals of Central America and Southeast Mexico. Second edition. Oxford University Press, New York.

Rogers, D. S., C. C. Funk, J. R. Miller, and M. D. Engstrom. 2007. Molecular phylogenetic relationships among crested-tailed mice (genus *Habromys*). Journal of Mammalian Evolution 14:37-55.

Saiki, R. K., et al. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science 239:487-491.

Sánchez-Hernández, C., M. de Lourdes Roméro-Almaraz, R. D. Owen, A. Núñez-Garduño, and R. López-Wilchis. 1999. Noteworthy records of mammals from Michoacán, México. The Southwestern Naturalist 44:231-235.

Smith, M. F., and J. L. Patton. 1993. The diversification of South American rodents: Evidence from mitochondrial sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149-177.

Sullivan, 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, J., E. Arellano, and D. S. Rogers. 2000. Comparative phylogeography of Mesoamerican highland rodents: Concerted versus independent response to past climatic fluctuations. The American Naturalist 155:755-768.

The Mathworks, Inc. 2006. MATLAB® version 6.5. http://www.mathworks.com/company.

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.

Timm, R. M., and R. K. LaVal. 2000. Mammals. Pp. 223-244 in Monteverde: Ecology and Conservation of a Tropical Cloud Forest (N. M. Nadkarni and N. T. Wheelwright, eds.). Oxford University Press, New York.

Toledo, V. M. 1982. Pleistocene changes of vegetation in tropical Mexico. Pp. 93-111 in Biological Diversification in the Tropics (G. T. Prance, ed.). Columbia University Press, New York.

Whiting, A. S., A. M. Bauer, and J. W. Sites, Jr. 2003. Phylogenetic relationships and limb loss in sub-Saharan African scincines (Squamata: Scincidae). Molecular Phylogenetics and Evolution 29:582-598.

Addresses of authors:

MEGAN S. CORLEY

Department of Biological Sciences
Texas Tech University
Lubbock, Texas 79409-3131
megan.corley@ttu.edu

NICTÉ ORDÓÑEZ-GARZA

Department of Biological Sciences
Texas Tech University
Lubbock, Texas 79409-3131
nicte.ordonez-garza@ttu.edu

DUKE S. ROGERS

Department of Biology and
Monte L. Bean Life Science Museum
Brigham Young University
Provo, Utah 84602
duke_rogers@byu.edu

ROBERT D. BRADLEY

Department of Biological Sciences and
Natural Science Research Laboratory, The Museum
Texas Tech University
Lubbock, Texas 79409-3131
robert.bradley@ttu.edu

Editor for this manuscript was Robert J. Baker.

APPENDIX

Specimens from which the cytochrome-*b* gene was sequenced are listed below with: locality information, museum voucher numbers, collection or tissue number, and GenBank accession numbers. The remaining sequences were obtained from GenBank (sequences generated in previous studies) and are listed by GenBank accession number.

Nyctomys sumichrasti colimensis.—MEXICO: Jalisco; 6 km SE Chamela, UNAM Estacíon de Biología (Locality 1, TTU37743, TK19590, JQ183066).

Nyctomys sumichrasti decolorus.—GUATEMALA: Petén; San Jose; Límite Oeste Biotopo San Miguel La Palotada-El Zotz, 17.17241ºN, 89.88585ºW, elev = 215 m (Locality 3, TTU115406, TK169284, JN851816). HONDURAS: Atlantida; Lancetilla Botanical Garden (Locality 4, TTU84484, TK101827, AF195801).

Nyctomys sumichrasti florencei.—EL SALVAOR: La Paz; about 3 mi NW San Luis Talpa (Locality 5, TTU111528, TK34799, JQ183063; TTU111529, TK34801, JQ183064). NICARAGUA: Chinandega; Chichigalpa, Belle Vista (Locality 6, TTU105094, TK113517, JQ183061); Atlantico Norte; Siuna, El Balsamo (Locality 7, TTU100336, TK121424, JQ183062).

Nyctomys sumichrasti salvini.—MEXICO: Chiapas; Municipio Chamela, Cerro Tzontehuitz, 13 km NE San Cristóbal de las Casas, 2,880 m (Locality 8, BYU14466, DSR4226, JQ183065).

Nyctomys sumichrasti sumichrasti.—MEXICO: Oaxaca; Distrito Ixtlán, 28 km SW (by road) La Esperanza, 17°35'08"N, 96°30'41"W, 2,950 m (Locality 9, CMC101, DSR5788, JQ183067).

Reference samples obtained from GenBank:

Neotominae.—*Baiomys taylori* (AF548469), *Scotinomys teguina* (JN851815), *Hodomys alleni* (AF186801), *Xenomys nelsoni* (AF307838), *Neotoma mexicana* (AF294345), *Ochrotomys nutalli* (AY195798), *Onychomys arenicola* (AY195793), *Reithrodontomys fulvescens* (AF176257), *Isthmomys pirrensis* (FJ214681), *Habromys ixtlani* (DQ973099), *Neotomodon alstoni* (AY195796), *Megadontomys thomasi* (AY195795), *Podomys floridanus* (EF989977), *Osgoodomys banderanus* (DQ000473), *Peromyscus californicus* (AF155393), and *Peromyscus maniculatus* (AY322503).

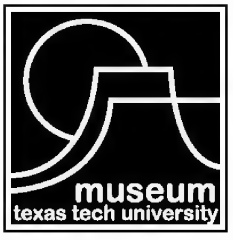
Tylomyinae.—*Otonyctomys hatti* (JQ183060), *Tylomys nudicaudus* (AF307839), and *Ototylomys phyllotis* (AY009789).

Sigmodontinae.—*Oryzomys palustris* (DQ185382) and *Sigmodon hispidus* (AF155420).

Publications of the Museum of Texas Tech University

Institutional subscriptions to Occasional Papers are available through the Museum of Texas Tech University, attn: NSRL Publications Secretary, Box 43191, Lubbock, TX 79409-3191. Individuals may also purchase separate numbers of the Occasional Papers directly from the Museum of Texas Tech University.

Series Editor: Robert J. Baker
Production Editor: Lisa Bradley



ISSN 0149-175X

Museum of Texas Tech University, Lubbock, TX 79409-3191