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Author(s): Sergio Solari, Víctor Pacheco, Elena Vivar, and Louise H. Emmons
Source: Proceedings of the Biological Society of Washington, 125(3):295-307. 2012.
Published By: Biological Society of Washington
URL: http://www.bioone.org/doi/full/10.2988/11-33.1

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
125(3):295–307. 2012.

A new species of *Monodelphis* (Mammalia: Didelphimorphia: Didelphidae) from the montane forests of central Perú

Sergio Solari*, Víctor Pacheco, Elena Vivar, and Louise H. Emmons

(SS) Instituto de Biología, Universidad de Antioquia, A.A. 1226, Medellín, Colombia, e-mail: ssolari@matematicas.udea.edu.co;
(VP, EV) Departamento de Mastozoología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Aptdo. 14 0434, Lima 14, Perú;
(LHE) Department of Vertebrate Zoology, National Museum of Natural History, P.O. Box 37012, MRC 108, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A.

Abstract.—With more than 20 recognized species, *Monodelphis* is the most species-rich genus of living Didelphidae. Recent research on these opossums revealed additional species from Perú and Venezuela, and herein we describe a new species from the montane forests of the eastern slope of the central Andes in Perú. *Monodelphis gardneri*, new species, is a small taxon with three black dorsal stripes, more similar in external appearance and cranial features to taxa from eastern Brazil, such as *M. theresa* or *M. americana*, than to Andean species, like *M. osgoodi*. Phylogenetic analyses of cytochrome *b* gene sequences recovered this new species as closer to *M. americana* from eastern Brazil than to *M. theresa* (another species in our analyses with three black dorsal stripes). In spite of this external resemblance, the molecular phylogeny indicates that species with dorsal stripes, including *M. americana*, *M. theresa*, and the new species, do not form a monophyletic group. Although weakly supported, a relationship between *M. americana* and the new species suggests a biogeographic connection between these disjunct distributions, i.e., from eastern Brazil and the eastern versant of the Andes.

Keywords: biogeography, *Monodelphis gardneri*, systematics, taxonomy

The systematics of the short-tailed opossums of the genus *Monodelphis* Burnett, 1830 is still poorly known, in spite of recent efforts to summarize generic diversity (Pine & Handley 2008). At least 18 nominal species were recognized in the most recent world's listing of mammals (Gardner 2005), but three new species, *M. ronaldi* Solari (2004), *M. reigi* Lew & Pérez-Hernández (2004), and *M. handleyi* Solari (2007), were subsequently described, and others have been recognized but are still unnamed (see Pine & Handley 2008). Gomes (1991) described three new species in his systematic review of Brazilian forms, but these are nomina nuda (Gardner pers. comm.) because they were never published in the meaning of the Code (ICZN 1999). Currently, no fewer than 22 species are recognized, making *Monodelphis* the most speciose genus of living didelphids (Voss & Jansa 2009).

In Perú, apart from the two recently described species from lowland forests (Solari 2004, 2007), a third was listed by some authors (Emmons et al. 2001, Solari et al. 2001, Voss & Jansa 2003, Pine & Handley 2008, Pacheco et al. 2009) as a new species present in montane forest of the central Andes. Although this species was originally identified as *M. theresa* by Gardner (1993) and Pacheco et al. (1995),

* Corresponding author.

they remarked that it was a provisional identification and might represent a new species. At the time of those accounts, the record was based on a single animal (LSUMZ 14019) caught in montane forest of the Department of Huánuco, around 2400 m, central Perú, in 1968. In the last 15 years, additional specimens were added: one was caught in the Yanachaga-Chemillén National Park, Pasco, in 1996 (Vivar 2006); two more were later collected in the northern Cordillera Vilcabamba, Junín, in 1997 (Emmons et al. 2001); and another in the southern range of the Cordillera Vilcabamba, Cusco, in 1998 (Solari et al. 2001). More recently (2003), a team from the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Perú, collected two specimens at the same locality where the first individual was captured, i.e., Cordillera Carpish, and in 2007, another one was obtained from the Yanachaga-Chemillén National Park. Thus, eight specimens of this taxon are now known from four localities (Fig. 1).

Patton & Costa (2003) included mtDNA sequences for the individuals of "*M. theresa*" from northern Vilcabamba (Emmons et al. 2001), which showed no close phylogenetic affinity with sequences from Brazilian material of *M. theresa* sensu stricto (Patton pers. comm.). Similar results were obtained by Solari (2010) for a larger dataset including 17 putative *Monodelphis* species (Fig. 2). Those works and our unpublished morphological comparisons confirmed that the Peruvian animals and *M. theresa* represent different species, but no further morphological distinctions between or phylogenetic analyses of black-striped species of *Monodelphis* have been reported (but see Gomes 1991). The aims of this paper are to diagnose and describe the new species and to update its geographic distribution in Perú. Solving the complex relationships among all black-striped species, however, is beyond the scope of this paper.

Materials and Methods

Material examined.—Specimens examined for this study (see Appendix) are housed in the following collections: American Museum of Natural History (AMNH, New York); Field Museum of Natural History (FMNH, Chicago); Museum of Natural Sciences, Louisiana State University (LSUMZ, Baton Rouge); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM, Lima, Perú); and the National Museum of Natural History, Smithsonian Institution (USNM, Washington, D.C.).

Measurements.—Standard external measurements in millimeters (total length [TL], length of tail [LT], length of hind foot with nail [HF], length of ear from notch [E]), and weight [W] in grams were taken directly from collector's labels or field notes. Head-and-body length [HBL] was obtained by subtracting LT from TL. Only adult *Monodelphis* were used in univariate morphometric comparisons (Table 1), corresponding to age class 5, i.e., individuals with permanent teeth fully erupted and in place, M4 with little or no wear (Pine et al. 1985), or older. Craniodental measurements (condylobasal length, maxillary toothrow, molar length, M3–M3 breadth, least interorbital breadth, and zygomatic breadth) are those of Voss et al. (2001), except for breadth across the upper third molars (M3–M3 breadth), which follows Pine (1981). Measurements were taken to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm.

Morphological characters.—Capitalized color names are from Ridgway (1912). Anatomical terminology for relevant characters in opossums is described by Pine (1981), Hershkovitz (1992), Voss & Jansa (2003), Wible (2003), and Pine & Handley (2008). Nomenclature for cranial osteology follows Wible (2003), except for the palatal fenestrae and foramina, and dental anatomy whose terminology follows Voss & Jansa (2003).

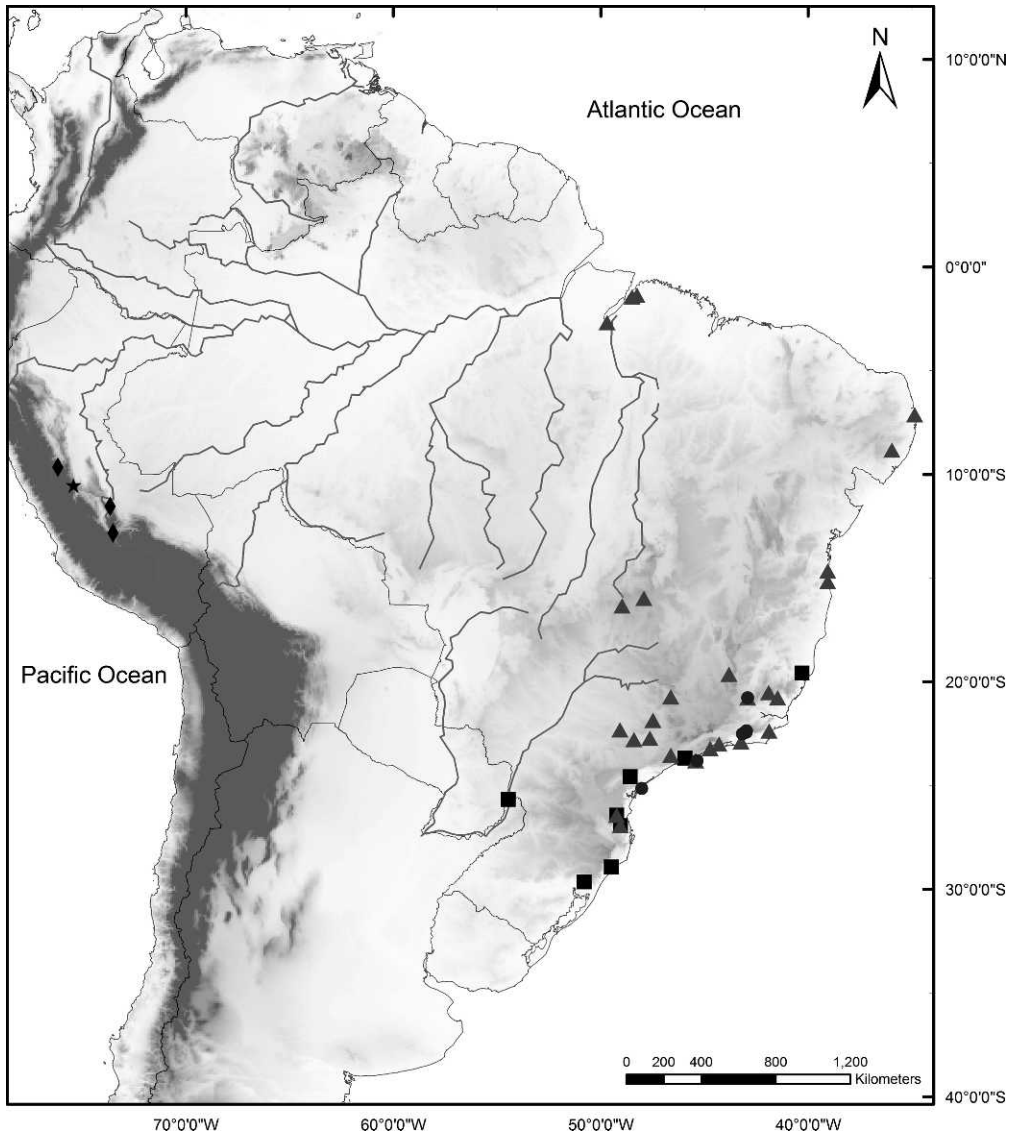

Fig. 1. Geographic distribution of *Monodelphis gardneri* and selected records for other taxa with three dark stripes on the back. In Perú, the black star represents the type locality of *M. gardneri*, and black diamonds are additional records of *M. gardneri* (Central Perú). In eastern South America, triangles identify geographic records for *M. americana*, squares for *M. iheringi*, and dots for *M. theresa*. Geographic records were obtained from specimens we examined (Appendix) and from the species accounts of Pine & Handley (2008).

Molecular and phylogenetic analyses.—All molecular analyses, including DNA extraction, amplification, and sequencing of cytochrome *b*, follow protocols of Patton & Costa (2003) and Solari (2007, 2010). Phylogenetic relationships were inferred by Maximum Likelihood analysis as implemented in PAUP* 4.0b 10 (Swofford 2002) and by Bayesian analysis implemented in MrBayes 2.01 (Huelsenbeck & Ronquist 2001). All analyses and results were detailed by Solari (2010), so

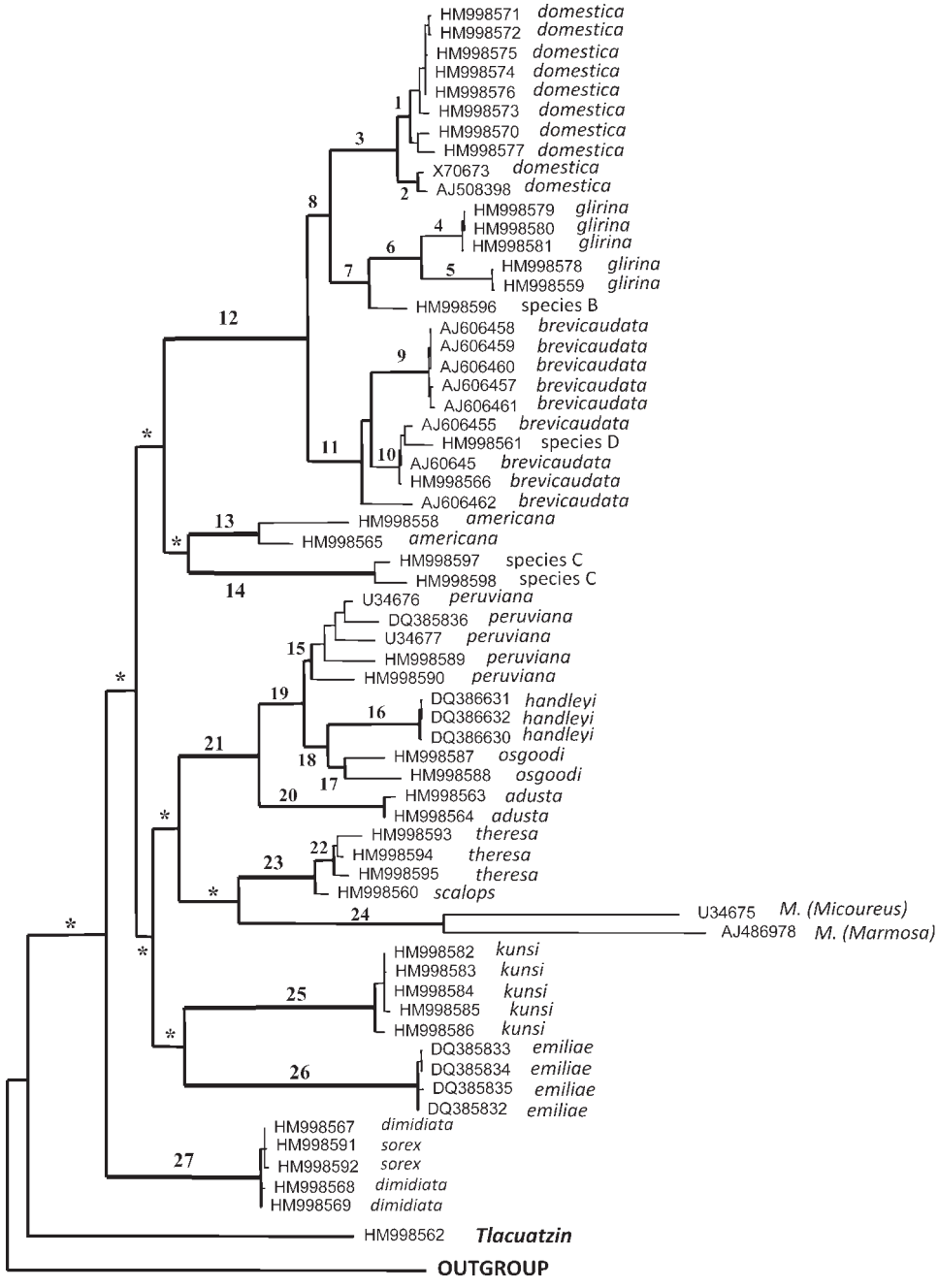

Fig. 2. Optimal tree obtained by Maximum Likelihood analyses of cytochrome *b* gene sequences by Solari (2010). The clade labeled "species C" (stem 14) represents *Monodelphis gardneri* described in this paper. Reprinted with permission from Mastozoología Neotropical, vol. 17(2), © SAREM (Sociedad Argentina para el Estudio de los Mamíferos).

Table 1.—External and craniodental measurements (mm) for specimens of *Monodelphis gardneri*, *M. americana*, and *M. theresa*. For *M. americana*, range of measurements is also included. Specimens of *M. americana* include: AMNH 37492, 61836, 133241 (females), and AMNH 37490, 37493, 75170, 203353, 203354 (males).

Taxa	*gardneri*	*gardneri*	*gardneri*	*gardneri*	*gardneri*	*americana*	*theresa*
n / sex	MUSM 18944 female	LSU 14019 male	MUSM 14631 female	MUSM 24216 female	USNM 582109 male	5 males 3 females	FMNH 141587 female
Head & body length	83.5	100.0	76.0	89.0	93.0	133–173 157.1 (4)	168.0
Length of tail	42.5	49.0	39.0	53.0	52.0	49.5–65.0 54.3 (4)	62.0
Hind foot	15.5	–	14.0	16.0	16.0	12.0–18.0 16.4 (4)	19.0
Condylobasal length	23.1	23.1	21.8	25.3	27.0	31.4–35.0 32.93 (3)	29.6
Maxillary toothrow	–	10.6	–	10.6	11.2	10.7–12.9 14.0 (6)	11.9
Length of upper molars	–	5.4	–	5.4	5.7	4.9–6.4 6.0 (8)	5.9
M3–M3 breadth	7.4	7.9	–	8.1	7.9	8.7–10.3 9.6 (6)	8.7
Least interorbital breadth	5.6	5.7	5.6	5.8	5.7	5.0–5.9 5.6 (7)	5.4
Zygomatic breadth	12.3	13.9	11.8	13.5	14.0	16.6–18.2 11.8 (3)	14.2

here we emphasize only the relationships among species of *Monodelphis* with black dorsal stripes as included in that study.

Results

Monodelphis gardneri, new species

Figs. 3, 4, Table 1

Holotype.—MUSM 24216, a skin, skull, and alcoholic carcass, all in good condition, of an adult female caught by Elena Vivar (field number EV 1570) on 11 Sep 2007.

Type locality.—Abra Esperanza, San Alberto (Fig. 1, black star), Oxapampa Province, Pasco Department, Perú, elev. 2784 m; GPS coordinates, taken in the field, are 11°56′S, 71°17′W.

Paratypes.—We designate seven specimens as paratypes: one trapped near the type locality, at Estación "El Cedro", San Alberto, 2400 m (MUSM 11334, adult male, fluid specimen); three from the eastern slope of the Cordillera Carpish, Huánuco Department (LSUMZ 14019, adult male, skin, skull and skeleton; MUSM 18943, adult male, fluid specimen; 18944, sub-adult female, skin and skull); two from Cordillera Vilcabamba, 2050 m, Junín Department (MUSM 13007, adult female, skin, skull and alcoholic carcass; USNM 582109, adult male, skin and skull); and one from La Convención, Wayrapata, 2445 m, Cusco Department (MUSM 14631, juvenile female, skin, skull and skeleton).

Distribution.—Montane forests on the eastern slope of the Andes in central and southern Perú (Fig. 1, black diamonds). At present, *M. gardneri* is known from the departments of Huánuco, Pasco, Junín, and Cuzco, from 1785 to 2800 m elevation.

Diagnosis.—A species of *Monodelphis* characterized by three conspicuous blackish stripes on the back; median stripe extending from between ears to base of tail, wider at mid-back, with two shorter, prominent lateral stripes extending from shoulders to base of tail. Size small, especially as reflected in head-and-body length (76–100 mm) and condylobasal length (21.8–27 mm); tail absolutely short (42.5–53 mm) but relatively long (LT 49–52% of HBL). Braincase globular; infraorbital foramen dorsal to M1; alisphenoid portion of bulla relatively inflated, with anterior elongated projection or alisphenoid strut forming a secondary foramen ovale (see Voss & Jansa 2003); (primary) foramen ovale almost entirely limited by alisphenoid, the petrosal delimiting the narrow posterior end. No contact between premolars, either upper or lower; molars small and delicate, with poorly developed ectoflexi on M1 but well-developed on M3–M4.

Description.—*Monodelphis gardneri* is a small species (HBL $<$ 150 mm), with short dorsal fur (4 mm); Prout Brown to Mummy Brown, grizzled in dorsal view, three conspicuous blackish dorsal stripes (Fig. 3). Median stripe reaching from between ears to base of tail, widest at mid-back; lateral stripes equally evident, but shorter, extending from shoulders to base of tail. Rump tinged rufous in most specimens, but not conspicuously so (rufous expression may be age related). Rhinarium blackish; pinnae sparsely covered by fine short hairs, appearing macroscopically naked, dark brown, blackish in juvenile. Underparts are Brussels Brown in adults, but Mummy Brown in juveniles; no evidence of throat gland. Tail slightly shorter than half of the head-and-body length; but relatively longer than in similar species (see Comparisons); only slightly paler ventrally; well covered by dense and dark scale-hairs. Dorsal surface of manus and pes well furred, but fingers and toes may appear naked at first glance.

Skull small, braincase globular and not flattened (Fig. 4). Inter- and post-orbital constrictions are evident (Fig. 4a). Braincase lacking parietal ridges or sagittal crest. Anterior projection of premaxillae without rostral process. Posterodorsal

Fig. 3. Juvenile individual of *Monodelphis gardneri*, photographed by F. Schmitt along the Villa Rica-Oxapampa road, Pasco Department, around 2200 m. Photograph courtesy of Mr. Fabrice Schmitt.

projection of premaxillae elongated, interposed between maxilla and nasal, reaching the root of P1; infraorbital foramen dorsal to M1 (Fig. 4c). Maxillopalatine fenestrae elongated, from posterior border of P3 to level of M3 protocone, posterolateral palatal foramina small (Fig. 4b). Alisphenoid portion of bulla well inflated, with anterior elongated projection or alisphenoid strut (Fig. 4b) forming a secondary foramen ovale (see Voss & Jansa 2003, Fig. 8c); (primary) foramen ovale almost entirely limited by alisphenoid, the petrosal delimiting the narrow posterior end (Fig. 4b). Basioccipital short, wide, its anterolateral suture with petrosal a raised crest. Crowns of I2, I3, I4, and I5 increasing in width from front to back; anterior cusps present on P1 and P2; no contact between C1, P1, and P2 (Fig. 4c). Small gaps present between lower premolars. Molars small and delicate, poorly developed ectoflexi on M1 but well-developed on M3–M4.

External measurements in mm of the holotype (and range of three paratypes): HBL 126 (93–149), LT 42.5 (39–52), HF 15.5 (14–15), E 10 (12–14); W 10.25 g.

Comparisons.—Monodelphis gardneri is somewhat smaller than sympatric *M. peruviana* in every external and craniodental measurement but larger than *M. osgoodi*. Compared to similar looking species, it is smaller than *M. americana* or *M. theresa*, except in least interorbital breadth (Table 1) but larger than *M. iheringi* (measurements reported by Gomes 1991); on average, the tail of *M. gardneri* is relatively longer although shorter in absolute length (Table 1). *Monodelphis americana* exhibits a longer, wider, and more defined medial stripe that reaches the top of the head (sometimes to the tip of the

Fig. 4. Skull of the holotype of *Monodelphis gardneri* (adult female, MUSM 24216), showing its diagnostic characteristics. A, dorsal view of cranium; B, ventral view of cranium; C, lateral view of cranium and mandible. Scale bar = 10 mm.

nose), a condition that is never present in *M. gardneri* or *M. theresa*.

Because of the mistaken use of the name *M. theresa* in previous references to *M. gardneri*, we emphasize cranial comparisons between it, *M. theresa*, and *M. americana*. In dorsal view of the skull, the squamosal portion of the zygomatic arch joins the skull almost perpendicularly in *M. gardneri*, but this union is slightly oblique (anteriorly oriented) in *M. theresa* and *M. americana*. In ventral view, the maxillopalatine fenestrae are elongated and straight in *M. gardneri* and *M. theresa* but slightly concave (to the labial side) in *M. americana*; the postpalatine torus is straight in *M. gardneri* and *M. americana* but slightly arched in *M. theresa*. The tympanic portion of the auditory bulla is much more inflated in *M. gardneri*, reaching anteriorly to the base of the zygoma, compared with those of *M. americana* or *M. theresa*; the alisphenoid tympanic process elongates to a thin process in *M. gardneri*, but this forms a medial lamina in *M. theresa* and *M. americana*. The foramen ovale is almost concealed between the petrosal and the alisphenoid in *M. gardneri*, but clearly exposed in *M. theresa* and *M. americana*; and finally, the paracanine fossa of *M. gardneri* reaches the level of the posterior edge of C1 but extends only to its anterior edge in *M. theresa* and *M. americana*. The most distinctive characteristic of *M. iheringi* is its flattened braincase, which contrasts with the rounded one of *M. gardneri*; the former trait represents a unique condition within the genus.

Phylogenetic relationships.—Partial sequences (801 bp) of the cytochrome *b* gene were obtained from 60 individuals representing 17 species of *Monodelphis*. The GTR+Γ+I model generated significantly better likelihood scores and was used in all maximum likelihood analyses, recovering a single tree (–ln L = 8592.478) with eight monophyletic and well-supported species-groups (Fig. 2), seven with bootstrap support $\geq$ 90. However, the relative position, as well as the relationships among the groups, did not receive enough support to allow further discrimination (Solari 2010).

A noteworthy phylogenetic result from the genetic analyses is that the species with three dark dorsal stripes, i.e., *Monodelphis americana*, *M. theresa*, and *M. gardneri*, do not form a monophyletic group (Fig. 2), as would be implied by use of the name *Microdelphys* for *americana* and related species (see Bugher et al. 1941). A sister relationship between *Monodelphis americana* and *M. gardneri* obtained low support in both topologies (Bootstrap $<$ 75; Bayesian $<$ 0.65). The genetic divergence between them is considerable (almost 16%) and is closer to that separating other pairs of species groups, rather than species within a group. Therefore, until more evidence can be obtained, we consider *M. americana* and *M. gardneri* as isolated lineages rather than as members of a single species group with an ancient divergence. The other black-striped species, *M. theresa*, appears to be only distantly related to the *M. americana* + *M. gardneri* pair, and it is placed in a species group with *M. scalops* (Fig. 2; see Solari 2010 for further discussion on nodes).

Habitat.—At the type locality in Cordillera San Alberto, Vivar (field notes) described the habitat as dense and semi-open montane forest, with varying degrees of intergradation. At Cordillera Carpish, Pacheco (field notes) characterized the habitat as pristine, very humid elfin forest. The two collected by Emmons at Cordillera Vilcabamba were collected in Sherman and pitfall traps at the edge between forest and an open sphagnum bog in thickets of dense brush and bamboo, and the one from the southern Cordillera Vilcabamba was caught in a Sherman live trap on the ground; the forest both in southern Junín and northern Cusco, is reported as wet, dense montane forest (Emmons et al. 2001, Solari et al. 2001). In addition to these records, Fabrice Schmitt photographed a

single individual (apparently a juvenile; Fig. 3) along the road from Villa Rica to Oxapampa, at ca. 2200 m. This area consists of almost undisturbed montane forest; when photographed, the weather was cold and cloudy (F. Schmitt, pers. comm., 7 November 2007).

Etymology.—We are pleased to name this short-tailed opossum for Dr. Alfred L. Gardner, United States Geological Survey, Washington, D.C., in recognition of his outstanding contributions to systematic mammalogy and to Peruvian mammalogy in particular, e.g., Gardner 1976, Gardner & Patton 1976. Dr. Gardner also took the first specimen of this beautiful opossum.

Discussion

Monodelphis gardneri is recorded in sympatry with *M. peruviana* at Cordillera Vilcabamba (Emmons et al. 2001, Solari et al. 2001; although both articles reported the latter as *M. osgoodi*) and is potentially sympatric with other species in central Perú. However, no other Peruvian species of *Monodelphis* has the distinctive black-striped pattern that characterizes *M. gardneri*. *Monodelphis gardneri* bears some superficial similarities, i.e., three dorsal black stripes, infraorbital foramen dorsal to M1, a globular alisphenoid tympanic process, and presence of a secondary foramen ovale, to non-Andean species, such as *M. theresa* from southeastern Brazil, and a slight resemblance to *M. americana*. Both *M. theresa* and *M. americana* exhibit significant morphological differences from *M. gardneri* (see Comparisons, above), and genetic differentiation among the three is substantial. The external resemblance of *M. gardneri* to *M. theresa* is so striking that many authors (Gardner 1993, Pacheco et al. 1995, Emmons & Feer 1997, Eisenberg & Redford 1999) used this name for the Cordillera Carpish animal, and Patton & Costa (2003) mapped it among other records of that species. Besides the indicated morphological differences, the phylogenetic cytochrome *b* analysis puts these species in two distinct groups (Solari 2010), with *M. theresa* as sister species to *M. scalops*. Some authors have suggested that *M. theresa* represents immature *M. scalops*, based on comparison of age series from southeastern Brazil (Gomes 1991); genetic analyses also support that interpretation, showing only 3% divergence among individuals of these species (Fig. 2; Solari 2010). If future studies support this assertion, the name *M. scalops* (Thomas, 1888) would have priority over *M. theresa* Thomas, 1921. Resolving this issue is beyond the scope of our paper.

Currently, the name *M. americana* refers to a three-striped taxon from eastern Brazil that has a northern and a southern range that could represent two species (Gomes 1991); museum specimens document an extensive range in eastern Brazil (see Pine & Handley 2008). The absence of a type specimen and lack of a definite type locality (Voss pers. comm.) prevent a precise diagnosis of this taxon. Samples of *M. americana* from Bahia (northeast) and São Paulo (southeast) clustered together with an 8.1% divergence, which is only slightly lower than the average divergence between any other pair of species in this analysis, e.g., 9.2% between *M. handleyi* and *M. osgoodi*. Our two sequences of *M. gardneri* from localities in central Perú (Fig. 1, black diamonds) diverge by only 3.5%, and when compared with other partial sequences (shorter than 500 bp) from the whole geographic range of the species, average divergence is less than 4%.

Species groups have been recognized in *Monodelphis* and even granted genus-level names, e.g., Matschie 1916, Cabrera 1919. Monophyly of *Monodelphis* and of some of the supposed species groups was tested by Solari (2010), using genetic data for 17 taxa. The monophyly of *Monodelphis* could not be supported or rejected in

Solari's cytochrome-*b* analysis, contrary to the findings of Voss & Jansa (2003), who recovered a monophyletic *Monodelphis* using morphological and molecular data for four species. As discussed above, there is no support for grouping all of the back-striped species under a single name as proposed by Bugher et al. (1941). If genus-group names are to be assigned to well-defined species groups, then *Microdelphys* Matschie (1916) should be restricted to *M. americana*, as type species, and its closest relatives, if any (none was identified by Solari 2010).

An ancient connection between species with distributions in eastern Brazil (*M. americana*) and along the eastern versant of the Andes (*M. gardneri*) is suggested by the phylogenetic relationship of these taxa (Solari 2010, Fig. 2), paralleling the novel biogeographic pattern recently hypothesized for certain sigmodontine rodents. The latter examples include species of *Rhagomys* (Luna & Patterson 2003, Villalpando et al. 2006) and *Eremoryzomys* + *Drymoreomys* (Percequillo et al. 2011). Furthermore, the *Monodelphis* results expand the connection to northern Brazil (Bahia) in the east and to the central sector of the eastern versant of the Andes in the west. Future studies may add other taxa that conform to this distribution or supply a precise splitting date for this disjunction, but our results (although with low statistical support) point toward an ancient Andean-Mata Atlantica link. Considering the antiquity of opossum lineages (see Steiner et al. 2005) and the large sequence divergence between *M. americana* and *M. gardneri* (almost 16% in cytochrome *b*), this could represent the oldest documented divergence among living small mammal congeners, and, therefore, between these biogeographic regions.

Acknowledgments

For loan of specimens and tissues relevant to this study, we thank R. S. Voss and E. Westwig (AMNH), B. D. Patterson and W. Stanley (FMNH), M. S. Hafner (LSUMZ), J. L. Patton and C. Cicero (Museum of Vertebrate Zoology, Berkeley), and R. J. Baker and H. Garner (Natural Science Research Laboratory, Texas Tech University, Lubbock). All molecular analyses were completed during the graduate studies of Solari at Texas Tech University, under guidance of R. J. Baker; we express our gratitude for facilitating use of the molecular lab. A. L. Gardner and D. E. Wilson (USNM) supported Solari during his visit to Washington, D.C. Support was provided by Texas Tech through a J. Knox Jones Memorial Fund (2004) and a Cash Family Endowment (2006). Solari was also supported by an Albert R. and Alma Shadle Fellowship (2005) and an ASM Fellowship (2006) from the American Society of Mammalogists. Figure 4 was prepared by J. Pacheco. Additional specimens from Carpish were obtained through a grant from CONCYTEC to Pacheco; and those from Parque Nacional Yanachaga-Chemillén through a consultancy for Protección de Áreas Naturales – PAN - II of PROFONANPE to Vivar. Reproduction of Fig. 2, originally published in Mastozoología Neotropical, vol. 17, was facilitated by U. Pardiñas. We thank R. S. Voss and R. H. Pine for critical review and comments on previous drafts.

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Associate Editor: Michael D. Carleton.

Appendix

Specimens examined for this study, arranged by species, then by country and by specific locality. Museum catalog numbers follow the institutional acronym (see Materials and Methods).

Monodelphis americana (13): BRAZIL: Bahia, Ilhéus, Urucutuba (FMNH 63767, 63768); Goiás, Annapolis, 1000 m (AMNH 133241); Minas Gerais, Viçosa, 6 km SW, Mata da Prefeitura (USNM 552401, 552402); Minas Gerais, Passos (USNM 304593); Minas Gerais / Espírito Santo, Serra do Caparaó, Fazenda Cardosa, 1000 m (AMNH 61836); Pará, Belém (AMNH 203353, 203354); Pará, Benevides (AMNH 37490); Pará, Patagonia, km 72 (AMNH 75170); Pará, Vorsladt (AMNH 37492); Pará, no locality (AMNH 37493).

Monodelphis gardneri (8): PERÚ: Huánuco, San Pedro de Carpish, 1785 m (LSUMZ 14019; MUSM 18943, 18944); Junín, Cordillera Vilcabamba, headwaters of Río Poyeni, 2015 m (MUSM 13007, USNM 582109); Cusco, La Convención, Wayrapata, 10 km NW of Pueblo Libre, 2445 m (MUSM 14631); Pasco, Parque Nacional Yanachaga-Chemillén, Refugio El Cedro, San Alberto, 10 km E of Oxapampa, 2430 m (MUSM 11334) and Abra Esperanza, San Alberto, 2784 m (MUSM 24216).

Monodelphis iheringi (2): BRAZIL: São Paulo, Ipiranga, 728 m (FMNH 94736); São Paulo, Ribeirão da Lagoa (USNM 484015).

Monodelphis theresa (5): BRAZIL: Rio de Janeiro, Teresópolis, 3800 ft (FMNH 25738, 25739); São Paulo, Parque Estadual de Ilhabela, Ilha de São Sebastião, 650 m (MZUSP 29200, MVZ 182776); São Paulo, Ilha do Cardoso, 105 m (FMNH 141587).