PHYLOGENETICS AND BIOGEOGRAPHY OF MOUSE OPOSSUMS (DIDELPHIDAE: *MARMOSA*)

By

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Abstract

PHYLOGENETICS AND BIOGEOGRAPHY OF MOUSE OPOSSUMS

(DIDELPHIDAE: *MARMOSA*)

By

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Advisor: Dr. Robert P. Anderson

This research focused on the systematics and biogeography of mouse opossums of the genus *Marmosa* (Mammalia: Didelphimorphia: Didelphidae), with special emphasis on species found in the complicated geography of north-central South America. Via the four chapters of this dissertation, I presented information obtained through fieldwork, examination of museum specimens, DNA sequencing, phylogenetic analyses, georeferencing (including consultation of field notes and collectors), and ecological niche modeling. In Chapter 1, I conducted phylogenetic analyses of species of *Marmosa* based on sequence data of the mitochondrial cytochrome-*b* gene (CYTB), in part to test the monophyly of species previously recognized based on morphological criteria. This study revealed the existence of unrecognized species and identified novel interspecific relationships. All trans-Andean species of the subgenus *Marmosa* were recovered as a clade, suggesting that the uplift of the Andes might have played an important role in the diversification of the genus. In Chapter 2, I documented the presence of *M. waterhousei* in the Venezuelan Andes. This finding implied that the species might have crossed the dry Depresión del Táchira during a glacial period. In Chapter 3, I investigated the

phylogeography of *M. robinsoni*, a species predominately distributed across the dry forests of northern South America. I conducted phylogenetic analyses based on sequence data of one mitochondrial and one nuclear gene. The results confirmed the monophyly of a dry-forest clade formed by *M. robinsoni* and *M. xerophila* and showed the existence of two major clades within *M. robinsoni* that corresponded roughly to an east/west division. Results of ancestral area reconstructions identified multiple dispersal events out of the greater Maracaibo basin. Lastly, in Chapter 4 I used ecological niche modeling to test the geographic predictions of competition between a sister species pair, *M. robinsoni* and *M. xerophila.* The results strongly suggest that *M. xerophila* may isolate populations of *M. robinsoni* in the Península de Paraguaná of northern Venezuela—representing a novel example of geographic isolation caused by competition. Together, these studies contributed to a better understanding of the taxonomy, phylogenetics, and biogeography of the genus *Marmosa*; provide novel information relevant to the biogeography of dry-forest species in northwestern South America; and propose a refinement of the concept of ecological vicariance to incorporate the possibility that biotic interactions could lead to geographic isolation.

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PREFACE

In this dissertation, I investigated phylogenetic and biogeographic aspects of a diverse, widespread group of Neotropical marsupials, the genus *Marmosa*. When I started the CUNY Ph.D. program, I was interested in conducting revisionary taxonomic work and learning how to generate and analyze molecular data for systematic research. Shortly afterwards, I became fascinated with the tremendous power of ecological niche modeling in many areas of research, in particular systematics and biogeography. With extensive advice from my mentor, Robert Anderson, I designed a dissertation that would allow me to gain experience using all of these methodological tools to address questions that I found exciting. Activities necessary to accomplish objectives of the dissertation included fieldwork, examination of museum specimens, DNA sequencing, phylogenetic analyses, exhaustive georeferencing (including consultation of field notes and collectors), and cutting-edge ecological niche modeling.

In this dissertation, I addressed questions at various taxonomic levels of mouse opossums (Mammalia: Didelphimorphia: Didelphidae) of the genus *Marmosa*, with special emphasis on the species found in the complicated geography of north-central South America. In Chapter 1, I conducted phylogenetic analyses based on the mitochondrial cytochrome-*b* gene, in part to test the monophyly of species previously recognized based on morphological criteria. In Chapter 2, I documented for the first time the presence of *M. waterhousei* in the Venezuelan Andes and discussed the biogeographic implications of this finding. In Chapter 3, I conducted a phylogeographic study on *M. robinsoni*, a species widely distributed in both the cis- and trans-Andean regions of northern South America, and for which moderately high levels of sequence divergence were revealed in Chapter 1. Lastly, in Chapter 4, I employed ecological niche modeling to test the geographic predictions of competition between a pair of sister species—*M.*

robinsoni and *M. xerophila*—and explored the possibility that this putative biotic interaction may have created, or at least maintained, geographic isolation among populations of the former. Together, the chapters in this dissertation contribute to a better understanding of the systematics and biogeography of the genus *Marmosa*, and provide novel information relevant to the biogeography dry-forest species in northwestern South America. In addition, this dissertation provides insights on the mechanisms that might promote ecological vicariance, with important implications for several fields within evolutionary biology. Although I led the work necessary to address each of the objectives of this research, and actively worked in all aspects of it, collaboration with several colleagues was key for me to learn and accomplish all of the aims.

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Molecular systematics of mouse opossums (Didelphidae: *Marmosa*): assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography

(Adapted from Gutiérrez EE, Jansa SA, and Voss RS. 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).

INTRODUCTION

Species of the didelphid marsupial genus *Marmosa* inhabit tropical and subtropical vegetation from Mexico to northern Argentina, including such diverse habitats as xerophytic thorn scrub, savannas, lowland rain forests, and humid-montane ("cloud") forests from sea level to about 3000 meters (Creighton and Gardner, 2008). As currently understood (Voss and Jansa, 2009), the genus contains 15 species, of which nine are referred to the paraphyletic subgenus *Marmosa* Gray, 1821, and six to the monophyletic subgenus *Micoureus* Lesson, 1842. By virtue of its wide ecogeographic range, the genus is of exceptional biogeographic interest, but effective analysis of distributional patterns is prevented by a host of taxonomic problems, not the least of which concerns species delimitation.

Tate (1933) recognized ten species referable to the subgenus *Marmosa* (sensu Voss and Jansa, 2009), which he organized into "sections" based on subjectively inferred relationships (Table 1). Subsequently, Hershkovitz (1951) synonymized all of the taxa in Tate's Mitis Section (for which the oldest available name is *robinsoni*; Cabrera, 1958), and new species were later described by Pine (1972) and Handley and Gordon (1979). As a result, recent taxonomic synopses (Gardner, 2005; Creighton and Gardner, 2008; Voss and Jansa, 2009) have recognized nine species: *M. andersoni*, *M. lepida, M. mexicana*, *M. murina*, *M. quichua*, *M. robinsoni*, *M. rubra*, *M. tyleriana*, and *M. xerophila*. Despite such consensus, several of these species have improbably wide geographic distributions (e.g., *M. mexicana*, *M. murina*, and *M. robinsoni*), and previously published analyses of mitochondrial gene sequences suggest that at least some include genetically divergent forms (Steiner and Catzeflis, 2003, 2004; Patton and Costa, 2003).

In a recent revisionary study, Rossi (2005) recognized 14 valid species in the nominotypical subgenus of *Marmosa*. Based on his examination of approximately 2500 specimens (including most of the relevant type material), he resurrected five species that had previously been treated as junior synonyms or subspecies: *M. simonsi* and *M. isthmica* (formerly synonymized with *M. robinsoni*); *M. zeledoni* (formerly synonymized with *M. mexicana*); and *M. tobagi* and *M. waterhousei* (formerly synonymized with *M. murina*)[1]. Although Rossi's unpublished results (summarized, in part, by Rossi *et al.*, 2010) are compellingly supported by morphometric analyses and by qualitative characters of the integument, skull, and dentition, his proposed taxonomy (Table 1) remains to be tested with molecular data.

Herein we report phylogenetic analyses of DNA sequences from the mitochondrial cytochrome-*b* gene representing most of the species recognized by Rossi (2005) in the subgenus *Marmosa* as well as several species of the subgenus *Micoureus*. These data provide a basis for testing the monophyly of Rossi's morphologically defined species, and they afford an opportunity to infer phylogenetic relationships among the majority of species currently referred to the genus. Although our results include novel insights concerning biogeography and subgeneric classification, we defer formal treatment of these topics to future reports that will incorporate additional sequence data from other genes.

MATERIALS AND METHODS

SOURCE OF MATERIAL: Except as noted, all voucher specimens and associated tissues are preserved in the following collections (listed alphabetically by institutional abbreviation):

[1] Rossi (2005) additionally suggested that *macrotarsus* Wagner, 1842, is the oldest available name for the species formerly known as *quichua* Thomas, 1899. Contra Creighton and Gardner (2008), *macrotarsus* Wagner, 1842, is not preoccupied by *macrotarsos* Schreber, 1777 (a

AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); CM, Carnegie Museum of Natural History (Pittsburg); EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquizas da Amazônia (Manaus); ISEM, Institut des Sciences de l'Evolution de Montpellier (Montpellier); LSUMZ, Louisiana State University, Museum of Natural Science (Baton Rouge); MHNG, Muséum d'Histoire Naturelle de Genève (Geneva); MNK, Museo de Historia Natural Noel Kempff Mercado (Santa Cruz); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); ROM, Royal Ontario Museum (Toronto); T-, tissue collection of the Laboratoire de Paleontologie at the Institut des Sciences de l'Evolution de Montpellier (ISEM; Montpellier); TTU, Museum of Texas Tech University (Lubbock); UFMG, Universidade Federal de Minas Gerais (Belo Horizonte); UMSNH, Universidad Michoacana de San Nicolas de Hidalgo (Morelia); USNM, United States National Museum of Natural History (Washington); V-, voucher collection of Francois M. Catzeflis (currently at ISEM, these specimens will eventually be deposited either at the Muséum National d'Histoire Naturelle [Paris] or at MHNG; F. M. Catzeflis, in litt).

TAXON SAMPLING: Our taxonomic sample (Table 2) includes 71 individuals representing 12 of the 14 species of *Marmosa* (*Marmosa*) recognized by Rossi (2005) together with four of the six currently recognized species of the subgenus *Micoureus*. We were unable to obtain samples of *Marmosa* (*M.*) *andersoni*, *M.* (*M.*) *tobagi*, *M.* (*Mi.*) *alstoni,* or *M.* (*Mi.*) *phaea* for this study. Among other didelphid genera, *Tlacuatzin* and *Monodelphis* have been identified as

Table 1. Species of *Marmosa* (subgenus *Marmosa*) recognized as valid by authors[a]

Tate (1933)[b]	Gardner (2005)[c]	Rossi (2005)
Murina Section	*M. andersoni*[d]	*M. mexicana*
M. murina	*M. lepida*	*M. zeledoni*[g]
M. rubra	*M. mexicana*	*M. isthmica*[h]
M. tyleriana	*M. murina*	*M. robinsoni*
M. quichua	*M. quichua*	*M. simonsi*[h]
Mitis Section	*M. robinsoni*[e]	*M. xerophila*
M. mitis	*M. rubra*	*M. rubra*
M. chapmani	*M. tyleriana*	*M. andersoni*
M. simonsi	*M. xerophila*[f]	*M. tyleriana*
M. ruatanica		*M. lepida*
Mexicana Section		*M. murina*
M. mexicana		*M. macrotarsus*[i, j]
Lepida Section		*M. waterhousei*[i]
M. lepida		*M. tobagi*[i]

[a] Only taxa referable to the nominotypical subgenus (as recognized by Voss and Jansa, 2009) are listed. Taxa are listed in the same order as in the cited works.

[b] Note that species were organized by "sections" within Tate's (1933) system.

[c] Also the taxonomy followed by Creighton and Gardner (2008) and Voss and Jansa (2009). Names are used in the same sense as by Tate (1933) except as noted otherwise.

[d] Described by Pine (1972).

[e] Senior synonym of *mitis*. Includes *chapmani*, *simonsi*, and *ruatanica* (after Hershkovitz, 1951).

[f] Described by Handley and Gordon (1979).

[g] Formerly included in *M. mexicana.*

[h] Formerly included in *M. robinsoni* (sensu Gardner, 2005).

[i] Formerly included in *M. murina*.

[j] Includes *quichua*.

phylogenetically closest to *Marmosa* (e.g., by Voss and Jansa [2009] and references cited therein); therefore, we used sequences from two individuals of *Tlacuatzin canescens* and one of *Monodelphis brevicaudata* as outgroups to root our trees.

Within each recognized species of *Marmosa* (*Marmosa*), we chose individuals to represent as many nominal taxa (subspecies or subjective synonyms) and regions of vertebrate endemism (Müller, 1973; Cracraft, 1985) as available tissue resources would allow (Figure 1). For the majority of our samples (60 out of 71), we extracted high-molecular-weight DNA from field-preserved tissues. We extracted relatively poor-quality DNA from museum skins of five individuals (two of *M. tyleriana*, and one each of *M. rubra*, *M. zeledoni*, and *M. xerophila*), and we obtained six additional sequences from GenBank: three of *M. murina* (AJ486984, AJ486990, AJ486995), two of *M. demerarae* (AJ487005, AJ487006), and one of *M. mexicana* (AJ606454). After removing identical haplotypes, our phylogenetic analyses were based on a matrix that included cytochrome-*b* sequences from 66 individuals.

Although many sequences identified as *Marmosa murina* are available in GenBank, most of them are from localities on the Guiana Shield, where there is very little genetic variation and apparently no phylogeographic structure (Steiner and Catzeflis, 2003, 2004); therefore, we included only three (all from French Guiana) in our study. Two other GenBank sequences reported as *M. murina* in previous studies are from Peru and correspond to *M. macrotarsus* (sensu Rossi, 2005). We resequenced the tissues from which these published sequences were obtained and found several discrepancies. For example, our sequence of AMNH 272816 should be identical to GenBank accession number AJ487003, but these differ in an A/C mutation at position 783 (as numbered from the start codon). Additionally, our sequence of AMNH 272870 was generated from the same specimen as GenBank accession AJ487002, but the two differ at

four sites (59 A/G, 246 C/T, 813 G/A, 819 T/C). Our sequences, which were generated from at least two strands, are unambiguous at these sites. Any number of reasons, including error incorporated by Taq polymerase, could explain such differences. However, because we do not have the original chromatograms from the GenBank reports, we used the sequences generated in our lab from these specimens.

LABORATORY METHODS: Genomic DNA was extracted from all samples using DNeasy extraction kits (Qiagen, Inc.). Whenever possible, we amplified the entire cytochrome-*b* gene using primers CYTB-F1 and CYTB-R1 (Table 3) located in the flanking tRNAs. To generate fragments of a suitable size for sequencing, we used this PCR product in two separate reamplification reactions, one using primer CYTB-F1 paired with CYTB-730R and one using either CYTB-540F or CYTB-650F paired with CYTB-R1. In cases where we extracted poor-quality DNA from skin samples (two samples of *Marmosa tyleriana* and one each of *M. xerophila*, *M. zeledoni,* and *M. rubra*), we generated a short (~400 bp) PCR product using CYTB-F1 paired with CYTB-420R and sequenced it directly using amplification primers.

Initial PCR amplifications using genomic DNA as a template were performed in 20 μL reactions using GoTaq DNA polymerase (Promega Corp.) and recommended concentrations of primers, unincorporated nucleotides, buffer, and $MgCl_2$. These reactions were performed in a four-stage touchdown protocol. The first stage consisted of 5 cycles of denaturation at 95°C for 20 seconds, annealing at 59°C for 20 seconds, and extension at 72°C for 30 seconds. The second and third stages were identical to the first except for lowered annealing temperatures of 57°C and 55°C, respectively. The final stage consisted of 25 cycles with an annealing temperature of 52°C. Subsequent reamplification reactions using this product as a template consisted of a single stage of 25 cycles of denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, and

extension at 72°C for 1 minute. All reactions were preceded by an initial denaturation at 95°C for 2 minutes and followed by a 7-minute extension at 72°C.

Gene fragments were sequenced in both directions using amplification primers and ABI BigDye version 3.1 terminator chemistry (Applied Biosystems, Inc.). Reactions were run on either an ABI 3130xl or ABI 3730xl capillary sequencer. Sequences were edited and compiled using Sequencher version 4.8 (Gene Codes Corporation, 2007). All sequences, along with their specimen voucher numbers, have been deposited in GenBank with accession numbers HM106338–HM106402.

ANALYTICAL METHODS: We performed multiple sequence alignment in Clustal X version 2.0 (Larkin *et al.*, 2007) and adjusted the resulting alignment with reference to translated amino-acid sequences. We used maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) to analyze the resulting data matrix; missing bases were coded as unknown for all phylogenetic analyses. To assess nodal support, we used nonparametric bootstrapping (Felsenstein, 1985) for the MP and ML analyses and nodal posterior probability estimates for the BI analysis (Ronquist and Huelsenbeck, 2003). Parsimony analyses were performed in PAUP* 4.0b10 (Swofford, 2002) using equal weighting and the heuristic search option with 1000 replicate searches, 10 random-addition replicates, and tree bisection-reconnection (TBR) branch swapping. Maximum-parsimony bootstrap analyses were performed in PAUP* using 1000 pseudodoreplicated data matrices, each with 5 random-addition sequences and TBR branch-swapping. To determine the appropriate model of evolution for ML and BI analyses, we considered both hierarchical likelihood-ratio tests (hLRT) and the Akaike information criterion (AIC) as implemented in ModelTest v. 3.7 (Posada and Crandall, 1998) and PAUP* (Swofford, 2002). For ML analyses, we performed 20 independent searches in GARLI 0.96 beta (Zwickl,

2006) using the default settings. Maximum-likelihood bootstrap analyses were performed in GARLI 0.96 beta using 100 pseudoreplicated data matrices, with 10 searches performed on each. Bayesian analyses were performed using the Markov Chain Monte Carlo (MCMC) sampling approach in MrBayes v. 3.1.2 (Huelsenbeck and Ronquist, 2001; Altekar *et al.*, 2004; Ronquist *et al.*, 2005) through the Computational Biology Service Unit from Cornell University (http://cbsuapps.tc.cornell.edu/mrbayes.aspx). The search started with a random tree, and consisted of one cold chain and three heated chains (temperature = 0.2) and default priors. The Markov chains were run for $1x10^6$ generations, and trees were sampled every 1000 generations. Default values were kept for the "relburnin" and "burninfrac" options in MrBayes (i.e., relburnin = yes and burninfrac = 0.25); therefore, the first 250,000 generations (250 trees) were discarded as burn-in, and posterior probability estimates of all model parameters were based on the remaining (750) trees.

To estimate genetic divergence, we calculated average uncorrected (p) distance within each species and average pairwise p distances among species. In addition, we report K2P-corrected distances for interspecific comparisons. These model-corrected statistics are the traditional metric for genetic divergence in the didelphid literature (e.g., Patton *et al.*, 2000; Patton and Costa, 2003), so we computed them to allow comparisons with values reported in previous studies. All distances were calculated using MEGA version 4 (Tamura *et al.*, 2007).

Table 2. Sequenced specimens of ingroup and outgroup taxa.

Taxon	Tissue/DNA#[a]	Voucher[b]	Locality[c]	bp[d]
Ingroup				
M. (*Marmosa*) *isthmica*	TK 135686	TTU 102969	Ecuador: Esmeraldas (17)	1145
M. (*Marmosa*) *isthmica*	FMG 2716	USNM 575395[e]	Panama: Bocas del Toro (37)	1140
M. (*Marmosa*) *isthmica*	FMG 2736	USNM 575397[e]	Panama: Bocas del Toro (37)	1146
M. (*Marmosa*) *isthmica*	TK 22555	TTU 39118[e]	Panama: Darién (39)	1146
M. (*Marmosa*) *lepida*	F 38809	ROM 107034[e]	Guyana: Potaro-Siparuni (30)	1146
M. (Marmosa) lepida	JLP 7844	MVZ 155245[e]	Peru: Amazonas (42)	1146
M. (Marmosa) lepida	DWF 717	AMNH 273186[e]	Peru: Loreto (46)	1146
M. (Marmosa) macrotarsus	LHE 1516	USNM 584462[e]	Bolivia: Santa Cruz (3)	797
M. (Marmosa) macrotarsus	LHE 1548	MNK [uncataloged]	Bolivia: Santa Cruz (3)	1146
M. (Marmosa) macrotarsus	JRM 202	MVZ 191187[f]	Brazil: Amazonas (5)	1146
M. (Marmosa) macrotarsus	MNFS 746	INPA 2912[f]	Brazil: Amazonas (6)	1087
M. (Marmosa) macrotarsus	JRM 450	INPA 2911[f]	Brazil: Amazonas (9)	1146
M. (Marmosa) macrotarsus	RSV 2303	AMNH 272816[e]	Peru: Loreto (46)	1146

Table 2. continued.

M. (Marmosa) macrotarsus	RSV 2413	AMNH 272870[e]	Peru: Loreto (46)	860
M. (Marmosa) mexicana A	MHNG 1812007	MHNG 1812007	Belize: Corozal (1)	800[i]
M. (Marmosa) mexicana A	FN 32277	ROM 99608[e]	Guatemala: El Petén (26)	1146
M. (Marmosa) mexicana A	FN 34135	ROM 99776[e]	Guatemala: El Progreso (27)	1146
M. (Marmosa) mexicana A	FN 30771	ROM 96968[e]	Mexico: Campeche (31)	1146
M. (Marmosa) mexicana A	FN 30134	ROM 96318[e]	Mexico: Campeche (32)	1145
M. (Marmosa) mexicana A	FN 29881	ROM 96090[e]	Mexico: Campeche (34)	1144
M. (Marmosa) mexicana A	FN 29586	ROM 95795[e]	Mexico: Campeche (33)	1146
M. (Marmosa) mexicana B	JOM 7269	USNM 569858[e]	Guatemala: Alta Verapaz (24)	1087
M. (Marmosa) mexicana B	FN 31448	ROM 98459[e]	Guatemala: Baja Verapaz (25)	1146
M. (Marmosa) mexicana B	WB 8515	USNM 570071[e]	Guatemala: Zacapa (28)	1146
M. (Marmosa) murina	LPC 436	MVZ 197421[f]	Brazil: Mato Grosso (11)	1146
M. (Marmosa) murina	JLP 16986	UFMG 2599[f]	Brazil: Mato Grosso do Sul (10)	1146
M. (Marmosa) murina	LHE 503	USNM 549291[e]	Brazil: Pará (12)	1146
M. (Marmosa) murina	LHE 582	USNM 549292[e]	Brazil: Pará (12)	1146
M. (Marmosa) murina	LPC 715	MVZ 197433[f]	Brazil: Tocantins (14)	1092

Table 2. continued.

M. (Marmosa) murina	T 2704	MHNG 1885048	French Guiana: Cayenne (21)	820[i]
M. (Marmosa) murina	T 2084	V-909[g]	French Guiana: Cayenne (22)	820[i]
M. (Marmosa) murina	T 2471	V-1206[g]	French Guiana: Cayenne (23)	820[i]
M. (Marmosa) murina	F 50629	ROM 113649[e]	Guyana: Demerara-Mahaica (29)	1146
M. (Marmosa) murina	F 41351	ROM 114321[h]	Surinam: Brokopondo (47)	770
M. (Marmosa) murina	TK 17359	CM 68346[e]	Surinam: Para (49)	1146
M. (Marmosa) murina	TK 17387	CM 68353[e]	Surinam: Para (49)	1146
M. (Marmosa) robinsoni	NK 101529	MSB 94363[e]	Panama: Los Santos (40)	1146
M. (Marmosa) robinsoni	NK 101606	MSB 94366[e]	Panama: Los Santos (40)	1146
M. (Marmosa) robinsoni	NK 101633	MSB 94368[e]	Panama: Veraguas (41)	1146
M. (Marmosa) robinsoni	NK 101634	MSB 94369[e]	Panama: Veraguas (41)	1146
M. (Marmosa) robinsoni	RPA 262	EBRG 25389[e]	Venezuela: Falcón (52)	1146
M. (Marmosa) rubra	F 54196	ROM 118744[e]	Ecuador: Orellana (20)	1146
M. (Marmosa) rubra	—	FMNH 84253[e]	Peru: Cusco (43)	402
M. (Marmosa) simonsi	NK 37836	MSB 87086[e]	Ecuador: El Oro (16)	1146
M. (Marmosa) simonsi	NK 37837	MSB 87087[e]	Ecuador: El Oro (16)	1146

Table 2. continued.

M. (Marmosa) simonsi	TK 134911	TTU 103308[e]	Ecuador: Guayas (18)	1146
M. (Marmosa) tyleriana	—	AMNH 130510[e]	Venezuela: Bolívar (50)	398
M. (Marmosa) tyleriana	—	AMNH 130511[e]	Venezuela: Bolívar (50)	399
M. (Marmosa) waterhousei	F 40140	ROM 105889[e]	Ecuador: Orellana (19)	1146
M. (Marmosa) waterhousei	F 37580	ROM 105257[e]	Ecuador: Orellana (20)	727
M. (Marmosa) waterhousei	JLP 7480	MVZ 154754[e]	Peru: Amazonas (42)	726
M. (Marmosa) waterhousei	TK 73294	TTU 98717[e]	Peru: Loreto (44)	1146
M. (Marmosa) waterhousei	TK 73276	TTU 100922[e]	Peru: Loreto (44)	1050
M. (Marmosa) waterhousei	JMC 88	LSU 28017[e]	Peru: Loreto (45)	1146
M. (Marmosa) xerophila	—	USNM 443814[e]	Colombia: La Guajira (15)	402
M. (Marmosa) xerophila	RPA 315	AMNH 276582[e]	Venezuela: Falcón (51)	1146
M. (Marmosa) xerophila	RPA 324	AMNH 276586	Venezuela: Falcón (51)	1146
M. (Marmosa) zeledoni	—	AMNH 269997[e]	Panama: Chiriquí (38)	402
M. (Micoureus) constantiae	NK 15501	MSB 59883[e]	Bolivia: Santa Cruz (2)	1146
M. (Micoureus) constantiae	NK 23272	AMNH 275466[e]	Bolivia: Santa Cruz (4)	1146
M. (Micoureus) demerarae	T 2006	V-972	French Guiana: Cayenne (22)	820[i]

Table 2. continued.

M. (Micoureus) demerarae	T 2083	V-884[e]	French Guiana: Cayenne (22)	820[i]
M. (Micoureus) demerarae	RSV 2029	AMNH 272667[e]	Peru: Loreto (46)	1146
M. (Micoureus) demerarae	RSV 2085	MUSM 13294[e]	Peru: Loreto (46)	1146
M. (Micoureus) paraguayana	MAM 46	MVZ 182064[e]	Brazil: São Paulo (13)	1146
M. (Micoureus) paraguayana	MAM 47	MVZ 182065[e]	Brazil: São Paulo (13)	1146
M. (Micoureus) regina	JLP 15435	MVZ 190323[e]	Brazil: Amazonas (7)	1146
M. (Micoureus) regina	MNFS 1232	MVZ 190332[e]	Brazil: Amazonas (8)	402
Outgroups				
Monodelphis brevicaudata	TK 17069	CM 68359[e]	Surinam: Nickerie (48)	1146
Tlacuatzin canescens	TK 11826	TTU 37700[e]	Mexico: Jalisco (35)	1146
Tlacuatzin canescens	TK 45085	UMSNH 2993[e]	Mexico: Michoacán (36)	1146

[a] Alphanumeric identifiers used by institutional tissue collections (and to label terminals in accompanying trees; Figures 2, 3). Sequences amplified from morphological specimens lack tissue/DNA numbers.
[b] See Materials and Methods for names of museum collections identified by acronyms in this table.
[c] Country and next-largest administrative unit (state, department, province, etc). Numbers in parentheses refer to gazetteer entries (Appendix 1), which provide additional geographic information.
[d] Number of base pairs sequenced. All sequences were obtained by us except as indicated otherwise.
[e] Examined by the authors.
[f] Examined by Rossi (2005).
[g] Examined by Steiner and Catzeflis (2003).

Table 2. continued.

[h] Examined by Lim *et al.* (2005).
[i] From GenBank.

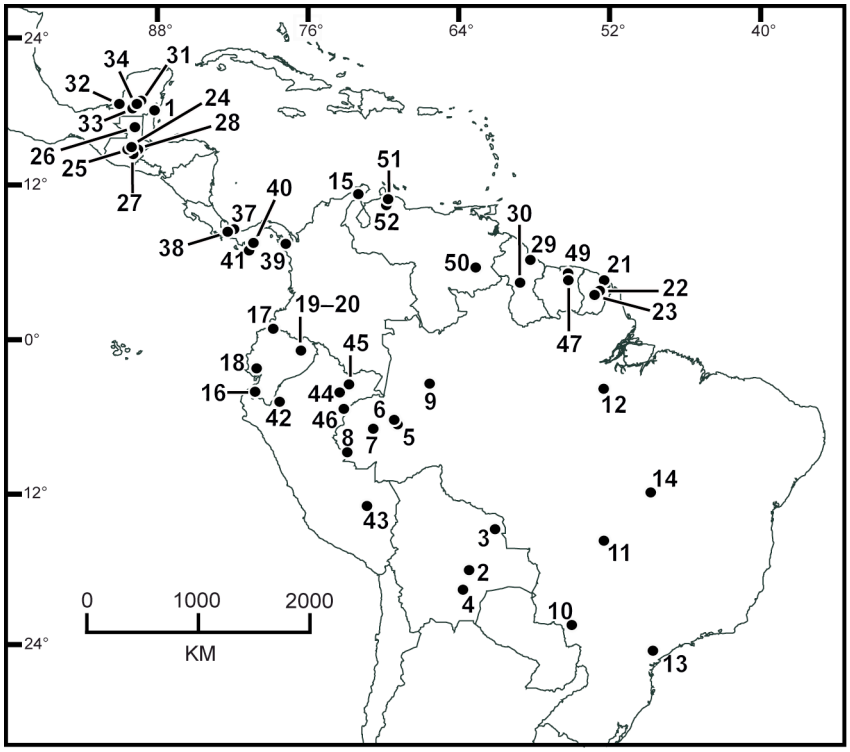
Table 3. Name and DNA sequence of primers used for DNA amplification and sequencing.

Primer name	Primer sequence
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG
CYTB-R1-Didelphidae	5′ CCTTCATTGCTGGCTTACAAGGC
CYTB-420R-Didelphidae	5′ GCTCCTCAGAAGGATATTTGTCCTCA
CYTB-730R-*Marmosa*	5′ TCWCCTAATARRTCWGGTGARAATATTGC
CYTB-540F-*Marmosa*	5′ GAGGAGGMTTYTCHGTTGATAAAGC
CYTB-650F-*Marmosa*	5′ CTATTCCTTCACGAAACAGGCTC
CYTB-217R-*Marmosa*	5′ TCTGTAGCCCAYATYTGYCGWGAYG
CYTB-70F-*Marmosa*	5′ CCMTCAAATATTTCAGCCTGATG

FIGURE 1.

Provenance of sequenced specimens of *Marmosa* (localities of collected outgroup specimens are not shown). Numbers in parentheses refer to entries in the Gazetteer (Appendix 1).

Figure 1.


88°
76°
64°
52°
40°
24°
12°
0°
12°
24°
0
1000
2000
KM
1
2
3
4
5
6
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19–20
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RESULTS

There are five pairs of identical haplotypes among our 71 sequences: two specimens of *Marmosa simonsi* (NK37836 and NK37837) from Ecuador, two specimens of *M. robinsoni* (NK101606 and NK101633) from Panama, two specimens of *M. murina* (TK17359 and TK17387) from Surinam, two specimens of *M. murina* (T2471 and T2704) from French Guiana, and two specimens of *M. paraguayana* (MAM46 and MAM47) from Brazil. In each of these cases, we excluded the sequence corresponding to the second-listed specimen from all subsequent phylogenetic analyses, resulting in a final data matrix comprising 42 complete cytochrome-*b* sequences (each with 1146 bp) and 24 partial sequences (ranging in length from 398 to 1145 bp; Table 2). As expected of mitochondrial sequences, average base composition across this dataset is relatively poor in guanine (30.7% A, 22.9% C, 12.5% G, 33.9% T), but there is no significant departure from base-compositional stationarity among taxa ($\chi^2 = 121.83$, df = 186, $p = 0.99$; see Saccone *et al.*, 1989). All sequences translate to open reading frame.

Our dataset contains 508 variable characters, 465 of which are parsimony-informative. Maximum-parsimony analysis recovered 96 minimum-length trees, the strict consensus of which is shown in Figure 2. For the model-based analyses (ML and BI), the hierarchical likelihood-ratio test (hLRT) selected the most complex model (GTR+I+Γ), whereas the simpler HKY+I+Γ model was preferred using the AIC. To test for possible effects of model selection on our phylogenetic analyses, we performed ML analyses specifying each of these models and obtained identical topologies; therefore, we report only the results obtained under the more complex GTR+I+Γ model (Table 4; Figure 3).

SPECIES LIMITS: We were able to test the monophyly of just 11 of the 14 morphologically defined species in the subgenus *Marmosa* recognized by Rossi (2005) because we lacked

samples of two taxa (*Marmosa andersoni* and *M. tobagi*), and we had only a single representative sample of *M. zeledoni*. For 10 of these 11 cases, morphologically defined species were recovered as monophyletic groups, usually with moderate to very strong support in both the MP and the model-based analyses (Figures 2, 3). The only noteworthy exception concerns *M. mexicana*, samples of which form two deeply divergent haplogroups (hereafter referred to as "*M. mexicana* A" and "*M. mexicana* B") that were not consistently recovered as sister taxa. Although the model-based analyses recovered these two haplogroups as a clade, the MP analysis placed *M. zeledoni* as the sister taxon to *M. mexicana* A and *M. isthmica* as sister to *M. mexicana* B; as might be expected, both of these alternatives are weakly supported.

Mean uncorrected sequence divergence within species (provisionally including *Marmosa mexicana* A and *M. mexicana* B, see below; Table 5) ranges from 0.2 to 4.2%. However, sequence divergence across the basal split within some species is considerably higher than these average within-group values. In particular, Panamanian sequences of *M. robinsoni* differ from the single available Venezuelan sequence by 6.2%, Bolivian sequences of *M. macrotarsus* differ from Brazilian and Peruvian sequences by 6.5%, and Peruvian sequences of *M. demerarae* differ from French Guianan sequences by 5.7%. By contrast, average interspecific divergence values within three consistently recovered sister-species pairs (*M. constantiae* + *M. regina*, *M. demerarae* + *M. paraguayana*, and *M. robinsoni* + *M. xerophila*) range from 9.5% to 18.6%.

PHYLOGENETIC RELATIONSHIPS: Whereas cytochrome-*b* sequences are clearly useful for testing the monophyly of morphologically defined species and for assessing intraspecific genetic divergence, they are less consistently informative about phylogenetic relationships among species. Approximately half of the interspecific nodes resolved in our trees were recovered with strong support in both MP and model-based analyses. Among these well-supported nodes are

the sister-species pairs *Marmosa robinsoni* + *M. xerophila*, *M. constantiae* + *M. regina*, and *M. demerarae* + *M. paraguayana*. At deeper levels, all of our phylogenetic analyses supported the monophyly of the genus *Marmosa* sensu Voss and Jansa (2009). Also, all analyses recovered a well-supported group comprising *M. robinsoni*, *M. xerophila*, *M. isthmica*, *M. mexicana*, *M. zeledoni* and *M. simonsi* (hereafter the "*mexicana-robinsoni* clade"); within this group, *M. simonsi* was consistently recovered as the sister taxon to the remaining species with moderate to strong support. *Marmosa murina* and three other species (*M. tyleriana*, *M. waterhousei*, and *M. macrotarsus*) formed another consistently well-supported clade, and the subgenus *Micoureus* (represented by *M. constantiae*, *M. regina*, *M. demerarae*, and *M. paraguayana*) was also recovered as monophyletic in all of our analyses.

By contrast, our MP and model-based analyses were notably inconsistent in their placement of *Marmosa lepida* and *M. rubra*. Whereas model-based analyses recovered *M. lepida* as sister to the *murina* cluster + *Micoureus* (with weak ML bootstrap but 100% Bayesian support), the parsimony analysis recovered *M. lepida* as the sister taxon to *Micoureus* (with negligible bootstrap support). In the model-based analyses, *M. rubra* was recovered as the sister taxon to the *mexicana-robinsoni* clade (again with weak ML bootstrap but impressive Bayesian support), whereas *M. rubra* was recovered as the sister taxon to all other analyzed congeners in the parsimony tree (with <50% bootstrap support).

The remaining interspecific nodes either agree or differ between the MP and model-based analyses, but all have uniformly weak support values. Within the *mexicana-robinsoni* clade, for example, the ML analysis recovered the two haplogroups of *M. mexicana* (A and B) as a clade, with *M. zeledoni* and *M. isthmica* as sequentially less closely related sister taxa (Figure 3), whereas the MP analysis placed *M. zeledoni* as sister to *M. mexicana* A and *M. isthmica* as sister

FIGURE 2.

Strict consensus of 96 equally most-parsimonious trees (L = 2198; CI = 0.36; RI = 0.80). Bootstrap support values are indicated above branches subtending species and conspecific haplogroups discussed in the text. For each terminal, the country of origin, next-largest political unit (state, department, province, etc.), and an alphanumeric specimen identifier (from Table 2) are provided. Numbers in parentheses refer to localities mapped in Figure 1 and listed in the Gazetteer (Appendix 1).

Figure 2.

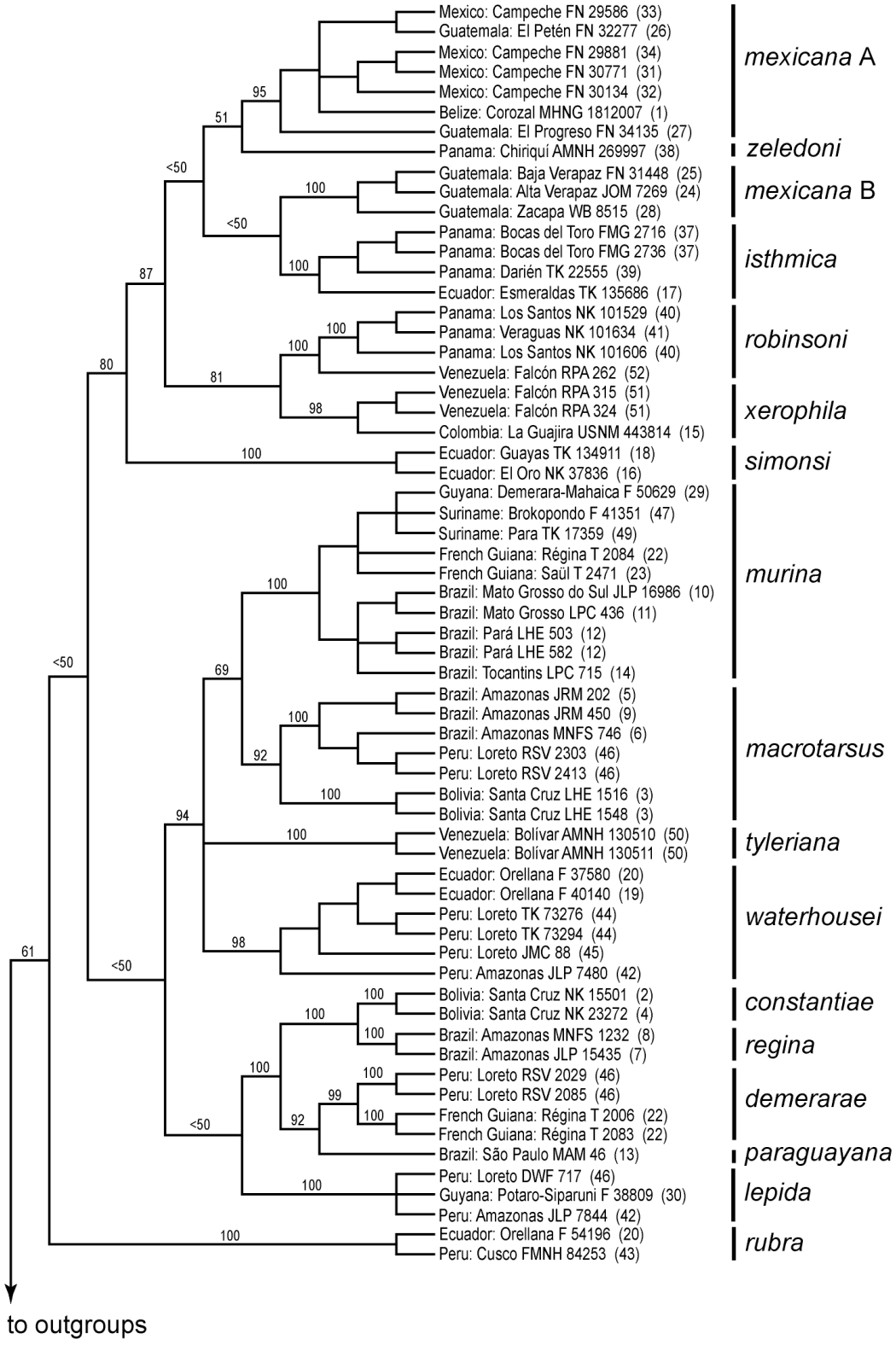

Mexico: Campeche FN 29586 (33)
Guatemala: El Petén FN 32277 (26)
Mexico: Campeche FN 29881 (34)
Mexico: Campeche FN 30771 (31)
Mexico: Campeche FN 30134 (32)
Belize: Corozal MHNG 1812007 (1)
Guatemala: El Progreso FN 34135 (27)
Panama: Chiriquí AMNH 269997 (38)
Guatemala: Baja Verapaz FN 31448 (25)
Guatemala: Alta Verapaz JOM 7269 (24)
Guatemala: Zacapa WB 8515 (28)
Panama: Bocas del Toro FMG 2716 (37)
Panama: Bocas del Toro FMG 2736 (37)
Panama: Darién TK 22555 (39)
Ecuador: Esmeraldas TK 135686 (17)
Panama: Los Santos NK 101529 (40)
Panama: Veraguas NK 101634 (41)
Panama: Los Santos NK 101606 (40)
Venezuela: Falcón RPA 262 (52)
Venezuela: Falcón RPA 315 (51)
Venezuela: Falcón RPA 324 (51)
Colombia: La Guajira USNM 443814 (15)
Ecuador: Guayas TK 134911 (18)
Ecuador: El Oro NK 37836 (16)
Guyana: Demerara-Mahaica F 50629 (29)
Suriname: Brokopondo F 41351 (47)
Suriname: Para TK 17359 (49)
French Guiana: Régina T 2084 (22)
French Guiana: Saül T 2471 (23)
Brazil: Mato Grosso do Sul JLP 16986 (10)
Brazil: Mato Grosso LPC 436 (11)
Brazil: Pará LHE 503 (12)
Brazil: Pará LHE 582 (12)
Brazil: Tocantins LPC 715 (14)
Brazil: Amazonas JRM 202 (5)
Brazil: Amazonas JRM 450 (9)
Brazil: Amazonas MNFS 746 (6)
Peru: Loreto RSV 2303 (46)
Peru: Loreto RSV 2413 (46)
Bolivia: Santa Cruz LHE 1516 (3)
Bolivia: Santa Cruz LHE 1548 (3)
Venezuela: Bolívar AMNH 130510 (50)
Venezuela: Bolívar AMNH 130511 (50)
Ecuador: Orellana F 37580 (20)
Ecuador: Orellana F 40140 (19)
Peru: Loreto TK 73276 (44)
Peru: Loreto TK 73294 (44)
Peru: Loreto JMC 88 (45)
Peru: Amazonas JLP 7480 (42)
Bolivia: Santa Cruz NK 15501 (2)
Bolivia: Santa Cruz NK 23272 (4)
Brazil: Amazonas MNFS 1232 (8)
Brazil: Amazonas JLP 15435 (7)
Peru: Loreto RSV 2029 (46)
Peru: Loreto RSV 2085 (46)
French Guiana: Régina T 2006 (22)
French Guiana: Régina T 2083 (22)
Brazil: São Paulo MAM 46 (13)
Peru: Loreto DWF 717 (46)
Guyana: Potaro-Siparuni F 38809 (30)
Peru: Amazonas JLP 7844 (42)
Ecuador: Orellana F 54196 (20)
Peru: Cusco FMNH 84253 (43)
mexicana A
zeledoni
mexicana B
isthmica
robinsoni
xerophila
simonsi
murina
macrotarsus
tyleriana
waterhousei
constantiae
regina
demerarae
paraguayana
lepida
rubra
to outgroups

FIGURE 3.

The maximum-likelihood tree inferred from the best-fit model of nucleotide substitution (Table 4). ML bootstrap support values and Bayesian posterior probabilities are indicated above and below branches, respectively. Branch and terminal labels follow the same conventions explained in the caption to Figure 2.

Figure 3.

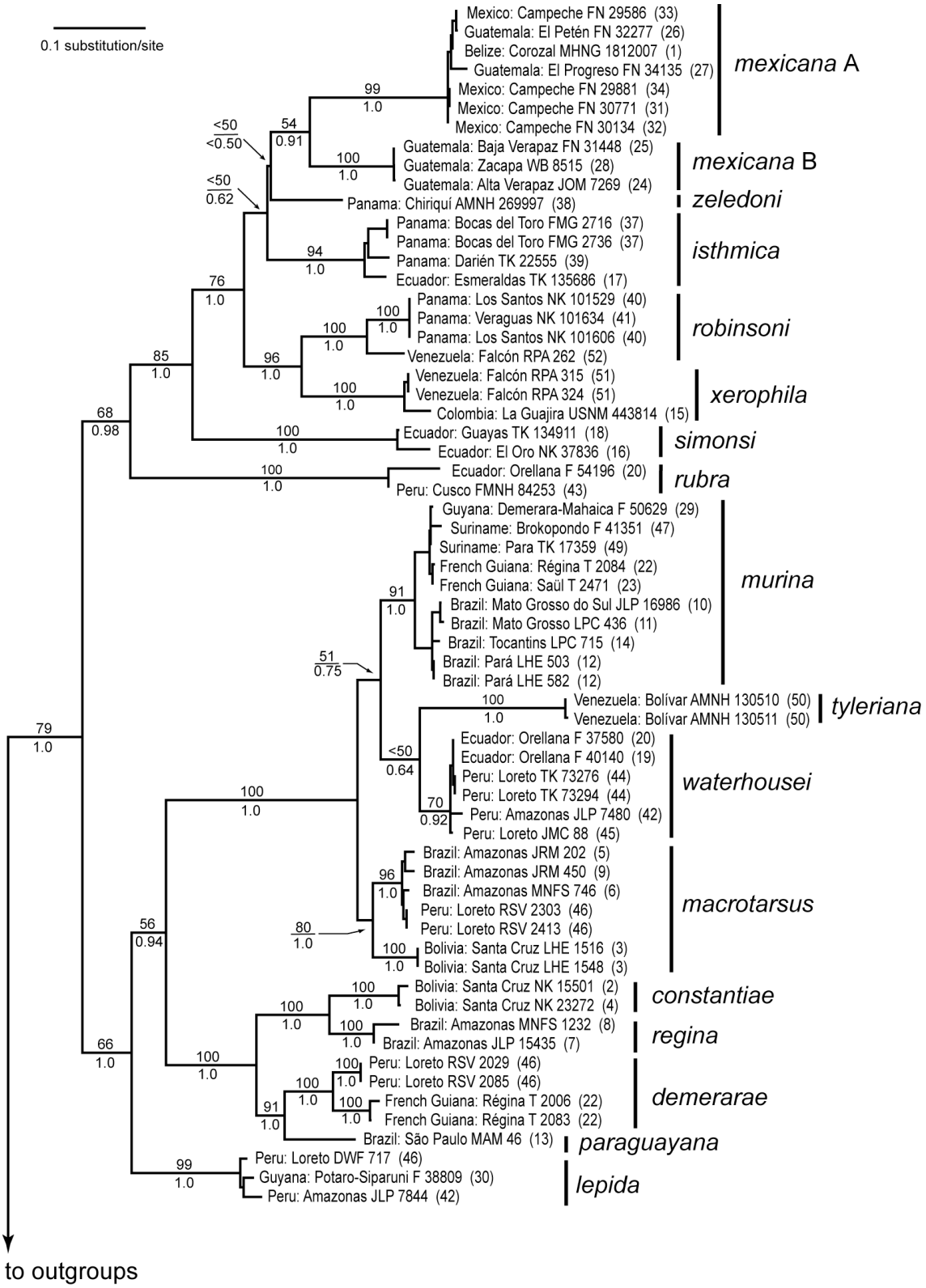

0.1 substitution/site
Mexico: Campeche FN 29586 (33)
Guatemala: El Petén FN 32277 (26)
Belize: Corozal MHNG 1812007 (1)
Guatemala: El Progreso FN 34135 (27)
Mexico: Campeche FN 29881 (34)
Mexico: Campeche FN 30771 (31)
Mexico: Campeche FN 30134 (32)
mexicana A
Guatemala: Baja Verapaz FN 31448 (25)
Guatemala: Zacapa WB 8515 (28)
Guatemala: Alta Verapaz JOM 7269 (24)
mexicana B
Panama: Chiriquí AMNH 269997 (38)
zeledoni
Panama: Bocas del Toro FMG 2716 (37)
Panama: Bocas del Toro FMG 2736 (37)
Panama: Darién TK 22555 (39)
Ecuador: Esmeraldas TK 135686 (17)
isthmica
Panama: Los Santos NK 101529 (40)
Panama: Veraguas NK 101634 (41)
Panama: Los Santos NK 101606 (40)
Venezuela: Falcón RPA 262 (52)
robinsoni
Venezuela: Falcón RPA 315 (51)
Venezuela: Falcón RPA 324 (51)
Colombia: La Guajira USNM 443814 (15)
xerophila
Ecuador: Guayas TK 134911 (18)
Ecuador: El Oro NK 37836 (16)
simonsi
Ecuador: Orellana F 54196 (20)
Peru: Cusco FMNH 84253 (43)
rubra
Guyana: Demerara-Mahaica F 50629 (29)
Suriname: Brokopondo F 41351 (47)
Suriname: Para TK 17359 (49)
French Guiana: Régina T 2084 (22)
French Guiana: Saül T 2471 (23)
Brazil: Mato Grosso do Sul JLP 16986 (10)
Brazil: Mato Grosso LPC 436 (11)
Brazil: Tocantins LPC 715 (14)
Brazil: Pará LHE 503 (12)
Brazil: Pará LHE 582 (12)
murina
Venezuela: Bolívar AMNH 130510 (50)
Venezuela: Bolívar AMNH 130511 (50)
tyleriana
Ecuador: Orellana F 37580 (20)
Ecuador: Orellana F 40140 (19)
Peru: Loreto TK 73276 (44)
Peru: Loreto TK 73294 (44)
Peru: Amazonas JLP 7480 (42)
Peru: Loreto JMC 88 (45)
waterhousei
Brazil: Amazonas JRM 202 (5)
Brazil: Amazonas JRM 450 (9)
Brazil: Amazonas MNFS 746 (6)
Peru: Loreto RSV 2303 (46)
Peru: Loreto RSV 2413 (46)
Bolivia: Santa Cruz LHE 1516 (3)
Bolivia: Santa Cruz LHE 1548 (3)
macrotarsus
Bolivia: Santa Cruz NK 15501 (2)
Bolivia: Santa Cruz NK 23272 (4)
constantiae
Brazil: Amazonas MNFS 1232 (8)
Brazil: Amazonas JLP 15435 (7)
regina
Peru: Loreto RSV 2029 (46)
Peru: Loreto RSV 2085 (46)
French Guiana: Régina T 2006 (22)
French Guiana: Régina T 2083 (22)
demerarae
Brazil: São Paulo MAM 46 (13)
paraguayana
Peru: Loreto DWF 717 (46)
Guyana: Potaro-Siparuni F 38809 (30)
Peru: Amazonas JLP 7844 (42)
lepida
to outgroups

Table 4. Parameter estimates from the best-fit model of nucleotide substitution for cytochrome b.

-ln L	10807.817
Base frequencies	
pA	0.349
pC	0.251
pG	0.059
pT	0.341
Rate matrix R	
rA-C	1.320
rA-G	13.495
rA-T	1.026
rC-G	1.500
rC-T	13.189
rG-T	1.000
Proportion of invariant sites	0.515
Shape parameter for the gamma distribution (α)	1.139

to *M. mexicana* B (Figure 2); neither alternative received strong Bayesian or bootstrap support. Although both ML and MP analyses recovered the more inclusive clade comprised of *M. mexicana*, *M. isthmica*, and *M. zeledoni*, Bayesian and bootstrap support for this relationship is negligible.

Patterns of interspecific relationships within the robustly supported *murina* cluster are similarly equivocal. Whereas the ML analysis recovered the sister-species pair *M. tyleriana* + *M. waterhousei*, with *M. murina* and *M. macrotarsus* as sequentially more distantly related sister taxa (Figure 3), the MP analysis placed *M. murina* and *M. macrotarsus* as sister taxa and left the positions of *M. tyleriana* and *M. waterhousei* unresolved (Figure 2); neither of these alternatives received compelling support. A clade comprising the four species of *Micoureus* was recovered as the sister taxon to the *murina* clade in both of our model-based analyses, but always with low support.

DISCUSSION

Despite ongoing debate about species concepts in the systematic literature (reviewed by de Queiroz, 1998; Mayden, 1999; Coyne and Orr, 2004; Baker and Bradley, 2006), most researchers agree that genetically independent lineages are fundamentally important units of evolutionary diversification. We therefore adopt a lineage-based concept of species (after de Queiroz, 1998), for which we use mtDNA haplotype monophyly (as recovered by this study) and morphological diagnosability (as documented by Rossi, 2005; Rossi *et al.*, 2010) as operational criteria for species recognition. Whereas mtDNA sequences provide crucial information about lineage membership based on maternally inherited genes, morphological diagnosability is important (1) as a proxy measure of evolutionary divergence at biparentally inherited nuclear

loci, (2) because it enables mitochondrial clades to be associated with name-bearing types for which sequence data are not available, and (3) because it allows other unsequenced specimens to be used for mapping geographic ranges and for niche-based distributional modeling (Graham *et al.*, 2004; Phillips *et al.*, 2006). Although a high degree of sequence divergence is neither necessary nor sufficient for species recognition (Ferguson, 2002; Baker and Bradley, 2006), pairwise distances provide a heuristically useful basis for comparisons of genetic variation within and among lineages, whether or not the latter are formally recognized as taxa.

In general, our analyses of mitochondrial sequence data from the subgenus *Marmosa* corroborate the morphology-based taxonomy proposed by Rossi (2005), most of whose species (Table 1) were recovered as well-supported monophyletic groups. Among the noteworthy taxonomic changes proposed by Rossi (2005) and by Rossi *et al.* (2010) that are unambiguously supported by our results are the recognition of *M. isthmica* and *M. simonsi* as species distinct from *M. robinsoni*, and the recognition of *M. macrotarsus* and *M. waterhousei* as species distinct from *M. murina*. Indeed, our failure to recover *Marmosa murina* (sensu lato: including *macrotarsus* and *waterhousei*) and *M. robinsoni* (sensu lato: including *isthmica* and *simonsi*) as clades convincingly refutes hoary taxonomic concepts dating back to the middle of the last century (Tate, 1933; Hershkovitz, 1951). The validity of three other species long recognized as distinct (*M. rubra, M. tyleriana,* and *M. xerophila*) is also clearly supported by our sequencing results.

The only exception in this context is *Marmosa mexicana* (sensu Rossi, 2005; Rossi *et al.*, 2010), sequenced exemplars of which were not consistently recovered as a clade, and which exhibit very high sequence divergence (>13%) between two well-supported haplogroups. One haplogroup (*M. mexicana* A) is represented by samples from seven lowland localities (< 300 m

above sea level) in Belize, Guatemala, and southeastern Mexico, whereas the other haplogroup (*M. mexicana* B) is represented by samples from three localities in the Guatemalan highlands (> 1500 m; Figure 4). Although examined voucher material of both haplogroups fits the morphological diagnosis of *M. mexicana* (sensu Rossi [2005] and Rossi *et al.*, [2010]), noteworthy phenotypic variation does exist among our tissue vouchers. Among other differences, skins of *mexicana* A are distinctly paler than those of *mexicana* B, and skulls of *mexicana* A are visibly broader in proportion to their length than like-aged skulls of *mexicana* B. Additionally, small postorbital processes of the frontals are present in most examined adult specimens of *mexicana* A, whereas no examined adult specimen of *mexicana* B has any trace of a postorbital process. Although these differences are not taxonomically compelling due to small sample sizes, they do suggest the likelihood that more than one species is represented in our material.

Several names that are currently regarded as synonyms or subspecies of *Marmosa mexicana* might apply to these haplogroups, but we lack sequence data from samples adjacent to any of the relevant type localities: Juquila (Mexico, Oaxaca; type locality of *mexicana* Merriam, 1897), Isla de Roatán (Honduras, Islas de la Bahía; type locality of *ruatanica* Goldman, 1911), Izamal (Mexico, Yucatán; type locality of *mayensis* Osgood, 1913), and Boquerón (Panama, Chiriquí; type locality of *savannarum* Goldman, 1917). In the absence of relevant genetic data, we note that the best phenotypic and ecogeographic match for haplogroup A is *mayensis*, a pale-furred form from the same dry Yucatecan forest biome where at least some of our voucher material was collected. By contrast, the darker pelage and montane provenance of haplogroup B more closely resembles the phenotypic and ecogeographic attributes of the nominotypical form

(*mexicana*). Obviously, future studies based on denser geographic sampling and more extensive sequencing within the *mexicana* complex will be necessary to test these conjectures.

Although other species of *Marmosa* were consistently recovered as monophyletic groups, unusual levels of sequence variation that we observed in some of them merit comment. In the case of *M. robinsoni*, moderately high divergence (ca. 6%) between Venezuelan and Panamanian sequences provides the first genetic evidence that this species, even in the restricted sense that it is now understood (Rossi, 2005; Rossi *et al.*, 2010), might be geographically variable. Although the data at hand are too few to sustain taxonomic interpretation, we note that *M. robinsoni* is widely distributed and still includes several subjective synonyms representing insular and continental populations alleged to differ in size and pelage coloration (*casta*, *chapmani*, *fulviventer*, *grenadae*, *luridavolta*, *mitis*, *nesaea*, and *pallidiventris*; Rossi, 2005; Rossi *et al.*, 2010). Therefore, assessing the significance of mtDNA divergence between our Panamanian and Venezuelan samples will require much broader geographic sampling. Future studies with this objective should include sequence data from as many nominal taxa as possible, including the typical form *robinsoni* Bangs, 1898 (from Isla de Margarita, Venezuela).

Another noteworthy example of intraspecific sequence variation concerns *Marmosa macrotarsus*, Bolivian samples of which differ by about 6% from Peruvian and western Brazilian material. Interestingly, both Bolivian samples come from the same region in northeastern Santa Cruz from which new cricetid rodent species have recently been described (Emmons and Patton, 2005; Carleton *et al.*, 2009). Morphological exemplars of both haplogroups were examined by Rossi (2005), who referred the Peruvian and Brazilian material to *M. macrotarsus* but did not make a definitive taxonomic determination of the Bolivian material (which he referred to "*Marmosa* cf. *macrotarsus*"). Our preliminary examination of Bolivian voucher material, which

we compared side-by-side with sequenced specimens from Peru did not reveal any consistent differences in characters of the skin, skull, or dentition.

The last example of unusual intraspecific sequence variation in our study involves *Marmosa demerarae*, a member of the subgenus *Micoureus*. Consistent with the results of Patton and Costa's (2003) analysis of a 630 bp fragment of cytochrome *b* from 19 geographic populations referred to this species, our French Guianan sequences (representing their "northeastern" clade) differ from Peruvian sequences (representing their "southwestern" clade) by almost 6%. As documented elsewhere (Patton *et al.*, 2000; Costa and Patton, 2006), the *demerarae* complex of *Micoureus* involves several additional phylogroups with equally divergent mtDNA sequences, the taxonomic interpretation of which is beyond the scope of this study.

Other geographically widespread species represented by multiple samples in our study (*Marmosa isthmica, M. lepida, M. murina,* and *M. waterhousei*) exhibit only modest sequence variation. Although phylogeographic structure is apparent in some cases (e.g., the discrete Guianan versus Brazilian clusters of *M. murina*), there are no clear indications in these results to challenge Rossi's (2005) interpretation that each of these taxa represents a single valid species. Indeed, the low level of sequence variation observed in *M. lepida*—a tiny species represented in our study by specimens from distant Guyanese and Peruvian localities—is at least as remarkable as the high levels of sequence variation that we discovered in other taxa.

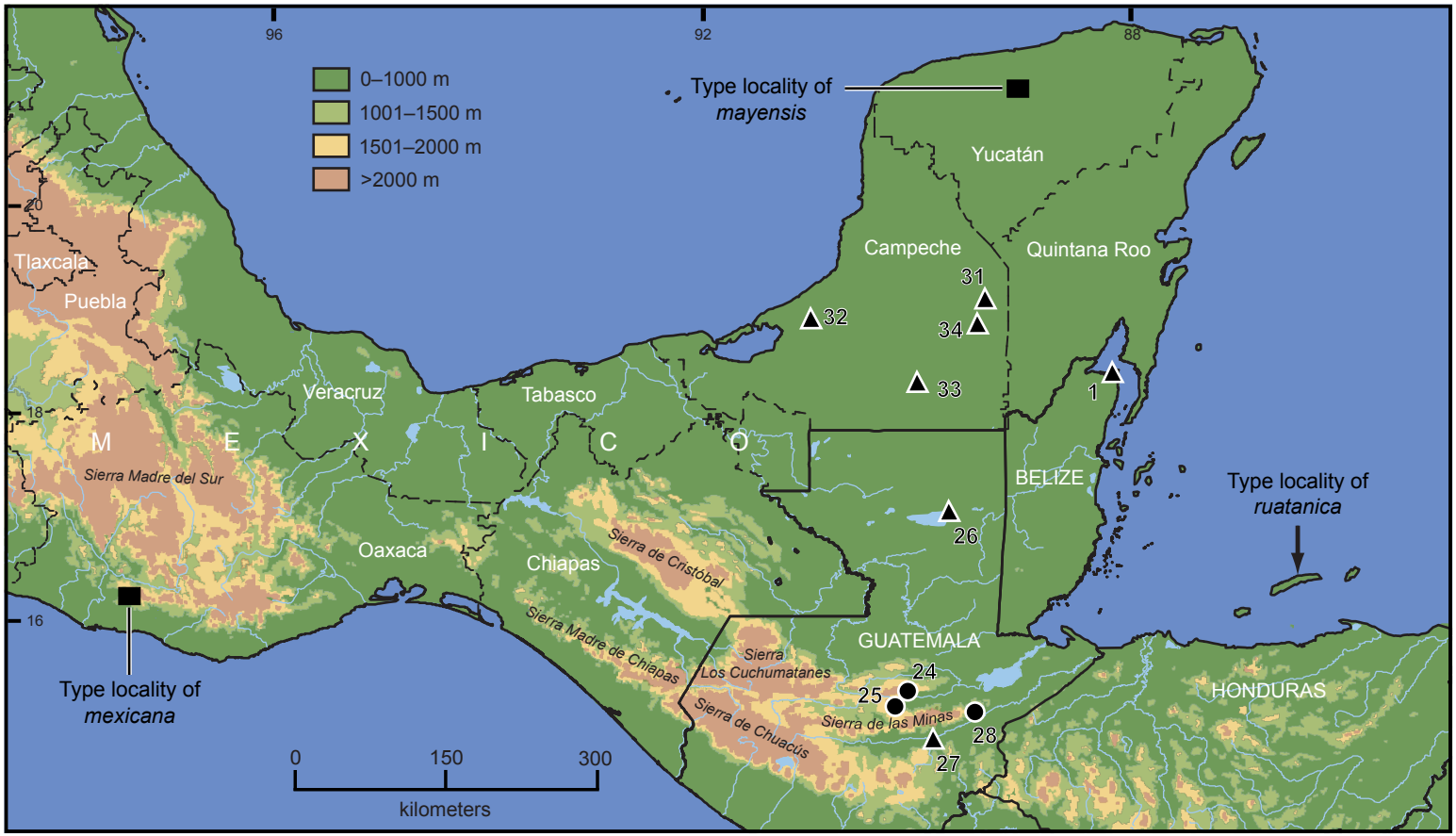
Phylogenetic Relationships.—Because the strength of the phylogenetic signal provided by the cytochrome-*b* gene typically declines with evolutionary depth (Meyer, 1994; Yoder *et al.*, 1996; Zardoya and Meyer, 1996; Gissi *et al.*, 2000; Springer *et al.*, 2001), it is not surprising that

FIGURE 4.

Provenance of sequenced specimens of *Marmosa mexicana* A (▲) and *M. mexicana* B (●).

Numbers refer to entries in the Gazetteer (Appendix 1).

Figure 4.


96
92
88
20
18
16
0–1000 m
1001–1500 m
1501–2000 m
>2000 m
Type locality of
mayensis
Yucatán
Campeche
Quintana Roo
Tlaxcala
Puebla
31
32
34
33
1
Veracruz
Tabasco
M E X I C O
Sierra Madre del Sur
BELIZE
Type locality of
ruatanica
26
Oaxaca
Chiapas
Sierra de Cristóbal
Sierra Madre de Chiapas
GUATEMALA
Sierra
Los Cuchumatanes
24
25
HONDURAS
Sierra de las Minas
28
Sierra de Chuacús
27
Type locality of
mexicana
0
150
300
kilometers

few of the deeper nodes in our trees are well supported. Among those interspecific relationships with strong nodal support are (1) monophyly of the subgenus *Micoureus*; (2) monophyly of a group comprised of *M. macrotarsus*, *M. murina*, *M. tyleriana*, and *M. waterhousei*; (3) a sister-group relationship between *M. robinsoni* and *M. xerophila*; and 4) monophyly of a group comprised of *M. robinsoni*, *M. xerophila*, *M. isthmica*, *M. mexicana*, *M. zeledoni* and *M. simonsi*. Whereas some of these relationships have previously been recovered by authors, others are unique to this report.

The monophyly of the subgenus *Micoureus*—represented in our study by the species *M. constantiae, M. demerarae, M. paraguayana,* and *M. regina*—is a noncontroversial result previously reported by other sequence-based phylogenetic analyses (e.g., Patton *et al.*, 1996; Voss and Jansa, 2003, 2009; Jansa and Voss, 2005; Jansa *et al.*, 2006). Although *M. alstoni* and *M. phaea* are the only currently recognized species of *Micoureus* that are absent from our analyses, we caution that the subgenus has not been revised for many years and that several nominal taxa now considered to be synonyms or subspecies of *M. demerarae* and *M. regina* were treated as valid species by Tate (1933). Because no substantive analyses of character data have ever been published to support currently accepted synonymies in this group, it is expected that additional species of *Micoureus* will be recognized as valid by future taxonomic researchers. If so, then our taxon sampling in *Micoureus* may be far from complete and our recovered support for subgeneric monophyly correspondingly less compelling.

Strong support for a group that includes *Marmosa murina, M. macrotarsus, M. tyleriana,* and *M. waterhousei* has not previously been reported in the literature. Although this clade approximates the membership of Tate's "Murina Section" (Table 1), it differs from Tate's

concept[2] by excluding *M. rubra*, which might either be a basal lineage in the genus (Figure 2) or the sister taxon to the *mexicana-robinsoni* clade (Figure 3). Of these alternatives, the latter is strongly supported by recent analyses of concatenated nuclear-gene sequence data (Voss and Jansa, 2009). Whereas some previous analyses of mtDNA sequence data with much sparser taxonomic sampling (Steiner *et al.*, 2005) have recovered *M. lepida* and *M. murina* as sister species, the relationships of *lepida* were not consistently resolved in our results. However, analyses of concatenated nuclear-gene sequence data (Voss and Jansa, 2009) suggest that *lepida* is sister to a group comprised of *Micoureus* and the *murina* cluster, as recovered by our model-based analyses (Figure 3).

A close relationship between *Marmosa robinsoni* and *M. xerophila* was implied by Handley and Gordon (1979), but our results provide the first phylogenetic evidence to support this notion. Although the data at hand suggest that these are reciprocally monophyletic sister taxa, we note that the range of *xerophila* is entirely contained within that of *robinsoni* (see Rossi *et al.*, 2010: Figures 25, 26), and that the latter species includes numerous nominal taxa currently treated as synonyms. Because our geographic sampling of *robinsoni* haplotypes is sparse, the possibility exists that *xerophila* is a divergent peripheral isolate of a widespread and possibly paraphyletic complex of morphologically similar forms currently lumped together in *robinsoni*. Any future study focused on scenarios of speciation in the genus should include many more sequences from geographically representative populations of the latter taxon.

The discovery of a well-supported clade that includes *Marmosa isthmica, M. mexicana, M. robinsoni, M. simonsi, M. xerophila,* and *M. zeledoni* is a novel result of this study. This clade does not coincide in membership with any of Tate's "sections" (Table 1), nor had its

[2] Note that Tate (1933) considered *waterhousei* as a subspecies of *murina* and used the name *quichua* for the taxon herein referred to as *macrotarsus*.

member taxa been explicitly associated with one another until the revisionary work by Rossi *et al.* (2010). To be sure, nuclear-gene datasets have consistently clustered *mexicana* with *isthmica* (previously reported as "*robinsoni*" by Voss and Jansa, 2003, 2009; Jansa and Voss, 2005; Jansa *et al.*, 2006; Gruber *et al.*, 2007), but no phylogenetic analysis of morphological or molecular data has hitherto included representative material of *robinsoni* (sensu stricto), *simonsi*, *xerophila*, or *zeledoni*. To our knowledge, no morphological character is uniquely shared by all of these forms to the exclusion of other species of *Marmosa*. Instead, their unifying characteristic seems to consist in a biogeographic criterion that has emerged in recent years as a fundamental dichotomy within several groups of co-distributed Neotropical organisms.

Biogeographic Implications.—The Andes are a formidable barrier to dispersal of lowland and lower-montane organisms that occur on opposite sides of the main cordilleras. Following Haffer (1967), we refer to the lowlands west and north of the Andes as trans-Andean, and those east and south of the Andes as cis-Andean. Examples of trans-Andean landscapes include those in Central America, the contiguous Pacific lowlands of western Ecuador and Colombia, and the Caribbean lowlands of northern Colombia and northwestern Venezuela. Cis-Andean regions include most of the remainder of tropical and subtropical South America, including Amazonia and the Atlantic Forest of southeastern Brazil.

The *mexicana-robinsoni* clade includes all of the trans-Andean species currently assigned to the subgenus *Marmosa*. Of these, five species (*isthmica, mexicana*, *simonsi, xerophila,* and *zeledoni*) are trans-Andean endemics, and one (*robinsoni*) occurs on both sides of the Andes (see Rossi *et al.* [2010] for range maps of all of these taxa). Although at least two species of the subgenus *Micoureus* (not represented in this study) also occur west of the Andes, the results in

hand suggest that these mountains may have played a significant role in constraining the early biogeographic radiation of *Marmosa*.

Phylogenetic evidence for separate cis- and trans-Andean radiations has recently been reported for a number of terrestrial and freshwater organisms (e.g., Harvey and Gutbertlet, 2000; Perdices, 2002; Ribas *et al.*, 2005; Noonan and Wray, 2006), suggesting that Andean crossings are rare events in some clades. However, cis- and trans-Andean taxa are sometimes scattered throughout recovered phylogenies (Weksler, 2006), implying that such events may have occurred frequently in other groups. In some studies, clades on opposite sides of the Andes are represented by distinct genera (Harvey and Gutbertlet, 2000). In others, cis- versus trans-Andean distributions distinguish reciprocally monophyletic groups of congeneric species (Perdices *et al.*, 2002; Ribas *et al.*, 2005), whereas distinct cis- and trans-Andean phylogroups have been discovered within certain widespread "species" (e.g., the tree *Symphonia globulifera*; Dick *et al.*, 2003).

The origin of cis- versus trans-Andean distributions has been attributed to a variety of historical scenarios, including Andean uplift, marine transgressions, and Pleistocene climatic fluctuations (reviewed by Cracraft and Prum, 1988; Brumfield and Capparella, 1996). Because some of these postulated tectonic and paleoclimatic events occurred at vastly different times, molecular dates are useful for assessing the relevance of competing historical explanations. Estimated dates for phylogenetic nodes that separate cis- versus trans-Andean clades of parrots (Ribas *et al.*, 2005) and pimelodid fishes (Perdices *et al.*, 2002), for example, are in the range of 6–8 million years, much too old to support a Pleistocene origin for this distributional pattern (contra Haffer, 1967). In this context, time-calibrating the present molecular phylogeny of *Marmosa* will contribute toward the causal analysis of a taxonomically widespread

biogeographic phenomenon, a goal that we defer to a subsequent report pending the analysis of sequence data from additional loci.

CHAPTER 2

Occurrence of *Marmosa waterhousei* in the Venezuelan Andes, with comments on its biogeographic significance

(Adapted from Gutiérrez EE, Soriano PJ, Rossi RV, Murillo JJ, Ochoa-G. J, and Aguilera M. 2011. Occurrence of *Marmosa waterhousei* in the Venezuelan Andes, with comments on its biogeographic significance. Mammalia, 75, 381–386).

INTRODUCTION

Species of the genus *Marmosa* collectively range from Mexico to northern Argentina, and are also found on the islands of Trinidad, Tobago, and Granada. The genus occurs in a diverse number of habitats, including xerophytic thorn scrub, savannas, lowland rain forests, and humid-montane forests, at elevations from sea level to about 3000 meters. By virtue of its wide ecogeographic range, and for being a member of the Didelphidae—the most diverse surviving lineage of the endemic mammalian fauna that evolved in South America during its Tertiary isolation (Voss and Jansa, 2003)—the genus *Marmosa* is of exceptional biogeographic interest. Nevertheless, effective assessments of distributional patterns of species in the genus have been prevented by taxonomic problems.

The genus *Marmosa* contains 20 species—14 in the subgenus *Marmosa* (sensu Rossi 2005) and 6 in subgenus *Micoureus* (Voss and Jansa, 2009). Although the subgenus *Micoureus* has not yet been treated in a modern taxonomic revision, the subgenus *Marmosa* was recently revised employing morphometric analyses and comparisons of qualitative traits of approximately 2500 specimens, including most relevant type material (Rossi, 2005, partially summarized in Rossi *et al.*, 2010). Subsequent phylogenetic analyses of cytochrome-*b* sequences (Gutiérrez *et al.*, 2010) supported most of the alpha-level taxonomy proposed in the aforementioned revision. Consequently, six taxa that had been traditionally treated as subspecies or minor synonyms of *Marmosa mexicana*, *M. robinsoni*, or *M. murina* are now recognized as valid species. One of these cases is represented by *Marmosa waterhousei*, which for decades was treated either as a subspecies (Tate, 1933; Cabrera, 1958; Pérez-Hernández *et al.*, 1994; Linares, 1998) or synonym (Gardner, 2005; Creighton and Gardner, 2008) of *M. murina*.

While treating *Marmosa waterhousei* as a subspecies of *M. murina*, publications that listed the species of mammals present in Venezuela have indicated the occurrence of *M. waterhousei*, sometimes inferring an extensive distribution throughout areas covered by humid forest north of the Río Orinoco. In these reports, no voucher material (i.e., museum cataloge numbers) to document this distributional pattern was mentioned—see maps of "*M. murina waterhousei*" in Pérez-Hernández *et al.*, 1994 and Linares, 1998. A reexamination of the only Venezuelan voucher of *Marmosa* "*waterhousei*" reported in the literature (see Tate, 1933, p. 103)—collected in "La Azulita, south of Lake Maracaibo, Zulia", and currently housed in the Field Museum of Natural History (FMNH 22176)—identified it as *Marmosa* cf. *murina* (see Rossi, 2005). Therefore, until this report, no correctly identified voucher specimens of *Marmosa waterhousei* exist in the literature to document the presence of the species in Venezuela. Herein, we present the first two confirmed records of the species for the Venezuelan Andes, discuss their biogeographic implications, and provide a dichotomous key for identification of the species of *Marmosa* present in Venezuela.

MATERIALS AND METHODS

Because specimens housed in Central- and most South American collections were not included in the recent revision of the subgenus *Marmosa*, their taxonomic identities are yet to be determined under the current classification criteria (i.e. sensu Rossi, 2005; Rossi *et al.*, 2010). As a first step to that end, we have examined specimens of the subgenus *Marmosa* in the Colección de Vertebrados de la Universidad de los Andes (CVULA), located in Mérida, Venezuela. Based on this effort, we can confirm the presence of the Waterhouse Mouse Opossum, *Marmosa waterhousei* (Tomes 1860), in the country. We compared data for mass,

four external and 19 craniodental measurements of adult (age classes 6–9) male specimens of *Marmosa waterhousei* reported herein from the Cordillera de Mérida (CVULA I-5994, I-6349), with those from other localities throughout the known distribution of the species. Data of non-Venezuelan specimens were taken from Rossi (2005). We report mass and external measurements from specimen labels. We employed a digital caliper to take the craniodental measurements to the nearest 0.01 mm. The mass is reported in grams, and all external and craniodental measurements in millimeters. For definitions, illustrations, and methods for taking measurements see Rossi *et al.* (2010).

RESULTS

Two specimens collected in the Cordillera de Mérida, the main mountain range of the Venezuelan Andes, represent the basis for this report. The first specimen (CVULA I-6349; Figure 5) was collected in 1994 in "La Palmita, 1 km N La Azulita, Estado Mérida", at an elevation of 1000 m (geographic coordinates: 08º44′N, 71º27′W; DCN 1977c; locality 20 in Figure 6). The second specimen (CVULA I-5994) was collected in 1995 in "Cucuchica, 6 km E Tovar, Estado Mérida" at an elevation of 1200 m (geographic coordinates: 08º21′N, 71º42′W; DCN 1977a; locality 19 in Figure 6). According to the collector, both specimens were captured in secondary semideciduous forest. The locally focused classification of habitat types of the Mérida state considers that the forest type at these localities correspond to semideciduous montane forest ("selva semicaducifolia montana"; see Attarof, 2003; Attarof and Sarmiento, 2004), which is found in the humid versants of the cordillera, or close to rivers in the dry versants, at elevations from 800 to 1700 m. This type of forest occupied extensive areas of the cordillera in the past, but it has been largely replaced with coffee plantations.

Integumental and cranial diagnostic traits used in the recent revision of the subgenus *Marmosa* (Rossi, 2005; Rossi *et al.*, 2010) allowed us to unambiguously identify specimens reported herein as *Marmosa waterhousei*. These traits are as follows: absence of the palatine fenestrae; long rostral process of premaxillae; supraorbital ridges oriented both laterally and dorsally; anterior and posterior margins of superior canine not parallel at the base of the tooth; dorsal pelage grayish-brown; ventral pelage with broad and conspicuous lateral zones of gray-based hairs on the neck, on the chest, belly, inguinal region, and ventral side of the limbs; dark brown tail, slightly paler on the ventral side. The two Venezuelan male specimens reported here (age class 6) are slightly smaller than those male specimens (age classes 6–9) reported by Rossi (2005; Table 1) from localities throughout the known range of the species (Figure 6; see criteria for age classification in Rossi *et al.*, 2010).

Marmosa waterhousei can be easily distinguished from other species of the subgenus *Marmosa* occurring in Venezuela—i.e., *M. lepida, M. murina, M. robinsoni, M. tyleriana*, and *M. xerophila* (see Soriano *et al.*, 1999; Rossi, 2005; Ochoa, 1985; Ochoa *et al.*, 2008; Rossi *et al.*, 2010)—using the following dichotomous key (based on information from Rossi, 2005 and Rossi *et al.*, 2010):

1a. Presence of palatine fenestrae ……...…...…..……... 2

1b. Absence of palatine fenestrae …..…….……..…..……...…. 4

2a. Gular gland absent; dorsal pelage dark brown; hairs of tail scales apparently absent when the specimen is examined without magnification; central triplet hairs as long as 1.5 scale; rostral process of premaxillae long (slightly shorter than I1 is tall) ……. ……...……... *M. tyleriana*

2b. Gular gland present; dorsal pelage dark or pale grayish brown, reddish brown, or yellowish brown; hairs of tail scales visible without magnification; central triplet hairs as long as or slightly longer than 2 scales; rostral process of premaxillae short (about half as long as I1 is tall) or absent ……..……..... 3

3a. Rostral process of premaxillae absent; dorsal fur color pale grayish-brown .....

……..…… *M. xerophila*

3b. Rostral process of premaxillae short; dorsal fur color yellowish-brown …...…….……

…….……...…..… *M. robinsoni*

4a. Gular gland absent; dorsal pelage shiny reddish brown; length of rostral process of premaxillae varying from as long as I1 is tall to twice as long as I1 tall …….…….

…….……. *M. lepida*

4b. Gular gland absent or present; dorsal pelage grayish-brown; rostral process of premaxillae about as long as I1 is tall ……...……...……..… 5

5a. Gular gland present; at the middle of the tail, the central hair of each caudal dorsal scale is tiny—shorter than the scale from which it emerges; supraorbital ridges conspicuously dorsally projected ……..……....… *M. waterhousei*

5b. Gular gland absent; at the middle of the tail, the central hair of each caudal dorsal scale is as long as the length of the scale from which it emerges; supraorbital ridges slightly or not at all dorsally projected (only laterally projected in this case) …….

…….……..…..……..… *M. murina*

FIGURE 5.

Lateral (top), dorsal (bottom left), and ventral (ventral right) views of skull of *Marmosa waterhousei* (CVULA I-6349). Note the presence of a long rostral process of premaxillae, dorsally projected supraorbital ridges, and the absence of palatine fenestrae.

Figure 5.

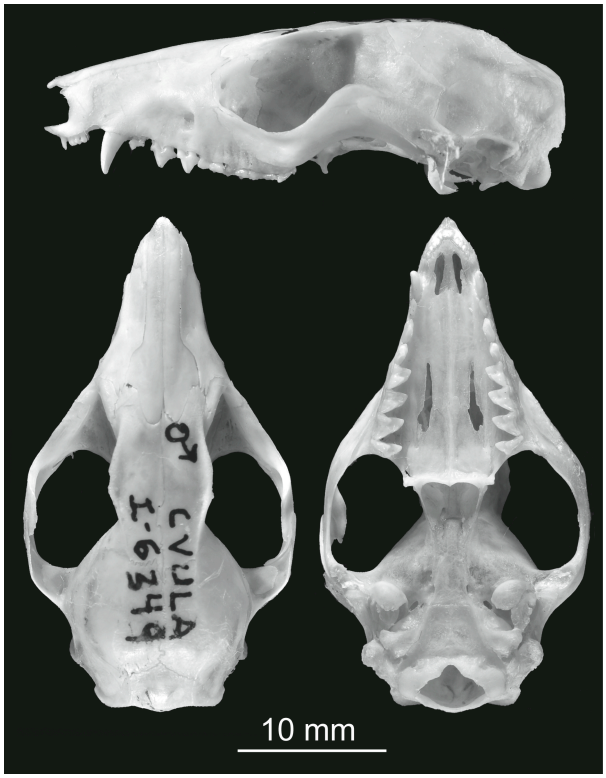


FIGURE 6.

Map showing the known collection localities of *Marmosa waterhousei*. Circles show previously known records of *M. waterhousei* (solid circles) and *Marmosa* cf. *waterhousei* (open circles) from Rossi (2005); squares show the Venezuelan records reported herein. Progressively darker shading indicates the following elevations: pale gray ≥ 500 m, medium gray ≥ 1000 m, and dark gray ≥ 1500 m. Abbreviated locality information, including country, largest political unit (state, department, or province) within each country, approximated geographic coordinates, and elevational data (in meters, if any), is as follows: **Brazil** : Amazonas: 1. Comunidade Colina (00°7′ N, 69°00′ W); 2. Macaco (02°05′ S, 62°07′ W); **Colombia**: Antioquia: 3. Medellín (06°15′ N, 75°35′ W, 1538 m); 4. Valdivia (07°11′ N, 75°27′ W, 950 m); Boyacá: 5. Muzo (05°32′ N, 74°07′ W, 1000 m); Cundinamarca: 6. Paime (05°22′ N, 74°09′ W, 1038 m); Meta: 7. Caño Guapaya (02°54′ N, 73°39′ W; 305 m); Putumayo: 8. Río Mecaya (00°28′ N, 75°20′ W, 185 m); **Ecuador**: Morona-Santiago: 9. Gualaquiza (03°24′ S, 78°33′ W, 971 m); Napo: 10. Puerto Napo (01°03′ S, 74°47′ W, 731 m); Pastaza: 11. Río Pindo (01°32′ S, 77°57′ W); Zamora-Chinchipe: 12. Zamora (04°04′ S, 78°57′ W, 990 m); **Peru**: Amazonas: 13. Huampam (04°28′ S, 78°10′ W); 14. La Poza (04°03′ S, 77°46′ W, 180 m); 15. Nazareth (05°08′ S, 78°19′ W, 335 m); Loreto: 16. Boca del Río Curaray (02°22′ S, 74°05′ W); 17. Laguna Miraño (03°24′ S, 73°08′ W); 18. San Lorenzo (04°49′ S, 76°36′ W, 152 m); **Venezuela**: Mérida: 19. Cucuchica (08°21′ N, 71°42′ W, 1200 m); 20. La Palmita (08°44′ N, 71°27′ W, 1000 m). For exact localities previously known for the specimens, see text for Venezuelan specimens and Rossi (2005) for non-Venezuelan specimens.

Figure 6.

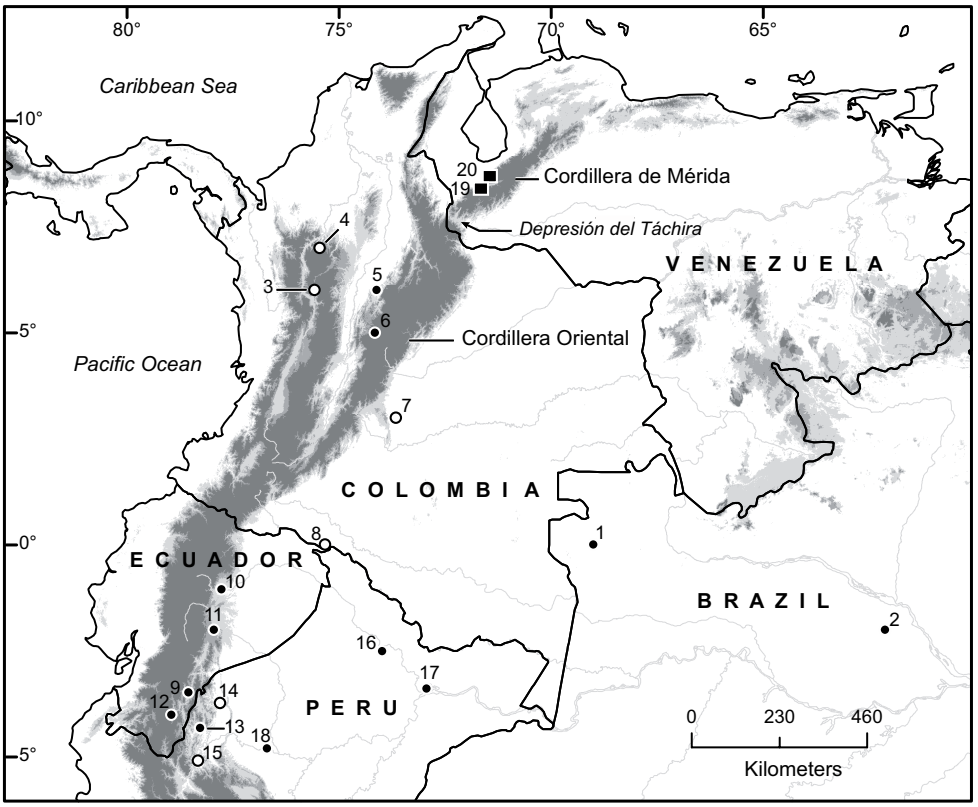

80°
75°
70°
65°
Caribbean Sea
10°
20
19
Cordillera de Mérida
Depresión del Táchira
4
3
5
6
Cordillera Oriental
VENEZUELA
5°
Pacific Ocean
7
COLOMBIA
8
1
0°
ECUADOR
10
11
BRAZIL
2
16
17
9
14
12
PERU
13
18
15
5°
0
230
460
Kilometers

Table 5. Mass, external and craniodental measurements of specimens of *Marmosa waterhousei* (age classes 6–9; males) reported herein from the Cordillera de Mérida (CVULA I-5994, I-6349), and from other localities throughout the known distribution of the species (Figure 6). Data of non-Venezuelan specimens were taken from Rossi (2005). We report mass and external measurements from specimen labels. The mass is reported in grams, and all external and craniodental measurements in millimeters. For definitions, illustrations, and methods for taking measurements see Rossi *et al.* (2010).

	CVULA I-5994	**CVULA I-6349**	**Non-Venezuelan specimens mean±SD (n)/min–max**
Mass	40	50	65.00±1.41 (2) 64–66
Length of head-and-body	220	134	137.40±10.21 (5) 125–149
Length of tail	80	178	199.17±18.21 (6) 172–223
Length of hind foot	25	22	23.17±1.72 (6) 21–25
Length of ear	28	25	24.40±1.95 (5) 21–26
Greatest length of skull	—	34.80	37.02±1.17 (7) 35.42–38.54
Condylobasal length	—	33.87	36.19±1.28 (7) 34.5–37.93
Nasal length	13.11	13.93	16.32±0.84 (8) 14.87–17.6
Palatal length	19.17	19.35	20.60±0.67 (8) 19.49–21.57
Length of maxillary tooth row	13.15	13.22	14.00±0.46 (8) 13.51–14.78
Length of upper molar series	6.52	6.56	7.02±0.21 (8) 6.71–7.28
Length of M4	1.15	1.24	1.07±0.07 (8) 0.95–1.18
Width of M2	1.68	1.70	1.87±0.07 (7) 1.79–1.98
Width of M4	2.35	2.24	2.33±0.11 (8) 2.14–2.45

Table 5. continued.

Postpalatal breadth	10.79	10.67	11.02±0.27 (7) 10.63–11.37
Breadth of basicranium	—	6.27	6.85±0.27 (4) 6.51–7.1
Breadth across tympanic bullae	—	11.39	11.40±0.3 (4) 11.12–11.76
Length of tympanic bulla	—	5.42	5.45±0.15 (4) 5.22–5.54
Breadth of rostrum between jugals	11.55	11.80	10.33±0.61 (4) 9.43–10.74
Least interorbital breadth	5.61	6.09	5.97±0.51 (4) 5.28–6.43
Postorbital constriction	6.35	6.02	6.26±0.65 (4) 5.47–6.83
Breadth of braincase	—	12.24	13.51±0.26 (3) 13.27–13.78
Zygomatic breadth	—	17.56	19.45±0.79 (4) 18.65–20.17
Nasal breadth	4.38	4.86	4.52±0.37 (4) 4.08–4.98

DISCUSSION

Venezuelan records of *Marmosa waterhousei* reported herein substantially extend the known distribution of the species. Previous to this report, *M. waterhousei* was known to occur at 50–1100 m elevations in humid forests (sensu classification of Olson *et al.*, 2001) of Brazil (northeastern Amazonas state), northern Peru, eastern Ecuador, and the valley of Río Magdalena in Colombia (Rossi, 2005; Figure 6). The locality of specimen CVULA I-6349, from the Cordillera de Mérida, is 422 km (straight airline) from the nearest locality previously known for *M. waterhousei* (i.e. Muzo, in the Boyacá department, Colombia; loc. 4 in Figure 6; see Rossi, 2005), and represents the northern extreme of the species' range. Non-Venezuelan specimens examined are as follows: *Marmosa waterhousei*: AMNH 47186, 69181, 71959; BM 7.1.1.215 (holotype of *Didelphys waterhousii* Tomes, 1860), 32.8.4.33, 14.4.25.85, 24.2.22.65, 34.9.10.242; FMNH 70940-41, FMNH 43184; MVZ 153279, 153286, 154754; 154756; INPA 2513. *Marmosa* cf. *waterhousei*: AMNH 70564, 71963; BM 78.8.31.8, 23.11.13.15; FMNH 69824, 69827, 69850, 70942, 70980, 87923; MVZ 139955, 154761, 155243, 155244, 153284, 153285, 157632. Abbreviations of museums follow Hafner *et al.* (1997).

The Depresión del Táchira, a low, dry saddle that separates mesic habitats of the Cordillera Oriental (Colombia) from those in the Cordillera de Mérida, is probably too xeric for *M. waterhousei* to disperse across it. Therefore, *M. waterhousei* might have crossed the Depresión del Táchira during glacial periods, similar to what has been proposed to explain the presence of *Heteromys australis* east of this depression (Anderson and Soriano, 1999). The presence of *M. waterhousei* in Amazonia and in the northern Andes might be explained by a corridor of forest habitat existing between the Amazonian region and the piedmont of the northern Andes, which have connected these regions even during warm-dry climatic periods of

the Pleistocene (see "Napo refuge" in Haffer, 1969, p. 134). This corridor has been invoked to explain the presence in the Andes of some amphibians and reptiles more widely distributed south of the Río Orinoco (e.g. Barrio-Amorós, 1998; Barrio-Amorós and Molina-Rodríguez, 2010 and references cited therein).

Analyses of cytochrome-*b* sequences have recently revealed high and moderately high levels of sequence divergences within two species of the subgenus *Marmosa*, *M. mexicana* and *M. robinsoni*, and suggested the possibility that the Andes might have played an important role in the diversification of the genus (Gutiérrez *et al.*, 2010). Because of these precedents, future studies focused on *M. waterhousei* should include assessments of the genetic divergence between samples from the cis-Andean (east of the Andes) and trans-Andean (west of the Andes) regions—note that analyses by Gutiérrez *et al.* (2010) only included samples from the cis-Andean region. Dating nodes of the resulting phylogeograghic tree, and coupling the phylogeographic information with projections of niche models onto past climate scenarios (Kozak *et al.*, 2008) might be particularly insightful for understanding the origin of the biogeographic pattern exhibited by *M. waterhousei*.

CHAPTER 3

Phylogeography of a dry-forest specialist in northern South America, the mouse opossum *Marmosa robinsoni*

INTRODUCTION

Marmosa robinsoni and *M. xerophila* represent useful focal taxa to gain insight into the biogeographic history of organisms predominantly distributed in the tropical dry forests of northern South America. A previous study (Gutiérrez *et al.*, 2010) suggested a sister-taxon relationship between *M. robinsoni* and *M. xerophila*; however, this relationship was based on limited geographic samples of both species, and the reciprocal monophyly of these species has never been rigorously assessed. Although the distribution of *M. xerophila* is limited to xerophytic lowland habitats of northeastern Colombia and northwestern Venezuela, at elevations from sea level to 350 m, *Marmosa robinsoni* has a much wider distribution, occurring in eastern Panama (including Isla del Rey and Isla Saboga in the Pacific), the inter-Andean valley of the Río Magdalena in Colombia, the Río Chama valley in the Cordillera de Mérida in Venezuela, the Venezuelan llanos, along the Caribbean coast of Colombia and Venezuela, and on the Caribbean islands of Margarita, Trinidad, Tobago, and Grenada (Rossi *et al.*, 2010). *Marmosa robinsoni* inhabits deciduous forests, savannas, and xeric shrublands at elevations from sea level to ca. 1200 meters; however, the species has also been collected in a very few localities with more mesic conditions at 1200–2000 meters. The species also inhabits mesic habitat in the tiny, isolated Cerro Santa Ana, Península de Paraguaná, Venezuela, where evergreen and cloud forests are present at atypically low elevations (350–700 meters), perhaps because of the Massenerhebung Effect (Anderson *in litt.*). Furthermore, it inhabits lowland rainforest on the islands of Trinidad and Tobago (a niche shift previously observed in other dry-forest small mammals; Voss, 1991).

Throughout the distributions of *Marmosa robinsoni* and *M. xerophila*, the Andes of Colombia and Venezuela interrupt the matrix of lowland dry forests. In Colombia, the Andes are

divided into the Cordillera Occidental, the Cordillera Central, and the Cordillera Oriental, separated by the valley of the Río Cauca (between the cordilleras Occidental and Central) and the valley of the Río Magdalena (between the cordilleras Central and Oriental). At the northern terminus of the Cordillera Oriental, near the border with Venezuela, the Serranía de Perijá extends northward to the base of the Península de la Guajira, and the Cordillera de Mérida extends to the northeast. A low, dry saddle, the Depresión del Táchira separates the Cordillera Oriental of Colombia from the Cordillera de Mérida in Venezuela. The Maracaibo basin lies between the Cordillera de Mérida and the Serranía de Perijá (Monasterio and Reyes, 1980; Schubert and Vivas, 1993; Josse *et al.*, 2011; Figure 7). Environmental conditions at higher elevations (above 2000 meters for *M. robinsoni*) in all of these Andean mountains likely act as barriers for *M. robinsoni* and *M. xerophila*; therefore, a phylogeographic study of these taxa should provide insights about the role of the Andean cordilleras in Colombia and Venezuela as possible vicariant agents, and about past corridors that may have allowed dry forest species to disperse across ecologically unfavorable terrain.

In this study, we used DNA sequence data to test the reciprocal monophyly of *Marmosa robinsoni* and *M. xerophila*, and subsequently used the phylogeographic structuring within the former species to identify temporal and geographic congruencies with geologic, hydrographic, and eustatic events that might have promoted haplotype divergence. These events include Andean uplifts in the Miocene, the subsequent changes in the course of the proto-Orinoco (Hoorn *et al.,* 1995; Díaz de Gamero, 1996), marine transgression along the Caribbean coast of present-day Venezuela and Colombia in the late Miocene (Rasänen *et al*., 1995; Paxton *et al*., 1996; Lovejoy *et al*., 1998), and Pleistocene glacial and interglacial periods (Webb and Bartlein, 1992).

MATERIALS AND METHODS

Sources of material.—Our analyses were based on sequences of the mitochondrial cytochrome-*b* (CYTB; ~1 kb) and the X-linked intron O-linked N-acetylglucosamine transferase (OGT; ~660 bp) genes. We used 14 CYTB sequences from GenBank and generated the remaining sequences (Table 6). Just over half of our sequences were generated from freshly preserved tissue samples (18 CYTB, 4 OGT), but to increase our geographic sampling, we also obtained sequences from DNA isolated from pieces of dried tissue snipped from skins or scraped from skeletal material of museum specimens (16 CYTB, 4 OGT). All sequences, along with their specimen voucher numbers, will be deposited in GenBank. Voucher specimens and associated tissues from which sequences were obtained are housed in the following institutions (Table 6): American Museum of Natural History (AMNH), New York; Museo de la Estación Biológica de Rancho Grande (EBRG), Maracay, Venezuela; Museum of Southwestern Biology (MSB), University of New Mexico, Albuquerque; Royal Ontario Museum (ROM), Toronto; Museum of Texas Tech University (TTU), Lubbock; United States National Museum of Natural History (USNM), Washington, DC.; Universidad Simón Bolívar (Laboratorio de Biología de Poblaciones y Evolución), Caracas, Venezuela.

Geographic sampling.—The use of DNA from skin and dried tissues from museum specimens allowed us to sample most of the known geographic distribution of *Marmosa robinsoni* (Figure 7). The only substantial gaps in the present geographic sampling for this species corresponded to the eastern portion of the Caribbean coast of Colombia, the eastern Venezuelan Llanos, and the islands of Grenada and Margarita. Unfortunately, we were not able to obtain sequences of the nuclear OGT gene from most of the DNA isolated from dried skins of museums specimens; however, we generated at least one sequence of that gene from individuals

of each lineage previously identified with analyses of the CYTB sequence data. The latter was important because the strength of the phylogenetic signal provided by the CYTB gene typically declines with evolutionary depth (Zardoya and Meyer, 1996; Springer *et al.*, 2001).

Laboratory methods.—All genomic DNA extractions were carried out using DNeasy extraction kits (Qiagen, Inc.). When the sources of DNA were dried tissues, we avoided contamination with foreign DNA by extensively washing (prior to extractions) each tissue using decreasing concentrations of ethanol (see Giarla *et al.*, 2010). That procedure and subsequent settings of PCR reactions based on DNA obtained from museum specimens were conducted in a UV-sterilized hood located in a laboratory where mammalian DNA had never been present.

Because DNA was extracted from both freshly preserved samples and museum specimens, different strategies were necessary to generate sequences. For freshly preserved samples, amplification of both genes CYTB and OGT required two steps: one round to amplify the whole gene, followed by a second round of amplification using internal primers, which yielded fragments of suitable lenght for sequencing. In cases where we extracted highly degraded DNA from museum specimens, we used various combinations of primers that amplified short fragments. PCR protocols followed Materials and Methods described in Chapter 1, but see Table 7 for primer sequences and annealing temperatures. We used Exonuclease I and Shrimp Alkaline Phosphatase (Hanke and Wink, 1994) to prepare PCR products for sequncing. All PCR products were sequenced in both directions using amplification primers and dye-terminator chemistry (BigDye ver. 3.1 Cycle Sequencing Kit, Applied Biosystems Inc., Foster City, California). We used Sequencher 4.7 (Gene-Codes Inc., Ann Arbor, Michigan) to compile and edit the sequences.

Phylogenetic analyses.—We first conducted a set of phylogenetic analyses based on the CYTB sequence data to test both the sister-taxon relantionship and the reciprocal monophyly of *Marmosa robinsoni* and *M. xerophila*. The former was suggested by results of a previous study based on very limited geographic sampling for *M. robinsoni* (Gutiérrez *et al.*, 2010). Based on results of that study, in our first set of analyses we used as ingroup all of the species forming the immediately larger clade in which the putative *M. robinsoni* + *M. xerophila* clade was included: *M. mexicana* A, *M. mexicana* B, *M. isthmica*, *M. robinsoni*, *M. xerophila*, and *M. zeledoni*. As the outgroup, we used *M. simonsi,* which was recovered with moderate or strong support as sister to the described ingroup (Gutiérrez *et al.*, 2010).

Based on the results of the first set of analyses, we assessed the phylogeographic structure of *Marmosa robinsoni*, the new ingroup, with *M. xerophila* designated as the outgroup. This second set of analyses was conducted separately for each gene (CYTB, OGT). The OGT matrix did not have a sampling equivalent to that of the CYTB matrix; it only contained representatives of clades of *M. robinsoni* circumscribed by the CYTB data, as well as one sequence of *M. xerophila* (see *Geographic sampling*, above).

All models were selected based on the Akaike Information Criterion (AIC; Akaike 1974) as implemented in MrModelTest ver. 2.3 (Nylander, 2004). In order to prevent possible deleterious effects of missing data entries in the CYTB matrices (Table 6) for selection of models of nucleotide substitution, we selected models using trimmed matrices. Although the existence of missing data entries might not be problematic for phylogenetic reconstructions under some conditions (Wiens, 2006; Wiens and Moen, 2008; but see Siddall, 2009), the effect

FIGURE 7.

Top: Provenance of sequenced specimens of *Marmosa robinsoni* (solid circles) and *M. xerophila* (open circles); localities of sequenced outgroup specimens are not shown (localities 5–10). Numbers refer to entries in the Gazetteer (Appendix 2). Bottom: geographic delimitation of areas used in reconstructions of ancestral areas (see Materials and Methods). Regions shown in increasingly darker tones of grey shading correspond to those with elevations of ≥ 500 m, ≥ 1000 m, and ≥ 1500 m, respectively.

Figure 7.

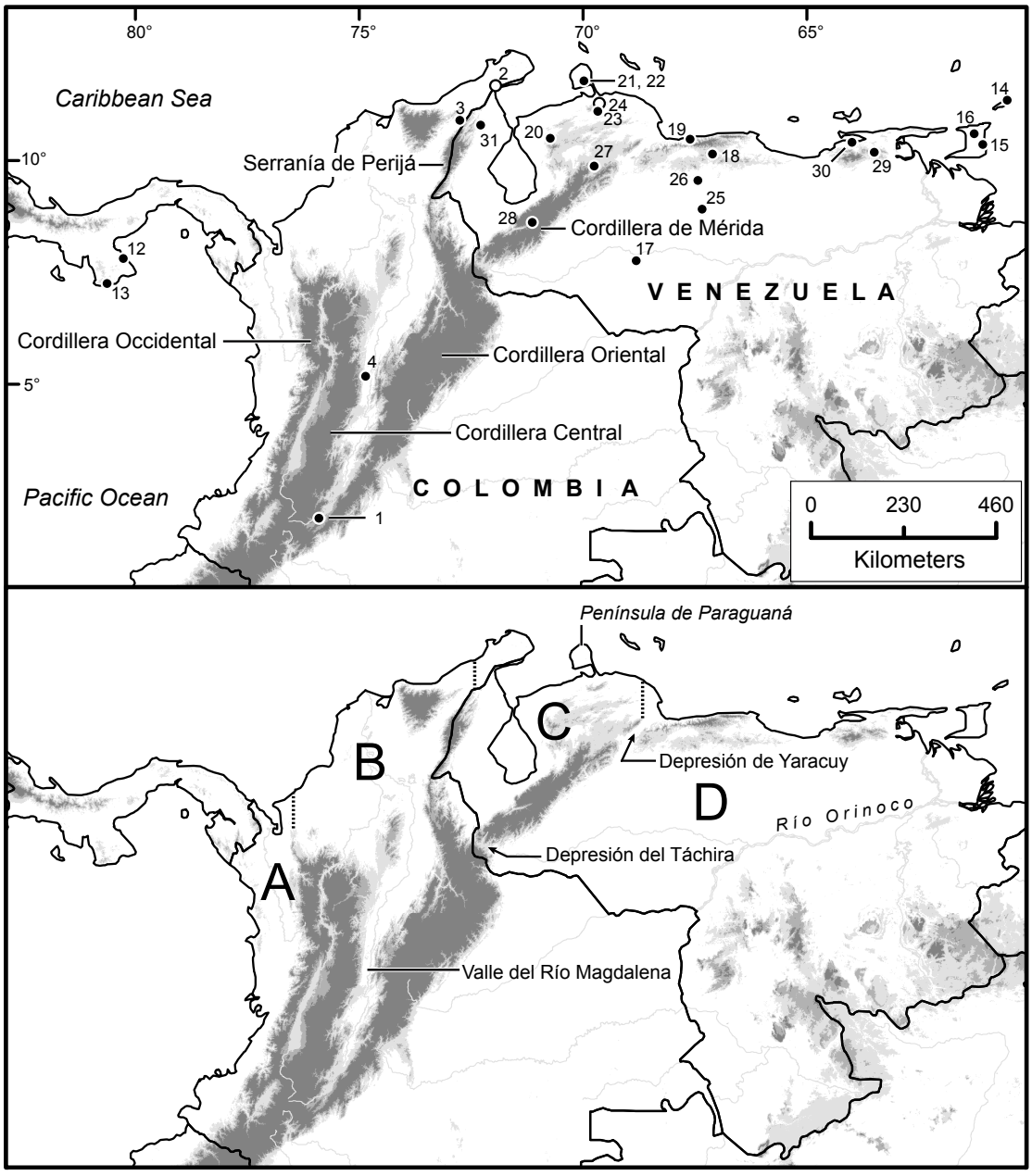

80°
75°
70°
65°
Caribbean Sea
10°
Serranía de Perijá
Cordillera de Mérida
V E N E Z U E L A
Cordillera Occidental
Cordillera Oriental
5°
Cordillera Central
Pacific Ocean
C O L O M B I A
0 230 460
Kilometers
Península de Paraguaná
A
B
C
D
Depresión de Yaracuy
Río Orinoco
Depresión del Táchira
Valle del Río Magdalena

Table 6. Sequenced specimens used to both test the sister-taxon relationship between *Marmosa robinsoni* and *M. xerophila* and assess the phylogeography structure of the former. a. Alphanumeric identifiers (including various personal field number series) used by institutional tissue collections (and to label terminals in accompanying Figs. 2–5); sequences amplified from morphological specimens lack tissue/DNA numbers. b. See Materials and Methods for names of museum collections identified by acronyms and abbreviations in this table. c. Country and next-largest administrative unit (state, department, province, etc.); numbers in parentheses refer to gazetteer entries (Appendix 2), which provide additional geographic information. d. Number of base pairs sequenced. *. CYTB sequences downloaded from GenBank.

Taxon	Tissue/DNA#[a]	Voucher[b]	Locality[c]	CYTB (bp)[d]	OGT (bp)[d]
Ingroups					
M. robinsoni	—	USNM 541860	Colombia: Huila (1)	192	—
M. robinsoni	—	USNM 280883	Colombia: La Guajira (3)	180	—
M. robinsoni	JRT 1198	AMNH 207766	Colombia: Tolima (4)	402	—
M. robinsoni	NK 101529	MSB 94363*	Panama: Los Santos (12)	1146	668
M. robinsoni	NK 101606	MSB 94366*	Panama: Los Santos (12)	1146	—
M. robinsoni	NK 101633	MSB 94368*	Panama: Veraguas (13)	1146	—
M. robinsoni	NK 101634	MSB 94369*	Panama: Veraguas (13)	1146	—
M. robinsoni	RSV 2450	AMNH 276741	Trinidad & Tobago: Tobago (14)	1136	—

Table 6. continued.

M. robinsoni	RSV 2451	AMNH 276742	Trinidad & Tobago: Tobago (14)	1136	—
M. robinsoni	RSV 2453	AMNH 276744	Trinidad & Tobago: Tobago (14)	1142	—
M. robinsoni	RSV 2455	AMNH 276746	Trinidad & Tobago: Tobago (14)	1140	664
M. robinsoni	RSV 2457	AMNH 276748	Trinidad & Tobago: Tobago (14)	1138	—
M. robinsoni	RSV 2458	AMNH 276749	Trinidad & Tobago: Tobago (14)	1138	—
M. robinsoni	RSV 2461	AMNH 276752	Trinidad & Tobago: Tobago (14)	1140	—
M. robinsoni	RSV 2464	AMNH 276755	Trinidad & Tobago: Tobago (14)	1140	—
M. robinsoni	RSV 2465	AMNH 276756	Trinidad & Tobago: Tobago (14)	1138	—
M. robinsoni	TRVL 4816	AMNH 206596	Trinidad & Tobago: Trinidad (15)	192	—
M. robinsoni	—	AMNH 169671	Trinidad & Tobago: Trinidad (16)	384	192
M. robinsoni	—	USNM 448524	Venezuela: Apure (17)	206	192
M. robinsoni	—	USNM 314171	Venezuela: Aragua (18)	352	—
M. robinsoni	—	USNM 517270	Venezuela: Aragua (19)	206	—
M. robinsoni	—	USNM 418532	Venezuela: Falcón (20)	206	—
M. robinsoni	RPA 199	EBRG 25349	Venezuela: Falcón (21)	726	—

Table 6. continued.

M. robinsoni	RPA 208	AMNH 276533	Venezuela: Falcón (21)	1146	—
M. robinsoni	JOG 4501	AMNH 276496	Venezuela: Falcón (22)	1146	—
M. robinsoni	RPA 215	EBRG 25357	Venezuela: Falcón (22)	726	—
M. robinsoni	RPA 280	AMNH 276562	Venezuela: Falcón (22)	1146	668
M. robinsoni	RPA 289	AMNH 276568	Venezuela: Falcón (22)	726	—
M. robinsoni	RPA 262	EBRG 25389 *	Venezuela: Falcón (23)	1146	664
M. robinsoni	—	USNM 443905	Venezuela: Guárico (25)	402	—
M. robinsoni	—	USNM 418519	Venezuela: Guárico (26)	367	—
M. robinsoni	—	USNM 443797	Venezuela: Guárico (26)	180	—
M. robinsoni	—	USNM 443913	Venezuela: Lara (27)	385	192
M. robinsoni	—	AMNH 24323	Venezuela: Mérida (28)	402	328
M. robinsoni	—	AMNH 33166	Venezuela: Mérida (28)	192	—
M. robinsoni	—	USNM 406951	Venezuela: Monagas (29)	389	—
M. robinsoni	—	USNM 388377	Venezuela: Sucre (30)	180	—
M. robinsoni	—	USNM 443803	Venezuela: Zulia (31)	402	—

Table 6. continued.

M. xerophila	—	USNM 443814 *	Colombia: La Guajira (2)	402	—
M. xerophila	RPA 315	AMNH 276582 *	Venezuela: Falcón (24)	1146	—
M. xerophila	RPA 324	AMNH 276586 *	Venezuela: Falcón (24)	1146	665
Outgroups					
M. isthmica	TK135686	TTU 102969 *	Ecuador: Esmeraldas (5)	1145	—
M. isthmica	TK22555	TTU 39118 *	Panama: Darién (11)	1146	—
M. mexicana A	FN34135	ROM 99776 *	Guatemala: El Progreso (8)	1146	—
M. mexicana A	FN30771	ROM 96968 *	Mexico: Campeche (9)	1146	—
M. mexicana B	JOM7269	USNM 569858 *	Guatemala: Alta Verapaz (7)	1087	—
M. simonsi	TK134911	TTU 103308 *	Ecuador: Guayas (6)	1146	—
M. zeledoni	—	AMNH 269997 *	Panama: Chiriquí (10)	402	

Table 7. Name and DNA sequences of pairs of primers used for amplification and sequencing of the CYTB and OGT genes. Touchdown PCRs are labeled as "TD" and their range of annealing temperatures are indicated (ºC); otherwise PCRs were conducted using a single annealing temperature (see Materials and Methods; see also Chapter 1).

Primer name	Primer sequence	Annealing temperature
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG	TD 59–52
CYTB-R1-Didelphidae	5′ CCTTCATTGCTGGCTTACAAGGC	
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG	52
CYTB-217R-*mexicana*	5′ CRTCWCGRCARATRTGGGCTACAGA	
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG	52
CYTB-420R-*Marmosa*	5′ GCTCCTCAGAAGGATATTTGTCCTCA	
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG	55
CYTB-730R-*Marmosa*	5′ TCWCCTAATARRTCWGGTGARAATATTGC	
CYTB-540F-*Marmosa*	5′ GAGGAGGMTTYTCHGTTGATAAAGC	55
CYTB-R1-Didelphidae	5′ CCTTCATTGCTGGCTTACAAGGC	
CYTB-650F-*Marmosa*	5′ CTATTCCTTCACGAAACAGGCTC	55
CYTB-R1-Didelphidae	5′ CCTTCATTGCTGGCTTACAAGGC	
OGT-F1-Didelphidae	5′ AAATCATTTCATCGACCTTTCTCAG	TD 55-52
OGT-R1-Didelphidae	5′ GCTGCTTTTCCATTACAGGGAAT	
OGT-F1-Didelphidae	5′ AAATCATTTCATCGACCTTTCTCAG	TD 55-52
OGT-360R-Didelphidae	5′ CATCCCYGCTTGGCCCAACCACA	

Table 7. continued.

OGT-300F-Didelphidae	5′ GTGATTTTGACTTTTCTCCTGGCCT	TD 55-52
OGT-R1-Didelphidae	5′ GCTGCTTTTCCATTACAGGGAAT	
OGT-120F-Didelphidae	5′ GGACATGGAAGAATTTGCTTTTGG	TD 55-52
OGT-540R-Didelphidae	5′ GCTCTGAATTCACAGCATCACCA	

of missing data entries on model selection remains poorly understood. When we used the untrimmed CYTB matrix, models with unrealistic rates were selected; therefore we trimmed the CYTB matrix to include only the first 200 bp. It was not necessary to trim the OGT matrix prior to model selection, as it contained very few entries with missing data.

All phylogenetic analyses were conducted using untrimmed matrices. For each set of analyses, we used maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) as optimality criteria. First, since base-compositional heterogeneity represents a potential problem for phylogenetic inference (Gruber *et al.*, 2007), we tested for departure from base-compositional stationarity among individuals. For each gene, we then performed multiple sequence alignment in Clustal X version 2.0 (Larkin *et al.*, 2007). We removed identical sequences[1], and coded missing bases as unknown. Parsimony analyses were performed in TNT ver. 1.1 (Goloboff *et al.*, 2008) using equal weighting with 1000 replicate searches, 10 random-addition replicates, and tree bisectionreconnection (TBR) branch swapping. For MP analyses based on the CYTB matrix, we used the *traditional search* option of TNT, but since the OGT matrix was small, we analyzed it using the *implicit enumeration*, which provides exact solutions within reasonable times. For ML analyses, we conducted 20 independent searches in GARLI 0.96 beta (Zwickl, 2006) using the default settings. Bayesian inference analyses were performed using the Markov Chain Monte Carlo (MCMC) sampling approach implemented in MrBayes ver. 3.1.2 (Ronquist and Huelsenbeck, 2003). A random tree was used to start each search, which used default priors and consisted of one cold chain and three heated chains (temperature = 0.2). The Markov chains were run for 1×10^7 generations, and trees were sampled every 1000^{th} generation. Default values were kept for the *relburnin* and *burninfrac* options in MrBayes (i.e.

[1] We only removed identical sequences if they had the same length.

relburnin = yes; burninfrac = 0.25). We examined a plot of the log-likelihood scores per generation to confirm that these 7,500 trees were generated after the log-likelihood scores stabilized.

To assess nodal support, we used nonparametric bootstrapping (Felsenstein, 1985) for the MP and ML analyses and posterior probabilities estimates for the BI analysis (Ronquist and Huelsenbeck, 2003). Maximum parsimony bootstrap analyses were performed in TNT using 1000 pseudodoreplicated data matrices with 10 random addition sequences and TBR branch-swapping. Maximum-likelihood bootstrap analyses were performed in GARLI 0.96 beta using 100 pseudoreplicated data matrices, with 10 searches performed on each. Bayesian posterior probabilities were calculated from the majority rule consensus tree of the 7,500 trees kept from the tree search performed in MrBayes.

We indicate to the degree of support received by individual nodes as follows. For the MP and ML bootstrap analyses, we use the following categories: *strong support*, for bootstrap values ≥ 75%; *moderate support*, for bootstrap values between 50% and 75%; *negligible* or *not supported* for values < 50%. For BI analyses, we considered that nodes were strongly supported (significantly supported) when posterior their probability values were ≥ 0.95, and weakly supported (or, not significantly supported) when their posterior probability values were < 0.95.

Ancestral area reconstructions.—We used two methods of ancestral area reconstructions, the parsimony criterion for optimization of unordered characters (Mesquite ver. 2.73; Maddison and Maddison, 2010) and Bayesian inference (RASP ver. 1.103; Yu *et al.,* 2010, 2011). We coded each tip (haplotype at the end of a tree branch) as occurring in one of four regions according to the specimen's locality relative to the major cordilleras of the Colombian and Venezuelan Andes, as follows (Figure 7): *region A*, west of Cordillera Occidental; *region B*, east

of the Cordillera Occidental and west of the Cordillera Oriental (including Serranía de Perijá); *region C*, east of the Serranía de Perijá and west of the Cordillera de Mérida and the Sierra de Aroa (hereafter, we refer to this latter region as the greater Maracaibo basin); *region D*, east of the Cordillera de Mérida. We delimited adjacent regions using as boundaries the crests of the cordillera that separates them. However, the northern extremes of these cordilleras typically become diffuse fans without meaningful distinct crests; hence, when each cordillera fell to the elevation of 500 meters, we delimited adjacent regions by drawing a line to the north to the Caribbean (Figure 7). For each analysis, we optimized the coded geographic distributions on the CYTB ML tree to interpret the phylogeographic structure of *M. robinsoni*. For the Bayesian inference method, we report the combined results from two independent analyses, each of them performed using 50000 generations sampled every 100th generations, and allowing for a widely distributed ancestor (i.e., root distribution = wide).

Divergence-time estimation.—After selecting a model of nucleotide-substitution (see *Phylogenetic analyses*, above) on a matrix containing all CYTB sequences of *Marmosa robinsoni* and one of *M. xerophila*, we employed that model (Table 8) to conduct a likelihood ratio test (LRT). Because the LRT indicated that our data could not reject a clock (see Results), we conducted a BI analysis in Beast ver. 1.5.4. (Drummond and Rambaut, 2007). We were not able to implement a relaxed-clock approach due to the lack of fossil records that would otherwise might serve as calibration points; therefore, we used a strict-clock approach to infer times since divergence between CYTB lineages of *M. robinsoni*, with *M. xerophila* designated as the outgroup. For this analysis, we used a substitution rate of 2% per million years (Brown *et al.*, 1979, 1982) and a Yule process tree prior (Yule, 1925). This assumes a constant speciation rate per lineage and is recommended for analyses based on sequences that were not collected from a

panmictic population (see Drummond *et al.*, 2007). All other priors were kept as default. The analysis was run for 5 x 10^6 generations and sampled every 100^{th} generation.

RESULTS

Molecular data and models of molecular evolution.—We obtained a total of 48 CYTB and 8 OGT sequences. For CYTB, 24 sequences were ~1146 bp in length, and another 24 ranged in length from 180 to 1087 bp. Overall, 36.59% of the untrimmed CYTB matrix entries were coded as missing data. For OGT, four sequences were ~668 kb in length, and four ranged in length from 192 to 328 bp (Table 6). For the CYTB matrix that we used to test the sister-taxon relantionship and reciprocal monophyly of *M. robinsoni* and *M. xerophila*, the Akaike information criterion selected the HKY+I model as optimal, whereas the HKY model was optimal for the OGT matrix (Table 8). For the CYTB matrix used to estimate time since divergence events within *M. robinsoni*, the AIC selected the HKY+G model. Average base composition across the ~1.1 kb CYTB matrix untrimmed (including all sequences in Table 6) was relatively poor in guanine (30.86% A, 22.37% C, 12.06% G, 34.72% T), but there was no significant departure from base-compositional stationarity among individuals ($\chi^2 = 40.29$, df = 111, $P = 1.00$; see Saccone *et al.* 1989). Average base composition across the OGT dataset comprised 22.37% A, 19.73% C, 25.55% G, 32.34% T, with no significant departure from base-compositional stationarity among individuals ($\chi^2 = 7.83$, df = 36, $P = 0.99$).

Monophyly of Marmosa robinsoni *and* M. xerophila.—All three optimality criteria used for phylogenetic analyses of the CYTB matrix recovered *Marmosa robinsoni* and *M. xerophila* as reciprocally monophyletic sister taxa (Figure 8; Table 9). Whereas the sister-taxon

Table 8. Parameter estimates from the best-fit models of nucleotide substitution for the CYTB and OGT datasets used in phylogenetic analyses and divergence-time estimations (see Materials and Methods).

	CYTB phylogenetic analyses (HKY+I)	**CYTB divergence-time estimations (HKY+G)**	**OGT phylogenetic analyses (HKY)**
-ln L	671.9958	422.8202	1350.8699
Base frequencies			
πA	0.3074	0.3118	0.2193
πC	0.2596	0.2526	0.2005
πG	0.0763	0.0939	0.2642
πT	0.3568	0.3417	0.3160
Proportion of invariant sites	0.6143	0.0000	0.0000
Shape parameter for the Γ distribution (α)	—	0.3345	—

FIGURE 8.

The maximum-likelihood tree (-lnL 4535.0002) resulting from analysis of the cytochrome-*b* (CYTB) sequence data to test the monophyly of *Marmosa robinsoni* and *M. xerophila* as a clade. The latter two species and *M. mexicana, M. isthmica,* and *M. zeledoni* formed the ingroup, and *M. simonsi* was designated as outgroup. Nodal support from parsimony and maximum-likelihood bootstrap analyses and a Bayesian analysis are indicated with shaded pie diagrams at nodes. For the maximum-parsimony and maximum-likelihood bootstrap analyses (MP and ML portions of the circle, respectively), black indicates bootstrap values ≥ 75%, gray indicates bootstrap values between 50% and 75%, and white indicates bootstrap values < 50%. For the Bayesian analysis (BPP; lower right one-third of circle), black indicates posterior probability values ≥ 0.95, and white indicates posterior probability values < 0.95. The northwestern South American lineage is abbreviated as "NW SA". For each terminal, political unit (state, department, province, etc.) of collection locality, and an alphanumeric specimen identifier (from Table 6) are provided. Numbers in parentheses refer to localities mapped in Figure 7 and listed in the Gazetteer (Appendix 2).

Figure 8.

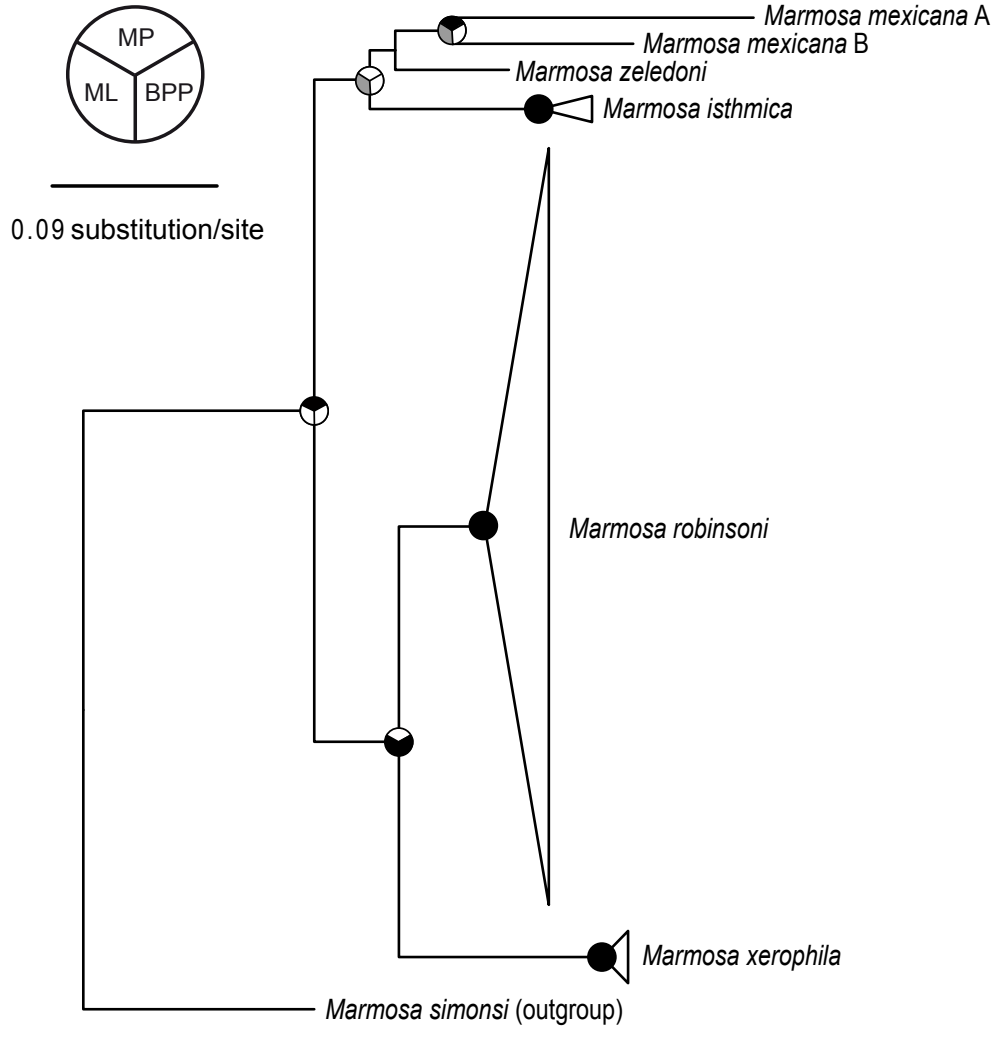

MP
ML
BPP
0.09 substitution/site
Marmosa mexicana A
Marmosa mexicana B
Marmosa zeledoni
Marmosa isthmica
Marmosa robinsoni
Marmosa xerophila
Marmosa simonsi (outgroup)

Table 9. Values of trees resulting from maximum-parsimony analyses. The first analysis was conducted to test the reciprocal monophyly and sister-taxon relationship between *Marmosa robinsoni* and *M. xerophila*, whereas the other two analyses were conducted to assess the phylogeographic structure of *M. robinsoni*. See Materials and Methods for outgroups used in each analysis.

	Test of reciprocal monophyly and sister-taxon relationship	**Assessment of phylogeographic structure**	
	CYTB	**CYTB**	**OGT**
Number of equally most-parsimonious trees	70	3300	1
Tree length	702	231	63
Consistency index	0.64	0.91	1.00
Retention index	0.69	0.97	1.00

relationship between *Marmosa robinsoni* and *M. xerophila* was only weakly supported by parsimony, this clade received strong support from our model-based analyses.

Phylogeographic structure of Marmosa robinsoni.—We found substantial phylogeographic structure within *Marmosa robinsoni*. All of the analyses (MP, ML, BI) based on the CYTB matrix revealed the existence of two major haplogroups, which were always strongly supported (Figure 9). One of these—hereafter referred to as the *eastern clade*—included haplotypes from the non-peninsular part of Falcón state, Lara state, the Llanos, and north central and northeastern Venezuela, as well as from the islands of Trinidad and Tobago (Figure 9, node B; see Figure 7 for map of collection localities). The second major haplogroup—hereafter referred to as the *western clade*—included haplotypes from Panama, Colombia, Zulia and Mérida states and the Península de Paraguaná of Falcón state in northwestern Venezuela (node E).

We found remarkably low geographic structure within the eastern clade of *Marmosa robinsoni* despite the existence of marine barriers to dispersal among several populations. Within this clade, model-based analyses recovered a strongly supported group formed by haplotypes from the Llanos and north-central and northeastern Venezuela, and from the islands of Trinidad and Tobago—hereafter we refer to this haplogroup as the *Venezuela-Trinidad-Tobago lineage* (Figure 9, node C). This lineage and four other sequences from northern Venezuela formed a polytomy at the most basal node within the eastern clade in MP and BI analyses; however, the ML analysis provided moderate support for the reciprocal monophyly of the latter sequences (comprising node D) and the Venezuela-Trinidad-Tobago lineage (node D).

In contrast, we identified three CYTB lineages within the western clade, as follows: the first includes all of the haplotypes from the Península de Paraguaná (hereafter the *Paraguaná*

lineage; Figure 9, node F); the second includes haplotypes from Colombia and the Venezuelan states Zulia and Mérida (hereafter the *northwestern South American lineage*; node H); and the third includes haplotypes from Panama (hereafter the *Panama lineage*; node I). All of the analyses provided strong support for the monophyly of both the Paraguaná and Panama lineages; however, the monophyly of the northwestern South American lineage was only moderately supported by the ML bootstrap analysis and was recovered with only weak support by the MP and BI analyses.

Analyses of the CYTB matrix did not provide strong support for any particular set of relationships among lineages of the western clade of *Marmosa robinsoni*. Model-based analyses recovered the (putative) northwestern South American lineage sister to the Panama lineage (node G) with negligible support, whereas results from the MP analysis showed a polytomy at the most basal node within the western clade (not shown). Thus, we tested whether the ML tree was significantly more likely than trees that lack node G. To do so, we used a one-tailed Shimodaira–Hasegawa test (Shimodaira and Hasegawa, 1999) as implemented in PAUP* 4.0 (Swofford 2002), with 1000 bootstrap replicates by resampling the partial likelihoods for each site (RELL model). That yielded *P*-values well above 0.05, indicating that (statistically) all compared topologies are equally good explanations for our CYTB dataset.

Results from phylogenetic analyses based on the nuclear OGT matrix—which include sequences representing each of the aforementioned lineages—recovered the eastern and western clades of *Marmosa robinsoni* as reciprocally monophyletic groups (Figure 10, nodes B and E, respectively). Nevertheless, as a result of the presence of missing data (see below), the monophyly of the western clade was not supported by the BI analysis, and it was only moderately by the bootstrapt MP and ML analyses. Topologies of the best trees that resulted

from the ML (Figure 10) and BI analyses, and that of the single tree found by the parsimony search were highly concordant. Within the eastern clade, two smaller clades were recovered, one representing the Venezuela-Trinidad-Tobago lineage (node C) and another formed by sequences from the Venezuelan states of Lara and Falcón (node D). All of the terminals within each of these small clades had the same base sequences, but some of them had large amounts of missing data (Table 6). Similarly, the three terminals for the western clade (node E) had the same base sequences, but the sample from the Cordillera de Mérida had a large amount of missing data (Table 6).

Ancestral area reconstructions.—Because phylogenetic analyses did not provide strong support for any relationship among lineages within the western clade of *Marmosa robinsoni*, we conducted ancestral area reconstructions based on three possible resolutions within that clade using the ML tree obtained from analysis of the CYTB data. These analyses rest on the assumption that samples from northwestern South America (mainland of northern Colombia and Venezuela) form a lineage—the latter was recovered in all of the phylogenetic analyses, but only moderately supported by the ML analyses (and weakly by the other two optimality criteria). All parsimony analyses optimized the coded areas in five steps. The distance between the two runs of the Bayesian analyses was 0.001, indicating that they had reached convergence. All analyses inferred the same ancestral area for *M. robinsoni*: the greater Maracaibo basin (Figure 11; region C). This was also true for various lineages within the species: the eastern clade, the western clade, and (at a shallower level) the (putative) northwestern South American and Paraguaná lineages. Moreover, all of the analyses inferred that the ancestor of the Panama lineage and its sister lineage (either the Paraguaná or the northwestern South American lineage) occurred also in the greater Maracaibo basin. Within the northwestern South American lineage, all analyses

suggested two possible, mutually exclusive scenarios: the first implied a single dispersal event from the greater Maracaibo basin (region C) to the west of the Serranía de Perijá (region B), and then a dispersal event back to the greater Maracaibo basin; the second scenario implied two independent dispersal events from the greater Maracaibo basin to the west of the Serranía de Perijá (region B).

Divergence-time estimation.—We conducted three analyses to estimate divergence times in *Marmosa robinsoni*, one for each possible resolution within the western clade (see above). For the first of these analyses we used the ML tree obtained produced with the CYTB data (Figure 9), and for the other two analyses we imposed topological constraints in this tree. Thus, for one of the analyses we enforced a sister-taxon relationship between the Panama and Paraguaná lineages, and for the other we enforced a sister-taxon relationship between the northwestern South American and Paraguaná lineages. These analyses yielded similar results; most of the estimates of time since ancestral divergence (stem origin) and of time to the most recent common ancestor of extant haplotypes (tmrca) correspond to Pliocene and Pleistocene events (Table 10).[4] The eastern and western clades of *M. robinsoni* were estimated to have diverged between ~3.33 and 3.91 Ma, but these estimates have wide 95% highest posterior densities (HPD) encompassing from the late Miocene to the early Pleistocene (Table 10). Based on mean estimates, extant haplotypes from within each of the two major clades shared a most recent common ancestor in the Pleistocene, but again each of the individual mean estimates had a wide 95% HPD (Table 10).

[4] We followed divisions of geologic time approved by the U.S. Geological Survey Geologic Names Committee (2010), which reflects ratified boundary estimates from the International Commission on Stratigraphy.

FIGURE 9.

The maximum-likelihood tree (-lnL 4122.5228) resulting from analysis of the cytochrome-*b* (CYTB) sequence data to assess the phylogeographic structure of *Marmosa robinsoni*; *M. xerophila* was designated as outgroup. Conventions for representation of nodal support, and of terminal names and geographic provenance are described in the caption to Figure 8.

Figure 9

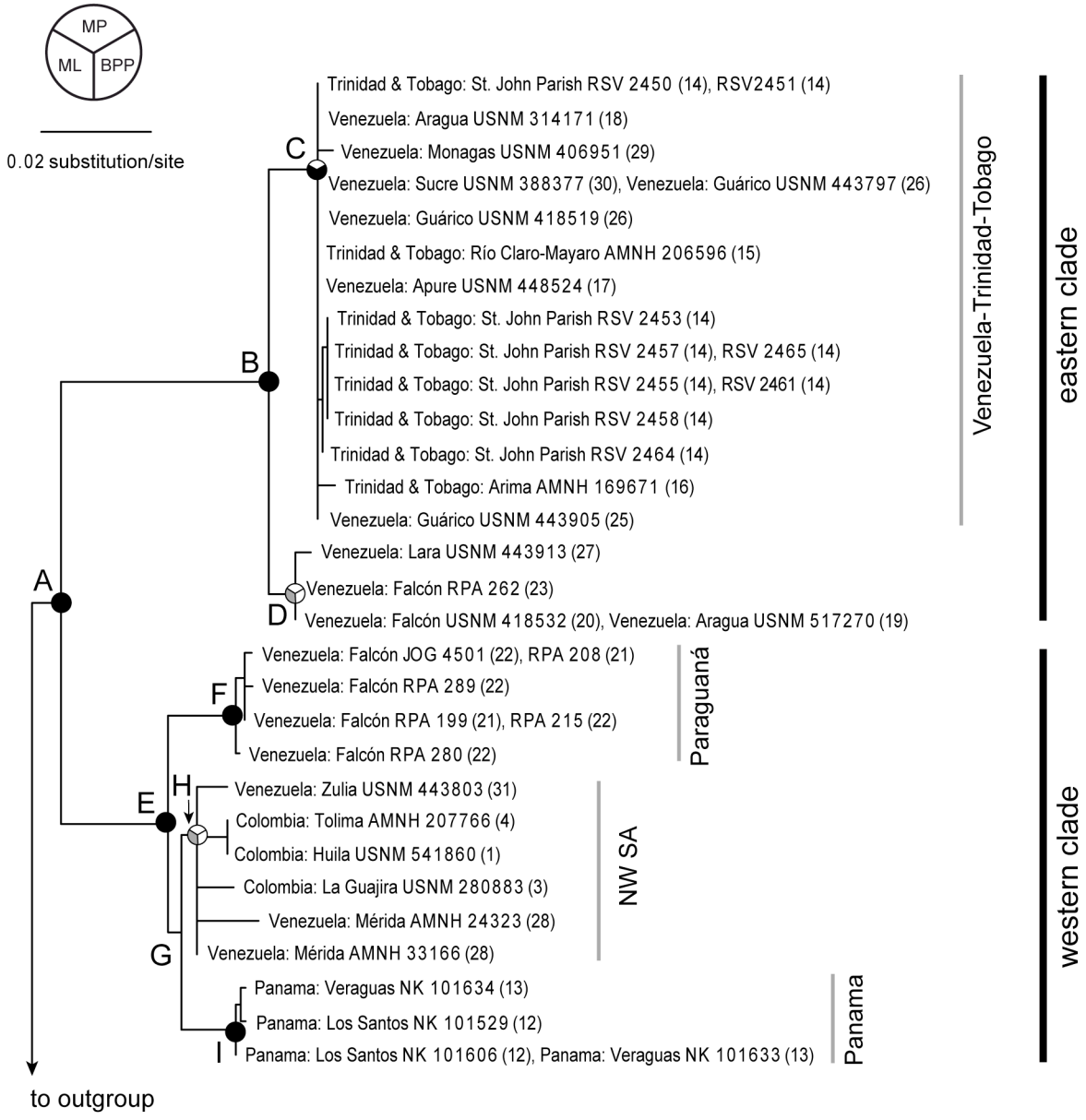

MP
ML
BPP
0.02 substitution/site
Trinidad & Tobago: St. John Parish RSV 2450 (14), RSV2451 (14)
Venezuela: Aragua USNM 314171 (18)
C
Venezuela: Monagas USNM 406951 (29)
Venezuela: Sucre USNM 388377 (30), Venezuela: Guárico USNM 443797 (26)
Venezuela: Guárico USNM 418519 (26)
Trinidad & Tobago: Río Claro-Mayaro AMNH 206596 (15)
Venezuela: Apure USNM 448524 (17)
Trinidad & Tobago: St. John Parish RSV 2453 (14)
B
Trinidad & Tobago: St. John Parish RSV 2457 (14), RSV 2465 (14)
Trinidad & Tobago: St. John Parish RSV 2455 (14), RSV 2461 (14)
Trinidad & Tobago: St. John Parish RSV 2458 (14)
Trinidad & Tobago: St. John Parish RSV 2464 (14)
Trinidad & Tobago: Arima AMNH 169671 (16)
Venezuela: Guárico USNM 443905 (25)
Venezuela-Trinidad-Tobago
eastern clade
Venezuela: Lara USNM 443913 (27)
A
Venezuela: Falcón RPA 262 (23)
D
Venezuela: Falcón USNM 418532 (20), Venezuela: Aragua USNM 517270 (19)
Venezuela: Falcón JOG 4501 (22), RPA 208 (21)
F
Venezuela: Falcón RPA 289 (22)
Venezuela: Falcón RPA 199 (21), RPA 215 (22)
Venezuela: Falcón RPA 280 (22)
Paraguaná
H
E
Venezuela: Zulia USNM 443803 (31)
Colombia: Tolima AMNH 207766 (4)
Colombia: Huila USNM 541860 (1)
Colombia: La Guajira USNM 280883 (3)
Venezuela: Mérida AMNH 24323 (28)
NW SA
G
Venezuela: Mérida AMNH 33166 (28)
Panama: Veraguas NK 101634 (13)
Panama: Los Santos NK 101529 (12)
I
Panama: Los Santos NK 101606 (12), Panama: Veraguas NK 101633 (13)
Panama
western clade
to outgroup

FIGURE 10.

The maximum-likelihood tree (-lnL 1350.8699) resulting from analysis of the O-linked N-acetylglucosamine transferase (OGT) sequence data to assess the phylogeographic structure of *Marmosa robinsoni*; *M. xerophila* was designated as outgroup. Conventions for representation of nodal support, and of terminal names and geographic provenance are described in the caption to Figure 8.

Figure 10.

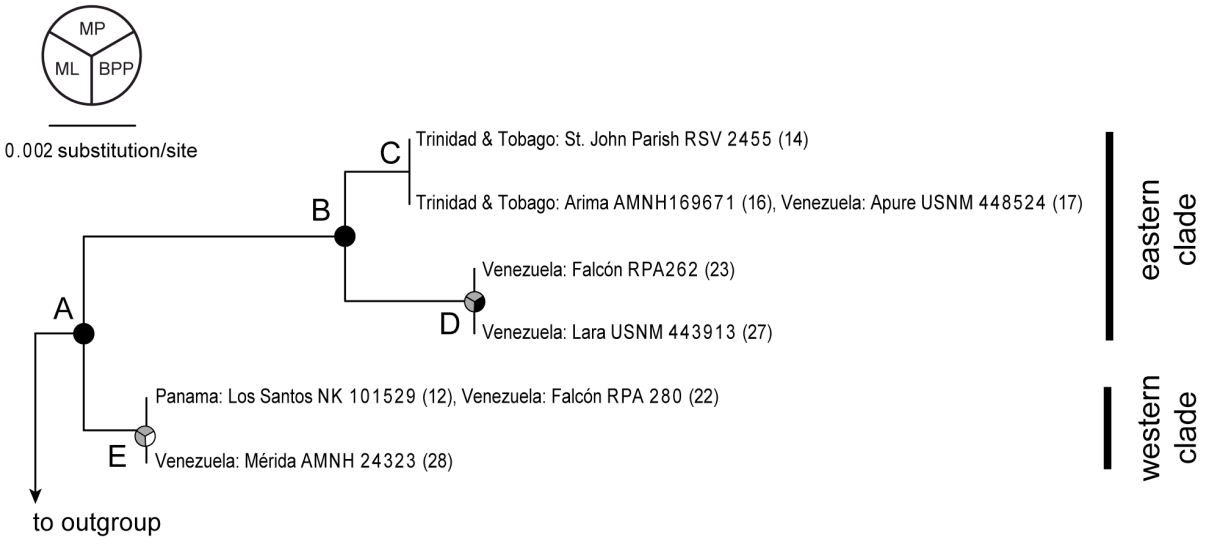

MP
ML
BPP
0.002 substitution/site
C
Trinidad & Tobago: St. John Parish RSV 2455 (14)
B
Trinidad & Tobago: Arima AMNH169671 (16), Venezuela: Apure USNM 448524 (17)
Venezuela: Falcón RPA262 (23)
A
D
Venezuela: Lara USNM 443913 (27)
eastern clade
Panama: Los Santos NK 101529 (12), Venezuela: Falcón RPA 280 (22)
E
Venezuela: Mérida AMNH 24323 (28)
western clade
to outgroup

FIGURE 11.

Results from parsimony and Bayesian reconstructions of ancestral areas onto the best tree resulting from maximum-likelihood analysis of the cytochrome-*b* (CYTB) sequence data (see Figure 9 and Materials and methods). Results from Bayesian reconstruction of ancestral areas are shown at each node of biogeographic interest. For each terminal, political unit (state, department, province, etc.) of collection locality, and an alphanumeric specimen identifier (from Table 6) are provided. Numbers in parentheses refer to localities mapped in Figure 7 and listed in the Gazetteer (Appendix 2). The northwestern South American lineage is abbreviated as "NW SA". Results of both parsimony and Bayesian ancestral area reconstructions based on alternative topologies within the western clade inferred the same ancestral areas (not shown).

Figure 11.

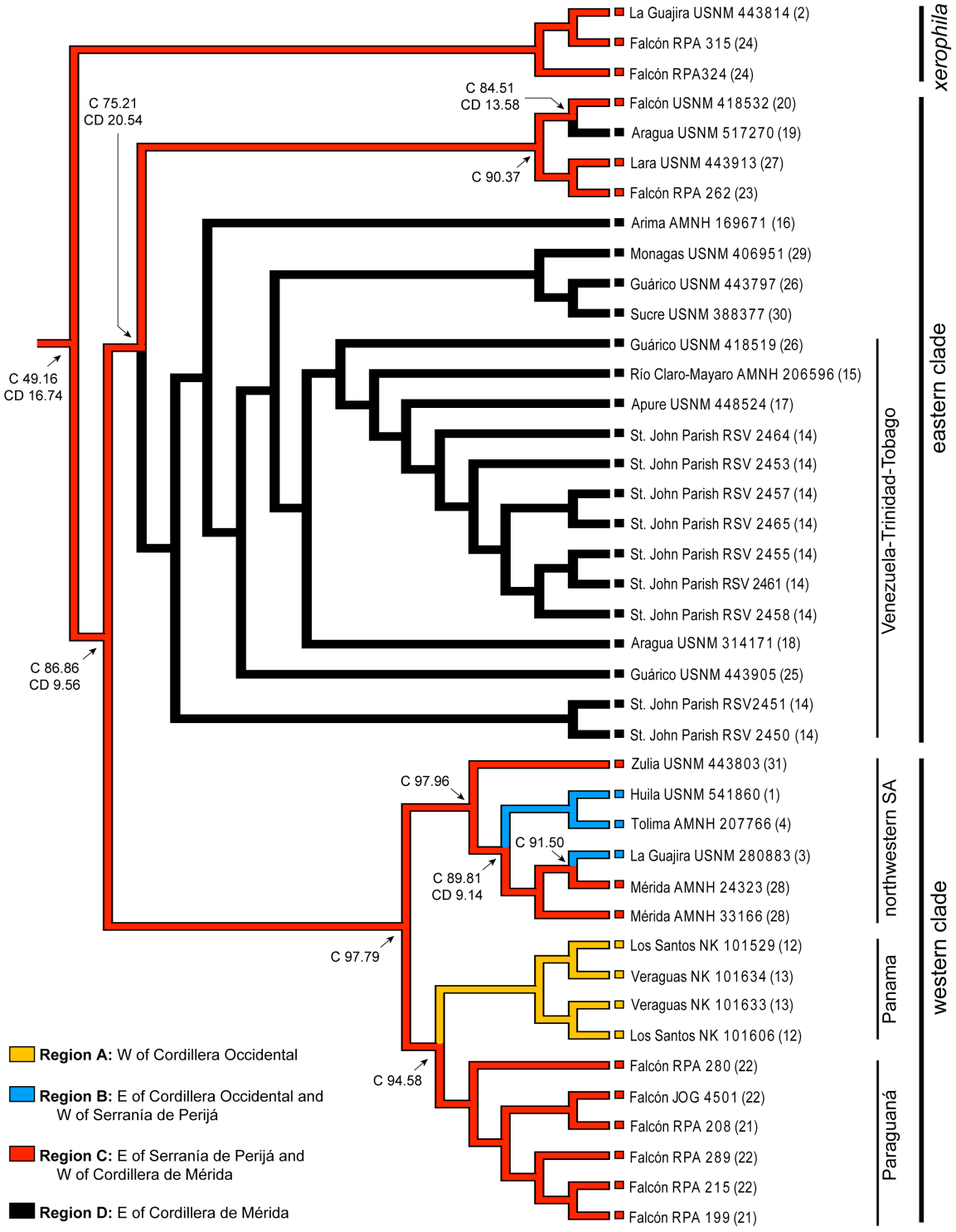

La Guajira USNM 443814 (2)
Falcón RPA 315 (24)
Falcón RPA324 (24)
Falcón USNM 418532 (20)
Aragua USNM 517270 (19)
Lara USNM 443913 (27)
Falcón RPA 262 (23)
Arima AMNH 169671 (16)
Monagas USNM 406951 (29)
Guárico USNM 443797 (26)
Sucre USNM 388377 (30)
Guárico USNM 418519 (26)
Río Claro-Mayaro AMNH 206596 (15)
Apure USNM 448524 (17)
St. John Parish RSV 2464 (14)
St. John Parish RSV 2453 (14)
St. John Parish RSV 2457 (14)
St. John Parish RSV 2465 (14)
St. John Parish RSV 2455 (14)
St. John Parish RSV 2461 (14)
St. John Parish RSV 2458 (14)
Aragua USNM 314171 (18)
Guárico USNM 443905 (25)
St. John Parish RSV2451 (14)
St. John Parish RSV 2450 (14)
Zulia USNM 443803 (31)
Huila USNM 541860 (1)
Tolima AMNH 207766 (4)
La Guajira USNM 280883 (3)
Mérida AMNH 24323 (28)
Mérida AMNH 33166 (28)
Los Santos NK 101529 (12)
Veraguas NK 101634 (13)
Veraguas NK 101633 (13)
Los Santos NK 101606 (12)
Falcón RPA 280 (22)
Falcón JOG 4501 (22)
Falcón RPA 208 (21)
Falcón RPA 289 (22)
Falcón RPA 215 (22)
Falcón RPA 199 (21)
C 84.51
CD 13.58
C 75.21
CD 20.54
C 90.37
C 49.16
CD 16.74
C 86.86
CD 9.56
C 97.96
C 91.50
C 89.81
CD 9.14
C 97.79
C 94.58
xerophila
eastern clade
Venezuela-Trinidad-Tobago
western clade
northwestern SA
Panama
Paraguaná
Region A: W of Cordillera Occidental
Region B: E of Cordillera Occidental and W of Serranía de Perijá
Region C: E of Serranía de Perijá and W of Cordillera de Mérida
Region D: E of Cordillera de Mérida

Table 10. Time since ancestral divergence (stem origin) and time to the most recent common ancestor (tmrca) of CYTB lineages of *M. robinsoni*. The values below resulted from three analyses: one with no topological constraint, one enforcing a sister relationship between the Paraguaná and Panama lineages, and another enforcing a sister relationship between the Paraguaná and the northwestern South American lineages. Estimates are in mega-annum (Ma; 1 Ma equals $1x10^6$ years); 95% highest posterior densities are shown within parentheses.

Clade/Linage	Not constraining topology Panama sister to NW SA		Constraining Paraguaná sister to Panama		Constraining Paraguaná sister to NW SA	
	Stem origin	tmrca extant haplotypes	Stem origin	tmrca extant haplotypes	Stem origin	tmrca extant haplotypes
Marmosa robinsoni	NA	3.91 (1.94–5.56)	NA	3.46 (1.96–5.58)	NA	3.33 (1.84–5.60)
Eastern clade	3.91 (1.94–5.56)	1.02 (0.40–1.45)	3.46 (1.96–5.58)	0.83 (0.41–1.45)	3.33 (1.84–5.60)	0.87 (0.40–1.48)
Venezuela-Trinidad-Tobago lineage	1.02 (0.40–1.45)	0.63 (0.13–0.66)	0.83 (0.41–1.45)	0.37 (0.13–0.66)	0.87 (0.40–1.48)	0.28 (0.13–0.65)
Western clade	3.91 (1.94–5.56)	1.94 (0.74–2.32)	3.46 (1.96–5.58)	1.32 (0.76–2.05)	3.33 (1.84–5.60)	1.53 (0.69–2.28)
Paraguaná linage	1.94 (0.74–2.32)	0.48 (0.08–0.50)	1.29 (0.63–2.05)	0.16 (0.08–0.48)	0.76 (0.57–2.00)	0.33 (0.08–0.47)
Panama linage	1.20 (0.46–1.81)	0.28 (0.03–0.34)	1.29 (0.63–2.05)	0.12 (0.04–0.33)	1.53 (0.69–2.28)	0.29 (0.04–0.35)
NW SA lineage	1.20 (0.46–1.81)	1.03 (0.30–1.37)	1.32 (0.76–2.05)	0.64 (0.36–1.60)	0.76 (0.57–2.00)	1.35 (0.31–1.40)
Panama + NW SA	1.94 (0.74–2.32)	1.20 (0.46–1.81)	NA	NA	NA	NA
Paraguaná + Panama	NA	NA	1.32 (0.76–2.05)	1.29 (0.63–2.05)	NA	NA
Paraguaná + NW SA	NA	NA	NA	NA	1.53 (0.69–2.28)	1.41 (0.57–2.00)

DISCUSSION

Biogeography of Marmosa robinsoni *and* M. xerophila.—Our reconstructions of ancestral areas in combination with our divergence-time estimates provide novel inferences about the biogeographic history of *M. robinsoni* and *M. xerophila*, and (to the best of our knowledge) reveal dispersal hypotheses for the first time in any widespread vertebrate species inhabiting these dry forests. In particular, our results suggest that the Cordillera de Mérida may have played a key role in the genetic divergence of eastern and western elements of the dry-forest biota. The common ancestor of the eastern and western clades of *M. robinsoni* was inferred to have occured in the greater Maracaibo basin (area C in Figure 7) about 1.84 to 5.60 Ma ago. Because most of the uplift of the Cordillera de Mérida—which had high exhumation rates from about 10 Ma until to 4 Ma (Bermúdez *et al.*, 2011)—occurred before the estimated divergence between the eastern and western clades, it is unlikely that uplift of this cordillera have created vicariance—in contrast to what has been suggested for other vertebrates (e.g. Littman *et al.*, 2000; Albert *et al.*, 2006; Schargel *et al.*, 2007). The Cordillera de Mérida and the string of lower cordilleras that almost connect the Merida-Trujillo massif with the Cordillera de la Costa (in north central Venezuela), however, might have together represented a barrier to dispersal and gene flow. This conclusion is also suggested by intraspecific geographic variation in qualitative morphological traits of several other small mammals, including *Zygodontomys brevicauda* and *Sylvilagus floridanus* (Voss, 1991: his Figures 24 and 40).

Our analyses also suggest the historical absence of effective barriers to gene flow among populations of *Marmosa robinsoni* on the northeastern Venezuelan mainland and the adjacent continental-shelf islands of Trinidad and Tobago. A recent origin for the eastern clade was suggested by the relative short time to the most recent common ancestor (tmrca) of analyzed

haplotypes, and the lack of phylogeographic structure within this clade. Strikingly, populations from north-central (locality 18) and northeastern Venezuela (localities 29, 30) and from the Venezuelan Llanos (localities 17, 25, 26) are intermingled with those from Trinidad (localities 15, 16) and Tobago (locality 14) in our ML topology (Figure 9). Two mutually exclusive scenarios that have been invoked to explain the presence of various mainland taxa on Trinidad and Tobago could account for the presence of *M. robinsoni* in these islands (e.g. Boos and Ratcliffe, 1985; Camargo *et al.*, 2009; Manzanilla *et al.*, 2009; Jowers *et al.*, 2011). One scenario implies that species dispersed to Trinidad and Tobago during the Miocene, when these present-day islands were connected to continental Venezuela (Liddle, 1946; Comeau, 1991), with subsequent vicariance separating the insular populations. The other scenario implies a dispersal event during the Pleistocene glacial cycles (Augustin *et al.*, 2004), when lowered sea levels exposed dry-land connections between Trinidad and mainland Venezuela, and between Trinidad and Tobago (Comeau, 1991; see also Murphy, 1997). Our estimates of tmrca for the Venezuela-Trinidad-Tobago lineage (Table 10) unambiguously support the latter (Pleistocene-glacial) scenario. Lastly, the Río Orinoco seems to have limited dispersal of *M. robinsoni* to southern Venezuela (south of that river), from where only one record of the species is known despite extensive small-mammal surveys conducted south of Río Orinoco.

Habitat fragmentation and eustatic fluctuations of sea level during the Pleistocene may also explain the origin of phylogeographic structure we discovered within the western clade of *Marmosa robinsoni*. Although our phylogenetic analyses did not allow us to robustly infer relationships among lineages within this clade, ancestral area reconstructions and dating analyses considering three alternative phylogenetic resolutions yielded similar results in several aspects of biogeographic interest. For example, all reconstructions inferred that the common ancestor of all

lineages within the western clade occurred in the greater Maracaibo basin. Both estimates of stem origin and tmrca of each individual lineage (Table 10) well postdate the uplift of the Cordillera de Mérida and marine transgression of the late Miocene (see Lovejoy *et al.*, 2006; Bermúdez, 2011). Instead, sea level and vegetation changes during glacial and interglacial periods (Webb and Bartlein, 1992) may have played an important role in the differentiation among these lineages. Climatic changes during these periods may have fragmented or connected patches of dry forest and rain forest. Although *M. robinsoni* has been collected in a few sites with mesic conditions, the species is predominately distributed in dry-forest habitat; therefore, it is likely that isolation of dry-forest habitat during interglacial periods may have decreased gene flow among populations. In addition, current sea levels in the Golfo de Venezuela are remarkably shallow, with most depths less than 45 meters, and a maximum depth of ~75 meters (see Zeigler, 1964; DMAHTC, 1981). Therefore, during glacial periods, broad land connections must have existed between the present-day Península de Paraguaná and northeastern Colombia, including intervening areas currently covered by the Caribbean Sea. These broad land connections may have allowed the most recent common ancestor of lineages within the western clade to disperse widely from the greater Maracaibo basin (including the Península de Paraguaná) to northwestern Colombia during glacial periods. Sea level rise during subsequent interglacial periods could have isolated populations in Paraguaná from the mainland (see Rodríguez, 2000; Nores, 2004), a phenomenom that might also explain the differentiation of other vertebrates endemic to that peninsula (see Anderson, 2003; Gutiérrez and Molinari, 2008 and references therein). Under this scenario, populations of *M. robinsoni* eventually dispersed through northern Colombia and reached Panama well after the final closure of the Panamanian

Isthmus (Bartoli *et al.,* 2005) and the subsequent pulses of major faunal exchanges of the Great American Biotic Interchange (Woodburne, 2010).

Biogeography of dry-forests of northern South America and future directions.—Our results suggest the historical importance and probably long-term continuity of a dry-forest refugium in the greater Maracaibo basin. Floristic affinities among disjunct dry forests of South America formed the basis of the Dry Forest Refugia Hypothesis, which states that present-day dry forests are remmants of a more widespread dry forest biome that existed during the cool, dry conditions of the Last Glacial Maximum, but contracted during the current interglacial period (Prado and Gibbs, 1993; Pennington *et al.*, 2000; but see Mayle, 2004). Future biogeographic studies of other dry-forest organisms in northern South America are necessary to test the generality of our results. Indeed, comparative phylogeographic analyses, ideally based on geographically dense sampling and multilocus approaches, coupled with ecological niche modeling analyses represent the most promising approach to gain insights on the poorly studied, but biogeographically fascinating dry forest of northern South America (Kozak *et al.*, 2008; Peterson *et al.*, 2011).

CHAPTER 4

Can interspecific competition cause allopatry?

Insights from ecological niche models of mouse opossums (genus *Marmosa*)

INTRODUCTION

Despite ongoing debate about species concepts in the systematic literature, most researchers agree that the origin of independent lineages in allopatry is the prevalent mode of animal speciation (Mayr, 1963; Futuyma and Mayer, 1980; Coyne, 1992; de Queiroz, 1998, 2007; Futuyma, 1998; Mayden, 1999; Barraclough and Vogler, 2000; Wheeler and Meier, 2000; Salomon, 2001; Gavrilets, 2003; Coyne and Orr, 2004; Baker and Bradley, 2006; Sobel *et al.*, 2009; but see Via, 2001; Berlocher and Feder, 2002; Fitzpatrick and Turelli, 2006). Geographic isolation, which has key ramifications for population-level divergences whether or not speciation eventually occurs (e.g., Holycrossa and Douglasb, 2007; Kraaijeveld *et al.*, 2009), can occur through two different mechanisms: either due to the presence of a barrier to dispersal, or because individuals from a previously widespread population have become extinct (Mayr, 1963; Futuyma, 1998). As perceived by most authors either explicitly or implicitly, and as defined in several classic textbooks, the barriers that promote allopatry are physical or climatic in nature (Mayr, 1963; Futuyma, 1998; Coyne and Orr, 2004; Lomolino *et al*., 2006). Typical examples of these barriers include mountain ranges, rivers, and marine transgressions for terrestrial organisms; or the emergence of land bridges severing bodies of water for aquatic species. The disappearance of suitable habitat as a consequence of climatic changes can also act as a vicariant agent (Pyron and Burbrink, 2010). These notions, however, neglect the possibility that geographic isolation—and therefore allopatric speciation—could also be promoted by the emergence and persistence of biotic interactions acting as barriers to dispersal. Examples of these biotic interactions might include the presence of particularly effective predators, strong competitors, or the absence of important prey or essential mutualistic species in intervening areas of otherwise connected populations. The possibility that biotic interactions could create and/or

maintain vicariance has been contemplated (Wiens, 2004), but little empirical evidence exists to support the idea (e.g., Jaeger, 1971). We explore this possibility, specifically with regard to interspecific competition.

A battery of technological, methodological, and conceptual advances has empowered researchers to document how competition acts as an important evolutionary force. Empirical evidence demonstrates that interspecific competition is capable of driving phenotypic diversification (e.g., Schluter, 2000; Kingsolver and Pfennig, 2004; Hone and Benton, 2005; Moen and Wiens, 2009), causing extinctions (e.g., Mooney and Cleland, 2001; Banks *et al.*, 2008), and shaping both species' distributional ranges (e.g., Bullock *et al.*, 2000; Leathwick and Austin, 2001; Leathwick, 2002; Arif *et al.*, 2007; but see Cadena, 2007) and the composition of communities (e.g., Cooper *et al*., 2008; Kamilar and Ledogar, 2011; but see Götzenberger *et al.*, 2011). In particular, one methodological advance allows for testing the geographic predictions of competitive exclusion based on GIS-based niche modeling (Anderson *et al.*, 2002b). The principle of competitive exclusion states that species that are ecologically too similar will be unable to coexist due to exclusion of the inferior competitor (Gause, 1934; see also Hardin, 1960). This principle and niche theory lead to the following predictions regarding the distributional patterns of a pair of species experiencing competitive exclusion (Anderson *et al.*, 2002b; see Materials and Methods for assumptions). If competitive exclusion does not occur between the focal species pair, then records of the two species should be present in approximately equal proportions in areas of potential sympatry (where both species are predicted to be present due to an overlap between their existing fundamental niches) along real contact zones. Alternatively, if competitive exclusion occurs between the focal species pair, then the

superior competitor will predominate (in terms of the number of occupied localities) in areas of potential sympatry along real contact zones.

In order to test these hypotheses, the focal species pair must meet certain requirements (Anderson *et al.*, 2002b). First, either prior studies or examination of occurrence records should indicate that the species do not co-occur broadly in sympatry, but rather show parapatric distributions with narrow contact zones. This requirement implies that competition may exist and yield geographic manifestations in their occupied distributional areas. Secondly, one or more areas of potential sympatry along real contact zones must exist, so competitive exclusion could occur in these areas. In addition, it is desirable (but not required) that the focal species possess two characteristics commonly presented by species involved in intense competition: morphological similarity (Darwin, 1859; Gause, 1934; MacArthur and Levins, 1967; see Abrams, 1983 for a review; e.g. Juliano and Lawton, 1990) and a close phylogenetic relationship (Darwin, 1859; e.g. Burns and Strauss, 2011; Violle *et al.*, 2011).

In this study, we test the aforementioned hypotheses for a pair of sister species of small didelphid marsupials ("mouse opossums"), *Marmosa robinsoni* and *M. xerophila*, and explore the possibility that competitive exclusion might have created and/or maintained geographic isolation of some populations. Although these correlational methods cannot conclusively demonstrate competitive exclusion, they can generate specific and directional hypotheses to be tested in experimental field and laboratory studies (e.g., Koplin and Hoffmann, 1968; Brown, 1971; Murie, 1971; Chappell, 1978; Higgs and Fox 1993; Thompson and Fox, 1993; Eccard and Ylönen, 2002; LeBrun *et al.*, 2007). If corroborated, such a phenomenon would represent a novel case of competition acting as a biotic barrier that creates and/or maintains geographic isolation. This possibility has implications for research on population-level divergence, and even

speciation itself, as competition might represent a cryptic yet currently overlooked factor driving genetic differentiation.

MATERIALS AND METHODS

Focal species and requirements for testing the geographic predictions of competitive exclusion.—Marmosa robinsoni and *M. xerophila* fulfill the requirements for testing the geographic predictions of competitive exclusion. The distribution of *M. xerophila* is restricted to xerophytic lowland habitats of northeastern Colombia (Departamento La Guajira) and northwestern Venezuela (Estados Falcón and Zulia), at elevations from sea level to ca. 350 m (Anderson *in litt.;* Rossi *et al.*, 2010; Appendix 3). *Marmosa robinsoni* has a much wider distribution, being found in Panama (including the islands of Isla del Rey and Isla Saboga in the Golfo de Panamá), Colombia, Venezuela (including Isla de Margarita), Trinidad and Tobago, and Grenada. The majority of known records of *M. robinsoni* correspond to deciduous forests, savannas, and xeric shrublands at elevations from sea level to ca. 1200 m; however, the species has also been collected in very few localities with more mesic conditions at 1200–2000 m (Appendix 3). Furthermore, it inhabits mesic habitat in the tiny, isolated Cerro Santa Ana, on the Península de Paraguaná in northern Venezuela, where evergreen and cloud forests are present at low elevations (350–700 m; see Anderson *in litt.*). The distributional ranges of these species do not broadly overlap, with only one real, narrow contact zone documented to date: on the Península de Paraguaná at the base of the Cerro Santa Ana and its immediately surrounding lowlands (ca. 80–120 meters elevations; Figures 1 and 2; Anderson *in litt.*; see also Bisbal, 1990; Appendix 3). Records of both species occur ca. 14 km apart in mainland Estado Falcón and ca.

46 km apart near the base of the Península de La Guajira; hence, despite relative geographic proximity of both species in these two areas, currently available distributional data do not allow us to consider them as a contact zone. These distributional patterns fulfill the requirement for testing the geographic prediction of competitive exclusion (Anderson *et al.*, 2002b). In addition, the two species are morphologically similar (Rossi *et al.*, 2010), and phylogenetic analyses have yielded strong evidence of a sister-taxon relationship between them (Chapter 3; see also Gutiérrez *et al.*, 2010). Moreover, *M. robinsoni* and *M. xerophila* appear similar with regard to feeding habits and habitat use (Alvizu and Aguilera, 1998; Zambrano, 2001; Thielen *et al.*, 1997, 2009). These characteristics make our focal species excellent candidates for the current study.

Data sources.—To model the existing fundamental niche and identify the abiotically suitable areas for each species (see Peterson *et al.*, 2011 for terminology), two sources of information are necessary: geographic coordinates of sites where the species is known to be present (occurrence records), and environmental data from such sites. We gathered high-quality occurrence records by using only information from voucher specimens with taxonomic identification derived either from our examination or from a recent revisionary work (Rossi *et al.*, 2010; Appendix 3). Several qualitative morphological traits permitted unambiguous taxonomic identifications of these taxa. Key among these, the rostral process of the premaxillae is almost always distinct in *Marmosa robinsoni* but absent in *M. xerophila* (Rossi *et al.*, 2010). In addition, the rostrum is proportionately longer and more slender and the orbits proportionately smaller in *M. robinsoni* than in *M. xerophila*; the postorbital processes are less often distinct in *M. robinsoni* than in *M. xerophila*; and the temporal ridges are less strongly convergent posteriorly in *M. robinsoni* than in *M. xerophila*. Regarding external traits, the dorsal pelage of *M. robinsoni* is usually darker than that of *M. xerophila*; the ventral pelage of *M. robinsoni* is

usually yellowish, whereas the ventral pelage of *M. xerophila* is usually whitish; and the lateral zones of gray-based ventral fur are more conspicuous in *M. robinsoni* than in *M. xerophila* (Rossi *et al.*, 2010; see also Rossi, 2005; and Chapter 2). Genetic data support the species-level distinctiveness of these two taxa (see above).

We georeferenced all occurrence records using information from collectors' field notes, specimen tags, and publications, and then consulting topographic maps, gazetteers, and other sources (see Appendix 3), with the exception of those cases for which collectors reported coordinates (either in their field notes or specimen tags). We also refined georeferenced occurrence records in Rossi *et al*. (2010), which were too coarse for the present niche modeling analyses. Because georeferencing errors can misinform the algorithms used to create niche models (see below), we discarded occurrence records whose estimated georeference errors exceeded 5 km in mountainous areas with high topographic relief (elevation >500 m) and 10 km in much more climatically homogeneous lowland areas (below 500 m elevation). In addition, since clusters of localities—typically resulting from more sampling in areas easily accessible to researchers (Reddy and Dávalos, 2003; Hortal *et al.*, 2008)—might create bias in environmental space, we followed Anderson and Raza (2010) in randomly filtering localities of each species to obtain the maximum number that were at least 10 km apart. When multiple equally optimal solutions were possible for a given cluster of localities, we retained the combination of localities with the lowest total possible georeference error. Final (filtered) datasets contained 133 unique localities for *M. robinsoni* and 10 for *M. xerophila* (Appendix 3).

For the environmental data, we used 19 bioclimatic variables from WorldClim 1.4 (Hijmans *et al.*, 2005; http://biogeo.berkeley.edu/worldclim/worldclim.htm, at 30" resolution (0.93 km x 0.93 km = 0.86 km^2 at the equator). These variables are based on average monthly

climatic data and reflect various aspects of temperature, precipitation, and seasonality. They are likely important in determining species distribution and have been used successfully for small non-volant mammals in the region (e.g., Anderson and Raza, 2010; Anderson and Gonzalez, 2011).

Study region.—The selection of the study region is a critical issue in model calibration (VanDerWal *et al.*, 2009); most niche-modeling algorithms based on presence-only data characterize the environmental conditions that the species is known to inhabit by comparing them with conditions available in the study region (Phillips *et al.*, 2006; Elith *et al.*, 2006). For example, it has been shown that excessively large study regions negatively affect model evaluation (Lobo *et al.*, 2008). In particular, study regions for calibration and evaluation should not include areas that might contain suitable environmental conditions for the species but that it does not occupy because of either: 1) dispersal limitations (e.g., via the presence of physical barriers to dispersal) or 2) biotic interactions with other species (e.g., the presence of a stronger competitor; Anderson and Raza, 2010; Barve *et al.*, 2011; Peterson *et al.*, 2011). Clearly, detailed information regarding dispersal limitations and biotic interactions generally is difficult to obtain (and often represents one of the goals of the modeling exercise). Nevertheless, reasonable study regions can be approximated by taking into account known occurrence records for both the focal species and closely related species, as well as the distributions of major vegetation types.

We selected study regions based on these principles and using a set of simple operational rules. For each species, we created minimum convex polygons (using Hawth's Analysis Tools for ArcGIS ver. 3.27; Beyer, 2004) surrounding major groups of occurrence records, and then delimited regions for background selection by setting buffers of 0.5 decimal degrees around each

polygon. Because occurrence records of *M. robinsoni* are geographically distributed in three major groups, the study region for this species is comprised of three sections: one enclosing occurrence records from northeastern Colombia, northern Venezuela, and the islands of Trinidad, Tobago, and Grenada; another for records from the upper valley of the Río Magdalena in Colombia; and one containing records from Panama (Figure 12). Only one polygon (and its corresponding buffer) was needed to create the study region of *Marmosa xerophila* (Figure 13). When calibrating models for each species, MAXENT sampled background data of environmental variables only from study regions (i.e., within the minimum convex polygons and their respective buffers), by use of a mask as a dummy variable.

These study regions likely match the relevant assumptions of modeling much more closely than the excessively expansive study regions typically employed in recent studies. However, we make the cautionary note that the study regions partially overlap, and therefore—if competitive exclusion plays a large role in reducing either or both of the species' distributions—these study regions may partially violate the assumptions of modeling and lead to underestimates of their niches. Such a possibility seems more problematic for *Marmosa xerophila* (Figure 13), which has a limited distribution surrounded by records of *M. robinsoni*; in contrast, *M. robinsoni* (Figure 12) inhabits broad and varied geographic areas, most of them without the possibility of contact with *M. xerophila*. If so, the niche models for *M. xerophila* may underestimate its abiotically suitable areas.

Tuning MAXENT settings, calibration of preliminary models.—To model the species' existing fundamental niches, we employed the software MAXENT ver. 3.3.3h, which implements the maximum entropy method (Phillips *et al.*, 2006; Phillips and Dudík, 2008). This presence-background modeling technique has performed well in recent comparisons with other such

techniques (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Wisz *et al.*, 2008; see also Phillips, 2008). To produce the best possible models—i.e. those with optimal complexity and the least overfitting—we conducted "model tuning." We first created preliminary models of each species to identify the combination of feature classes (in the case of *Marmosa robinsoni*) and regularization multiplier (for both species; see below). Since we had only a few occurrence records for *M. xerophila* (which should require very simple models), we used the simple combination of feature classes suggested by default settings and created preliminary models by varying only the regularization multiplier. In contrast, for *M. robinsoni*, represented by numerous occurrence records, we created preliminary models varying both feature classes and regularization multiplier values.

Together, feature class and regularization multiplier affect model complexity. The regularization multiplier controls the strength of the penalties for complex models (the stronger the multiplier, the stronger the penalty for a complex model; Phillips *et al.*, 2006; Warren and Seifert, 2011). Complex models, unfortunately, are more prone to overfitting. Here, the term overfitting refers to situations in which a model is more complex than the real relationships between the species' niche and the examined environmental variables (Anderson and Gonzalez, 2011; Peterson *et al.*, 2011). Feature classes represent the kinds of mathematical responses that the program is allowed to consider. For *M. robinsoni*, we considered combinations of feature classes that were judged to be reasonable given the number of occurrence records available (see Phillips *et al*. 2006; Phillips and Dudík, 2008; Anderson and Gonzalez, 2011), as follows: linear, quadratic, hinge features (LQH); linear, quadratic, product features (LQP); linear, quadratic, product, hinge features (LQPH), linear, quadratic, product, threshold features (LQPT), linear, quadratic, product, hinge, threshold features (LQPHT; the default combination of feature classes

for this number of records). For *M. xerophila*, we used linear and quadratic features (LQ; the default combination of feature classes for this number of records). For each of these instances, we constructed models using regularization multiplier values of 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0, and implemented replicates to identify the settings that led to the highest performance on independent data (see below).

Tuning MAXENT settings, evaluation of preliminary models.—We employed threshold-independent and threshold-dependent criteria to evaluate two aspects of preliminary-model performance: 1) the degree to which they avoided *overfitting* and 2) their *discriminatory power*. Our primary criterion for these evaluations was a model property that we refer to as *least degree of overfitting*. Overfit models underestimate species' existing fundamental niches, with various detrimental effects (Phillips and Dudík, 2008; Anderson and Raza, 2010; Anderson and Gonzalez, 2011). We assessed overfitting with both a threshold-independent and a threshold dependent approach. For the former, we used AUC_{Diff} (Warren and Seifert, 2011), which is based on the area under the curve (AUC) of the receiver operating characteristic (ROC) plot. For any given model, AUC_{Diff} equals its calibration AUC minus its evaluation AUC (AUC_{Train} - AUC_{Test} in Warren and Seifert, 2011). Because overfitting typically results in high calibration AUCs and low evaluation AUCs, the optimality criterion implemented herein preferred MAXENT settings that yielded the lowest possible AUC_{Diff}. We also used omission rate (OR), a threshold-independent measure, to assess overfitting. An OR indicates the proportion of the localities of the focal species that fall outside of (are omitted from) areas predicted to be suitable by the model (Anderson *et al.*, 2003; Phillips *et al.*, 2006). Overfit models tend to yield large omission rates. Because of this, the optimality criterion preferred those MAXENT settings that yielded the least possible ORs and best approximated to the theoretical expectation of the thresholding rule

applied. To calculate the ORs, we applied the 10 percentile threshold (i.e. 10 percentile training omission threshold of MAXENT; "T10" of Pearson *et al.*, 2007). When this threshold rule is applied, an ideal model is expected to yield approximately 10% omission in an independent, unbiased sample of localities of the species (Phillips and Dudík, 2008).

Our secondary criterion for preliminary-model evaluation, *high discriminatory power,* refers to models' capacity to correctly distinguish between unsuitable and suitable conditions for the focal species. This desirable property was gauged with a threshold-independent measure, the AUC of the ROC plot obtained based on evaluation data. This optimality criterion preferred Maxent settings that yielded the highest evaluation AUC.

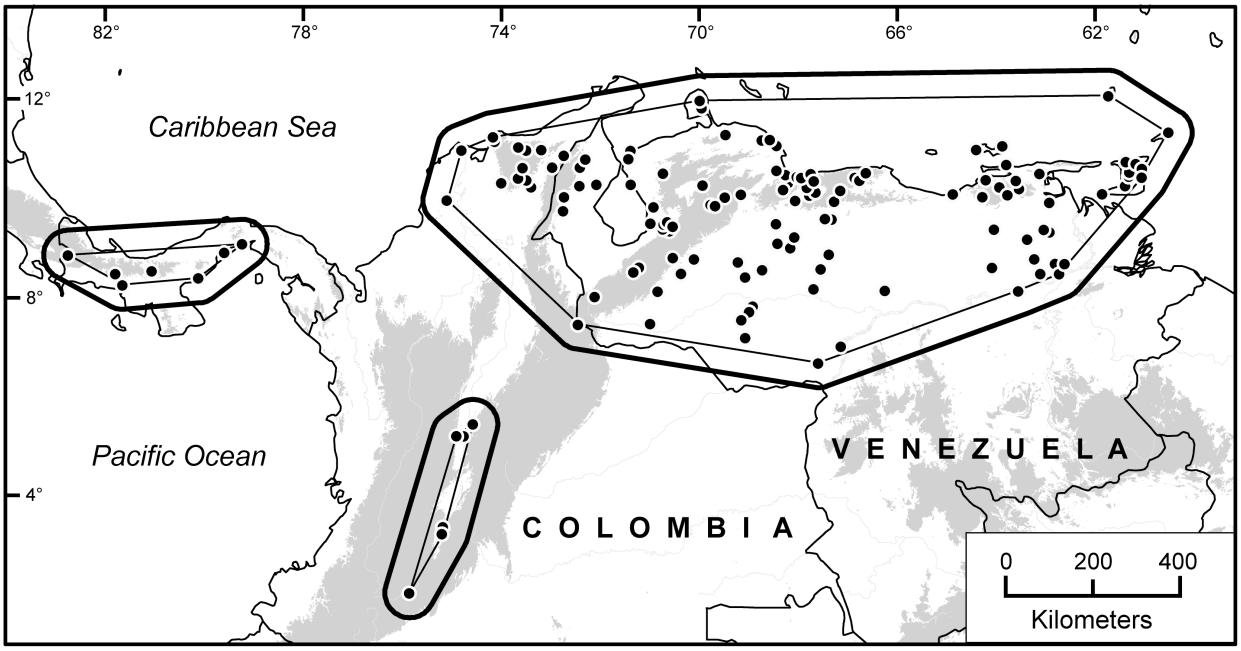
To implement these threshold-dependent and threshold-independent measures of model performance, we cross-validated preliminary models, with five random replicates for *M. robinsoni* and ten for *M. xerophila.* The ten partitions for the latter species allowed assessment of model performance and significance with the n-1 jackknife approach proposed by Pearson *et al.* (2007), for cases in which only a small number of records are available. For *M. robinsoni*, we implemented k-fold cross validation, with k = 5 groups (Peterson *et al.*, 2011). These numbers of partitions per species allowed us to produce final models with similar numbers of occurrence records; thus, we expect that optimal settings selected on the basis of preliminary model performances will be optimal to calibrate the final models.

Assessments of significance of preliminary models.—We assessed the significance of the preliminary models built with the MAXENT settings that yielded optimal performance using each individual replicate generated during the tuning experiments. For each model, we converted the continuous predictions produced by MAXENT into binary predictions by applying the 10 percentile threshold. We then used one-tailed binomial probabilities to determine whether

FIGURE 12.

Spatially filtered localities of and study region used to calibrate preliminary and final models of existing fundamental niche of *Marmosa robinsoni*. For each section of the study region, minimum convex polygons (thin lines) and their corresponding buffer (thick lines) are indicated (see Materials and Methods). Shaded areas represent elevations ≥ 500 m.

Figure 12.


82°
78°
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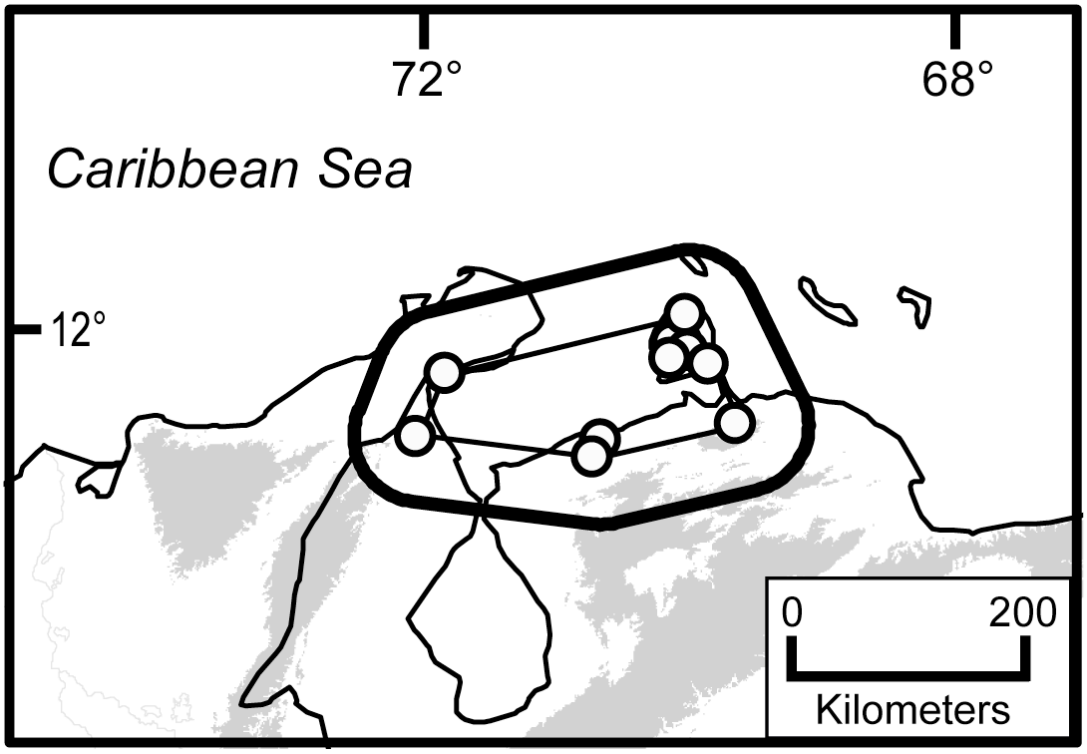
70°
66°
62°
12°
8°
4°
Caribbean Sea
Pacific Ocean
COLOMBIA
VENEZUELA
0
200
400
Kilometers

Figure 13.

Spatially filtered localities of and study region used to calibrate preliminary and final models of existing fundamental niche of *Marmosa xerophila*. Minimum convex polygon (thin line) and its corresponding buffer (thick line) are indicated (See Materials and Methods). Shaded areas represent elevations ≥ 500 m.

Figure 13.



evaluation localities fell into regions of predicted presence more often than expected by chance (Anderson *et al.*, 2002a; Fielding, 2002; Phillips *et al.*, 2006).

We visually inspected geographic projections of preliminary models made with the settings that led to the best performance. For each species, we projected those preliminary models produced by MAXENT onto a rectangular area surrounding the *M. robinsoni* study region and averaged the replicates. We selected this area because we later used the study region of *M. robinsoni* to identify areas of potential sympatry (see below). In our visual inspections, we searched for high predictions in regions that should be considered unsuitable these typically dry-forest species.

*Calibration of final models***.—**We used the best MAXENT settings to calibrate final models for our focal species with all of the filtered occurrence records available for each species. Lastly, to confirm that the models do not yield strong predictions in areas with unreasonably mesic and/or cold conditions, we visually inspected geographic projections of final models onto the study region of *Marmosa robinsoni* (following the criteria explained earlier; see *Tuning MAXENT settings, calibration of preliminary models*).

Test of predicted geographic patterns of competitive exclusion.—The final model of existing fundamental niche of each species was projected onto geographic space to identify abiotically suitable areas and areas of potential sympatry. These projections were made onto rectangular environmental layers (extent: 10–13° N and 60–76° W) that included the northern portion of the occupied distributional area of *M. robinsoni* and the entire occupied distributional area of *M. xerophila*. We selected this region because we were primarily interested in identifying areas of potential sympatry—i.e., areas with suitable climatic conditions for both

species—adjacent to real contact zones. To identify areas of potential sympatry, we superimposed the binary predictions of both models in this region.

We analyzed the proportions of species records in areas of potential sympatry along their real contact zone, directly testing the geographic pattern predicted under competitive exclusion (Anderson *et al.*, 2002b). We tested for the patterns expected under competitive exclusion under two scenarios, both assessed in areas of potential sympatry along the real contact zone: first, one species consistently dominates; and second, each species dominates wherever environments are more suitable for it than for the other species. In the first scenario, if neither species consistently excludes the other—assuming both are equally likely to be captured by the sampling methods used to obtain the occurrence records, see below—records of the two species should be present in approximately equal proportions in areas of potential sympatry along their real contact zone. Deviations from expectated values generated from overall proportions of (filtered) unique species localities were determined using two tailed tests (χ^2 statistic). To avoid bias toward the more widely distributed species. The latter test was conducted generating expected values using unique localities of each species only in the greater Maracaibo basin (27 of *M. robinsoni*; 10 of *M. xerophila*). Based on known natural history information (Anderson *in litt.*; Handley, 1976; Thielen *et al.*, 1997; Alvizu and Aguilera, 1998; Zambrano, 2001; Rossi *et al.*, 2010), the assumption regarding probability of capture (see above) seems reasonable for our focal species.

For the second scenario, we examined areas of potential sympatry in more detail, and determined which species was more strongly predicted in each pixel. We used this information to assess the predicted outcome of competition between the species, if the relative strength of the prediction (environmental suitability) influenced that interaction. In this scenario, a stronger

model prediction for a species indicates a higher likelihood of being present (in comparison with the other species, which showed a weaker prediction at that particular site [= pixel]).

RESULTS

Performance and significance of preliminary models.—Among all 200 preliminary models of *Marmosa robinsoni*, those that showed the least overfitting and the highest discriminatory power were calibrated with linear, quadratic, and hinge (LQH) feature classes and a regularization multiplier value of 2.5. Using this regularization multiplier value, the average evaluation omission rate (OR) yielded by LQH feature classes (13.45% omission) was both the lowest and the closest to the theoretically expected omission (i.e., 10.00%) for the applied 10 percentile threshold rule. Each of the five preliminary models calibrated with those settings predicted evaluation localities significantly better than a random model (Peterson *et al.*, 1999, 2004). Also, using this regularization multiplier, the LQH feature classes yielded the lowest average AUC_{DIFF}. With regard to discriminatory power, the usage of the LQH features and a regularization multiplier value of 2.5 also yielded the highest average evaluation AUC. Based on these results, we calibrate the final model of *M. robinsoni* using the LQH feature classes and a regularization multiplier value of 2.5.

As mentioned earlier, we used default feature classes to calibrate the model of the existing fundamental niche of *Marmosa xerophila* (i.e. linear and quadratic; LQ)—and the regularization multiplier selected as optimal was 1.5. That value yielded the lowest average evaluation omission rate (20.00%). This omission rate is higher than that theoretically expected (10.00%) for the used threshold rule; this probably reflects the inclusion of a single occurrence record used for evaluation in each replicate, and possibly also the low number of records used for

calibration in each iteration. The small study region, which resulted in a very large proportional predicted area (ca. 73% on average for the ten replicates), probably explains the insignificant value resulting from the jackknife method of Pearson *et al.* (2007; $P = 0.755$).

Visual inspections indicated reasonable predictions for each species. Specifically, for *M. robinsoni* the map of the average of the geographic projections of the preliminary models produced by optimal settings did not reveal strong predictions for areas that are unreasonably mesic and/or cold for the species. The corresponding map for *M. xerophila* indicated strong prediction only for reasonable areas, for example showing low prediction for cool, wet sections of the Serranía de San Luis.

Abiotically suitable areas and areas of potential sympatry.—Superimposition of final models of abiotically suitable areas for the two species (Figures 14 and 15) revealed limited areas of potential sympatry (Figure 16). The models predicted potential sympatry in the northern extreme of Península de La Guajira (northeastern Colombia); lowlands of the Estado Falcón in northwestern Venezuela; narrow strip-shaped coastal areas of north central and northeastern Venezuela (including the Península de Paria); and in the islands of Aruba, Curacao, Bonaire, Margarita, Tobago, St. Lucia, and some of the smaller islands nearby. Examination of multivariate environmental similarity surfaces (as reported by Maxent; see Elith *et al.*, 2010) indicated that no areas of potential sympatry showed environmental variables outside the range present in the calibration data.

Species predominance in areas of potential sympatry along real contact zones via binary tests.—*Marmosa xerophila* predominated in areas of potential sympatry along its contact zone with *M. robinsoni* (on the Península de Paraguaná; Figure 17, Appendix 3). Seven collection localities fell in such areas, two corresponding to *M. robinsoni* and five to *M. xerophila*. This ratio

significantly deviated from species' relative proportions expected by chance (χ^2=6.997, *P*=0.03). Inspection of the observed counts revealed that the number of localities of *M. xerophila* was higher than expected by chance.

Comparison of prediction strengths in areas of potential sympatry along the real contact zone.—Along the real contact zone and nearby areas in the Estado Falcón, localities of each species fell in areas more strongly predicted for that same species, with few exceptions (see below). *Marmosa xerophila* was more strongly predicted in most of the Península de Paraguaná, and in part of the "mainland" (i.e. not peninsular) Estado Falcón (Figure 17). On the other hand, *M. robinsoni* was more strongly predicted in the Istmo de Médanos and extensive areas of mainland Estado Falcón, but only very restricted parts of the Península de Paraguaná. Eight of the ten localities of *M. xerophila* fell in areas more strongly predicted for that species (Figure 17); the only two localities of that species falling in areas more strongly predicted for *M. robinsoni* were Capátarida and La Chapa (localities 178 and 179 in Appendix 3, respectively). Similarly, one locality of *M. robinsoni* (near Fila de Monte Cano, locality 101 in Appendix 3) was more strongly predicted for *M. xerophila* (Figure 17) but occurred extremely close to a pixel more strongly predicted for *M. robinsoni*.

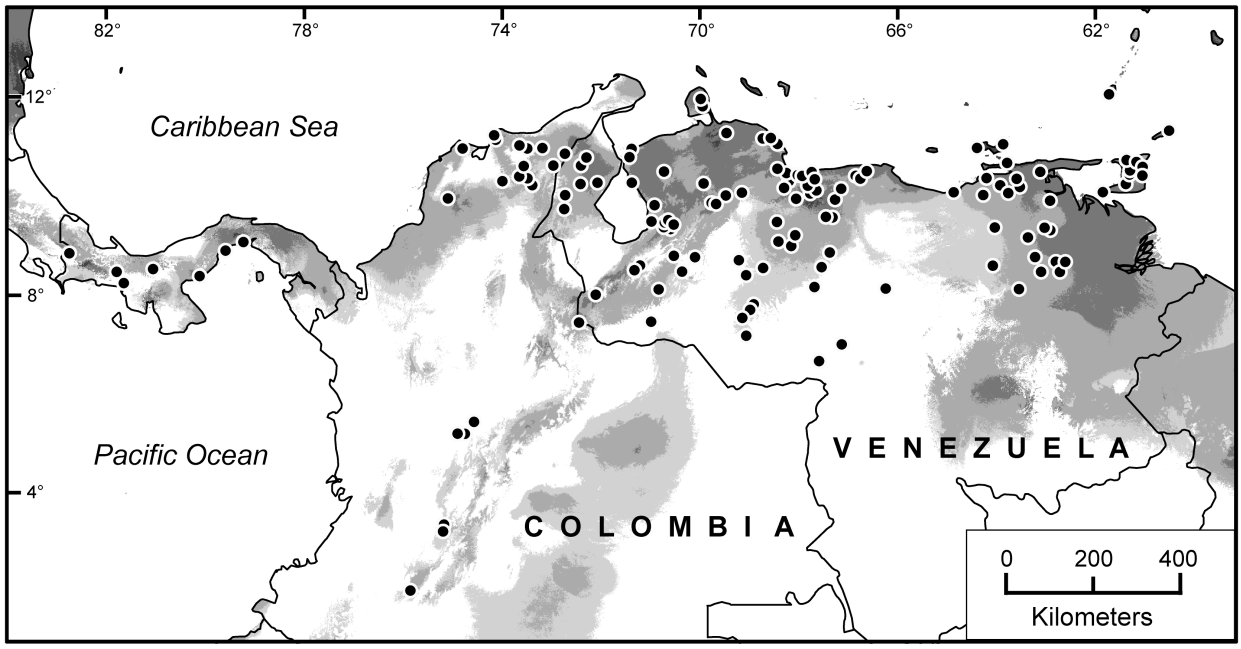
DISCUSSION

Competitive exclusion as possible vicariant agent.—The strong (and statistically significant) predominance of localities of *Marmosa xerophila* in areas of potential sympatry along its real contact zone with *M. robinsoni* is congruent with the predictions of competitive

FIGURE 14.

Final MAXENT model of abiotically suitable areas of *Marmosa robinsoni*. Abiotically suitable areas (given the 0.1 fixed threshold; see Materials and Methods) are indicated with shades; increasingly stronger predictions are indicated with increasingly darker shades.

Figure 14.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Caribbean Sea
Pacific Ocean
VENEZUELA
COLOMBIA
0
200
400
Kilometers

FIGURE 15.

Final MAXENT model of abiotically suitable areas of *Marmosa xerophila*. Abiotically suitable areas (given the 0.1 fixed threshold; see Materials and methods) are indicated with shades; increasingly stronger predictions are indicated with increasingly darker shades.

Figure 15.

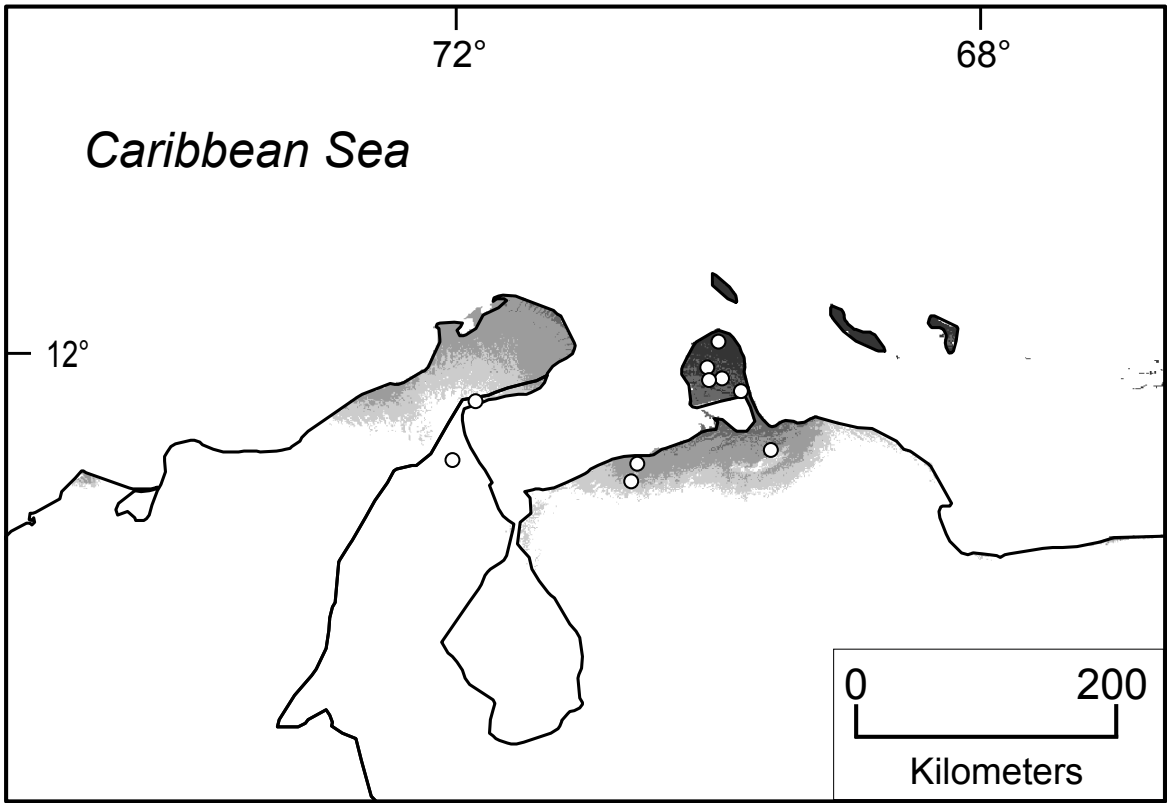


FIGURE 16.

Areas of potential sympatry. Top: Areas of potential sympatry for *Marmosa robinsoni* and *M. xerophila* (where suitable environmental conditions exist for both species) in northcentral South America. Bottom: Areas of potential sympatry indicating where each species was more strongly predicted than the other: areas with stronger predictions for *M. robinsoni* are indicated with black, whereas those with stronger predictions for *M. xerophila* are indicated with light grey.

Figure 16.

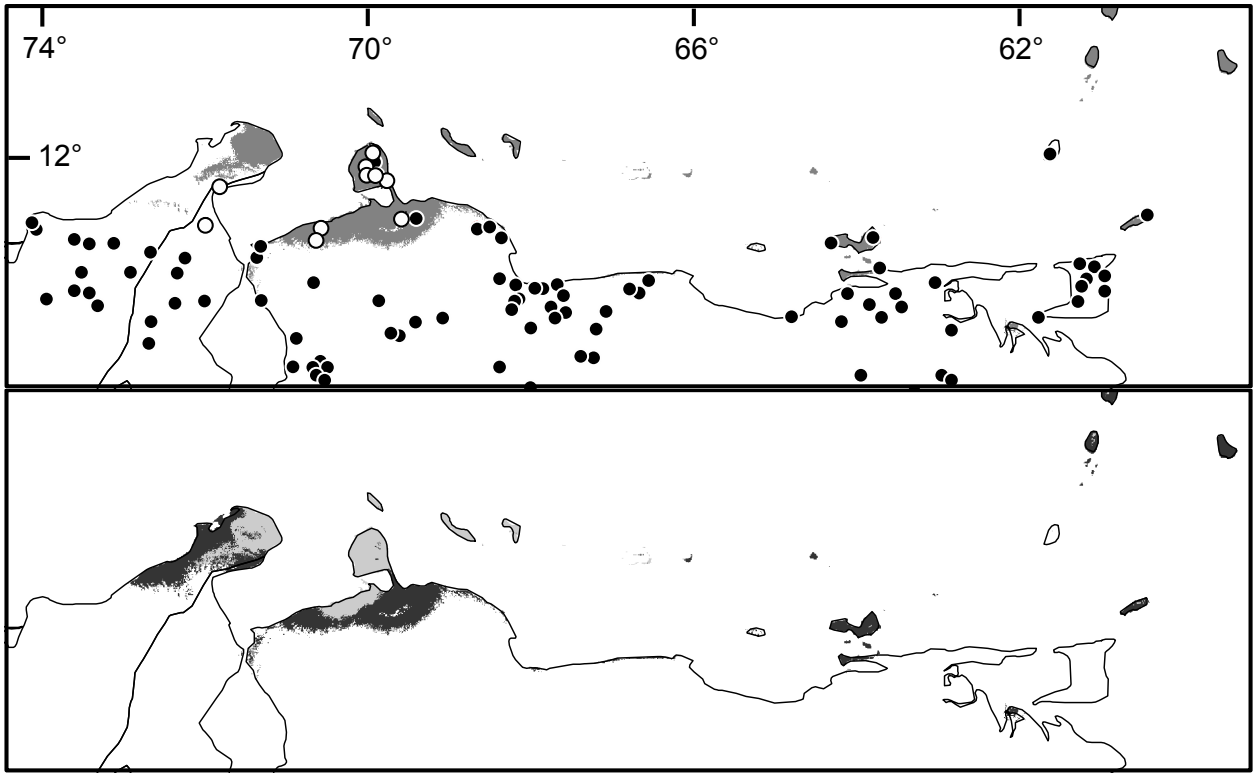
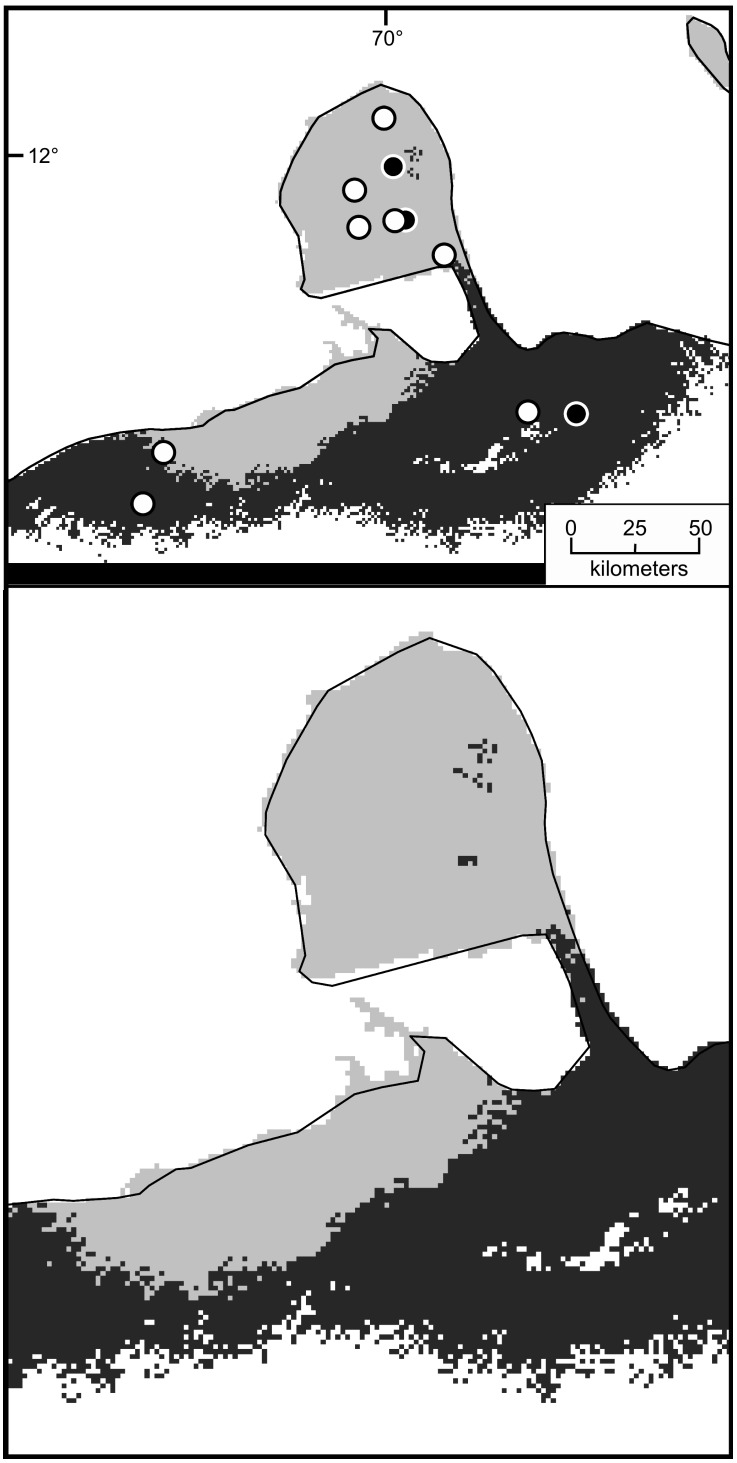


FIGURE 17.

Top: Areas of potential sympatry in northern Estado Falcón (Venezuela) more strongly predicted for each species. Areas more strongly predicted for *M. robinsoni* are indicated with black shading, whereas those of *M. xerophila* are indicated with grey shading. Bottom: Zoomed-in view of areas of potential sympatry along the documented real contact zone between focal species. Note that areas more strongly predicted for *M. robinsoni* are isolated from sites with similar environmental conditions in the adjacent "mainland" by areas more strongly predicted for, and predominantly occupied by *M. xerophila*, its putative superior competitor (see Discussion). Black circles represent localities of *M. robinsoni*; white circles represent localities of *M. xerophila*.

Figure 17.



exclusion, and suggests that the former species may be a superior competitor to the latter in areas suitable for both. Close examination of the Península de Paraguaná revealed the striking existence of small areas more strongly predicted for *M. robinsoni* embedded in a matrix of pixels with more suitable conditions for *M. xerophila* (Figure 17). These ”islands” more favorable for *M. robinsoni* corresponded to the Cerro de Santa Ana and the Fila de Monte Cano, where occurrence records of *M. robinsoni* exist. These results strongly suggest that competition may maintain (and possibly may even have created) allopatric conditions for *M. robinsoni*. Specifically, areas in the Península de Paraguaná suitable for *M. robinsoni* are disjunct from optimally suitable areas on the mainland because intervening regions harbor climatic conditions even more suitable for, and occupied by *M. xerophila*. This finding is based on three uncontroversial facts: 1) our models identified suitable conditions for both species in the peninsula, the adjacent mainland, and the isthmus connecting the two; 2) records of *M. xerophila* predominate in areas of potential sympatry in this region; 3) *M. xerophila* (the putative superior competitor) predominates in environments that are more strongly predicted to be suitable for it.

Caveats.—Local factors could explain why three localities fell in areas more strongly predicted for the other species. Two of these corresponded to *Marmosa xerophila* in areas more strongly predicted for *M. robinsoni*. This might be explained by the presence/abundance of critical resources for *M. xerophila* in areas climatically more suitable for *M. robinsoni*. Unless the presence/abundance of such resources strongly depends on the climatic variables used to calibrate the models, such factors would represent additional important (but not modeled) niche dimensions (see Bullock *et al.*, 2000 for a similar case in which physical rather than climatic factors may determine the outcome of competition at ranges boundaries). In our study system, one resource that could potentially drive the occupancy by *M. xerophila* of areas with more

suitable climate for *M. robinsoni* may be the abundance of columnar cacti, whose fruits are reported to be consumed by *M. xerophila* and *M. robinsoni* (Alvizu and Aguilera, 1998; Zambrano, 2001; Thielen *et al.*, 1997). In addition, one locality of *M. robinsoni* fell in a site (pixel) more strongly predicted for *M. xerophila*. Based on available natural history information, this exceptional locality likely corresponds to gallery forest habitat along a stream, a case of local conditions not reflected in the climatic variables employed here (Soley *in litt*.; see Austin and Van Neil, 2011).

Revisiting the concept of ecological vicariance.—Our results strongly suggest that competition may maintain (and may even have created) allopatric conditions for *M. robinsoni* in the Península de Paraguaná (see also Wiens, 2004; Jaeger, 1971). If demonstrated, this situation could have tremendous implications for studies of speciation, as similar cases could be taxonomically and geographically widespread (see below). The possible role of competition as a vicariant agent invites a reconsideration of the mechanisms that lead to *ecological vicariance*. *Ecological vicariance* (as conceived by most authors, e.g. Haffer, 1969, 1997, 2008; Vuilleumier, 1971; Cracraft and Prum, 1988; Hardy and Linder, 2005; Escudero *et al.*, 2009) is not equivalent to *soft vicariance*. Soft vicariance refers to cases in which isolation is incomplete (regardless of whether the barrier is physical or not; Fransen, 2007; see also Fransen, 2002; Hickerson and Meyer, 2008). Instead, *ecological vicariance*—whether leading to complete (hard) or incomplete (soft) isolation—is currently understood as the result of intrinsic organismal response to large-scale ecological variation, via the fragmentation of a single population into areas divided by ecologically, but not physically, unsuitable habitat (sensu Pyron and Burbrink, 2010, who used the terms *soft vicariance* and *soft allopatry*). Whereas this mechanism indeed leads to geographic isolation (e.g., Moritz *et al.*, 2000; Wiens, 2004; Kozak and Wiens, 2006;

Waltari *et al.*, 2007), we argue that limiting the notion of ecological vicariance only to those cases in which large-scale habitat-related changes have occurred excludes the possibility that important, (likely local-scale) biotic interactions might also isolate populations in the absence of physical or habitat-related barriers. In fact, we argue that biotic interactions are capable of creating and maintaining geographic isolation at a local scale (i.e., at particular sites), and likely also at a large scale (e.g., along extensive portions of their distributions). The latter possibility seems plausible as studies have documented that local competition can lead to extirpation of populations at a large scale (Bullock *et al.*, 2000; Leathwick and Austin, 2001).

Implications for speciation research.—Together with findings from a previous study (Jaeger, 1971; see also Wiens, 2004), our results imply that biotic interactions could directly promote genetic differentiation, and eventually speciation via geographic isolation. This possibility will depend at least on the degree by which biotic interactions prevent gene flow between the populations, and of the length of time they operate. Analogous to speciation events of insular populations far from the source of species (see Heaney, 2000; Whittaker *et al.*, 2008; Kisel and Barraclough, 2010), low levels of gene flow and long periods of isolation caused by biotic interactions would promote speciation. Given the dynamic nature of biotic interactions, it is expected that often biotic interactions will not persist as long as some physical barriers; however, they might still prevent gene flow long enough to promote phylogeographic divergences. In the case of competition, the exclusion of the inferior competitor from the intervening areas between its populations should effectively prevent gene flow. Thus, biotic interactions represent alternative causal explanations for recent divergence in phylogeographic trees that cannot be plausibly explained by geologic or other physical-environmental events. In this respect, the methodological approach implemented here holds great promise for future

research. Finally, projections of ecological niche models onto past climatic scenarios could be tremendously insightful in investigating the possible role of competition as a vicariant agent.

CONCLUSIONS

This research contributes to better understanding of the taxonomy, phylogenetics, and biogeography of the genus *Marmosa*; provides novel information relevant to the biogeography dry-forest species in northwestern South America; and proposes a refinement of the concept of *ecological vicariance* to incorporate the possibility that biotic interactions could lead to geographic isolation. Results from Chapter 1 support the validity of most of the species of the subgenus *Marmosa* previously recognized based on morphological criteria, and suggest the existence of more species than recognized in the current taxonomy of the genus. Chapter 1 also represents the first assessment of the phylogenetic relationships among most of the species in the genus *Marmosa*, with a dense taxonomic and geographic sampling within the subgenus *Marmosa*. The results identified several clades above the species level, including a clade formed by all of the species of the subgenus *Marmosa* predominantly distributed to the west of the Andes (the trans-Andean region). The discovery of this clade suggests that the Andes may have played an important role in the early evolution of the genus *Marmosa*.

In Chapter 2, examination of museum specimens allowed documentation of the presence of *Marmosa waterhousei* in the Cordillera de Mérida, Venezuela, and provided an opportunity to discuss likely events that may explain the current distribution of the species. Because the Depression del Táchira is probably too dry for the species to disperse across, *M. waterhousei* might have crossed it during glacial periods. The presence of *M. waterhousei* in Amazonia and in the northern Andes is likely explained by a corridor of forest habitat existing between the Amazonian region and the piedmont of the northern Andes, connecting these regions even during dry climatic periods of the Pleistocene. In addition, a dichotomous taxonomic key that allows identifications of the six species of the subgenus *Marmosa* known to occur in Venezuela was

provided, which should facilitate future work by researchers interested in the mammalian fauna of that country.

Chapter 3 focused on the phylogeography of *Marmosa robinsoni*, which is predominately distributed in the dry forests of northern South America. Phylogenetic analyses identified two clades that seem to correspond to an east-west divergence event. The results imply that the Cordillera de Mérida and associated mountain ranges have represented an important barrier to gene flow between populations at opposite sides of this system. In addition, the results show that repeated dispersal events of *M. robinsoni* lineages out of the greater Maracaibo basin have occurred. The results generate novel hypotheses for future studies of other elements of the northern South American dry-forest biota.

Chapter 4 explored the possibility that geographic isolation among conspecific populations might be caused (or at least maintained) by interspecific competition. Results of Ecological Niche Modeling (ENM) analyses tested whether the distributions of *Marmosa robinsoni* and *M. xerophila* fit the geographic pattern predicted under competitive exclusion. The results suggest that populations of *Marmosa robinsoni* from the Península de Paraguaná are isolated from those on the adjacent "mainland" due to competitive exclusion by *M. xerophila*. If corroborated, the competitive relationship between these species would represent a novel example of allopatry caused, or at least maintained, by competitive exclusion. Hence, in this chapter a modification to the concept of *ecological vicariance* is proposed to allow for the possibility that biotic interactions can geographically isolate populations.

Thus, the first two chapters provided information on systematic and biogeographic aspects of most of the species of the subgenus *Marmosa*, whereas the last two chapters focused on a sister-species pair (*Marmosa robinsoni* and *M. xerophila*) predominately distributed in the

poorly-studied dry-forest habitats of northern South America. While the first two chapters might be mostly of the interest of mammalogists working in the Neotropics, results from the last two chapters should be of the interest of a broader audience, which include researchers in several disciplines within evolutionary biology.

APPENDIX 1

(Gazetteer of sequenced specimens for Chapter 1)

Below we list all of the (abbreviated) localities from which specimens of *Marmosa* and outgroup taxa were sequenced for this report. Italicized place names are those of the largest political unit (state, department, province, etc) within each country. Elevational data (if any) are reproduced verbatim from specimen tags in meters (m) or feet (ft). Geographic coordinates and their cited source are provided in parentheses.

BELIZE

1. *Corozal,* Shipstern Nature Reserve (18°18' N, 88°09' W; Quang Minh, 2007).

BOLIVIA

2. *Santa Cruz,* 27 km SE Santa Cruz (17°58' S, 63°03' W; Anderson, 1997).
3. *Santa Cruz,* El Refugio (14°43' S, 61°02' W; Emmons and Patton, 2005).
4. *Santa Cruz,* Estancia Isibobo (19°31' S, 63°36' W; Anderson, 1997).

BRAZIL

5. *Amazonas,* Altamira (6°35' S, 68°54' W; Patton *et al.*, 2000).
6. *Amazonas,* Barro Vermelho (6°28' S, 68°46' W; Patton *et al.*, 2000).
7. *Amazonas,* Igarapé Nova Empresa, left bank Rio Juruá (6°48' S, 70°44' W; collector's label).
8. *Amazonas,* Igarapé Porongaba, right bank Rio Juruá, Acre (8°40' S, 72°47' W; collector's label).

9. *Amazonas,* Ilhazinha (3°17' S, 66°14' W; Patton *et al.*, 2000).

10. *Mato Grosso do Sul,* Fazenda Cedro, 517 m (22°17' S, 54°54' W; Rossi, 2005).

11. *Mato Grosso,* Fazenda São Luís, 389 m (15°38' S, 52°21' W; Rossi, 2005).

12. *Pará,* E bank Rio Xingu (3°39' S, 52°22' W; Voss and Emmons, 1996 [appendix 8]).

13. *São Paulo,* Capão Bonito, Fazenda Intervales, 700 m (24°20' S, 48°25' W; collector's label).

14. *Tocantins,* Rio Santa Teresa, 205 m (11°51' S, 48°38' W; Rossi, 2005).

COLOMBIA

15. *La Guajira,* La Isla (11°41' N, 71°55' W; Gardner, 2008).

ECUADOR

16. *El Oro,* Río Puyango, 370 m (3°53' S, 80°07' W; collector's label).

17. *Esmeraldas,* Comuna San Francisco de Bogotá (1°06' N, 78°42' W; Porter *et al.*, 2007).

18. *Guayas,* B.P. [Bosque Protector] Cerro Blanco (2°11' S, 80°01' W; collector's label).

19. *Orellana,* 35 km S Pompeya Sur (0°41' S, 76°28' W; GE, 2008).

20. *Orellana,* 38 km S Pompeya Sur (0°39' S, 76°28' W; Gardner, 2008).

FRENCH GUIANA

21. *Cayenne,* Cayenne (4°56' N, 52°20' W; Stephens and Traylor, 1985).

22. *Cayenne,* Nouragues (4°05' N, 52°40' W; Voss and Emmons, 1996 [appendix 5]).

23. *Cayenne,* Pic Matecho (3°45' N, 53°02' W; GE, 2008).

GUATEMALA

24. *Alta Verapaz,* Chelem Há (Yalijux Mtn.), 2090 m (15°22' N, 90°03' W; Renner, 2003).

25. *Baja Verapaz,* 5 km E Purulhá, 1550 m (15°14' N, 90°11' W; GE, 2008).

26. *El Petén,* Biotopo Cerro Cahui, El Remate, 120 m (17°00' N, 89°44' W; collector's label).

27. *El Progreso,* Río Uyús, 5 km E San Cristóbal, Acasaguascatlán, 240 m (14°51' N, 89°50' W; collector's label).

28. *Zacapa,* 9.5 km NW Gualán, 1973 m (15°11' N, 89°27' W; GE, 2008).

GUYANA

29. *Demerara-Mahaica,* Ceiba Biological Station (6°30' N, 58°13' W; Lim *et al.*, 2008).

30. *Potaro-Siparuni,* Iwokrama Reserve, 42 km WNW Siparuni, Pakatau Mt. (4°45' N, 59°01' W; Lim and Engstrom, 2001).

MEXICO

31. *Campeche,* 10 km N El Refugio (18°58' N, 89°19' W; GE, 2008).

32. *Campeche,* 3.7 km SE Chekubul (18°48' N, 90°58' W; GE, 2008).

33. *Campeche,* 44 km S Constitución (18°15' N, 90°04' W; ROM collection database).

34. *Campeche,* Xpujil, 25 km N of Xpujil (18°44' N, 89°24' W; GE, 2008).

35. *Jalisco,* 6 km SE Chamela (19°30' N, 105°03' W; Ceballos, 1990).

36. *Michoacán,* 1 km E Playa Azul, 25 m (17°59' N, 102°20' W; collector's label).

PANAMA

37. *Bocas del Toro,* Ñuri (8°55' N, 81°49' W; NGA, 2009).

38. *Chiriquí,* Reserva Forestal Fortuna, 1100 m (8°44' N, 82°16' W; NGA, 2009).

39. *Darién,* Cana, 600 m (7°47' N, 77°42' W; NGA, 2009).

40. *Los Santos,* Los Cuernitos (7°51' N, 80°16' W; collector's label).

41. *Veraguas,* Río Portabelo (7°14' N, 80°37' W; collector's label).

PERU

42. *Amazonas,* Río Cenepa, vecinity of Huapami, 700 ft (4°40' S, 78°12' W; collector's label).

43. *Cusco,* Hacienda Villa Carmen (12°50' S, 71°15' W; Stephens and Traylor, 1983)

44. *Loreto,* 25 km S Iquitos (3°58' S, 73°25' W; Hice *et al.*, 2004).

45. *Loreto,* Quebrada Orán (3°25' S, 72°35' W; Capparella *et al.*, 1997).

46. *Loreto,* Río Gálvez, Nuevo San Juan (5°15' S, 73°10' W; Simmons *et al.*, 2002).

SURINAM

47. *Brokopondo,* Brownsberg Nature Park, Km 1.2 Mazaroni trail (4°56' N, 55°11' W; Lim *et al.*, 2005).

48. *Nickerie,* Kayserberg Airstrip (3°06' N, 56°28' W; Lim *et al.*, 2008).

49. *Para,* Zanderij (5°27' N, 55°12' W; collector's label).

VENEZUELA

50. *Bolívar,* Auyantepui (5°55' N, 62°32' W; Gardner, 2008).

51. *Falcón,* Serranía de San Luis; ca. La Chapa; ca. 15 km N Cabure, ca. 350–380 m (11°17' N, 69°36' W; collector's label).

52. *Falcón,* Serranía de San Luis, ca. 4 km S and 3 km W Cabure, ca. 425 m (11°07' N, 69°38' W; collector's label).

APPENDIX 2

(Gazetteer of analyzed specimens in Chapter 3)

Below we list all of the (abbreviated) localities from which sequences of *Marmosa* were analyzed for this report. Italicized place names are those of the largest political unit (state, department, province, etc) within each country. Elevational data (if any) are reproduced verbatim from specimen tags in meters (m) or feet (ft). Geographic coordinates and their cited source are provided in parentheses.

COLOMBIA

1. *Huila*, Valle de Suaza (02°01' N, 75°51' W; NGA, 2010).
2. *La Guajira*, 119 km N and 32 km W of Maracaibo (La Isla), 15 m (11°41'N, 71°55'W; Gardner, 2008).
3. *La Guajira*, Las Marimondas (10°52'N, 72°43'W; Hershkovitz, 1947).
4. *Tolima*, Mariquita, ca. 535 m (5°12'N, 74°54'W; Paynter 1982).

ECUADOR

5. *Esmeraldas*, Comuna San Francisco de Bogotá (01°06'N, 78°42'W; Porter *et al.*, 2007).
6. *Guayas*, B.P. [Bosque Protector] Cerro Blanco (02°11'N, 80°01'W; collector's label).

GUATEMALA

7. *Alta Verapaz*, Chelem Ha´ (Yalijux Mtn.), 2090 m (15°22'N, 90°03'W; Renner, 2003).

8. *El Progreso*, Río Uyús, 5 km E San Cristóbal, Acasaguascatlán, 240 m (14°51'N, 89°50'W; collector's label).

MEXICO

9. *Campeche,* 10 km N El Refugio (18°58'N, 89°19'W; GE, 2010).

PANAMA

10. *Chiriquí,* Reserva Forestal Fortuna, 1100 m (08°44'N, 82°16'W; NGA, 2010).

11. *Darién,* Cana, 600 m (07°47'N, 77°42'W; NGA, 2010).

12. *Los Santos*, Los Cuernitos (07°51'N, 80°16'W; collector's label).

13. *Veraguas*, Río Portabelo (07°14'N, 80°37'W; collector's label).

TRINIDAD & TOBAGO

14. *Tobago* [*St. John Parish*], near Charlotteville, 275 m (11°18.789'N, 60°32.918'W; collector's field notes).

15. *Trinidad* [*Río Claro-Mayaro*], Bush Bush, ca. 0 m (10°24'N, 61°03'W; Anderson and Gutiérrez, 2009).

16. *Trinidad* [*Arima*], St. Patricks, ca. 30 m (10°38'N, 61°17'W; Anderson and Gutiérrez, 2009).

VENEZUELA

17. *Apure*, Hato El Frío, 30 km W (By Road) El Saman (07°49'N, 68°54'W; GE, 2010).

18. *Aragua*, Campamento Rangel, 800–1200 m (10°09'N, 67°09'W; Anderson and Gutiérrez, 2009).

19. *Aragua*, Ocumare de la Costa, 2 km NE, 1 m (10°28'N, 67°45'W; DCN, 1971).

20. *Falcón*, 24 km S and 93 km E of Maracaibo (Cerro Socopo), 1258 m (10°30'N, 70°44'W; Handley, 1976).

21. *Falcón*, Península de Paraguaná; Cerro Santa Ana; ca. 3 km N Santa Ana, ca. 200 m (11°48.352'N, 69°56.667'W; collector's field notes).

22. *Falcón*, Península de Paraguaná; Cerro Santa Ana; ca. 4 km N Santa Ana, ca. 520–570 m (11°49'N, 69°57'W; collector's label).

23. *Falcón*, Serranía de San Luis; ca. 4 km S + 3 km W Cabure, ca. 425 m (11°06.672'N, 69°38.263'W; collector's field notes).

24. *Falcón*, Serranía de San Luis; ca. La Chapa; ca. 15 km N Cabure, ca. 350–380 m (11°16.911'N, 69°36.370'W; collector's field notes).

25. *Guárico*, 7 km S and 5 km E of Calabozo (Estación Biológica de Los Llanos), 100 m (08°52'N, 67°23'W; Handley, 1976).

26. *Guárico*, Hto. Las Palmitas, 35 Km SSW San Juan de Los Morros [includes "34 Km S and 12 km W of San Juan de Los Morros (Hato Las Palmitas)"], 181 m (09°36'N, 67°27'W; Handley, 1976).

27. *Lara*, El Tocuyo, 10 Km N of El Tocuyo, caserio Boro, 528 m (09°53'N, 69°47'W; DCN, 1975b; see Handley, 1976).

28. *Mérida*, Cafetos de Chama, ca. 1600 m (08°36'N, 71°08'W; Paynter, 1982; coordinates correspond to the city of Mérida, where the Río Chama matches the indicated elevation).

29. *Monagas*, 2 km N and km W of Caripe [number of km W of Caripe not written on collector's label] (Nr. San Agustin) [= San Agustin, 5 Km NW Caripe], 1150 m (10°12'N, 63°32'W; Handley, 1976).

30. *Sucre*, 16 km E Cumaná (Quetepe), 0 m (10°27'N, 64°02'W; Gardner, 2008; see Handley, 1976).

31. *Zulia*, 18 km N and 56 km W of Maracaibo (Nr. Hacienda El Rodeo) [= Nr. Cerro Azul, 40 Km NW La Paz; = Hda. El Trigre], 80 m (10°48'N, 72°18'W; GE, 2008).

APPENDIX 3

(Gazetteer of analyzed specimens in Chapter 4)

Below we list all of the localities and specimens of *Marmosa robinsoni* and *M. xerophila* examined and whose associated data were used in this study. Elevation, geographic coordinates, and sources for coordinates are indicated in brakets. Elevational data (if any) are reproduced verbatim from either specimen tags or Rossi *et al.* (2010) in meters (m) or feet (ft). For each entry, boldface type indicates the place name to which geographic coordinates correspond. Estimated georreference error is indicated for each entry in kilometers (km). Museum catalog numbers for specimens examined follow each locality, using the abbreviations provided in Materials and Methods in Chapter 4. Early specimens in the AMNH for which the osteological portion was cataloged in a separate numbering sequence from the skin are indicated as skin number/osteological number. Localities that were not used in analyses because they fell out of the environmental layers (numbers: 29, 37, 99, 150, 151, 186) or because of their large georreference error (numbers: 43, 79, 94, 106, 146, 162) are listed here as well.

Marmosa robinsoni

COLOMBIA

ATLÁNTICO

1. **Barranquilla** [ca. 100 m, 10°59´N, 74°48´W; Paynter, 1997], MVZ 135234–135243; "**Barranquilla**" [place of shipment]: MVZ183339; Vicinity **Barranquilla**: MVZ 183334–183338. Georeference error: ca. 2 km.

BOLÍVAR

2. **San Juan Nepomuceno** [167 m, 09°57´N, 75°05´W; Paynter, 1997], FMNH 69315. Georeference error: ca. 2km.

CESAR

3. Río Cesar [=**El Orinoco**; 158 m, 10°13´N, 73°23´W; Hershkovitz, 1960], USNM 280820, 280886–280888; Río Guaimaral [= El Guaimaral, 5 km from **El Orinoco**; coordinates correspond to **El Orinoco**, which is located 5 km from El Guaimaral; see Hershkovitz, 1960; Anderson, 2003], USNM 280817, 280819. Georeference error: ca. 1 km.
4. **Colonia Agrícola de Caracolicito** [400 m, 10°18´N, 74°00´W; Hershkovitz, 1947], USNM 280806. Georeference error: ca. 1 km.
5. **El Salado** [430 m, 10°22´N, 73°29´W; Hershkovitz, 1947], USNM 280814–280816. Georeference error: ca. 1 km.
6. **Pueblo Bello** [1067 m, 10°24´N, 73°39´W; Hershkovitz, 1947], USNM 280807–280813. Georeference error: ca. 1 km.
7. **San Sebastián** [1900–2000 m, 10°37´N, 73°34´W; Hershkovitz, 1947], FMNH 69320, 69321. Georeference error: ca. 1 km.

CUNDINAMARCA

8. **Bogotá** ["**Volcan**"; 2590 m, 05°26´N, 74°34´W; Anderson, 1999 (p. 618) cited Hernández-Camacho 1956 (p. 3) and clarified that this locality corresponded to "*Volcanes, cerca a la cabecera del corregimiento de Córdoba, Municipio Caparrapí, Departamento de Cundinamarca; vertiente occidental de la Cordillera Oriental. Colombia. Alt. 250*

metros"; not Rossi *et al*., 2010, who, mistakenly provided coordinates for Bogotá (at an elevation of 2590 m) while ignoring the mention of "*Volcanes*" in the original collector's tag], AMNH 143521. Georeference error: ca. 2 km.

HUILA

9. Valle de Suaza, **Naranjal** [02°01´N, 75°51´W; NGA, 2010], USNM 541857–541861, 543120. Georeference error: ca. 2 km.
10. **7.5 km E Villavieja** [488 m, 03°14´N, 75°10´W; GE, 2010], specimens from this locality are reported by Rossi *et al*., 2010 under locality "*16 km NE Villavieja*" (see below). Georeference error: ca. 1 km.
11. **5 km N Villavieja** [488 m, 03°16´N, 75°12´W; IGAC, 1985a], specimens from this locality are reported by Rossi *et al*., 2010 under locality "*16 km NE Villavieja*" (see below). Georeference error: ca. 1 km.
12. **16 km NE Villavieja** [488 m, 03°21´N, 75°10´W; IGAC, 1985a], MVZ 113366, 113367, 113833–113840. Georeference error: ca. 1 km.

LA GUAJIRA

13. Sierra Negra, **Villanueva**, Valledupar District [274 m, 10°37´N, 72°58´W; Hershkovitz, 1960], USNM 280821–280852; **Villanueva**, Valledupar District, USNM 280853–280875. Georeference error: ca.1 km.
14. **Las Marimondas**, Fonseca District [1000 m, 10°52´N, 72°43´W; Hershkovitz, 1947], USNM280876–280880, 280882, 280883, 280885. Georeference error: ca. 1 km.

15. **San Miguel** [1700 m, 10°58´N, 73°29´W; Paynter, 1997], FMNH 18506. Georeference error: ca. 1 km.

16. Santa Marta, **Pueblo Viejo** [610 m, 10°59´N, 73°10´W; IGAC, 1988; see Anderson, 2003], FMNH 18508. Georeference error: ≤ 5 km.

17. **Pueblo Viejo [= El Pueblito**; 610 m, 10°59´N, 73°27´W; IGAC, 1988; see Anderson, 2003], FMNH 18509; BMNH 9.4.15.18–9.4.15.20; MCZ B8117–B8122, B8123, B8125–B8127, B8132, B8143;USNM85531, 85532. Georeference error: ≤ 5 km.

18. **La Concepción** [ca. 800 m, 11°03´N, 73°27´W; Paynter, 1997; not Rossi *et al.*, 2010], FMNH 18507. Georeference error: ca. 1 km.

MAGDALENA

19. **Palomino** [ca. 600 m, 11°02´N, 73°39´W; Paynter, 1997], USNM 85533. Georeference error: ca. 1 km.

20. **Minca** [670 m, 11°09´N, 74°07´W; Paynter, 1997], AMNH 23293. Georeference error: ca. 1 km.

21. **Bonda** [46 m, 11°14´N, 74°08´W; Paynter, 1997], AMNH 14610, 14611, 15357–15361, 23273–23276, 23280, 23281, 23292, 23627. Georeference error: ca. 1 km.

22. **Mamatoco** [ca. 25 m, 11°14´N, 74°10´W; Paynter, 1997], AMNH 15362. Georeference error: ca. 1 km.

23. **Taganga** [0 m, 11°16´N, 74°12´W; Paynter, 1997], AMNH 15363. Georeference error: ca. 1 km.

NORTE DE SANTANDER

24. Cucuta, 10 mi N [= **10 miles N Cúcuta**; 215 m, 08°02´N, 72°08´W; IGAC, 1985b], FMNH 18692. Georeference error: ca. 1 km.

TOLIMA

25. Madalegna River, **Honda** [183 m, 05°12´N, 74°45´W; Paynter, 1997], AMNH 34602–34604. Georeference error: ca. 1 km.

26. **Mariquita** [535 m, 05°12´N, 74°54´W; Paynter, 1997], AMNH 207766. Georeference error: ca. 1 km.

GRENADA

SAINT GEORGE

27. Annandale [=**Annandale waterfalls**; 12°05´N, 61°43´W; NGA, 2010], BMNH 87.6.30.5. Georeference error: ca. 1 km.

PANAMA

CANAL ZONE

28. **Fort Kobbe** [08°54´N, 79°36´W; Fairchild and Handley, 1966], USNM298697, 298698, 300329, 300330, 301141, 303049. Georeference error: ca. 1 km.

29. **Quarry Heights** [08°57´N, 79°34´W; Fairchild and Handley, 1966], USNM 303281–303283. Georeference error: ca. 1 km.

30. 8 km W Balboa, **Rodman Naval Ammo** [=Ammunition] **Depot** [=Rodman Naval Station; 08°57´N, 79°37´W; Fleming, 1970], USNM 456818, 456822. Georeference error: ca. 1 km.

31. **Miraflores** [08°59´N, 79°36´W; Fairchild and Handley, 1966], USNM 396415. Georeference error: ca. 1 km.

CHIRIQUÍ

32. **2 mi NE Tolé** [08°15´N, 81°39´W, GE, 2010], USNM 331071. Georeference error: ca. 2 km.

33. **Colorado Camp. [=Campamento Cerro Colorado**; 08°29´N, 81°48´W, GE, 2010], USNM 541324. Georeference error: ca. 2 km.

34. **23–25 km NNE San Felix** [=Near Escopeta Camp; 08°30´N, 81°47´W; Rossi *et al.*, 2010], USNM 541000, 541002. Georeference error: ca. 4 km.

35. **Finca Santa Clara, 14.5 km NW El Volcán** [08°51´N, 82°45´W; GE, 2010], USNM 520772. Georeference error: ca. 2 km.

COCLÉ

36. **2 mi E Río Hato** [08°23´N, 80°08´W; GE, 2010; also see Fairchild and Handley, 1966], USNM331069. Georeference error: ca. 2 km.

PANAMÁ

37. **Saboga Island** [08°37´N, 79°04´W; GE, 2010], MCZ 10809. Georeference error: ca. 2 km.

38. **4 mi E, 1 mi S Pacora** [09°04´N, 79°14´W; GE, 2010], USNM 305146. Georeference error: ca. 4 km.

VERAGUAS

39. **Río Santa María, Santa Fé** [08°31´N, 81°04´W; Fairchild and Handley, 1966], USNM 304696–304709. Georeference error: ca. 1 km.

TRINIDAD & TOBAGO

TOBAGO

40. **Speyside** [11°18´N, 60°32´W; Anderson and Gutiérrez, 2009], AMNH 184845, 184846, 184848, 184849. Georeference error: ca. 3 km.
41. **1 km E Charlotteville** [11°19´N, 60°32´W; GE, 2010], Rossi *et al.*, 2010 lumped this locality and specimens with "Near Charlotteville"; Near Charlotteville [=**1 km E Charlotteville**], AMNH 259973, 259983; USNM 537898, 537899, 538075–538078. Georeference error: ca. 1 km.

TRINIDAD

42. **Bush Bush Forest** [10°24´N, 61°03´W; Downs *et al.*, 1968; Rossi *et al.*, 2010 lumped this locality with "Nariva Swamp, **Bush Bush Forest**"; Nariva Swamp, **Bush Bush Forest**] AMNH 188357, 189314–189316, 204855–204857, 206595–206597, 206761, 206762, 206764–206768. Georeference error: ca. 2 km.
43. El Cerro del Oropuche [10°46´N, 61°09´W; NGA, 2010], AMNH 31229–31231. Georeference error: ca. 12 km.

TRINIDAD, CARONI

44. **Caparo** [10°27´N, 61°19´W; Anderson and Gutiérrez, 2009], AMNH 7426, 7429, 7660/6046–7664/6050. Georeference error: ca. 3 km.

TRINIDAD, SAINT ANDREW

45. **Fishing Pond** [10°35´N, 61°03´W; Anderson and Gutiérrez, 2009], AMNH 173997. Georeference error: ca. 4 km.

46. **Sangre Grande** [10°35´N, 61°07´W; Anderson and Gutiérrez, 2009], AMNH 173984, 173996, 174000, 174007, 174008, 174012, 174162, 188356; El Reposo Rd., **Sangre Grande**, AMNH 173990; Maingot Estate, 5 miles from **Sangre Grande**, AMNH 173998. Georeference error: ca. 10 km.

47. Tamana Ward, **Cumuto**, St. Andrew [10°35´N, 61°12´W; Anderson and Gutiérrez, 2009], AMNH 212303–212305. Georeference error: ca. 3 km.

48. **Cumaca** [10°42´N, 61°10´W; Anderson and Gutiérrez, 2009], AMNH 188354, 208996, 208999–209003, 212128–212130, 214425–214438, 214444, 234963–234970; Valencia Ward, **Cumaca**, St. Andrew (Rossi *et al.*, 2010 lumped this locality with "**Cumaca**"). Georeference error: ca. 4 km.

TRINIDAD, SAINT GEORGE

49. **Brazil village** [10°33´N, 61°17´W; GE, 2010], AMNH 208997, 208998. Georeference error: ca. 3 km.

50. **Caura** [10°43´N, 61°21´W; Anderson and Gutiérrez, 2009], AMNH 7665/6051, 7666/6052, 7667/6053–7670/6056, 7672/6058, 7674/6060–7676/6062; USNM 85556; **Caura** Mts., AMNH 7430. Georeference error: ca. 3 km.

TRINIDAD, SAINT PATRICK

51. Cedros [coordinates correspond to **Bonasse**, near Cedros Bay; 10°05´N, 61°51´W; O.S. 1930], AMNH 234960, 234961; Cedros Ward, Cedros, St. Patrick Co. [coordinates correspond to **Bonasse**, near Cedros Bay] (AMNH 214424). Georeference error: ca. 5 km.

TRINIDAD, VICTORIA

52. **Princestown [= Princes Town**;10°16´N, 61°23´W; Anderson and Gutiérrez, 2009], AMNH 4799–4802, 6046, 6049, 6121, 6123, 6045/4767, 6047/4768, 6048/47669, 6050/4770–6053/4773, 6055/4775, 6056/4776, 6058/4778. Georeference error: ca. 4km.

VENEZUELA

ANZOÁTEGUI

53. **Mamo** [08°28´N, 63°06´W; Gardner, 2008], MHNLS 6463. Georeference error: ca. 2 km.

54. Paso "**Los Cocos**" Río Caris S de El Trigre [08°36´N, 64°04´W; Anderson and Gutiérrez, 2009], MBUCV 3131–3134; Sabana "**Los Cocos**", Río Caris, S El Tigre, MBUCV 3135. Georeference error: ca. 2 km.

55. **Morichal Largo [= Río Morichal Largo]**, **límite de los Estados Anzoátegui y Monogas** [08°46´N, 63°13´W; SAGCN, 1996], MHNLS 5611, 5612. Georeference error: ca. 5 km.

56. **Hato Real Campo Matas** [09°22´N, 64°02´W; collector's label], EBRG 24174. Georeference error: < 5 km.

57. **Complejo De Joces, 15 km E Puerto Piritu** [10°05´N, 64°53´W; collector's label], EBRG 22811, 22812; **Quebrada Hoces 15 km E Puerto Piritu,** EBRG 22231, 22232. Georeference error: < 5 km.

APURE

58. **Caño la Guardia, afluente del Río Capanaparo** [90 m, 06°40´N, 67°35´W; collector's label], MHNLS 7600, 7601, 7984, 7985. Georeference error: < 5 km.

59. "Mata Salado", **Hato Acapulco**, entre Capanaparo y Arauca [07°00´N, 67°07´W; Gardner, 2008], MBUCV 1423, 1424. Georeference error: ca. 5 km.

60. La Trinidad (**Hato La Trinidad de Arauca**) [07°11´N, 69°04´W; Voss, 1991], MBUCV 1414, 1415. Georeference error: ca. 5 km.

61. **El Mantecal** [07°33´N, 69°09´W; Paynter, 1982], CVULA I-952. Georeference error: ca. 5 km.

62. **Hato El Frío; 30 km W. del Saman de Apure** [60 m, 07°43´N, 68°58´W; collector's label], MHNLS 8234. Georeference error: < 5 km.

63. **Hato El Frío** [60 m, 07°49´N, 68°54´W; collector's label], MHNLS 7942; USNM 448524. Georeference error: < 5 km.

ARAGUA

64. **Fundo Paso del Medio, 10 km ENE San Juan de los Morros** [400–458 m, 09°56´N, 67°16´W; collector's label], EBRG 24083–24086. Georeference error: < 5 km.

65. **Hacienda Macapo, Lago de Valencia** [10°08´N, 67°39´W; collector's label], EBRG 22154, 22158, 22159, 22390. Georeference error: < 5 km.

66. **Camp Rangel** [10°09´N, 67°09´W, Anderson and Gutiérrez, 2009], USNM 314171. Georeference error: ca. 5 km.

67. **Rancho Grande** [1050–1100 m, 10°21´N, 67°40´W; Anderson and Gutierrez, 2009], USNM 517262–517270; Parque Nacional Henri Pittier, **Rancho Grande**, Guamitas (EBRG 16903). Georeference error: ca. 2 km.

68. **2 km NE Ocumare de La Costa** [183 m, 10°28´N, 67°45´W; DCN, 1971], USNM 517271–517280. Georeference error: ca. 1 km.

BARINAS

69. **Reserva Forestal Caparo, 30 km E del Cantón** [200 m, 07°28´N, 71°00´W; GE, 2010], CVULA I-6539. Georeference error: ca. 3 km.

70. **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 [200 m, 08°07´N, 70°50´W; Ochoa *et al.*, 1988; GE, 2010], EBRG 15757, 15758, 15761; **Reserva Forestal Ticoporo Unidad II**, Compartimiento 16 (EBRG 10151, 10274); **Reserva Forestal Ticoporo Unidad II**, área intervenida (EBRG 6386); **Reserva Forestal Ticoporo Unidad II**, 8 km ESE Miri (EBRG 15789); **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 Río Quiu (EBRG 10133–10135, 10251, 10252); **Reserva Forestal Ticoporo Unidad II**,

Compartimiento 9 (EBRG 10284, 15762); **Reserva Forestal Ticoporo Unidad II**, Parcela 15 (EBRG 6387). Georeference error: ca. 5km.

71. La Erika [= **La Erica**], 20 km SW Barinas [08°29´N, 70°22´W; DCN, 1970], CVULA I-073. Georeference error: ca. 3km.

72. **El Irel** [90 m, 08°46´N, 70°06´W; GPS coordinates taken by Thalia Paparoni in 2010], CVULA I-3375. Georeference error: ca. 1 km.

73. **Río Barragán [= Quebrada Barragan]**, Barinitas [440 m, 08°48´N, 70°27´W; coordinates correspond to a place along the river with the indicated elevation; DCN, 1975a], CVULA I-0347. Georeference error: ca. 1 km.

74. La Quinta, **5 km SW Altamira** [697 m, 08°48´N, 70°32´W; DCN, 1976a], USNM 418540. Georeference error: ca. 1 km.

75. **Altamira de Caceres** [830 m, 08°50´N, 70°30´W; DCN, 1976a], CVULA I-0847. Georeference error: ca. 1 km.

BOLÍVAR

76. **Ciudad Bolívar** [ca. 100 m, 08°08´N, 63°33´W; Paynter, 1982], AMNH 16132. Georeference error: ca. 1 km.

CARABOBO

77. **Pira-Pira [= Pirapira**; 09°57´N, 68°04´W; Paynter, 1982], EBRG 47. Georeference error: ca. 2 km.

78. **El Trompillo** [ca. 500 m, 10°04´N, 67°46´W; Paynter, 1982], BMNH 14.9.1.86–14.9.1.97. Georeference error: ca. 1 km.

79. **Valencia** [10°11´N, 68°00´W; Paynter, 1982], EBRG 125. Georeference error: >10 km.

80. **6 km SSE Montalban, Sabana Aguirre** [562 m, 10°11´N, 68°18´W; DCN. 1976b; A. L. Tuttle's field notes (1967); Tuttle corrected elevation is 562 m, not 1055 m as indicated on specimen label)], EBRG 3972. Georeference error: ca. 1 km.

81. **Punta Cabito**; Lago de Valencia [420 m, 10°12´N, 67°50´W; Mavárez *et al.*, 2002], MHNLS 2979, 2980, 3188–3194, 3295. Georeference error: ca. 1 km.

82. **1 km E Montalban, Sanjon** [579–598 m, 10°12´N, 68°20´W; DCN, 1976b; A. L. Tuttle's field notes (1967) (Tuttle corrected elevation is 598 m, not 1091 m as indicated on specimen label)], EBRG 3975; 2.5 km SE Montalban, El Castaño (EBRG 3977); Montalban, Potrerito (EBRG 3973, 3974, 3976, 3978). Georeference error: ca. 1 km.

83. Embalse Río Moron, **Campamento Palmichal** [10°18´N, 68°14´W; Anderson and Gutiérrez, 2009], EBRG 17081. Georeference error: ca. 2 km.

84. Bahía de **Patanemo** [10°26´N, 67°55´W; Anderson and Gutiérrez, 2009], MHNLS 3732. Georeference error: ca. 3 km.

85. **San Esteban** [ca. 200 m, 10°26´N, 68°01´W; Paynter, 1982], AMNH 31532; BMNH 11.5.25.178–11.5.25.183, 11.5.25.184, 11.5.25.185, 11.5.25.187; **San Esteban** Valley: BMNH 11.5.25.186. Georeference error: ca. 1km.

86. **Caño Alpargatón**, Petroquímica de Moron [10°28´N, 68°15´W; DCN, 1976a], MBUCV 4078; La Batea, 5 km SO [SW]. de Moron (MBUCV 4097, 4101–4104). Georeference error: ca. 3 km.

87. **10 km NO [NW] Urama, Río Yaracuy** [125 m, 10°32´N, 68°23´W; DCN, 1983; not Rossi *et al.*, 2010], EBRG 3959. Georeference error: ca. 2 km.

88. **El Central**, 10 km NW Urama, Río Yaracuy [25 m, 10°33´N, 68°25´W; Gardner, 2008; see also Handley, 1976], USNM372938–372940, 372942–372944, 372947. Georeference error: ca. 1 km.

COJEDES

89. **Finca El Piñero, 25 km E El Baul** [08°59´N, 68°09´W; GE, 2010; see also Polisar *et al.*, 2003], EBRG 8174. Georeference error: ca. 5 km.
90. **Hato El Piñero a 20 km N de El Baul** [09°00´N, 68°10´W; GE, 2010], MBUCV 5157. Georeference error: ca. 5 km.90. Hato El **Tirado** [100 m, 09°05´N, 68°25´W; Anderson and Gutiérrez, 2009], MHNLS 3812, 3889, 3890. Georeference error: ca. 2 km.
91. Hato El **Tirado** [100 m, 09°05´N, 68°25´W; Anderson and Gutiérrez, 2009], MHNLS 3812, 3889, 3890. Georeference error: ca. 2 km.
92. **Hato Nuevo** [09°13´N, 68°05´W; Gardner, 2008], EBRG 364, 458–461, 464, 465. Georeference error: ca. 2 km.
93. **Hato de Itabana** [80 m, 09°28´N, 68°27´W; Paynter, 1982], MHNLS 4405. Georeference error: ca. 5 km.

DISTRITO CAPITAL

94. **Caracas** [950 m, 10°30´N, 66°55´W; Paynter, 1982], AMNH 130586–130589. Georeference error: ca. 15 km.

FALCÓN

95. 20 km S and 98 km E Maracaibo (**Hacienda Socopito**) [470–480 m, 10°30´N, 70°44´W; Handley, 1976; see also Anderson, 2003], USNM 443801; 24 km S and 94 km E Maracaibo (**Hacienda Socopito**), USNM 418531, 418532. Georeference error: ≤ 5 km.

96. **Near Mirimire** [coordinates correspond to the site closet to Mirimire (visited by collector) at indicated elevation; see Handley, 1976] [250 m, 11°10´N, 68°44´W; Handley, 1976], USNM 406953. Georeference error: ca. 8 km.

97. 5 km N and 13 km E Mirimire (cerca **La Pastora**) [122 m, 11°11´N, 68°35´W; Anderson, 2003], EBRG 3979. Georeference error: ≤ 5 km.

98. **Parque Nacional Juan Cristofono Falcón, sector Acurigua** [650 m, 11°17´N, 69°28´W; collector's label], EBRG 23773, 23887, 23888. Georeference error: ca. 2 km.

99. **Campechano cerca Boca Río Hueque, Municipio Píritu** [0 m, 11°27´N, 68°57´W; collector's label], EBRG 22549, 22556, 22558, 22560. Georeference error: < 5 km.

100. **Cerro Santa Ana**, Península de Paraguaná [300–615 m, 11°49´N, 69°57´W; Anderson, 2003; SAGCN. 1990], EBRG 3698, 3707, 15977, 15982, 15986; 49 km N and 32 km W Coro, **Cerro Santa Ana** (EBRG 3993–3997); Península de Paraguaná, **Cerro Santa Ana**, 4 km N Santa Ana (AMNH 276478 (previously EBRG 25353), 276479 (previously EBRG 25352), 276487 (previously EBRG 25464), 276489 (previously EBRG 25467), 276496 (previously EBRG 25481), 276502 (previously EBRG 25488), 276530 (previously EBRG 25356), 276531 (previously EBRG 25355), 276537 (previously EBRG 25368), 276541 (previously EBRG 25509), 276543 (previously EBRG 25370), 276562 (previously EBRG 25358); EBRG 25346–25351, 25357, 25359, 25367, 25371, 25465, 25496, 25498, 25512, 25514); 15 km SSW Pueblo Nuevo [=49 km and 32 km of Coro], **Cerro Santa Ana**, Península de Paraguaná (USNM 442907); 49 km N and 32 km

W Coro (**Cerro Santa Ana**) (USNM 443870–443874, 443877, 443880–443888, 443890–443896). Georeference error: ca. 1 km.

101. **Reserva Biológica Monte Cano**, 5 km de Pueblo Nuevo Península de Paraguaná [200 m, 11°58´N, 69°59´W; Soley-G. *in litt*.], EBRG 23557–23566; Estacion Biólogica Monte Cano, San Jose de Cocodite (EBRG 24097–24099); Montecano Pueblo Nuevo Península Paraguaná (EBRG 20677–20679); San José de Cocodite Estación Biológica de Monte Cano Municipio Falcón Península de Paraguaná (EBRG 23585–23591). Georeference error: ca. 1 km.

102. Reserva de Fauna Silvestre Tucurere, **Hacienda Somosagua** [near Boca de Tocuyo], Municipio Acosta [40 m, 11°03´N, 68°26´W; GE, 2010], EBRG 24923. Georeference error: ca. 3 km.

103. Península de Paraguaná, **Cerro Santa Ana, 3 km N Santa Ana** [120–200m, 11°48´N, 69°57´W; collectors' label], AMNH 276533 (previously EBRG 25354); EBRG 25366; Cerro Santa Ana, Península Paraguaná (EBRG 12342). Georeference error: ca. 1 km.

GUÁRICO

104. **Santa Rita, cerca Río Manapiare** [08°08´N, 66°15´W; Gardner, 2008], MBUCV 2435. Georeference error: ca. 2 km.

105. Paso Mereyal, **Hato La Muerta**, Espino [08°17´N, 65°46´W; www.fallingrain.com . Specifically: http://www.fallingrain.com/world/VE/12/Hato_La_Muerta.html], MBUCV 1469. Georeference error: ca. 12 km.

106. **Hato La Fé**, Caserio Corozopando [90 m, 08°30´N, 67°35´W; Voss, 1991], MHNLS 6723. Georeference error: ca. 5 km.

107. **Carretera Calabozo-San Fernando, nivel Hato Flores Moradas** [08°34´N, 67°33´W; Anderson and Gutiérrez, 2009; not Paynter, 1982], EBRG 8078. Georeference error: ca. 4 km.

108. **Estación Biológica de los Llanos** [110–115 m, 08°52´N, 67°23´W; Handley, 1976], USNM 385052; Estación Biológica de Calabozo (MBUCV 1416–1422); **Estación Biológica de Los Llanos**, Calabozo (MBUCV 1429–1433, 1934–1937, 1952, 2032); 7 km S and 5 km E Calabozo [= **Estacion Biológica de los Llanos**] (USNM 443897, 443901–443905, 443911); 9 km SE Calabozo, **Estación Biológica de los Llanos** (USNM 442908, 443906, 443908, 443910). Georeference error: ca. 2 km.

109. **Dos Caminos** (50 km S, San Juan de Los Morros) [09°35´N, 67°18´W; Gardner, 2008], CVULA I-0261, I-0117. Georeference error: ca. 2 km.

110. **Hato Las Palmitas** [181 m, 09°36´N, 67°27´W; Handley, 1976], EBRG 3980; 34 km S and 12 km O [W] San Juan de Los Morros, **Hato Las Palmitas** (EBRG 3971, 3981–3992); Hato La Palmita [=**Hato Las Palmitas**], San Francisco de Tiznados (MBUCV 1557); 34 km S and 12 km W San Juan de los Morros, **Hto. Las Palmitas** (USNM 385053–385056, 418518, 418519, 443794, 443797, 443798, 443800). Georeference error: ca. 5 km.

111. **Río Portuguesa 18 km NO [NW] Camaguan, Municipio Camaguan** [69 m, 08°11´N, 67°42´W; collector's label], EBRG 24980. Georeference error: ca. 2 km.

LARA

112. 14 km NE El Tocuyo, **Puerta Vieja** [616 m, 09°51´N, 69°41´W; DCN, 1975b; see also Handley, 1976], USNM 443914. Georeference error: ca. 1 km.

113. 10 km N El Tocuyo, **caserio Boro** [528 m, 09°53´N, 69°47´W; Handley, 1976; DCN, 1975b], USNM 443913. Georeference error: ca. 2 km.

114. 8 km SW Barquisimeto, **La Concordia** [592 m, 10°01´N, 69°29´W; NGA, 2010; see also Handley, 1976], USNM 443912. Georeference error: ca. 1 km.

115. **Río Tocuyo** [500 m, 10°16´N, 69°56´W; Voss, 1991, AMNH 130577–130585, 130600. Georeference error: ca. 1 km.

MÉRIDA

116. **Laguna de Caparú, 3 km SE San Juan de Lagunillas** [900 m, 08°29´N, 71°20´W; Sosa and Soriano, 1996], CVULA I-2964, I-3863, I-3867, I-3868. Georeference error: ca. 2 km.

117. **Las Gonzalez** [800–900 m, 08°30´N, 71°19´W; DCN, 1977b], CVULA I-1218, I-1223, I-1318, I-1319, I-1515. Georeference error: ca. 1 km.

118. **Lagunillas** [08°30´N, 71°22´W; Handley, 1976], CVULA I-1760. Georeference error: ca. 3 km.

119. Cafetos de **Milla** [ca. 1100 m, 08°36´N, 71°08´W; DCN, 1977b; elevation likely wrong in Rossi *et al.*, 2010; see Gardner, 2008], BMNH98.7.1.21; USNM 149005. Georeference error: ca. 1 km.

120. **Pedregosa** [=Quebrada La Pedregosa; 1630 m, 08°36´N, 71°12´W; Paynter, 1982], BMNH 98.7.1.19. Georeference error: ca. 1 km.

121. **Turgua** [10°22´N, 66°45´W; DCN, 1964], MBUCV 1411, 1412. Georeference error: ca. 1 km.

122. **8 km S Caracas, cerca Turagua [=Turgua**; 1144 m, 10°22´N, 66°50´W; Anderson and Gutiérrez, 2009], EBRG 3960, 3961. Georeference error: ca. 2 km.

123. **8 km SSE Caracas** [1144 m, 10°25´N, 66°51´W; DCN, 1964; see also Handley, 1976], USNM 385047–385049. Georeference error: ca. 1 km.

124. **19 km E Caracas (Curapao)** [1160–1630 m, 10°31´N, 66°38´W; Anderson and Gutiérrez, 2009], EBRG 3962–3965; Estanque de Curupao, N. de Guarenas (MBUCV 2033); **19 km E Caracas, Curupao** (USNM 385057–385060). Georeference error: ca. 2 km.

MONAGAS

125. **Los Pozos** [08°28´N, 62°43´W; SAGCN, 1996], MHNLS 4727, 4728; Carretera **Los Pozos** (MHNLS 4732). Georeference error: ca. 3 km.

126. **Carretera Los Barrancos-Chaguaramas**, km 20 [coordinates correspond to 20 km N Los Barrancos on the indicated road] [08°32´N, 62°45´W; SAGCN, 1996], MHNLS 4723, 4724, 4726, 4729–4731. Georeference error: ca. 5 km.

127. **Uverito**, 35 km S Temblador Distrito Sotillo [40 m, 08°40´N, 62°37´W; SAGCN, 1996], EBRG 16226, 16228, 16229, 16232. Georeference error: ca. 6 km.

128. **Campamento El Merey**, cerca Chaguaramas, 45 km SSO [SSW] Temblador, Distrito Sotillo [30 m, 08°40´N, 62°48´W, GE, 2010], EBRG 16863. Georeference error: ca. 2 km.

129. **Río Ñato, 4 km N Las Gaviotas, Municipio Aguasay** [09°10´N, 63°22´W; collector's label], EBRG 22378. Georeference error: < 5 km.

130. 55 km SSE Maturín, **Hato Mata de Bejuco** [18 m, 09°19´N, 62°56´W; Handley, 1976], Rossi *et al.*, 2010 lumped this locality with "*Hato Mata de Bajuco*" (USNM 443915–443917, 442720). Georeference error: ca. < 5 km.

131. **47 km SE Maturín**, Hato Santa Barbara [18 m, 09°22´N, 63°01´W; GE, 2010; see also Handley, 1976], USNM 385068–385072. Georeference error: ca. 1 km.

132. **Campamento MARNR**, Río Guarapiche [09°55´N, 62°55´W; DCN, 1978], EBRG 17569. Georeference error: ca. 2 km.

133. **Entre Arbolito y Buena Vista, Suroeste de San Antonio de Capayacual** [850 m, 10°04´N, 63°46´W; collector's label], MHNLS 9912, 9914. Georeference error: < 5 km.

134. San Antonio [= **San Antonio de Maturin**; 549 m, 10°07´N, 63°43´W; Paynter, 1982], AMNH 69939, 69940. Georeference error: ca. 1 km.

135. **Caripe** [860 m, 10°11´N, 63°30´W; DCN, 1969], MBUCV 397–400. Georeference error: ca. 2 km.

136. 5 km NW Caripe, **San Agustín** [1150 m, 10°12´N, 63°32´W; Handley, 1976], USNM 406951. Georeference error: ca. 2 km.

137. **Ipuré**, Cumaná [10°22´N, 64°08´W; Anderson and Gutiérrez, 2009], BMNH0.5.1.59. Georeference error: ca. 7 km.

NUEVA ESPARTA

138. **Península de Macanao, Quebrada La Chica** [50 m, 10°02´N, 64°16´W; collector's label], EBRG 24297. Georeference error: < 5 km.

139. Península de Macanao, **Punta Arenas** [10°59´N, 64°24´W; DCN, 1979a], EBRG 3133, 3134. Georeference error: ca. 1 km.

140. **La Sierra**, Isla de Margarita [100 m, 11°01´N, 63°52´W; DCN, 1979b], MHNLS 198; . Georeference error: ca. 1 km.

141. **3 km S La Asunción**, Isla Margarita [38 m, 11°01´N, 63°53´W; DCN, 1979; see also Handley, 1976], USNM 388398. Georeference error: ca. 1 km.

142. 2 km N and 1 km E La Assunción (**Salamanca**) [38 m, 11°03´N, 63°52´W; DCN, 1979; see also Handley, 1976], USNM 388381, 388388–388397, 388399, 388400. Georeference error: ca. 1 km.

PORTUGUESA

143. Palmarito Curbeleno [= **Palmerita Curbelero**], near Guanarito [08°24´N, 69°04´W, NGA, 2010], AMNH 266951–266954. Georeference error: ca. 1 km.

144. **Refugio de Fauna Silvestre Estero de Chiriguare, Río Guanare** [ca. 60 m, 08°33´N, 68°44´W; collector's label], EBRG 20681–20683. Georeference error: < 5 km.

145. Near **Guanarito** [08°42´N, 69°13´W; Anderson, 2003], Rossi *et al.*, 2010 lumped this locality with "*Palmarito Curbeleno, near Guanarito*"; La Arenosa, near Guanarito; La Hoyada, near Guanarito. Note: Rossi *et al.*, 2010 lumped this locality and specimens with "*Palmarito Curbeleno, near Guanarito*; therefore, see the just mentioned locality for specimen numbers". Georeference error: ≤ 5 km.

SUCRE

146. **Embalse Turimiquire**, campamento Inos [ca. 300 m, 10°10´N, 64°19´W; GE, 2010], EBRG 16814. Georeference error: ca. 11 km.

147. **Cuchivano** [213 m, 10°14´N, 63°56´W; Anderson and Gutiérrez, 2009], AMNH 69938. Georeference error: ca. 3 km.

148. **Río Clavellinos Abajo Embalse Clavellinos Municipio Ribero** [300 m, 10°22´N, 63°36´W; collector's label], EBRG 23204. Georeference error: < 5 km.

149. **Campo Alegre**, Cumaná [411 m, 10°22´N, 64°12´W; Anderson and Gutiérrez, 2009], BMNH 0.5.1.58. Georeference error: ca. 4 km.

150. **21 km E Cumaná,** cerca Sotillo [25 m, 10°27´N, 63°58´W; Gardner, 2008; see also Handley, 1976], EBRG 3967. Georeference error: ca. 2 km.

151. **16 km E Cumaná,** Hacienda Quetepe [0 m, 10°27´N, 64°02´W; Gardner, 2008; see also Handley, 1976], EBRG 3966, 3968–3970; **16 km E Cumaná** (Quetepe) (USNM 388377–388379, 388385, 388386). Georeference error: ca. 2 km.

152. **Finca Vuelta Larga**, 9.7 km (by road) SE Guaraúnos [10–20 m, 10°30´N, 63°07´W; Anderson and Gutiérrez, 2009], AMNH 257208–257210; **Finca Vuelta Larga**; 9.7 km SE. de Guaraunos (MHNLS 8805–8813, 8162, 8164, 8181); **Finca Vuelta Larga**, Guaraunos (MHNLS 8802). Georeference error: ca. 2 km.

153. **Carretera Cariaco-Chacopata** [10°39´N, 63°43´W; Anderson & Gutiérrez, 2009], MHNLS 6669. Georeference error: ca. 10 km.

154. Península de Araya, **Laguna Chacopata** [10°41´N, 63°48´W; DCN, 1990], EBRG 20680. Georeference error: ca. 2 km.

TÁCHIRA

155. **Buena Vista** [07°27´N, 72°26´W; Handley, 1976], MBUCV 2772. Georeference error: ca. 3 km.

TRUJILLO

156. **Valera** [645 m, 09°19´N, 70°37´W; Paynter, 1982], FMNH 22175. Georeference error: < 5 km.

157. 10 km WNW Valera, Nr. **Isnotú** [930 m, 09°22´N, 70°42´W; Anderson, 2003], USNM 370050. Georeference error: ≤ 5km.

158. **18 km N Valera, Nr. Agua Viva** [164 m, 09°28´N, 70°34´W; GE, 2010], USNM 371304. Georeference error: ca. 2 km.

159. 30 km NW Valera, Nr. **El Dividive** [90 m, 09°29´N, 70°44´W; Anderson, 2003], USNM 371305, 371315, 371316. Georeference error: ≤ 5 km.

160. **Hacienda Valle Verde** [29 m, 09°29´N, 70°59´W; GE, 2010 (coordinates in Handley, 1976 correspond to La Ceiba, which is located ca. 8 km W of Hacienda)], USNM 371317; **Hda. Valle Verde** [= 46 km WNW Valera; see Handley, 1976], vía Puerto La Ceiba (CVULA I-3231). Georeference error: ca. 5 km.

161. 23 km NW Valera, Nr. **Agua Santa** [90 m, 09°32´N, 70°39´W; Anderson, 2003], USNM 370048, 370049. Georeference error: ≤ 5 km.

VARGAS

162. **Canales de Naiguata**, Parque Nacional El Avila, DF [720–750 m, 10°35´N, 66°44´W; Anderson and Gutiérrez, 2009], MHNLS 8577; **Canales de Naiguata**, DF (MHNLS 7166); Los **Canales de Naiguata**, Naiguata, DF (MBUCV 2971, 2972). Georeference error: > 10 km.

YARACUY

163. **Agua Negra** [80 m, 10°04´N, 69°09´W; SAGCN, 1994], MHNLS 3294. Georeference error: ca. 2 km.

YARACUY-CARABOBO

164. **19 km NO [NW] Urama**, km 40 [5–25 m, 10°33´N, 68°27´W; Anderson, 2003], EBRG 3946–3958. Georeference error: ≤ 5 km.

ZULIA

165. **El Tukuko; Perijá** [300 m, 09°45´N, 72°45´W; collector's label], MHNLS 7775. Georeference error: < 5 km.

166. **Mene Grande** [70 m, 09°49´N, 70°56´W; Paynter, 1982], CVULA I-1320. Georeference error: ca. 2 km.

167. 3 km S and 19 km W Machiques [= **Novito**; 1132 m, 10°02´N, 72°43´W; Handley, 1976], USNM 418529, 418530. Georeference error: ca. 1 km.

168. **Hato El Mango; 8 km S. La Villa** [200 m, 10°15´N, 72°25´W; collector's label], MHNLS 7061. Georeference error: < 5 km.

169. **La Soledad; Hacienda Grano de Oro; Campo Boscán; Cuenca Baja del Río Palmar** [10°16´N, 72°04´W; collector's label], MHNLS 11929. Georeference error: < 5 km.

170. **Planta Ule**, 20 km de Cabimas, Carretera Cabimas-Ciudad Ojeda [5 m, 10°17´N, 71°23´W; GE, 2010], EBRG 24078, 24080, 24081. Georeference error: ca. 2 km.

171. **Río Palmar** [110 m, 10°37´N, 72°24´W; DCN. 1974a], EBRG 17066. Georeference error: ca. 2 km.

172. **Refugio de Fauna Silvestre y Reserva de Pesca Los Olivitos, Municipio Miranda** [0 m, 10°48´N, 71°26´W; collector's label], EBRG 22568. Georeference error: < 5 km.

173. **17 km N and 55 km W Maracaibo (Hacienda El Tigre)** [80 m, 10°48´N, 72°18´W; NGA, 2010; not Musser *et al.*, 1998 who provided coord. for Maracaibo], USNM443807; 18 km N and 56 km W Maracaibo [= Hda. El Tigre] (USNM 443802–443804). Georeference error: ca. 2 km.

174. 39 km NW La Paz, Nr. **Cerro Azul** [80 m, 10°51´N, 72°16´W; Anderson, 2003], USNM 443805, 443806. Georeference error: ≤ 5 km.

175. **Refugio de Fauna Silvestre y Reserva de Pesca Los Olivitos, Municipio Miranda** [note that same collector reported different coordinates for other locality (number 169. above) within the protected area, but described such locality in the same way as this one] [0 m, 10°57´N, 71°23´W; collector's label], EBRG 22545. Georeference error: < 5km.

Marmosa xerophila

COLOMBIA

LA GUAJIRA

176. 114 km N and 32 km O [W] Maracaibo (**Cojoro**) [15 m, 11°39´N, 71°51´W; GE, 2010; not Handley, 1976], EBRG 4003, 4005; 114 km N and 32 km W Maracaibo (La Isla) [= 37 km NNE Paraguaipoa; = **Cojoro**] (USNM 443810, 443811, 443832); 37 km NNE Paraguaipoa, near **Cojoro** (USNM 443812–443818, 443819, 443820–443831). Georeference error: ca. 2 km.

VENEZUELA

FALCÓN

177. **18 km WSW Capatárida**, Capatárida [75 m, 11°02´N, 70°40´W; DCN, 1963], USNM 442728. Georeference error: ca. 3 km.

178. **Capatárida** [40–75m, 11°10´N, 70°37´W; DCN, 1963; A. L. Tuttle's field notes (1968); see also Handley, (1976), who reported the same coordinates], EBRG 4004, 4006–4031; USNM 442721–442727, 442729–442731, 442733–442735, 442744, 443918–443925, 443927–443929, 443931, 443936–443938, 443940–443942, 443946, 443947, 443951, 443952, 443955–443957, 443959, 443960, 443963–443972, 443974–443978. Georeference error: ca. 2 km.

179. Serranía de San Luis, **La Chapa**, 15 km N Cabure [350–380 m, 11°17´N, 69°36´W; collectors' label], AMNH 276582 (previously EBRG 25427), 276586 (previously EBRG 25433); EBRG 25432, 25437, 25439. Georeference error: ca. 1 km.

180. **Tacuato**, N Península Paraguaná [11°43´N, 69°50´W; DCN, 1974b], EBRG 20670. Georeference error: ca. 3 km.

181. 48 km N and 46 km W Coro, **Yabuquiva** [= 25 km SW Pueblo Nuevo; Handley, 1976] [13 m, 11°48´N, 70°04´W; N. E. Peterson field notes, 1968; SAGCN, 1990; DCN. 1962], EBRG 4035–4045; 25 km SW Pueblo Nuevo, **Yabuquiva**, Península de Paraguaná (USNM 442906); 48 km N and 46 km W Coro (**Yabuquiva**) (USNM 443852, 443854–443856, 443862, 443863, 443868–443869). Georeference error: < 5 km.

182. 49 km N and 33 km W Coro (**Moruy**) [80–90m, 11°49´N, 69°58´W; N. E. Peterson field notes, 1968; Soley-G., *in litt.*; not Anderson (2003)], EBRG 4032, 4033; USNM 443834–443848, 443851. Georeference error: ca. 2 km.

183. 49 km N and 34 km W Coro (**Moruy**) [55 m, 11°50´N, 69°59´W; Anderson, 2003], EBRG 4034. Georeference error: ≤ 5 km.

184. San Pedro, **Jadacaquiva**, Península de Paraguaná [11°54´N, 70°05´W; DCN, 1962], EBRG 22111. Georeference error: ca. 3 km.

185. **Guaidabacoa**, 22 km NW Pueblo Nuevo, Paraguaná [60 m, 12°06´N, 70°00´W; Diaz and Granadillo, 2005], CVULA I-3498, I-3499; **Guaidabacoa**, Península de Paraguaná (EBRG 22112, 22115–22117, 22119); Hato **Guaidabacoa**, Península Paraguaná (EBRG 20671, 22113, 22114, 22118). Georeference error: ca. 2 km.

186. La Voz de Venezuela, Puerto Tumatey [= **Punta Tumatey**], Península de Paraguaná [12°10´N, 69°56´W; DCN, 1974c], EBRG 20668, 20669. Georeference error: ca. 2 km.

ZULIA

187. **Las Mentiras, Municipio Paez** [20–30 m, 11°12´N, 72°02´W; collector's label], EBRG 21810, 21817, 21819, 21820. Georeference error: < 5 km.

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