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Phylogenetic Relationships of Mouse Opossums (Didelphidae, *Marmosa*) with a Revised Subgeneric Classification and Notes on Sympatric Diversity

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ABSTRACT

To resolve phylogenetic relationships among species of *Marmosa* we analyzed DNA sequences from one mitochondrial and three nuclear genes for every member of the nominotypical subgenus and from four species of the subgenus *Micoureus*. As reported in previous studies, the subgenus *Marmosa* was found to be paraphyletic, whereas *Micoureus* was recovered as a robustly supported clade. Species currently referred to the subgenus *Marmosa* form four strongly supported and morphologically diagnosable groups. Based on these results we recognize a total of five subgenera: *Marmosa* Gray, 1821 (for *macrotarsus*, *murina*, *tyleriana*, and *waterhousei*); *Micoureus* Lesson, 1842 (for *alstoni*, *constantiae*, *demerarae*, *paraguayana*, *phaea*, and *regina*); *Stegomarmosa* Pine, 1972 (for *andersoni* and *lepida*); *Eomarmosa,* new subgenus (for *rubra*); and *Exulomarmosa,* new subgenus (for *isthmica*, *mexicana*, *robinsoni*, *simonsi*, *xerophila*, and *zeledoni*). The best-supported hypothesis of relationships among these clades is

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((*Stegomarmosa* (*Marmosa* + *Micoureus*)) (*Eomarmosa* + *Exulomarmosa*)), and our results additionally resolve many interspecific relationships within each subgenus. These clades have broadly overlapping geographic distributions, especially in western Amazonia, where the arboreal insectivorous-frugivorous niche of *Marmosa* is apparently partitioned among multiple sympatric congeners.

INTRODUCTION

As currently recognized (Voss and Jansa, 2009), the didelphid marsupial genus *Marmosa* Gray, 1821, is a robustly supported monophyletic group containing 19 species assigned to two subgenera (table 1). Recent morphology-based revisionary work (Rossi, 2005; Rossi et al., 2010) has resolved many long-standing taxonomic problems in the nominotypical subgenus, but the subgenus *Micoureus* Lesson, 1842, remains unrevised. Although analyses of DNA sequence data provide strong support for the monophyly of *Micoureus*, the same analyses suggest that the subgenus *Marmosa* is paraphyletic (Voss and Jansa, 2009; Gutiérrez et al., 2010; Faria et al., 2013). The nomenclatural solution to this problem has so far been elusive because sequence data are lacking for *Marmosa andersoni*, type species of *Stegomarmosa* Pine, 1972. The latter name, currently treated as a subjective junior synonym of *Marmosa*, is available for subgeneric usage, but its application is uncertain until the relationships of *M. andersoni* can be determined.

Marmosa andersoni was redescribed by Solari and Pine (2008) based on recently collected material, but they were not able to resolve the relationships of this species using the morphological data matrix of Jansa and Voss (2005). Solari (unpublished) subsequently obtained a partial cytochrome-*b* sequence from dry tissue of *M. andersoni*, and we were later successful in obtaining nuclear-gene sequences from DNA extracts of the same material. In this report, we analyze these new sequence data, which now suffice to securely place *M. andersoni* in a well-resolved phylogenetic context.

Additionally, we analyze sequence data from *Marmosa "tobagi,"* an insular form originally described by Thomas (1911). Long considered a subspecies or synonym of *M. murina* (e.g., by Goodwin, 1961; Creighton and Gardner, 2008), *tobagi* was recognized as a valid species in Rossi's (2005) still-unpublished revision of the *murina* complex. A recent collecting trip to Tobago provided fresh tissues for a molecular appraisal of the relationships of this nominal taxon. With these additions, our species-level molecular sampling of the nominotypical subgenus is complete, and the sequence data now in hand provide a secure basis for a revised classification of the genus *Marmosa*.

Materials and Methods

Source of Material: All voucher specimens and associated tissues mentioned in this report are preserved in the following collections (listed alphabetically by institutional abbreviation; in the United States except as noted): AMNH, American Museum of Natural History (New York); CM, Carnegie Museum of Natural History (Pittsburg); EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay, Venezuela); FMNH, Field Museum of Natural History (Chicago); LSU, Louisiana State University, Museum of Natural Science (Baton Rouge);

TABLE 1. Currently Recognized Species of the Genus *Marmosa*[a]

Subgenus *Marmosa*	Subgenus *Micoureus*
M. andersoni[b]	*M. alstoni*
M. isthmica[c]	*M. constantiae*
M. lepida[b]	*M. demerarae*
M. macrotarsus[d]	*M. paraguayana*
M. mexicana[c]	*M. phaea*
M. murina	*M. regina*
M. robinsoni[c]	
M. rubra[e]	
M. simonsi[c]	
M. tyleriana	
M. waterhousei	
M. xerophila[c]	
M. zeledoni[c]	

[a] After Voss and Jansa (2009), Rossi et al. (2010), and Gutiérrez et al. (2010), except as noted below. See taxonomic accounts for authors and dates of species epithets.
[b] Referred to the subgenus *Stegomarmosa* in this report.
[c] Referred to *Exulomarmosa* (new subgenus) in this report.
[d] According to Rossi (2005), this is the correct name for the taxon previously known as *M. quichua* (e.g., by Voss and Jansa, 2009; Gutiérrez et al., 2010).
[e] Referred to *Eomarmosa* (new subgenus) in this report.

MNK, Museo de Historia Natural Noel Kempff Mercado (Santa Cruz, Bolivia); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima, Peru); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); ROM, Royal Ontario Museum (Toronto, Canada); TTU, Museum of Texas Tech University (Lubbock); USNM, National Museum of Natural History (Washington).

Taxon Sampling and Laboratory Methods: We analyzed all the cytochrome-*b* (CYTB) sequences published by Gutiérrez et al. (2010), and we sequenced CYTB from nine additional specimens representing nominal taxa or geographic populations that were not included in that report (table 2). This new material includes two museum specimens of *Marmosa andersoni* (from which only fragments of dry skin were available), together with fresh tissue from one specimen of *M. robinsoni* (representing the nominal taxon *M. r. luridivolta*, from Tobago) and six specimens of *M. "tobagi"* (also from Tobago). We extracted DNA from skin fragments of *M. andersoni* using a phenol/chloroform/isoamyl alcohol protocol developed by K. Nelson and the late M.C. Knapp; to sequence CYTB from this material, we used laboratory protocols described by Solari (2007) with internal primers MVZ 04, MVZ 16, and MVZ 11 (Patton et al., 1996). To sequence CYTB from the Tobago specimens we used primers and laboratory protocols described by Gutiérrez et al. (2010).

In addition to CYTB, we analyzed nuclear-gene sequences that we obtained from 24 specimens of *Marmosa* (including multiple individuals of some widespread species) and from two

TABLE 2. Additional Specimens of *Marmosa* Sequenced for Cytochrome *b*

Taxon	Tissue/DNA#[a]	Voucher	Locality	CYTB[b]
Marmosa andersoni	TK 125320	MUSM 14154	Peru: Cusco, Camisea	810
Marmosa andersoni	TK 125321	MUSM 14155	Peru: Cusco, Camisea	810
Marmosa robinsoni	RSV 2455	AMNH 276746	Trinidad & Tobago: Tobago, near Charlotteville	1138
Marmosa "tobagi"	RSV 2452	AMNH 276743	Trinidad & Tobago: Tobago, near Charlotteville	1140
Marmosa "tobagi"	RSV 2454	AMNH 276745	Trinidad & Tobago: Tobago, near Charlotteville	1140
Marmosa "tobagi"	RSV 2460	AMNH 276751	Trinidad & Tobago: Tobago, near Charlotteville	1137
Marmosa "tobagi"	RSV 2462	AMNH 276753	Trinidad & Tobago: Tobago, near Charlotteville	1140
Marmosa "tobagi"	RSV 2463	AMNH 276754	Trinidad & Tobago: Tobago, near Charlotteville	1140
Marmosa "tobagi"	RSV 2466	AMNH 276757	Trinidad & Tobago: Tobago, near Charlotteville	1140

[a] Alphanumeric identifiers used by collectors and/or institutional tissue collections.
[b] Number of base pairs sequenced.

specimens representing outgroup taxa (table 3). Using the primers listed in appendix 1, we amplified part of exon 11 from the breast cancer type 1 susceptibility gene (BRCA1), intron 14 from the X chromosome-linked gene O-linked N-acetylglucosamine transferase (OGT), and intron 7 from the autosomal gene sodium-coupled neutral amino acid transporter 2 (SLC38). We amplified BRCA1 using the primer pair F1163a/R2151, and we subsequently reamplified and sequenced this product using primer pairs F1163a/R1780 and F1697/R2151. To obtain shorter fragments of BRCA1 from degraded DNA, we used four sets of primer pairs: F1163a/R1475, F1360/R1750, F1620/R1980, and F1850/R2151. In most cases, we amplified and sequenced the entire OGT intron using primer pair OGTF1/OGTR1; for specimens with low-quality DNA, we amplified and sequenced portions of the intron using primer pairs OGT-F1/OGT-R360, OGT-F120/OGT-R540, and OGT-F300/OGT-R1. We amplified the SLC38 intron using primer pair SLC38-F1/SLC38-R1 or primer pairs SLC38-F1/SLC38-R350 and SLC38-F250/SLC38-R1. All genes were PCR-amplified in 12.5 μL reactions using either GoTaq (Promega Corp.) or Platinum Taq (Life Technologies Corp.) with recommended reagent concentrations. Initial amplifications were performed using a four-stage touchdown protocol as described in Voss and Jansa (2009). When necessary, reamplification reactions were performed as 12.5 μL reactions using GoTaq. The resulting PCR products were sequenced using amplification primers and dye-terminator chemistry on an ABI-3730xl automated sequencer. All new sequences obtained for this study have been deposited in GenBank (CYTB: KM819039-KM819047; BRCA1 KM819017-KM819038; OGT: KM819048-KM819065; SLC 38: KM819066-KM819086).

Phylogenetic Analyses: We aligned orthologous gene sequences using default settings of MUSCLE (Edgar, 2004) as implemented in Geneious v. 7.0.5 (Biomatters, Inc.). For the CYTB dataset, we determined the optimal nucleotide substitution model by comparing the likelihood scores of 55 candidate models using the Bayesian Information Criterion (BIC) as implemented in jModelTest 2.1.1 (Darriba et al., 2012). We analyzed this dataset using maximum likelihood (ML) as implemented in GARLI ver. 2.0 (Zwickl, 2006), specifying five search replicates, the optimal substitution model, and default search parameters. To estimate nodal

TABLE 3. Specimens Sequenced for Nuclear Genes

	Tissue/DNA#[a]	Voucher	BRCA1[b]	OGT[b]	SLC38[b]
Ingroup[c]					
Marmosa (Ma.) andersoni	TK 125320	MUSM 14154	729	334	76
Marmosa (Ma.) isthmica	TK 135686	TTU 102969	878	659	612
Marmosa (Ma.) isthmica	TK 22555	TTU 39118	884	659	612
Marmosa (Ma.) lepida	DWF 717	AMNH 273186	878	645	639
Marmosa (Ma.) macrotarsus	LHE 1548	MNK [uncataloged]	879	644	644
Marmosa (Ma.) macrotarsus	RSV 2303	AMNH 272816	884	644	642
Marmosa (Ma.) mexicana A	FN 30771	ROM 96968	879	657	613
Marmosa (Ma.) mexicana B	JOM 7269	USNM 569858	876	658	615
Marmosa (Ma.) murina	LHE 503	USNM 549291	879	644	641
Marmosa (Ma.) murina	F 50629	ROM 113649	NA	644	642
Marmosa (Ma.) robinsoni	NK 101529	MSB 94363	884	668	628
Marmosa (Ma.) robinsoni	RPA 262	EBRG 25389	879	664	626
Marmosa (Ma.) robinsoni	RSV 2455	AMNH 276746	884	662	629
Marmosa (Ma.) rubra	JLP 6930	MVZ 153280	884	336	538
Marmosa (Ma.) simonsi	NK 37836	MSB 87086	884	657	623
Marmosa (Ma.) "tobagi"	RSV 2452	AMNH 276743	881	644	642
Marmosa (Ma.) tyleriana	—	AMNH 130510	884	644	479
Marmosa (Ma.) waterhousei	JMC 88	LSU 28017	879	644	644
Marmosa (Ma.) xerophila	RPA 324	AMNH 276586	867	665	628
Marmosa (Ma.) zeledoni	—	AMNH 269997	884	657	615
Marmosa (Mi.) constantiae	NK 15501	MSB 59883	875	644	644
Marmosa (Mi.) demerarae	RSV 2085	MUSM 13294	884	645	661
Marmosa (Mi.) paraguayana	MAM 46	MVZ 182064	884	645	632[d]
Marmosa (Mi.) regina	JLP 15435	MVZ 190323	878[e]	643	635
Outgroup[c]					
Monodelphis brevicaudata	TK 17069	CM 68359	876	650	652
Tlacuatzin canescens	TK 11826	TTU 37700	884	621	564

[a] Alphanumeric identifiers used by collectors and/or institutional tissue collections. Sequences amplified from DNA extracted from dried tissue lack entries in this column (except for *Marmosa andersoni* for which dried-tissue DNA extracts are stored at TTU).
[b] Number of base pairs sequenced.
[c] Based on the results of prior analyses (e.g., Voss and Jansa, 2009), we assumed the monophyly of the genus *Marmosa* and used exemplar species from other marmosine genera to root our trees.
[d] SLC38 of *Marmosa paraguayana* was amplified and sequenced from voucher MVZ 182065
[e] BRCA1 of *Marmosa regina* was amplified and sequenced from voucher MVZ 190332.

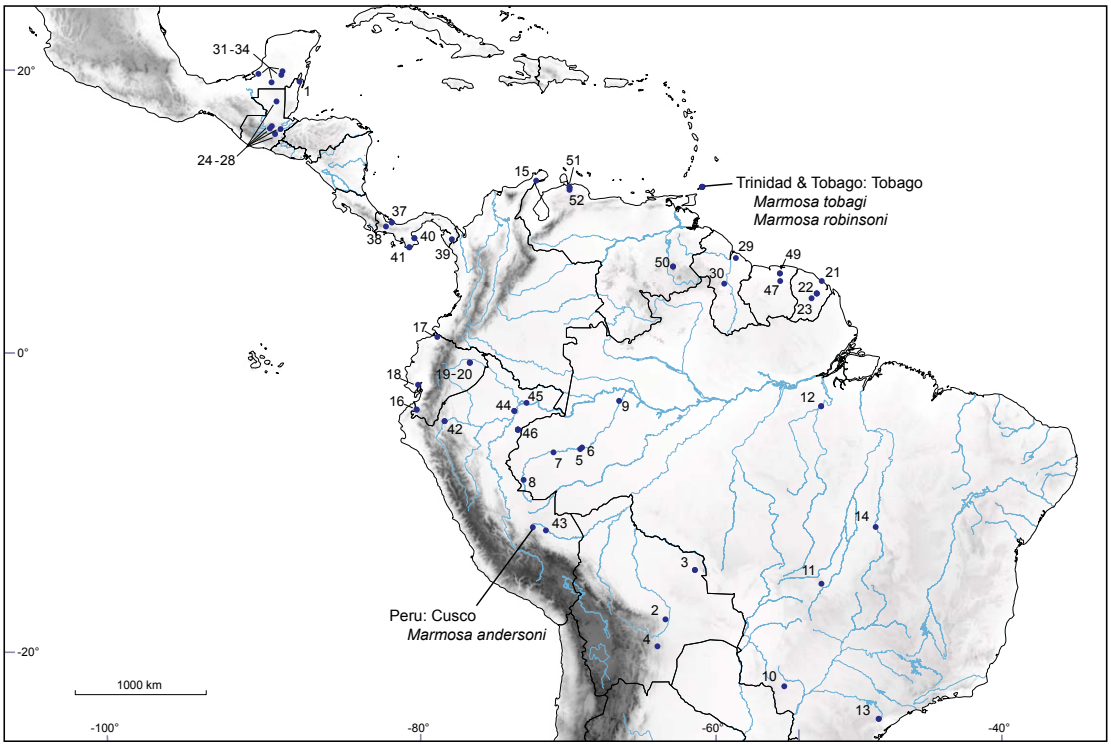


FIG. 1. Localities where sequenced specimens of *Marmosa* were collected. Numbers correspond to gazetteer entries in Gutiérrez et al. (2010: appendix) and to branch-tip labels in figure 2 of this report. Collection localities of specimens newly sequenced for this report are labeled with country of origin, next-largest political unit, and species.

support values, we ran 1000 bootstrap replicates also using GARLI ver. 2.0. We analyzed each of the three nuclear-gene datasets separately assuming the GTRGAMMA model on the RAxML BlackBox server (Stamitakis et al., 2008), using full maximum-likelihood optimization for the tree search and 100 rapid bootstrap searches to assess nodal support.

We used the BIC implemented in PartitionFinder (Lanfear et al., 2012) to determine the best partitioning scheme and substitution models for two different concatenated-gene matrices: one that contained only the three nuclear genes and a second that also included CYTB from the same specimens sequenced for nuclear loci. For the first dataset, we partitioned by locus and by codon for the protein-coding gene BRCA1, and we used a single partition for each of the introns (for a total of five partitions). For the nuclear + CYTB dataset we additionally partitioned CYTB by codon for a total of eight partitions. For both datasets, we used the *greedy* search algorithm for model comparison. We performed partitioned ML analyses on each of the two datasets using five search replicates, optimal substitution models, and default search parameters as specified in GARLI ver. 2.0. We assessed nodal support from the multigene datasets in RAxML ver. 8.0 (Stamitakis, 2014) using 1000 bootstrap replicates with the optimal partitioning scheme and a GTRGAMMA model.

Finally, we conducted a species-tree analysis (Maddison and Knowles, 2006; Degnan and Rosenberg, 2009) as implemented by *BEAST ver. 1.7.4 (Heled and Drummond, 2010) using

the 80-terminal CYTB matrix and the three 26-terminal nuclear-gene matrices. We assigned each individual to a species; specified the best-fitting model of sequence substitution and ploidy level for each locus; assumed a Yule process for the species tree with a piecewise linear, constant root model for the population size model; and modeled rates according to an uncorrelated lognormal relaxed clock with an exponential prior (mean = 1.0; standard deviation = 0.33). We ran the MCMC chain for 5×10^7 generations and assessed convergence using ESS values derived from Tracer ver. 1.5.

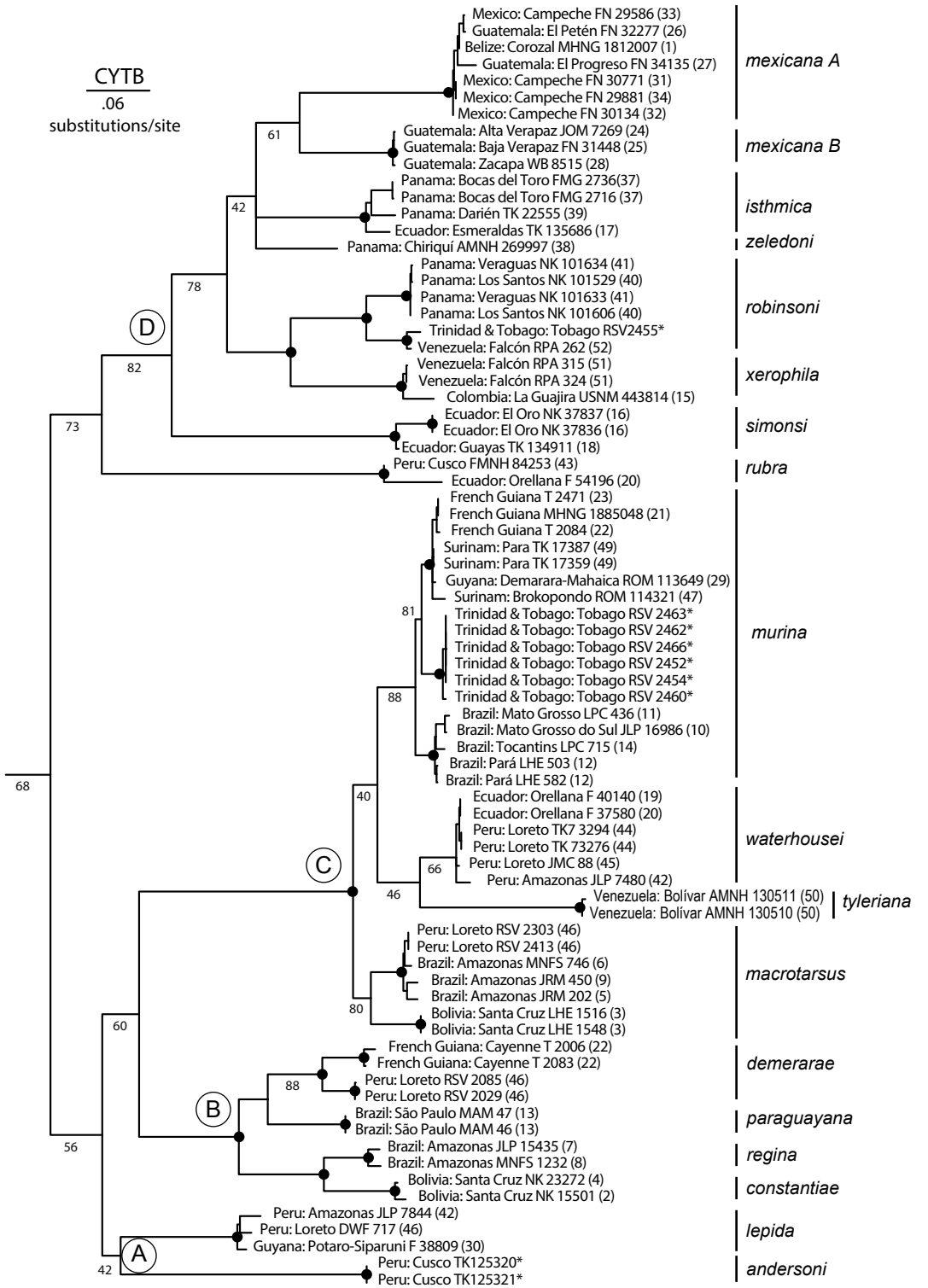
RESULTS

The optimal substitution model for our cytochrome-*b* data matrix (with 77 ingroup and three outgroup terminals) was HKY+I+Γ. The best tree resulting from maximum-likelihood (ML) analysis under this model (fig. 2) is almost identical to the ML topology obtained by Gutiérrez et al. (2010: fig. 3), with only three noteworthy differences concerning terminals new to this study. First, *Marmosa andersoni* was recovered as the sister taxon of *M. lepida*. Although these taxa are highly divergent (uncorrected pairwise distance = 13.5%; appendix 2), they form a weakly supported lineage (clade A). Second, the six specimens of *M. "tobagi"* were recovered as one of three geographically structured haplogroups within *M. murina*; average pairwise distances are 2.8% between *"tobagi"* and a cluster of Guianan haplotypes and 3.7% between *"tobagi"* and a cluster of Brazilian sequences. Lastly, our single sequence from a specimen of *M. robinsoni* collected on Tobago was recovered as minimally divergent (1.5%) from a conspecific sequence from mainland Venezuela.

A conspicuous pattern in these CYTB results is lack of strong support for deep structure in the tree. Although clade B (representing the subgenus *Micoureus*) and clade C (the cluster of forms associated with *M. murina*) are each strongly supported, support for clade D (the mostly trans-Andean *"mexicana-robinsoni"* group of Gutiérrez et al., 2010) is somewhat less convincing, and the novel pairing of *M. andersoni* + *M. lepida* is weakly supported. Only moderate ML bootstrap support was obtained for the sister-group relationship between *M. rubra* and clade D, and for the group that includes clades B and C.

Each of our nuclear-gene datasets consists of 24 ingroup and two outgroup sequences except BRCA1, for which we lack sequence from one specimen of *Marmosa murina* (table 3). Separate ML analyses of each nuclear-gene dataset (results not shown) consistently recovered many relationships in common with those seen in the CYTB tree (fig. 2) including clades A, B, C, and D; a group that includes clades A, B, and C; a group that includes clade D and *Marmosa rubra*; a group that includes *M. robinsoni* and *M. xerophila*; and a group that includes *M. isthmica*, *M. mexicana*, and *M. zeledoni*. All of the nuclear loci also support the same pattern of interspecific relationships within clade B that was supported by cytochrome *b*. By contrast, one or more nuclear-gene trees conflict with the CYTB topology concerning relationships within clade D and/or clade C, and our analysis of OGT sequences uniquely supports a sister-group relationship between clades A and C.

The concatenated nuclear-gene dataset consists of 2317 aligned sites, and the concatenated nuclear + CYTB dataset consists of 3463 aligned sites; both datasets include 24 ingroup and


CYTB
.06
substitutions/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 30771 (31)
Mexico: Campeche FN 29881 (34)
Mexico: Campeche FN 30134 (32)
mexicana A
Guatemala: Alta Verapaz JOM 7269 (24)
Guatemala: Baja Verapaz FN 31448 (25)
Guatemala: Zacapa WB 8515 (28)
mexicana B
Panama: Bocas del Toro FMG 2736(37)
Panama: Bocas del Toro FMG 2716 (37)
Panama: Darién TK 22555 (39)
Ecuador: Esmeraldas TK 135686 (17)
isthmica
Panama: Chiriquí AMNH 269997 (38)
zeledoni
Panama: Veraguas NK 101634 (41)
Panama: Los Santos NK 101529 (40)
Panama: Veraguas NK 101633 (41)
Panama: Los Santos NK 101606 (40)
Trinidad & Tobago: Tobago RSV2455*
Venezuela: Falcón RPA 262 (52)
robinsoni
Venezuela: Falcón RPA 315 (51)
Venezuela: Falcón RPA 324 (51)
xerophila
Colombia: La Guajira USNM 443814 (15)
Ecuador: El Oro NK 37837 (16)
Ecuador: El Oro NK 37836 (16)
Ecuador: Guayas TK 134911 (18)
simonsi
Peru: Cusco FMNH 84253 (43)
Ecuador: Orellana F 54196 (20)
rubra
French Guiana T 2471 (23)
French Guiana MHNG 1885048 (21)
French Guiana T 2084 (22)
Surinam: Para TK 17387 (49)
Surinam: Para TK 17359 (49)
Guyana: Demarara-Mahaica ROM 113649 (29)
Surinam: Brokopondo ROM 114321 (47)
Trinidad & Tobago: Tobago RSV 2463*
Trinidad & Tobago: Tobago RSV 2462*
Trinidad & Tobago: Tobago RSV 2466*
Trinidad & Tobago: Tobago RSV 2452*
Trinidad & Tobago: Tobago RSV 2454*
Trinidad & Tobago: Tobago RSV 2460*
Brazil: Mato Grosso LPC 436 (11)
Brazil: Mato Grosso do Sul JLP 16986 (10)
Brazil: Tocantins LPC 715 (14)
Brazil: Pará LHE 503 (12)
Brazil: Pará LHE 582 (12)
murina
Ecuador: Orellana F 40140 (19)
Ecuador: Orellana F 37580 (20)
Peru: Loreto TK7 3294 (44)
Peru: Loreto TK 73276 (44)
Peru: Loreto JMC 88 (45)
Peru: Amazonas JLP 7480 (42)
waterhousei
Venezuela: Bolívar AMNH 130511 (50)
Venezuela: Bolívar AMNH 130510 (50)
tyleriana
Peru: Loreto RSV 2303 (46)
Peru: Loreto RSV 2413 (46)
Brazil: Amazonas MNFS 746 (6)
Brazil: Amazonas JRM 450 (9)
Brazil: Amazonas JRM 202 (5)
Bolivia: Santa Cruz LHE 1516 (3)
Bolivia: Santa Cruz LHE 1548 (3)
macrotarsus
French Guiana: Cayenne T 2006 (22)
French Guiana: Cayenne T 2083 (22)
Peru: Loreto RSV 2085 (46)
Peru: Loreto RSV 2029 (46)
demerarae
Brazil: São Paulo MAM 47 (13)
Brazil: São Paulo MAM 46 (13)
paraguayana
Brazil: Amazonas JLP 15435 (7)
Brazil: Amazonas MNFS 1232 (8)
regina
Bolivia: Santa Cruz NK 23272 (4)
Bolivia: Santa Cruz NK 15501 (2)
constantiae
Peru: Amazonas JLP 7844 (42)
Peru: Loreto DWF 717 (46)
Guyana: Potaro-Siparuni F 38809 (30)
lepida
Peru: Cusco TK125320*
Peru: Cusco TK125321*
andersoni
A
B
C
D
61
42
78
82
73
81
88
68
40
66
46
80
60
88
56
42

two outgroup terminals. Maximum-likelihood analysis of these two matrices under their optimal partitioning schemes and substitution models (appendix 3) resulted in highly congruent topologies (fig. 3). Although most nodes in both trees are strongly supported, several key relationships remain weakly supported: (1) alternative resolutions of *Marmosa simonsi* within clade D; (2) the group that includes clades B and C; and (3) alternative resolutions of *M. murina*, *M. macrotarsus*, and *M. waterhousei* within clade C.

The species tree (fig. 4) convincingly resolves much of the conflict among the individual gene trees and provides improved support for some of the nodes that remain weakly supported in our concatenated-gene trees. In particular, the position of *Marmosa simonsi* is resolved in favor of the topology supported by OGT and CYTB, and the position of clade A is resolved in accordance with the topology supported by all the sequenced genes except OGT. In effect, the only region of the tree that remains poorly supported is the branching order among *M. murina*, *M. waterhousei*, and *M. macrotarsus* within clade C.

TAXONOMIC SYNTHESIS

Our molecular results provide unambiguous evidence for robust phylogenetic structure among the species currently referred to the paraphyletic subgenus *Marmosa*, and it now seems appropriate to propose a revised classification of the genus based on the relationships discussed above. Although taxonomic rank is biologically arbitrary, it is a matter of practical importance that nomenclature provide a stable basis for biological communication, so unnecessary changes of rank are to be avoided. The rank of subgenus has not been widely used in mammalian taxonomy, but this category usefully serves to label clades of closely related species while preserving traditional binomial usage. An alternative is to use informal nomenclature, such as Tate's (1933) "sections" and "groups," but informal names have two disadvantages. The first is that hierarchical relationships are inapparent (for example, do sections contain groups or do groups contain sections?). The second disadvantage is that informal names are not regulated by widely accepted conventions: clade D, for example, could just as easily be called something else (the trans-Andean group, for example, or the *mexicana-robinsoni* complex) without any rules to mediate alternative usage. By contrast, subgenera are regulated by the ICZN (1999), so usage is constrained (and stability promoted) by typification and priority.

FIG. 2. Phylogeny of *Marmosa* inferred by maximum-likelihood analysis of CYTB sequences (lnL = -11360.78). Branch tips are sequenced specimens labeled by geographic origin and a tissue identifier (see table 2 of Gutierrez et al. [2010] and table 2 of this report); numbers in parentheses refer to localities mapped in figure 1 and georeferenced by Gutiérrez et al. (2010: appendix). Outgroup taxa are not shown. Bootstrap values below 90% are shown along branches, whereas bootstrap values ≥ 90% are indicated with filled circles at relevant nodes. For simplicity, we do not show support values for relationships among very similar sequences. Individuals marked with asterisks were newly sequenced for this report. Capital letters (A–D) indicate clades discussed in the text.

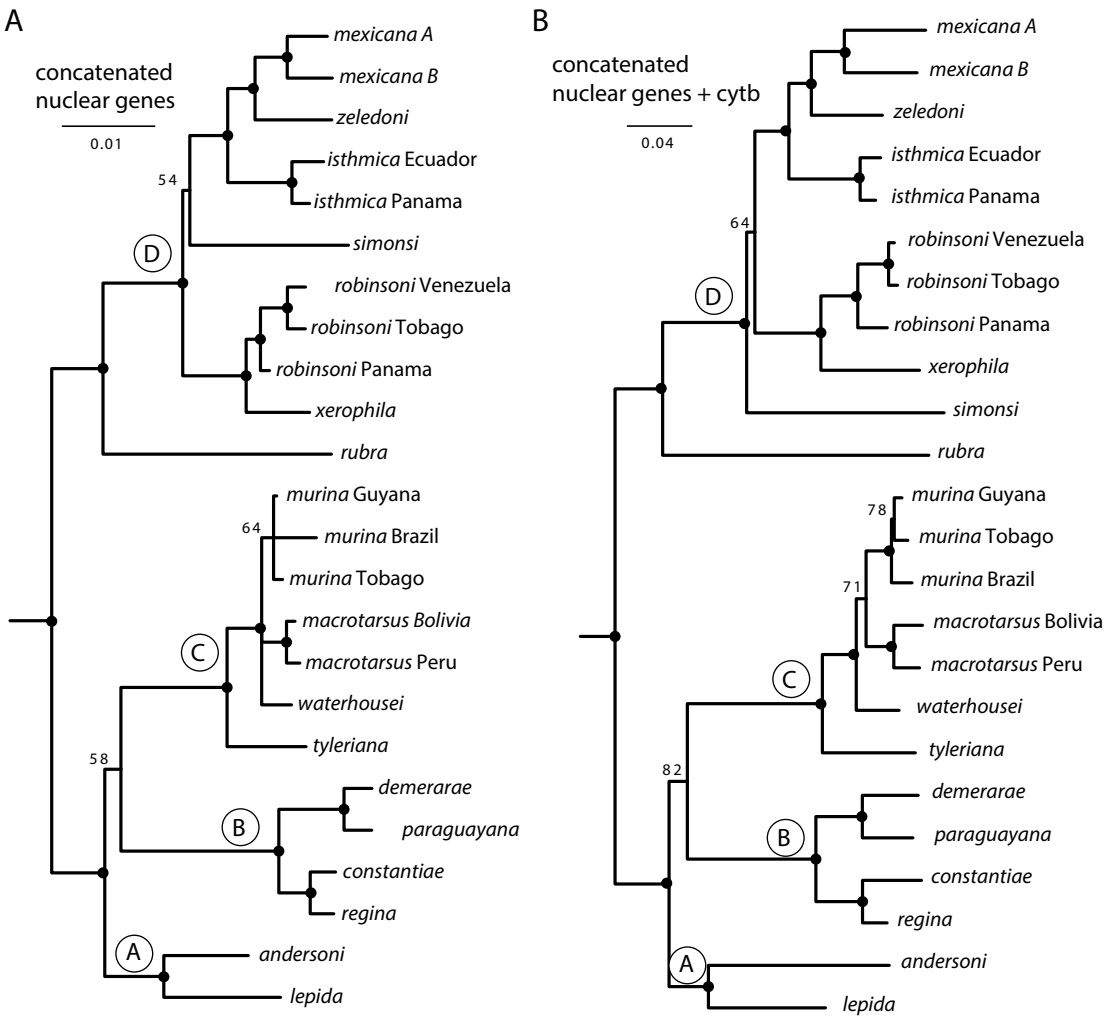


FIG. 3. Phylogeny of *Marmosa* inferred by (**A**) maximum-likelihood analysis of concatenated nuclear genes (lnL = -7351.13) and (**B**) maximum-likelihood analysis of concatenated nuclear genes plus CYTB (lnL = -16236.59). Terminals are species or mtDNA haplogroups represented by exemplar specimens sequenced for nuclear loci (table 3). Outgroup taxa are not shown. Capital letters (A–D) indicate clades discussed in the text.

We propose recognizing five subgenera of *Marmosa:* four for the clades designated alphabetically in figures 2–4 and another for *M. rubra*. As explained below, appropriate names are already available for three of these groups, so only two new names are required. All five subgenera can be diagnosed morphologically. Below we summarize morphological character data for all of the supraspecific taxa treated in this report using anatomical terminology defined and illustrated or referenced by Voss and Jansa (2009) and Rossi et al. (2010). We also take this opportunity to provide a revised morphological description of the genus *Marmosa* to correct a few errors of commission and omission in Voss and Jansa (2009).

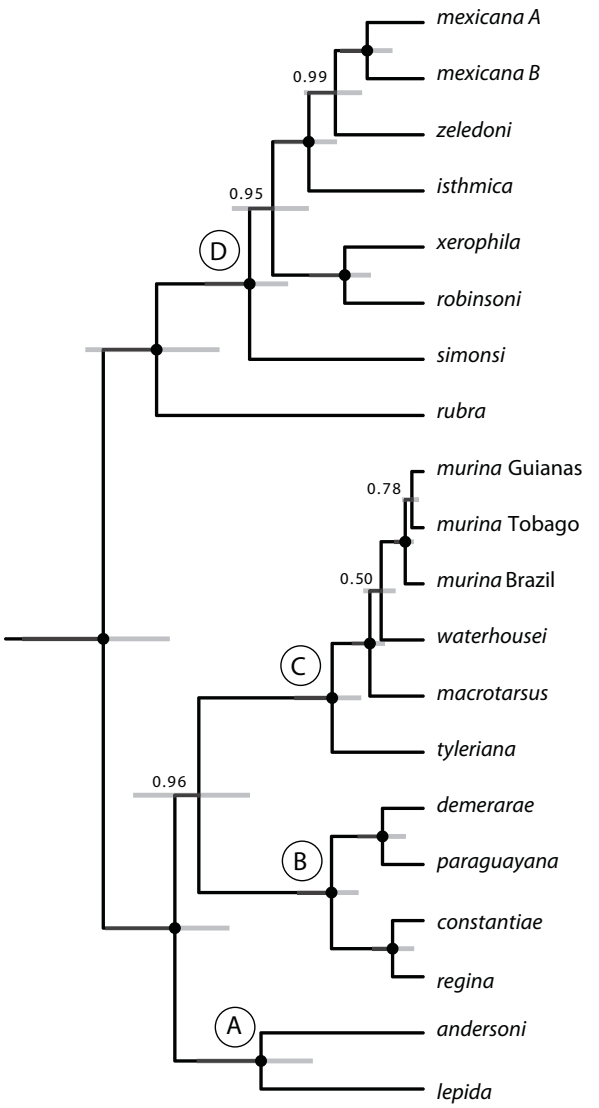


FIG. 4. Species tree computed from four single-gene data matrices (see text). Outgroup taxa are not shown. Filled circles indicate posterior probability values of 1.0 and numbers indicate posterior probabilities < 1.0. Gray bars indicate 95% credibility intervals for relative branching times. Capital letters (A–D) indicate clades discussed in the text.

Genus *Marmosa* Gray, 1821

Type Species: *Marmosa murina* (Linnaeus, 1758).

Contents: Five subgenera, as diagnosed below.

Morphological Description: Combined length of adult head and body ca. 80–210 mm; adult weight ca. 20–170 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe

TABLE 4. Diagnostic Characters and Geographic Distribution of Subgenera Recognized in this Report

	Eomarmosa	*Exulomarmosa*	*Marmosa*	*Micoureus*	*Stegomarmosa*
Gular gland	absent	present	variable[a]	absent	variable[a]
Manual claws	small	small	small	large	small
Medial carpal tubercles	present	present	absent	present	variable[a]
Lateral carpal tubercles	present	present	absent	present	present
Tail scales	usually spiral[b]	spiral & annular	usually spiral[b]	usually spiral[b]	spiral & annular
Prehensile fringe on tail	absent	absent	absent	absent	present
Postorbital processes	indistinct/absent	variable[a]	variable[a]	usually present	present
Palatine fenestrae	absent	variable[a]	variable[a, b]	variable[a]	variable[a]
Fenestra cochleae	concealed	usually exposed[b]	exposed	exposed	exposed
M2 preparacrista	to stA	to stB	to stB	usually to stB[b]	to stB
Geographic distribution	cis-Andean	mostly trans-Andean[c]	mostly cis-Andean[d]	cis- & trans-Andean	cis-Andean

[a] Differs among member species.
[b] Some intraspecific variation.
[c] *Marmosa robinsoni* also occurs in cis-Andean northern Venezuela, and on Isla Margarita, Trinidad, Tobago, and Grenada.
[d] *Marmosa murina* also occurs in the trans-Andean lowlands of NW Venezuela (Handley, 1976; Rossi, 2005: fig. 56), and *M. waterhousei* occurs in the inter-Andean valleys of northern Colombia (Rossi, 2005: fig. 63).

absent or indistinct; throat gland absent in some species but present in adult males of others. Dorsal pelage unpatterned, superficially brownish, reddish, or grayish, but dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur superficially whitish, yellowish, or orange, wholly or partly gray based (apparently never completely self-colored). Manus paraxonic (dIII = dIV); manual claws about as long as or slightly longer than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely covered with flattened tubercles (never densely tuberculate); carpal tubercles absent in some species, or only lateral carpal tubercles present in adult males, or both medial and lateral carpal tubercles present in adult males. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel macroscopically naked. Pouch absent; mammae 3–1–3 = 7 to 7–1–7 = 15, all abdominal-inguinal; cloaca present. Tail substantially longer than combined length of head and body; slender and muscular (not incrassate); without a conspicuously furred base in some species, or tail base conspicuously furred to about the same extent dorsally as ventrally; naked caudal integument unicolored (all dark) in most species but mottled distally with white spots and/or white tipped in others; caudal scales in spiral series or in both spiral and annular series; each caudal scale usually with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface always modified for prehension distally (the prehensile surface naked, consisting of a long, shallow midventral groove or sulcus and an apical pad bearing dermatoglyphs).

Premaxillary rostral process present in most species (absent only in *M. xerophila*). Nasals long, extending anteriorly beyond I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately

branched. Lacrimal foramina usually two on each side, exposed to lateral view on or near anterior orbital margin. Supraorbital margins with distinct beads or prominent crests; postorbital processes usually present in mature adults but substantially larger in some species than in others (and absent or indistinct in some). Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest usually absent (occasionally present in old adult males of *M. robinsoni* and *M. xerophila*). Petrosal usually not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent in almost all examined specimens). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae consistently absent in some species but consistently present in others; maxillary fenestrae absent; posterolateral palatal foramina small, never extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process usually without anteromedial process or posteromedial lamina enclosing the maxillary nerve (secondary foramen ovale almost always absent), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended directly from basicranium. Stapes usually triangular, with large obturator foramen (microperforate and imperforate stapes occur as rare variants in several species). Fenestra cochleae exposed in most species (but concealed in a sinus formed by the caudal and rostral tympanic processes of the petrosal in *M. rubra*). Paroccipital process small, rounded, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals (incisura occipitalis present).

Two mental foramina usually present on lateral surface of each hemimandible (one foramen or three foramina occur as rare, usually unilateral variants in some species); angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, and increasing in length (mesio-distal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 usually simple, without accessory cusps (but posterior accessory cusp consistently present in *M. lepida*). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars moderately carnassialized (postmetacristae are visibly longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus indistinct or absent on M1, shallow but usually distinct on M2, and consistently deep on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Unworn lower canine (c1) usually semiprocumbent, with flattened bladelike apex, with or without distinct posterior accessory cusp. Second lower premolar (p2) taller than p3; lower milk premolar (dp3) trigonid incomplete

(bicuspid). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

Eomarmosa, new subgenus

Type Species: *Marmosa rubra* Tate, 1931.

Contents: *rubra* Tate, 1931.

Diagnosis: Gular gland absent; manual claws small (not extending beyond fleshy apical pads of fingers); medial and lateral carpal tubercles present in large adult males (e.g., AMNH 71950); dorsal tail scales rhomboidal and arranged in predominantly spiral series; ventral prehensile surface of tail not densely fringed by long hairs. Postorbital processes absent, indistinct, or very small; palatine fenestrae absent; fenestra cochleae concealed; M2 preparacrista attaches to stylar cusp A.

Comparisons: *Eomarmosa* differs from other subgenera of *Marmosa* in petrosal and dental characters. Specifically, the fenestra cochleae of *Eomarmosa* is concealed within a sinus formed by the caudal and rostral tympanic processes of the petrosal, whereas the fenestra cochleae in other subgenera is normally exposed because the rostral and caudal tympanic processes of the petrosal are widely separated. Additionally, the preparacrista on M2 of *Eomarmosa* attaches to stylar cusp A (or to the corresponding anterolabial corner of the stylar shelf when a discrete cusp is missing), whereas the M2 preparacrista of other subgenera usually passes straight labially to terminate at or near stylar cusp B.

Other characters distinguish *Eomarmosa* from some, but not all, other congeners. For example, *Eomarmosa* differs from *Exulomarmosa* by its lack of a gular gland—consistently present as a hairless patch of (often greasy) skin in adult male specimens of the latter subgenus—and by the spiral arrangement of its caudal scales (the arrangement of tail scales of *Exulomarmosa* usually includes at least some in annular series). *Eomarmosa* differs from members of the subgenus *Marmosa* by the presence of well-developed medial and lateral carpal tubercles in large adult males (sexually dimorphic carpal tubercles are consistently absent in *Marmosa*). *Eomarmosa* has small manual claws, the tips of which do not extend distally beyond the fleshy apical pads of the fingers, whereas the manual claws of *Micoureus* are larger, stronger, and (unless blunted) usually extend slightly beyond the fleshy apical pads of the fingers. Lastly, *Eomarmosa* lacks the dense fringes of long silvery hairs that border the caudal prehensile surface in both species of *Stegomarmosa*.

Etymology: From the ancient Greek ἕως (“dawn”), by metonymy, for the reddish fur of the single included species.

Remarks: A detailed description of *Marmosa* (*Eomarmosa*) *rubra* was provided by Rossi et al. (2010), who also mapped the collection localities of all known specimens. Based on those data, the geographic range of *M. rubra* appears to be restricted to western Amazonia, where it is known to occur from southeastern Colombia to southeastern Peru (Rossi et al., 2010: fig. 30). This taxon occurs sympatrically—but perhaps not syntopically—with members of the subgenera *Marmosa* and *Micoureus*, (e.g., at Boca Río Curaray, Departamento Loreto, Peru; Tate,

1933) and with *Stegomarmosa* (e.g., at Hacienda Villa Carmen, Departamento Cusco, Peru; Pine, 1972).

Exulomarmosa, new subgenus

Type Species: *Marmosa robinsoni* Bangs, 1898.

Contents: *isthmica* Goldman, 1912 (including *mimetra* Thomas, 1921); *mexicana* Merriam, 1897 (including *mayensis* Osgood, 1913; *ruatanica* Goldman, 1911; and *savannarum* Goldman, 1917); *robinsoni* Bangs, 1898 (including *casta* Thomas, 1911; *chapmani* J.A. Allen, 1900; *fulviventer* Bangs, 1901; *grenadae* Thomas, 1911; *luridavolta* Goodwin, 1961; *mitis* Bangs, 1898; *nesaea* Thomas, 1911; and *pallidiventris* Osgood, 1912); *simonsi* Thomas, 1899; *xerophila* Handley and Gordon, 1979; and *zeledoni* Goldman, 1917.

Diagnosis: Gular gland consistently present and well developed in adult males; manual claws small (not extending beyond fleshy apical pads of fingers); medial and lateral carpal tubercles present in large adult males[6]; dorsal tail scales rhomboidal or oblong, usually in both spiral and annular series on most specimens, but one or the other pattern sometimes predominating; ventral prehensile surface of tail not densely fringed with long hairs. Postorbital processes usually absent, indistinct, or very small in some species (e.g., *Marmosa zeledoni*) but consistently large and well developed in adults of other species (e.g., *M. simonsi*); palatine fenestrae consistently absent in some species (e.g., *M. isthmica*) but consistently present in others (e.g., *M. xerophila*); fenestra cochleae usually exposed (but partially concealed in a few examined specimens of *M. robinsoni*, *M. simonsi*, and *M. xerophila*); M2 preparacrista attaches to or terminates near stylar cusp B.

Comparisons: Comparisons of *Exulomarmosa* with *Eomarmosa* have already been provided (see above). Species of *Exulomarmosa* differ consistently from members of the subgenus *Marmosa* in sexually dimorphic features of the carpal (wrist) region: whereas large adult male specimens of *Exulomarmosa* have well-developed lateral and medial carpal tubercles, neither sex has large carpal tubercles in the subgenus *Marmosa*. Additionally, gular glands are consistently well developed (especially in adult males) in *Exulomarmosa*, but gular glands are absent in most species of *Marmosa* (appearing polymorphically only in *M. waterhousei*; Rossi, 2005). *Exulomarmosa* also differs from *Micoureus* in possessing gular glands, and these subgenera further differ in manual claw morphology (small in *Exulomarmosa*, large in *Micoureus*). In *Exulomarmosa* the caudal prehensile surface lacks the dense lateral fringes of long hairs that occur in both species of *Stegomarmosa*.

Remarks: Morphological diagnoses of the species in this subgenus were provided by Rossi et al. (2010), who also discussed relevant synonymies. At least two species (*Marmosa mexicana* and *M. robinsoni*) contain highly divergent mtDNA haplotype groups that might represent cryptic taxa (Gutiérrez et al., 2010; Gutiérrez et al., in press).

[6] Exemplar adult male specimens in which these tubercles are well developed include AMNH 12454 (*Marmosa mexicana*), AMNH 37890 (*M. isthmica*), AMNH 66852 (*M. simonsi*), AMNH 69939 (*M. robinsoni*), USNM 443920 (*M. xerophila*), and AMNH 147759 (*M. zeledoni*). The same specimens also exhibit the well-developed gular gland that characterizes this subgenus.

Species of *Exulomarmosa* are mostly trans-Andean (sensu Haffer, 1967), but the geographic range of *Marmosa robinsoni* extends east of the Andes into the dry coastal forests of northern Venezuela, several Caribbean islands (Isla Margarita, Trinidad, Tobago, Grenada), and the llanos (Rossi et al., 2010: fig. 25). *Exulomarmosa* and *Micoureus* have broadly overlapping geographic distributions in Central America and northwestern South America, where they have been collected together at numerous localities.[7] Although the distributions of *Exulomarmosa* and the subgenus *Marmosa* narrowly overlap in Colombia and northernmost Venezuela, they are seldom collected sympatrically at mainland localities. By contrast, *M. (Ma.) murina* and *M. (Ex.) robinsoni* occur syntopically in abandoned cacao plantations on Tobago (e.g., near Charlotteville at 11°19′N, 60°33′W; Voss, 1991).

Etymology: From the Latin *exul* ("a banished or exiled person"), in reference to the isolation of this trans-Andean clade (Gutiérrez et al., 2010) from the cis-Andean distribution of most of the rest of the genus.

Subgenus *Marmosa* Gray, 1821

Type Species: *Marmosa murina* (Linnaeus, 1758).

Contents: *macrotarsus* Wagner, 1842 (including *madeirensis* Cabrera, 1913; *musicola* Osgood, 1913; and *quichua* Thomas, 1899); *murina* Linnaeus, 1758 (including *chloe* Thomas, 1907; *dorsigera* Linnaeus, 1758; *duidae* Tate, 1931; *guianensis* Kerr, 1792; *klagesi* J.A. Allen, 1900; *meridionalis* Miranda-Ribeiro, 1936; *moreirae* Miranda-Ribeiro, 1936; *muscula* Cabanis, 1848; *parata* Thomas, 1911; *roraimae* Tate, 1931; and *tobagi* Thomas, 1911); *tyleriana* Tate, 1931 (including *phelpsi* Tate, 1939); and *waterhousei* Tomes, 1860 (including *bombascarae* Anthony, 1922; and *maranii* Thomas, 1924).

Diagnosis: Gular gland consistently absent in some species (e.g., *Marmosa tyleriana*), usually present in adult males of other species (e.g., *M. murina*), and apparently polymorphic in some (e.g., *M. waterhousei*); manual claws small (not extending beyond fleshy apical pads of fingers); medial and lateral carpal tubercles consistently absent; dorsal tail scales rhomboidal and arranged in spiral series (except in *M. tyleriana*, in which the scale arrangement is sometimes predominantly annular); ventral prehensile surface of tail not densely fringed with long hairs. Postorbital processes usually well developed in large adults (but absent in *M. tyleriana*); palatine fenestrae usually absent in most species (but consistently present in *M. tyleriana*); fenestra cochleae exposed; M2 preparacrista consistently attaches to or terminates near stylar cusp B.

Comparisons: Members of the nominotypical subgenus uniquely lack sexually dimorphic carpal tubercles. By contrast, large adult males belonging to species in other subgenera have well-developed medial and lateral carpal tubercles that are absent in females and less well

[7] For example, at Armila (8°40′N, 77°27′W; Rossi et al., 2010) in the Panamanian province of San Blas, where *Marmosa* (*Exulomarmosa*) *isthmica* was collected sympatrically with a small species of *Micoureus* said to resemble *M. phaea* (see Handley, 1966). At Curupao (10°31′N, 66°38′W; Handley, 1976) in the Venezuelan state of Miranda several specimens of *M. (Ex.) robinsoni* were collected sympatrically with specimens of a large form resembling *M. (Mi.) demerarae*. Representative specimens from both localities are at the USNM.

developed in smaller (presumably younger) males. Additionally, species of *Marmosa* (*Marmosa*) consistently differ from species in the subgenus *Micoureus* by their smaller manual claws, and from species of *Stegomarmosa* by lacking dense fringes of long hairs along the margins of the caudal prehensile surface. Comparisons with *Eomarmosa* and *Exulomarmosa* were summarized in the preceding accounts.

Remarks: Our synonymies for species in the nominotypical subgenus of *Marmosa* follow Rossi (2005), except that we treat *tobagi* (recognized as a valid species by Rossi, 2005) as a subjective synonym of *murina* for reasons explained earlier in this report. Diagnostic morphological comparisons among *macrotarsus*, *murina*, and *waterhousei* were provided by Rossi (2005), and characters distinguishing *murina* from *waterhousei* were discussed by Gutiérrez et al. (2011).

Species of *Marmosa* (*Marmosa*) occur in lowland moist forests from northern Venezuela to eastern Bolivia and south-central Brazil (Mato Grosso), and along the Atlantic coast of Brazil southward to Espírito Santo. Apparently they are everywhere sympatric with members of the subgenus *Micoureus* (e.g., at all the cis-Andean inventory sites analyzed by Voss and Emmons, 1996: appendices 4–11). Additionally, species of the subgenus *Marmosa* are broadly sympatric with *Stegomarmosa* in northeastern and western Amazonia—for example, at Huampami (4°28′S, 78°10′W) in Amazonas department, Peru (specimens at MVZ)—and they are also sympatric with *Eomarmosa* from southeastern Colombia to southeastern Peru (see above).

Subgenus *Micoureus* Lesson, 1842

Type Species: *Didelphis cinerea* Temminck, 1824, by subsequent designation (Thomas, 1888). According to Gardner and Creighton (2008: 79), *cinerea* Temminck, 1824, is an unavailable name (preoccupied by *cinerea* Goldfuss, 1812) for the southeastern Brazilian species currently known as *Marmosa* (*Micoureus*) *paraguayana* Tate, 1931.

Contents: *alstoni* J.A. Allen, 1900 (including *nicaraguae* Thomas, 1905); *constantiae* Thomas, 1904 (including *budini* Thomas, 1920); *demerarae* Thomas, 1905 (including *areniticola* Tate, 1931; *domina* Thomas, 1920; *esmeraldae* Tate, 1931; *limae* Thomas, 1920; *meridae* Tate, 1931); *paraguayana* Tate, 1931 (including *cinerea* Temminck, 1824 [preoccupied]); *phaea* Thomas, 1899 (including *perplexa* Anthony, 1922); *regina* Thomas, 1898 (including *germana* Thomas, 1904; *mapiriensis* Tate, 1931; *parda* Tate, 1931; *rapposa* Thomas, 1899; *rutteri* Thomas, 1924).

Diagnosis: Gular gland consistently absent; manual claws relatively larger than in other congeners (usually extending just beyond fleshy apical pads of fingers); medial and lateral carpal tubercles present in large adult males; caudal scales usually rhomboidal in spiral series; ventral prehensile surface of tail not densely fringed with long hairs. Postorbital processes usually well developed in large adults; palatine fenestrae absent in most species (but consistently present in some); fenestra cochleae usually exposed (partially concealed in some specimens of at least two species); M2 preparacrista usually attaches to or terminates near stylar cusp B.

Comparisons: Members of the subgenus *Micoureus* tend to have slightly larger manual claws than species in other subgenera, but share no other unique trait (see Remarks, below).

Instead, they are distinguished by a unique combination of traits, including those previously discussed in comparisons with *Eomarmosa*, *Exulomarmosa*, and the nominotypical subgenus (above). They can be distinguished from species of *Stegomarmosa* by the lack of dense fringes of long hairs along the caudal prehensile surface.

Remarks: Although species of *Micoureus* are commonly known as "woolly mouse opossums" and are said to differ from other species of *Marmosa* in pelage length and texture (e.g., by Gardner, 2008: 2), we have not found pelage length or texture to be consistently useful as diagnostic traits. To be sure, some species of *Micoureus* (e.g., *M. demerarae*) have longer and woollier pelts than sympatric members of the nominotypical subgenus (e.g., *M. murina*). However, other species of *Micoureus* (e.g., lowland populations of the yellowish eastern Bolivian form currently known as *M. constantiae*) have short fur, some highland forms of *Marmosa* (e.g., *M. tyleriana*) have long fur, and we are unable to define "woolliness" by any satisfactory (nonsubjective) criterion. Species of *Micoureus* are also said to be larger than other marmosines (Gardner, 2008), but small species of *Micoureus*—such as the southwestern Ecuadorean taxon that Anthony (1922) described as *M. perplexa*—exhibit broad morphometric overlap with large species in other subgenera (such as *M. isthmica*). Other traits that have sometimes been used to diagnose *Micoureus* include the prominent extension of body fur onto the base of the tail, and the presence of a white tail-tip. Although it is true that species in other subgenera do not commonly exhibit either of these traits, neither is consistently exhibited by all of the phenotypes that seem to belong in *Micoureus* based on molecular analyses. Despite the fact that it was once ranked as a genus, *Micoureus* is, paradoxically, one of the least morphologically distinctive clades within the genus *Marmosa.*

Species of *Micoureus* occur in moist lowland and montane forests from Belize southward to Paraguay and northern Argentina. The contents of this subgenus are unrevised, and current taxonomic usage is impossible to reconcile either with DNA sequencing results or with our examination of relevant type material (Voss and Jansa, in prep.). Therefore, the species-level taxonomy used in this report uncritically follows Gardner and Creighton (2008) pending analyses of relevant morphological and molecular data.

Species of *Micoureus* occur sympatrically with members of every other subgenus, including *Eomarmosa*, *Exulomarmosa*, and *Marmosa* (see above). *Micoureus* and *Stegomarmosa* are probably sympatric throughout the Guiana Region (e.g., at Nouragues, French Guiana; Guillemin et al., 2001) and western Amazonia. At least two species of *Micoureus* occur sympatrically (but perhaps not syntopically) throughout most, if not all, of western Amazonia (e.g., along the Rio Juruá; Patton et al., 2000). This subgenus includes the largest members of the genus, with some specimens of several species weighing > 150 grams, but other species of *Micoureus* are substantially smaller (with adult weights consistently < 100 g).

Subgenus *Stegomarmosa* Pine, 1972

Type species: *Marmosa andersoni* Pine, 1972.

Contents: *andersoni* Pine, 1972; and *lepida* Thomas, 1888.

Diagnosis: Gular gland present (*andersoni*) or absent (*lepida*); manual claws small (not extending beyond fleshy apical pads of fingers); medial carpal tubercle present (in the type and

only examined adult male specimen of *andersoni*) or absent (*lepida*); lateral carpal tubercle present; caudal scales in both spiral and annular series; prehensile caudal surface densely fringed with long hairs; postorbital processes well developed in mature adult specimens; palatine vacuities present (*andersoni*) or absent (*lepida*); fenestra cochleae exposed; M2 preparacrista attaches to or terminates near stylar cusp B.

Comparisons: Comparisons of *Stegomarmosa* with other subgenera have already been summarized in the preceding accounts.

Remarks: *Marmosa andersoni* and *M. lepida* differ in several characters, but they uniquely share twin rows of long, silvery hairs that flank the median prehensile sulcus on the underside of the distal part of the tail. Additionally, mature adults of these species resemble one another—and differ from most other congeners—by having a very long rostral process of the premaxillae; large, triangular postorbital processes; and distinctly reddish dorsal fur. Both species occur in western Amazonia, although the range of *Marmosa lepida* also extends eastward into the Guiana Region (NE Amazonia). Examples of sympatry between *Stegomarmosa* and other subgenera of *Marmosa* have already been mentioned in the preceding accounts.

Several discrepancies between our diagnosis of *Stegomarmosa* and published descriptions of *Marmosa andersoni* merit discussion. (1) Solari and Pine (2008: 56) suggested that "The normal condition of the palate may be completely without fenestration" in *M. andersoni*, but all the adult specimens we examined (FMNH 84252; MUSM 14154, 14155) have well-developed maxillopalatine and palatine fenestrae.[8] (2) Voss and Jansa (2003: 64) described the caudal scales of FMNH 84252 as arranged in spiral series, but our reexamination of this specimen and other newly available material convinces us that Solari and Pine (2008) were correct in describing the arrangement as spiral and annular. (3) Rossi (2005: 80) described the medial carpal tubercle as absent, but close inspection reveals that a small medial tubercle is present on the wrist of FMNH 84252, the only known adult male specimen. Because FMNH 84252 is a young adult (with fully erupted P3 but unworn posterior molars), the tubercle is probably larger on older males.

NOTES ON SYMPATRIC DIVERSITY

Based on a review of available ecobehavioral information (Voss and Jansa, in prep.), the genus *Marmosa* appears to be the dominant clade of small insectivorous-frugivorous arboreal opossums throughout most of the forested Neotropical lowlands.[9] Members of other sympatric arboreal clades are larger and perhaps more frugivorous (e.g., *Caluromys* spp.), whereas sympatric clades that overlap *Marmosa* in size and appear to have similar diets are apparently scansorial (e.g., *Marmosops*). In dry forests south of Amazonia, *Marmosa* seems to be replaced ecologically by *Gracilinanus*. However, species of *Marmosa* occupy dry forests where *Gracilina-*

[8] The palatine fenestrae are covered by a membrane on the incompletely cleaned skull of MUSM 14154, which accounts for their indistinct appearance in Solari and Pine's (2008: fig. 2) photograph of that specimen.

[9] For exemplar accounts of local species, see Enders (1935), Charles-Dominique et al. (1981), Thielen et al. (1997), and Pinheiro et al. (2002).

nus does not occur—for example, *M. mexicana* in Central America, *M. xerophila* in northern Venezuela, and *M. simonsi*, in western Ecuador (Rossi et al., 2010).

Interestingly, two or more species of *Marmosa* occur sympatrically at many rainforested localities. Based on geographic range overlap (see maps in Rossi, 2005), most western Amazonian sites probably have one species each of the subgenera *Marmosa* (either *M. waterhousei* or *M. macrotarsus*) and *Stegomarmosa* (usually *M. lepida*) and two species each of *Micoureus* (usually one each of the taxa currently known as *M. regina* and *M. demerarae*), and some sites close to the base of the Andes could have additional species of *Eomarmosa* and *Stegomarmosa*. Therefore, some western Amazonian sites might have as many as six sympatric species of *Marmosa*, although no more than four seem to have been collected to date at any one site.

These observations suggest that the adaptive zone occupied by small, arboreal, insectivorous-frugivorous opossums can be subdivided, and it would be interesting to know whether the clades recognized as subgenera in this report are ecobehaviorally distinctive. Some field observations (e.g., Charles-Dominique et al., 1981; Malcolm, 1990) suggest that *Marmosa (Micoureus) demerarae*, for example, is active in the forest canopy and subcanopy, whereas sympatric *Marmosa (Marmosa) murina* is primarily active in understory vegetation. In western Amazonia, *M. (Mi.) demerarae* appears to be more common in terra firme forest, whereas sympatric *M. (Mi.) regina* prefers seasonally flooded forest (Patton et al., 2000). In central Panama, *M. (Exulomarmosa) isthmica* is more abundant in secondary vegetation than in undisturbed old-growth forest (Enders, 1935). Such observations, few as they are, suggest that both vertical and horizontal habitat segregation may be important correlates of sympatry in this widespread genus of small opossums.

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APPENDIX 1

Primers Used to Amplify BRCA1, OGT, and SLC38

Gene	Primer Name	Primer Sequence
SLC38	SLC38-F1	5' TGGTTTCAGTGGTGCTTATT
SLC38	SLC38-F150	5' CCCAGCATGCCCAGTTTGTTA
SLC38	SLC38-F250	5' CCAAGCTCCGTGTTCATACACTG
SLC38	SLC38-R1	5' CAATCAGAAAGAACACCATACACA
SLC38	SLC38-R350	5' CACTGTAAGAGGTCAAACTGGGA
OGT	OGT-F1	5' AAATCATTTCATCGACCTTTCTCAG
OGT	OGT-F120	5' GGACATGGAAGAATTTGCTTTTGG
OGT	OGT-F300	5' GTGATTTTGACTTTTCTCCTGGCCT
OGT	OGT-R1	5' GCTGCTTTTCCATTACAGGGAAT
OGT	OGT-R360	5' CATCCCYGCTTGGCCCAACCACA
OGT	OGT-R540	5' GCTCTGAATTCACAGCATCACCA
BRCA	BRCA-F1163a	5' AATGAGACTGAACTACAGATCGAT
BRCA	BRCA-F1360	5' GTGATCAAATGTTAGCTAGCTGCAG
BRCA	BRCA-F1620	5' AAATAATGGAAACCCCAAAGGA
BRCA	BRCA-F1697	5' TTWGATGRTTGTTCATCYRAAAACAC
BRCA	BRCA-F1850	5' GTGCTATTTCTCAGGCTTTACATCAGC
BRCA	BRCA-R1475	5' TTTGGCTCTCTGGCCTTGTGA
BRCA	BRCA-R1750	5' CCTCCATTTCTGTGGTTGTCTCTGA
BRCA	BRCA-R1780	5' TAAATAYTGGGTRTCRAGTTCACT
BRCA	BRCA-R1980	5' TCATGACTGTAGACTTTGCTTGCA
BRCA	BRCA-R2151	5' TCCTTTTGATYAGGAACTTGTGAAATT

APPENDIX 2

Mean Sequence Divergence at the Cytochrome-*b* Locus within and among Species of *Marmosa*[a]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. *M. (Eo.) rubra*	**4.2**																
2. *M. (Ex.) isthmica*	12.8	**3.3**															
3. *M. (Ex.) mexicana*	11.8	9.1	**6.6**[b]														
4. *M. (Ex.) robinsoni*	13.1	9.9	10.0	**3.5**													
5. *M. (Ex.) simonsi*	15.9	13.1	12.7	12.0	**2.0**												
6. *M. (Ex.) xerophila*	14.5	10.1	9.8	8.6	14.5	**1.7**											
7. *M. (Ex.) zeledoni*	15.0	8.4	7.7	9.7	13.7	9.8	—										
8. *M. (Ma.) macrotarsus*	15.0	15.0	13.2	13.9	13.7	16.3	15.7	**3.7**									
9. *M. (Ma.) murina*	15.0	15.0	13.8	14.7	14.0	15.8	13.8	5.7	**2.8**[c]								
10. *M. (Ma.) tyleriana*	15.3	14.5	15.0	15.2	15.0	17.4	17.4	11.2	9.6	**0.3**							
11. *M. (Ma.) waterhousei*	14.8	15.7	14.6	14.9	14.8	16.2	15.4	7.1	7.0	8.5	**0.7**						
12. *M. (Mi.) constantiae*	15.4	16.4	14.6	16.5	18.1	16.4	16.6	15.0	15.8	17.1	15.9	**1.2**					
13. *M. (Mi.) demerarae*	14.3	12.4	13.1	14.5	15.7	14.9	14.5	13.0	12.9	15.1	14.0	11.7	**4.1**				
14. *M. (Mi.) paraguayana*	15.1	15.6	15.7	16.8	17.3	16.2	16.2	15.7	16.0	17.1	16.6	12.3	7.4	**0.0**			
15. *M. (Mi.) regina*	15.3	15.9	14.0	15.8	17.7	16.3	17.5	14.9	15.3	18.1	15.6	6.9	9.9	11.3	**2.1**		
16. *M. (S.) andersoni*	15.4	15.4	14.2	15.4	16.6	15.1	16.9	16.0	16.6	18.3	16.8	15.7	12.9	14.5	14.3	**0.0**	
17. *M. (S.) lepida*	13.0	13.5	13.3	14.2	14.8	14.2	14.7	12.4	13.1	14.9	13.6	13.8	11.8	14.0	13.1	13.5	**2.4**

[a] Uncorrected (p) distances scaled as percentages. Intraspecific distances are in boldface type.
[b] Includes haplogroups "*mexicana* A" and "*mexicana* B" discussed by Gutiérrez et al. (2010).
[c] Includes *tobagi*.

APPENDIX 3

Optimal Partitioning Schemes and Substitution Models for Two Concatenated-gene Datasets[a]

Nuclear only (BIC = 15252.51)

Partition	Characters included	Model
1	BRCA1 position1	HKY+Γ
	BRCA1 position2	
	BRCA1 position3	
2	OGT	GTR+Γ
	SLC38	

Nuclear + mitochondrial (BIC = 33260.66)

Partition	Characters included	Model
1	BRCA1 position1	HKY+Γ
	BRCA1 position2	
	BRCA1 position3	
2	OGT	GTR+Γ
	SLC38	
3	CYTB position 1	SYM+Γ
4	CYTB position 2	HKY+I
5	CYTB position 3	GTR+I+Γ

[a] Results obtained by comparing substitution models using the BIC as implemented in PartitionFinder (Lanfear et al., 2012).

APPENDIX 4

Exemplar Series of Morphological Specimens Examined

Marmosa (Eomarmosa) rubra (*N* = 11): AMNH 68128, 68129, 71950, 71952, 71974, 71976; MVZ 153280, 154759, 154765; USNM 274577, 274578.

Marmosa (Exulomarmosa) isthmica (*N* = 9): USNM 306415–306422, 456814.

Marmosa (Exulomarmosa) mexicana "A" (*N* = 9): AMNH 277680–277682; ROM 95795, 96090, 96318, 96968, 99608, 99776.

Marmosa (Exulomarmosa) mexicana "B" (*N* = 4): AMNH 79250; ROM 98459; USNM 569858, 570071.

Marmosa (Exulomarmosa) robinsoni (*N* = 9): USNM 372938–372940, 372942–372944, 372947, 385068, 385069.

Marmosa (Exulomarmosa) simonsi (*N* = 15): AMNH 61195, 63350, 63404, 63407, 63413, 64525, 64532, 66873, 66883; USNM 121155, 121156, 121158, 461643, 513423, 551640.

Marmosa (Exulomarmosa) xerophila (*N* = 9): USNM 443920, 443929, 443840, 443845, 443847, 443920, 443924, 443947, 443951.

Marmosa (Exulomarmosa) zeledoni (*N* = 11): AMNH 28283, 29541, 269997; USNM 361194–361201.

Marmosa (Marmosa) macrotarsus (*N* = 11): AMNH 268214, 272816, 273062, 273063, 273178, 273188; MUSM 13283, 15293, 15294, 15296, 15297.

Marmosa (Marmosa) murina (*N* = 13): AMNH 266416, 266417, 267368, 267816; USNM 393480–393482, 393484, 393485, 578006–578008, 588119.

Marmosa (Marmosa) tyleriana (*N* = 8): AMNH 130501, 130503, 130504, 130507, 130509–130511, 130559.

Marmosa (Marmosa) waterhousei (*N* = 8): AMNH 47186, 68127; TTU 98654, 98717, 98934, 100922, 101098, 101153.

Marmosa (Micoureus) alstoni (*N* = 10): AMNH 131732, 131737, 136863, 136865, 136866, 137288, 137997, 137999, 139280, 139780.

Marmosa (Micoureus) constantiae (*N* = 9): AMNH 209159, 209160, 210398–210400, 275463, 275465–275467.

Marmosa (Micoureus) demerarae (*N* = 12): AMNH 266427–266434, 267369–267371, 267818.

Marmosa (Micoureus) paraguayana (*N* = 7): FMNH 141586, 211415, 211416; MVZ 182063–182065; UMMZ 134551).

Marmosa (Micoureus) phaea (*N* = 8): FMNH 88543, 88545, 89364, 90101, 90102; Rom 57242, 57243, 57245).

Marmosa (Micoureus) regina (*N* = 5): MVZ 190323, 190324, 190328, 190332, 190333.

Marmosa (Stegomarmosa) andersoni (*N* = 4): FMNH 84252; MUSM 14154, 14155; USNM 582777.

Marmosa (Stegomarmosa) lepida (*N* = 7): AMNH 78001, 98656, 182937, 273186; FMNH 140824; USNM 461467, 461468

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