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# NEW SPECIES OF *MONODELPHIS* (DIDELPHIMORPHIA: DIDELPHIDAE) FROM PERU, WITH NOTES ON *M. ADUSTA* (THOMAS, 1897)

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*Monodelphis* (short-tailed opossums) is the most diverse genus in the family Didelphidae, including at least 20 recognized species. This paper describes a new species of short-tailed opossum from the lowland forests of Loreto, northeastern Peru. The new species is intermediate in size and coloration between *M. ronaldi*, a species recently described on the basis of 1 specimen from southeastern Peru, and *M. adusta*, a more common species distributed across western Amazonia. However, the new species is sympatric only with *M. emiliae*. Diagnostic characters include overall large size, conspicuously wide buffy stripe on the venter, wide rostrum, narrow postorbital constriction, rounded posterior border of the infraorbital foramen, small and well-separated tympanic processes of alisphenoid, conspicuous posttympanic processes, enlarged canines, small 1st upper premolars, and enlarged cingula on premolars and molars. Whereas morphologically the new species closely resembles *M. ronaldi* and *M. adusta*, a phylogenetic analysis of mitochondrial DNA sequences (which did not include *M. ronaldi*) indicates *M. osgoodi* as its sister taxon. Examination of molecular data also indicates that *M. adusta* is paraphyletic relative to *M. osgoodi* and the new species, and that populations currently referred to *M. a. adusta* and to *M. a. peruviana* each represent 2 distantly related and clearly distinct species.

Key words: *Monodelphis adusta*, new species, Peru, phylogeography, systematics

The neotropical genus *Monodelphis* Burnett, 1830, short-tailed opossums, is the most diverse genus of living American marsupials, but their systematics and taxonomy remain problematic. Gardner (2005) recognized 18 species, whereas Pine and Handley (in press) included 2 species recently described, 1 from Peru (Solari 2004) and the other from Venezuela (Lew and Pérez-Hernández 2004), and suggest that at least 5 additional ones remain unnamed. *Monodelphis* species are widely distributed (Brown 2004), and constitute a distinctive component of the nonvolant mammalian fauna in temperate and tropical habitats of the Neotropics, from southeastern Panama (*M. adusta* [sepia short-tailed opossum]—Handley 1966) through Amazonia and the eastern slope of the Andes to southeastern Brazil (*M. iheringi* [Ihering's three-striped opossum]—Pine 1977) and east-central Argentina (*M. dimidiata* [yellow-sided opossum]—Mares and Braun 2000). These short-tailed opossums occur in a variety of habitats, ranging from Andean elfin forests to lowland rain forests, and include savannas, grasslands, arid Chaco, and the Caatinga (Patton and Costa 2003), over an elevational range from near sea level to near 3,500 m.

At least 5 species are thought to be sympatric in the lowland forests of western Amazonia: *M. adusta* (Thomas), Emilia's short-tailed opossum (*M. emiliae* (Thomas)), Amazonian red-sided opossum (*M. glirina* (Wagner)), pigmy short-tailed opossum (*M. kunsi* Pine), and Pine's short-tailed opossum (*M. ronaldi* Solari). A specimen of *Monodelphis* was obtained during a mammal survey conducted in the rainy season (March) of 1997 in the lowland forests of Loreto, northeastern Peru. This specimen is intermediate in size and coloration between *M. adusta* and *M. ronaldi*, and clearly distinguishable from *M. emiliae*, *M. glirina*, and *M. kunsi*. Recent surveys at the same locality (June–July 2003, dry season) yielded a series of specimens representing the same morphotype. In this study, I have compared morphological and morphometric characteristics among specimens representing the holotype of *M. ronaldi*, the 3 nominal taxa currently synonymized with *M. adusta*, and the unidentified specimens from northeastern Peru. I also performed a phylogeographic analysis on DNA sequences of the mitochondrial cytochrome-*b* gene from samples from specimens representing these taxa, along with an Andean relative, Osgood's short-tailed opossum (*M. osgoodi*), as well as samples of *M. emiliae*, *M. brevicaudata* (northern red-sided opossum), and *M. domestica* (gray short-tailed opossum).

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## Materials and Methods

*Specimens examined*.—The specimens examined in this study are housed in the following collections: American Museum of Natural History (AMNH, New York), Academy of Natural Sciences (ANSP, Philadelphia), Colección Boliviana de Fauna (CBF, La Paz, Bolivia), Field Museum of Natural History (FMNH, Chicago), Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN, Bogotá, Colombia), University of Kansas Museum of Natural History (KU, Lawrence), Museum of Southwestern Biology (MSB, Albuquerque), Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM, Lima, Peru), Museum of Vertebrate Zoology (MVZ, Berkeley), Museum of Texas Tech University (TTU, Lubbock), and the National Museum of Natural History (USNM, Washington, D.C.). Specimens examined are listed by taxon (species and subspecies), then by country, and last by specific locality. If a museum catalog number has not yet been assigned or is unknown, an original field number follows the acronym representing the repository institution. Tissue catalog numbers (e.g., FM, MVZ, NK, and TK), or GenBank accession numbers, are enclosed in brackets for specimens used in molecular analyses.

*Monodelphis adusta adusta (27)*.—COLOMBIA: Antioquia, La Cabaña, 1,200 m (FMNH 70538, female); Antioquia, Zaragoza, La Tirana (ICN 14387, female); Boyacá, Santa Maria, Río Bata (ICN 15047, male); Cesar, Colonia agrícola de Caracolicito, 400 m (USNM 280894, male); Cundinamarca, Guaicáramo (AMNH 75232, male); Cundinamarca, Paime, 1,038 m (FMNH 140244, female); Cundinamarca, San Francisco, Finca Tacaloa, 1,700 m (ICN 12927, male); Meta (AMNH 202650, female); Meta, Acacias, Brisas del Guayoriba, 470 m (ICN 13829, female); Meta, Villavicencio (ICN 5201, 14388, 14389, 14390, all males). ECUADOR: Napo, Lumbaqui (USNM 534286, male); Napo, San José (AMNH 68136, female); Pastaza, 5 km E Puyo (TTU 84865 [TK 104093], 84899 [TK 104127], both males); Pastaza, Mera (AMNH 67274, male); Pastaza, Palmera (AMNH 67275, female); Zamora–Chinchipe, Zamora, 3,250 feet (AMNH 47189, male). PERU: Loreto, Maynas, Estación Biológica Allpahuayo, 110–180 m (TTU 98864 [TK 73633], 101075, both females; TTU 98686 [TK 73228], 98923, 101019 [TK 73496], 101164, all males); Loreto, Teniente López, 1.5 km N (KU 157978 [TK 125211], male).

*Monodelphis adusta melanops (3)*.—PANAMA: Darién, Tacarcuna, 3,200 feet (USNM 309263, male); Cana, 2,800 feet (USNM 179609, male, type of *Peramys melanops*); Guayabo (ANSP 19676, male).

*Monodelphis adusta peruviana (38)*.—BOLIVIA: Cochabamba, Serranía Mosetenes, 1,400–2,200 m (CBF—FGS 03-50 [TK 125206], TTS 717 [TK 125210]); La Paz, La Reserva, 840 m (AMNH 264562 [NK 25662], MSB 68336 [NK 25587], both females). PERU: Cusco, 3 km E Amaybamba, 2,200 m (MVZ 173928 [U34677], male); Cusco, 72 km NE Paucartambo [by road, km 152], 1,460 m (MVZ 166497, 166498, 166499, all females; 171412 [U34676], male); Cusco, Cordillera Vilcabamba, 1,050 m (MUSM 13416 [LHE 1442], female); Cusco, La Convención, Camisea, Cashiriari, 694 m (USNM 582782 [TK 55303], male); Cusco, Paucartambo, Pillahuata, 2,460 m (FMNH 172032 [FM 172032], male); Cusco, Paucartambo, Suecia, 1,920 m (MUSM 16805, 16807, 16809, 16810; FMNH 169807 [FM 169807], 169812 [FM 169812], BDP3781, LLW 655, all males); Huánuco, Hacienda Buena Vista, 3,500 feet (FMNH 23778, 23780, both females); Huánuco, Hacienda Éxito, 3,000 feet (FMNH 23772, 24756, both males); Huánuco, Hacienda San Antonio, 3,000 feet (FMNH 23773, female; 23774, 23775, 23776, all males; USNM 259433, male); Junín, Cordillera Vilcabamba, 2,015 m (MUSM 13006 [LHE 1379]); USNM 582110 [LHE 1395], female); Loreto, Nuevo San Juan, Río Gálvez, 148 m (AMNH 272695 [RSV 2086], female; 272781, male; MUSM 13297, female); Madre de Dios, Tambopata, Reserva Cusco Amazónico, 200 m (MUSM 7157, male); Puno, Zona Reservada Tambopata–Candamo, 450 m (MUSM—HZP 1249, male); San Martín, Moyobamba, 860 m (FMNH 19362, male, type of *Peramys peruvianus*; 19361, female).

*Monodelphis osgoodi (9)*.—BOLIVIA: Cochabamba, 4.4 km N Tablas Monte, 1,833 m (AMNH 264922 [NK 30257], female); Cochabamba, Ayopaya, El Choro, 3,500 m (FMNH 74861, male); Cochabamba, Incachaca, 2,600 m (CM 5248, male, topotype); Cochabamba, Serranía Mosetenes, 1,400–2,200 m (CBF - EY 1915 [TK 125205], TTS 708 [TK 125207], 712, 713 [TK 125209]); La Paz, Nor Yungas, Bajo Hornuni, 1,860 m (CBF 7640 [TK 125204], male). PERU: Cusco, Ocobamba Valley, 3,000 m (USNM 194379, male); Puno, Sandia, Oconeque, Río Quitun, 1,956 m (FMNH 52714, male).

*Monodelphis ronaldi (1)*.—PERU: Madre de Dios, Manu, Pakitza, 365 m (MUSM 17027, male, holotype).

*Monodelphis sp. nov. (8)*.—PERU: Loreto, Requena, Centro de Investigaciones Jenaro Herrera, 135 m (MUSM 15991 [TK 125118], male; DPL 1621, male; JAA 849 [TK 82889], female; JAA 856, male; JAA 857, male; MVC 355, male; MVC 362 [TK 82890], male; MVC 368 [TK 82891], male).

*Measurements*.—Standard external measurements in millimeters (total length [TL], length of tail [LT], length of hind foot [HF], length of ear [E]) and weight (W) in grams were taken directly from collector's tags or field notes. Head-and-body length (HBL) was obtained by subtracting LT from TL. I used only adult specimens in the morphometric comparisons, corresponding to age class 5 (i.e., permanent teeth fully erupted and in place and M4 with little or no wear [Pine et al. 1985]) and older. The craniodental measurements are those of Voss et al. (2001), except for M3M3 (see Pine 1981). Measurements were taken to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm. Because of sexual dimorphism in opossums, measurements of males and females are listed separately.

*Morphological characters and nomenclature*.—Capitalized color names are from Ridgway (1912). The anatomical terminology for relevant characters in opossums was described by Pine (1981), Creighton (1984), Pine and Handley (1984), Reig et al. (1987), Hershkovitz (1992), Voss and Jansa (2003), and Wible (2003). Nomenclature for cranial osteology follows Wible (2003), but names for palatine fenestrae and foramina, and dental features follow Voss and Jansa (2003).

*Molecular analyses*.—Tissues used in this study were collected in the field and either frozen in liquid nitrogen or stored in 96% ethanol. DNA was extracted following standard phenol–chloroform, proteinase K–ribonuclease protocols (Longmire et al. 1997; Sambrook et al. 1989) or following manufacturer's protocol of the DNeasy tissue kit (Qiagen Inc., Valencia, California). Amplification of the entire cytochrome-*b* gene was performed via polymerase chain reaction by using primers MVZ 05 and MVZ 14 (Patton et al. 1996). Conditions for these reactions were: 35 cycles of 94°C for 30 s, 45°C for 1.5 min, and 72°C for 1.5 min; a final 30-min 72°C extension also was used. Polymerase chain reaction products were purified by using a QIAquick polymerase chain reaction purification kit (Qiagen Inc.) following manufacturer's instructions. Internal sequencing primers were the same as those used in previous studies (MVZ 04, MVZ 16, and MVZ 11—Patton and Costa 2003; Patton et al. 1996), and 3 newly designed primers (mono700H1: 5′-CCTAGRGCRTCTTTRATAG-3′; mono480L: 5′-YTAGTAGARTGAATYTGAGG-3′; and mono860L: 5′-AGTAYTAGCYCTCTTAGC-3′). DNA was sequenced in both directions by using ABI Big Dye Chain Terminators, followed by electrophoresis on an ABI Prism 3100-*Avant* Genetic Analyzer (Perkin Elmer, Applied Biosystems, Foster City, California).

Sequence alignment of the resulting fragments was performed using the Vector NTI Suite 6.0 (Informax Inc., Bethesda, Maryland), specifically the ContigExpress (for sequence assembling) and Align X (for sequence alignment) components. Sequences in GenBank (*M. adusta* [U34676, U34677], *M. domestica* [X70673], and *M. brevicaudata* [AJ606461, AJ606462]) were added to verify alignments. Vouchers for both specimens identified as *M. adusta* in GenBank were reexamined and assigned to *M. a. peruviana*.

Phylogenetic relationships were inferred by Bayesian analysis implemented in MrBayes 2.01 (Huelsenbeck and Ronquist 2001) and by maximum-likelihood and parsimony analyses implemented in PAUP (test version 4.0b 10—Swofford 2002). The general time reversible (GTR) model, with allowance for gamma distribution of rate variation ($\Gamma$) and for a proportion of invariant sites (I), best fit the cytochrome-*b* data set using both the Akaike information criterion and hierarchical likelihood ratio tests implemented in Modeltest 3.06 (Posada and Crandall 1998). I calculated Kimura 2-parameter distances for all pairwise comparisons to facilitate comparisons with previous studies.

For Bayesian analyses, 4 simultaneous Markov chains ran for $1 \times 10^6$ generations, with random starting trees for each chain, and trees sampled (saved) every 10 generations. Model parameters were treated as unknown variables (with uniform priors) to be estimated in each Bayesian analysis. I performed 2 sets of independent analyses with changed outgroups, to assess whether or not outgroup choice affects topology; burn-in values were determined by empirical evaluation of likelihood scores. A 50% majority-rule consensus tree was calculated from the sample of stabilized trees in PAUP, with branch lengths obtained via the "sumt" option in MrBayes. Clade reliability was assessed via posterior probabilities and values $\geq 0.95$ were regarded as significant.

Maximum-likelihood analyses used the GTR+$\Gamma$+I model and parameters (as obtained by Modeltest) and full heuristic searches with starting trees by simple addition and with tree-bisection-reconnection branch swapping. For parsimony analysis, all characters and substitution types were treated with equal probability and conducted under full heuristic search with 10 random sequence addition, starting trees by simple addition, and tree-bisection-reconnection branch swapping. Reliability of clades was evaluated by bootstrap analyses (Felsenstein 1985) with 100 replicates for both maximum-likelihood and parsimony analyses.

Originally, trees were rooted by designating *Micoureus regina* and *Marmosa lepida* as outgroups (Voss and Jansa 2003), but recent analyses suggested that *Tlacuatzin canescens* is a more appropriate outgroup (Jansa and Voss 2005). However, based on preliminary phylogenetic analysis of several *Monodelphis* species (S. Solari, in litt.), 5 sequences of *M. emiliae* (MNFS 524, 1150, 1195; LHE 837; and RSV 2083), were selected to work as the closest outgroup and sequences from *M. domestica* and *M. brevicaudata* were used as more distantly related outgroups.

## Results

*Phylogenetics relationships in the M. adusta species complex*.—I obtained 31 cytochrome-*b* sequences ranging between 420 and 1,149 base pairs (bp) from the available samples. These represent 5 *Monodelphis* species and are deposited in GenBank (accession numbers DQ385832–385840, DQ386611–386632). Only 28 of these sequences ($\geq$600 bp), plus 5 available sequences in GenBank, were used in the phylogenetic analyses.

Supported topologies from maximum-parsimony, maximum-likelihood, and Bayesian analyses were nearly identical (Fig. 1). There were no major conflicts among analyses; most of the unsupported differences involved terminal relationships within species. Maximum-parsimony analysis identified 171 (out of 600 bp) parsimony-informative characters that resulted in 8 most-parsimonious trees (436 steps; consistency index = 0.58; retention index = 0.86), and maximum-likelihood analysis resulted in a single optimal tree ($-\ln L = 2{,}720.27$). Independent Bayesian analyses agreed regardless of outgroup choice. Burn-in value for each was 1,000 trees, leaving 9,000 trees for calculation of posterior probabilities.

The most basal clade within the ingroup corresponds to specimens from the northern geographic area, including lowland forests in eastern Ecuador and northern Loreto (Peru), for which the name *M. adusta* (sensu stricto; see "Discussion") is valid (Fig. 1). Divergence values within this clade range from 0.3% to 0.5%, diverging from *peruviana* (see below) by 12.0%, from *osgoodi* by 11.9%, and from the Jenaro Herrera specimens by 12.9%. Specimens from south of the Amazon River correspond to *M. peruviana* (called *M. peruanus* by Emmons and Feer 1990); its 2 main clades, 1 from Peru and another from Bolivia, differ by 6.1%; divergence values within each of these geographic clades range from 0.8% to 2.6%. *M. peruviana* differs from *M. osgoodi* by 9.3% and from the

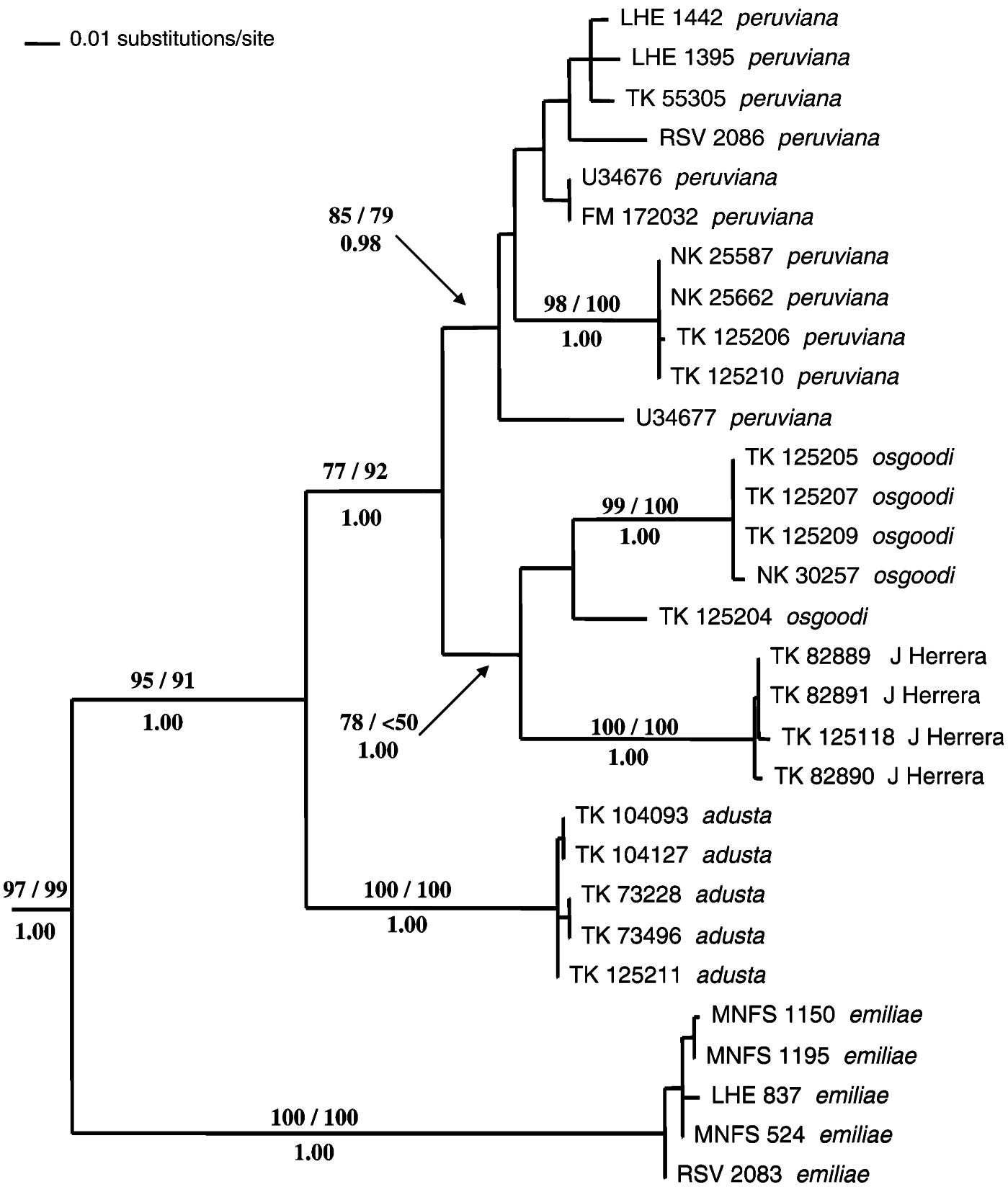



**Fig. 1.**—Optimal tree obtained by maximum-likelihood analysis ($-\ln L = 2{,}720.27$) based on 600 base pairs of cytochrome-*b* gene and GTR+Γ+I model. Outgroups were *Monodelphis emiliae*, plus *M. domestica* and *M. brevicaudata* (not shown). Numbers above branches are bootstrap support values based (100 replicates) from maximum-likelihood and parsimony analyses, and those below are Bayesian posterior probabilities.

Jenaro Herrera specimens by 10.3%. *M. osgoodi* also is composed of 2 groups, 1 from northern (La Paz) and 1 from central (Cochabamba) Bolivia, which differ by 6.0%. Internal divergence in the central Bolivian clade is 0.1%, and *M. osgoodi* diverges from its sister clade (the Jenaro Herrera specimens) by 9.2%. Specimens from Jenaro Herrera average 0.3% in internal divergence, and they are clearly divergent from all other recognizable taxa included in this analysis. Although tissue samples were not available from *M. ronaldi*, its degree of morphological distinction from the Jenaro Herrera specimens (see below) justifies the recognition of the latter as a new species, which is named and described below.

*Monodelphis handleyi,* new species

*Holotype*.—An adult male, MUSM 15991 (skin and skull in good condition, plus tissues in alcohol), caught by Jessica Amanzo A. (original field number JAA 277), on 5 February 1997, at Centro de Investigaciones Jenaro Herrera, 2.8 km E of Jenaro Herrera, on the east bank of Río Ucayali, Requena Province, Department of Loreto, Peru. The coordinates of Jenaro Herrera are 4°52′S, 73°39′W, and elevation is 135 m (Pacheco 1991).

*Paratypes*.—Seven additional specimens collected at the type locality during June and July 2003 are hereby designated as paratypes. All currently are housed at the AMNH, but half of them will eventually be deposited at the MUSM, Lima. Their original field numbers are: DPL (D. P. Lunde) 1621, male, in alcohol with skull removed; JAA (J. Amanzo A.) 849, juvenile female, in alcohol with skull removed; JAA 856, male, skin, skull, and carcass in alcohol; JAA 857, juvenile male, in alcohol; MVC (M. Villalobos C.) 355, male, in alcohol with skull removed; MVC 362, male, in alcohol with skull removed; MVC 368, male, skin, skull, and carcass in alcohol. Tissues were saved for all specimens and are on deposit at the AMNH.

*Distribution*.—Known only from the type locality. Based on information provided by the collectors, specimens of *M. handleyi* were trapped in terrestrial habitats within both swampy and well-drained forests bordering primary and secondary forests, usually with some degree of selective logging and exploitation. In addition, small patches of white sand (podzol soils) were common, but no specimens were recorded near the swamp itself. There was no evidence of heavy leaf litter. Tree canopy height was 25–30 m, understory was dense, and palms were abundant (D. P. Lunde's and J. Amanzo's field notes). One specimen (JAA 857) was caught in a snap trap on the ground, but all the others were taken in pitfall arrays that extended for approximately 100 m within these habitats. General descriptions of habitats at Centro de Investigaciones Jenaro Herrera also were given by Ascorra et al. (1993) and Pacheco (1991).

*Etymology*.—I name this species after the late Dr. Charles O. Handley, Jr. (1924–2000) in recognition of his outstanding contributions to our knowledge of neotropical mammals, and his special fondness for *Monodelphis*. According to R. H. Pine (pers. comm.), Handley recognized this form as an undescribed species (see ''*Remarks*'').

*Diagnosis*.—A robust, large species of *Monodelphis*. Dorsal fur short; hairs with pale gray bases and buffy or brown tips that impart an overall Brussels Brown appearance. Underparts dull cream (self-colored hairs) throughout, with a paler midventral stripe, which is readily noticeable despite the low contrast. Rostrum and anteorbital regions of the skull are wide and robust; postorbital constriction is narrow, delimiting the comparatively small braincase; and a low sagittal crest is sometimes present in adults. The zygomatic arches are robust, wide, and convergent anteriorly. The infraorbital foramen is very large, its outer margin protrudes over the maxilla. The lacrimal foramina lie within the anterior margin of the orbit. The intermaxillary and the interpalatine sutures form a raised crest, and the glenoid process of the jugal is enlarged and forms a conspicuous part of the fossa. The posttympanic processes of the squamosal are enlarged and projected laterally, whereas the tympanic processes of the alisphenoid are small. Canines are greatly enlarged, anterior cingula on premolars and molars are well developed, but the 1st upper premolars are comparatively small. Coronoid processes are wide and low, and the masseteric fossa has a robust posterior shelf.

Additional support for recognizing *M. handleyi* as a species comes from phylogenetic analysis of the first 600 bp of the mitochondrial cytochrome-*b* gene. Sequences available from different geographic populations of putatively related taxa, show *M. handleyi* as a divergent lineage within a group including *M. osgoodi* and *M. peruviana*. Morphologically, *M. handleyi* is distinguishable (see under ''*Description*'') from its sister species (*M. osgoodi*), and does not show a close genetic relationship with its morphologically most similar taxon, *M. adusta* (sensu stricto). Therefore, *M. handleyi* conforms to the criteria suggested by Bradley and Baker (2001) to identify separate evolutionary lineages.

*Description*.—*Monodelphis handleyi* is a medium-sized species (HBL $>$ 105 mm), larger than either *M. adusta* or *M. peruviana* in all external and craniodental measurements examined, but smaller than *M. ronaldi* (Table 1). *M. handleyi* has short ($<$ 5-mm) dorsal fur, hairs have pale gray bases, and buffy or brown tips that produce an almost entirely Brussels Brown coloration in dorsal view, with brownish (Prout's Brown) head and rump; there is no evidence of conspicuous dark dorsal stripes, or of lateral reddening or yellowing. A faint dark midline along the posterior back is evident in the holotype but not in any of the paratypes. Facial vibrissae (Brown 1971) include mystacial and genal series; both are short and white, except for a few mystacial vibrissae that are blackish basally (50–80% of their length). When laid back along the head, the mystacial vibrissae do not extend beyond the ears. There is 1 pair of supraorbital vibrissae, white and unequal in size. In addition, there are 3 pairs each of white submental and interramal vibrissae on the chin. The pinnae are uniformly brownish and appear naked. Underparts have self-colored, dull cream hairs (Ochraceous-Tawny to Buffy Brown) from chin to anus. A throat gland is present as indicated by a yellowish to orange-tinged spot. There is a pale (Light Ochraceous Buff to Ochraceous-Salmon) stripe on the venter. This stripe is wider at midlength and is noticeable despite its low contrast with more lateral hairs on the venter. The limbs are short and robust; plantar surfaces are typical for the genus (Creighton 1984).

**Table 1.**—External and craniodental measurements (in mm) for relevant specimens of *Monodelphis adusta*, *M. peruviana*, *M. melanops*, *M. ronaldi*, and *M. handleyi*. Acronyms are defined in the "Materials and Methods," Voss et al. (2001), and Pine (1981).

| | *adusta* | *adusta* | *peruviana* | *peruviana* | *melanops* | *ronaldi* | *handleyi* | *handleyi* |
|---|---|---|---|---|---|---|---|---|
| No. and sex | 5 ♀ | 9 ♂ | 11 ♀ | 20 ♂ | 2 ♂ | 1 ♂, holotype | 1 ♂, holotype | 5 ♂, paratypes |
| HBL | 107.5 (2) | 110.78 (8) | 96.4 (10) | 96.3 (18) | 102.5 | 141.5 | 124.0 | 122.9 |
| LT | 56.0 (2) | 55.4 (8) | 58.1 (10) | 56.4 (18) | 55.0 | 72.5 | 68.0 | 69.3 |
| HF | 15.0 (2) | 15.1 (8) | 14.7 (10) | 15.1 (17) | 15.3 | 20.0 | 16.0 | 17.5 |
| CBL | 27.5 (4) | 28.1 (8) | 26.1 | 26.1 (17) | 26.7 | 35.3 | 31.9 | 31.6 |
| MTR | 10.9 | 11.4 | 10.6 | 10.7 | 10.4 | 14.5 | 13.1 | 13.2 |
| LM | 6.0 | 6.2 | 5.7 | 5.7 | 5.6 | 8.1 | 7.4 | 7.3 |
| M3M3 | 8.9 | 9.1 | 8.5 | 8.2 | 8.7 | 12.8 | 11.2 | 10.7 |
| LIB | 5.5 | 5.4 (7) | 5.3 | 5.4 (18) | 5.9 (1) | 5.3 | 4.8 | 4.8 |
| ZB | 14.5 (4) | 15.1 | 13.5 | 13.4 (18) | 13.6 (1) | 20.7 | 17.8 | 17.7 |

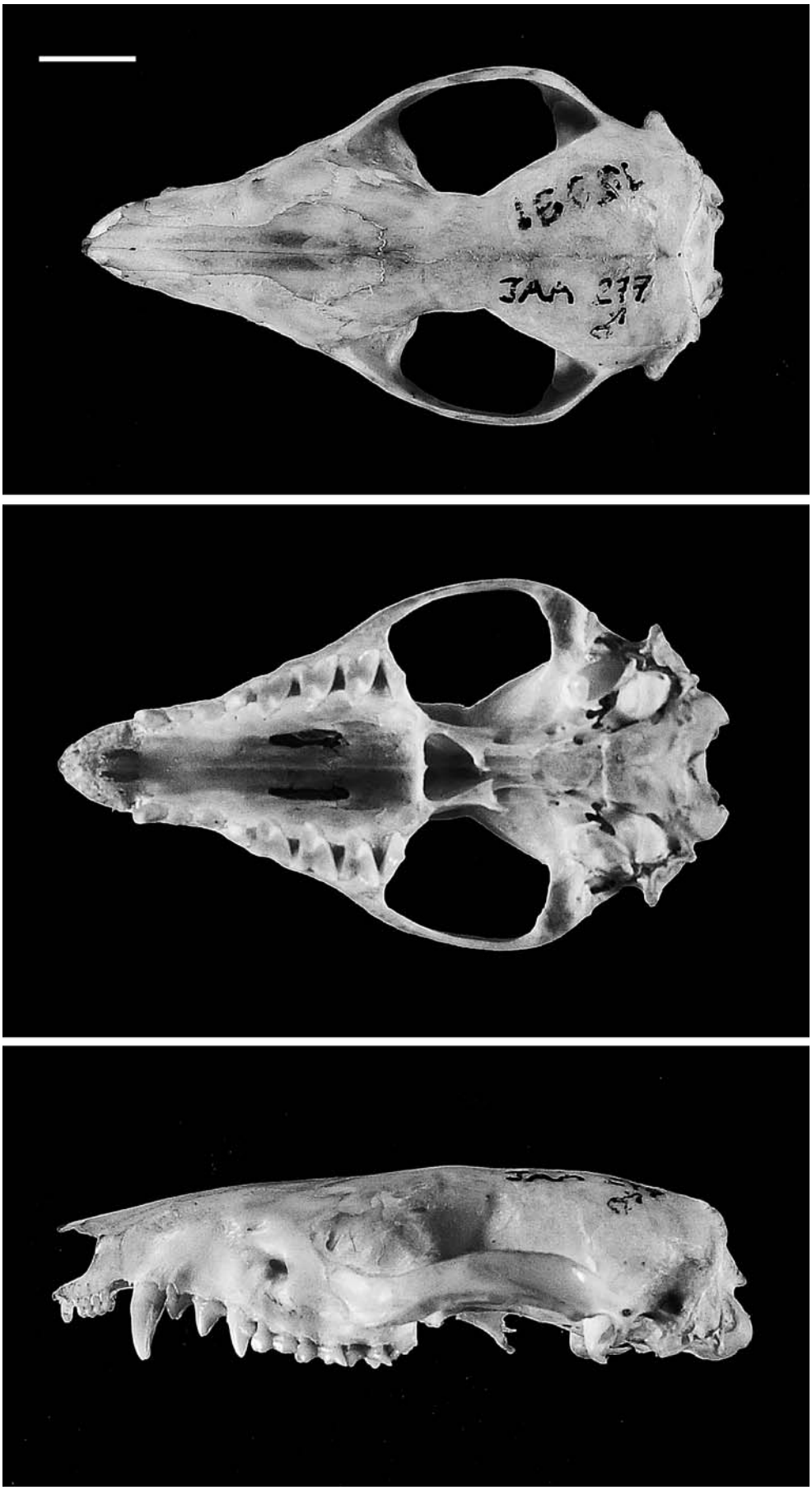
Metacarpals and metatarsals are densely covered with brownish hairs; the digits are sparsely clothed with shorter whitish hairs. Ungual tufts on toes are short, not reaching the tips of the claws. The scrotal skin is whitish and clothed by pale-buffy hairs. The mammary formula is unknown because no adult females are available at present. The tail is short and stout, almost 55% of head-and-body length, and is practically unicolored (dark fuscous). Body fur barely extends onto the base of tail, less than 5 mm dorsally and 8–10 mm ventrally. The pattern of epidermal scales is predominantly annular; there are approximately 20 scale rows/cm, each scale has 3 hairs projecting from under its posterior border. The central hair is darker (blackish), larger, and thicker (petiolate) than the lateral ones. Scalar hairs are no more than 1.5 scale rows long, do not conceal the scales, and are similar on both dorsal and ventral surfaces of the tail.

The skull is distinctively stout and flattened, with weak temporal lines (frontal processes) that may or may not converge to form a low sagittal crest over the parietals (lacking in the holotype, but extending onto the frontals in MVC 362) and intersects the well-developed nuchal crest (Fig. 2a). The posterior one-third of the nasals is conspicuously widened near the frontomaxillary suture, but it is narrowed posteriorly, somewhat diamond-shaped, and blunt at the nasofrontal suture. The postorbital constriction is pronounced, and clearly demarcates the smaller braincase from the much enlarged rostrum. The infraorbital foramen is enlarged; its lateral border protrudes over the maxilla in adults, whereas its posterior border (which is rounded), defines an oblique angle with the horizontal plane of the skull (Fig. 2c). The zygomatic arches are robust, expanded, and convergent anteriorly (Fig. 2b). The lacrimal foramina consist of 1 or more openings; although the number on each side is variable, it is not age-dependent, and the foramina are always located within the orbit (not on its external margin as in most other congeneric species). The superior border of the lacrimal bone projects posterolaterally, creating a shallow sulcus on the anteromedial wall of the orbit. The incisive foramina are short, their posterior borders extending back only as far as the anterior base of canines; the medial palatine processes of the premaxillae are wider posteriorly. The intermaxillary and interpalatine sutures are raised and form a midventral crest, which is evident even in juveniles. The maxillopalatine fenestrae extend from the anterior border of M1 back to the anterior border of M3. There are no palatine fenestrae. The jugal contribution to the glenoid fossa is comparatively large, forming a conspicuous portion of the fossa in ventral view; the postglenoid process is high and wide. A well-developed nuchal crest marks the posterior end of the skull; its most lateral expansions merge with the enlarged posttympanic processes of the squamosal. The alisphenoid tympanic processes are small, and no secondary foramen ovale is present, although a shallow groove for the maxillary nerve runs over the inner side of each bulla. The paracondylar (paroccipital) processes of the exoccipital are elongated. The upper canines are enlarged. The 1st upper premolars are relatively small (less than half the height of the 2nd) and nearly parallel; behind them, the upper toothrows diverge posteriorly. Well-developed anterior cingulae are present and conspicuous on both the premolars and molars; upper molars are large (M1–M4 length $>$ 7.2 mm) and massive. There is a small gap between the lower canine and the 1st lower premolar. There are no accessory cuspulids on the posterior border of the lower canines. The lower premolars are set close to each other, but are not in contact. The trigonid of the deciduous 3rd lower premolar (dp3) is tricuspid. The mandibular rami are not excessively bowed, and the comparatively wide and low coronoid processes are oriented almost perpendicular to the lower toothrow. The posterior shelf of the masseteric fossa and the rami connecting the angular process and the mandibular condyle are robust.

*Remarks.*—The type locality of *M. handleyi* lies between the Ucayali and Yavari rivers (Fig. 3), an area where only *Amphinectomys savamis* Malygin, a semiaquatic sigmodontine rodent, has previously been reported as endemic (Malygin et al. 1994). *Scolomys ucayalensis* Pacheco, originally described from Jenaro Herrera, now includes *S. juruaense* Patton and da

→

**Fig. 2.**—Skull of the holotype of *Monodelphis handleyi*, new species (male adult, MUSM 15991), showing its diagnostic characteristics. a) Dorsal view. b) Ventral view. c) Lateral view. Scale bar = 5 mm.



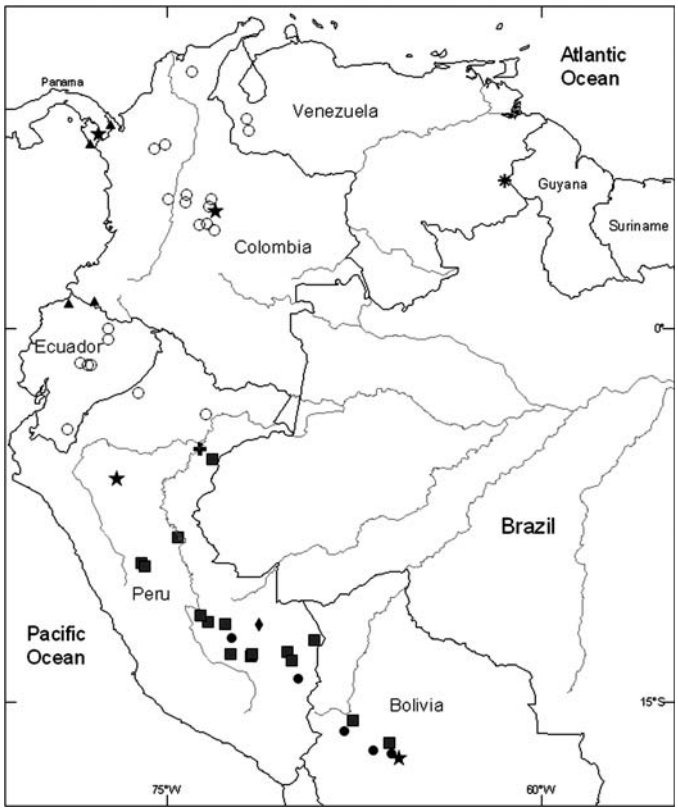



**Fig. 3.**—Geographic distribution of *Monodelphis handleyi* and other taxa related to *M. adusta* in South America. Records of *M. adusta* and *M. osgoodi* are represented by open and filled circles (respectively), *M. melanops* by triangles, and *M. peruviana* by squares. Black stars = type localities of *M. adusta* (Cundinamarca, Colombia), *M. melanops* (Cana, Panama), *M. peruviana* (San Martín, Peru), and *M. osgoodi* (Cochabamba, Bolivia); plus = type locality of *M. handleyi* (Loreto, Peru), black diamond = type locality of *M. ronaldi* (Madre de Dios, Peru), and asterisk = type locality of *M. reigi* (El Dorado, Venezuela).

Silva (see Gomez-Laverde et al. 2004) and its range therefore extends into western Brazil. There are no records of similar *Monodelphis* in northeastern Peru or northwestern Brazil, despite recent collection efforts (Hice 2001; Patton et al. 2000). Other small mammals recorded at Jenaro Herrera by Pacheco (1991) include: *Metachirus nudicaudatus*, *Philander opossum* (Didelphidae); *Neacomys spinosus*, *Oecomys bicolor*, *Oryzomys perenensis*, *S. ucayalensis* (Cricetidae); *Proechimys brevicauda*, and *P. steerei* (Echimyidae). Recent records of sympatric opossums include: *Caluromys lanatus*, *Didelphis marsupialis*, *Hyladelphys kalinowskii*, *Marmosa* sp., *Marmosops* cf. *bishopi*, *Marmosops impavidus*, *Micoureus* cf. *demerarae*, and *Monodelphis emiliae* (R. S. Voss, pers. comm.).

An additional specimen from Jenaro Herrera, examined by Handley at the Smithsonian Institution, and borrowed from the Moscow State University Zoological Museum (catalog number S-155520) also may correspond to *M. handleyi*. When the specimen was brought to the USNM for identification (early 1990s), Handley thought it represented an undescribed species (R. H. Pine, pers. comm.) but he never made a definitive or formal statement to that effect. The specimen now appears to have been lost.

## Discussion

*Comparisons with similar species*.—Morphologically, *M. handleyi* is most similar to *M. ronaldi*, the latter known only by the holotype from southeastern Peru (Solari 2004). Both species are unusual in having ventral fur composed of self-colored hairs; however, there are several discrete cranial and dental characters that distinguish them. *M. ronaldi* is larger in all external and craniodental measurements (Table 1), has paler dorsal pelage (described as Broccoli Brown in Solari [2004] but meant to be Brussels Brown), with a larger portion of the hair tips being buffy. Cranially, *M. ronaldi* has a flatter skull, conspicuous temporal lines, a well-developed sagittal crest, and shorter premaxillae in which the 1st upper incisor is very close to the 2nd. Although the infraorbital foramen also is enlarged in *M. ronaldi*, its posterior edge forms nearly a right angle to the horizontal plane of the skull, not an oblique angle as seen in *M. handleyi*. There are gaps between each of the lower premolars in *M. ronaldi*, but only a small gap between the 1st and 2nd lower premolars in *M. handleyi*.

*Monodelphis handleyi*, *M. adusta* (sensu stricto), and *M. peruviana* are all similar in having uniformly colored dorsal fur color and being relatively small (HBL $< 150$ mm), and having nearly naked tails. Skulls of all the species are flattened, especially at the frontal region, and have low and small bullae. However, *M. handleyi* can be distinguished from the other species by its larger size and paler coloration. *M. handleyi* also has a wider rostrum, narrower postorbital constriction, and a well-developed sagittal crest in adults. The posterior border of the anteorbital foramen is rounded, and defines an oblique angle with the horizontal plane of the skull, lacrimal foramina are always within the orbit (not exposed laterally), alisphenoid tympanic processes are smaller, and posttympanic processes of the squamosal are conspicuous in *M. handleyi*.

Compared to the other taxa in this group of species, *M. handleyi* is larger in all external and craniodental measurements examined (Table 1). *Monodelphis melanops*, which is similar in size and coloration to *M. adusta* (sensu stricto), is restricted to the western side of the Andes. Because of its uniform coloration, *M. handleyi* needs no further comparisons with western Amazonian species of *Monodelphis* that have conspicuously patterned dorsal fur (e.g., *M. emiliae* and *M. glirina*).

No other *Monodelphis* species had been reported at Jenaro Herrera until recently, when a single specimen of *M. emiliae* (MVC 364) was caught during the last trapping season (2003). At Nuevo San Juan (05°15′S, 73°10′W, 148 m—Simmons et al. 2002), a Matses Indian village about 100 km southeast of Jenaro Herrera, *M. peruviana* and *M. emiliae* have been collected in sympatry (Jansa and Voss 2000), and at the Allpahuayo–Mishana Reserved Zone (03°28′S, 73°25′W, 110–180 m), almost 75 km north of Jenaro Herrera, *M. adusta* (sensu stricto) was reported by Hice (2001). Another nearby

record of *M. peruviana* (as originally identified by Ceballos [1959]) comes from Pucallpa (08°23′S, 74°32′W), in Ucayali Department (Fig. 3).

*Taxonomy of the M. adusta species complex.*—The composition of *M. adusta* was reviewed by Solari (2004), who suggested that *M. melanops* (Goldman 1912) is a junior synonym of *M. adusta*, but that *M. peruviana* (Osgood 1913) should be considered a recognizable subspecies. This taxonomy was based on morphological examination of specimens representing those names, including holotypes of *melanops* and *peruviana*. Availability of tissues from specimens of *M. adusta* (sensu lato) throughout its geographic range (from Ecuador to Bolivia) now permits comparisons of mitochondrial DNA sequences to evaluate the applicability of these names. For comparative purposes, I included samples representing *M. osgoodi* from Peru and Bolivia in the analysis (S. Solari et al., in litt.).

Some of the cranial characters originally used to distinguish *M. peruviana* from *M. osgoodi* were smaller skull, more delicate and more slender construction of the skull, a proportionally and absolutely narrower palate, and smaller teeth in the latter (Doutt 1938). However, the present study reveals that *M. peruviana* displays a considerable degree of geographic variation in morphological characters. Specimens from the lowlands (below 1,000 m) in the departments of Loreto, Cusco, and Madre de Dios (Peru) and La Paz (Bolivia) resemble *M. adusta*, but are slightly more delicate in cranial construction, whereas specimens from montane habitats (above 1,000 m) in Cusco and Junín (Peru) appear to be more similar to *M. osgoodi*. Further discussion of the distinction between *M. peruviana* and *M. adusta* is detailed in Solari (2004). A taxonomic review of all taxa in this group, along with an emended morphological diagnosis of *M. osgoodi*, is necessary and is presently in preparation.

Because of morphological and morphometric differences between these taxa, supported by the level of molecular divergence, and geographic separation by the Amazon River, *M. peruviana* should be considered a distinct species, rather than a subspecies of *M. adusta*, with an even larger distribution than previously thought (Solari 2004). *M. peruviana* is now represented by specimens from the departments of Cusco, Huánuco, Junín, Loreto, Ucayali, San Martín, Madre de Dios, and Puno in Peru, and from the departments of La Paz and Cochabamba in Bolivia.

The Andean Cordillera has led to Trans-Andean speciation in several groups (e.g., *Lophostoma aequatorialis* [Baker et al. 2004], *Oryzomys bolivaris* and *O. talamancae* [Musser et al. 1998], and *Proechimys decumanus* and *P. semispinosus* [Gardner 1983; Patton 1987]), and the Amazon River has had a similar influence (e.g., *Philander andersoni* versus *P. mcilhennyi* [Patton and da Silva 1997]). The influence of these geographic features on the diversification of *Monodelphis* and other groups of small mammals demonstrates that geographic disjunction can be associated with or contribute to speciation events. Given the major affect of the Andean Cordillera, and the limited use of morphological data to recognize species in this group, the taxonomic status of *M. melanops* (from Darien, southeastern Panama) also should be reevaluated. Animals from the Chocó biogeographic region, in Colombia (Nariño—Muñoz-Saba and Alberico 2004) and Ecuador (Esmeraldas—L. Albuja, pers. comm.), agree with the expected distributional pattern of that taxon and suggest specific status. However, the verification of this hypothesis, and the elucidation of its phylogenetic affinities should await appropriate geographic sampling.

## Resumen

*Monodelphis* (raposas colicortas) es el género más diverso de la familia Didelphidae, incluyendo no menos de 20 especies reconocidas. Aquí, se describe una nueva especie de raposa colicorta de los bosques húmedos tropicales de Loreto, en el noreste de Perú. Esta nueva especie es intermedia en tamaño entre *M. ronaldi*, recientemente descrita de un único ejemplar del sureste de Perú, y *M. adusta*, la cual es ampliamente distribuida en la Amazonia occidental. Sin embargo, esta nueva especie es simpátrica únicamente con *M. emiliae*. Sus caracteres diagnósticos incluyen una talla grande, una banda ventral de color ante bastante ancha, rostro ancho, constricción postorbital angosta, borde posterior del foramen infraorbital redondeado, procesos timpánicos del alisfenoides pequeños y bastante aparte uno del otro, procesos posttimpánicos conspicuos, caninos grandes, primer premolar superior comparativamente pequeño, y cíngulos desarrollados en los premolares y molares. Morfológicamente, la nueva especie estaría más relacionada a *M. adusta* o *M. ronaldi*, pero el análisis filogenético de secuencias del ADN mitocondrial (que no incluye a *M. ronaldi*) indica que la nueva especie es hermana a *M. osgoodi*. Adicionalmente, los datos moleculares muestran que *M. adusta* es parafilético con respecto a *M. osgoodi* y la nueva especie, con poblaciones asignables a *M. a. adusta* y *M. a. peruviana* representando especies distantemente relacionadas.

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