MAMMALIAN DIVERSITY AND MATSES ETHNOMAMMALOGY IN AMAZONIAN PERU

PART 3: MARSUPIALS (DIDELPHIMORPHIA)

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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ABSTRACT

This report is the third in our monographic series on mammalian diversity and Matses ethnomammalogy in the Yavarí-Ucayali interfluvial region of northeastern Peru. Based on taxonomic analysis of specimens collected in the region, we document the occurrence of 19 species of marsupials in the genera Caluromys, Glironia, Hyladelphys, Marmosa, Monodelphis, Metachirus, Chironectes, Didelphis, Philander, Gracilinanus, and Marmosops. Our principal taxonomic results include the following: (1) we provide a phylogenetic analysis of previously unpublished mitochondrial DNA (mtDNA) sequence data for Caluromys that supports the reciprocal monophyly of all currently recognized species in the genus but reveals substantial heterogeneity in one extralimital taxon; (2) we explain why Marmosa constantiae is the correct name for the southwestern Amazonian taxon previously known as Mar. demerarae, and we diagnose Mar. constantiae from Mar. rapposa, a superficially similar species from southern Peru, eastern Bolivia, and central Brazil; (3) we explain why Mar. rutteri is the correct name for one of the Amazonian species currently known as Mar. regina, and we restrict the latter name to the transAndean holotype; (4) we recognize Metachirus myosuros as a species distinct from Met. nudicaudatus based on morphological comparisons and a phylogenetic analysis of new mtDNA sequence data; and (5) we name a new species of Marmosops to honor the late Finnish-Peruvian naturalist Pekka Soini.

Of the 19 marsupial species known to occur in the Yavarí-Ucayali interfluve, 16 have been recorded in sympatry at Nuevo San Juan, the Matses village where we based most of our fieldwork from 1995 to 1999. We explain why we believe the marsupial species list from Nuevo San Juan to be complete (or nearly so), and we compare it with a species list obtained by similarly intensive fieldwork at Paracou (French Guiana). Although Nuevo San Juan and Paracou are 2500 km apart on opposite sides of Amazonia, the same opossum genera are present at both sites, the lists differing only in the species represented in each fauna. We briefly discuss current explanations for spatial turnover in species of terrestrial vertebrates across Amazonian landscapes and provide evidence that the upper Amazon is a significant dispersal barrier for marsupials.

Marsupials are not important to the Matses in any way. In keeping with their cultural inattention to mammals that are inconspicuous, harmless, and too small to be of dietary significance, the Matses lexically distinguish only a few kinds of opossums, and they are not close observers of opossum morphology or behavior.

INTRODUCTION

This report is the third installment of a monographic series on mammalian diversity and ethnomammalogy in a sparsely inhabited rainforested region between the Yavarí and Ucayali rivers in northeastern Peru. Like those that preceded it, the present study is based on collections made in this region between 1926 and 2003, and on our long-term ethnological and linguistic fieldwork with the Matses, a Panoan-speaking group of indigenous Amazonians who still obtain most of their dietary protein by hunting mammals. The primary objectives of these monographs are to document the species

richness of the regional fauna through taxonomic analysis of collected specimens, and to assess the extent of Matses knowledge of mammalian natural history based on linguistic analysis of recorded interviews.

The introductory report in this series (Voss and Fleck, 2011) summarized current knowledge about the physical geography and floristics of the Yavarí-Ucayali interfluve (figs. 1, 2), provided background information about the indigenous cultures of the region, and analyzed taxonomic and ethnographic data on primates. Our second report (Voss and Fleck, 2017) provided equivalent taxonomic and ethnographic treatments for the larger mammals, including xenarthrans, carnivores, ungulates, and

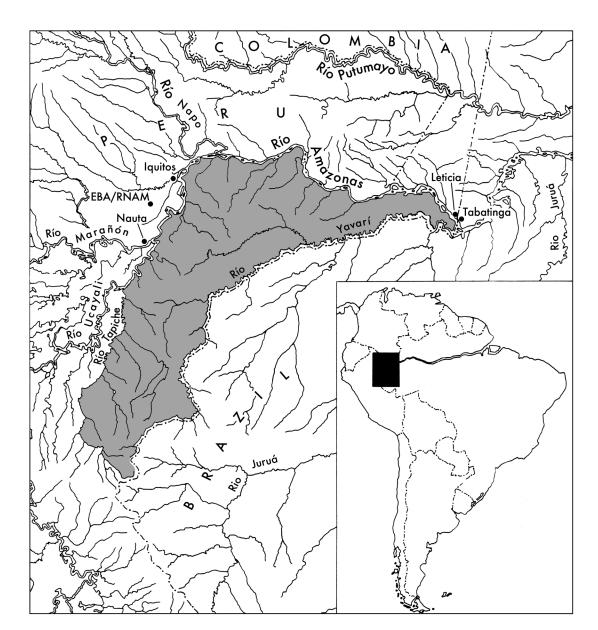


FIG. 1. The Yavarí-Ucayali interfluve (shaded) in relation to surrounding geographic features of western Amazonia. EBA/RNAM = Estación Biológica Allpahuayo, a biological field station in the Reserva Nacional Allpahuayo-Mishana).

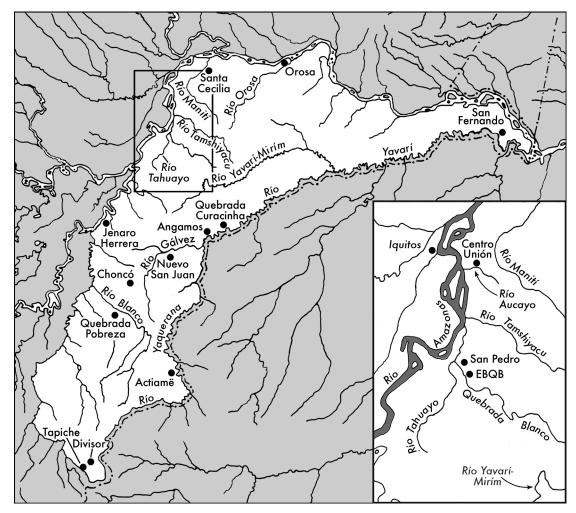


FIG 2. Faunal inventory sites and other collecting localities within the Yavarí-Ucayali interfluve (see appendix 1 for geographic coordinates and other information). EBQB = Estación Biológica Quebrada Blanco.

aquatic species. In this report, we turn to the marsupial fauna, which is uniquely challenging from a taxonomic perspective.

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Whereas Amazonian primates and larger mammals are, with few exceptions, reasonably well understood taxonomically, or at least have reasonably well-circumscribed taxonomic problems, Amazonian marsupials have received little revisionary attention. Therefore, literature resources for specimen identification are limited, and first-hand inspection of type material is a necessity. To support our taxonomic decisions we examined and measured large series of specimens, and in two

cases we analyzed new molecular datasets. Inevitably, the systematic accounts in this report are longer than most of those in our previous reports. By way of compensation, our results include novel insights about Amazonian marsupial taxonomy, species richness, and faunal complementarity.

MATERIALS AND METHODS

Faunal Sampling Methods

A few marsupial specimens reported here were obtained by commercial collectors (Voss

and Fleck, 2011: 9-10), but most were collected by biologists using more or less standard trapping methods and equipment (e.g., Victor rat traps, Sherman live traps, and Tomahawk live traps deployed at ground level; Voss and Emmons, 1996: 14-17). Standard trapping efforts that resulted in specimens examined for this report were carried out at Jenaro Herrera by personnel from the Universidad Nacional Mayor de San Marcos at irregular intervals from the early 1990s to 2003 (e.g., Pacheco, 1991), at San Pedro by Michael H. Valqui from 1994 to 1999 (Valqui, 1999, 2001), and at Nuevo San Juan by D.W.F. and R.S.V. from 1995 to 1999 (figs. 3, 4). Other specimens were taken in deadfalls, captured by hand, or trapped using equipment borrowed from us by Matses men, women, and children at Nuevo San Juan from 1995 to 2003.1 All the latter material was measured and preserved following standard protocols by D.W.F. (in 1995, 1996, and 1999) or by R.S.V. (in 1998).

Additionally, some marsupial specimens were collected by pitfall trapping and arboreal trapping at Jenaro Herrera, where Darrin P. Lunde and D.W.F. installed traplines that were subsequently maintained by Jessica Amanzo and Lynne Villalobos from 8 June to 24 July 2003. The pitfall-trapping effort consisted of five lines, each with 11 plastic buckets sunk flush to the soil surface and spaced 5 m apart; a continuous sheet-plastic drift fence supported by wooden stakes ran the whole length of each line (Voss et al., 2001: fig. 6). The arboreal trapping effort consisted of 25 stations, each with one $145 \times 145 \times$ 410 mm Tomahawk trap and a piggy-backed 80 \times 90 \times 230 mm Sherman trap hoisted into the subcanopy at heights ranging from 6-20 m above the ground (mean height = 12 ± 5 m). An effort was made to site pitfall traplines and arboreal traps in a variety of recognizable biotopes surrounding the field station at Jenaro Herrera.

Lastly, several Matses men were employed to hunt at night in the vicinity of Nuevo San Juan in 1999. Each man was provided with a singleshot 16-gauge shotgun, ammunition suitable for small game (including .410 and .22 caliber shotshells loaded into auxiliary barrels), headlight, digital watch, waterproof notebook, and mechanical pencil. Hunters were instructed to walk slowly along trails scanning the vegetation for eyeshine (especially in the canopy and subcanopy), to record every mammal sighted, and to collect every marsupial and rodent encountered. The data recorded for each sighting or collected specimen included time, species, habitat, and other relevant circumstances. Hunters' notebook entries (fig. 5) were written in the Matses language, which is rich in descriptive terminology for both mammals and local habitats (Fleck and Harder, 2000); these were subsequently translated by D.W.F. and transcribed to loose-leaf field journals that are now bound and archived at the AMNH.

Ethnobiological Methods

RECORDED MONOLOGS: From May to July of 1998 we elicited monologs about the natural history of local mammals from hunters at four different Peruvian Matses villages, and we recorded these interviews on digital minidisk. All monologs were recorded in the Matses language. To elicit these texts, informants were asked to talk about a single mammalian folk taxon (e.g., cheka bëbëdi, "four-eyed opossums"), which was mentioned only once by the interviewer (Fleck). Informants were asked to say as much as they liked about any topic relating to the taxon in question (see Voss and Fleck, 2017: appendix 1 for a free English translation of a recorded monolog about armadillos). Each informant's monologs were recorded with no other adults present in order to achieve independence of response. For each taxon, the interview was replicated a total of seven or eight times with different informants. These recordings were subsequently tran-

¹ We encouraged such donations by rewarding successful trappers with small gifts, but juvenile collectors were sometimes inarticulate with shyness, so many of their specimens are data deficient (e.g., lacking definite information about the habitats in which they were taken).



FIG. 3. Satellite view of Nuevo San Juan (arrow: 5°15′S, 73°10′W), on the right bank of the Río Gálvez, Loreto, Peru. The town is surrounded by swidden-agricultural fields (pale green) in a matrix of primary forest (dark green) that extends for many kilometers in all directions. Inventory fieldwork at this locality documented sympatry of 16 didelphid species.

scribed and translated by Fleck and literate Matses assistants. The texts were then checked with speakers other than the narrators to obtain second opinions on the validity of some of the less commonly asserted natural history details.

Sentences in the translated texts were sorted by topic (physical appearance, habitat preference, social behavior, vocalizations, daily activities, and food), and then combined to obtain composite essays for each taxon. These essays, which are presented under the heading "Matses natural history" in the accounts that follow, are supplemented by parenthetical editorial comments only as necessary to interpret otherwise obscure passages or to identify botanical taxa corresponding to Matses plant names. To provide a more complete ethnographic picture, topics concerning Matses nomenclature, classification, hunting strategies, and cultural significance (summarized under the heading "Ethnobiology" in each species account) were elaborated using data from additional sources, including interview-style question-and-answer sessions.

PLANT IDENTIFICATIONS: Most of the plants mentioned by the Matses in their monologs were identified by various means. Palms were collected by Fleck in 1998 and 1999 from the area surrounding Nuevo San Juan with the help





FIG. 4. Our house at Nuevo San Juan in 1998 (above) and specimens drying in the sun (below), including *Marmosa constantiae*, *Metachirus myosuros*, and *Philander mcilhennyi* (both photos by R.S.V.).

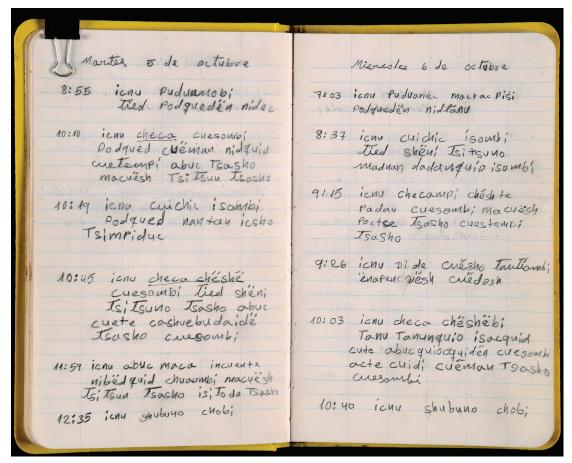


FIG. 5. Two pages from the field notes of a Matses man employed to hunt for marsupials and rodents at Nuevo San Juan. On the left-hand page, which records observations made on 5 October 1999, the second entry reads, "10:10 [pm] I killed an opossum in primary forest on the lower slope of a hillside. It was up in a slender tree." The corresponding voucher is MUSM 15311, a specimen of *Marmosa constantiae*.

of Matses assistants, who named the palms while in the forest, prior to being collected. Palm specimens were identified in the field using published identification guides (Henderson, 1994; Henderson et al., 1995), and voucher material was subsequently deposited at the herbarium of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima) and in the New York Botanical Garden (New York). Other plants, particularly dicotyledonous trees, were identified by Fleck and two Matses assistants at the arboretum of the Instituto de Investigaciones de la Amazonía Peruana. This arboretum is maintained at the Centro

de Investigaciones Jenaro Herrera, a forestry research station located about 80 km west of Nuevo San Juan, where Swiss botanists have identified all trees >10 cm at breast height (Spichiger et al., 1989, 1990). Plants and trees in the proximity of Nuevo San Juan were also identified by Fleck using identification keys in Gentry (1993).

Botanical taxa corresponding to Matses plant names are provided according to the following conventions: (1) Only the generic name is given if the Matses plant name corresponds to all the species in a locally polytypic genus (e.g., bin, which refers to all the local species

of the genus Castilla [Moraceae]). (2) The generic name is followed by "sp." if the Matses plant name corresponds to just one unidentified local species in a genus (e.g., ichibin, which refers to an unidentified species of Matisia and another of Eriotheca [Bombacaceae]). (3) The generic name is followed by "spp." if the Matses plant name corresponds to two or more unidentified species, but not to all the local species of that genus (e.g., shankuin, which refers to multiple unidentified local species of Pourouma [Moraceae]). Where alternative technical names for plant families are current in the literature (e.g., Palmae vs. Arecaceae, Clusiaceae vs. Guttiferae), the nomenclature used here follows Gentry (1993).

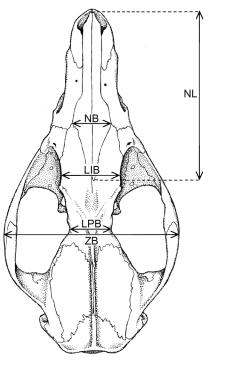
Taxonomic Methods

Specimens: The morphological specimens we examined and others mentioned below are preserved in the following collections (listed in order of their standard institutional abbreviations): AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, London), CM (Carnegie Museum, Pittsburgh), EBD, Estación Biológica Doñana (Sevilla), FMNH (Field Museum, Chicago), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), KU (University of Kansas Biodiversity Research Center, Lawrence), LACM (Los Angeles County Museum, Los Angeles), LSUMZ (Louisiana State University Museum of Zoology, Baton Rouge), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MHNG (Muséum d'Histoire Naturelle de Genève, Geneva), MNCN (Museo Nacional de Ciencias Naturales, Madrid), MNHN (Muséum National d'Histoire Naturelle, Paris), MNHNP (Museo Nacional de Historia Natural del Paraguay, Asunción), MNK (Museo de Historia Natural Noel Kempff Mercado, Santa Cruz), MNRJ (Museu Nacional, Rio de Janeiro), MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque), MUSM (Museo de Historia Natural, Universidad Nacional Mayor

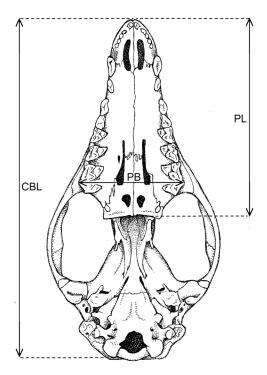
de San Marcos, Lima), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), MZUSP (Museu de Zoologia da Universidade do São Paulo, São Paulo), NMW (Naturhistorisches Museum Wien, Vienna), OMNH (Sam Noble Oklahoma Museum of Natural History, Norman), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito), RMNH (Naturalis Biodiversity Center, Leiden), ROM (Royal Ontario Museum, Toronto), TTU (Museum of Texas Tech University, Lubbock), UF (Florida Museum of Natural History, University of Florida, Gainesville), UMSPH (Université de Montpellier Service du Patrimoine Historique, Montpellier), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), USNM (National Museum of Natural History, Washington), and ZMB (Museum für Naturkunde, Berlin).

MEASUREMENTS: For specimens measured in the field according to the American protocol (Hall, 1962), we transcribed total length (nose to fleshy tail tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field catalogs, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight as recorded in the field, but we sometimes remeasured HF on dried skins and fluid-preserved specimens to check the accuracy of the collector's values, and we used our values whenever large discrepancies were found. (In a few instances we omitted problematic collectors' measurements when computing sample means and reporting observed ranges.) All external measurements are reported here to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers as skulls were viewed under low $(6-12\times)$ magnification. Measurement values were recorded to the nearest 0.01 mm, but those reported here are rounded to the nearest 0.1 mm. The following dimensions were measured (fig. 6):



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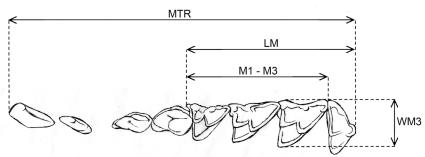


FIG. 6. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of an opossum (*Philander*), illustrating the anatomical limits of craniodental measurements defined in the text.

Condylobasal length (CBL): measured from the occipital condyles to the anteriormost point of the premaxillae.

Nasal length (NL): the greatest anteroposterior dimension of either bone.

Nasal breadth (NB): measured between the triple-point sutures of the nasal, frontal, and maxillary bones on each side.

Least interorbital breadth (LIB): measured at the narrowest point across the frontals between the

orbits (anterior to the postorbital processes, if present). This measurement cannot be taken on specimens lacking postorbital processes if there is no distinct interorbital constriction.

Least postorbital breadth (LPB): measured at the narrowest point across the frontals between the temporal fossae (posterior to the postorbital processes, if present).

Zygomatic breadth (ZB): measured at the widest point across both zygomatic arches.

Palatal length (PL): measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present).

Palatal breadth (PB): measured across the labial margins of the M4 crowns, at or near the "stylar A" position.

Maxillary toothrow length (MTR): measured from the anterior margin of C1 to the posterior margin of M4.

Length of upper molar series (LM): crown length, measured from the anteriormost labial margin of M1 to the posteriormost point on M4

Length of M1–M3 (M1–M3): measured from the anteriormost labial margin of M1 to the posteriormost point on M3.

Width of M3 (WM3): measured from the labial margin of the crown at or near the "stylar A" position to the lingual apex of the protocone.

Morphological Terminology: Most of the terms for external morphology in this report follow Voss and Jansa (2003, 2009). An important exception (not defined in those references) are descriptors of ventral fur coloration. Following Tate (1933), we refer to hairs that are the same color from root to tip as "self-colored"; fur that is composed of such hairs is then referred to as self-whitish, self-yellowish, etc. By contrast, "gray-based" fur is composed of hairs that have gray bases and paler (e.g., whitish or yellowish) tips. Both kinds of fur (self-colored and gray-based) can occur together, and their distribution in the ventral pelage is an important taxonomic criterion for species identification in several genera.

AGE CRITERIA: Age determination is crucial for many aspects of didelphid taxonomy. Unless otherwise noted below, we recorded measurements and scored qualitative morphological data from adult specimens only. Following Voss et al. (2001), a specimen was judged to be juvenile if dP3 is still in place, subadult if dP3 has been shed but P3 and/or M4 is still incompletely erupted, and adult if the permanent upper dentition is complete. Because didelphid

deciduous premolars are molariform, juveniles have only two premolariform teeth (P1 and P2) between the upper canine and the first molariform tooth (dP3), whereas adults have three fully erupted premolariform teeth (P1, P2, and P3) between the upper canine and the first molariform tooth (M1). Note that "juvenile," "subadult," and "adult" as used herein are descriptors of skeletal rather than reproductive maturity (many didelphids are reproductively active before the permanent dentition has completely erupted; Díaz and Flores, 2008).

Molecular Data: We analyzed DNA sequence data to supplement our morphologybased taxonomic accounts for Caluromys and Metachirus. DNA was extracted from ethanolpreserved tissues or from fragments of dried skin obtained from museum specimens (listed in appendices 3 and 4, respectively) using methods described by Voss and Jansa (2009) and Giarla et al. (2010). To minimize risk of contamination, all extractions from dried tissues were performed in an isolated laboratory where mammalian polymerase chain reaction (PCR) products were not present. We PCR-amplified the mitochondrial gene encoding cytochrome b (CYTB) using the primers listed in appendix 5 and the methods described by Gutiérrez et al. (2010). For most samples, the gene was amplified using primer DidMVZ05 paired with Did1260R. In some cases, shorter, overlapping fragments were generated with the internal forward primers Cal610F or Met690F paired with Did1260R and Did-MVZ05 paired with Phil730R or Cal750R. The resulting PCR products were Sanger-sequenced using amplification primers on an ABI 3730xl automated sequencer. All the new CYTB sequences generated for this report (including those from ingroup and outgroup taxa; see below) have been deposited in GenBank with accession numbers MK817273-MK817330.

The best-fitting nucleotide substitution model for these data was determined under the corrected Akaike Information Criterion (AICc) in jModelTest (Posada, 2008). We conducted maximum-likelihood analyses of the aligned sequence

matrices using the GTRGAMMA model implemented in RAxML ver. 8.2.10 (Stamatakis, 2014), with 1000 replicates of rapid bootstrapping to evaluate nodal support. All phylogenetic analyses were implemented in the CIPRES Science Gateway (Miller et al., 2010). We estimated uncorrected genetic distances within and among species and haplogroups using MEGA7 (Kumar et al., 2016).

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SYSTEMATIC ACCOUNTS

The following accounts summarize taxonomic and ethnographic information about the marsupial taxa collected or observed in the Yavarí-Ucayali interfluve. To organize such information we use several indented headings.

Under the heading Voucher Material (for species), we list all the museum specimens that we personally examined from each locality in our region. Under Other Interfluvial Records we list unvouchered published records of the species, or published records based on specimens that we did not personally examine; in some cases, such records employ different names than those used in this report (e.g., Marmosa murina for M. macrotarsus), but the implied synonymies are explained in the text that follows. Under Identification we explain the taxonomic criteria we used, or the published revisions we consulted, to assign a Latin binomial to the species in question; sometimes this is straightforward, but entries under this heading can be extensive when current usage is problematic. Under Remarks we provide a summary of the ecological circumstances in which specimens of each species were collected or observed in our region (if known) and comment on other relevant topics. When we examined specimens from outside the Yavarí-Ucayali interfluve to confirm our identifications, to determine the geographic range of a local species, or to provide a larger morphometric sample, we list this material under Other Specimens Examined. Examined specimens of additional species are listed separately.

Ethnographic information is summarized under two headings that sometimes appear in

species accounts (as in Voss and Fleck, 2011, 2017) but more often, in this report, under higher-taxonomic headings. (Morphologically similar marsupial species are not lexically distinguished by the Matses, whose opossum names typically refer to several zoological taxa.) Under the heading Ethnobiology we describe Matses names associated with the taxa in question, explain their cultural significance (if any), and describe any relevant folk beliefs. Under Matses Natural History we summarize allegedly factual information about each species obtained from the interview methods described above; although translated and edited by us, the text provided under this heading is, as nearly as possible, in the Matses' own words.

Family Didelphidae

All the marsupials that occur in Amazonia are members of the order Didelphimorphia, which contains this single family of living species, commonly known as opossums. The marsupial fauna of the Yavarí-Ucayali interfluve includes members of all four extant didelphid subfamilies: one species each of Caluromyinae, Glironiinae, and Hyladelphinae, plus 16 species of Didelphinae. At least one additional caluromyine species and another three didelphine species are known from localities north and south of our region and might also be expected to occur there as well (appendix 2). The following accounts follow the classification of Voss and Jansa (2009), who provided a key and morphological diagnoses for the genera, tribes, and subfamilies of Recent opossums. Emmons' (1997) field guide contains illustrations and descriptions of external characters for all the genera and some of the species mentioned below, but recent revisionary work (e.g., Rossi et al., 2010; Díaz-Nieto and Voss, 2016; Voss et al., 2018) has resulted in numerous changes to Emmons' species-level taxonomy.

ETHNOBIOLOGY: The Matses classify opossums into three categories: (1) <u>cheka</u>, which includes everything except short-tailed opossums and the common opossum; (2) <u>yama</u>, which includes sev-

eral local species of short-tailed opossums (Monodephis spp.); and (3) mapiokos, the common opossum (Didelphis marsupialis). Only the first category is divided into named subtypes: abuk cheka, the "woolly opossum" (Caluromys lanatus); cheka bëbëdi, "four-eyed opossums" (Metachirus and Philander spp.); and chekampi, "mouse opossums" (including all local species of small, long-tailed, black-masked didelphines plus Hyladelphys kalinowskii).

Subfamily Caluromyinae

Only a single species of caluromyine, the woolly opossum (*Caluromys lanatus*), is known from the Yavarí-Ucayali interfluve, but a second species (the black-shouldered opossum, *Caluromysiops irrupta*) could reasonably be expected to occur in our region (appendix 2).

Caluromys lanatus (Olfers, 1818)

VOUCHER MATERIAL (TOTAL = 6): Jenaro Herrera (AMNH 276706), Nuevo San Juan (AMNH 273038, 273059; MUSM 11024, 15290, 15291).

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (Fleck and Harder, 1995), San Pedro (Valqui, 1999).

IDENTIFICATION: Caluromys lanatus has never been revised, and several subspecies are currently recognized as valid (Gardner, 2008). To assess the taxonomic significance of the current trinomial classification, we analyzed sequence data from the mitochondrial gene encoding cytochrome *b*, and we examined specimens from throughout western Amazonia, where no fewer than three subspecies—C. l. nattereri (Matschie, 1917), C. l. ochropus (Wagner, 1842), and C. l. ornatus (Tschudi, 1845)—are said to occur. Unfortunately, representative sequence data are currently unavailable from the nominotypical subspecies (in Paraguay), C. l. cicur (Bangs, 1898; in transAndean Colombia), and C. l. vitalinus (Miranda-Ribeiro, 1936; in southeastern Brazil), so the materials at hand are insufficient for a comprehensive revision of the species.

The results of our molecular analysis (figs. 7, 8; table 1; appendix 3) provide robust support for the reciprocal monophyly of all three currently recognized species of *Caluromys*, but only weak support for monophyly of the subgenus *Mallodelphys* (= *C. derbianus* + *C. lanatus*). Remarkably, we recovered only shallow phylogeographic structure in *C. derbianus* and none at all in *C. lanatus*, both of which exhibit negligible sequence variation among samples collected at widely scattered localities. By contrast, our samples of *C. philander* reveal noteworthy genetic heterogeneity in that species, which clearly merits revisionary attention.²

The absence of phylogeographic structure among genetic samples of Caluromys lanatus from widely scattered populations in western Amazonia and central Brazil suggests that the subspecies currently recognized from these regions are based on nothing more than coatcolor variants. In fact, western Amazonian specimens of C. lanatus exhibit considerable variation in pelage coloration. Whereas some individuals are almost uniformly reddish brown dorsally (e.g., MVZ 157611), others have distinctly grayish fore- and hind limbs (e.g., MVZ 190249, USNM 546177), and others are almost uniformly brownish (e.g., MUSM 15291). The base of the tail is reddish in some specimens, but grayish in others. A patch of grayish hair between the shoulders (said to be diagnostic of C. derbianus; Cáceres and Carmignotto, 2006) is present in several specimens among those we examined (e.g., MVZ 157608, 190249, 190250). Most specimens have uniformly gray-based fur on the throat, chest, and upper abdomen as well as on the ventral surfaces of the forelimbs, but others have irregular patches of self-cream fur on the throat and in the forelimb axillae; the lower abdomen and groin are seemingly always

² Our geographic samples of *Caluromys philander* are far too few to support taxonomic conclusions, but it should be pointed out that the haplogroups we recovered are impossible to reconcile with the current trinomial nomenclature for this species, nor do they correspond to the taxa recognized by López-Fuster et al. (2008), who suggested, inter alia, that the Trinidadian form (*trinitatis* Thomas, 1894) is a distinct species.



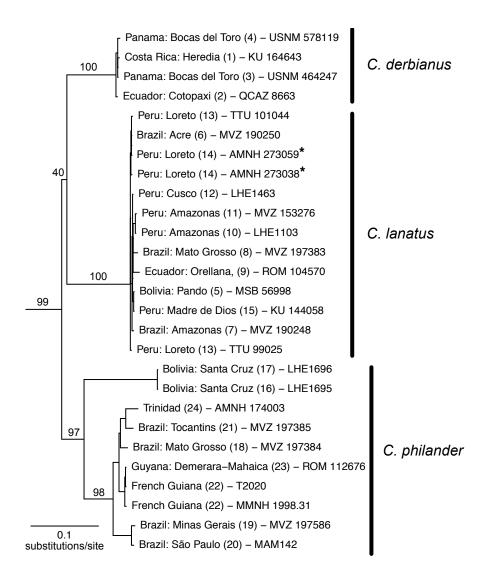


FIG. 7. Results of maximum-likelihood analysis ($\ln L = -5514.25$) of cytochrome b sequences of *Caluromys* (outgroups used for rooting are not shown). Branch tips are sequenced specimens labeled by geographic origin and a sequence identifier (see appendix 3); numbers in parentheses refer to localities mapped in figure 8. Branch support values above selected branches are bootstrap frequencies. Asterisks mark specimens from the Yavarí-Ucayali interfluve.

self-cream, but parous females have orangestained fur surrounding the pouch. Although some of this pelage variation might be geographic, there are substantial differences in coloration among sympatrically collected skins, and intermediates exist among most coat-color phenotypes. Cranial size and shape differences among the specimens we examined do not suggest anything more than individual and ontogenetic variation. In effect, we concur with Fonseca and Astúa's (2015) suggestion that only a single phenotypically distinguishable taxon, which they called *C. lanatus ochropus*, occurs in the Amazon and Cerrado.

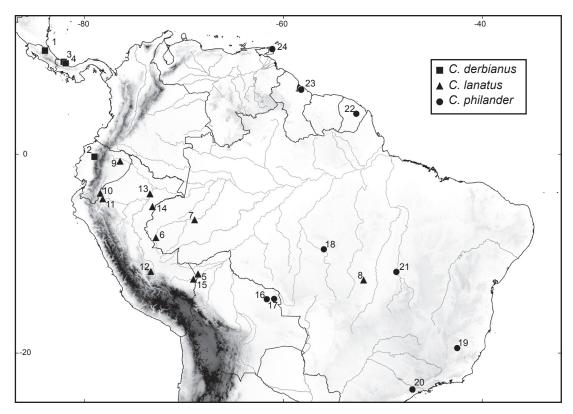


FIG. 8. Collecting localities of sequenced specimens of *Caluromys*. Numbers are keyed to gazetteer entries in appendix 3.

The holotype of Caluromys lanatus, a juvenile specimen from Paraguay collected in the late 18th century, was originally preserved in alcohol; its pelage is discolored, and few useful measurements can be obtained from the incompletely erupted dentition (Voss et al., 2009a). However, recently collected Paraguayan adults (AMNH 66780, UMMZ 134007) have very pale, almost entirely grayish fur that lacks the rich reddish-brown pigments seen in most western Amazonian specimens; additionally, the naked caudal skin (distal to the furry basal portion) is completely unpigmented, whereas most western Amazonian specihave dark-spotted tails. Metrical comparisons (table 2) indicate that these Paraguayan specimens are smaller than western Amazonian material in several dimensions (e.g., condylobasal length), but both of them are young adults, and measurements of age-invariant structures (e.g., LM, WM3) are within the observed range of western Amazonian variation. With just two Paraguayan examples at hand, and in the absence of any relevant molecular data, it is hard to assess the taxonomic significance of such comparisons, or to properly evaluate Fonseca and Astúa's (2015) suggestion that *C. l. ochropus* is really distinct from the nominotypical form.

ETHNOBIOLOGY: The Matses name for the woolly opossum is <u>abuk cheka</u>, which literally means "up opossum," in reference to its arboreal habits. The Matses do not eat or use the woolly opossum for any purpose, nor do they seem to have any particular beliefs about it.

Matses Natural History: The woolly opossum is reddish. It has a stripe going down its rostrum. Its tail is partly bare. Its ears are large.

The woolly opossum is arboreal, but it sometimes descends to the ground to forage. It

descends by climbing down a vine. It is found in all rainforest habitat types. It makes its nest in tree cavities that it lines with leaves. It also makes nests in the branches of dicot trees, or in leaf litter that collects in palm crowns.

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The woolly opossum is nocturnal. After foraging for dicot tree fruits and insects during the night, it returns to its nest at dawn. It climbs quickly on vines.

The woolly opossum is solitary. It gives birth to many young that it keeps in its pouch. The young suck milk inside the pouch. When the young get big, they leave their mother, one by one.

Margays and snakes prey on the western woolly opossum.

When the wooly opossum sees people, it opens its mouth and hisses, wanting to bite them.

The woolly opossum eats crickets/katydids (the Matses do not distinguish lexically between crickets and katydids), cockroaches that live up in trees, armored millipedes (*Barydesmus*) that are on the ground, dicot tree fruits including those of the bata (*Pseudolmedia* spp. and/or ?*Maquira* spp.; Fam. Moraceae), kuëte bata trees (?*Pseudolmedia*; Fam. Moraceae), kuëte mëdiad (unidentified tree with starchy fruits that the Matses cook before eating), and vine fruits. It also eats the mesocarp of ripe isan palms (*Oenocarpus bataua*) that have not fallen to the ground yet.

Remarks: Four of our six vouchers were shot from trees at night by Matses hunters, three in secondary forest (abandoned swiddens) and one in hilltop primary forest; heights were not recorded, but the specimen shot in primary forest was said to be "very high up in a big tree" (English translation from Matses field notes). One specimen was captured by hand in the late afternoon by several boys, who shook it from the crown of a small guaba tree (Fabaceae: *Inga edulis*) on the outskirts of the village. The specimen from Jenaro Herrera was trapped on a liana 18 m above the ground in disturbed primary forest.

OTHER SPECIMENS EXAMINED (TOTAL = 29): **Bolivia**—*Pando*, Isla Gargantua (MSB 56998). **Brazil**—*Acre*, Nova Vida on right bank Rio Juruá (MVZ 190250, 190251), opposite Igarapé

TABLE 1
Percent Uncorrected Pairwise Sequence Divergence within and among Species of Caluromys^a

	derbianus	lanatus	philander
derbianus	0.6		
lanatus	11.7	0.9	
philander	11.5	11.9	6.0

 $^{\mathrm{a}}$ At the cytochrome b locus; diagonal elements (in boldface) are mean uncorrected within-group distances.

Porongaba on left bank Rio Juruá (MVZ 190249), Sena Madureira (USNM 546177); Amazonas, opposite Altamira on left bank Rio Juruá (MVZ 190248), Rosarinho (AMNH 92760), Sacado on right bank Rio Juruá (MVZ 190247). Ecuador— Napo, San Jose Abajo (AMNH 68282); Orellana, Parque Nacional Yasuní (ROM 104570). Paraguay—Caazapá, Caazapá (MNCN-M2630 [holotype]; Canendiyu, 13.3 km N Curuguaty (UMMZ 134007); Guairá, Villarrica (AMNH 66780). Peru—Amazonas, La Poza on Río Santiago (MVZ 157608, 157611, 157612); Huánuco, Tingo Maria (MVZ 140041); Loreto, Boca Río Curaray (AMNH 71979, 71983, 71984), Estación Biológica Allpahuayo (TTU 99025, 101044); Madre de Dios, Reserva Cusco Amazónico (KU 144058, MVZ 168852); Pasco, Nevati Mission (AMNH 230001), San Juan (USNM 364160); Ucayali, Boca Río Urubamba (AMNH 75911), Lagarto (AMNH 78951). Venezuela-Amazonas, Esmeralda (AMNH 76970).

Subfamily Glironiinae

The only species of this subfamily that is currently recognized as valid, *Glironia venusta*, is known to occur in our region from a single specimen.

Glironia venusta Thomas, 1912

Voucher Material (total = 1): Quebrada Vainilla (LSUMZ 28421).

OTHER INTERFLUVIAL RECORDS: None.

TABLE 2	
Measurements (mm) and Weights (g) of Caluromys lanatus from Paraguay and Western Amazor	nia

		Males	I	Gemales
	Paraguay (AMNH 66780)	Western Amazonia ^a	Paraguay (UMMZ 134007)	Western Amazonia ^b
HBL	_	271 ± 25 (225–300) 8	265	289 ± 12 (270-303) 7
LT	_	420 ± 21 (380–446) 8	386	433 ± 14 (410-451) 7
HF	_	45 ± 3 (40–49) 9	46	47 ± 3 (43–51) 7
Ear	_	34 ± 2 (30–38) 9	40	35 ± 1 (34–36) 6
CBL	52.2	$59.5 \pm 2.0 \ (54.8 - 62.1) \ 11$	54.0	59.6 ± 1.8 (56.4–62.5) 11
NL	23.1	$25.4 \pm 1.0 \ (23.3 - 26.6) \ 10$	23.2	$25.3 \pm 1.1 \ (22.8-26.5) \ 11$
NB	8.0	$8.7 \pm 0.8 \ (7.2 - 10.1) \ 11$	8.7	$8.8 \pm 0.6 \ (8.0 - 9.7) \ 11$
LIB	10.0	$10.9 \pm 0.8 \ (9.8 - 13.0) \ 11$	10.0	$10.7 \pm 0.5 \ (9.9 - 11.6) \ 11$
LPB	9.3	$8.7 \pm 0.9 \ (7.6 - 10.4) \ 11$	8.6	$8.4 \pm 0.4 \ (7.5 - 9.3) \ 11$
ZB	31.7	$35.4 \pm 1.8 \ (31.5 - 37.9) \ 10$	32.2	34.4 ± 1.2 (32.9–36.7) 10
PL	27.8	$31.8 \pm 1.0 \ (29.6 - 33.2) \ 11$	28.5	$31.8 \pm 1.0 \ (30.2 - 33.2) \ 11$
PB	16.0	$17.4 \pm 0.7 \ (16.5 - 18.8) \ 11$	16.1	$17.2 \pm 0.4 \ (16.6 - 17.7) \ 9$
MTR	20.0	$21.7 \pm 0.5 \ (20.8 – 22.4) \ 11$	19.6	$21.4 \pm 0.6 \ (20.4 - 22.1) \ 11$
LM	10.0	$10.3 \pm 0.2 \ (10.0 - 10.7) \ 11$	9.9	$10.2 \pm 0.3 \ (9.5 - 10.8) \ 11$
M1-3	8.3	$8.5 \pm 0.2 \ (8.2 - 8.9) \ 11$	8.1	$8.4 \pm 0.3 \ (7.9 - 8.9) \ 11$
WM3	2.9	$3.0 \pm 0.1 \ (2.8 – 3.1) \ 11$	2.8	$2.9 \pm 0.2 \ (2.6 - 3.1) \ 11$
Weight		403 ± 81 (243–500) 8	320	396 ± 32 (349–430) 5

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (asterisks identify Yavarí-Ucayali vouchers): AMNH 71983, 75911, 23001, 273038*, 273059*; MUSM 11024*; MVZ 140041, 157611, 157612, 190249; USNM 546177).

IDENTIFICATION: As currently understood, Glironia venusta ranges across much of Amazonia but remains known from only a few specimens (Barkley, 2008; Ardente et al., 2013). Among the handful that we were able to examine for this report were the holotypes of two nominal species—aequatorialis Anthony, 1926, and criniger Anthony, 1926—that have long been regarded as junior synonyms of venusta. Whereas the type localities of aequatorialis (Boca Río Lagartococha, on the Peruvian-Ecuadorian frontier) and criniger (Boca Río Curaray, in Loreto department) are both north of the Amazon,³ the type locality of venusta (Pozuzo, in Pasco depart-

ment) is south of the Amazon. In addition to these and our single specimen from Quebrada Vanilla, we examined a fourth specimen, from eastern Ecuador.

Although Barkley (2008) said that LSUMZ 28421 was an adult, it is really a subadult with a still incompletely erupted P3 on each side. The immaturity of this specimen plausibly explains why it is smaller than the others we measured (table 3) in several cranial dimensions subject to postweaning growth (e.g., CBL, ZB, PB), but not in age-invariant molar dimensions (LM, M1–3, WM3). We did not note any conspicuous craniodental differences among these specimens, but the tip of the tail is abruptly white for about 2 cm in LSUMZ 28421, a marking that is also present

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 68282, 71979, 71984, 78951, 92760; MVZ 157608, 168852, 190247, 190250, 190251; USNM 364160.

 $^{^{\}rm 3}$ See Wiley (2010) for information about these historically important localities.

Measurements (mm) and Weights (g) of Glironia venusta AMNH 71395d LSUMZ 28421a BMNH 12.1.15.7b AMNH 713949 FMNH 41440 Age subadult adult adult adult adult female female female Sex male male "160" **HBL** 180 185 "195" LT 190 210 HF "2.7" 2.7 31e 309 2.8 23 "25" Ear 22 "43.5" CBL. 42.0 43.4 NL 19.1 "19.8" 18.8 19.8 20.5 "6.4" NB 7.6 7.1 6.9 6.8 LIB 7.0 "7.1" 7.2 7.4 7.4 LPB 8.6 9.7 9.6 8.9 ZΒ 23.2 25.6 26.4 PL "23.5" 26.6 24.7 25.4 26.0 PB 11.5 12.0 12.4 11.9 MTR 17.5 17.8 18.4 18.5

TABLE 3

Measurements (mm) and Weights (g) of Glironia venusta

8.8

7.2

2.5

98

"7.0"

8.3

6.7

2.5

LM

M1 - 3

WM3

Weight

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on BMNH 12.1.15.7 (Thomas, 1912b), but not in any of the specimens we examined from the left ("north") bank of the Amazon, which all have grayish or brownish tail tips.

Preliminary genetic data suggest that distinct haplotypes of *Glironia venusta* occupy opposite banks of the Amazon. Patton et al. (1996) obtained 1140 bp of cytochrome *b* from a single specimen (INPA 2570) collected on the upper Rio Urucu, a right-bank tributary of the upper Amazon (Solimões) in western Brazil. This sequence differs by about 6% (uncorrected) from two large fragments (both >500 bp) that we obtained from the left-bank holotypes of *criniger* (AMNH 71394)

and aequatorialis (AMNH 71395); by contrast, the latter two sequences differ from one another by just a single base-pair substitution (an uncorrected distance of just 0.2%). Although it might make some sense in the light of these results to recognize two subspecies, *G. v. criniger* (including aequatorialis) on the north bank and *G. v. venusta* on the south bank, we are reluctant to formalize any taxonomic conclusions on such an inadequate basis. Nevertheless, the trivial genetic distance between the two left-bank specimens does tend to support the conclusions of previous taxonomists that the allegedly diagnostic morphological differences between *criniger* and *aequatorialis* reported

8.8

7.1

2.6

8.8

7.3

2.6

^a From Quebrada Vainilla (in the Yavarí-Ucayali interfluve).

^b Holotype of *venusta*; measured by Thomas (1912b). Measurements are in quotes because external dimensions were measured according to the British protocol (Lankester, 1904), and craniodental measurements may have been affected by preservational artifacts (Thomas, 1912b).

^c Holotype of criniger.

d Holotype of aequatorialis.

e Estimated values.

by Anthony (1926) are nothing more than intraspecific variation.

ETHNOBIOLOGY: The Matses have no definite knowledge of this species, and therefore do not have a name for it or any particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no knowledge of the appearance or behavior of this species.

REMARKS: According to Barkley (2008), LSU 28421 was captured at night in a mist net set for bats in primary forest. Local habitats at the capture site, which is not subject to seasonal inundation, were described by Robbins et al. (1991).

OTHER SPECIMENS EXAMINED (TOTAL = 3): Ecuador—Pastaza, Montalvo (FMNH 41440). Peru—Loreto, Boca Río Curaray (AMNH 71394). Peru (Loreto) or Ecuador (Orellana)—Boca Río Lagartococha (AMNH 71395).

Subfamily Hyladelphinae

The only currently recognized species in the subfamily Hyladelphinae is known from our region on the basis of just two specimens from a single locality.

Hyladelphys kalinowskii (Hershkovitz, 1992)

Figures 9A, 10A

Voucher Material (total = 2): Nuevo San Juan (AMNH 276725; MUSM 11031).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: This tiny marsupial, long unknown to science and only recently recognized as the sole survivor of an ancient lineage, is still represented by fewer than two dozen museum specimens despite its wide Amazonian distribution and apparent lack of habitat specificity (Hershkovitz, 1992; Voss et al., 2001; Jansa and Voss, 2005; Astúa, 2006; Hice and Velazco, 2012; Catzeflis, 2018). Our two specimens consist of the damaged skull of a juvenile that retains the diagnostically reduced milk dentition (Voss et al., 2001: figs. 17, 18), and the fluid-preserved carcass and extracted skull of an adult female.

Díaz (2014) erroneously reported that the latter specimen (AMNH 276725) was collected at Jenaro Herrera.

Hyladelphys kalinowskii is one of three superficially similar species in our region, all of which are very small (<30 g) opossums with long tails, black masks, and reddish-brown dorsal fur. Despite these resemblances, they are only distantly related to one another, and specimens in hand are easily identified by numerous integumental and craniodental differences (figs. 9, 10; table 4). Traits unique to H. kalinowskii among this trio of tiny didelphids include the posterior extent of its blackish facial markings, possession of just four mammae, an indistinctly banded tail (due to paler skin over the vertebral articulations), lack of a premaxillary rostral process, absence of a posterior accessory cusp on C1, a third upper premolar (P3) that is conspicuously smaller than P2, and an exceptionally short upper molar row (LM ≤4.6 mm). Hyladelphys kalinowskii additionally differs from Marmosa lepida by its exclusively self-white ventral fur and lack of postorbital processes. Hyladelphys kalinowskii additionally differs from Gracilinanus emiliae by having a much shorter tail, and by lacking a gular gland, palatine fenestrae, and secondary foramina ovales.

Both of our specimens conform in all qualitative traits to the emended description of Hyladelphys kalinowskii provided by Jansa and Voss (2005). Measurements of our adult female specimen are a bit smaller than those of the adult female holotype from Cuzco department and the adult female paratype from Junin (table 5), but without any adequate population sample to assess individual (nongeographic) variation in this species, such differences are hard to interpret. Although Jansa and Voss (2005) discussed the possibility that multiple species of Hyladelphys might be represented among the specimens currently referred to H. kalinowskii, ours are so similar to Hershkovitz's (1992) original material that this identification would seem to be beyond dispute.

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FIG. 9. Dorsal and ventral cranial views of three small opossums. **A,** *Hyladelphys kalinowskii* (AMNH 267338, an adult male from French Guiana); **B,** *Marmosa lepida* (AMNH 273186, an adult male from the Yavarí-Ucayali interfluve); **C,** *Gracilinanus emiliae* (MUSM 15292, an adult female from the Yavarí-Ucayali interfluve). Abbreviations: **amp,** anteromedial process of the alisphenoid bulla (enclosing a secondary foramen ovale); **pal,** palatine fenestra; **pop,** postorbital process (of frontal); **rp,** rostral process (of premaxilla).

10 mm

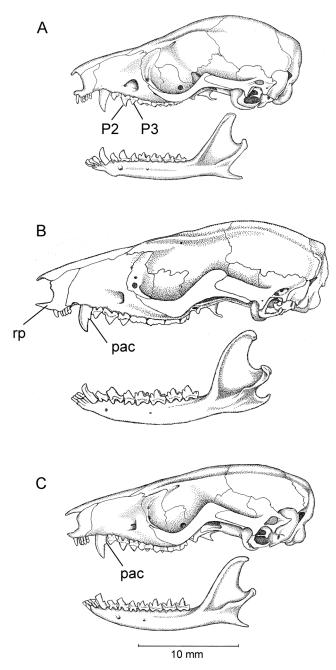


FIG. 10. Lateral cranial views of three small opossums (same specimens as in fig. 9). **A,** *Hyladelphys kalinowskii*; **B,** *Marmosa lepida*; **C,** *Gracilinanus emiliae*. Abbreviations: **P2,** second upper premolar; **P3,** third upper premolar; **pac,** posterior accessory cusp (of upper canine); **rp,** rostral process (of premaxilla).

Diagnostic Morphological Halls of Three Species of Small Opossums from the Tavari-Ocayan Internuve					
	Hyladelphys kalinowskii	Marmosa lepida	Gracilinanus emiliae		
Ventral pelage	completely self-white	gray-based laterally	completely self-white		
Black eye mask	extends to ear	extends just behind eye	extends just behind eye		
Gular gland	absent	absent	present		
Mammary formula	2-0-2=4	3-1-3=7	3-1-3 = 7 or 4-1-4 = 9		
Tail coloration	indistinctly banded	uniformly dark	uniformly dark		
Tail ratio (TL/HBL \times 100)	121%-147%	143%-168%	164%-196%		
Postorbital processes of frontals	absent	present, large	absent		
Rostral process of premaxillae	absent	present, very long	present		
Palatine fenestrae	absent	absent	present		
Secondary foramen ovale	absent	usually absent ^a	present		
C1 posterior accessory cusp	absent	present	present		
Heights of P2, P3	P2 > P3	P2 ≈ P3	P2 ≈ P3		
Length upper molars (LM) ^b	4.2-4.6 mm	5.6-6.1 mm	4.8-5.1 mm		

 ${\it TABLE~4}$ Diagnostic Morphological Traits of Three Species of Small Opossums from the Yavarı́-Ucavali Interfluve

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums, all of which are known indiscriminately as chek-ampi (see the account for *Marmosa*, below). Therefore, they have no particular beliefs about it, nor is it of any cultural importance.

Matses Natural History: The Matses have no definite knowledge of this species.

REMARKS: Our juvenile specimen was captured during the day by a Matses boy when it ran out of some leaf litter.⁴ Another was captured by a Matses hunter in unknown circumstances.

OTHER SPECIMENS EXAMINED (TOTAL = 5): French Guiana—Paracou (AMNH 267003, 267338, 267339). Peru—Cuzco, Hacienda

Cadena (FMNH 89991 [holotype]; *Junín*, Chanchamayo (FMNH 65754).

Subfamily Didelphinae

Species of the subfamily Didelphinae that occur in the Yavarí-Ucavali interfluve are classified into four tribes. The tribe Marmosini is locally represented by four species of mouse opossums (Marmosa) and three species of short-tailed opossums (Monodelphis); the tribe Didelphini is represented by the water opossum (Chironectes minimus), the so-called common opossum (Didelphis marsupialis), and two species of gray four-eyed opossums (Philander); the tribe Metachirini is represented by the brown four-eyed opossum (Metachirus myosuros); and the tribe Thylamyini is represented by one species of gracile mouse opossum (Gracilinanus emiliae) and three species of slender mouse opossums (Marmosops). Geographic range data suggest that three additional species known from specimens collected

^a Present unilaterally in AMNH 273186.

^b Tabulated ranges are based on measurements of inventory vouchers and extralimital material (e.g., specimens measured by Voss et al., 2001).

⁴ Although the original phrasing of the Matses conversation that elicited this information was not recorded, the usual term for leaf litter is <u>shapu</u>, which can either refer to a thick layer of dead leaves on the ground or to an accumulation of dead leaves in the crown of a stemless palm (typically 1–2 m above the ground). Unfortunately, this ambiguity cannot now be resolved, but the latter interpretation would be more consistent with what is currently known about the nesting habits of *Hyladelphys* (Catzeflis, 2018).

TABLE 5

Measurements (mm) of *Hyladelphys kalinowskii* from Eastern Peru^a

	FMNH 89991 ^b	FMNH 65754 ^c	AMNH 276725 ^d
Sex	female	female	female
HBL	89	91	_
LT	117	110	_
HF	16	15	15e
Ear	18	15	16e
CBL	23.6	23.7	21.6
NL	9.9	9.7	9.3
NB	3.5	3.5	3.0
LIB	3.8	3.9	3.6
ZB	15.0	_	13.8
PL	12.6	_	11.6
PB	7.3	7.4	6.7
MTR	8.7	8.9	8.2
LM	4.6	4.6	4.4
M1-3	3.8	3.9	3.6
WM3	1.3	1.4	1.2

- ^a None accompanied by weight data.
- ^b Holotype.
- ^c Paratype.
- ^d Voucher from Nuevo San Juan.
- ^e Measured from fluid specimen.

north and south of our region might also occur locally (appendix 2).

Tribe Marmosini

Amazonian members of the tribe Marmosini include small but otherwise strikingly dissimilar taxa. Whereas species of *Marmosa* are longtailed, black-masked, and almost exclusively arboreal, species of *Monodelphis* are short-tailed, maskless, and strictly terrestrial. Field identification of *Monodelphis* is not problematic because these shrewlike opossums do not closely resemble any other Amazonian mammals (Emmons, 1997), but species of *Marmosa* bear a superficial

resemblance to members of several thylamyine genera, notably *Marmosops* and *Gracilinanus*, both of which include species that occur in our region. Voss et al. (2004) and Voss and Jansa (2009) provide descriptions and illustrations of external and craniodental characters that unambiguously distinguish *Marmosa* from *Marmosops* and *Gracilinanus*.

Marmosa Gray, 1821

Members of the genus *Marmosa* are among the most abundant species of nocturnal-arboreal insectivorous-frugivorous small mammals throughout lowland Amazonia. By contrast with previous classifications (e.g., in Gardner, 2005, 2008), the species referred to *Marmosa* are now allocated among five subgenera (Voss et al., 2014). In the Yavarí-Ucayali interfluve, the nominotypical subgenus is represented by *M. macrotarsus*, the subgenus *Micoureus* by *M. constantiae* and *M. rutteri*, and the subgenus *Stegomarmosa* by *M. lepida*. In addition to these four species, *M. (Eomarmosa) rubra* might also be expected to occur in our region (appendix 2).

The Matses do not lexically distinguish the various species of small, long-tailed, black-masked didelphids that occur in their tribal territory (*Hyladelphys kalinowskii*, *Marmosa* spp., *Gracilinanus emiliae*, *Marmosops* spp.), but this seems as good a place as any to summarize relevant ethnological information.

ETHNOBIOLOGY: The opossums that the Matses call <u>chekampi</u> ("little opossums") are superficially similar (small, black-masked, long-tailed, and pouchless), although some of our interviewees acknowledged that <u>chekampi</u> come in different sizes and in different shades of gray and brown. Some Matses use <u>mapiokosëmpi</u> (the name of the common opossum with a diminutive suffix) as an alternative name.

Mouse opossums come into Matses houses and eat their food. Sometimes they make nests in Matses houses, but they seldom stay long. The Matses say that mouse opossums usually enter their houses during heavy rains.

Matses Natural History: Mouse opossums have long tails and large ears. Some are gray, while others are reddish, and others are dark-colored. They are similar to four-eyed opossums, but much smaller.

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Mouse opossums are arboreal and terrestrial. They are abundant in the forest and sometimes come into Matses swiddens. They make nests of dry leaves in thick vegetation up in trees, in cavities in tree branches, or in leaf litter that accumulates in the crowns of palms. In Matses swiddens they make nests among plantain plants using dead plantain leaves. In houses they make nests in containers where clothes are kept.

Mouse opossums are strictly nocturnal. They give birth to many young. They always carry their young with them. Otherwise they are solitary.

Mouse opossums are eaten by margays and snakes. They make a high-pitched hiss when they are threatened.

Mouse opossums eat all sorts of things. They eat crickets/katydids; large cockroaches; and small birds, eggs, and hatchlings that they find at night in nests. They also eat dicot tree fruits, including those of the mannan tsipuis tree (*Inga* spp.; Mimosoideae) and the mesocarp of swamppalm (*Mauritia flexuosa*) fruits.

Marmosa (Marmosa) macrotarsus (Wagner, 1842)

Voucher Material (Total = 20): Nuevo San Juan (268214, 272816, 272870, 273062, 273063, 273140, 273178, 273188, 276726; MUSM 11028, 11029, 13283, 15293–15297, 23798), Orosa (AMNH 73855, 73856).

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (as *Marmosa murina*; Fleck and Harder, 1999), San Pedro (as *M. murina*; Valqui, 1999).

IDENTIFICATION: The species currently recognized as *Marmosa macrotarsus* and *M. waterhousei* (Tomes, 1860), both of which occur in eastern Peru, were long treated as subspecies or synonyms of *M. murina* (Linnaeus, 1758), but Rossi (2005) summarized evidence that these

three taxa are phenotypically distinct, and Gutiérrez et al. (2010) subsequently recovered them as reciprocally monophyletic mtDNA clades with average sequence divergence values of about 9% in all pairwise comparisons. According to Rossi's (2005) still incompletely published revision, the species belonging to this complex are allopatric. Whereas Marmosa murina occurs in eastern Amazonia and the Atlantic Forest, M. waterhousei is in northwestern Amazonia, and M. macrotarsus is in southwestern Amazonia. In eastern Peru, M. waterhousei is said to occur north of the Amazon-Marañón (in Amazonas and northern Loreto departments), whereas M. macrotarsus is distributed south of the river (e.g., in Cuzco, Huánuco, Junín, Madre de Dios, Pasco, Ucayali, and southern Loreto).5

To assess the diagnostic morphological traits attributed to Marmosa macrotarsus and M. waterhousei, we examined Peruvian specimens of the nominotypical subgenus from both sides of the Amazon. According to Rossi (2005) and Díaz (2015), M. macrotarsus can be distinguished from M. waterhousei by the absence of a gular gland (said to be present in M. waterhousei) and by the form of the base of the upper canine (said to be less curved than in M. waterhousei), but neither character seems to be taxonomically useful. None of the Peruvian specimens we examined from south of the Amazon (nominally M. macrotarsus) showed any trace of a gular gland, but of the seven adult males we examined from north of the Amazon (nominally M. waterhousei), only three showed any sign of glandular activity on the chest or throat. We observed considerable variability in canine curvature in specimens from both sides of the Amazon, and we were unable to consistently distinguish north-bank

⁵ According to Díaz (2014: 125), two Orosa specimens ("AMNH 73855, 73853") identified by Rossi (2005) as *Marmosa macrotarsus* were subsequently reidentified by Gutiérrez et al. (2010) as *M. waterhouesi*, but this statement is erroneous on two counts: (1) Rossi (2005) did not examine AMNH 73853 (a specimen of *Marmosops noctivagus*; see below), and (2) no Orosa material was examined or reidentified by Gutiérrez et al. (2010).

TABLE 6

Measurements (mm) and Weights (g) of Marmosa macrotarsus and M. waterhousei from Eastern Peru

	Ma	ales	Fen	nales
•	M. macrotarsus ^a M. waterhousei ^b		M. macrotarsus ^c	M. waterhousei ^d
HBL	123 ± 6 (112–129) 7	148 ± 7 (140–156) 4	117 ± 11 (102–131) 6	135 ± 8 (130-148) 5
LT	197 ± 10 (185–209) 7	214 ± 6 (211–223) 4	184 ± 14 (169–205) 6	203 ± 5 (196–208) 5
HF	22 ± 1 (20–24) 8	23 ± 1 (21–25) 6	21 ± 1 (20-21) 6	21 ± 2 (20–23) 3
Ear	25 ± 1 (24–27) 7	25 ± 1 (24–27) 6	24 ± 1 (23–25) 3	24 ± 1 (23–25) 4
CBL	$33.2 \pm 0.7 \ (32.2 - 34.3) \ 8$	37.4 ± 0.5 (36.6–37.9) 5	32.2 ± 1.5 (29.6-33.8) 6	34.5 ± 0.7 (33.8–35.2) 3
NL	$15.1 \pm 0.3 \ (14.7 - 15.6) \ 7$	16.6 ± 1.0 (15.0–17.6) 7	14.5 ± 1.0 (12.8–16.1) 8	$15.6 \pm 0.5 \ (14.9 - 15.9) \ 4$
NB	$4.7 \pm 0.2 \ (4.5 - 5.1) \ 8$	$5.1 \pm 0.2 \ (4.8 - 5.4) \ 7$	$4.5 \pm 0.4 \ (4.1 - 5.1) \ 9$	$4.5 \pm 0.2 \ (4.2 - 4.8) \ 5$
LIB	$5.8 \pm 0.1 \ (5.7 - 6.1) \ 8$	$6.6 \pm 0.1 \ (6.4 - 6.8) \ 7$	$5.6 \pm 0.4 \ (5.1 - 6.1) \ 8$	$6.0 \pm 0.3 \ (5.6 - 6.5) \ 5$
LPB	$6.5 \pm 0.2 \ (6.1 - 6.7) \ 8$	$6.2 \pm 0.2 (5.9 - 6.6) 7$	$6.5 \pm 0.5 \ (6.0 - 7.4) \ 7$	$6.4 \pm 0.4 \ (5.8 - 6.8) \ 5$
ZB	$19.0 \pm 0.7 \ (18.2 - 20.0) \ 8$	$20.6 \pm 0.7 \ (19.6 - 21.4) \ 7$	$18.5 \pm 0.7 \ (17.0 - 19.0) \ 7$	$19.7 \pm 0.6 \ (19.1 - 20.3) \ 5$
PL	$18.6 \pm 0.4 \ (17.9 - 19.3) \ 8$	$21.2 \pm 0.6 \ (20.3-21.7) \ 5$	$18.0 \pm 0.9 \ (16.8 - 19.2) \ 9$	$19.5 \pm 0.6 (19.0 - 20.1) 3$
PB	$10.4 \pm 0.3 \; (10.0 – 10.7) \; 8$	$11.1 \pm 0.2 \ (10.8 – 11.2) \ 7$	$10.2 \pm 0.2 \ (10.0 - 10.6) \ 9$	$10.9 \pm 0.2 (10.6 - 11.1) 5$
MTR	$13.0 \pm 0.2 \ (12.8 - 13.3) \ 8$	$14.3 \pm 0.2 \ (13.9 - 14.5) \ 7$	$12.7 \pm 0.2 \ (12.2 - 13.0) \ 9$	$13.7 \pm 0.3 \ (13.4 - 14.2) \ 5$
LM	$6.6 \pm 0.2 \ (6.4 - 6.9) \ 8$	$7.0 \pm 0.1 \ (6.8 - 7.2) \ 7$	$6.6 \pm 0.1 \ (6.5 - 6.8) \ 9$	$7.0 \pm 0.2 (6.7 - 7.1) 5$
M1-3	$5.6 \pm 0.1 \ (5.3-5.7) \ 8$	$5.9 \pm 0.1 \ (5.7 - 6.0) \ 7$	$5.6 \pm 0.2 \ (5.4 - 5.9) \ 9$	$5.9 \pm 0.1 (5.7 - 6.0) 5$
WM3	$2.1 \pm 0.1 \ (2.0 - 2.1) \ 8$	$2.2 \pm 0.1 \ (2.0 - 2.3) \ 7$	$2.1 \pm 0.1 \ (2.0 – 2.2) \ 9$	$2.3 \pm 0.0 \ (2.3 - 2.3) \ 4$
Weight	41 ± 4 (34–47) 7	61 ± 8 (50-71) 7	35 ± 5 (30-40) 3	45 ± 4 (40-50) 5

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (asterisks identify Yavarí-Ucayali vouchers): AMNH 268214*, 272816*, 273062*, 273063*, 273188*; MUSM 11029*, 15296*; MVZ 136370.

from south-bank material by this criterion. Instead, the only trenchant difference we observed between Peruvian specimens of *Marmosa* (*Marmosa*) from opposite banks of the Amazon is size: specimens from the north side of the river are substantially larger, on average, than specimens from the south bank (table 6), and although our samples are inadequate to show the full range of intraspecific morphometric variation that might be expected, the lack of overlap in same-sex comparisons for several dimensions (e.g., HBL, LT, CBL, LIB, PL, PB, and MTR for

males) seems noteworthy. Altogether, the morphometric evidence for genetically distinct populations on opposite banks of the upper Amazon seems reasonably compelling (Rossi, 2005), although additional phenotypic criteria for species recognition would be very welcome.

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the follwing series: LACM 96112; MVZ 154754; TTU 98717, 98934, 100922, 101153, 124790.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (asterisks identify Yavarí-Ucayali vouchers): AMNH 73856*, 254508, 273178*; FMNH 19352, 19357, 24754, 24755; MUSM 15293*; MVZ 136368.

^d The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: MVZ 153286, 157632; TTU 98654, 98716, 124796.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

2019

REMARKS: Of the 13 specimens from Nuevo San Juan for which we have habitat information, 12 were trapped, shot, or captured by hand in secondary vegetation; only one specimen is known to have been taken in primary forest. Three additional specimens trapped by children in unrecorded circumstances at Nuevo San Juan were probably also taken in secondary growth (children seldom enter primary forest except in the company of adults). Most specimens were trapped, shot, or caught by hand at night, but two were taken in the daytime by men weeding gardens or clearing trash piles, who presumably disturbed sleeping individuals in their daytime refugia. Most specimens were taken at or near ground level (on the ground or on fallen logs), but one was caught by hand at a height of 2 m above the ground in a small tree, and another was shot from a tree at an unrecorded height above the ground.

OTHER SPECIMENS EXAMINED (TOTAL = 8): **Peru**—*Huánuco*, Pozuzo (FMNH 24754, 24755); *Pasco*, Nevati (AMNH 254508); *San Martín*, Moyobamba (FMNH 19352, 19357); *Ucayali*, Balta (MVZ 136368–136370).

SPECIMENS OF *MARMOSA WATERHOUSEI* EXAMINED (TOTAL = 14): **Peru**—*Amazonas*, Huampami on Río Cenepa (MVZ 154754, 154761), Kayamas on Río Cenepa (MVZ 153286), La Poza on Río Santiago (MVZ 157632), 12 mi SSW Nazareth (MVZ 139955); *Loreto*, 25 km S Iquitos (LACM 96112; TTU 98654, 98716, 98717, 98934, 100922, 101153), 61.5 km S Iquitos (TTU 124790, 124796).

Marmosa (Micoureus) constantiae Thomas, 1904

Figure 11A

VOUCHER MATERIAL (TOTAL = 21): Nuevo San Juan (AMNH 268219, 268220, 272667, 272832, 273052, 273079, 273113, 273118; MUSM 11060, 11062, 11064, 13294–13296, 15317, 15310–15313), Jenaro Herrera (MUSM 23806), Santa Cecilia (FMNH 87117).

OTHER INTERFLUVIAL RECORDS: None that can be confidently associated with this species (see below).

IDENTIFICATION: Two species of the subgenus Micoureus ("woolly mouse opossums," formerly recognized as a distinct genus; Gardner and Creighton, 2008) are sympatric at Nuevo San Juan, and the same two species occur sympatrically at several other localities south of the Amazon in eastern Peru and western Brazil. Specimens of both species collected sympatrically in western Brazil were identified as Micoureus demerarae (Thomas, 1905) and Mic. regina (Thomas, 1898) by Patton et al. (2000), who, however, cautioned that different names might apply to their material. Among other possibilities, they (Patton et al., 2000: 72) suggested that "constantiae might best be considered a junior synonym of demerarae," but the former name has priority. Therefore, Marmosa constantiae is the binomen used in this report for the demeraraelike woolly mouse opossum of southwestern Amazonia.⁶ For reasons explained in the next account, we use the name Mar. rutteri Thomas, 1924, for the woolly mouse opossum that Patton et al. (2000) called Mic. regina.

Marmosa constantiae and M. rutteri are large mouse opossums with broadly overlapping external and craniodental measurements (table 7). Where they occur sympatrically in eastern Peru and western Brazil, both have drab, somewhat woolly dorsal fur; long, all-dark tails with rhomboidal scales arranged in spiral series; almost completely ossified palates (lacking palatine fenestrae, and with short-narrow maxillopalatine openings); well-developed postorbital processes (in most mature adults); and small auditory bullae. As in other members of the subgenus Micou-

⁶ Based on our unpublished sequence results (which are too extensive to effectively summarize in this report), the material we refer to this species forms a distinct haplogroup within a large and complex clade that also includes voucher material referable to the nominal taxa *demerarae*; *domina* Thomas, 1920; *limae* Thomas, 1920; and *phaea* Thomas, 1899. The species we provisionally recognize as *Marmosa constantiae* occurs south of the Amazon from the base of the Andes to the left bank of the Tapajós.

TABLE 7
Measurements (mm) and Weights (g) of Marmosa constantiae and M. rutteri from Eastern Peru

-	Ma	ales	Fem	nales
	M. constantiae ^a M. rutteri ^b		M. constantiae ^c	M. rutteri ^d
HBL	179 ± 14 (159–203) 22	199 ± 24 (164-240) 5	157 ± 11 (138–175) 19	170 ± 15 (152–197) 10
LT	246 ± 20 (218–289) 22	272 ± 15 (252–291) 5	222 ± 20 (186–250) 19	240 ± 14 (225–269) 10
HF	29 ± 2 (26–32) 22	29 ± 3 (25–33) 5	26 ± 3 (20-30) 20	28 ± 2 (25–30) 11
Ear	27 ± 2 (24–30) 21	27 ± 2 (24–28) 5	26 ± 2 (23–29) 20	25 ± 1 (24–28) 10
CBL	$43.7 \pm 2.1 \ (40.4 - 47.4) \ 21$	$44.9 \pm 2.6 \ (41.6 - 49.7) \ 11$	$41.2 \pm 2.1 \ (37.8 - 45.3) \ 20$	42.7 ± 2.4 (39.6–46.5) 12
NL	19.3 ± 1.1 (17.4–21.1) 18	19.7 ± 1.7 (17.4–22.8) 14	$18.3 \pm 1.0 \ (16.7 - 20.4) \ 17$	19.5 ± 1.2 (17.5–21.6) 11
NB	$6.0 \pm 0.4 \ (5.2 - 7.4) \ 23$	$6.3 \pm 0.7 \ (5.5 - 7.7) \ 17$	$5.6 \pm 0.5 \ (4.7 - 7.0) \ 20$	$6.2 \pm 0.6 \ (4.8 - 6.9) \ 13$
LIB	$7.7 \pm 0.5 \ (6.8 - 8.6) \ 23$	$8.2 \pm 0.7 \ (7.2 - 9.6) \ 17$	$7.0 \pm 0.5 \ (6.4 - 8.5) \ 20$	$8.0 \pm 0.6 \ (7.4 - 9.2) \ 13$
LPB	$6.7 \pm 0.6 \ (5.8 - 8.0) \ 23$	$7.3 \pm 0.4 \ (6.4 - 7.9) \ 17$	$6.7 \pm 0.4 \ (6.1 - 8.1) \ 20$	$7.6 \pm 0.5 \ (6.9 - 8.2) \ 13$
ZB	24.6 ± 1.2 (22.6–27.2) 23	25.6 ± 1.7 (23.4–28.7) 14	$23.0 \pm 1.3 \ (21.0 - 25.5) \ 20$	24.7 ± 1.6 (22.4–27.4) 13
PL	24.4 ± 1.0 (22.8–26.4) 23	24.6 ± 1.5 (22.5–27.6) 15	$23.2 \pm 1.1 \ (21.4 - 25.1) \ 20$	24.1 ± 1.3 (22.2–26.6) 13
PB	$14.0 \pm 0.6 \ (13.0 - 15.0) \ 22$	14.3 ± 0.8 (13.1–15.7) 16	$13.5 \pm 0.5 \ (12.6 - 15.0) \ 20$	$14.5 \pm 0.7 \ (13.5 - 16.2) \ 13$
MTR	$17.6 \pm 0.7 \ (15.9 - 18.7) \ 23$	$17.7 \pm 1.0 \ (16.7 - 19.4)17$	17.1 ± 0.6 (15.8–18.4) 20	17.7 ± 0.7 (16.7–18.8) 13
LM	$9.0 \pm 0.3 \ (8.5 - 9.7) \ 23$	$8.9 \pm 0.4 \ (8.3 - 9.8) \ 17$	$8.9 \pm 0.2 \ (8.4 – 9.3) \ 21$	$9.2 \pm 0.3 \ (8.6 - 9.6) \ 13$
M1-3	$7.5 \pm 0.3 \ (7.1 - 8.1) \ 23$	$7.5 \pm 0.4 \ (7.0 - 8.2) \ 17$	$7.6 \pm 0.2 \ (7.2 - 8.0) \ 21$	$7.8 \pm 0.2 \ (7.2 - 8.1) \ 13$
WM3	$2.9 \pm 0.2 \ (2.6 – 3.4) \ 23$	$2.9 \pm 0.2 \ (2.6 – 3.3) \ 17$	$2.9 \pm 0.1 \ (2.6 – 3.1) \ 21$	$3.1 \pm 0.1 \ (2.9 – 3.2) \ 13$
Weight	124 ± 34 (78–185) 20	168 ± 14 (148–180) 4	81 ± 23 (50–142) 19	103 ± 29 (63–151) 8

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (asterisks identify Yavarí-Ucayali vouchers): AMNH 272832*, 273052*, 273118*; FMNH 19348, 84255, 87117*, 138852, 174443, 203510; KU 144094; MUSM 6084, 6107, 6108, 13295*, 13296*, 13414, 13415, 14141, 19830; MVZ 136374–136377.

reus, gular glands are absent in both sexes, and large adult males have well-developed medial and lateral carpal tubercles (Voss et al., 2014). Although there are several pelage and craniodental differences that allow confident identification of specimens in hand (table 8), *M. constantiae* and *M. rutteri* are otherwise so alike that unvouchered records (e.g., of "Micoureus cinereus" at Jenaro Herrera; Fleck and Harder,

1995) cannot be confidently associated with one or the other species.

As described and illustrated by Patton et al. (2000: 65–77), the ventral pelage is mostly gray-based in *Marmosa constantiae*, but it is mostly self-yellowish in *M. rutteri*. In the former species, self-yellowish fur is restricted to the throat, groin, and (sometimes) to a narrow streak along the midline of the chest and abdomen: the fur on

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (all from south of the Amazon/Marañón; asterisks identify Yavarí-Ucayali vouchers): AMNH 76302, 230021; BMNH 24.2.22.67, 28.5.2.231–28.5.2.235, 28.5.2.237, 28.5.2.240, 28.5.2.241; FMNH 46110, 46111; KU 144110; MUSM 11055*, 11063*, 15316*.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (asterisks identify Yavarí-Ucayali vouchers): AMNH 268219*, 268220*, 273113*; FMNH 84254, 98029; KU 144092, 144096–144099, 144103; MUSM 6085, 6089, 6109, 11060*, 11060*, 11064*, 13412, 14139, 15310*, 15312*, 15317*.

^d The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (all from south of the Amazon/Marañón; none are Yavarí-Ucayali vouchers): AMNH 74087, 273164; FMNH 19635, 55467, 75100; KU 144093, 144095, 144100, 144102, 144107; LSUMZ 15674; MUSM 6086, 6087.

M. rapposa^a

broadly self-yellowish

short-furred

white-tipped

present

long

usually present on m1-m3

 $8.3 \pm 0.2 \text{ mm}$

short

absent

 $9.0 \pm 0.3 \text{ mm}$

TABLE 8

Diagnostic Morphological Traits of Three Species of Marmosa (Micoureus)

^a Not a member of the Yavarí-Ucayali interfluvial fauna (see text).

2019

Postprotocristae

 LM^c

Posterior cingulids

- ^b Geographically variable (see text); tails are all-dark in eastern Peru.
- ^c Crown length M1–M4 (see Materials and Methods); tabulated statistics are the sample mean plus or minus one standard deviation.

long

usually present on m2

 $9.0 \pm 0.4 \text{ mm}$

the insides of the fore- and hind limbs is always gray-based. In *M. rutteri*, by contrast, self-yellowish fur extends over the chin, throat, chest, and groin, and along the insides of the fore- and hind limbs; a median abdominal band of self-yellowish fur is always present, and it is at least as broad as or broader than the flanking lateral zones of gray-based fur.

Another taxonomically informative external trait is the length of the dorsal fur, which appears to be consistently longer in *Marmosa constantiae* than in sympatric *M. rutteri*. In our material from the Yavarí-Ucayali interfluve, the middorsal fur of adult *M. constantiae* is about 12–15 mm long, whereas the dorsal fur of *M. rutteri* from our region and adjacent lowlands is only about 8–11 mm. Although these observed ranges almost overlap, the modal fur lengths for these species (about 13 mm and 9 mm, respectively) correspond to visibly and tactilely distinct phenotypes.

A third diagnostically useful external trait (illustrated by Patton et al., 2000: fig. 53) concerns the tail, which has a more conspicuously furry base in *Marmosa constantiae* than in *M. rutteri*. Not only does the caudal fur (identical in color and texture to the fur of the rump) extend distally further along the tail in *constantiae*, but the hairs that comprise the caudal fur are longer in this species than in *rutteri*. Measured from

skins in our material of *constantiae*, this fluffy-furred tail base extends distally for about 28 mm (on average) with hairs that are about 10 mm long, whereas the homologous average values for *rutteri* are about 16 mm and 5 mm.

Although Patton et al. (2000: table 13) found statistically significant differences for most craniodental measurements in same-sex comparisons of Marmosa constantiae ("Micoureus demerarae") and M. rutteri ("Micoureus regina"), these species have broadly overlapping morphometric distributions, such that no measurement (nor any ratio of measurements that we computed) is diagnostic. Unmagnified comparisons of cranial morphology are likewise uninformative, but two dental features (visible under low magnification) are useful for species recognition. In constantiae the postprotocrista (the posteriormost of the two enamel crests that pass labially from the apex of the protocone; Voss and Jansa, 2009: fig. 20) is short, because it terminates at or near the base of the metacone, whereas the postprotocrista is much longer in rutteri, extending labially well beyond the base of the metacone on the posterior surface of the tooth. On the lower molars, a posterior cingulid (a small enamel shelf at the posterolabial base of the hypoconid) is consistently absent in constantiae, whereas a small but persistent posterior cingulid is usually present, at least on m2, in rutteri.

Unlike the Peruvian material described above, the holotype of Marmosa constantiae (BMNH 3.7.7.157, from Chapada dos Guimarães, Mato Grosso, Brazil; Thomas, 1904a), other specimens from Mato Grosso, and many specimens from eastern Bolivia (Beni and Santa Cruz departments, see below) have tails that are one-third to one-half whitish distally. Nevertheless, all the material that we refer to M. constantiae is morphologically similar in other respects, and sequenced specimens from Mato Grosso and eastern Peru belong to the same well-defined mtDNA haplogroup (the "SW-S" clade of Patton and Costa, 2003: fig. 9). Therefore, we interpret geographic differences in caudal markings as intraspecific variation.

Unfortunately, the epithet constantiae has often been misapplied (e.g., by Tate, 1933; Flores et al., 2007; Gardner and Creighton, 2008; Gutiérrez et al., 2010; de la Sancha et al., 2012; Voss et al., 2014) to another widespread species of woolly mouse opossum, for which the oldest available name is Marmosa rapposa Thomas, 1899. As recognized in this report, M. rapposa (with type locality at Huadquiña, near Cusco, Peru; Ceballos-Bendezu, 1981) ranges at middle elevations in Andean cloud forests from Junin department, Peru, throughout the Bolivian Yungas to northeastern Argentina (budini Thomas, 1920, from Jujuy is a junior synonym); at lower elevations, this species occurs in Cerrado woodlands from eastern Bolivia across central Brazil to eastern Paraguay. Although specimens of M. rapposa resemble the holotype of *M. constantiae* in having white-tipped tails and yellowish underparts, they differ in other respects (table 8), most notably in having well-developed palatine fenestrae (fig. 11B), long postprotocristae, well-developed posterior cingulids on m1-m3, and highly divergent mtDNA sequences (Voss et al., in prep.).

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the 19 specimens of *Marmosa constantiae* collected at Nuevo San Juan, 11 were trapped or shot in primary upland forest; 2 were trapped in primary floodplain forest; 4 were trapped, shot, or caught by hand in secondary growth (abandoned swiddens); and 2 were caught by hand in Matses houses. Of 10 specimens accompanied by information about capture height, 2 were trapped on the ground, 1 was trapped on a fallen log, and 7 were trapped or shot in trees or on lianas at estimated heights ranging from 0.4 to 4 m above the ground. Our single specimen from Jenaro Herrera was trapped at a height of 17 m in a tree at the edge of a clearing.

OTHER SPECIMENS EXAMINED (TOTAL = 62): Bolivia—Beni, Río Iténez frente Costa Marques (AMNH 209158-209162), Río Mamoré lado este frente Cascajal (AMNH 210397); Pando, La Cruz (MSB 57001). Brazil—Amazonas, Altamira on right bank of Rio Juruá (MVZ 190309-190312), Coleção Vira-Volta on left bank of Rio Juruá (MVZ 190316-190318), Penedo on right bank of Rio Juruá (MVZ 190301-190303), Seringal Condor on right bank of Rio Juruá (MVZ 190305-190307), Ilhazinha on left bank of Rio Juruá (MVZ 190313, 190314); Mato Grosso, Chapada dos Guimarães (AMNH 384, BMNH 3.7.7.157 [holotype], OMNH 37209), Fazenda Noirumbá (MVZ 197415), Reserva Ecológica Cristalino (MVZ 197407-197414). Peru-Cuzco, 15.9 km SW Pilcopata (FMNH 174443), 2 km SW Tangoshiari (MUSM 13412, 13414, 13415), Pagoreni (MUSM 14139, 14141); Madre de Dios, Altamira (FMNH 98029), 13.5 km NW Atalaya (MUSM 19830), Hacienda Amazonía (FMNH 138852), Itahuanía (FMNH 84254, 84255), Reserva Cuzco Amazónico (KU 144092, 144094, 144096-144099, 144103); Pasco, Pozuzo (BMNH 12.1.15.18); San Martín, Área de Conservación Municipal Mishquiyacu Rumiyacu-Almendra (FMNH 203510), Moyobamba (FMNH 19348), Yurac Yacu (BMNH 27.1.1.174-27.1.1.176); Ucayali, Balta (MVZ 136374-136377).

Marmosa (Micoureus) rutteri Thomas, 1924

VOUCHER MATERIAL (TOTAL = 6): Nuevo San Juan (AMNH 273164; MUSM 11055, 11063, 15315, 15316), Orosa (AMNH 74087).

OTHER INTERFLUVIAL RECORDS: None that can be confidently associated with this species.

IDENTIFICATION: As explained in the preceding account, this is the species that Patton et al. (2000) called Micoureus regina, but their usage is taxonomically indefensible. As those authors noted, regina is based on a specimen collected in the Magdalena Valley of Colombia, so it seems biogeographically improbable that the name could validly apply to an Amazonian taxon. Additionally, the type of regina (BMNH 98.5.15.4, an old adult male) does not closely resemble any Amazonian woolly mouse opossum that we have seen. Among other traits that do not fit the present species, the dorsal fur of BMNH 98.5.15.4 is redder (near Prout's Brown according to Tate [1933: 83], who saw the type when it was less than 40 years old), the upper molars are smaller (LM = 8.1 mm), and the postprotocristae are short. Like Tate (1933), we restrict the application of Marmosa regina to the holotype, and we reject the application of this name to any of the Amazonian nominal taxa treated as subjective junior synonyms or subspecies by Gardner (1993, 2005).

According to Patton et al. (2000), the nextoldest name for this species is Marmosa germana Thomas, 1904, which was treated as a synonym of M. regina by Gardner (1993), but as a valid subspecies of M. regina by Gardner (2005) and by Gardner and Creighton (2008). However, the type of germana (BMNH 80.5.6.77, an adult female from eastern Ecuador; Thomas, 1904b) more closely resembles the species that Patton and his colleagues called *M*. demerarae than the species that they called M. regina. Among other traits that do not match the present species, BMNH 80.5.6.77 has completely gray-based ventral fur; a long (30 mm), fluffy-furred tail base; and short postprotocristae. Unpublished DNA sequence data (Voss et

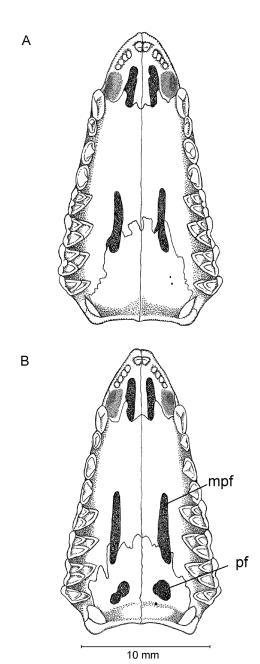


FIG. 11. Ventral views of palates of **A**, *Marmosa constantiae* (AMNH 209162) and **B**, *M. rapposa* (MSB 140347). Both specimens are from Bolivia, where these species are externally similar (with mostly self-yellow ventral fur and half-white tails; see text). Both species have maxillopalatine fenestrae (**mpf**), but only *M. rapposa* consistently has well-developed palatine fenestrae (**pf**).

al., in preparation) suggest that *M. germana* is a distinct species, restricted to the left (north) bank of the upper Amazon.

Thomas (1924) described Marmosa rutteri as a valid species, but Tate (1933: 81) considered rutteri to be a subspecies of M. germana, and most subsequent authors have considered rutteri to be a junior synonym of germana (now usually ranked as a subspecies of regina; e.g., by Gardner, 2005; Gardner and Creighton, 2008). In fact, M. rutteri is a distinct species with the diagnostic traits listed in table 8, and analyses of DNA sequence data (Voss et al., in prep.) suggest that it is more closely related to M. rapposa and other extralimital species than to M. germana. The holotype (BMNH 24.2.22.67, an adult male) is from Tushemo, on the right bank of the upper Ucayali. As recognized in this report, the species is widely distributed in western Amazonia, but different haplogroups are found north and south of the Amazon; the specimens listed below, which include all of those with measurement data summarized in table 7, are from south of the Amazon.

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of our four specimens from Nuevo San Juan, one was captured by hand inside a Matses house, one was trapped on top of a fallen log in primary upland forest, one was shot from a tree (at an unrecorded height) in primary upland forest, and one was taken by hand inside a hollow tree at the edge of the Río Gálvez.

OTHER SPECIMENS EXAMINED (TOTAL = 84): **Brazil**—*Acre*, Igarapé Porongaba (MVZ 190332), Nova Vida (MVZ 190333); *Amazonas*, Boa Esperança (MVZ 190330, 190331), Igarapé Nova Empresa (MVZ 190321, 190323–190325), opposite Altamira (MVZ 190328, 190329), Penedo (MVZ 190319, 190320), Seringal Condor (MVZ 190326). **Colombia**—*Caquetá*, Tres Troncos

(FMNH 70964-70966). Ecuador—Napo, San José de Payamino (FMNH 124613). Peru—Amazonas, La Poza (MVZ 157629), mouth of Río Cenepa (AMNH 98712), vicinity of Huampami (MVZ 153278, 154749, 154751, 154755, 154758, 154762, 154764, 154766, 157628, 157630, 157631), vicinity of Kayamas (MVZ 153281); Ayacucho, Santa Rosa on Río Santa Rosa (LSUMZ 15674); Cuzco, Quincemil (FMNH 75100); Loreto, Boca Río Curaray (AMNH 71951, 71956, 71958, 71964, 71966, 71968, 71975, 72010), Otorongo (MUSM 33443), Pampa Chica (FMNH 87118), San Antonio (AMNH 98655), San Jerónimo (BMNH 28.5.2.231-28.5.2.241; FMNH 46110, 46111), Sarayacu (AMNH 76302, 76303), El Triunfo (TTU 124799), Yurimaguas (FMNH 19635); Madre de Dios, Blanquillo (MUSM 8399), Reserva Cuzco Amazónico (KU 144091, 144093, 144095, 144100, 144102, 144107, 144110, 144111; MUSM 6083, 6086-6088, 6090-6092, 6100, 6101); Pasco, San Pablo (AMNH 230019, 230021); Ucayali, Tushemo (BMNH 24.2.22.67 [holotype]), Yarinacocha (FMNH 55467). Peru (Loreto) or Ecuador (Orellana)-Boca Río Lagartococha (AMNH 72008, 72009)

Marmosa (Stegomarmosa) lepida (Thomas, 1888)

Figures 9B, 10B

Voucher Material (Total = 1): Nuevo San Juan (AMNH 273186).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: Our unique voucher, an adult male preserved in fluid with the skull extracted and cleaned, exhibits all the diagnostic traits of the nominotypical form (*Marmosa lepida lepida*), including small size, reddish dorsal fur, a midventral zone of self-whitish fur flanked by lateral zones of gray-based fur, a long tail with dense fringes of silvery hairs flanking the distal prehensile surface, a very long rostral process of the premaxillae, large postorbital processes, and small posterior accessory cusps on C1 and c1. Additionally,

our specimen lacks any trace of a gular gland, and palatine fenestrae are absent. Morphometric comparisons with other specimens from western Amazonia, including the holotype, suggest striking uniformity in most craniodental dimensions, especially of the molar dentition (table 9). A cytochrome *b* sequence obtained from AMNH 273186 was analyzed by Gutiérrez et al. (2010), who reported that it formed a strongly supported clade with sequences from other specimens that also exhibit the distinctive morphological traits of *M. lepida*.

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The only local taxa with which Marmosa lepida could possibly be confused in the field are Hyladelphys kalinowskii and Gracilinanus emiliae, both of which are also small, reddish, black-masked, and long-tailed. Comparisons with Hyladelphys kalinowskii have already been described, but it remains to compare M. lepida with G. emiliae. The chief external character distinguishing these taxa (table 4) is the ventral coloration (self-whitish and gray-based in M. lepida versus entirely self-white in G. emiliae). Crania of these species (figs. 9, 10) are most easily distinguished by the occurrence of postorbital processes (present in M. lepida, absent in G. emiliae), palatine fenestrae (absent in M. lepida, present in G. emiliae), and secondary foramina ovales (usually absent in M. lepida, consistently present in G. emiliae); additionally, the upper molar series is much longer in M. lepida (LM = 5.6-6.1 mm) than in G. emiliae (LM = 4.8-5.1 mm).

Two subspecies of *Marmosa lepida* were recognized by Tate (1933), of which our material is unambiguously referable to the nominotypical form. *Marmosa l. lepida* occurs on both sides of the Amazon, from the base of the Andes to the Atlantic coast, with remarkably little evidence of geographic variation in either morphology or cytochrome *b* sequences (Tate, 1933; Gutiérrez et al., 2010; Guimarães et al., 2018). By contrast, *M. l. grandis* Tate, 1931, is known only from Buenavista in Santa Cruz province, Bolivia. We examined the young

adult female holotype of grandis (BMNH 26.12.4.94), which differs from other specimens of M. lepida in ventral pelage color (entirely gray-based buffy) and in lacking posterior accessory cusps on C1 and c1. Given the morphological uniformity exhibited by Amazonian specimens of M. lepida, we are not persuaded that grandis is really conspecific. Although Tate (1933: 205) listed two specimens that he identified as M. l. lepida from Buenavista (paradoxically implying sympatry of two subspecies), the specimens in question are offspring of the holotype of grandis (as documented by notes on the skin tags). We have not examined any Bolivian specimen definitely referable to typical M. lepida as diagnosed by the suite of traits listed in the first paragraph of this account.

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Our single specimen was shot at night by a Matses hunter as it perched in the subcanopy of tall primary forest.

OTHER SPECIMENS EXAMINED (TOTAL = 13): Brazil-Amazonas, Igarapé Grande on Rio Juruá (FMNH 140824). Colombia—Amazonas, 20 km downstream from La Chorrera on Río Igaraparaná (MNHN 1982-653). French Guiana-Les Nouragues (MNHN 1998-306). Guyana-Potaro-Siparuni, 42 km WNW Siparuni (ROM 107034). Ecuador-Pastaza, Río Tigre (AMNH 182937); Sucumbíos, Lago Agrio (KU 135118). Peru-Amazonas, Huampami on Río Cenepa (MVZ 154750, 154752, 155245); Loreto, Río Pisqui (AMNH 98656), Santa Cruz on Río Huallaga below Yurimaguas (BMNH 69.3.31.4 [holotype]); Ucayali, Lagarto (AMNH 78001). Venezuela-Amazonas, El Platanal (EBD, uncataloged).

Sex

HBI.

LT

HF

Ear

CBL. NL

NB

LIB

LPB

ZB

PL

PR

MTR

LM

M1 - 3

WM3

Weight

4.8

16.0

8.7

11.0

5.8

5.0

23

IADLE 9						
Measureme	ents (mm) and	Weights (g) o	f Marmosa lep	oida from Ecu	ador and Peru	
AMNH 98656	AMNH 182937	AMNH 273186 ^a	KU 135118	AMNH 78001	BMNH 69.3.31.4 ^b	MVZ 154750
male	male	male	male	female	female	female
_	_	96	_	_	_	104
_	_	161	_	_	_	155
_	_	17	_	_	17 ^c	17
_	_	20	_	_	_	18

27.1

11.3

3.0

4.3

6.1

14.6

15.5

7.8

10.6

5.6

26.2

11.4

2.9

4.5

6.6

14.8

15.2

8.4

10.7

5.6

1.9

5.0

6.6

8.4

10.7

5.6

4.8

1.9

TARIFO

11.5

2.7

4.5

6.8

15.4

8.6

10.9

5.8

1.9

Monodelphis Burnett, 1830

29.1

13.0

3.6

4.9

6.5

16.3

17.0

8.8

11.1

5.8

5.0

1.9

27.4

11.6

3.4

4.8

7.1

15.9

15.6

8.7

10.6

5.7

1.9

2.2.

Three species of Monodelphis are known from the Yavarí-Ucayali interfluve, and no others seem likely to occur in the region. Two of the five subgenera recognized by Pavan and Voss (2016) are represented locally, Mygalodelphys with two species and Pyrodelphys with one. All three species are readily identified by external, craniodental, and morphometric traits (table 10). Because the Matses do not distinguish different species of Monodelphis, we summarize ethnobiological observations and Matses natural history under this generic heading.

ETHNOBIOLOGY: The Matses name for short-tailed opossums is yama, a term that is not linguistically analyzable. Curiously, yama

is also used to refer to the turnip-tailed gecko (Gekkonidae: Thecadactylus solimoensis) and to an unidentified arboreal rat that was formerly used for black magic.7 The Matses do not consider yama to be a type of cheka.

^a Specimen from the Yavarí-Ucayali interfluve.

^b Holotype.

^c Measurement of dried hind foot.

⁷ Several generations ago, according to the Matses, men of evil intention would concoct a poison from yama rats, which are said to be found on leafless trees that have recently died. The poisoner would place a large clay pot containing ripe plantains at the base of such a tree at night and hide nearby to wait. When the rat entered the pot and began to eat the plantains, the poisoner would place a lid over the pot and take it to an isolated hut. There, without lifting the lid, he would place the pot over a fire until the contents were completely burned. Next, he would gather the burned remnants into a length of bamboo, which was used as a mortar to grind the contents to dust and ash. This pulverized substance was then sprinkled on the head of a sleeping victim, who would breathe in the rat ashes, become insane, and die shortly afterward.

M. emiliae

red and gray exposed (outside orbit)

present

usually present

present

laterally exposed

broad & rounded

concealed

absent

broadf

distinct

6.3-7.1 mm

	Selected
Ι	Porsal pelage
Ι	acrimal foramina
F	Frontal process of jugal ^a
S	agittal crest
F	Parietal/mastoid contact ^b
E	Basioccipital (inside orbit) ^c
F	Rostral tympanic process ^d
P	Anterior process of malleus ^d
(C1 accessory cusps

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TABLE 10
Selected Morphological Comparisons among Three Species of *Monodelphis*

M. peruviana

uniformly brownish

exposed (outside orbit)

absent/indistinct

absent

absent

concealed

triangular

exposed

present in females

narrowe

indistinct

5.6-6.1 mm

M. handleyi

uniformly brownish

concealed (inside orbit)

absent/indistinct

usually present

absent

concealed

triangular

exposed

absent

narrowe

indistinct

7.2-7.5 mm

Crown length M1-M4 (LM)			
^a See Pavan and Voss (2016: fig. 6).			

Anterior cingulids (m2, m3)

Entoconids (m1-m3)g

The Matses do not eat short-tailed opossums and have no other use for them. Not all Matses are familiar with them.

MATSES NATURAL HISTORY: Short-tailed opossums are similar to mouse opossums, but they have very short tails. They are terrestrial, diurnal, solitary, and make nests in cavities among the roots of bottle palms (*Iriartea deltoidea*) and in hollows at the bases of trees. They are eaten by jaguarundi cats.

Monodelphis (Mygalodelphys) handleyi Solari, 2007

VOUCHER MATERIAL (TOTAL = 7): Jenaro Herrera (AMNH 276698, 276704, 276709; MUSM 15991, 23808–23810).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: Our voucher material was examined by Solari (2007) and served as the basis for his description of the species, which remains known only from Jenaro Herrera. Among other

congeners, *Monodelphis handleyi* most closely resembles *M. ronaldi* (described by Solari, 2004), formerly known only from the holotype collected at Pakitza (11°56′S, 71°17′W) in Madre de Dios department, about 800 km southeast of Jenaro Herrera. Solari (2007) compared *M. handleyi* with *M. ronaldi*, which, among other differences, is substantially larger, but recently collected new material of *M. ronaldi* should allow a more complete differential diagnosis of these apparently closely related species (D. Ruelas, personal commun.). With the exception of a single juvenile female (AMNH 276704), all specimens of *M. handleyi* collected to date are male.

Several aspects of Solari's (2007) original description merit comment. The ventral pelage was described as entirely self-cream from chin to anus with a somewhat paler streak along the midline, but in one topotypical skin (MUSM 23810) most of the ventral fur is distinctly brownish and the hairs have pale-gray bases except on the center of the chest and upper

^b See Pavan and Voss (2016: fig. 7).

^c See Pavan and Voss (2016: fig. 8).

^d See Pavan and Voss (2016: fig. 10).

e Lingual to hypoconids of m1 and m2, respectively.

^fLevel with hypoconids of m1 and m2, respectively.

g See Pavan and Voss (2016: fig. 12).

abdomen, which is marked by a broad self-cream blaze. Whereas the central hair of each caudal-scale triplet was described as "thicker (petiolate) than the lateral hairs" (Solari, 2007: 324), the scale triplets we examined on several specimens had subequal lateral and central hairs. Both of the adult male skulls at hand (AMNH 276709, MUSM 23809) have distinct sagittal crests, which are also present but less distinct on all three sub-adults (AMNH 276698; MUSM 23808, 23810). The upper and lower canines lack accessory cusps in both sexes.

Monodelphis handleyi is much the larger of the two local members of the subgenus Mygalodelphys. Although only two fully adult specimens of M. peruviana from the Yavarí-Ucayali interfluve are available for comparisons, measurements of other material referable to M. peruviana suggest that these species have nonoverlapping craniodental measurements (tables 11, 12). Additionally, several qualitative differences inferred from our small samples merit evaluation when more specimens of both species become available: (1) The lacrimal foramina are concealed from lateral view inside the anterior margin of the orbit in M. handleyi, whereas these foramina are laterally exposed just anterior to the orbit in M. peruviana. (2) Most subadult and adult specimens of M. handleyi have a sagittal crest, but the left and right temporalis scars are separated and a sagittal crest is absent in all examined specimens of M. peruviana. (3) The upper and lower canines lack accessory cusps in both sexes of M. handleyi, whereas both upper and lower canines have small but distinct accessory cusps in female specimens of M. peruviana.

ETHNOBIOLOGY: The Matses do not distinguish this species from other short-tailed opossums (all known as <u>yama</u>; see the account for *Monodelphis*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the six specimens for which we have capture information, five were taken in pit-falls along a single trapline flanked by swampy primary forest. The sixth specimen was taken in

a pitfall trapline sited in a small patch of whitesand forest.

Monodelphis (Mygalodelphys) peruviana (Osgood, 1913)

Voucher Material (Total = 4): Nuevo San Juan (AMNH 272695, 272781; MUSM 13297, 15318).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: This taxon was long treated as a synonym or subspecies of Monodelphis adusta (Thomas, 1897)—for example, by Cabrera (1958), Gardner (2005), and Pine and Handley (2008)—but it was recognized as a valid species by Solari (2007), largely on the basis of mtDNA sequence analyses. In fact, phylogenetic analyses of multiple genes provide compelling evidence that M. adusta and M. peruviana are not sister taxa: whereas *M. peruviana* belongs to a robustly supported clade that includes M. handleyi, M. osgoodi Doutt, 1938, and M. saci Pavan et al., 2017, the sister taxon of *M. adusta* (as currently recognized; see below) is M. reigi Lew and Pérez-Hernández, 2004 (Pavan et al., 2014, 2017). In light of those results, it seems reasonable to treat M. adusta and M. peruviana as distinct species, but the absence of unambiguously diagnostic morphological characters (Solari, 2004) is a relevant problem. In effect, M. adusta and M. peruviana are names applied to haplogroups vouchered by morphologically similar material collected north and south of the Amazon, respectively. Although the application of peruviana to material from the Yavarí-Ucayali interfluve seems adequately justified by proximity to the type locality (Moyobamba, only about 200 km west of our region; Osgood, 1913), the application of adusta to the haplogroup that occurs on the north bank of the Amazon is more problematic.8 Nevertheless, we maintain

⁸ The type locality of *Monodelphis adusta* is in the valley of the Río Magdalena ("W[est]. Cundinamarca, in the low-lying hot regions" [Thomas, 1897: 220]), so this name properly belongs to trans-Andean populations, from which sequence data are currently unavailable.

current conventions for applying these epithets to small specimens of *Mygalodelphys* from western Amazonia.

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To assess the problem of species diagnosis, we compared our voucher material and other referred specimens of Monodelphis peruviana with cis-Andean specimens of M. "adusta," including several from the Reserva Nacional Allpahuayo-Mishana (RNAP), a north-bank locality adjacent to our region (fig. 1). Sequence data from one of our vouchers (AMNH 272695 [= RSV 2086]) and from specimens collected at RNAP (TTU 101019 [= TK 73496], TTU 101164 [= TK 73868]) document their membership in the haplogroups currently associated with these binomina (e.g., by Solari, 2007; Pavan et al., 2014). Contra Solari (2004: 150), we found no external morphological differences between these taxa: whereas he reported that adusta has shorter dorsal fur than peruviana, our measurements indicate that both species have dorsal fur that ranges from 3 to 4 mm long, and we were unable to distinguish the "ill-defined blackish area on the posterior dorsum and the rump" that was said to be present in adusta, but absent in peruviana. Likewise, we observed no consistent qualitative craniodental differences between specimens collected on opposite banks of the Amazon. Sample sizes are too small for confident statistical comparisons of craniodental measurements, but broadly overlapping ranges for most dimensions (table 12) suggest that morphometric differences, if any, are unlikely to provide a secure basis for species separation. Although we are currently unable to provide diagnoses of the taxa currently associated with these names, it seems prudent to maintain current usage pending a comprehensive revision of the subgenus Mygalodelphys.

ETHNOBIOLOGY: The Matses do not distinguish this species from other short-tailed opossums (all known as <u>yama</u>; see the account for *Monodelphis*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: One of our four vouchers (AMNH 272695) was trapped on the ground in well-

TABLE 11

Measurements (mm) and weights (g) of Monodelphis handleyi

		,	
	MUSM 15991 ^a	MUSM 23809	AMNH 276709
Sex	male	male	male
HBL	124	131	117
LT	68	72	74
HF	16	18	16
Ear	13	14	14
CBL	31.8	32.0	33.1
NL	15.0	14.9	16.6
NB	4.8	4.7	4.6
LIB	_	_	_
LPB	5.5	5.0	5.7
ZB	17.8	18.6	18.8
PL	17.6	17.6	18.2
PB	11.1	10.9	11.2
MTR	13.0	13.3	13.6
LM	7.4	7.3	7.2
M1-3	6.4	6.3	6.2
WM3	2.8	2.5	2.7
Weight	40	51	52

^a Holotype.

drained (hill-slope) primary forest; another (AMNH 272781) was trapped under a log in what was said to be primary forest by the Matses boy who caught it; a third (MUSM 13297) was trapped by another Matses child at an undisclosed location near the village; and the fourth (MUSM 15318) was caught by hand by a Matses man at the edge of his swidden.

OTHER SPECIMENS EXAMINED (TOTAL = 9): Peru—Cuzco, Camisea (USNM 582782), 2 km SW Tangoshiari (USNM 588019); Huánuco, Hacienda Exito (FMNH 23772), Hacienda San Antonio (FMNH 23774, 23775; USNM 259433); Madre de Dios, Reserva Cuzco Amazónico (MUSM 7157); San Martín, Moyobamba (FMNH 19361, 19362 [holotype]).

Specimens of *Monodelphis adusta* Examined (total = 9): **Ecuador**—*Pastaza*, Mera

TABLE 12
Measurements (mm) and weights (g) of Monodelphis peruviana and M. "adusta'

	Ma	ales	Females		
-	M. peruvianaª	M. adusta ^b	M. peruviana ^c	M. adusta ^d	
HBL	101 ± 11 (90–118) 7	111 ± 4 (105–115) 6	107 ± 5 (101-112) 4	98	
LT	54 ± 5 (47–59) 7	54 ± 8 (40–66) 6	59 ± 5 (54-64) 4	53	
HF	17 ± 1 (16–19) 6	16 ± 1 (15–17) 6	17 ± 1 (16–17) 3	15	
Ear	12 ± 2 (10-13) 2	12 ± 1 (11-14) 4	12 ± 1 (11-13) 3	_	
CBL	27.6 ± 1.2 (26.0–28.9) 4	$27.9 \pm 1.0 \ (26.7 - 29.2) \ 6$	$27.6 \pm 0.6 \ (26.8 - 28.3) \ 4$	26.8	
NL	$13.1 \pm 1.0 \ (11.7 - 14.6) \ 6$	$14.0 \pm 0.1 \ (13.9 - 14.1) \ 2$	$12.6 \pm 0.6 \ (12.0 - 13.5) \ 4$	12.1	
NB	$3.9 \pm 0.4 \ (3.3 - 4.4) \ 7$	$4.2 \pm 0.3 \ (3.9 - 4.7) \ 6$	$3.5 \pm 0.6 \ (2.9 – 4.3) \ 4$	4.1	
LPB	$5.2 \pm 0.3 \ (4.9 - 5.7) \ 6$	$5.5 \pm 0.2 (5.2 - 5.7) 5$	$5.2 \pm 0.2 \ (4.9 - 5.4) \ 4$	5.8	
ZB	$14.7 \pm 0.7 \ (14.0 - 16.0) \ 6$	$15.1 \pm 0.6 \ (14.6 - 15.8) \ 3$	$14.7 \pm 0.3 \ (14.4 - 15.2) \ 4$	_	
PL	$15.1 \pm 0.9 \ (13.6 - 16.3) \ 6$	$15.0 \pm 0.7 \ (14.1 - 15.8) \ 6$	$14.7 \pm 0.3 \ (14.4 - 15.2) \ 4$	14.6	
PB	$9.1 \pm 0.5 \ (8.3 - 9.6) \ 7$	$9.2 \pm 0.2 \ (8.9 - 9.5) \ 5$	9.3± 0.5 (8.8-9.9) 4	8.2	
MTR	$11.2 \pm 0.6 \ (10.6 - 12.4) \ 7$	$11.2 \pm 0.4 \ (10.8 - 11.8) \ 5$	$11.0 \pm 0.2 \ (10.8 – 11.1) \ 4$	10.7	
LM	$6.1 \pm 0.3 \ (5.9 - 6.7) \ 7$	$6.1 \pm 0.2 \ (5.8 - 6.3) \ 6$	$5.9 \pm 0.2 \ (5.6 - 6.0) \ 4$	5.5	
M1-3	$5.3 \pm 0.2 \ (5.1 - 5.6) \ 7$	$5.3 \pm 0.2 \ (5.0 - 5.5) \ 6$	$5.1 \pm 0.2 \ (4.9 - 5.2) \ 4$	4.7	
WM3	$2.1 \pm 0.1 \ (1.9 - 2.3) \ 7$	$2.1 \pm 0.1 \ (2.0 - 2.2) \ 6$	$2.0 \pm 0.1 \ (2.0 – 2.2) \ 4$	1.9	
Weight	26 ± 11 (18–33) 2	30 ± 3 (28–35) 4	26 ± 2 (25–28) 3	_	

^a From eastern lowland Peru (south of the Amazon and below about 1000 m). Tabulated values include the mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size of the following series (none is from the Yavarí-Ucayali interfluve): FMNH 19362 [holotype], 23772, 23774, 23775; MUSM 7157; USNM 259433, 582782.

^d AMNH 67275.

(AMNH 67274); Sucumbíos, km 61 on Lago Agrio-Quito highway (USNM 534286); Tungurahua, Palmira (AMNH 67275); Zamora-Chinchipe, Zamora (AMNH 47189). Peru—Loreto, 25 km S Iquitos (TTU 98686, 98923, 101019, 101164).

Monodelphis (Pyrodelphys) emiliae (Thomas, 1912)

Figure 12

Voucher Material (total = 7): Jenaro Herrera (AMNH 276721, MUSM 23807), Nuevo San

Juan (AMNH 268221; MUSM 11065, 13298), Río Aucayo (FMNH 58955), San Pedro (MUSM 22333).

OTHER INTERFLUVIAL RECORDS: Quebrada Curacinha (photograph, fig. 12).

IDENTIFICATION: Our voucher material exhibits all of the distinctive phenotypic traits of the monotypic subgenus *Pyrodelphys*, including disruptively colored dorsal pelage (a reddish head and rump separated by grizzled-grayish middorsal fur), contact or fusion of the thenar and first interdigital pads of the hind foot, a rounded but distinct frontal process of the jugal, parietal-mastoid contact, exposure of the basioccipital in the rear of the orbit, a broadly rounded rostral tym-

^b From eastern lowland Ecuador and Peru (north of the Amazon and below about 1000 m). Tabulated values include the mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size of the following series: AMNH 47189, 67274; TTU 98686, 101019, 101164; USNM 534286.

^c From eastern lowland Peru (south of the Amazon and below about 1000 m). Tabulated values include the mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size of the following series (specimens marked with asterisks are from the Yavarí-Ucayali interfluve): AMNH 272695*, FMNH 23780, MUSM 13297*, USNM 588019.

panic process of the petrosal, broad lower-molar anterior cingulids, and distinct entoconids on m1-m3 (Pavan and Voss, 2016).

2019

A cytochrome *b* sequence from MUSM 13298 was analyzed by Pavan et al. (2014), who recovered it as part of a strongly supported haplogroup with other specimens that exhibit the diagnostic morphological traits of *Monodelphis emiliae*. Although substantial phylogeographic structure was reported among the sequences that Pavan et al. (2014) identified as *M. emiliae*, morphological comparisons of our Peruvian specimens with the holotype and other material from eastern Amazonia have not revealed any consistent differences. At least for the time being, we recognize *M. emiliae* as a widespread and morphologically uniform species.

According to Pine and Handley (1984: 242), Monodelphis emiliae has "well-defined postorbital processes on the frontals," but among the specimens we examined this trait is developed in just a few old adult males (e.g., BMNH 20.7.14.44, MUSM 20452). By contrast, females and other adult males (some of which have wellworn teeth; e.g., FMNH 58955) lack any trace of frontal processes. The same authors (op. cit.: 241) described the tail of M. emiliae as "furred throughout its length," but only the base of the tail bears soft fur on the specimens we examined, the remainder of that organ being covered with the usual caudal bristles (albeit thicker, longer, and more densely crowded than in many other congeneric species). The measurements of M. emiliae reported by Patton et al. (2000: table 15) include several values that are smaller than any obtained by us (table 13) or by Pine and Handley (1984); although we have not examined all of Patton et al.'s material, at least one of their measured specimens (MVZ 190335) is a subadult. This species is one of the few didelphid species that is polymorphic for presence/absence of secondary foramina ovales, which are formed by stout medial bullar laminae in some specimens (e.g., AMNH 96810, MUSM 20452), but not in others (e.g., AMNH 268221, BMNH 20.7.14.44). The fugitive ventral coloration origi-



FIG. 12. Bothriopsis taeniata (Serpentes: Viperidae) eating Monodelphis emiliae at Quebrada Curacinha, Loreto, Peru (photo and observation by Roosevelt García). Although no voucher specimen was preserved, M. emiliae is unambiguously identifiable in the photograph by its diagnostic dorsal coloration (see text).

nally reported by Thomas (1912a) and subsequently noted by Pine and Handley (1984), Patton et al. (2000), and Pavan and Voss (2016: fig. 14) was also seen in our fresh material. The ventral fur of MUSM 2083 (an adult female), for example, was bright pink in life (on 27 May 1998), but it soon faded to a dull beige on the dried skin. Although sample sizes are small, it seems noteworthy that adult males and adult females in our Peruvian material have nonoverlapping measurements for many craniodental dimensions (table 13).

ETHNOBIOLOGY: The Matses do not distinguish this species from other short-tailed opossums (all known as <u>yama</u>; see the account for *Monodelphis*, above) and therefore have no particular beliefs about it.

Sex HBL LT HF Ear CBL. NL NB LIB LPB

ZB

PL

PR

MTR

LM

M1-3

WM3

Weight

18.2

18.1

11.0

13.6

7.1

2.4

40

Measure	ments (mm)	and weights	(g) of Mono	delphis emil	iae from eas	tern Peru ^a	
AMNH 268221*	AMNH 276721*	MUSM 22333*	MUSM 14148	MUSM 20452	MUSM 13298*	MUSM 14146	MUSM 14149
male	male	male	male	male	female	female	female
113	142	129	132	144	116	_	_
57	69	71	55	61	53	_	_
22	24	24	21	24	19	_	_
15	15	15	13	16	15	_	_
33.4	33.8	33.9	33.2	35.5	29.9	28.9	28.9
16.6	_	16.0	15.6	16.4	14.2	12.8	_
5.6	4.9	5.8	5.6	6.1	4.9	4.6	4.7
_	_	_	_	8.0	6.2	_	6.2
5.5	5.2	5.7	5.8	5.4	6.1	6.0	6.2

21.2

19.1

11.6

13.2

6.8

5.8

2.4

72

17.6

16.8

10.8

11.9

6.5

5.5

2.3

35

16.4

15.6

10.4

11.8

6.6

5.6

2.3

17.0

15.6

10.3

11.2

6.3

5.5

2.2

TABLE 13

18.7

17.6

10.7

13.0

7.0

5.9

2.2

43

19.3

18.2

11.6

13.4

7.1

5.9

2.3

72

19.0

18.4

10.9

13.4

7.1

5.9

2.3

64

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the five specimens we collected, one (AMNH 268221) was captured in a Matses house surrounded by secondary vegetation; another (MUSM 11065) was captured by hand in old secondary vegetation near a Matses swidden; another (MUSM 13298) was trapped on the ground in valley-bottom primary forest; a third (MUSM 23807) was trapped on the ground in primary forest growing on white sand; and the last (AMNH 276721) was taken in a pitfall in swampy primary forest. The specimen from San Pedro was trapped "on a hilltop in a primary terra firme forest" (Valqui, 2001). Based on these observations, it would seem that Monodelphis emiliae is a habitat generalist, although Patton et al.'s (2000) trapping results suggest that it might not occur in seasonally flooded forests. One of our specimens

(MUSM 13298) was taken on the same date, along the same trapline, and in the same habitat (primary upland rainforest) as a specimen of M. peruviana (AMNH 272695). Consistent with the Matses' observation that short-tailed opossums are diurnal, MUSM 11065 was captured by hand at 07:30 hrs, and MUSM 13298 was found at 17:00 hrs in a trap that had previously been checked and found empty at dawn.

Although Monodelphis emiliae was reported from the "Iquitos area" by Patton et al. (2000), all the specimens known to have been collected in northeastern Peru are from the right ("south") bank of the Amazon.9 Despite many decades of collecting near Iquitos—on the left

^a Specimens marked with an asterisk are from the Yavarí-Ucayali interfluve.

⁹ Note that, due to the river's convoluted course, the right bank of the Amazon near Iquitos is actually the east side and the left bank is the west side (fig. 2, inset). To avoid confusion, however, we use "south" and "north" with respect to the river's macrogeographic orientation.

("north") bank of the river—including the impressive faunal survey effort monographed by Hice and Velazco (2012), no specimens or sightings of *M. emiliae* have been reported from there. Nor has *M. emiliae*, which is very widely distributed along the right bank of the lower Amazon (Pine and Handley, 2008: map 41), been reported to occur at any other leftbank locality. Thus, it seems reasonable to conclude that the Amazon effectively limits the northward distribution of this species.

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OTHER SPECIMENS EXAMINED (TOTAL = 12): **Brazil**—Amazonas, Igarapé Porongaba (MVZ 190335), Seringal Condor (MVZ 190334); Pará, Baião (AMNH 96810), Boim (AMNH 37491, BMNH 11.12.22.16 [holotype]), Vila Braga (BMNH 20.7.14.44). **Peru**—Cusco, Cashiriari (MUSM 14146, 14148), Pagoreni A (MUSM 36686), San Martín (MUSM 14149); Loreto, Cerros de Canchaguaya (MUSM 18028), Cerros de Contaya (MUSM 20452).

Tribe Metachirini

Members of this tribe are commonly known as "brown four-eyed opossums" or "pouchless four-eyed opossums" to distinguish them from the grayish, pouched four-eyed opossums referred to Philander. The only included genus, Metachirus, was long thought to be monotypic, but molecular sequence analyses reported by Patton et al. (2000) and Patton and Costa (2003) recovered several mtDNA haplogroups, some of which were so highly divergent as to suggest the existence of multiple species. Indeed, there is no lack of available names for brown four-eyed opossums: in the last synthesis of the taxonomic literature (Gardner and Dagosto, 2008), no fewer than 11 epithets were treated as synonyms or subspecies of M. nudicaudatus (Geoffroy, 1803), the type locality of which is in northeastern Amazonia (French Guiana). In the account that follows, we explain why we use a different binomen for the brown four-eyed opossums of the Yavarí-Ucayali interfluve.

Metachirus myosuros (Temminck, 1824)

Figures 13B, 14B, 15B

VOUCHER MATERIAL (TOTAL = 12): Nuevo San Juan (AMNH 268217, 268218, 272780, 273057; MUSM 11049, 11051, 11053, 11054, 13293, 15308, 15309), San Fernando (FMNH 89001).

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (as *Metachirus nudicaudatus*; Pacheco, 1991; Pavlinov, 1994; Fleck and Harder, 1995), San Pedro (as *M. nudicaudatus*; Valqui, 1999, 2001).

IDENTIFICATION: Same-sex morphometric comparisons of our voucher material and other specimens from southwestern Amazonia with typical examples of Metachirus nudicaudatus (from northeastern Amazonia) document broad overlap in most external and craniodental dimensions (table 14). However, side-by-side visual comparisons of skulls reveal consistent differences in other aspects of craniodental morphology (table 15). Most conspicuously, the left and right scars that mark the dorsalmost origin of the temporalis muscle on each side of the skull are only weakly convergent posteriorly in most specimens of typical M. nudicaudatus, usually remaining widely separated over the parietals and interparietal (fig. 13A); if a sagittal crest is formed, usually in large adult male specimens, it is restricted to the midline of the interparietal. By contrast, the temporalis scars are more strongly convergent posteriorly in fully adult specimens from southwestern Amazonia, often uniting on the midline of the posterior braincase to form a low sagittal crest over the interparietal and along the mid-parietal suture (fig. 13B). Additionally, the rostrum tends to be more robust and the zygomatic arches tend to be more rounded laterally in southwestern Amazonian material than in M. nudicaudatus, which typically has a longer, narrower rostrum

TABLE 14
Measurements (mm) and Weights (g) of Metachirus nudicaudatus and M. myosuros

	Males		Fen	nales
	M. nudicaudatus ^a	M. myosuros ^b	M. nudicaudatus ^c	M. myosuros ^d
HBL	276 ± 17 (255–298) 8	254 ± 18 (217–285) 23	259 ± 17 (240-290) 7	250 ± 17 (218-278) 10
LT	347 ± 25 (302–380) 8	303 ± 21 (256–336) 23	344 ± 14 (326–370) 7	297 ± 22 (265–336) 10
HF	47 ± 3 (44–51) 9	$43 \pm 2 \ (40-47) \ 24$	44 ± 2 (41–46) 7	41 ± 3 (37-46) 12
Ear	$38 \pm 2 \ (35-40) \ 9$	$35 \pm 2 (30-39) 22$	39 ± 2 (35–41) 7	35 ± 3 (30–39) 11
CBL	61.1 ± 1.9 (57.6–63.9) 10	57.3 ± 2.8 (51.2–62.9) 24	$58.0 \pm 1.4 \ (56.5 - 59.6) \ 7$	$54.9 \pm 2.8 \ (50.4 - 60.5) \ 14$
NL	$30.9 \pm 1.3 \ (29.0 - 33.2) \ 12$	28.7 ± 1.8 (25.4–32.4) 24	29.2 ± 1.2 (27.6–30.6) 7	$27.9 \pm 1.6 \ (25.0 - 30.7) \ 13$
NB	$8.8 \pm 0.4 \ (8.2 - 9.4) \ 11$	$8.6 \pm 0.6 \ (7.41 - 10.3) \ 26$	$8.6 \pm 0.4 \ (8.1 - 9.1) \ 8$	$8.5 \pm 0.8 \ (7.4 – 10.1) \ 14$
LPB	$9.7 \pm 0.4 \ (9.0 - 10.0) \ 12$	$9.3 \pm 0.4 \ (8.6 - 10.3) \ 26$	$9.3 \pm 0.3 \ (8.5 - 9.6) \ 9$	$9.3 \pm 0.4 \ (8.8 - 9.8) \ 14$
ZB	29.6 ± 0.9 (28.3–31.0) 10	29.5 ± 1.7 (25.7–32.6) 24	27.4 ± 1.1 (25.8–28.9) 7	27.7 ± 1.0 (25.2–29.8) 14
PL	34.6 ± 1.3 (32.7–36.3) 11	$32.9 \pm 1.6 (29.7 - 36.1) 25$	$33.3 \pm 0.6 \ (32.1 - 34.0) \ 9$	$31.9 \pm 1.6 \ (29.4 – 35.5) \ 14$
PB	$17.8 \pm 0.3 \ (17.3 - 18.2) \ 11$	17.6 ± 0.8 (16.0–19.2) 26	$17.4 \pm 0.7 \ (16.7 - 18.5) \ 9$	$17.4 \pm 0.6 \ (16.4 - 18.2) \ 14$
MTR	$25.7 \pm 0.6 \ (25.1 - 27.3) \ 12$	$24.1 \pm 0.9 \ (22.4 - 25.8) \ 26$	$25.2 \pm 0.3 \ (24.8 - 25.9) \ 9$	$23.4 \pm 0.9 \ (22.4 - 25.8) \ 14$
LM	$12.0 \pm 0.3 \ (11.3 - 12.6) \ 12$	11.5 ± 0.4 (10.7–12.4) 26	$11.9 \pm 0.4 \ (11.4 - 12.6) \ 9$	11.4 ± 0.4 (11.0–12.4) 14
M1-3	$10.0 \pm 0.4 \ (9.3 – 10.7) \ 12$	$9.4 \pm 0.3 \ (8.8 10.1) \ 26$	$9.8 \pm 0.3 \ (9.4 – 10.4) \ 9$	$9.4 \pm 0.3 \ (9.0 - 10.1) \ 14$
WM3	$3.8 \pm 0.2 \ (3.6 - 4.2) \ 12$	$3.8 \pm 0.2 \ (3.4 - 4.4) \ 26$	$3.7 \pm 0.2 \ (3.6 - 4.3) \ 9$	$3.7 \pm 0.2 \ (3.4 - 4.0) \ 14$
Weight	427 ± 51 (330–480) 9	387 ± 62 (248–485) 16	335 ± 56 (260–410) 7	325 ± 59 (270–430) 7

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from French Guiana, Guyana, Surinam, and Amapá): AMNH 266450, 267009, 267010; MNHN 1995.906; ROM 33051, 119571; USNM 393548, 393553, 461456, 461457, 545544, 548440.

and almost parallel-sided zygomatic arches. In ventral view, the maxillopalatine fenestrae are much shorter and narrower in southwestern Amazonian specimens than in typical M. nudicaudatus (fig. 14), and statistical comparisons of fenestral length and width confirm that these visually obvious differences are highly significant (p < 0.0001 by two-tailed Student's t tests). Although subtle differences in the dentition also appear to distinguish southwest-

ern Amazonian specimens from typical *M. nudicaudatus*, the only dental character that we were able to score with confidence was size of the entoconid. This is a small cusp, subequal to or sometimes smaller than the paraconid on unworn m1–m3 in *M. nudicaudatus* (fig. 15A), but it is a large cusp, substantially bulkier than the paraconid and almost equal in size to the hypoconid in southwestern Amazonian specimens (fig. 15B).

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from southwestern Amazonia; specimens from the Yavarí-Ucayali interfluve are marked with an asterisk): AMNH 268217*, 273057*; BMNH 1.6.7.69, 1.6.7.71; FMNH 20798, 24788, 75097, 75098, 169803, 174437, 174441; MSB 70283; MUSM 11054*, 15309*; MVZ 136383, 157634, 166501, 166504, 190287, 190288, 190297; USNM 364161, 390039, 390040, 499009, 546190.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from French Guiana, Guyana, Surinam, and Amapá): AMNH 266435, 266440, 266449, 266455; MNHN 1995.907; ROM 32459, 34252, 111938; USNM 393544.

^d The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from southwestern Amazonia; specimens from the Yavarí-Ucayali interfluve are marked with an asterisk): AMNH 272780*; BMNH 1.6.7.72–1.6.7.74; FMNH 18206, 20795, 84248, 87128; MVZ 136384, 166505, 190296, 190299; USNM 390036, 546191.

Diagnostic Haits of Incucan us numerous and M. myosuros				
	M. nudicaudatus	M. myosuros		
Temporal crests	usually weakly convergent	usually strongly convergent		
Sagittal crest	usually absent	usually present		
Length MPF ^a	$10.1 \pm 0.9 \text{ mm } (N = 19)$	$6.5 \pm 1.3 \text{ mm } (N = 34)$		
Width MPFa	$2.8 \pm 0.3 \text{ mm } (N = 19)$	$1.4 \pm 0.6 \text{ mm} (N = 34)$		
Entoconids	small	large		

TABLE 15

Diagnostic Traits of Metachirus nudicaudatus and M. myosuros

To supplement our morphological comparisons, we sequenced the entire mitochondrial gene encoding cytochrome b from ethanolpreserved tissues of 29 specimens of Metachirus from 27 localities in Central and South America representing most of the nominal taxa currently treated as synonyms or subspecies of Metachirus nudicaudatus (fig. 16, appendix 4). The best-fitting topology obtained from maximum-likelihood analysis of this dataset (fig. 17) recovered a strongly supported basal dichotomy between sequences from northeastern Amazonia (French Guiana, Guyana, and Surinam) and those from elsewhere in the geographic range of the genus; uncorrected pairwise distances across this basal split are about 11.2%, on average, and are much larger than any others we obtained from these data (table 16). The mtDNA haplogroup that includes our sequenced vouchers ("SW Amazonia") also includes sequences from southern Peru (Cuzco and Madre de Dios), eastern Bolivia (Cochabamba and La Paz), and western Brazil (Acre and Amazonas). Uncorrected pairwise distances within this group are uniformly small (about 1.4% on average), and visual inspection of the gene tree suggests that there is little (if any) internal phylogeographic structure. Sister to this clade is a group of sequences from the Atlantic Forest of southeastern Brazil, and these two haplogroups are sister to a clade that includes sequences from northwestern Amazonia and Central America.

Although a comprehensive revision of Metachirus is beyond the scope of this report, the results described in the preceding paragraphs clearly suggest that our southwestern Amazonian material is specifically distinct from M. nudicaudatus which, based on specimens we personally examined (see below), seems to be endemic to northeastern Amazonia (French Guiana, Guyana, Surinam, and the Brazilian state of Amapá). Of the many nominal taxa currently referred to the genus (table 17), the oldest that applies to our material is M. myosuros, which is based on a lectotype from southeastern Brazil. Specimens that we examined from southeastern Brazil (mostly from Rio de Janeiro and São Paulo at the AMNH, FMNH, and USNM; not listed below) closely

TABLE 16

Percent Uncorrected Sequence Divergence within and among Species and Haplogroups of Metachirus^a

	nudicaudatus	myosuros			
		SWA	AF	NWA	CA
nudicaudatus	0.8				
myosuros SWA	10.9	1.4			
myosuros AF	11.4	5.3	1.3		
myosuros NWA	11.6	7.6	7.4	0.3	
myosuros CA	11.6	6.8	7.2	6.5	4.6

 $^{^{\}rm a}$ At the cytochrome b locus; diagonal elements (in bold-face) are mean uncorrected within-group distances. Haplogroup abbreviations: AF, Atlantic Forest; CA, Central America; NWA, northwestern Amazonia; SWA, southwestern Amazonia.

^a MPF = maxillopalatine fenestrae; only one fenestra, either the right or the left, was measured per specimen. Tabulated statistics are the sample mean plus or minus one standard deviation computed from adult measurements of both sexes.

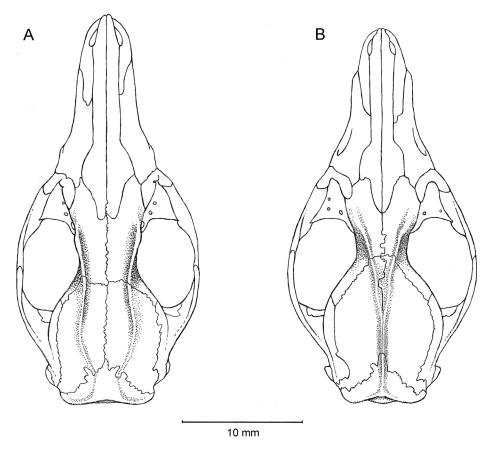
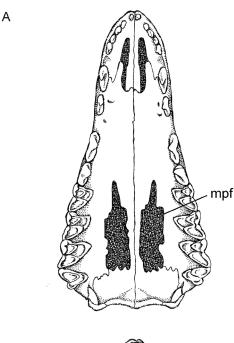


FIG. 13. Dorsal cranial views of **A**, *Metachirus nudicaudatus* (AMNH 267009, an adult male from French Guiana) and **B**, *M. myosuros* (AMNH 273057, an adult male from the Yavarí-Ucayali interfluve).

resemble our material from southwestern Amazonia in all the traits previously discussed, which we regard as diagnostic of the species. Because types and other material of the remaining nominal taxa currently referred to *Metachirus* more closely resemble *M. myosuros* than *M. nudicaudatus*, we provisionally treat them as junior synonyms of the former species; all are based on seemingly minor coat-color differences, and none appears to exhibit morphometric traits that exceed the range of variation in our southwestern Amazonian series.

The absence of any sequence data from southeastern Amazonia (south of the Amazon and east of the Rio Madeira) is a major hiatus in our genetic sampling, so only phenotypic traits are

available for identification of the populations that occur there. Specimens from localities on the right (east) bank of the Tocantins (e.g., Baião, Belém, Bragança, and Capim; at the AMNH and USNM) exhibit all the diagnostic craniodental traits of Metachirus myosuros, whereas those from the Tocantins-Xingu interfluve are morphologically distinctive (e.g., with large maxillopalatine fenestrae and small entoconids like M. nudicaudatus, but with strongly convergent temporalis scars like M. myosuros). Patton et al. (2000) reported a highly divergent cytochrome b sequence from this region, but we have not seen the voucher specimen (in Manaus), nor was this sequence included in a subsequent analyses of Metachirus mitochondrial DNA (Costa and Patton, 2006). Additional



2019

В

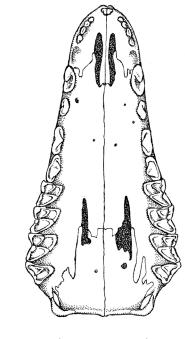


FIG. 14. Ventral views of palates of **A**, *Metachirus nudicaudatus* (AMNH 266449) and **B**, *M. myosuros* (MUSM 15309) illustrating species divergence in size of the maxillopalatine fenestrae (**mpf**).

10 mm

sequence data from this region would be very welcome, as would a careful assessment of associated morphological material.

ETHNOBIOLOGY: The Matses do not distinguish this species from other "four-eyed" opossums (all known as <u>cheka bëbëdi</u>; see the account for *Philander*, below) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the 11 specimens of *Metachirus myosuros* for which we have capture information, seven were trapped on the ground or near ground level (one was trapped on a fallen log), two were shot on the ground at night, one was caught by hand in the daytime as it ran out of a leaf nest on the ground, and another was caught by hand on the ground in the late afternoon as it was eating fallen guavas. One trapped specimen is also known to have been captured in the daytime (between 06:30 and 15:00 hours). Four of these specimens were taken in primary upland forest, whereas seven were in secondary growth (abandoned swiddens).

OTHER SPECIMENS EXAMINED FROM SW AMA-ZONIA (TOTAL = 39): Bolivia—Cochabamba, Cavernas de Repechón (MSB 70283); La Paz, Chulumani (BMNH 1.6.7.69-1.6.7.74 [type series of bolivianus]). Brazil—Acre, Nova Vida on right bank Rio Juruá (MVZ 190296, 190297), Sena Madureira (USNM 546190, 546191); Amazonas, Condor on left bank Rio Juruá (MVZ 190288), Penedo on right bank Rio Juruá (MVZ 190287), Vira Volta on left bank Rio Juruá (MVZ 190299); Rondônia, 8 km N Porto Velho (USNM 390034, 390035). **Peru**—*Cuzco*, Consuelo (FMNH 174437, 174441), Huajyumbe (FMNH 84248), Kiteni on Río Urubamba (MVZ 166505), Quincemil (FMNH 75097, 75098); Junín, Chanchamayo (FMNH 18206), San Ramón (FMNH 20795, 20798); Loreto, Santa Elena on Río Samiria (FMNH 87128); Madre de Dios, Hacienda Érica (MVZ 166501, 166504), "Inambari River" (BMNH 2.7.27.8 [holotype of infuscus]), Lago Sandoval (MVZ 157634), Puerto Maldonado (USNM 390040), 4 km S Puerto Maldonado (USNM 390036), 4 km W Puerto Maldo-

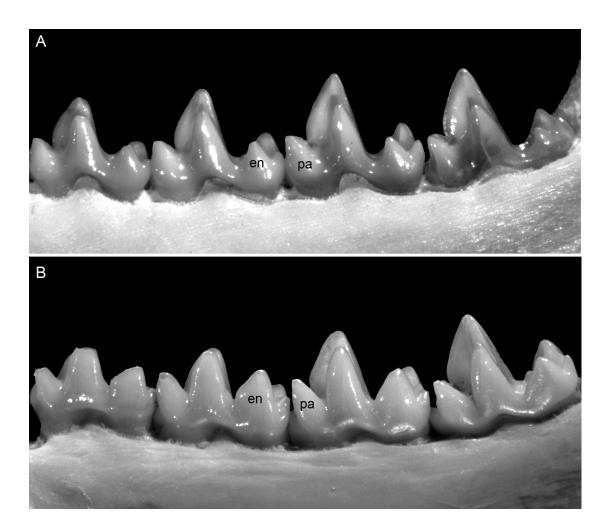


FIG. 15. Lingual views of lower molars of **A**, *M. nudicaudatus* (AMNH 266451) and **B**, *M. myosuros* (AMNH 268218) illustrating species divergence in relative size of the entoconid (**en**) and paraconid (**pa**).

nado (USNM 390039), 2.75 km E Shintuya (FMNH 169803); *Pasco*, Pozuzo (FMNH 24788), San Juan (USNM 364161); *Ucayali*, Balta (MVZ 136383, 136384), 59 km SW Pucallpa (USNM 499009).

Specimens of *Metachirus Nudicaudatus* Examined (Total = 33): **Brazil**—*Amap*á, Serra do Navio (USNM 393544–393553, 461456, 461457, 545544, 546189). **French Guiana**—Paracou (AMNH 266435, 266440, 266449, 266450, 266455, 267009, 267010; MNHN 1995.906, 1995.907), "River Arataye" (USNM 548440). **Guyana**—*East Berbice-Corentyne*, Amuku Creek (ROM 34252); *Potaro-Siparuni*, Iwokrama Forest (ROM 111938);

Rupununi, 30 mi E Dadanawa (ROM 32459), Kwitaro River (ROM 33051). **Surinam**—*Brokopondo*, Brownsberg Nature Park (ROM 114155); Sipaliwini, Bakhuis Transect 9 (ROM 117030), Bakhuis Transect 11 (ROM 117525), Iconja Landing (ROM 120317), Tafelberg (ROM 119571).

Tribe Didelphini

Members of the tribe Didelphini are large opossums (with average adults weights >300 g), and the three genera that occur in our region are all unambiguously distinguishable by exter-

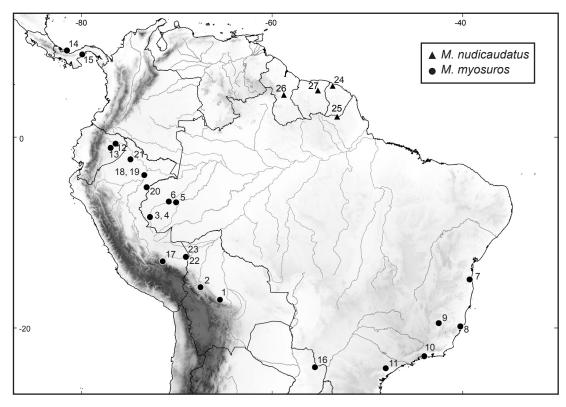


FIG. 16. Collecting localities of sequenced specimens of *Metachirus*. Numbers are keyed to gazetteer entries in appendix 4.

nal and craniodental characters (Emmons, 1997; Voss and Jansa, 2009). However, the water opossum is seldom observed, and the Matses do not distinguish among local species of "foureyed" opossums (*Philander* spp. and *Metachirus myosuros*); only the so-called common opossum (*Didelphis marsupialis*) has its own proper name in the Matses zoological lexicon.

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Chironectes minimus (Zimmermann, 1780) Figure 18

Voucher Material: Centro Unión (FMNH 106721).

OTHER INTERFLUVIAL RECORDS: Nuevo San Juan (this report), Quebrada Pobreza (Pitman et al., 2015), San Pedro (Valqui, 1999), Santa Rosa (this report).

IDENTIFICATION: With its boldly gray-andblack banded dorsal pelage, webbed hind feet, and semiaquatic habits, the water opossum cannot be confused with any other species of Neotropical mammal. The single specimen we examined from our region (FMNH 106721) is mounted in a crudely lifelike pose with the skull inside; stuffed with sawdust and with painted seeds for eyes, it was probably manufactured for the tourist trade. A penciled cardboard tag attached to the left hind foot indicates the locality (Río Aucayo), the collector (Pekka Soini), and the date (12 February 1972). An inked FMNH label tied to the right hind foot further resolves the locality as "Río Aucayo, Centro Unión." We infer that the specimen was probably purchased from a native taxidermist by Pekka Soini in the course of his fieldwork at Centro Unión in the

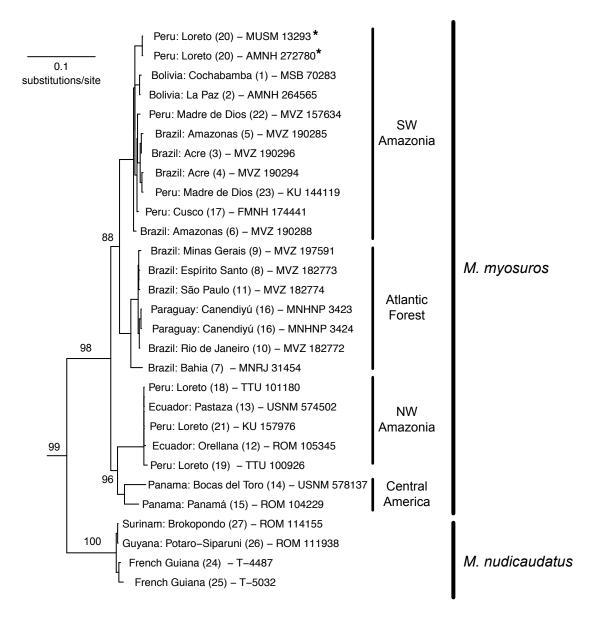


FIG. 17. Results of maximum-likelihood analysis (lnL = -5384.07) of cytochrome b sequences of *Metachirus* (outgroups used for rooting are not shown). Branch tips are sequenced specimens labeled by geographic origin and a sequence identifier (see appendix 4); numbers in parentheses refer to localities mapped in figure 16. Branch support values above selected branches are bootstrap frequencies. Asterisks mark specimens from the Yavarí-Ucayali interfluve.

	Туре	Type locality	Status (this report)
antioquiae Allen, 1916	AMNH 37751 ^a	La Frijolera, Antioquia, Colombia	synonym of M. myosuros
bolivianus Allen, 1901	BMNH 1.6.7.73 ^a	Chulumani, La Paz, Bolivia	synonym of M. myosuros
colombianus Allen, 1900	AMNH 15448 ^a	"Donamo," Magdalena, Colombia	synonym of M. myosuros
dentaneus Goldman, 1912	USNM 172732a	Gatun, Colón, Panama	synonym of M. myosuros
imbutus Thomas, 1923 ^b	BMNH 13.10.24.71 ^a	Mindo, Pichincha, Ecuador	synonym of M. myosuros
infuscus Thomas, 1923	BMNH 2.7.27.8 ^a	Inambari River, Madre de Dios, Peru	synonym of M. myosuros
modestus Thomas, 1923	BMNH 3.2.3.38 ^a	Sapucay, Paraguarí, Paraguay	synonym of M. myosuros
myosuros Temminck, 1824	NMW B-2589 ^c	Ipanema, São Paulo, Brazil ^d	valid species
nudicaudatus Geoffroy, 1803	MNHN 1990-420a	Cayenne, French Guiana	valid species
<i>personatus</i> Miranda-Ribeiro, 1936	MNRJ 1218 ^e	Serra da Piraquara, Rio de Janeiro, Brazil	synonym of M. myosuros
phaeurus Thomas, 1901	BMNH 1.3.19.44 ^a	San Javier, Esmeraldas, Ecuador	synonym of M. myosuros
tschudii Allen, 1900	AMNH 11815/10107 ^a	"Guayabamba," Amazonas, Peru	synonym of M. myosuros

TABLE 17
Nominal Species-group Taxa Referred to *Metachirus*

early 1970s (appendix 1), but there is no way to be certain about exactly where the animal was collected. Fortunately, there are other interfluvial records of *Chironectes*, one of which is documented by a photograph (fig. 18).

Although central Amazonia (including the Yavarí-Ucayali interfluve) falls outside the mapped geographic range of *Chironectes minimus* in most standard references (e.g., Stein and Patton, 2008), recent observations and gene-sequencing results (Ardente et al., 2013; Brandão et al., 2015; Oliveira et al., 2016; Voss and Jansa, 2018) suggest that the water opossum is continuously distributed from Central America to southeastern Brazil. Despite geographic variation in craniodental morphology reported by Damasceno and Astúa (2016) and Cerqueira and Weber (2017), this species seems to be genetically undifferentiated across most, if not all, of cis-Andean South America,

and it shows minimal genetic divergence even across the Andes (Voss and Jansa, 2018). Therefore, the "subspecies" of *C. minimus* currently recognized by authors (Gardner, 2005; Stein and Patton, 2008) are unlikely to represent valid taxa.

ETHNOBIOLOGY: Because the water opossum is unknown to most of the Matses, they have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: One of the previously unpublished records from our region is based on an unambiguous sighting made by Matses hunters near Nuevo San Juan and reported by them to D.W.F. in 2006. The second is based on a specimen killed by a Matses hunter on 27 January 2017 near the village of Santa Rosa and photographed by D.W.F. at Estirón on the following day; in the absence of collecting permits, it was not preserved.

^a Holotype by original designation.

^b Gardner and Dagosto (2008: 37) incorrectly spelled this epithet as "inbutus."

^c The lectotype designated by Pohle (1927). A specimen in the Berlin Museum (ZMB 2326) is incorrectly labelled as the type of *myosuros*: it is not the specimen designated as lectotype by Pohle and cannot have been part of the original material examined by Temminck (1824), who did not mention any specimens from Berlin.

^d Fixed by lectotype selection (Pohle, 1927).

^e Lectotype (Langguth et al., 1997).



FIG. 18. *Chironectes minimus* killed by a Matses hunter on the lower Quebrada Chobayacu (photographed by D.W.F. at Estirón, 2017). The webbed hind feet and black-and-gray banded dorsal pelage are unambiguously diagnostic traits.

Didelphis marsupialis Linnaeus, 1758

Voucher Material (Total = 7): Jenaro Herrera (AMNH 276703; MUSM 23797), Nuevo San Juan (AMNH 268213, 272836; MUSM 11025, 11027, 13282).

OTHER INTERFLUVIAL RECORDS: Actiamë (Vriesendorp et al., 2006a), Divisor (Vriesendorp et al., 2006b), Jenaro Herrera (Fleck and Harder, 1995), Nuevo San Juan (three unvouchered sightings), San Pedro (Valqui, 1999).

IDENTIFICATION: *Didelphis marsupialis*, the so-called common or black-eared opossum of Amazonia and Central America, is externally unmistakable (Husson, 1978; Emmons, 1997), and although similar in most qualitative aspects of craniodental morphology to species of *Philander* (Voss and Jansa, 2009), it is so much larger in all dimensions that skulls, and even isolated teeth, are

easily identified. There is remarkably little genetic variation in this species throughout its geographic range (e.g., <1.6% mean sequence divergence at the cytochrome b locus among samples from Costa Rica to central Amazonia; Patton et al., 2000: fig. 39). Measurements of the few adult specimens from our region (table 18) overlap the range of variation reported by Patton et al. (2000) for material collected along the Rio Juruá in western Brazil, but our specimens are large by comparison with their tabulated sample means.

Although the name *Didelphis marsupialis* has been used consistently for many years to refer to the black-eared Amazonian opossum, Gurgel-Filho et al. (2015) resurrected the obsolete synonym *D. karkinophaga* Zimmermann, 1780, for this species and proposed that Linnaeus's (1758) epithet be used for the white-eared species that has long been known

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	MUSM 13282	AMNH 276703	MUSM 23797
Sex	male	female	unknown
HBL	417	479	_
LT	425	429	_
HF	67	65	_
Ear	55	60	_
CBL	100.8	102.6	93.6
NL	46.8	47.9	42.4
NB	15.0	15.2	12.9
LIB	19.8	19.3	19.0
LPB	11.5	11.8	11.3
ZB	52.3	50.6	47.7
PL	61.7	63.3	57.4
PB	30.9	31.4	29.2
MTR	40.4	42.6	40.8
LM	19.8	19.7	19.9
M1-3	16.2	16.1	16.6
WM3	5.5	5.8	6.0
Weight	1200		_

as *D. albiventris* Lund, 1841. Their justification for thus disrupting current usage was discussed by Dias et al. (2018), who thought that a specimen in Uppsala might be the lectotype designated by Thomas (1911). Feijó and Voss (2019) disagreed, established that the lectotype is almost certainly lost, and designated a neotype for *D. marsupialis* to conserve prevailing usage of this name for the black-eared opossum of Amazonia.

ETHNOBIOLOGY: The common opossum is called <u>mapiokos</u> by the Matses, a term that is not analyzable and is not found in other Panoan languages. The Matses recognize its similarity to the opossums they call <u>cheka</u>, but they do not classify it as a type of cheka.

Common opossums are considered pests because they eat chickens at night. The Matses kill them when they find them near chicken coops. The Matses traditionally did not eat common opossums, but local nontribal Peruvians do, so a few Matses eat them now, but most do not because of their foul smell.

The Matses believe that when the common opossum vocalizes, it is a death omen. If it calls from the trees, a man will die, and if it calls from the ground a woman will die.

MATSES NATURAL HISTORY: The common opossum has a naked tail. It has dark hairs sprinkled with white hairs, as if its coat were turning gray. It has a white snout and large ears. It has a strong, foul odor that can be smelled from far away. One can readily detect its scent where it has passed by hours ago.

The common opossum is terrestrial and arboreal, but forages mostly on the ground. It is found in upland forest, floodplain forest, and along streams. It occurs in both primary and secondary forest. It comes to Matses swiddens to eat plantains and papayas. It makes its nest in hollow trees and in the crowns of <u>isan</u> palm trees (*Oenocarpus bataua*).

The common opossum is nocturnal and solitary. The female carries its young in its pouch and suckles them inside the pouch. It gives birth to many young.

The common opossum is eaten by jaguars, ocelots, and margays. It vocalizes saying "chocod chocod."

The common opossum eats spiny rats and birds, including tinamous, that it finds nesting on or near the ground at night. It enters coops to eat chickens, and it also eats pet guans, crickets/katydids, cockroaches, and rotten meat.

REMARKS: Of our seven specimens, two were trapped on the ground in a swamp-palm (*Mauritia flexuosa*) swamp, one was trapped on the ground in primary upland forest, one was trapped at a height of 9 m in a tree in primary upland forest, one was caught by hand 2 m above the ground on a sapling in primary upland forest, one was trapped by a Matses boy (probably on the ground in secondary forest), and one was shot by a mestizo hunter in unrecorded circum-

TABLE 19
Morphological Comparisons among Three Species of Gray Four-eyed Opossums (Philander)
from Eastern Peru

	P. mcilhennyi	P. pebas	P. canus ^a
Dorsal pelage	distinctly blackish middorsally	uniformly grayish ^b	uniformly grayish
Ventral pelage	dark grayish or blackish	mostly gray-based	mostly self-whitish
Naked (scaly) part of tail	usually ½ to ¾ white	usually < 1/4 white	usually ¼ to ½ white
Nasal bones	long ^c	intermediate in length	$short^d$
Unworn molar enamel	smooth	crenulated	smooth
Pre- and postprotocingula	absent	presente	absent
Posterior cingulids	absent	$present^{\rm f}$	absent

- ^a Not currently known to be a member of the Yavarí-Ucayali interfluvial fauna (see text).
- ^b Sometimes indistinctly darker middorsally than on flanks.
- ^c Often extending posteriorly to or between postorbital processes (see Voss et al., 2018: fig. 18B).
- d Apparently never extending posteriorly to level of postorbital processes (see Voss et al., 2018: fig. 18A).
- e See Voss et al. (2018: fig. 19A).
- f See Voss et al. (2018: fig. 20A).

stances (near Jenaro Herrera). The "common" opossum was far from common at Nuevo San Juan in 1999, when Matses hunters recorded only three sightings in 409 hours of night hunting: once perched at an unrecorded height on a vine in old secondary growth, once on a fallen tree next to a stream (habitat unrecorded), and once on the ground in hilltop primary forest.

Philander Brisson, 1762

Two species of gray four-eyed opossums, Philander mcilhennyi and P. pebas, are definitely known to occur in the Yavarí-Ucayali interfluve, and a third species (P. canus) could be expected to occur there based on geographic range data (appendix 2). Specimens of both P. pebas and P. canus have long been misidentified as P. opossum (an eastern-Amazonian taxon; Voss et al., 2018), so the identity of animals previously reported as P. opossum from the Yavarí-Ucayali interfluve (Pavlinov, 1994; Fleck and Harder, 1995) is unclear. To facilitate the identification of specimens collected in the course of future fieldwork, we summarize qualitative traits and morphometric variation for all three species (tables 19-21).

The Matses do not consistently recognize more than a single kind of opossum with pale supraocular spots, so the name they apply to such animals, <u>cheka bëbëdi</u>, could refer either to gray four-eyed opossums or to the superficially similar brown four-eyed opossum (*Metachirus myosuros*). Because species of *Philander* are more commonly encountered than *M. myosuros*, we summarize relevant ethnographic information here.

ETHNOBIOLOGY: Cheka bëbëdi, the most frequently used name for these species, literally means "spotted-forehead opossums," but in some Matses villages they are called cheka dëwisak "long-snouted opossums." They are sometimes also referred to as chekadapa "big opossum," but this is not considered a real name; rather it is a descriptive phrase used to distinguish these large species from mouse opossums. Some Matses recognize that there is more than one local type of cheka bëbëdi, but they do not differentiate them linguistically.

The Matses do not eat these opossums, although children sometimes shoot them with arrows. One informant mentioned that a four-eyed opossum ate his pet dove.

MATSES NATURAL HISTORY: Some four-eyed opossums are black, while others are gray,

		(11111) WILL (VOIGILES (B) OI IVINI	op comicine of 1 mmm.
	P. mcilhennyi ^a	P. pebas ^b	P. canus ^c
HBL	290 ± 10 (272–304) 13	279 ± 14 (253–297) 17	256 ± 19 (200-280) 20
LT	303 ± 22 (265–330) 13	$267 \pm 15 \ (241 - 300) \ 17$	282 ± 19 (245–319) 20
HF	$44 \pm 3 \ (40-49) \ 13$	44 ± 3 (40–48) 17	$40 \pm 2 (37-45) 20$
Ear	$40 \pm 3 \ (35-45) \ 13$	33 ± 2 (31–38) 16	37 ± 4 (29–42) 19
CBL	$75.2 \pm 2.4 \ (71.7 - 78.9) \ 12$	$70.6 \pm 2.8 \ (65.1 - 75.4) \ 27$	$64.0 \pm 2.6 \ (60.0 - 70.7) \ 21$
NL	$37.0 \pm 2.7 \ (31.7 - 39.9) \ 13$	$33.6 \pm 1.7 \ (30.6 - 36.4) \ 22$	$29.4 \pm 1.3 \ (26.8 - 31.4) \ 21$
NB	$8.8 \pm 1.0 \ (7.6 - 10.5) \ 12$	$7.8 \pm 0.8 \ (6.5 - 9.8) \ 27$	$7.4 \pm 0.9 \ (5.8 - 9.0) \ 21$
LIB	$13.7 \pm 1.2 \ (11.9 - 15.9) \ 13$	$12.2 \pm 0.7 \ (11.0 - 13.9) \ 27$	$10.6 \pm 0.6 \ (9.6 - 11.7) \ 21$
LPB	$8.9 \pm 0.5 \ (8.0 - 9.5) \ 13$	$8.7 \pm 0.3 \ (8.3 - 9.9) \ 27$	$7.9 \pm 0.3 \ (7.4 - 8.5) \ 21$
ZB	$38.3 \pm 2.1 \ (33.8 - 41.8) \ 12$	$35.8 \pm 2.3 \ (32.0 - 40.5) \ 27$	$34.0 \pm 1.7 \ (31.4 - 38.4) \ 21$
PL	$45.3 \pm 1.5 \ (42.2 - 48.0) \ 13$	$43.7 \pm 1.5 \ (40.5 - 46.3) \ 27$	$38.1 \pm 1.4 (36.2 - 41.5) 21$
PB	$22.1 \pm 0.9 \ (20.7 - 23.8) \ 13$	$20.0 \pm 0.8 \ (18.5 - 21.9) \ 27$	$19.3 \pm 0.7 \ (18.2 - 20.6) \ 21$
MTR	$31.5 \pm 0.7 \ (30.0 – 32.6) \ 13$	$30.6 \pm 0.8 \ (29.2 – 32.1) \ 27$	$27.4 \pm 0.8 \ (26.4 - 29.5) \ 21$
LM	$15.0 \pm 0.5 \ (13.9 - 15.9) \ 13$	$14.0 \pm 0.5 \ (13.4 - 15.1) \ 27$	$13.2 \pm 0.4 \ (12.4 - 13.7) \ 21$
M1-3	$12.6 \pm 0.5 \ (12.0 - 13.7) \ 13$	$11.7 \pm 0.5 \ (10.9 – 12.8) \ 27$	$11.1 \pm 0.4 \ (10.4 – 11.7) \ 20$
WM3	$4.6 \pm 0.3 \ (4.1 - 5.0) \ 13$	$4.2 \pm 0.2 \ (3.9 - 4.5) \ 27$	$4.1 \pm 0.2 \ (3.7 - 4.4) \ 21$
Weight	497 ± 95 (320–592) 10	416 ± 85 (310-610) 17	335 ± 52 (266–454) 14

TABLE 20
Summary Statistics for Measurements (mm) and Weights (g) of Male Specimens of *Philander*

and others are reddish/yellowish. They have a very long tail, a long snout, spots on their foreheads, and long whiskers.

2019

They are arboreal and terrestrial. They are common in all rainforest habitats but seem to be more common along streams.

Four-eyed opossums make nests in different places: in the leaf litter that collects at the base of large stemless palms; in hollow logs; in vine tangles up in the trees; on the ground at the base of two trees that are growing right next to each other; and in the crown of plantain plants. These they line with dry leaves.

Four-eyed opossums are nocturnal.

Four-eyed opossums have many young, which they carry around and suckle inside their pouches. The young leave the mother when they get about half the size of the mother. Other than mothers with young, they are solitary.

Four-eyed opossums are eaten by margays and ocelots.

Four-eyed opossums open their mouth very wide and hiss aggressively when found by people, and try to bite them if they get close.

Four-eyed opossums eat anything. They eat sweet tree fruits, the mesocarp of swamp-palm (*Mauritia*

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (specimens from the Yavarí-Ucayali interfluve are marked with an asterisk): AMNH 268224*, 273040*, 273054*, 273055*, 273089*; LSUMZ 14014; MUSM 11073*, 15322*; MVZ 136381; USNM 461133, 499003, 499006, 546220.

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements

⁶ The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (none from the Yavarí-Ucayali interfluve): LACM 91622; MUSM 33564, 33566, 33567, 33570, 33572, 33574, 33580, 33583, 33587, 33588, 33590, 33592, 33593, 33597–33600; MVZ 190343, 190344; TTU 98574, 98591, 98592, 98755, 101178, 101192, 101256.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (none from the Yavarí-Ucayali interfluve): AMNH 135887, 210402, 210410, 210411, 210413, 260037, 261269, 261271, 261272, 261278, 263966; FMNH 114707; MSB 55074, 55075 55854, 55856; USNM 390005, 390010–390012, 390562.

TABLE 21
Summary Statistics for Craniodental Measurements (mm) and Weights (g) of Female Specimens of Philander

	P. mcilhennyi ^a	P. pebas ^b	P. canus ^c
HBL	294 ± 12 (278–320) 10	279 ± 16 (255–303) 10	250 ± 17 (225–275) 19
LT	298 ± 15 (270-318) 10	264 ± 21 (244–312) 10	$280 \pm 20 \ (242 - 312) \ 20$
HF	43 ± 3 (39–50) 10	41 ± 2 (37–43) 10	39 ± 3 (35–43) 19
Ear	38 ± 2 (35–42) 10	32 ± 2 (30-36) 10	$38 \pm 3 \ (32-43) \ 20$
CBL	$72.4 \pm 2.6 \ (68.5 - 76.2) \ 8$	$68.5 \pm 3.3 \ (61.0 - 75.8) \ 23$	$62.1 \pm 3.0 \ (57.0 - 67.1) \ 22$
NL	$36.6 \pm 2.2 \ (33.6 - 41.4) \ 10$	$32.3 \pm 1.9 (29.2 - 35.1) 16$	$28.4 \pm 1.6 \ (25.2 - 31.0) \ 21$
NB	$8.2 \pm 0.5 \ (7.4 - 9.0) \ 10$	$7.3 \pm 0.8 \ (5.7 - 8.9) \ 23$	$7.1 \pm 0.6 \ (6.4 - 8.8) \ 22$
LIB	$12.8 \pm 0.7 \ (11.7 - 13.9) \ 10$	$11.6 \pm 1.0 \ (9.8 - 14.1) \ 22$	$10.1 \pm 0.5 \ (9.3 – 11.1) \ 22$
LPB	$9.0 \pm 0.3 \ (8.5 - 9.4) \ 10$	$8.8 \pm 0.3 \ (8.3 - 9.5) \ 23$	$7.8 \pm 0.3 \ (7.4 - 8.4) \ 22$
ZB	$36.1 \pm 1.5 (33.4 - 38.8) 10$	$34.2 \pm 1.9 (30.1 - 38.5) 23$	$32.4 \pm 1.6 \ (29.8 - 35.7) \ 22$
PL	$43.6 \pm 1.8 \ (41.1 - 47.0) \ 10$	$42.4 \pm 2.2 \ (37.8 - 46.7) \ 23$	$37.2 \pm 1.9 (33.8 - 40.1) 22$
PB	$22.0 \pm 1.2 \ (19.9 - 23.8) \ 10$	$19.7 \pm 0.7 \ (18.3 - 21.0) \ 22$	$19.0 \pm 0.8 \ (17.8 - 20.5) \ 22$
MTR	$30.6 \pm 1.2 \ (28.9 – 32.5) \ 10$	$29.4 \pm 1.1 \ (27.4 - 30.9) \ 23$	$26.7 \pm 1.0 \ (25.0 - 28.6) \ 22$
LM	$14.8 \pm 0.7 \ (13.8 - 15.9) \ 10$	$13.7 \pm 0.5 \ (12.7 - 14.5) \ 23$	$12.8 \pm 0.4 \ (12.2 - 13.6) \ 22$
M1-3	$12.5 \pm 0.7 \ (11.8 - 13.5) \ 10$	$11.4 \pm 0.4 \ (10.7 - 12.3) \ 23$	$10.8 \pm 0.3 \; (10.4 – 11.4) \; 22$
WM3	$4.5 \pm 0.3 \ (4.0 - 4.9) \ 10$	$4.0 \pm 0.2 \ (3.6 - 4.5) \ 23$	$4.0 \pm 0.2 \ (3.6 - 4.4) \ 22$
Weight	470 ± 35 (425–515) 5	$400 \pm 63 \ (320 - 500) \ 11$	$300 \pm 68 \ (210 - 420) \ 15$

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (specimens from the Yavarí-Ucayali interfluve are marked with an asterisk): AMNH 272818*; FMNH 87125; LSUMZ 14015, 16393, 16394; MUSM 13299*; MVZ 190337; USNM 499005, 499007, 546222.

flexuosa) fruits, crickets/katydids, spiders, and armored millipedes. They eat birds that they find nesting up in the trees or on the ground. If the bird flies off or is too large, they eat the eggs or hatchlings. Among the birds they prey upon are tinamous, ground doves, and rusty-belted tapaculos.

Philander mcilhennyi Gardner and Patton, 1972

Figure 19

Voucher Material (total = 18): Nuevo San Juan (AMNH 268223, 268224, 272818,

273039, 273040, 273054, 273055, 273089; MUSM 11068, 11070, 11071, 11073, 13299, 15319–15323), Orosa (AMNH 74088).

OTHER INTERFLUVIAL RECORDS: Choncó (Vriesendorp et al., 2006a), Divisor (Vriesendorp et al., 2006b), Jenaro Herrera (as *Philander andersoni*; Fleck and Harder, 1995).

IDENTIFICATION: Amazonian specimens of *Philander* with distinctly blackish middorsal fur belong to two strongly supported cytochrome *b* haplogroups (Patton and da Silva, 1997; Patton et al., 2000; Voss et al., 2018). One haplogroup is represented by specimens collected north of

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (none from the Yavarí-Ucayali interfluve): AMNH 74388, 76448–76450, 98642; LACM 91621; MUSM 6074, 33569, 33576, 33586, 33594, 33602, 33603, 34892; MVZ 190345, 190346; TTU 98583, 98953, 100984, 101142, 101186, 101253, 101258.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (none from the Yavarí-Ucayali interfluve): AMNH 210403, 210409, 210414, 210416, 260034, 261270, 261273, 261277, 263964; BMNH 47.11.22.15; FMNH 114685, 114694, 114701, 114714; MSB 55073, 55855, 58517, 59887, 67025; USNM 390009, 390564, 390565.

the Amazon (in northern Loreto, eastern Ecuador, southeastern Colombia, southern Venezuela, and northwestern Brazil), but it also includes a sequence obtained from a paratype of P. andersoni (Osgood, 1913), which was collected south of the upper Amazon at Yurimaguas, in western Loreto department. The other haplogroup, represented by specimens collected south of the Amazon in Peru and western Brazil, includes specimens that closely resemble the type series of P. mcilhennyi (from Balta in Ucayali department). Both haplogroups are currently recognized as valid species (Patton and da Silva, 2008), but Voss et al. (2018) noted that the material they referred to P. andersoni and P. mcilhennyi on the basis of cytochrome b sequences could not be consistently distinguished by morphological criteria.

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Most specimens of Philander mcilhennyi (e.g., the type series from Balta, Peru, and material from western Brazil) are very dark: completely blackish middorsally with dark-grayish flanks and underparts. Although the lateral and ventral fur is frosted with gray, the tonal contrast with the middorsal fur is not abrupt. Additionally, the middorsal fur is much longer than the lateral fur, giving some skins a distinctly shaggy appearance. By contrast, typical material of P. andersoni has paler-grayish flanks, such that the black middorsal stripe is more obvious; additionally, the middorsal fur of andersoni is said to be shorter than that of mcilhennyi, and the ventral fur is either self-whitish or gray-based whitish (rather than dark gray). Lastly, P. andersoni is said to have a medial patch of pale fur at the base of the ear that is absent from the entirely blackish crown of P. mcilhennyi (see Patton and da Silva, 1997, 2008).

Patton et al. (2000) remarked that *Philander andersoni* and *P. mcilhennyi* might be sympatric on the "lower Río Javarí in northeastern Peru," citing a personal communication with D.W.F., who had observed both phenotypes at Nuevo San Juan (on the Río Gálvez). In fact, our voucher material includes specimens that distinctly resemble *P. mcilhennyi* (e.g., AMNH 272818, MUSM 13299) and others that closely resemble *P. andersoni* (e.g.,

AMNH 273055; fig. 19). Cytochrome *b* sequences that we obtained from specimens of both phenotypes, however, all belong to the *mcilhennyi* haplogroup (Voss et al., 2018), so introgression rather than sympatry might be the more appropriate interpretation of pelage variation at this locality. Nevertheless, we maintain current binomial usage pending further genetic analysis of our material (Jansa and Voss, in prep.).

A curious aspect of intraspecific variation in both *Philander mcilhennyi* and *P. andersoni* is sexual dimorphism in the middorsal fur, which is significantly longer, on average, in females than in males (table 22). Same-sex comparisons, however, support Patton and da Silva's (1997, 2008) description of *P. mcilhennyi* as longerfurred than *P. andersoni*, although there is species overlap in our measurements of fur length even when comparing males with males and females with females. To our knowledge, sexual dimorphism in fur length has not been reported from other didelphid species.

ETHNOBIOLOGY: The Matses do not distinguish this species from other "four-eyed" opossums (all known as <u>cheka bëbëdi</u>; see the generic account for *Philander*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the 17 specimens for which we have definite habitat data, seven (41%) were trapped or shot in primary forest (usually at well-drained sites, but once in the narrow floodplain of the Río Gálvez), another nine (53%) were taken in secondary forest (regenerating abandoned swiddens), and one was taken in an active swidden. Of the 14 specimens with recorded capture heights, 10 (71%) were trapped or shot on the ground, whereas four (29%) were shot or trapped on elevated substrates. Of the latter, one was trapped on a log 1 m above the ground, another was shot 3 m above the ground in a tree, and two others were shot at unrecorded heights in trees (one said to be "not very high" and the other "high up" [English translations from Matses field notes]).



FIG. 19. Dorsal and ventral views of *Philander* skins from Nuevo San Juan (from left to right in each panel: MUSM 13299, AMNH 272818, AMNH 273089, AMNH 273055). Cytochrome *b* sequences obtained from all four specimens belong to the *P. mcilhennyi* haplogroup (Voss et al., 2018).

OTHER SPECIMENS EXAMINED (TOTAL = 17): **Brazil**—*Acre*, Sena Madureira (USNM 546220–546222), Sobral on left bank Rio Juruá (MVZ 190337). **Peru**—*Loreto*, Santa Elena on Río Samiria (FMNH 87125). *Ucayali*, Balta (LSUMZ 14014, 14015, 16393, 16394; MVZ 136379–136381), 59 km SW Pucallpa (USNM 461133, 499003, 499005–499007).

Philander pebas Voss et al., 2018

Voucher Material (total = 1): Orosa (AMNH 73852).

OTHER INTERFLUVIAL RECORDS: See Remarks (below).

IDENTIFICATION: Our single voucher specimen, the skin and skull of a juvenile female collected by the Olallas in 1926, is in poor shape, but it preserves all of the diagnostic traits of the

species (table 19). In particular, it has uniformly grayish dorsal pelage (only indistinctly darker middorsally than on the flanks), extensively gray-based ventral pelage (without any median streak of self-whitish fur), a short white tail tip (less than 1/5 of the unfurred part of the tail is unpigmented), upper molars with crenulated protocones and pre- and postcingula, and lower molars with small but distinct postcingulids on m1 and m2 (Voss et al., 2018).

ETHNOBIOLOGY: The Matses do not distinguish this species from other "four-eyed" opossums (all known as <u>cheka bëbëdi</u>; see the generic account for *Philander*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

Remarks: The grayish four-eyed opossums reported as *Philander "opossum"* from the Yavarí-

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	Males	Females	Sexual dimorphism ^b
P. mcilhennyi	14.67 ± 1.50 mm (12–17 mm, N = 12)	18.44 ± 2.83 mm (14–22 mm, N = 9)	t = 3.95, df = 19 p < 0.001
P. andersoni	$11.25 \pm 1.24 \text{ mm}$ (9–14 mm, $N = 16$)	$14.17 \pm 1.27 \text{ mm}$ (12–16 mm, $N = 12$)	t = 6.10, df = 26 p < 0.001
Species difference ^b	t = 6.60, df = 26 p < 0.001	t = 4.67, df = 19 $p < 0.001$	

TABLE 22

Comparisons of Dorsal Fur Length in *Philander mcilhennyi* and *P. andersoni*^a

Ucayali interfluve by Pavlinov (1994) and Fleck and Harder (1995) might have been *P. pebas* or they might have been *P. canus*. Unfortunately, the specimens collected as vouchers for Fleck and Harder's ecological study, which were deposited at the Instituto de Investigaciones de la Amazonía Peruana, appear to have been lost or stolen, and we have not examined Pavlinov's material (in Moscow).

OTHER SPECIMENS EXAMINED (TOTAL = 57): Brazil-Acre, Fazenda Santa Fé on Rio Juruá (MVZ 190345), opposite Ocidente on Rio Juruá (MVZ 190346); Amazonas, Igarapé Nova Empresa on Rio Juruá (MVZ 190343), Lago do Baptista on S bank of Amazon (FMNH 51095), Sacado on Rio Juruá (MVZ 190344), Santo Isidoro [near] Tefé on S bank of Amazon (AMNH 78954), Parintins ("Villa Bella Imperatriz") on S bank of Amazon (AMNH 92880, 92881, 93526-93528, 93968), Tapauá on Rio Purus (USNM 461374). Ecuador—Orellana, 42 km S Pompeya Sur (ROM 106101, 106139). Peru-Loreto, Apayacu (AMNH 74388), Avícola San Miguel (MUSM 33590, 33592, 33593), Cabo López (MUSM 33566, 33567, 33569, 33570, 33572), Carretera Iquitos-Nauta km 28.8 (MUSM 34892), Caserio Cahuide (MUSM 33564, 33574, 33576), El Paujil (MUSM 33580), El Triunfo (MUSM 33586, 33587, 33583), Iquitos (AMNH 98642), 19.7 km SW Iquitos (MUSM 33588), Mishana (MUSM 33597), Otorongo Army Base (LACM 91621, 91622), Peña Negra (MUSM

33598), Picuro Yacu (MUSM 33594), Quistococha (FMNH 122745–122748; MUSM 33599, 33600), San Gerardo (MUSM 33602), Santo Tomas (MUSM 33603), Sarayacu on Río Ucayali (AMNH 76448–76450); *Madre de Dios*, Cusco Amazónico (KU 144120, 144121; MUSM 6074); *Ucayali*, Balta (LSUMZ 12007, 12010, 14011), Yarinacocha (FMNH 55411).

Tribe Thylamyini

The thylamyine fauna of the Yavarí-Ucayali interfluve includes *Gracilinanus emiliae*, a diminutive species of gracile mouse opossum, and at least three species of slender mouse opossums (*Marmosops*). A fourth species of *Marmosops* could be expected to occur locally, perhaps in the seasonally flooded forests along the right banks of the Ucayali and Amazon rivers, a habitat that remains poorly sampled in our region (appendix 2).

Gracilinanus emiliae (Thomas, 1909)

Figures 9C, 10C

Voucher Material (total = 1): Nuevo San Juan (MUSM 15292).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: Our single voucher conforms in all respects to the morphological diagnosis of *Gracilinanus emiliae* provided by Voss et al. (2009b), who also tabulated external and craniodental measurements of MUSM

^a Tabulated sample statistics include the mean plus or minus one standard deviation, the observed range, and the sample size.

^b Results of two-tailed Student's *t* tests for equality of sample means.

15292 and compared them with homologous values from other specimens, including Thomas's (1909) subadult holotype. Within the Yavarí-Ucayali interfluve *G. emiliae* might be confused with two superficially similar sympatric species, *Hyladelphys kalinowskii and Marmosa lepida*, but numerous external and craniodental differences are sufficient for unambiguous identifications of specimens in hand (table 4).

Gracilinanus emilae is the only species of Gracilinanus expected to occur in the Yavarí-Ucayali interfluve, although G. peruanus—formerly synonymized with G. agilis (see Semedo et al., 2015)—is known from scattered localities in the lowlands and foothills of central and southern Peru. Based on material we examined, G. peruanus occurs in the departments of Cusco (e.g., at La Convención, Camisea, San Martín: MUSM 14086), Huánuco (Tingo Maria: BMNH 27.11.1.268, 27.11.1.269), Madre de Dios (Pakitza: MUSM 8922), Pasco (near Villa Rica: AMNH 67242), and Ucayali (Balta: LSUMZ 16378).¹⁰ The only other Peruvian congener, G. aceramarcae, appears to be a strictly montane taxon. Semedo et al. (2015: table 10) provided diagnostic comparisons among the three known Peruvian species of Gracilinanus.

Recently reported specimens of *Gracilinanus emiliae* from scattered localities in Brazil (Silva et al., 2013; Brandão et al., 2014; Rocha et al., 2015) confirm that this species is very widely distributed in Amazonia. Despite substantial (ca. 5%) divergence at the cytochrome *b* locus between our Peruvian voucher and the eastern Amazonian material analyzed by Rocha et al. (2015),

this appears to be a phenotypically homogeneous taxon, without any obvious morphological differences among the specimens we examined.

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Our single specimen was shot at night by a Matses hunter in hilltop primary forest as it perched low in the crown of an understory tree.

OTHER SPECIMENS EXAMINED (TOTAL = 11): **Brazil**—*Pará*, Belém (BMNH 9.3.9.10 [holotype]), Capím (AMNH 203363). **Colombia**—*Meta*, Los Micos (FMNH 87924). **French Guiana**—Paracou (AMNH 267006). **Guyana**—*Upper Takutu-Upper Essequibo*, 20 mi E Comiwariwau Head (ROM 33103), 12 km E Dadanawa (ROM 35465, 35466), 40 mi E Dadanawa (ROM 55519). **Peru**—*Loreto*, Zona Reservada Pucacuro (MUSM 24430). **Surinam**—*Marowijne*, Langamankondre (RMNH 18231). **Venezuela**—*Monagas*, 47 km SE Maturín (USNM 385066).

Marmosops Matschie, 1916

Species of *Marmosops* superficially resemble species of *Marmosa*, but external and craniodental traits that distinguish these distantly related taxa—first recognized as separate genera by Gardner and Creighton (1989)—were described and illustrated by Voss et al. (2004). Subsequent phylogenetic research revealed a deep dichotomy in the genus that was recently formalized by subgeneric nomenclature (Díaz-Nieto et al., 2016). Of the three species definitely known to occur in the Yavarí-Ucayali interfluve, two belong to the nominotypical subgenus and the other to the subgenus *Sciophanes*; each is easily distinguished from the others by size and qualitative characters (table 23). A fourth species, apparently associ-

¹⁰ The specimen that Huamani et al. (2009) reported as *Gracilinanus agilis* from the Zona Reservada Pucacuro in northern Loreto (MUSM 24430) is a juvenile specimen of *G. emiliae*. Another specimen that Huamani et al. (2009) identified as *G. agilis* (MUSM 14085) is an unidentifiable *Marmosops* with molar teeth worn almost to the roots. The specimens from Bellavista (in Cajamarca department [Stephens and Traylor, 1983]) that Tate (1933: 199) tentatively identified as "*Marmosa agilis peruana*" (MCZ 17057–17059) consist only of skins; although these are unambiguously identifiable as *Gracilinanus*, and are clearly not *G. emiliae* (the ventral fur is extensively gray-based), they are not identifiable to species without cranial material.

		·		
	M. (Marmosops) noctivagus	M. (Marmosops) soinii	M. (Sciophanes) bishopi	
Head-and-body length (HBL)a	150 ± 15 mm	117 ± 11 mm	102 ± 4 mm	
Length of tail (LT) ^a	196 ± 15 mm	172 ± 13 mm	141 ± 10 mm	
Hind foot (HF) ^a	20 ± 2 mm	18 ± 1 mm	18 ± 1 mm	
Ventral fur	completely self-white	broadly gray-based laterally	completely self-white	
Gular gland (males)	present	present	absent	
Supraorbital beads	present in both sexes	present in older adults	absent	
Postorbital processes	usually absent or indistinct	present in adult males	absent	
Palatine fenestrae	usually present	present	absent	
Subsquamosal foramen	short	short	elongate	
C1 accessory cusps	absent	absent	posterior cusp present	
Length of upper molars (LM) ^a	$7.9 \pm 0.3 \text{ mm}$	$6.8 \pm 0.2 \text{ mm}$	$5.9 \pm 0.2 \text{ mm}$	

TABLE 23

Diagnostic Morphological Comparisons among Three Species of Marmosops from the Yavarí-Ucavali Interfluve

ated elsewhere with *várzea* habitats, might also occur in our region (appendix 2).

Marmosops (Marmosops) noctivagus (Tschudi, 1845)

VOUCHER MATERIAL (TOTAL = 38): Nuevo San Juan (AMNH 272704, 272715, 272775, 272782, 272809, 273034, 273051, 273058, 273060, 273061, 273131; MUSM 11032–11036, 11038, 11041, 11042, 11044, 11048, 13288–13292, 15301–15305, 15314), Orosa (AMNH 73853, 73854), San Pedro (UF 30451–30454), Santa Cecilia (FMNH 87122).

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (Fleck and Harder, 1995).

IDENTIFICATION: Like other material traditionally referred to *Marmosops noctivagus* (e.g., by Tate, 1933; Patton et al., 2000; Voss et al., 2004; Hice and Velazco, 2012), specimens from the Yavarí-Ucayali interfluve are rather large mouse opossums (table 24) with mostly self-whitish ventral fur and conspicuously beaded interorbital regions, but without distinct postorbital processes at any age or in either sex.¹¹ As

reported by Díaz-Nieto et al. (2016), DNA sequences from specimens with these phenotypic traits form a geographically widespread clade that extends across much of western Amazonia and along the adjacent eastern foothills and lower slopes of the Andes. However, this clade includes several allopatric haplogroups, which differ among themselves by about 3%-5% in mean uncorrected sequence comparisons at the cytochrome b locus. Sequenced specimens from the Yavarí-Ucayali interfluve belong to the haplogroup that Díaz-Nieto et al. (2016) called "noctivagus C," which (in their analyses) also included other sequences from south of the Amazon in western Brazil, eastern Peru, and northeastern Bolivia. Although the "noctivagus C" haplogroup is widespread in lowland habitats, it is also known to extend to at least 2200 m above sea level in southeastern Peru (e.g., near Amaybamba in Cuzco department; Díaz-Nieto et al., 2016: appendix, locality 98).

Eleven nominal taxa are currently regarded as synonyms of *Marmosops noctivagus* (e.g., by Voss and Jansa, 2009), but it is currently difficult to determine the application of names to most of the haplogroups discovered by Díaz-Nieto et al. (2016), a problem that those authors discussed at

^a The mean plus or minus one standard deviation computed from adult measurements of both sexes.

 $^{^{\}rm 11}$ A few old a dult males (e.g., MUSM 15305, AMNH 73853) have in distinct processes.

TABLE 24
Measurements (mm) and Weights (g) of Marmosops noctivagus
from the Yavarí-Ucayali interfluve

		Females		
	Males ^a	AMNH 272782	AMNH 273051	AMNH 273061
HBL	154 ± 15 (137–179) 7	158	131	137
LT	202 ± 13 (180-217) 7	198	184	171
HF	21 ± 2 (18–24) 8	21	17	19
Ear	25 ± 2 (22–28) 8	23	23	23
CBL	40.1 ± 1.8 (37.9–43.0) 8	38.6	38.1	36.8
NL	$19.6 \pm 0.9 \ (18.5 - 20.8) \ 8$	18.8	18.8	17.5
NB	$4.5 \pm 0.2 \ (4.3 - 5.0) \ 8$	4.1	3.9	3.7
LIB	$6.9 \pm 0.4 (6.3 - 7.4) 7$	6.5	6.4	6.5
LPB	$6.3 \pm 0.5 (5.9 - 7.2) 7$	6.1	6.5	6.4
ZB	$20.8 \pm 0.2 \ (19.0 - 22.3) \ 8$	20.1	19.5	19.2
PL	$22.9 \pm 0.8 \ (21.9 - 24.3) \ 8$	22.0	21.8	21.3
PB	12.2 ± 0.4 (11.6–12.9) 8	11.9	11.6	11.6
MTR	16.8 ± 0.5 (16.1–17.5) 8	16.0	16.0	15.8
LM	$8.0 \pm 0.3 \ (7.4 - 8.4) \ 8$	7.7	7.9	7.8
M1-3	$6.8 \pm 0.3 \ (6.2 - 7.2) \ 8$	6.6	6.7	6.6
WM3	$2.7 \pm 0.1 \ (2.4 - 2.7) \ 8$	2.6	2.6	2.6
Weight	82 ± 17 (64–115) 7	66	63	57

 $^{^{\}rm a}$ The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 272809, 273034, 273058, 273060, 273131; MUSM 11032, 15302, 15305.

some length. The difficulty arises both from the lack of unambiguously diagnostic characters by which to distinguish taxa in the *M. noctivagus* complex and from the lack of sequence data from many type localities. Although geographically distant samples of *M. noctivagus* often exhibit modest morphological differences, such differences are hard to interpret in the absence of data from geographically intermediate sites and in the absence of relevant genetic information. Our material from the Yavarí-Ucayali interfluve, for example, averages larger in most measured dimensions than specimens collected near the type locality of *M. noctivagus* (in the Andean foothills of Junín department; Gardner, 2008), 12 but the differences

we observed are insufficient as a basis for taxonomic distinction, and we have no sequence data from the vicinity of the type locality, which is not, in fact, far outside the known geographic range of the "noctivagus C" haplogroup.

In the absence of a comprehensive revision of the *Marmosops noctivagus* complex based on better morphological samples and denser molecular sequencing than those available to us at present, it seems profitless to speculate about trinomial nomenclature. However, it is relevant for the purposes of this report to note that sequences obtained from specimens collected on the left ("north") bank of the Amazon (e.g., at the Estación Biológica Allpahuayo; fig. 1) belong to a different mtDNA haplogroup than those from the Yavarí-Ucayali interfluve, from which they

¹² For example, AMNH 230005, 230007-230013.

differ by about 3.9% at the cytochrome *b* locus (Díaz-Nieto et al., 2015: table S4). Because the left-bank haplogroup ("noctivagus A") also occurs in eastern Ecuador, the type locality of the nominal taxon politus Cabrera, 1913, that epithet would seem to apply to it if there were any point in recognizing subspecies. However, measurements and side-by-side comparisons of our vouchers with left-bank specimens (e.g., the LACM and TTU specimens reported by Hice and Velazco, 2012) did not reveal any consistent morphological differences between them.

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ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of 25 specimens accompanied by definite habitat information, 13 (52%) were taken in primary upland (unflooded) forest, 10 (40%) were taken in secondary growth (abandoned swiddens), and 2 (8%) were captured in houses. Of 12 specimens accompanied by substrate information, 9 (75%) were trapped on the ground or on fallen logs, 2 (17%) were trapped on lianas between 1.5 and 1.8 m above the ground, and one was taken by hand as it perched close to the ground on a small tree. A single specimen was taken in the daytime from a leaf nest in the crown of an Astrocaryum palm at an unrecorded height above the ground, and another specimen was found dead, but all the specimens shot or captured by hand while active were taken at night, and all of the specimens trapped by D.W.F. and R.S.V. were found at dawn in traps that had been baited in the late afternoon of the previous day.

Marmosops (Marmosops) soinii, new species

Figures 20-22, 23A

HOLOTYPE: MUSM 13284, an adult male specimen collected by the first author (original

number RSV 2114) on 1 June 1998 at Nuevo San Juan on the right bank of the Río Gálvez, Loreto department, Peru. The entire specimen was originally preserved in ethanol, but the skull was later extracted and cleaned. The holotype is additionally represented by frozen tissues in the Ambrose Monell Cryo Collection (AMNH), from which Díaz-Nieto et al. (2016) obtained a nearly complete (1148 bp) cytochrome *b* sequence (GenBank: KT437848) and a shorter (882 bp) fragment from exon 11 of the nuclear BRCA1 gene (KT454025).

OTHER VOUCHER MATERIAL (TOTAL = 24): Jenaro Herrera (AMNH 276714; MUSM 23804, 23805), Nuevo San Juan (AMNH 268215, 268216, 272709, 272760, 273050, 273078, 273151, 273189; MUSM 11040, 11046, 11047, 13285, 13286, 15298–15300, 15306, 15307), San Pedro (MUSM 22331; UF 30449, 30450).

OTHER INTERFLUVIAL RECORDS: None.

DISTRIBUTION: Known only from the Yavarí-Ucayali interfluve.

DESCRIPTION: A species of Marmosops conforming in all respects to the generic description provided by Díaz-Nieto and Voss (2016: 14-15), but distinguished from other congeneric taxa by the following combination of traits: Dorsal pelage (fig. 20) dull reddish-brown, somewhat resembling Ridgway's (1912) Natal Brown or Olive Brown, but slightly paler. Ventral pelage (fig. 21) continuously self-cream from chin to groin, but this median color much narrowed between the fore- and hind limbs by broad lateral zones of gray-based fur. Tail very long (>140%, on average) and uniformly dark from base to tip dorsally, but indistinctly paler ventrally in some specimens. Hands and feet covered dorsally with mostly pale hairs, but sometimes indistinctly darker over the metapodials. Gular gland present in adult males and adult females. Lateral carpal tubercle present as an anteroposteriorly elongated knob in adult males. Forearm with one antebrachial vibrissa. Mammae 3-1-3 = 7 (e.g., AMNH 272709, 273189; MUSM 15300) or 4-1-4 = 9 (e.g., AMNH 273151), all abdominal/inguinal. Scrotum unpigmented, white.



FIG. 20. Dorsal views of skins of *Marmosops soinii* (left to right: AMNH 272760, MUSM 15298, MUSM 23805) and M. ocellatus (left to right: USNM 584469, 584466, 584467).

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FIG. 21. Ventral views of skins of Marmosops soinii (left to right: AMNH 272760, MUSM 15298, MUSM 23805) and M. ocellatus (left to right: USNM 584469, 584466, 584467).



FIG 22. Dorsal, ventral, and left lateral cranial views of *Marmosops soinii* (AMNH 276714). All views about $\times 2.5$.

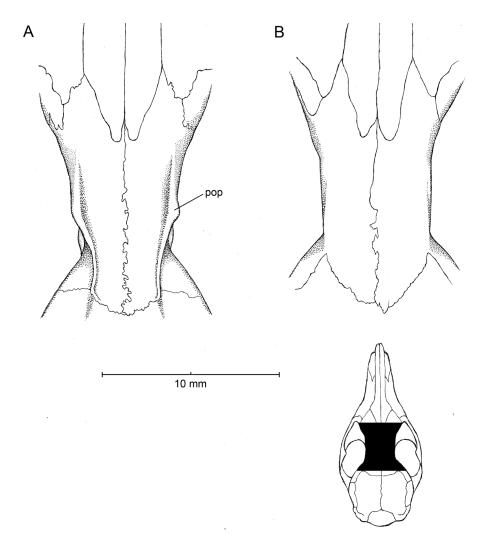


FIG. 23. Dorsal views of interorbital region of A, Marmosops soinii (AMNH 272760) and B, M. ocellatus (AMNH 261266).

Nasal bones conspicuously wider posteriorly (near the maxillary-frontal suture) than anteriorly, and long (extending posteriorly beyond the lacrimals). Lacrimal foramina concealed inside the orbit in some specimens, partially exposed to lateral view on the anterior orbital margin in others. Supraorbital margins smoothly rounded or with inconspicuous beading in juveniles, subadults, and young adult females (e.g., MUSM 15298, 15299), but distinctly beaded in older and larger adults, especially males (e.g., AMNH

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272760, 276714; MUSM 11046), which also develop small postorbital processes (fig. 23A). Incisive foramina short, not extending posteriorly beyond the canine alveoli; maxillopalatine fenestrae long and narrow, usually extending from between the upper third premolars (P3s) to between the third molars (M3s); palatine fenestrae always present, usually as multiple holes on each side. Subsquamosal foramen short (as in other members of the nominotypical subgenus), not exposing the lateral surface of the petrosal

TABLE 25

Measurements (mm) and Weights (g) of Marmosops soinii and M. ocellatus

	Males		Fen	nales
	M. soiniiª	M. ocellatus ^b	M. soinii ^c	M. ocellatus ^d
HBL	127 ± 9 (117-136) 4	123 ± 8 (109-132) 11	110 ± 2 (106–112) 5	110 ± 11 (90–121) 7
LT	$182 \pm 3 \ (177 - 185) \ 4$	167 ± 7 (158–178) 11	164 ± 13 (145–181) 5	148 ± 6 (141–160) 7
HF	19 ± 1 (18–20) 4	18 ± 1 (17–19) 11	17 ± 1 (16–18) 5	16 ± 1 (15–17) 7
Ear	23 ± 1 (21-24) 4	25 ± 2 (21–29) 10	23 ± 1 (22-24) 5	23 ± 1 (21–25) 8
CBL	$34.9 \pm 0.8 \ (34.0 - 35.7) \ 4$	$33.8 \pm 1.6 \ (31.6 - 36.8) \ 14$	$32.4 \pm 0.1 \ (32.2 - 32.5) \ 4$	$31.2 \pm 0.6 (30.3 - 31.8) 7$
NL	$16.5 \pm 0.5 \ (15.9 - 17.0) \ 4$	$16.1 \pm 0.9 \ (15.0 - 17.9) \ 13$	15.2 ± 0.2 (14.9–15.5) 5	14.7 ± 0.3 (14.4–15.1) 6
NB	$4.1 \pm 0.3 \; (3.8 – 4.5) \; 4$	$3.8 \pm 0.3 \ (3.2 - 4.3) \ 14$	$3.8 \pm 0.0 \ (3.8 – 3.9) \ 4$	$3.7 \pm 0.2 \ (3.4 - 4.0) \ 8$
LIB	$6.0 \pm 0.0 \ (6.0 - 6.0) \ 3$	$5.9 \pm 0.3 \ (5.3 - 6.3) \ 14$	$5.6 \pm 0.2 \ (5.5 - 6.0) \ 5$	$5.6 \pm 0.2 (5.3 - 5.9) 8$
LPB	$5.6 \pm 0.2 \ (5.4 - 5.8) \ 4$	$6.0 \pm 0.2 \ (5.6 - 6.3) \ 14$	$5.6 \pm 0.2 \ (5.3 - 5.8) \ 4$	$6.0 \pm 0.3 \ (5.6 - 6.5) \ 8$
ZB	$18.1 \pm 0.6 \ (17.4 - 18.6) \ 4$	$17.9 \pm 0.8 \ (16.7 - 19.8) \ 14$	$17.2 \pm 0.1 \ (17.0 - 17.3) \ 4$	$16.8 \pm 0.2 \ (16.5 - 17.2) \ 7$
PL	$19.8 \pm 0.4 \ (19.3 - 20.3) \ 4$	$19.2 \pm 0.8 \ (18.2 - 20.8) \ 14$	$18.6 \pm 0.1 \ (18.5 - 18.7) \ 4$	$17.8 \pm 0.4 \ (17.0 - 18.3) \ 8$
PB	$10.2 \pm 0.2 \ (10.0 - 10.4) \ 4$	$10.6 \pm 0.3 \ (10.0 - 11.0) \ 14$	$10.1 \pm 0.3 \ (9.8 – 10.5) \ 5$	$10.4 \pm 0.2 \ (10.0 - 10.6) \ 7$
MTR	$14.4 \pm 0.3 \ (13.9 - 14.6) \ 4$	$13.9 \pm 0.4 \ (13.3 - 14.7) \ 14$	$13.4 \pm 0.2 \ (13.1 - 13.7) \ 5$	$13.1 \pm 0.2 \ (12.7 - 13.3) \ 8$
LM	$7.0 \pm 0.2 \ (6.7 - 7.1) \ 4$	$6.8 \pm 0.2 \ (6.5 - 7.1) \ 14$	$6.7 \pm 0.2 \ (6.4 - 7.0) \ 5$	$6.7 \pm 0.1 \ (6.4 - 6.8) \ 8$
M1-3	$6.0 \pm 0.2 \ (5.8 - 6.1) \ 4$	$5.8 \pm 0.1 \ (5.6 - 6.0) \ 14$	$5.8 \pm 0.2 \ (5.5 - 6.0) \ 5$	$5.8 \pm 0.1 \ (5.6 - 5.9) \ 8$
WM3	$2.3 \pm 0.1 \ (2.2 – 2.4) \ 4$	$2.3 \pm 0.1 \ (2.2 – 2.5) \ 14$	$2.3 \pm 0.1 \ (2.1 – 2.4) \ 5$	$2.3 \pm 0.1 \ (2.2 - 2.4) \ 8$
Weight	41 ± 9 (33–54) 4	$39 \pm 6 (25-49) 10$	36 ± 2 (33–38) 5	27 ± 4 (19-31) 8

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 272760, 276714; MUSM 11046, 13284.

behind the sulcus for the prootic sinus (Díaz-Nieto and Voss, 2016: fig. 9).

Upper canine (C1) simple, without accessory cusps in either sex. M3 anterior cingulum incomplete (preprotocrista terminates at base of paracone, not continuous with anterolabial cingulum). Unworn lower canine (c1) distinctly taller than first lower premolar (p1), sometimes with a small but distinct posterior accessory cusp. Entoconids small, neither as tall nor as bulky as adjacent paraconids.

Comparisons: This species, previously referred to as *Marmosops* "Gálvez," was included

in molecular analyses reported by Díaz-Nieto et al. (2016), who recovered it within a strongly supported monophyletic group ("Clade E") that also included *M. ocellatus* Tate, 1931, and *M.* "Juruá" (another unnamed form). *Marmosops ocellatus*—resurrected from synonymy and redescribed by Voss et al. (2004)—occupies deciduous, semideciduous, and riparian forests in the Cerrado landscapes of eastern Bolivia and southwestern Brazil (Emmons et al., 2006; Cáceres et al., 2007; Semedo et al., 2013), whereas *M.* "Juruá" corresponds to the Amazonian species that Patton et al. (2000) called *M. impavidus*

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 247652, 260026, 260028, 261265, 261266, 263549, 275462; BMNH 26.1.5.25, 28.2.9.87, 28.2.9.90; USNM 390022, 390571, 390572, 584467.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 273151, 273189; MUSM 15298, 15299, 15300.

^d The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 260027, 261267, 275461; MSB 58512, 58513; USNM 581979, 584466, 584469.

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Tschudi, 1845 (a nomen dubium). ¹³ Comparisons with M. "Juruá" will be provided when that species is formally named in a subsequent publication. The following comparisons serve to distinguish M. soinii from M. ocellatus, its closest named relative as determined by Díaz-Nieto et al.'s (2016) results.

Marmosops soinii and M. ocellatus are morphometrically similar (table 25), with broad overlap in most measured dimensions (except male tail length). In qualitative comparisons (table 26), M. soinii differs from M. ocellatus by its reddish-brown dorsal pelage, which appears somewhat darker and more richly pigmented in side-by-side comparisons with the somewhat paler dorsal fur of the latter species (fig. 20). The wider lateral zones of gray-based fur in M. soinii are conspicuous in ventral pelage comparisons (fig. 21). Marmosops soinii has a relatively longer tail (about 147% of head-and-body length, on average) that is uniformly dark from base to tip, whereas the relatively shorter tail of *M. ocellatus* (about 136% of head-and-body length) is bicolored at its base (distinctly paler ventrally than dorsally) and particolored (paler distally than proximally, becoming completely unpigmented toward the tip in most examined specimens). Less conspicuously, a gular gland is present in adult males and at least some adult female specimens of M. soinii, whereas most examined adult specimens of *M. ocellatus*—the holotype (BMNH 28.2.9.87) is the unique exception—show no trace of glandular activity on the throat or upper chest. Lastly, adult female specimens of M. soinii have either 3-1-3 = 7 or 4-1-4 = 9 abdominalinguinal mammae, whereas M. ocellatus seems to consistently have 6-1-6 = 13 mammae (L.H. Emmons, personal commun.), of which the two anteriormost pairs are "thoracic" (sensu Tate, 1933), extending toward the lower chest from the

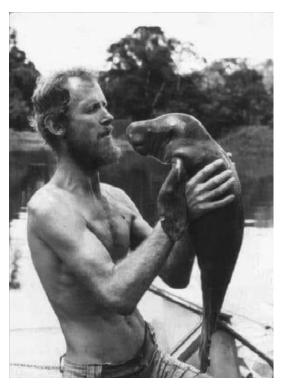


FIG. 24. Pekka Soini (1941–2004) with a young friend. Location and photographer unknown.

abdominal/inguinal positions occupied by the more posterior teats.

These species are craniodentally similar, but specimens of *M. ocellatus* seem to lack any trace of supraorbital beading, and none that we examined has postorbital processes (fig. 23B). In almost all examined specimens of *M. soinii* the basisphenoid is concealed from lateral view in the rear of the orbit (AMNH 272760 is the unique exception), but the basisphenoid is laterally exposed through an expanded sphenorbital fissure in the rear of the orbit in *M. ocellatus*. ¹⁴

ETYMOLOGY: For Pekka Soini (fig. 24), legendary field biologist and visionary conservationist, who lived and worked in Loreto for many years and made important contributions to the

¹³ As explained by Díaz-Nieto et al. (2016), the epithet *impavidus* has been used for at least two distinct species, of which one has traits that are inconsistent with the original description, and the other is not known to occur near the type locality. The type is apparently lost, and it is not certain that the animal described by Tschudi was even a species of *Marmosops*.

¹⁴ This interesting character, which is taxonomically useful in other genera and probably covaries with size of the optic nerve, was illustrated by Pavan and Voss (2016: fig. 8) for *Monodelphis*.

Diagnostic Traits of Marmosops sointi and M. occilatus				
	M. soinii	M. ocellatus		
Dorsal pelage	dull reddish brown	somewhat paler		
Ventral pelage	w/broad lateral zones of gray-based fur	mostly self-white		
Tail	uniformly dark	bicolored and particolored		
TL/HBL	1.47 ± 0.11	1.36 ± 0.10		
Gular gland	present in adults of both sexes	usually absent		
Mammae	3-1-3 = 7 or 4-1-4 = 9	6-1-6 = 13		
Supraorbital margins	distinctly beaded in older adults	smooth (no beading)		
Postorbital processes	present in adult males	absent		
Basisphenoid	usually concealed laterally	consistently exposed laterally		

TABLE 26

Diagnostic Traits of Marmosops soinii and M. ocellatus

herpetology and mammalogy of northeastern Peru (Mittermeier et al., 2004).

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, long-tailed, black-masked species of small opossums (all known as <u>chekampi</u>; see the account for *Marmosa*, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the 23 specimens for which we have capture information, 13 were trapped, shot, or captured by hand while climbing on saplings, lianas, logs, or fallen branches at estimated heights from 0.2 to 1 m above the ground; only five are definitely known to have been captured on the ground (of which three were taken in pitfalls). Most (15) specimens were taken in primary upland forest, but four were in secondary forest (abandoned swiddens), two were in swampy primary forest, one was in primary floodplain forest, and one was captured in a house. Ten specimens were shot or captured by hand while active at night, and another 10 were found at dawn in traps that had been baited in the late afternoon of the previous day (three specimens found at dawn in pitfalls might have been taken at any time in the previous 24 hours).

Specimens of *Marmosops ocellatus* Examined (total = 23): **Bolivia**—*Santa Cruz*, 7 km SE Ariruma (AMNH 275461), 6 km W

Ascención (AMNH 261265), Ayacucho (USNM 390571, 390572), Buenavista (BMNH 26.1.5.25 [holotype], 28.2.9.87, 28.2.9.90), El Refugio (USNM 584466, 584467, 584469), 3.5 km W Estación Pailón (AMNH 260026–260028), 7 km E and 3 km N Ingeniero Mora (AMNH 247652), Lago Caimán (USNM 581979), 2 km S Las Cruces (AMNH 263549), 10 km N San Ramón (AMNH 261266, 261267), 15 km S Santa Cruz (MSB 58512, 58513), Warnes (USNM 390022), 13 km N Zanja Honda (AMNH 275462). Brazil—Mato Grosso, 3 km W Cáceres on BR 30 (USNM 390026).

Marmosops (Sciophanes) bishopi (Pine, 1981)

VOUCHER MATERIAL (TOTAL = 12): Jenaro Herrera (AMNH 276697, 276700, 276705, 276718, 276723; MUSM 23799–23803), Nuevo San Juan (MUSM 13287), San Pedro (UF 30454).

OTHER INTERFLUVIAL RECORDS: None.

IDENTIFICATION: The small species of *Marmosops* formerly associated with the name *M. parvidens* (e.g., by Pine, 1981) were referred to the subgenus *Sciophanes* by Díaz-Nieto et al. (2016). Specimens from the Yavarí-Ucayali interfluve were subsequently examined by Díaz-Nieto and Voss (2016), who referred them to *M. bishopi*, a taxon originally described as a subspecies of *M. parvidens* on the basis of a female holotype collected in central Brazil. As recognized by

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Díaz-Nieto and Voss (2016), M. bishopi is a widespread species that includes several morphologically indistinguishable mtDNA haplogroups. Unfortunately, no sequence data is available from the holotype, nor did Díaz-Nieto et al. (2016) obtain sequences from specimens collected in the Yavarí-Ucayali interfluve. The holotype (USNM 393535) has paler fur and a much shorter tail (116 mm) than the single adult female from our region (table 27), but other measurement differences between these specimens seem unremarkable. Our material agrees with the emended description of this species by Díaz-Nieto and Voss (2016: 43-49), who provided cranial photographs of one of our vouchers (MUSM 23803).

ETHNOBIOLOGY: The Matses do not distinguish this species from other pouchless, longtailed, black-masked species of small opossums (all known as chekampi; see the account for Marmosa, above) and therefore have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Our single specimen from Nuevo San Juan was caught by hand at night by a Matses hunter, but no information was recorded about the habitat in which it was taken. The remaining 10 specimens (all from Jenaro Herrera) were taken in pitfall traplines: five in welldrained secondary growth, three in swampy primary forest, and two in white-sand forest.

DISCUSSION

With 19 species definitely known to occur in the Yavarí-Ucayali interfluve, marsupials are a major component of the regional mammalian fauna, ranking third in diversity after bats (ca. 100 species; Velazco et al., in prep.) and rodents (ca. 35 species; Voss and Fleck, in prep.). However, it is possible that even more marsupial species might occur locally but were not recorded by us or by the other collectors and researchers who previously worked in the region. Because inventory completeness is a potential problem for fau-

TABLE 27 Measurements (mm) and Weights (g) of Marmosops bishopi from the Yavarí-Ucayali interfluve

	Malesa	MUSM 23802 ^b
HBL	102 ± 4 (96-108) 8	101
LT	141 ± 11 (120–153) 8	141
HF	18 ± 1 (16–20) 8	17
Ear	21 ± 1 (20-22) 8	20
CBL	$28.2 \pm 0.5 \ (27.5 - 29.0) \ 8$	26.7
NL	$13.0 \pm 0.5 \ (12.1 - 13.6) \ 8$	11.9
NB	$3.4 \pm 0.2 \ (3.2 - 3.8) \ 8$	3.3
LIB	$5.5 \pm 0.2 (5.3 - 5.8) 8$	5.1
LPB	$5.6 \pm 0.1 \ (5.4 - 5.9) \ 8$	5.4
ZB	$14.8 \pm 0.3 \ (14.3 - 15.1) \ 8$	13.9
PL	$15.7 \pm 0.4 \ (14.9 - 16.3) \ 8$	15.0
PB	$8.6 \pm 0.3 \ (8.2 - 9.0) \ 8$	8.8
MTR	$11.5 \pm 0.3 \ (11.2 - 12.0) \ 8$	11.5
LM	$5.9 \pm 0.2 (5.5 - 6.2) 8$	6.0
M1-3	$5.1 \pm 0.1 \ (4.9 - 5.3) \ 8$	5.2
WM3	$1.9 \pm 0.1 \ (1.8 - 2.0) \ 8$	2.0
Weight	29 ± 3 (26-34) 8	25

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 276700, 276705; MUSM 15981, 15983, 23799-23801, 23803.

nal comparisons, the issue of missing species merits brief consideration.

Our knowledge of the interfluvial marsupial fauna is almost entirely based on taxonomic analysis of specimens collected from 1926 to 2003.15 Although our specimen tally (table 28) gives a very rough idea of species encounter rates, these data did not result from a uniform sampling process (sensu Colwell and Coddington, 1994), so they are not really suitable for diversity extrapolation or other forms of statisti-

^b Female.

¹⁵ Unlike primates and large mammals, most marsupials cannot be reliably identified without specimens in hand (Voss and Emmons, 1996) so visual transect-census results and interviews are generally not a relevant source of diversity information.

TABLE 28
Marsupial Specimens Examined and Locality Records
from the Yavarí-Ucayali Interfluve

	Specimens	Localitiesa			
	examined	NSJ	JH	SP	Others
Caluromys lanatus	6	X	X	(X)	
Glironia venusta	1				X
Hyladelphys kalinowskii	2	X			
Marmosa macrotarsus	20	X	(X)	(X)	X
Marmosa constantiae	21	X	X	?	X
Marmosa rutteri	6	X	?	?	X
Marmosa lepida	1	X			
Monodelphis handleyi	7		X		
Monodelphis peruviana	4	X			
Monodelphis emiliae	7	X	X	X	X
Chironectes minimus	1	(X)		(X)	X
Didelphis marsupialis	7	X	X	(X)	(X)
Philander mcilhennyi	18	X	(X)	?	X
Philander pebas	1	?	?	?	X
Metachirus myosuros	12	X	(X)	(X)	X
Gracilinanus emiliae	1	X			
Marmosops noctivagus	38	X	(X)	X	X
Marmosops soinii	25	X	X	X	
Marmosops bishopi	12	X	X	X	
TOTALS ^b	190	16 spp.	11 spp.	11 spp.	_

^a Column headings: NSJ, Nuevo San Juan; JH, Jenaro Herrera; SP, San Pedro. Column entries: X = known from examined specimens, (X) = unvouchered sighting or unexamined specimen, ? = equivocal record.

cal analysis. Instead, inventory completeness must be assessed by other means.

We note, first, that all the inventory methods known to be effective for Neotropical rainforest marsupials (Voss and Emmons, 1996) were employed intensively. Based on field notes and published sources cited in Materials and Methods (above), relevant sampling effort included ca. 63,000 trap-nights at ground level using standard equipment (commercially manufactured snaptraps and live traps), mostly at San Pedro and Nuevo San Juan; 2150 trap-nights of arboreal trapping at Jenaro Herrera; 409 hours of noctur-

nal hunting at Nuevo San Juan; and 2750 bucketnights of pitfall trapping at Jenaro Herrera. In addition, our fieldwork at Nuevo San Juan was supplemented by unquantified but frequent trapping and haphazard captures by Matses children and adults. The inventory methods used by previous collectors in the region are unknown, but this aggregate effort with methods of known efficacy and complementarity (Voss et al., 2001) suggests that few marsupials are likely to remain undetected in the region.

Second, only four additional species (species not represented in the material we examined;

^b Specimens or species (spp.). Species totals include only unambiguous occurrence records as discussed in the systematic accounts, but we assume that at least one species each of *Marmosa* (*Micoureus*) and *Philander* occur at San Pedro.

appendix 2) have geographic ranges that are known to overlap the Yavarí-Ucayali interfluve. Possibly, all of them are habitat specialists, and the most likely habitat in which they might occur, and which we certainly did not sample effectively, is the seasonally flooded forest (*várzea*) that occurs along the Ucayali and the Amazon. This riparian habitat is extensive in some places (at Orosa, for example, *várzea* is said to extend inland for 6–8 km from the right bank of the Amazon; Wiley, 2010), and it makes sense that it might harbor a distinctive fauna. If all four species with geographic ranges that overlap the Yavarí-Ucayali interfluve actually occur there, then our regional inventory is only about 83% complete.

Faunal-sampling effort was unevenly distributed among just a few localities in the region, with 9-16 marsupial species definitely known to occur at the three best-sampled sites. Of these, we feel reasonably confident that our species list from Nuevo San Juan is complete or nearly so. The habitat surrounding the village consists almost entirely of upland (well-drained, unflooded) forest, including both primary growth and patches of secondary (successional) vegetation from small-scale shifting cultivation; the nearby floodplain of the Río Gálvez is narrow, discontinuous, and seems unlikely to harbor undetected várzea specialists. We judge our faunal-sampling efforts at Nuevo San Juan sufficient to have detected most of the marsupials expected to occur locally, and the two "missing" arboreal species (Caluromysiops irrupta, Glironia venusta) are distinctive enough externally that even the Matses-inattentive to most nuances of marsupial external morphology-would surely have remembered them had either been encountered while felling trees for new swiddens, an annual activity.16 Therefore, we assume that the 16 species recorded from Nuevo San Juan is a meaningful estimate of sympatric species richness at

¹⁶ We questioned several Matses men for this purpose, and showed them pictures of both species from a field guide (Emmons, 1997), but obtained no evidence that either species occurs near the village.

TABLE 29
Distributions of Marsupial Species from the Yavarí-Ucayali Interfluve

	Amazonian distribution ^a			
	SW	NW	SE	NE
Caluromys lanatus	X	X		(X)
Glironia venusta ^b	X	X	X	X
Hyladelphys kalinowskii	X	X^{c}		X
Marmosa macrotarsus ^d	X		(X)	
Marmosa constantiae ^e	X		(X)	
Marmosa rutteri ^e	X	X		
Marmosa lepida	X	X	X^{f}	X
Monodelphis handleyi ^e	(X)			
Monodelphis peruviana ^e	X			
Monodelphis emiliae	X		X	
Chironectes minimus	X	X	X	X
Didelphis marsupialis	X	X	X	X
Philander mcilhennyi	X			
Philander pebas ^g	X	X		
Metachirus myosuros ^e	X	X	(X)	
Gracilinanus emiliae ^h	(X)	X	X	X
Marmosops noctivagus	X	X	(X)	
Marmosops soiniie	(X)			
Marmosops bishopi i	X	X		

^a Distributional records from Gardner (2008) except as noted. Column headings are quadrants defined by major rivers: SW (south of the Amazon and west of the Madeira), NW (north of the Amazon and west of the Negro), SE (south of the Amazon and east of the Madeira), NE (north of the Amazon and east of the Negro). Table entries: X = known from quadrant, (X) = known from part of quadrant but probably not widespread.

^b Ardente et al. (2013; Sant and Catzeflis, 2018).

^c Hice and Velazco (2012).

^d Rossi (2005).

^e This report.

f Guimarães et al. (2018).

g Voss et al. (2018).

h Brandão et al. (2014).

i Díaz-Nieto et al. (2016).

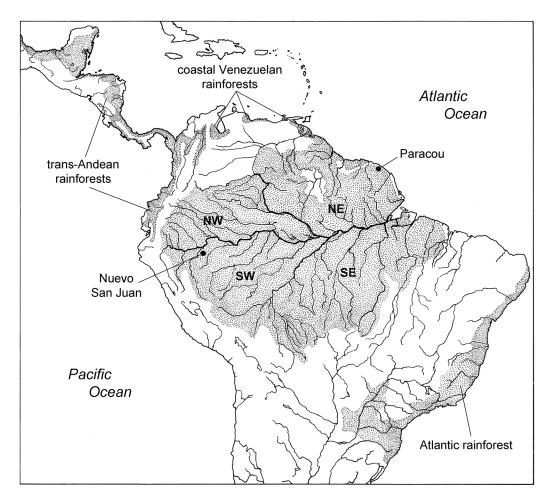


FIG. 25. Mammalian inventory sites at Nuevo San Juan (Peru) and Paracou (French Guiana) in biogeographic context. Stipple indicates lowland rainforest vegetation. Primary intercardinal directions (NE, NW, SE, SW) label quadrants of Amazonia defined by the Amazon, Madeira, and Negro rivers (after Wallace, 1852).

upland sites (remote from extensive tracts of *várzea*) within the Yavarí-Ucayali interfluve.

Comparisons with Other Amazonian Faunas

The marsupial fauna of the Yavarí-Ucayali interfluve includes two endemic species and 17 species with wider Amazonian distributions (table 29). Of the latter, five species—Glironia venusta, Marmosa lepida, Chironectes minimus, Didelphis marsupialis, and Gracilinanus emiliae—are known from every quarter of Amazonia, and four others (Caluromys lanatus,

Hyladelphys kalinowskii, Metachirus myosuros, Marmosops noctivagus) are almost as widespread. Of the remainder, three species (Marmosa rutteri, Philander pebas, Marmosops bishopi) are known only from southwestern and northwestern Amazonia, another three (Marmosa macrotarsus, M. constantiae, Monodelphis emiliae) are known only from southwestern and southeastern Amazonia, and two (Monodelphis peruviana, Philander mcilhennyi) are known only from southwestern Amazonia.

Conspicuously absent from the marsupial fauna of our region are any species known only

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from the southwestern and northeastern quadrants, opposite poles of Amazonian zoogeography in both traditional and modern analyses (e.g., Wallace, 1852; Godinho and da Silva, 2018). To assess faunal similarities and differences along this SW/NE axis, we compared our species list from Nuevo San Juan with a species list from Paracou, French Guiana (fig. 25), where we previously used similar faunal-sampling methods and expended comparable effort in essentially similar habitats (Voss et al., 2001). Remarkably, the same genera are present at both sites (table 30), which differ only in the species represented.

The 10 genera common to Nuevo San Juan and Paracou (Caluromys, Hyladelphys, Marmosa, Monodelphis, Metachirus, Chironectes, Didelphis, Philander, Gracilinanus, and Marmosops) probably occur sympatrically at most Amazonian sites that are not subject to periodic flooding. Although all of these taxa have seldom been documented in sympatry elsewhere, incomplete faunal sampling is a plausible explanation for missing marsupial taxa in most rainforest mammal inventories, especially those based on methodologically and temporally limited fieldwork (Voss and Emmons, 1996). By contrast, we are not aware of any compelling evidence for environmental "filtering" (sensu Kraft et al., 2015) or biotic interactions that might account for the absence of any of these genera at Amazonian rainforest sites where they are not known to occur.

Despite the generic-level homogeneity of Amazonian marsupial faunas, species turnover (beta diversity) along the SW/NE axis is substantial. Of the 25 marsupial species represented in the combined faunal lists from Nuevo San Juan and Paracou, 20 species (80%) are represented at one site or the other, but not at both. What dispersal barriers or environmental gradients might account for such numerous replacements of one congeneric species by another across the 2500 km that separate these inventory sites?

The short answer is, we do not yet know. Much of the literature on Amazonian tetrapod faunas has focused on rivers as limiting species distributions (e.g., Wallace, 1852; Cracraft, 1985;

TABLE 30

Rainforest Marsupials from Two Amazonian Localities

Two Amazoman Locanties			
Nuevo San Juan	Paracou		
(SW Amazonia) ^a	(NE Amazonia) ^b		
Caluromyinae	Caluromyinae		
Caluromys lanatus	Caluromys philander		
Hyladelphinae	Hyladelphinae		
Hyladelphys kalinowskii	Hyladelphys kalinowskii		
Didelphinae	Didelphinae		
Marmosini	Marmosini		
Marmosa macrotarsus	Marmosa murina		
Marmosa constantiae	Marmosa demerarae		
Marmosa rutteri	Marmosa lepida ^c		
Marmosa lepida	Monodelphis touan		
Monodelphis peruviana	Didelphini		
Monodelphis emiliae	Chironectes minimus		
Didelphini	Didelphis imperfecta ^d		
Chironectes minimus	Didelphis marsupialis		
Didelphis marsupialis	Philander opossum		
Philander mcilhennyi	Metachirini		
Metachirini	Metachirus nudicaudatus		
Metachirus myosuros	Thylamyini		
Thylamyini	Gracilinanus emiliae		
Gracilinanus emiliae	Marmosops parvidens		
Marmosops noctivagus	Marmosops pinheiroi		
Marmosops soinii			
Marmosops bishopi			

^a This report

Ayres and Clutton-Brock, 1992), but the general importance of fluvial barriers is far from established. Some major Amazonian tributaries (e.g., the Juruá; Gascon et al., 2000) are clearly ineffective as barriers, whereas other rivers are known to be a barrier for some species, but not for others (Pomara et al., 2014). Because most studies have analyzed distributional data from birds and

^b Species list from Voss et al. (2001) except as noted; taxonomy has been updated following Voss and Jansa (2009) and Pavan et al. (2012).

^c F. Catzeflis (personal commun.). Vouchers are MNHN 2001-1432, 2001-1434, and 2001-1451.

d Adler et al. (2006).

TABLE 31
Pairs of Species and Haplogroups in Marsupial Faunas North and South of the Upper Amazon

South-bank species/haplogroup ^a	North-bank species/haplogroup ^b	Status
Marmosa macrotarsus	Mar. waterhousei	not sister species (Voss et al., 2014)
Marmosa constantiae	Mar. germana	not sister species ^c
Marmosa rutteri (S haplogroup)	Mar. rutteri (N haplogroup)	sister groups ^c
Monodelphis peruviana	Mon. adusta	not sister species (Pavan et al., 2014)
Metachirus myosuros (SW haplogroup)	Met. myosuros (NW haplogroup)	not sister groups (this report)
Philander mcilhennyi	P. andersoni	not sister species (Voss et al., 2018)
Marmosops noctivagus (haplogroup C)	Mps. noctivagus (haplogroup A)	not sister groups (Díaz-Nieto et al., 2016)
Marmosops bishopi (haplogroup A)	Mps. bishopi (haplogroup F)	not sister groups (Díaz-Nieto et al., 2016)

^a In the Yavarí-Ucayali interfluve and elsewhere in SW Amazonia (this report).

primates, the importance of Amazonian rivers as barriers for other vertebrate groups cannot be assumed a priori.

Information summarized in this report suggests that the upper Amazon is an important dispersal barrier for marsupials. At least seven species or haplogroups present in the Yavarí-Ucayali interfluve are replaced by closely related congeneric taxa, or by conspecific haplogroups, on the left bank of the Amazon (table 31), and another three species from our region (Monodelphis handleyi, Mon. emiliae, Marmosops soinii) are unknown from any left-bank counterparts despite intensive recent collecting between Iquitos and Nauta (Hice and Velazco, 2012; Díaz, 2014). Therefore, dispersal of somewhat more than half of the regional marsupial fauna seems to be limited by the Amazon to one degree or another. Additionally, it seems noteworthy that few of the species or haplogroups that replace one another on opposite sides of the river are sister clades, a phenomenon that has previously been noted in studies of other organisms separated by Amazonian rivers (Naka and Brumfield, 2018).

By contrast, most (ca. 85%) of the species in the Yavarí-Ucayali marsupial fauna are widely distributed elsewhere in southwestern Amazonia, as are several haplogroups of species with strongly developed phylogeographic structure.¹⁷ Although not all species appear to be uniformly distributed south of the Amazon and west of the Madeira, our impression is that this quadrant of Amazonia is not partitioned by any strong barriers to marsupial dispersal, and we conjecture that edaphic discontinuities (Tuomisto et al., 2016), rainfall gradients, or other environmental factors might play a larger role than rivers in limiting species distributions there. Unfortunately, few localities in southwestern Amazonia have been thoroughly inventoried, and existing faunal lists from this quadrant need taxonomic updating to be useful for strong biogeographic inference.

Matses Ethnomammalogy

Matses knowledge of marsupials is very incomplete by comparison with their detailed knowledge about primates and large mammals (Voss and Fleck, 2011, 2017). This is not unexpected, because most opossums are small, nocturnal, and hard to distinguish from one another externally. None is hunted for food, and with the

^b Between Iquitos and Nauta (Hice and Velazco, 2012; Díaz, 2014) and elsewhere in NW Amazonia.

^c Unpublished sequencing results (Voss et al., in prep.).

¹⁷ Examples discussed in this report include the the southern haplogroup of *Mar. rutteri*, the SW Amazonian haplogroup of *Metachirus myosuros*, and haplogroup C of *Marmosops noctivagus*.

TABLE 32
Matses Folk Taxonomy for Opossums

Matses name	Variants	Referent
mapiokos		Didelphis marsupialis
<u>yama</u>		Monodelphis spp.a
<u>cheka</u>		
abuk cheka		Caluromys lanatus
cheka bëbëdi	chekadëwisak	Metachirus myosuros Philander mcilhennyi
chekampi	<u>mapiokosëmpi</u>	Hyladelphys kalinowskii Marmosa spp. Gracilinanus emiliae Marmosops spp.

^a Also *Thecadactylus solimoensis* (Squamata: Gekkonidae) and an unidentified rodent.

exception of the common opossum (*Didelphis marsupialis*)—which enters villages to eat chickens—they are seldom encountered.

Because opossums are culturally unimportant (inedible and not dangerous), the Matses seldom need to talk about them, so their marsupial lexicon is correspondingly underdifferentiated with respect to zoological taxa (table 32). Didelphis marsupialis has its own proper name, and short-tailed opossums (Monodelphis spp.) are also recognized, albeit collectively, as belonging to a distinct folk taxon, but all the rest are treated as kinds of cheka and labelled according to arboreality, size, or markings. The water opossum, unknown to most of the Matses, is not named. There is no Matses name, nor, apparently, even a covert category (sensu Berlin et al., 1968) that includes all local species of didelphids, although the variant term for chekampi implies some recognition of kinship between mouse opossums and the common opossum.

Matses inattention to opossum natural history and taxonomic diversity is consistent with their scant knowledge of (and rudimentary lexicons for) other small and culturally unimportant animals (e.g., bats; Fleck et al., 2002). It makes sense that the large, chicken-thieving, and externally unmistakable common opossum should have its

own name, but <u>yama</u> is something of an enigma. As noted earlier, this name applies not only to species of *Monodelphis*, but also to a lizard and to an unidentified rat formerly used for sorcery. It is not obvious what these animals have in common, but the supernatural powers of <u>yama</u> rats (which are not limited to their former use for magical murder) suggests that it might be some long-forgotten occult attribute.

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FIG. 26. A Matses hunter reclines in the informant's hammock and monologs about mammals while D.W.F. monitors sound quality on a digital minidisk recorder (Nuevo San Juan, 1998; photo by R.S.V.).

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APPENDIX 1

GAZETTEER

Below we list the principal localities from which marsupials have been collected or observed in the Yavarí-Ucayali interfluvial region. Boldface identifies locality names as they appear in the text (alternative names or spellings are cited parenthetically). Except as noted otherwise, all localities are mapped in figure 2.

- Actiamë (6°19′S, 73°09′W; Vriesendorp et al., 2006a): inventory site in the left-bank floodplain of the Río Yaquerana (q.v.) surveyed from 2–7 November 2004 (Amanzo, 2006).
- Angamos (also known as "Colonia Angamos"; 5°11'S, 72°53'W; DMA, 1989): military outpost on the left bank of the Río Yavarí (q.v.) just downstream from the confluence of the Río Gálvez (q.v.) and the Río Yaquerana.
- Centro Unión (ca. 3°47′ S, 73°09′ W): ribereño community on the right bank of the lower Río Aucayo (q.v.), where Pekka Soini and colleagues conducted field research and collected specimens in the early 1970s (Castro and Soini, 1977; Dixon and Soini, 1986).
- Choncó (5°33′S, 73°36′W; Vriesendorp et al., 2006a): inventory site in hilly terrain between the Río Tapiche (q.v.) and the Río Gálvez (q.v.) surveyed for large mammals by J. Amanzo from 25–28 October 2004 (Amanzo, 2006).
- **Divisor** (7°12′S, 73°53′W; Vriesendorp et al., 2006b): inventory site near Tapiche (q.v.) east of the upper Río Tapiche (q.v.) in the Sierra del Divisor (250–600 m), surveyed for mammals

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 - by M.L.S.P. Jorge and P.M. Velazco from 19 to 23 August 2005 (Jorge and Velazco, 2006).
- Estación Biológica Quebrada Blanco (4°21′S, 73°09′W; Heymann and Aquino, 2010): research station near San Pedro (q.v.) on the Quebrada Blanco.
- **Estirón** (not mapped; 5°35′ S, 73°01′ W): Matses village on the lower Quebrada Chobayacu, not far (about 7 km) from Santa Rosa (q.v.).
- Jenaro Herrera (sometimes misspelled "Genaro Herrera" or "Henaro Errera"; 4°55′S, 73°40′W): botanical field station ca. 2.5 km inland from the right bank of the Río Ucayali, surveyed for mammals by various research teams from 1978 to 2003 (Voss and Fleck, 2011: 10).
- Nuevo San Juan (5°15′S, 73°10′W; IGN, 1995): Matses village on the right bank of the Río Gálvez (q.v.), intensively sampled for mammals from 1995 to 1999 by D.W.F. and from 19 May to 12 July 1998 by R.S.V.
- Orosa (ca. 3°32'S, 72°11'W; Wiley, 2010): collecting locality on the right bank of the Amazon where Alfonso and Ramón Olalla worked from 30 August to 11 December 1926 (probably near the modern village of San José de Orosa with above coordinates; Wiley, 2010). Hershkovitz (1977: 928) placed this locality on the Río Marañón, but Orosa lies well below the confluence of the Marañón and the Ucayali, so it is unambiguously on the Amazon (Río Amazonas; for Peruvian fluvial nomenclature, see Faura-Gaig, 1964). Also erroneously, Díaz (2014: 125) placed Orosa on the Río Napo, a major left-bank tributary of the Amazon. According to Wiley (2010), seasonally flooded forest (várzea) extends inland for many kilometers from the right bank of the Amazon at Orosa.
- Quebrada Curacinha (5°03′S, 72°44′W; Pitman et al., 2003): inventory site on the left bank of the Río Yavarí, about 20 km downstream from Angamos (q.v.), briefly visited by a Rapid Biological Inventory team in 2003 (Pitman et al., 2003).

- Quebrada Pobreza (5°59′S, 73°46′W; Pitman et al., 2015): inventory site on the eponymous stream, a left-bank affluent of the Río Blanco (q.v.), surveyed for mammals by M. Escobedo-Torres from 20–26 October 2014 (Pitman et al., 2015).
- Quebrada Vainilla (not mapped; ca. 3°32′S, 72°44′W; Robbins et al., 1991): collecting site on the eponymous stream about 17 km NE of Santa Cecilia (q.v.), visited by LSUMZ ornithologists in 1983 (Robbins et al., 1991).
- **Río Aucayo** (mouth at ca. 3°50′S, 73°05′W): minor right-bank tributary of the Amazon where R. Castro and P. Soini carried out early field studies of callitrichine behavioral ecology (Castro and Soini, 1977).
- **Río Gálvez** (mouth at 5°12′S, 72°53′W; DMA, 1989): one of two principal headwater tributaries of the Río Yavarí (see Río Yaquerana, below). Our inventory site at Nuevo San Juan (q.v.) was on the right bank of the middle Gálvez.
- **Río Manití** (mouth at 3°27′S, 72°51′W; DMA, 1989): minor right-bank tributary of the Amazon downstream from Iquitos.
- **Río Orosa** (mouth at 3°29′S, 72°03′W; Wiley, 2010): minor right-bank tributary of the Amazon, probably with mouth near Orosa (q.v.) in the early 1900s but now shifted downstream (Wiley, 2010: 40).
- **Río Tapiche** (mouth at 5°03′S, 73°51′W; DMA, 1989): major right-bank tributary of the Ucayali upstream from Jenaro Herrera (q.v.).
- **Río Yaquerana** (mouth at ca. 5°12′S, 72°53′W): one of two principal headwaters of the Río Yavarí. The combined waters of the Yaquerana and the Río Gálvez (q.v.) form the Río Yavarí, but the Yaquerana is sometimes also known as the Alto Yavarí (Faura-Gaig, 1964), not the "Alto Yaquerana" (contra Stephens and Traylor, 1983).
- San Fernando (4°09′S, 70°14′W; DMA, 1989): collecting locality of C. Kalinowski on left bank of the lower Río Yavarí, 10–15 July 1957.
- **San Pedro** (4°20′S, 73°12′W; Valqui, 2001): ribereño village on the lower Quebrada Blanco,

site of a faunal inventory study by Valqui (1999, 2001), whose results were based on fieldwork conducted from 1993 to 1999. Local habitats include flooded and unflooded primary forest and secondary growth.

Santa Cecilia (3°33′S, 72°53′W; Robbins et al., 1991): collecting locality of Celestino Kalinowski on the right bank of the Río Manití (q.v.) from 27 December 1956 to 21 January 1957. According to Robbins et al. (1991), who collected birds around Santa Cecilia in 1983, the predominant natural habitat is well-drained forest on level terrain.

Santa Rosa (not mapped; 5°32′ S, 72°59′ W): Matses village on the lower Quebrada Chobayacu, a minor left-bank tributary of the Río Yaquerana, about 37 km SE of Nuevo San Juan (q.v.). Note that the positions of this village and the nearby community of Estirón are reversed on Vriesendorp et al's (2006a) satellite map of Matses territory.

Tapiche (7°12′S, 73°56′W; Vriesendorp et al., 2006b): inventory site on the right bank of the upper Río Tapiche (q.v.), surveyed for mammals by M.L.S.P. Jorge and P.M. Velazco from 12–17 August 2005 (Jorge and Velazco, 2006).

APPENDIX 2

EXPECTED SPECIES

CALUROMYSIOPS IRRUPTA: The black-shouldered opossum is an elusive arboreal species known to occur along the left (north) bank of the Amazon in Loreto department and in Madre de Dios (Emmons, 2008). The few published observations of *C. irrupta* accompanied by definite habitat information (e.g., Janson et al., 1981) suggests that it occurs in whitewater floodplains; therefore, if it occurs in our region, it is perhaps to be found in the still poorly sampled riparian forests along the lower Ucayali and the right bank of the Amazon.

PHILANDER CANUS: The Yavarí-Ucayali interfluve occupies a wide gap in the known distribution of this species (Voss et al., 2018: fig. 9), which is known to occur north of our region in Venezuela

and eastern Colombia (where it was formerly known as *P. mondolfii* Lew et al., 2006) and south of our region in Peru, Bolivia, Paraguay, central Brazil, and northern Argentina. The closest specimen personally examined by us is from Moyobamba (6°03′S, 76°58′W; the type locality) in San Martín department, but two specimen that Díaz (2014) identified as *P. olrogi* Flores et al., 2008 (a junior synonym of *P. canus*; Voss et al., 2018) were collected on the adjacent left (north) bank of the Amazon about 40 km SW of Iquitos. The geographic distribution of collection localities for this species suggests that it occurs in upland habitats, but we have not found any explicit description of the Amazonian habitats in which it has been taken.

MARMOSA RUBRA: This western Amazonian species is known from just 12 localities (Rossi et al., 2010), of which 11 are north of the Yavarí-Ucayali interfluve (in southeastern Colombia, eastern Ecuador, and northern Loreto) and one is to the south (in Cusco). The specimens closest to our region were collected by the Olallas in 1925 at a locality they called "Boca Río Curaray," about 180 km NW of Iquitos (Wiley, 2010: fig 2). Nothing is apparently known about the ecological circumstances in which this species occurs.

MARMOSOPS CAUCAE: This is the oldest available name for the species that Patton et al. (2000) called M. neblina Gardner, 1989. Based on specimens sequenced by Díaz-Nieto et al. (2016: fig. 1), this species—or species complex—occurs north, south, east, and west of the Yavarí-Ucayali interfluve; the closest to our region are from the Rio Juruá (e.g., at Igarapé Nova Impresa: 6°48′S, 70°44′W) in western Brazil, where they were taken in "várzea forest or disturbed river-edge areas" (Patton et al., 2000: 57). Other specimens collected not too far from the Yavarí-Ucayali interfluve include two (FMNH 87119, 87120) from Santa Elena (ca. 4°50′ S, 74°13′ W) on the Río Samiria. We have not examined the material that Díaz (2014) identified as M. neblina from the left bank of the Amazon south of Iquitos, but no specimens referable to M. caucae were among the many small didelphids previously collected from the same general area by Hice and Velazco (2012).

 ${\bf APPENDIX~3}$ Specimens of Caluromys Sequenced for Cytochrome ${\it b}$

Species	Vouchera	Field number	Locality ^b	bp ^c
derbianus	KU 164643	RMT 4743	Costa Rica: Heredia, La Selva (1)	1148
derbianus	QCAZ 8663*	MP 87	Ecuador: Cotopaxi, Otonga (2)	1148
derbianus	USNM 464247*	JFJ 131	Panama: Bocas del Toro, Isla Bastimentos, Salt Creek (3)	1148
derbianus	USNM 578119*	FMG 2587	Panama: Bocas del Toro, Valiente Peninsula (4)	1148
lanatus	MSB 56998*	NK 13951	Bolivia: Pando, Isla Gargantua (5)	1148
lanatus	MVZ 190250*	MNFS 1518	Brazil: Acre, Nova Vida, right bank Rio Jurua (6)	1148
lanatus	MVZ 190248*	MNFS 944	Brazil: Amazonas, opposite Altamira, left bank Rio Juruá (7)	1148
lanatus	MVZ 197383	LPC 735	Brazil: Mato Grosso, Fazenda Noirumbá (8)	1140
lanatus	ROM 104570*	_	Ecuador: Orellana, 40.5 km S Pompeya Sur (9)	1148
lanatus	[MUSM]	LHE 1103	Peru: Amazonas, Cordillera Condor, Alfonso Ugarte (10)	1148
lanatus	MVZ 153276	JLP 6880	Peru: Amazonas, Río Cenepa, vicinity of Huampami (11)	1148
lanatus	[MUSM]	LHE 1463	Peru: Cusco, 2 km SW Tangoshiari (12)	1148
lanatus	TTU 99025*	TK 75121	Peru: Loreto, 25 km S Iquitos (13)	1148
lanatus	TTU 101044*	TK 73551	Peru: Loreto, 25 km S Iquitos (13)	1148
lanatus	AMNH 273038*	DWF 383	Peru: Loreto, Río Gálvez, Nuevo San Juan (14)	1148
lanatus	AMNH 273059*	DWF 414	Peru: Loreto, Río Gálvez, Nuevo San Juan (14)	1148
lanatus	KU 144058*	RMT 3980	Peru: Madre de Dios, Reserva Cuzco Amazónico (15)	1148
philander	[MNK] ^d	LHE 1695	Bolivia: Santa Cruz, between Florida and Los Fierros (16)	1149
philander	[MNK] ^d	LHE 1696	Bolivia: Santa Cruz, Los Fierros (17)	1148
philander	MVZ 197384	LPC 526	Brazil: Mato Grosso, Reserva Ecológica Cristalino (18)	1148
philander	MVZ 197586	LPC 97	Brazil: Minas Gerais, Parque Estadual do Rio Doce (19)	1148
philander	[MZUSP]	MAM 142	Brazil: São Paulo, Cotia, Caucaia do Alto (20)	1148
philander	MVZ 197385	LPC 705	Brazil: Tocantins, Rio Santa Teresa, 20 km NW Peixe (21)	1147
philander	MNHN 1998.310*	V-823/T-1754	French Guiana, Les Nouragues (22)	1148
philander	UMSPH 1081-V*	V-960/T-2020	French Guiana, Les Nouragues (22)	1148
philander	ROM 112676*	F 45378	Guyana: Demerara-Mahaica, Ceiba Biological Station (23)	1148
philander	AMNH 174003*	WGD 390	Trinidad and Tobago: Trinidad, Sangre Grande (24)	516

^a Asterisks indicate specimens personally examined by us. Institutional abbreviations in square brackets are collections where voucher material is assumed to have been deposited.

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^b Country, first geographic subdivision, and locality name (some abbreviated for table entry). Bold numbers in parentheses correspond to symbols plotted on our map of collecting localities (fig. 8).

 $^{^{\}rm c}$ Base pairs of cytochrome b.

^d Photographs examined.

 ${\bf APPENDIX~4}$ Specimens of ${\it Metachirus}$ Sequenced for Cytochrome ${\it b}$

Species	Voucher ^a	Field number	Locality ^b	bp ^c
myosuros	MSB 70283*	NK 30229	Bolivia: Cochabamba, Cavernas de Repechón (1)	1149
myosuros	AMNH 264565*	NK 25664	Bolivia: La Paz, La Reserva (2)	1149
myosuros	MVZ 190296*	MNFS 1578	Brazil: Acre, Nova Vida, right bank Juruá (3)	1149
myosuros	MVZ 190294 ^d	MNFS 1529	Brazil: Acre, Sobral, left bank Juruá (4)	1149
myosuros	MVZ 190285 ^d	JLP 15305	Brazil: Amazonas, Penedo, right bank Juruá (5)	1149
myosuros	MVZ 190288*	JLP 15567	Brazil: Amazonas, Seringal Condor, left bank Rio Juruá (6)	1149
myosuros	MNRJ 31454	EDH 23	Brazil: Bahia, Fazenda Brejo Grande, 12 km S Itabuna (7)	1149
myosuros	MVZ 182773*	MAM 193	Brazil: Espírito Santo, Município de Aracruz (8)	1149
myosuros	MVZ 197591	LPC 85	Brazil: Minas Gerais, Parque Estadual do Rio Doce (9)	1149
myosuros	MVZ 182772	MAM 187	Brazil: Rio de Janeiro, Mangaratiba, Ibicui (10)	1149
myosuros	MVZ 182774	MAM 240	Brazil: São Paulo, Fazenda Intervales, Base Saibadela (11)	1149
myosuros	ROM 105345*	F 37674	Ecuador: Orellana, 42 km S Pompeya Sur (12)	1149
myosuros	USNM 574502*	JFJ 636	Ecuador: Pastaza, Tiguino, 130 km S Coca (13)	1149
myosuros	USNM 578137*	FMG 2601	Panama: Bocas del Toro, Peninsula Valiente (14)	1149
myosuros	ROM 104229*	F 38064	Panama: Panamá, Parque Nacional Altos de Campana (15)	1149
myosuros	MNHNP 3424e	TK 122295	Paraguay: Canendiyú, Reserva de Biósfera Mbaracayú (16)	1149
myosuros	MNHNP 3423e	TK 122424	Paraguay: Canendiyú, Reserva de Biósfera Mbaracayú (16)	1149
myosuros	FMNH 174441*	95	Peru: Cusco, Paucartambo, 15.9 km SW Pilcopata (17)	1149
myosuros	TTU 101180*	TK 73911	Peru: Loreto, 21 km S Iquitos (18)	1149
myosuros	TTU 100926*	TK 73286	Peru: Loreto, 25 km S Iquitos (19)	1149
myosuros	AMNH 272780*	RSV 2236	Peru: Loreto, Río Gálvez, Nuevo San Juan (20)	1149
myosuros	MUSM 13293*	RSV 2329	Peru: Loreto, Río Gálvez, Nuevo San Juan (20)	1149
myosuros	KU 157976*	NW 830	Peru: Loreto, San Jacinto (21)	1149
myosuros	MVZ 157634*	JLP 8282	Peru: Madre de Dios, Lago Sandoval (22)	1149
myosuros	KU 144119*	RMT 3958	Peru: Madre de Dios, Reserva Cuzco Amazónico (23)	1149
nudicaudatus	MNHN 2004-316	V-1860/T-4487	French Guiana, Angoulème (24)	726
nudicaudatus	MHNG 1995.070	V-2175/T-5032	French Guiana, Trois Sauts (25)	1149
nudicaudatus	ROM 111938*	F 45067	Guyana: Potaro-Siparuni, Iwokrama Forest (26)	1149
nudicaudatus	ROM 114155*	F 41230	Surinam: Brokopondo, Brownsberg Nature Park (27)	726

^a Asterisks indicate specimens personally examined by us. Institutional abbreviations in square brackets are collections where voucher material is assumed to have been deposited.

^b Country, first geographic subdivision, and locality name (sometimes abbreviated). Bold numbers in parentheses correspond to symbols plotted on our map of collecting localities (fig. 16).

^c Base pairs of cytochrome *b*.

^d Examined by Patton et al. (2000).

^e Examined at our request by Robert Owen (in litt., 29 May 2012).

APPENDIX 5 PRIMERS USED TO AMPLIFY CYTOCHROME B

Forward primers:	
DidMVZ05	5'ATAACCTATGGCATGAAAAACCATTGTTG
Cal610F	5'ACCTGCTCTTTCTACACGAAACAGG
Met690F	5'AGATAAAATTCCATTTCATCC
Reverse primers:	
Did1260R	5'CCTTCATTGCTGGCTTACAAGGC
Phil730R	5'TCTCCYAGRAGRTCTGGTGARAATATTGC
Cal750R	5'TGGTGTAAAGTTGTCAGGGTCACC

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[∞] This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

On the cover: An opossum visitor (probably Marmosa constantiae) at the Estación Biológica Quebrada Blanco, a research station in the Yavarí-Ucayali interfluve (photo by Eckhard Heymann).