Short Note

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

Eliécer E. Gutiérrez^{1,2,*}, Pascual J. Soriano^{3,4}, Rogério V. Rossi⁵, Johnny J. Murillo³, José Ochoa-G⁶ and Marisol Aguilera⁷

¹Department of Biology, 526 Marshak Science Building, 160 Convent Avenue, City College of the City University of New York, New York, NY 10031, USA,

e-mail: eeg@sci.ccny.cuny.edu

- ² Graduate School and University Center, City University of New York, New York, NY 10016, USA
- ³ Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela
- ⁴ Postgrado en Ecología Tropical, Instituto de Ciencias Ambientales y Ecológicas, Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela
 ⁵ Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Correa da Costa, 2367, Cuiabá,
- Mato Grosso 78060-900, Brazil ⁶Cabañas Bougainvillae, Los Taques, Paraguaná, Falcón,
- ⁷ Departamento de Estudios Ambientales, Universidad Simón Bolívar, Apartado 89.000, Caracas 1080-A, Venezuela

*Corresponding author

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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 rainforests, and humid-montane forests, at elevations from sea level to about 3000 m. 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 six in the 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 1957, Pérez-Hernández et al. 1994, Linares 1998) or synonym (Gardner 2005, Creighton and Gardner 2007) 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 catalogue numbers) to document this distributional pattern was mentioned (see maps of "M. murina waterhousei" in Pérez-Hernández et al. 1994 and Linares 1998). A re-examination (by RVR) 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.

Because specimens housed in Central American and most South American collections were not included in the 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.

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 1) was collected in 1994 in "La Palmita, 1 km N La



Figure 1 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.

Azulita, Estado Mérida", at an elevation of 1000 m (geographic coordinates: 08°44′N, 71°27′W; DCN 1977b; locality 20 in Figure 2). 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: 08°21′N, 71°42′W; DCN 1977a; locality 19 in Figure 2). According to the collector (JJM), both specimens were captured in secondary semi-deciduous forest. The locally focused classification of habitat types of the Mérida state considers that the forest type at these localities corresponds to semi-caducipholic montane forest ("selva semicaducifolia montana"; see Ataroff 2003, Ataroff 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 2; 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 Ochoa-G 1985, Soriano et al. 1999, Rossi 2005, Ochoa-G 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 fenestrae2
1b.	Absence of palatine fenestrae
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)
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
3a.	Rostral process of premaxillae absent; dorsal fur color pale grayish-brown
3b.	Rostral process of premaxillae short; dorsal fur color yellowish-brown
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
4b.	Gular gland absent or present; dorsal pelage grayish-brown; rostral process of premaxillae about as long as I1 is tall
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

Venezuelan records of Marmosa waterhousei reported herein substantially extend the known distribution of the

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 pro-

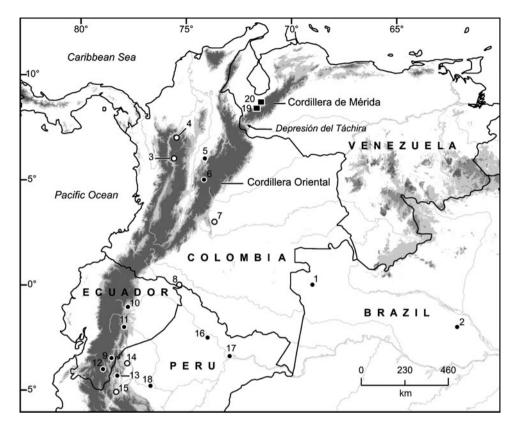


Figure 2 Map showing the known collection localities of *Marmosa waterhousei*. Circles show previously known records of *M. waterhousei* (solid circles) and *Marmosa* cf. *waterhousei* (open circles) from Rossi (2005); squares show the Venezuelan records reported herein. Progressively darker shading 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 of this report for Venezuelan specimens and Rossi (2005) for non-Venezuelan specimens.

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 (north-eastern Amazonas state), northern Peru, eastern Ecuador, and the valley of Río Magdalena in Colombia (Rossi 2005; Figure 2). 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. waterhouse (i.e., Muzo, in the Boyacá department, Colombia; locality 4 in Figure 1; see Rossi 2005), and represents the northern extreme of the species' range. Non-Venezuelan specimens examined (all by RVR) 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

Table 1 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), and from other localities throughout the known distribution of the species (Figure 2).

	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)
Toursday of the "I	00	170	125–149
Length of tail	80	178	199.17±18.21 (6)
Length of hind foot	25	22	172–223 23.17±1.72 (6)
Length of finid foot	25	22	23.17±1.72 (0) 21–25
Length of ear	28	25	24.40±1.95 (5)
Length of car	20	23	21–26
Greatest length of skull	-	34.80	37.02±1.17 (7)
Greatest length of skull			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)
	1.68	1.70	0.95-1.18
Width of M2			1.87±0.07 (7)
	2.35	2.24	1.79–1.98
Width of M4			2.33±0.11 (8)
D (1 (11 - 14	10.79	10.67	2.14–2.45
Postpalatal breadth			11.02±0.27 (7)
Breadth of basicranium		6.27	10.63–11.37
breadth of basicramum	_	0.47	6.85±0.27 (4) 6.51–7.1
Breadth across tympanic bullae	_	11.39	11.40 ± 0.3 (4)
breadin across tympanic bunac		11.37	11.12–11.76
Length of tympanic bulla	_	5.42	5.45±0.15 (4)
Length of tympanic band		3.12	5.22–5.54
Breadth of rostrum between jugals	11.55	11.80	10.33±0.61 (4)
J. B.			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

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)

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 phylogeographic 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.

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References

- Anderson, R.P. and P.J. Soriano. 1999. The occurrence and biogeographic significance of the southern spiny pocket mouse *Heteromys australis* in Venezuela. Z. Säugetierkunde 64: 121–125.
- Ataroff, M. 2003. Selvas y bosques de montaña. In: (M. Aguilera, A. Azócar and E. González-Jiménez, eds.) Biodiversidad en Venezuela. Vol. 2. FONACIT-Fundación Polar, Caracas, pp. 762–810.
- Ataroff, M. and L. Sarmiento. 2004. In: (E. La Marca and P.J. Soriano, eds.) Reptiles de los Andes de Venezuela. Fundación Polar, Conservación Internacional, CODEPRE-ULA, Fundacite Mérida, BIOGEOS, Mérida, Venezuela, pp. 9–26.

- Barrio-Amorós, C.L. 1998. Sistemática y biogeografíía de los anfibios (Amphibia) de Venezuela. Acta Biol. Venezuelica 18: 1–93.
- Barrio-Amorós, C.L. and C. Molina-Rodríguez. 2010. Herpetofauna del Ramal de Calderas, Andes de Venezuela. In: (B.A Rial, J.C. Señaris, C.A. Lasso and A. Flores, eds.) Evaluación rápida de la biodiversidad y aspectos socioecosistémicos del Ramal de Calderas, Andes de Venezuela. RAP Bulletin of Biological Assessment 56. Conservation International, Arlington, VA. pp. 74–80.
- Cabrera, A. 1957. Catálogo de los mamíferos de América del Sur [part 1]. Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadavia (Zool.) 4(1): i-iv, 1-307.
- Creighton, G.K. and A.L. Gardner. 2007. Genus Marmosa Gray, 1821. In: (A.L. Gardner, ed.) Mammals of South America. Vol. 1. Marsupials, xenarthrans, shrews, and bats. Chicago University Press, Chicago, IL, pp. 51–61.
- DCN. 1977a. Hoja 5841 (El Vigia), escala 1:100.000. Dirección de Cartografía Nacional, Ministerio de Obras Públicas, Caracas.
- DCN. 1977b. Hoja 5942 (La Azulita), escala 1:100.000. Dirección de Cartografía Nacional, Ministerio de Obras Públicas, Caracas
- Gardner, A.L. 2005. Order Didelphimorphia. In: (D.E. Wilson and D.M. Reeder, eds.) Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, MD, pp. 3–18.
- Gutiérrez, E.E., S.A. Jansa and R.S. Voss. 2010. Molecular systematics of mouse opossums (Didelphidae: *Marmosa*): assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. Am. Mus. Novitates 3692: 1–22.
- Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165: 131–137.
- Hafner, M.S., W.L. Gannon, J. Salazar-Bravo and S.T. Álvarez-Castañeda. 1997. Mammal collections in the western hemisphere: a survey and directory of existing collections. American Society of Mammalogists, Lawrence, KS.
- Kozak, K.H., C.H. Graham and J.J. Wiens. 2008. Integrating GIS-based environmental data into evolutionary biology. Trends Ecol. Evol. 23: 141–148.
- Linares, O.J. 1998. Mamíferos de Venezuela. Sociedad Conservacionista Audubon de Venezuela, Caracas, Venezuela.
- Ochoa-G, J. 1985. Nueva localidad para *Marmosa tyleriana* (Marsupialia: Didelphidae) en Venezuela. Doñana, Acta Vert. 12: 183–185.
- Ochoa-G, J., F. García, S. Caura and J. Sánchez-H. 2008. Mamíferos de la cuenca del Río Caura, Venezuela: listado taxonómico y distribución conocida. Mem. Fund. La Salle Cienc. Nat. 170: 41–117.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'amico, I. Itoua, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, T.H. Ricketts, Y. Kura, J.F. Lamoreux, W.W. Wettengel, P. Hedao and K.R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51: 933–938.
- Pérez-Hernández, R., P. Soriano and D. Lew. 1994. Marsupiales de Venezuela. Cuadernos Lagoven, Caracas.
- Rossi, R.V. 2005. Revisão taxonómico de *Marmosa* Gray, 1821 (Didelphimorphia, Didelphidae). Doctoral dissertation, Universidade de São Paulo, Brazil.
- Rossi, R.V., R.S. Voss and D.P. Lunde. 2010. A revision of the didelphid marsupial genus *Marmosa*. Part 1. The species in Tate's

- 'Mexicana' and 'Mitis' sections and other closely related forms.
- Soriano, P.J., A. Díaz de Pascual, J. Ochoa-G. and M. Aguilera. 1999. Biogeographic analysis of the mammal communities in the Venezuelan Andes. Interciencia 24: 17–25.

Bull. Am. Mus. Nat. Hist. 334: 1-83.

- Tate, G.H.H. 1933. A systematic revision of the marsupial genus *Marmosa* with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). Bull. Am. Mus. Nat. Hist. 66: 1–250.
- Voss, R.S. and S.A. Jansa. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bull. Am. Mus. Nat. Hist. 276: 1–82.
- Voss, R.S. and S.A. Jansa. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bull. Am. Mus. Nat. Hist. 322: 1–177.