

A Revision of the Didelphid Marsupial Genus *Marmosa* Part 3. A New Species from Western Amazonia, with Redescriptions of *M. perplexa* Anthony, 1922, and *M. germana* Thomas, 1904

ROBERT S. VOSS¹ AND THOMAS C. GIARLA²

ABSTRACT

We describe a new species of woolly mouse opossum from northwestern Amazonia, *Marmosa jansae*, based on museum specimens previously misidentified either as *M. germana* Thomas, 1904, or as *M. regina* Thomas, 1898. Instead of being closely related to either of those species, *M. jansae* appears to be the sister taxon of *M. perplexa* Anthony, 1922, a trans-Andean species previously synonymized with *M. phaea* Thomas, 1899. We redescribe *M. perplexa*, which inhabits critically endangered evergreen and semideciduous forests in southwestern Ecuador and northwestern Peru. We also redescribe *M. germana*, an Amazonian species that has long been synonymized with *M. regina*, but which molecular analyses now suggest is the sister taxon of a trans-Andean species complex that includes *M. alstoni* (Allen, 1900). These results substantially clarify the long-confused taxonomy of woolly mouse opossums (subgenus *Micoureus*), provide new examples of sister-group relationships between upper-Amazonian and trans-Andean taxa, and raise interesting questions about congeneric diversity in northwestern Amazonia, where as many as six species of *Marmosa* might occur sympatrically.

¹ Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.

² Department of Biology, Siena College, Loudonville, NY.

INTRODUCTION

Marmosa germana was originally described by Thomas (1904) based on specimens collected in the Amazonian lowlands of eastern Ecuador. Although *M. germana* was recognized as a distinct species in Tate's (1933) monographic revision of *Marmosa*, it has subsequently been treated—without explanation—as a junior synonym or subspecies of *M. regina* Thomas, 1898 (e.g., by Gardner, 1993; Gardner and Creighton, 2008). By contrast, *M. perplexa*, originally described by Anthony (1922) based on a single specimen collected in western Ecuador, was relegated by Tate (1933) to the synonymy of *M. phaea* Thomas, 1899, and as a junior synonym of the latter species it has been largely ignored ever since. In fact, both *M. germana* and *M. perplexa* are morphologically distinct from the taxa with which they were once synonymized, and recent analyses of mitochondrial and nuclear gene sequences (Voss et al., 2020) now support their recognition as valid species of the subgenus *Micoureus*.

We redescribe *Marmosa germana* and *M. perplexa* in this report, but to do so we must first describe a new species, *M. jansae*, which is closely related to *M. perplexa* but occurs sympatrically with *M. germana*. Surprisingly, specimens of *M. jansae* have occupied museum cabinets for over 100 years, where they have been misidentified as belonging to other taxa. In analyses of multigene datasets (fig. 1), *M. jansae* and *M. perplexa* are consistently recovered as sister taxa, whereas *M. germana* is recovered in a separate clade that includes *M. alstoni* (Allen, 1900). These relationships have biogeographic and ecological implications because *M. alstoni* and *M. perplexa* both occur west of the Andes, whereas their sister taxa *M. germana* and *M. jansae* are members of a uniquely diverse fauna of mouse opossums that inhabit the Amazonian lowlands of southeastern Colombia, eastern Ecuador, and northeastern Peru.

Materials and Methods

SPECIMENS EXAMINED: Specimens cited in our tables and text 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); FMNH, Field Museum of Natural History (Chicago); KU, University of Kansas Biodiversity Research Center (Lawrence); LSUMZ, Louisiana State University Museum of Natural Science (Baton Rouge); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); ROM, Royal Ontario Museum (Toronto); TTU, The Museum of Texas Tech University (Lubbock); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); and USNM, National Museum of Natural History (Washington, DC).

MEASUREMENTS: 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 notes, 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 from specimen labels or field notes, but we sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by the collector, and we used our values whenever large dis-

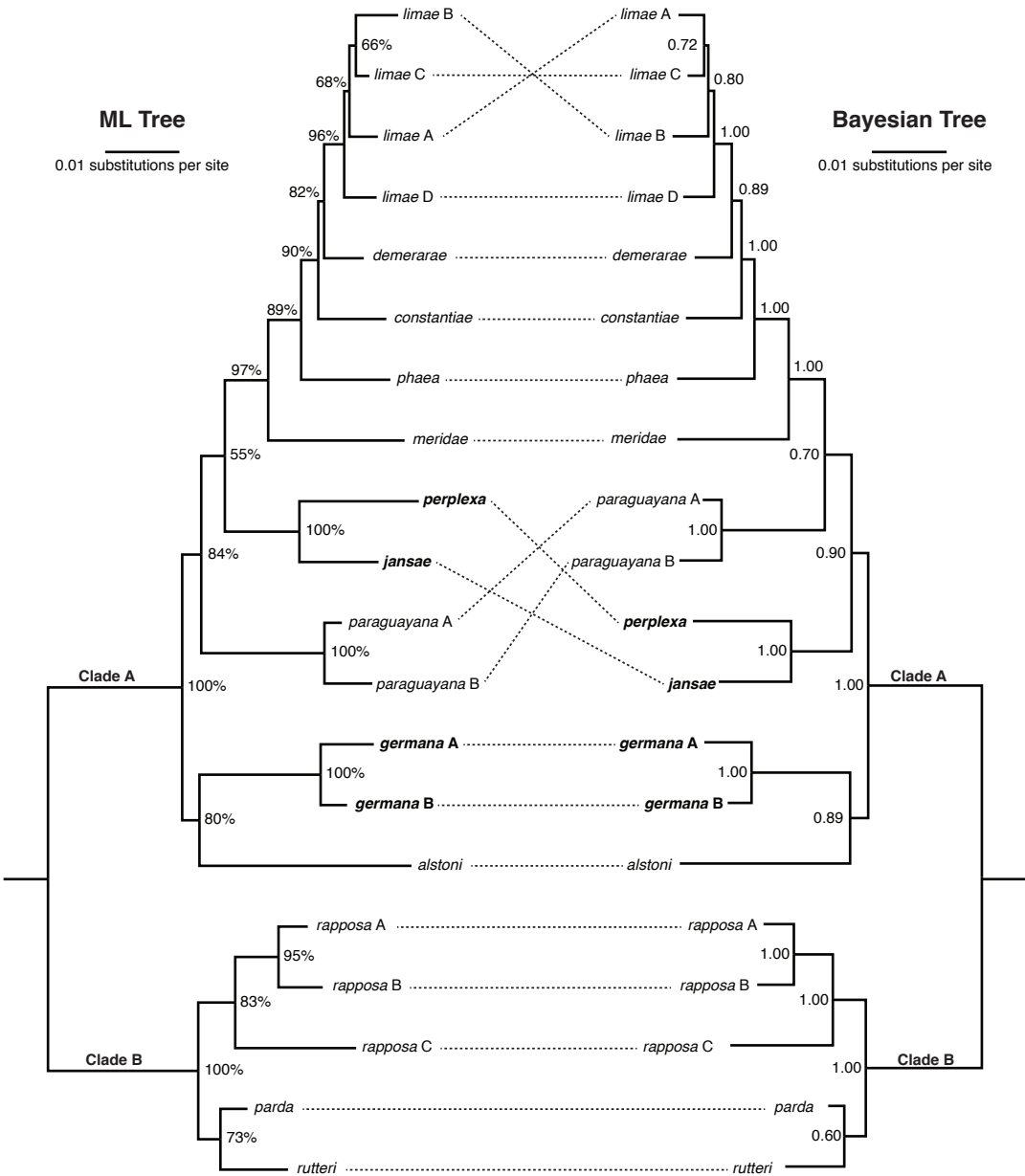


FIG. 1. Maximum-likelihood (ML; left) and Bayesian (right) phylogenetic trees for putative species of *Marmosa* (*Micoureus*) inferred from concatenated sequences of six genes (after Voss et al., 2020: fig. 6). Numbers at nodes denote ML bootstrap support or Bayesian posterior probabilities. Outgroups are not shown. Dotted lines connect the same taxa across the two trees to highlight differences. Names of species treated in this report are in boldface.

crepancies were found. All external measurements are reported to the nearest millimeter, and all weights are reported to the nearest gram.

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm; we computed sample statistics from these unrounded measurements, but values reported herein are rounded to the nearest 0.1 mm (the smallest decimal fraction that is consistently obtainable with repeated caliper measurements). The following dimensions were measured as illustrated by Voss et al. (2020: fig. 4):

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 across 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.

Least postorbital breadth (LPB): measured at the narrowest point across the frontals between the temporal fossae (behind the postorbital processes).

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 fourth molar (M4) crowns at or near the “stylar A” position.

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

Length of molars (LM): 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.

AGE DETERMINATION: Except as noted below, all analyzed character data were obtained from adult specimens as determined by dental criteria. A specimen was judged to be juvenile if dP3 is still in place; subadult if dP3 has been shed but P3 and/or M4 are still incompletely erupted; and adult if the permanent upper dentition is complete.

MORPHOLOGICAL TERMINOLOGY: Qualitative character variation is described herein using terminology that is explained or referenced by Voss and Jansa (2003, 2009). An exception (not defined by those authors) is the prefix “self-” as used in combination with descriptors of ventral pelage color, such as self-white or self-cream. This usage applies to hairs that have the same coloration from base to tip, as opposed to hairs that are basally gray and distally white or cream (for example).

DESCRIPTIVE STATISTICS: Estimates of central tendency and dispersion in our text and tables are the sample mean plus or minus one standard deviation.

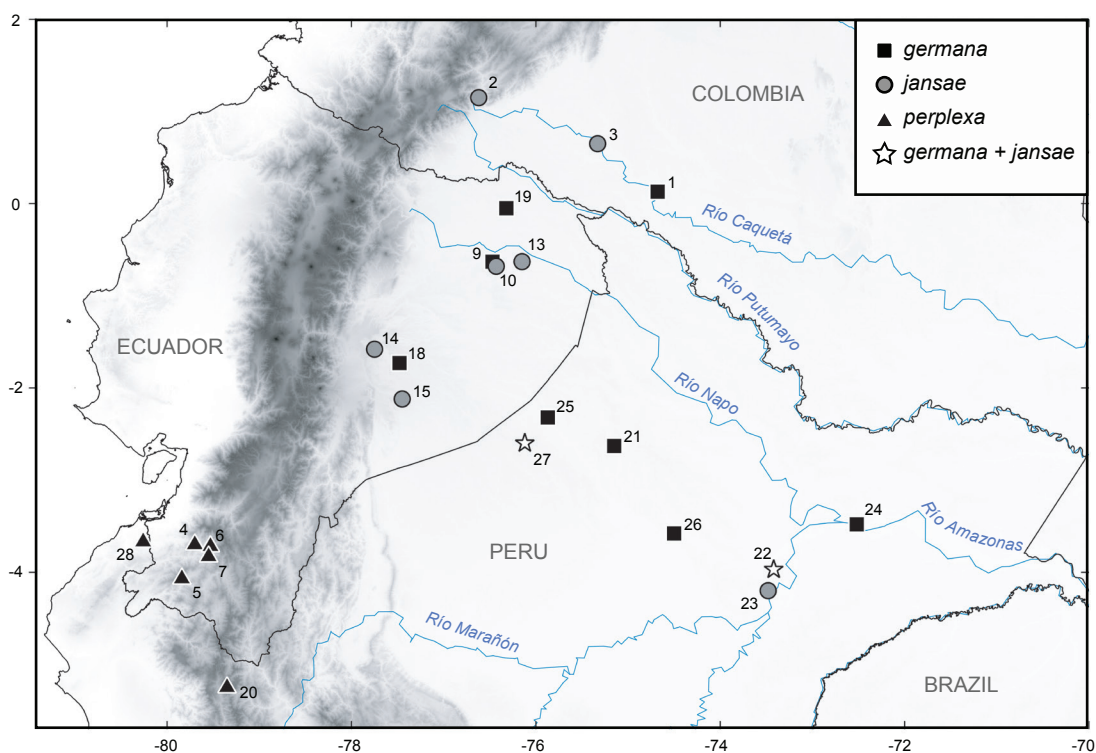


FIG. 2. Collection localities of examined specimens of *Marmosa germana*, *M. jansae*, and *M. perplexa*. Numbers are keyed to entries in our gazetteer (appendix 1).

SYSTEMATIC ACCOUNTS

Marmosa (Micoureus) jansae, new species

Marmosa “Yasuni” Voss et al., 2020: 11 (provisional name for a putative species identified by phylogenetic analyses of molecular sequence data).

TYPE MATERIAL AND TYPE LOCALITY: The holotype consists of the skin, skull, postcranial skeleton, and frozen tissues of an adult male (ROM 118880; original number F41891) collected 42 km south and 1 km east of Pompeya Sur in Parque Nacional Yasuní, Orellana province, Ecuador, on 29 May 2006 by M.D. Engstrom and S.L. Peters (see appendix 1 for geographic coordinates). Molecular sequence data obtained from the holotype by Voss et al. (2020) include the entire cytochrome *b* gene (1149 bp, GenBank accession number MN978679) together with fragments of the following loci (abbreviated as in Voss et al., 2020): Anon128 (690 bp, MN978693), BRCA1 exon 10 (949 bp, MN978705), IRBP exon 1 (1180 bp, MN978712), and OGT intron 14 (645 bp, MN978724).

DISTRIBUTION AND SYMPATRY: *Marmosa jansae* is currently known from the Amazonian lowlands of southeastern Colombia (Putumayo), eastern Ecuador (Orellana, Pastaza), and northeastern Peru (Loreto); the three Peruvian localities from which *M. jansae* has been collected (see Specimens Examined, below) are all on the north (left) bank of the



FIG. 3. Dorsal and ventral views of skins of *Marmosa jansae* (ROM 118880), *M. perplexa* (USNM 513425), and *M. germana* (FMNH 43179).

Amazon/Marañón (fig. 2). *Marmosa jansae* has been collected in sympatry with several congeners, including *M. (Eomarmosa) rubra*, *M. (Micoureus) germana*, and *M. (Marmosa) waterhousei* (appendix 2).

DESCRIPTION: The dorsal pelage of *Marmosa jansae* is dull grayish brown (fig. 3); in most specimens the color is close to Ridgway's (1912) Deep Grayish Olive, but in a few the color is closer to Hair Brown. Although this drab pigmentation is unremarkable (most other members of the subgenus *Micoureus* also have grayish-brown dorsal pelage), the fur of *M. jansae* is distinctively short, ranging in middorsal length from just 8 to 10 mm. The ventral pelage is almost entirely gray-based; self-colored (pale buff) fur is only consistently present ventrally on the chin and groin. In a few specimens (e.g., ROM 40399, TTU 157974) there is a narrow, discontinuous midventral streak of self-colored fur, but the fur of the chest and the insides of the forelimbs is always gray-based. The hind feet are covered dorsally with short, pale-buff hairs, but the metacarpals and proximal phalanges of the forefeet are covered with dark (brownish) hairs, such that only the distal manual phalanges are pale. The tail is about 137% of the combined length of the head and body, on average, and only 20 mm or less of the base of the tail is covered with short (≤ 5 mm) fur; the naked, scaly part of the tail is uniformly dark dorsally, but the ventral surface is sometimes indistinctly paler.

Adult skulls (fig. 4) are unremarkable in dorsal view, each with the widely flaring zygomatic arches, short, broad rostrum, and well-developed postorbital processes that are typical cranial features of the subgenus *Micoureus*. In ventral view, the skull is distinguished by short (3.8 ± 0.5 mm) maxillopalatine fenestrae that usually extend only from a point opposite the P3/M1 commissure to a point opposite the M2/M3 commissure, by the complete absence of palatine fenestrae, and by auditory bullae that often have well-developed anteromedial laminae. The latter are noteworthy because, in most marmosines (e.g., *Marmosa murina*; Voss and Jansa, 2009: fig. 16A), the extracranial course of the maxillary nerve is unenclosed by bone; the anteromedial lamina does not completely enclose the nerve in most specimens of *Marmosa jansae*, but in a few specimens (e.g., ROM 106151) it forms a secondary foramen ovale resembling the morphology sometimes seen in *Monodelphis* (Voss and Jansa, 2009: fig. 16C). The second upper premolar (P2) has an incomplete lingual cingulum, and the upper molar toothrow is short (LM = 7.9–8.5 mm) by comparison with other Amazonian species of *Micoureus* (see below). The postprotocrista of M3 terminates at or near the base of the metacone, and the lower molars lack posterior cingulids.³

COMPARISONS: *Marmosa jansae* averages larger than its trans-Andean sister species, *M. perplexa*, in all measured dimensions (tables 1, 3). Despite its larger body size, however, *M. jansae* has shorter (8–10 mm versus 11–13 mm) dorsal fur than *M. perplexa*, but these species are otherwise externally similar. In dorsal view, skulls of *M. jansae* (fig. 4A) have visibly shorter, broader rostrums in proportion to cranial length than skulls of *M. perplexa* (fig. 4B), but for lack of suitable landmarks these proportions are difficult to quantify. A more conspicuous difference is that the postorbital processes are always well developed in adult skulls of *M. jansae*, whereas the postorbital processes are never very large in *M. perplexa*. In ventral cranial view,

³ For illustrations of these and contrasting molar traits of other species, see Voss et al. (2020: figs. 10, 11).

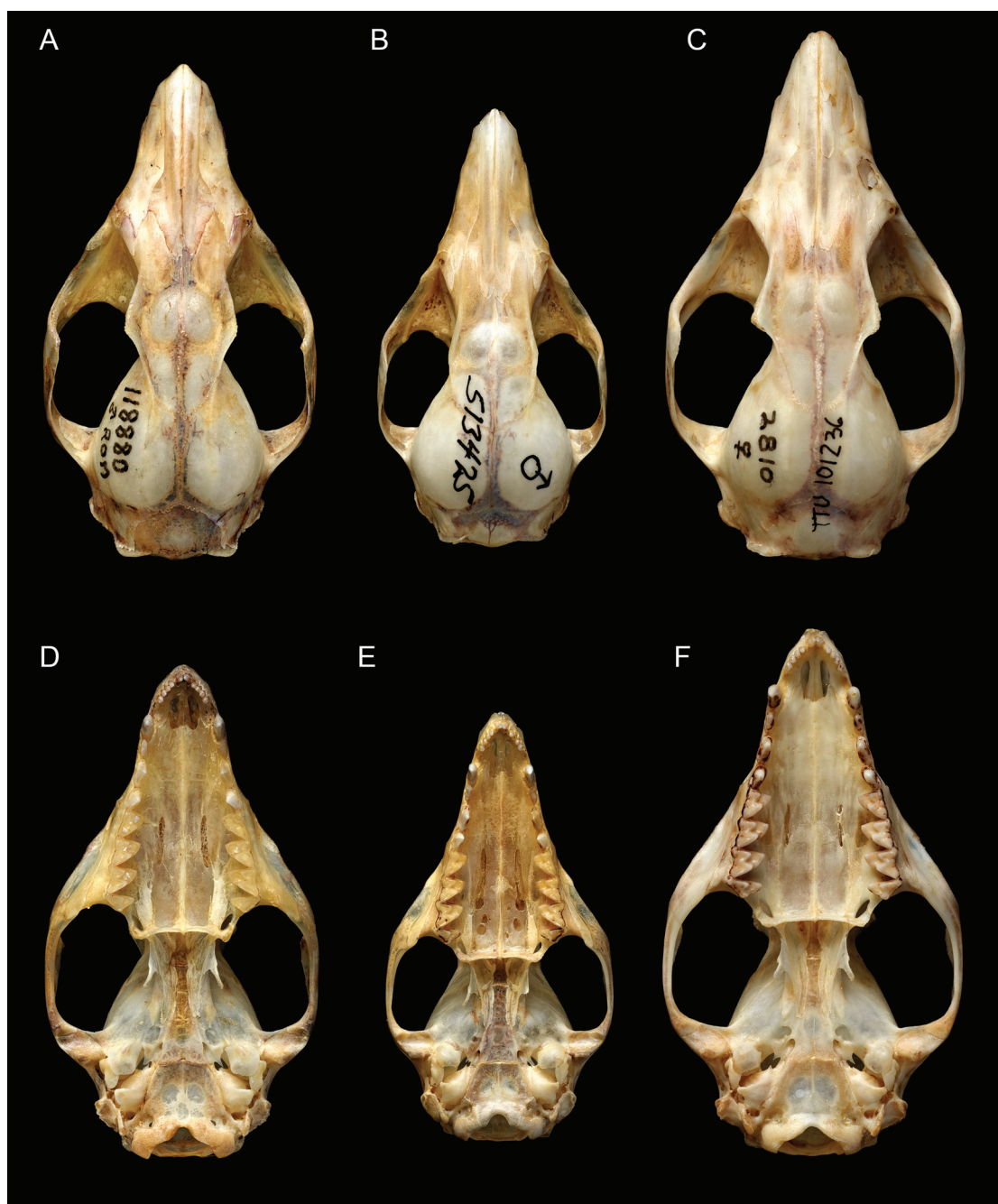


FIG. 4. Dorsal and ventral cranial views ($\times 1.75$) of *Marmosa jansae* (A, D; ROM 118880), *M. perplexa* (B, E; USNM 513425), and *M. germana* (C, F; TTU 101236).

TABLE 1. Measurements (mm) and weights (g) of *Marmosa (Micoureus) jansae*.

	Males ^a	Females ^b
HBL	165 ± 9 (153–177) 7	161 ± 10 (149–177) 6
LT	227 ± 9 (215–237) 7	218 ± 10 (209–237) 6
HF	25 ± 1 (25–27) 7	24 ± 1 (22–26) 9
Ear	24 ± 1 (23–25) 5	24 ± 1 (22–25) 5
CBL	39.9 ± 0.8 (39.0–40.6) 5	38.8 ± 0.9 (37.7–39.9) 6
NL	18.2 ± 1.1 (17.0–19.5) 6	17.3 ± 0.8 (16.2–18.3) 8
NB	5.6 ± 0.2 (5.3–6.0) 7	5.4 ± 0.3 (4.8–5.8) 9
LIB	7.3 ± 0.3 (6.9–7.8) 7	6.9 ± 0.2 (6.6–7.4) 10
LPB	7.1 ± 0.4 (6.7–7.7) 7	7.1 ± 0.3 (6.4–7.6) 10
ZB	22.7 ± 0.9 (21.3–24.4) 7	22.0 ± 0.8 (20.6–23.2) 8
PL	22.6 ± 0.7 (22.0–23.8) 7	21.8 ± 0.7 (20.9–22.8) 7
PB	12.7 ± 0.5 (12.0–13.3) 7	12.5 ± 0.4 (11.8–12.9) 10
MTR	16.3 ± 0.3 (15.7–16.7) 7	15.9 ± 0.3 (15.5–16.4) 10
LM	8.3 ± 0.2 (7.9–8.5) 7	8.2 ± 0.1 (8.0–8.3) 10
M1-3	7.0 ± 0.2 (6.6–7.2) 7	6.9 ± 0.1 (6.7–7.0) 10
WM3	2.6 ± 0.1 (2.5–2.7) 7	2.6 ± 0.1 (2.5–2.8) 10
Weight	90 ± 12 (80–103) 3	70 ± 10 (56–79) 4

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: FMNH 40399, 46430, 46431, 53351; ROM 106151, 118880; TTU 124793.

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: BMNH 11.7.19.20, 54.267; FMNH 70962, 70967, 70968; KU 157974; TTU 99000, 101208, 124792; USNM 267503.

M. jansae has absolutely and relatively shorter maxillopalatine fenestrae (on average) than *M. perplexa*, although there is some taxonomic overlap in measured fenestral lengths (2.8–4.4 mm in *M. jansae* versus 4.2–5.2 mm in *M. perplexa*). Lastly, none of our specimens of *M. jansae* has palatine fenestrae, whereas palatine fenestrae are consistently present in our material of *M. perplexa*. Such morphological differences, together with the 8% average divergence in cytochrome *b* sequences reported by Voss et al. (2020: table 4) seem sufficient to support the hypothesis that these are distinct species.

The geographic range of *Marmosa jansae* overlaps the distributions of two other Amazonian species of the subgenus *Micoureus*—*M. germana* and *M. rutteri*—but these taxa are not closely related (fig. 1) and they are morphologically dissimilar (table 2). By comparison with *M. jansae*, *M. germana* is much larger in all measured dimensions (table 4), has longer dorsal fur, has a much longer furry tail base, and lacks anteromedial bullar processes. *Marmosa rutteri* is also substantially larger than *M. jansae* (see measurement data summarized by Voss et al., 2020: table 9), but these two species have similarly short dorsal fur and short-furred tail bases. Instead, *M. jansae* and *M. rutteri* are most easily distinguished externally by ventral coloration: whereas *M. jansae* has almost entirely gray-based ventral fur, *M. rutteri* almost always has a broad midventral zone of self-colored (usually yellowish) fur that extends continuously from

TABLE 2. Morphological comparisons among three species of *Marmosa* (*Micoureus*) from northwestern Amazonia.

	<i>Marmosa germana</i>	<i>Marmosa jansae</i>	<i>Marmosa rutteri</i>
Middorsal fur length ^a	13 ± 1 mm	9 ± 1 mm	10 ± 1 mm
Ventral fur	mostly gray-based	mostly gray-based	partly self-colored
Length of furry tail base	usually ≥30 mm	usually ≤20 mm	usually ≤20 mm
Anteromedial bullar process	absent or inconspicuous	often well-developed	absent or inconspicuous
Lingual cingulum of P2	incomplete	incomplete	complete
Postprotocrista of M3	short	short	long
Postcingulids of m1–m3	absent	absent	usually present
Crown length of M1–M4 ^a	9.1 ± 0.3 mm	8.2 ± 0.2 mm	9.0 ± 0.4

^a The mean plus or minus one standard deviation.

chin to groin, and the insides of the forelegs are also self-colored. Additionally, *M. rutteri* has a complete lingual cingulum on P2, a long postprotocrista on M3, and small but usually persistent posterior cingulids on m1–m3.

REMARKS: One of the specimens we refer to *Marmosa jansae* (BMNH 11.7.19.20) was identified by Tate (1933: 80) as *M. germana germana*, but later in the same publication (on p. 82) he identified two other specimens (AMNH 64025, 68142) as *M. germana rutteri*.⁴ Such misidentifications exemplify the taxonomic confusion that has long prevailed regarding western Amazonian species of *Marmosa*, and they help explain why *M. jansae* (specimens of which were first collected >100 years ago) remained undescribed until now. More recently, specimens of *Marmosa jansae* were identified as *M. regina* by Hice and Velazco (2012), an identification consistent with the then-prevailing notion that *M. germana* and *M. rutteri* were synonyms or subspecies of *M. regina*. However, *M. regina* is not a member of the subgenus *Micoureus* (Giarla and Voss, 2020), and an application has been submitted to the International Commission on Zoological Nomenclature to suppress usage of the epithet (Voss and Giarla, 2020).

HABITATS: Lowland rainforest is the natural climax vegetation throughout the known geographic range of *Marmosa jansae*, but only two specimens (TTU 99000, 101208) are accompanied by explicit habitat descriptions. According to Hice and Velazco (2012: 27), who summarized the results of a multiyear faunal inventory project at the Reserva Nacional Allpahuayo-Mishana in Loreto department, Peru, these specimens were trapped “in *monte alto* forest several hours walk from the road.” The authors explained that *monte alto* (fig. 5) is the typical rainforest of the area, where it occurs on clayey soils in low-lying areas; among other attributes, *monte alto* forest has a high (30–40 m) canopy, abundant understory palms, and numerous lianas. By contrast, five sympatrically collected specimens of *M. germana* (TTU 98845, 98846, 98988, 101094, 101236) were trapped or shot “in *varillal* habitat and in older secondary growth” (Hice and Velazco, 2012: 25). *Varillal* is the local name for a distinctive type of stunted forest that grows on white sand on upland terrain; among other floristic and structural differences, it has

⁴ Only the skin of AMNH 64025 is from *Marmosa jansae*; the mismatched skull is from *Marmosops noctivagus*. This specimen was purchased from commercial collectors, who were probably responsible for the mismatched elements.

TABLE 3. Measurements (mm) and weights (g) of *Marmosa (Micoureus) perplexa*.

	MUSM 24484	USNM 513425	AMNH 47188 ^a	AMNH 61382	MUSM 24486	UMMZ 176563
Sex	male	male	female	female	female	female
HBL	130	114	127	151	127	—
LT	195	192	178	204	184	—
HF	23	24	22	25	22	24
Ear	25	22	—	—	24	21
CBL	35.5	35.7	—	37.5	35.2	38.0
NL	15.9	16.7	14.4	16.8	15.9	18.0
NB	4.9	4.6	4.9	5.2	4.9	6.0
LIB	6.5	6.1	6.1	6.6	6.4	7.0
LPB	8.0	7.1	—	6.8	8.0	7.2
ZB	19.4	19.2	19.5	21.0	19.3	21.3
PL	20.4	20.6	18.9	21.3	20.1	22.1
PB	10.9	11.2	12.4	11.9	11.3	12.4
MTR	14.9	15.0	14.6	15.1	15.0	15.6
LM	7.8	8.0	7.7	7.8	8.0	8.2
M1-3	6.7	6.7	6.8	6.6	6.6	7.0
WM3	2.5	2.6	2.7	2.4	2.5	2.6
Weight	43	35	—	—	39	—

^a Holotype.

a much lower canopy (with a maximum height of 20 m), fewer understory palms, and fewer lianas than does adjoining *monte alto* habitat.

Few as they are, these observations from the Reserva Nacional Allpahuayo-Mishana suggest that, within the matrix of what is broadly considered lowland rainforest, sympatric species of the subgenus *Micoureus* might occupy floristically and structurally distinct habitats correlated with soil types, successional stage, or (as discussed by Voss et al., 2020), seasonal flooding regimes. Although Hice and Velazco's (2012) results imply that *Marmosa jansae* prefers tall primary forest over secondary vegetation or white-sand forest, only future fieldwork carefully designed to assess faunal differences among adjacent vegetation types is likely to provide compelling evidence of such habitat associations.

ETYMOLOGY: For our friend, mentor (to T.C.G.), and colleague Sharon A. Jansa (fig. 6), whose molecular-phylogenetic research has produced major advances in systematic understanding of both marsupials and rodents.

SPECIMENS EXAMINED ($N = 22$): **Colombia**—*Putumayo*, Mocoa (ROM 40399, 46430, 46431), Río Mecaya (FMNH 70962, 70967, 70968). **Ecuador**—*Orellana*, Cerro Guataraco (USNM 267503), 42 km S and 1 km E Pompeya Sur (ROM 118880), Río Suno Abajo (AMNH 68142), Río Suno Arriba (AMNH 64025), Tiputini Biodiversity Station (ROM 106151); *Pastaza*, Canelos (BMNH 11.7.19.20), Río Copotaza (FMNH 53347, 53349, 53351), Río Pastaza (BMNH 54.267). **Peru**—*Loreto*, 25 km S Iquitos (TTU 99000, 101208), 52 km S Iquitos (TTU 124792, 124793), 1.5 km N Teniente López (KU 157974, 157875).

TABLE 4. Measurements (mm) and weights (g) of *Marmosa (Micoureus) germana*.

	BMNH 80.5.6.77 ^a	Adult males ^b	Adult females ^c
HBL	"187"	193 ± 9 (186–205) 4	171 ± 14 (154–187) 5
LT	"245"	267 ± 13 (254–282) 4	251 ± 18 (225–270) 6
HF	"23"	30 ± 2 (27–32) 4	27 ± 1 (25–29) 7
Ear	"19"	26 ± 2 (24–28) 4	25 ± 1 (24–26) 6
CBL	42.3	45.1 ± 2.6 (41.5–47.4) 4	43.6 ± 2.6 (39.9–46.9) 5
NL	—	20.6 ± 1.4 (18.8–22.3) 4	20.4 ± 1.9 (18.5–22.3) 3
NB	6.1	6.8 ± 0.4 (6.1–7.2) 6	6.2 ± 0.5 (5.7–6.9) 7
LIB	7.6	8.2 ± 0.5 (7.4–8.7) 6	7.4 ± 0.4 (6.9–8.0) 6
LPB	7.3	7.6 ± 0.2 (7.2–7.8) 5	7.3 ± 0.6 (6.5–8.3) 7
ZB	24.7	25.0 ± 1.9 (22.6–26.9) 4	24.5 ± 1.2 (23.1–26.3) 7
PL	23.8	25.5 ± 1.0 (23.9–26.7) 5	24.4 ± 1.3 (22.5–26.2) 5
PB	14.4	14.4 ± 0.8 (13.1–15.2) 5	14.1 ± 0.5 (13.5–14.7) 7
MTR	17.7	18.4 ± 0.6 (17.4–19.1) 6	17.5 ± 0.4 (17.0–18.0) 6
LM	9.3	9.2 ± 0.2 (8.8–9.5) 6	8.9 ± 0.2 (8.7–9.2) 7
M1-3	7.9	7.8 ± 0.3 (7.3–8.1) 6	7.5 ± 0.2 (7.2–7.7) 7
WM3	3.0	3.0 ± 0.1 (2.8–3.1) 6	3.1 ± 0.1 (3.0–3.2) 7
Weight	—	119 ± 30 (84–150) 4	88 ± 11 (75–95) 3

^a The subadult female holotype. External measurements in scare quotes were taken by Thomas (1904) from the stuffed skin according to British conventions (Lankester, 1904).

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: BMNH 80.5.6.76; FMNH 124606; MUSM 17588; ROM 105521; TTU 98846, 98988.

^c The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 67292; BMNH 54.265; FMNH 43179, 87116; KU 157973; TTU 101236.

Marmosa (Micoureus) perplexa Anthony, 1922

Marmosa perplexa Anthony, 1922: 3 (original description).

Marmosa phaea: Tate, 1933: 84 (part, *perplexa* treated as synonym).

Marmosa (Marmosa) phaea: Cabrera, 1958: 23 (part, *perplexa* treated as synonym).

Micoureus regina: Gardner, 1993: 20 (part, *perplexa* treated as synonym).

Micoureus phaeus: Gardner, 2005: 13 (part, *perplexa* treated as synonym).

Marmosa (Micoureus) phaea: Voss and Jansa, 2009: 101 (part, *perplexa* treated as synonym).

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation, AMNH 47188) consists of the skin and skull of a young adult female collected on the trail from Zaruma to Loja near Punta Santa Ana, 3650 feet (1113 m) above sea level, in the western Andean foothills of Loja province, Ecuador, by H.E. Anthony on 21 December 1920.

DISTRIBUTION AND SYMPATRY: Examined specimens of *Marmosa perplexa* are all from lowland, foothill, or lower-montane localities in southwestern Ecuador (Loja, El Oro) and northwestern Peru (Cajamarca, Tumbes). This species is not known to occur sympatrically with other congeners.



FIG. 5. Rainforest (*monte alto*) habitat of *Marmosa jansae* at the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru (photo by Christine L. Hice).

DESCRIPTION: The dorsal pelage of *Marmosa perplexa* is (as usual for the subgenus) dull grayish brown (fig. 3); among Ridgway's (1912) color swatches, the closest match seems to be Hair Brown, with remarkably little variation in side-by-side comparisons among five skins collected between 1920 and 2006.⁵ Measured at midback, the dorsal fur varies from 11 to 13 mm long in the same series. The ventral pelage is almost entirely gray-based, with self-colored (pale buff) fur only on the chin and groin. The hind feet of some specimens (e.g., AMNH 61382) seem to be almost entirely covered with pale fur, but in others (e.g., USNM 513425) some of the metatarsal fur is dark; the metacarpal fur of the forefeet seems to be consistently brownish, but the manual phalanges are pale. The tail averages about 148% of head-and-body length, but with such extreme individual variation in this proportion (from 135% to 168%) as to cast doubt on the accuracy of some collectors' measurements; excluding the highest and lowest computed fractions, however, the average is about the same (145%). Only 20 mm or less of the tail base is covered with short (ca. 5–6 mm) fur. The naked (scaly) caudal skin is completely dark from base to tip in some specimens (e.g., AMNH 61382, USNM 513425), but the tail of the holotype has pale mottling near the tip, and the tail of one specimen (UMMZ 176563) is almost half white.

In dorsal view, adult skulls of *Marmosa perplexa* (fig. 4B) are chiefly remarkable for their slender rostrums and for the absence of well-developed postorbital processes. In ventral view (fig. 4E), these skulls have long (4.8 ± 0.5 mm) maxillopalatine fenestrae that sometimes extend

⁵ But note that Anthony (1922) matched the dorsal pelage of the type with Saccardo's Umber, a decidedly more saturated color.



FIG. 6. Sharon A. Jansa (with *Marmosa robinsoni* on Tobago; photo by F. Keith Barker).

from a point opposite P3 to a point opposite the M3 protocone on each side; one specimen (MUSM 24484), however, has notably shorter maxillopalatine fenestrae. Another distinctive feature is the consistent presence of palatine fenestrae, either as one large hole or as multiple smaller perforations on each side. Lastly, several specimens (e.g., AMNH 47199, MUSM 24484, UMMZ 176563) have well-developed anteromedial bullar processes resembling those described above for *M. jansae*, and in one specimen (MUSM 24484) the anteromedial process forms a unilaterally complete secondary foramen ovale. The second upper premolar (P2) has an incomplete lingual cingulum, and the molar toothrow is among the shortest known in the subgenus (LM = 7.7–8.2 mm). The postprotocrista of M3 is short (terminating at or near the base of the metacone), and m1–m3 lack posterior cingulids.

COMPARISONS: Tate (1933) synonymized *Marmosa perplexa* with *M. phaea*, and it is hard to fault his decision, because these taxa are very similar morphologically. However, *M. perplexa* and *M. phaea* are not closely related (fig. 1), and they have highly divergent cytochrome *b* sequences (about 11% on average; Voss et al., 2020: table 4). Side-by-side comparisons of *M. perplexa* with typical examples of *M. phaea* (from the Colombian departments of Cauca, Huila, and Nariño) suggest that these species are externally indistinguishable, but skulls of *M. phaea* are slightly larger than those of *M. perplexa*, have better-developed postorbital processes, a complete lingual cingulum on P2, and long postprotocristae.

Morphological comparisons between *M. perplexa* and its allopatric sister species *M. jansae* were summarized in the preceding account.

REMARKS: In his original description of *Marmosa perplexa*, Anthony (1922: 3) emphasized the “peculiarly depressed frontal region” and the absence of postorbital processes in the type, a young adult, but Tate (1933) noted the absence of any frontal depression in a subsequently collected fully adult specimen (AMNH 61382) and suggested that the type skull was deformed. None of the other specimens that we assign to this species has a frontal depression resembling that of the type, but the absence of well-developed postorbital processes seems to be a valid diagnostic feature. Nevertheless, none of the material at hand is very old, and it is possible that specimens more mature than any we have yet seen might have better-developed processes.

Cytochrome *b* sequences that Voss et al. (2020) obtained from USNM 513425 (475 bp; GenBank accession MN978645) and UMMZ 176563 (1149 bp; MN978646) differ by about 5% (uncorrected), a noteworthy value, but maximum-likelihood analyses recovered these sequences as a strongly supported clade (with 100% bootstrap support; Voss et al., 2020: fig. 5) and we regard them as conspecific. Nevertheless, UMMZ 176563 is our only montane example of *Marmosa perplexa*, it is the only specimen we have seen with a half-white tail, and it is slightly larger than the other specimens we measured (table 3). A less conservative interpretation of such observations might conclude that two species are represented, but it seems prudent to await additional material from the mountains of northwestern Peru to establish whether these are consistent differences between lowland and highland populations that merit taxonomic recognition.

HABITATS: The vegetation of southwestern Ecuador and northwestern Peru is a complex mosaic of humid (evergreen or semi-evergreen) forest, dry (deciduous) forest, and arid scrub.

In general, the coastal lowlands are subject to the desiccating effect of the cold Humboldt Current, but a narrow strip of humid forest occurs along the foothills of the Andes, and condensation from nocturnal fogs can sustain patches of humid vegetation in otherwise arid landscapes (Chapman, 1926). Site descriptions are therefore crucial for understanding the habitat affinities of species in this region.

According to Chapman (1926: 716), the AMNH expeditionary camp at Punta Santa Ana—the type locality of *Marmosa perplexa*—was in “a heavy stand of fine forest” in a well-watered headwater valley of the Río Tumbes, but “the surrounding district is arid and desolate.” A typed itinerary of Anthony’s 1921 fieldwork in Ecuador provides more information.⁶

Punta Santa Ana is a high divide between two tributaries of the Río Tumbes, and our camp was at an elevation of 3650 feet in a splendid body of large timber. This forest was extremely local, not more than three or four miles wide at the southern end and extending as a long tongue down a valley ... Probably the greater part of this region is in the humid tropical zone, reaching [upslope] into the subtropics, but immediately to the west, south, and east lie great areas of the arid tropical [zone] so that, in a sense, it is an oasis of life in a great barren section.

Anthony’s handwritten fieldnotes describe the local vegetation as including large trees (among which “figs,” presumably *Ficus* spp., were very common), small tree ferns, and “cane” (probably dwarf bamboo, *Chusquea* sp. [Poaceae]). Mammals collected at this locality (in addition to *M. perplexa*) included such humid-forest taxa as *Alouatta palliata*, *Cebus albifrons*, *Potos flavus*, *Melanomys caliginosus*, and *Transandinomys talamancae*.

Only the most cursory habitat descriptions are available for other sites at which *Marmosa perplexa* has been collected in Ecuador, but G.H.H. Tate’s fieldnotes for 1921 indicate that humid tropical forest (or remnants of such vegetation) were present at Piñas (in El Oro province) and Guainche (in Loja). However, the habitat near Portovelo (in El Oro) may have been less humid, because dry-forest rodent species such as *Aegialomys xanthaeolus* (e.g., USNM 513559, 513560) were collected in sympatry with *M. perplexa* at this locality.

The vegetation surrounding Quebrada Faical in the Parque Nacional Cerros de Amotepe of northwestern Peru has been described as “dry deciduous forest” (Wiedenfeld et al., 1985: 305), “semi-deciduous forest” (Parker et al., 1995: 202), or transitional between “Equatorial Dry Forest” and “Pacific Tropical Rainforest” (Pacheco et al., 2007). According to Wiedenfeld et al. (1985), most of the trees had lost or were losing their leaves when researchers visited this site early in the dry season, but a photograph of the local habitat (presumably taken at the same time; Wiedenfeld et al., 1985: fig. 2) shows many still-leafy trees. The forest canopy is said to be about 20 m high, with such characteristic tree species as *Triplaris cumingiana* (Polygonaceae), *Cavanillesia plataniifolia* (Malvaceae), *Ficus jacobii* (Moraceae), *Ceiba trichastandra* (Malvaceae), *Muntingia calabura* (Muntingiaceae), *Tessaria integrifolia* (Asteraceae), and *Mimosa pellita* (Fabaceae) (Pacheco et al., 2007). Palms and giant herbs are conspicuously absent from photographs of the forest interior

⁶ These and other unpublished sources cited in the next paragraph are preserved in the AMNH Department of Mammalogy archives.



FIG. 7. Semideciduous forest understory near Quebrada El Faical, Tumbes department, Peru, habitat of *Marmosa perplexa* (photo by Elizabeth Escobar).

(e.g., fig. 7), additional indications of highly seasonal rainfall at this locality. Two specimens of *Marmosa perplexa* were captured in the kitchen of the biological station at El Faical, but two others were captured in the forest: one on the ground and another about 1 m above the ground on a tree branch; *Transandinomys talamancae* and *Proechimys decumanus* were taken in the same traplines that captured *M. perplexa* at this locality (V. Pacheco, personal commun.).

In summary, *Marmosa perplexa* appears to occur in a range of forest types in southwestern Ecuador and northwestern Peru. Based on the presence of tree ferns at Punta Santa Ana, the vegetation at the type locality was probably evergreen forest, and descriptions of similar sites in the immediate area (e.g., Robbins and Ridgley, 1990; Torres-Porras et al., 2017) suggest that this humid premontane vegetation is sustained by daily moisture from enveloping clouds. In the adjacent lowlands, *M. perplexa* seems to occur at drier sites where the forest is at least partially leafless in the dry season. Whether evergreen or semideciduous, however, the forests of southwestern Ecuador and northwestern Peru are among the most endangered habitats in the western hemisphere, and their endemic biotas are a focus of urgent conservation concern (Parker et al., 1995; Linares-Palomino et al., 2010; Ferrer-Paris et al., 2018; Rivas et al., 2020).

SPECIMENS EXAMINED ($N = 10$): **Ecuador**—*El Oro*, Piñas (AMNH 61382, 61391); *Loja*, Guainche (AMNH 61390), 12 km E by road Portovelo (USNM 513425), Punta Santa Ana (AMNH 47188). **Peru**—*Cajamarca*, Cerro La Viuda (UMMZ 176563); *Tumbes*, Quebrada Faical (MUSM 24483–24486).

Marmosa (Micoureus) germana Thomas, 1904

Marmosa germana Thomas, 1904: 143 (original description).

Marmosa (Marmosa) waterhousei: Cabrera, 1919: 39 (part, *germana* treated as synonym).

Marmosa germana germana: Tate, 1933: 80 (name combination).

Marmosa (Marmosa) germana germana: Cabrera, 1958: 15 (name combination).

Micoureus regina: Gardner, 1993: 20 (part, *germana* treated as synonym).

Micoureus regina germanus: Gardner, 2005: 13 (name combination).

Marmosa (Micoureus) regina: Voss and Jansa, 2009: 101 (part, *germana* treated as synonym).

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation, BMNH 80.5.6.77) consists of the skin and skull of a subadult female collected by Clarence Buckley at Sarayacu, a village on the Río Bobonaza in Pastaza province, Ecuador. No date of collection accompanies the holotype, nor was any mentioned by Thomas (1904), but Buckley's mammals from eastern Ecuador are thought to have been collected between July 1877 and September 1878 (Vane-Wright, 1991). An adult male paratype (BMNH 80.5.6.76), consisting of a skin and partial skull, was also collected by Buckley at Sarayacu.

DISTRIBUTION AND SYMPATRY: Examined specimens of *Marmosa germana* are from the Amazonian lowlands of southeastern Colombia (Caquetá), eastern Ecuador (Orellana, Pastaza), and northeastern Peru (Loreto); all the localities in the Peruvian department of Loreto are on the left (north) bank of the Amazon/Marañón (fig. 2). *Marmosa germana* has been collected sympatrically with several congeners including *M. (Eomarmosa) rubra*, *M. (Marmosa) waterhousei*, *M. (Micoureus) jansae*, *M. (Micoureus) rutteri*, and *M. (Stegomarmosa) lepida* (appendix 2).

DESCRIPTION: The dorsal fur of *Marmosa germana* (fig. 3) is distinctly browner than that of most other congeners; Thomas (1904) described the dorsal pelage color of *M. germana* as "rather paler" than Ridgway's (1912) Mummy Brown and "rather less yellow" than Burnt Umber, whereas Tate (1933: 81) described it as "between Mummy Brown and Bistre." With many more specimens at hand than either Thomas or Tate examined, including some reasonably fresh skins (<25 years old), these colors do not seem like good matches: all of them are far too dark. Better matches are to be found among paler shades in the same dilution series (e.g., Dresden Brown rather than Mummy Brown; Snuff Brown rather than Bistre), but somewhat less saturated colors (like Buffy Brown) are even closer matches. The ventral pelage is uniformly gray-based over the throat, chest, the insides of the forelegs, and the upper abdomen; self-colored (buffy) fur is present only on the chin and groin of most specimens, but one (LSUMZ 28018) has a very narrow and apparently continuous midventral streak of self-buffy fur. The dorsal surface of the hind feet is covered with short, pale fur, but the fur over the metacarpals and the proximal phalanges of the forefeet is usually dark, such that only the distal phalanges of the hand are pale. The tail is about 143% of head-and-body length on average, and about 30 mm or more of the base of the tail is covered with moderately long (ca. 10 mm) fur. The naked (scaly) part of the tail is uniformly dark (brownish), without any pale markings.

Skulls of *Marmosa germana* are large in all measured dimensions (figs. 4C, 4F; table 4) with broad rostrums, wide zygomatic arches, and well-developed postorbital processes. The palate is almost completely ossified, with short (3.3 ± 0.8 mm) maxillopalatine fenestrae that extend

only from M1 to M2 in most (10 out of 14) specimens scored for this trait, and palatine fenestrae are consistently absent. The auditory bullae are very small and lack well-developed antero-medial laminae; although some specimens have conventionally “globular” (roughly hemispherical) bullae, a few large specimens from eastern Ecuador (e.g., AMNH 67292; FMNH 43179, 124606) have “subconical” bullae (Tate, 1933: 80), so called because they have an apical process containing a vascular sinus. The second upper premolar (P2) has an incomplete lingual cingulum, the postprotocrista of M3 terminates at or near the base of the metacone, and the lower molars lack posterior cingulids.

COMPARISONS: In our phylogenetic analyses of molecular data (fig. 1), *Marmosa germana* is consistently recovered as the sister taxon of *M. alstoni*, from which it differs on average by about 9% in uncorrected pairwise sequence comparisons at the cytochrome *b* locus. *Marmosa alstoni* is the oldest name that applies to a putative species represented by nine sequences from Central America, western Colombia, and northwestern Ecuador (Voss et al., 2020: table 2, fig. 1). It is our belief that these sequences represent at least four distinct species, two of which are undescribed (Voss et al., in prep.). For simplicity, the following comparisons concern *M. alstoni* sensu stricto, which occurs in the volcanic cordilleras of Costa Rica.

Although *Marmosa germana* and *M. alstoni* are similar in size, with broadly overlapping external dimensions, they are easily distinguished by qualitative external features. In side-by-side comparisons, the dorsal pelage of *M. germana* appears browner, and it is coarser and less cohesive than that of *M. alstoni*, which is grayer, softer, and woollier. Less subjectively, the tail of *M. germana* has a shorter furry base (only about 25–35 mm of the base of the tail is furred), and the basal fur is shorter (usually about 10–11 mm long); by contrast, about 40–60 mm of the base of the tail is furred in *M. alstoni*, and the basal fur is about 20 mm long. Additionally, the naked (scaly) part of the tail is completely dark in *M. germana* whereas the distal two-thirds or more of the naked caudal epithelium is unpigmented (whitish) in *M. alstoni* (see Voss et al., 2020: fig. 8). These species are craniodentally similar, but *M. germana* has a narrower postorbital constriction than *M. alstoni* (e.g., 7.6 ± 0.2 mm versus 8.2 ± 0.4 mm in males); the corresponding proportional difference (e.g., $\text{LPB/CBL} \times 100 = 16.9\%$ on average in *M. germana* males versus 18.6% in *M. alstoni* males) is small but perceptible in side-by-side comparisons of representative series of skulls.

Marmosa germana occurs sympatrically with two other members of the subgenus *Micoureus*, from which it can be distinguished unambiguously by a combination of external and craniodental characters (table 2); descriptive comparisons among these taxa were provided in the preceding account for *M. jansae* and in Voss et al.’s (2020) account for *M. rutteri*. Unfortunately, it is much more difficult to distinguish *M. germana* from *M. constantiae*, an allopatric species that occurs south of the Amazon (Voss et al., 2019). *Marmosa germana* and *M. constantiae* are only distantly related (fig. 1), but they are morphologically similar, at least in northern Peru, where the local form of *M. constantiae* lacks the white caudal markings of Bolivian and central Brazilian specimens (Voss et al., 2019). Measurements of *M. constantiae* (Voss et al., 2019: table 7) broadly overlap those of *M. germana*, and careful side-by-side comparisons of skins and cranial material have not revealed any consistent qualitative differences.

For the moment, at least, the morphological discrimination of these phylogenetically distant and molecularly divergent taxa remains a research challenge.

REMARKS: Two putative species were associated with the name *Marmosa germana* by Voss et al. (2020), who assigned five cytochrome *b* sequences to the lineage they called “*germana* A” and a single sequence to its sister lineage “*germana* B.” The former sequences are from the Marañón-Napo interfluvium in eastern Ecuador and northern Peru (Voss et al., 2020: fig. 1), whereas the latter is from the Napo-Putumayo interfluvium. With so few sequences in hand, it is difficult to know whether the Napo really separates different mtDNA lineages of *M. germana*, but it seems harmless to adopt this as a working hypothesis. The sequence identified as *germana* B (obtained from LSUMZ 28018) differs from the sequences assigned to *germana* A (KU 157972, 157973; ROM 105521; TTU98988, 101236) by an average uncorrected distance of 4% (Voss et al., 2020: table 4), and the corresponding voucher material is also distinctive. Unlike any of the specimens from the Marañón-Napo interfluvium, which have almost entirely gray-based ventral fur, LSUMZ 28018 has a narrow but apparently continuous midventral streak of self-buffy fur, and it has slightly narrower nasal bones. These are not very impressive differences, however, particularly given the handful specimens at hand, so we are reluctant to provide a new name for this unique specimen.

HABITATS: The dominant climax formation throughout the geographic range of *Marmosa germana* is evergreen lowland rainforest, but western-Amazonian rainforests include different kinds of vegetation associated with characteristic edaphic factors and successional stage. At the Reserva Nacional Allpahuayo-Mishana (locality 22; fig. 2, appendix 1), Hice and Velazco (2012) trapped specimens of *M. germana* in vegetation locally known as *varillal*, which grows on patches of white sand on well-drained high ground (fig. 8). By contrast with tall *monte alto* vegetation (in which *M. jansae* was trapped at the same locality; see above), *varillal* habitat has a lower (20 m) canopy of smaller trees, some of which have multiple stems; very few palms or lianas; and abundant terrestrial bromeliads that often carpet the forest floor. However, other specimens of *M. germana* were captured at this locality “in older secondary growth where it grades into less disturbed forest.” According to the authors, secondary vegetation occurs on abandoned agricultural plots that are usually sited on loamy soils, so the association between *M. germana* and white-sand forest is evidently not obligatory. Unfortunately, no other useful information is available about the habitats in which this species has been taken.

SPECIMENS EXAMINED ($N = 18$): **Colombia**—Caquetá, Tres Troncos (FMNH 70979). **Ecuador**—Orellana, 35 km S Pompeya Sur (ROM 105521); Pastaza, Río Pastaza (BMNH 54.265), Río Pindo Yacu (FMNH 43179), Sarayacu (AMNH 67292; BMNH 80.5.6.76, 80.5.6.77); Sucumbios, Marian (FMNH 124606). **Peru**—Loreto, Collpa Salvador (MUSM 17588), 25 km S Iquitos (TTU 98845, 98846, 98988, 101094, 101236), Quebrada Orán (LSUMZ 28018), San Jacinto (KU 157972), Santa Luisa (FMNH 87116), Teniente López (KU 157973).

DISCUSSION

These results, together with those from previous reports (Voss et al., 2019, 2020), challenge the hitherto widely accepted notion that just two species in the subgenus *Micoureus* of *Marmosa* have broadly overlapping ranges in western Amazonia and account for multiple examples



FIG. 8. White-sand vegetation (*varillal*) at the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru, habitat of *Marmosa germana* (photo by Christine L. Hice).

of sympatry throughout the region. Whereas sympatric western-Amazonian species of *Micoureus* were formerly identified as *M. regina* and *M. demerarae* (e.g., by Emmons, 1997; Patton et al., 2000; Solari et al., 2001; Gardner and Creighton, 2008; Hice and Velazco, 2012), taxonomic analyses of morphological and molecular data (Voss et al., 2019, 2020; this report) have shown that the sympatric species in southwestern Amazonia are *M. constantiae* and *M. rutteri*, whereas the species that occur sympatrically in northwestern Amazonia are *M. germana*, *M. jansae*, and *M. rutteri*.

Additionally, this report documents new examples of upper-Amazonian species (*Marmosa germana*, *M. jansae*) that are the sister taxa of species (*M. perplexa*) or species complexes (*M. alstoni*; Voss et al., in prep.) that occur west of the Andes. Such biogeographic disjunctions are not unusual in birds—many species of which have cis- and trans-Andean populations (Cadena et al., 2016)—but they are seldom seen among nonvolant small mammals, for which the Andes seem to be a formidable dispersal barrier. However, some species of *Micoureus* are known to occur at moderately high elevations (e.g., >2500 m in *M. rapposa*; Voss et al., 2020), so it seems plausible that transmontane dispersal was at least occasionally possible over the Porculla Pass (Abra de Porculla, 2145 m: Duellman, 1979) in northern Peru or the Zamora Pass (ca. 2850 m) in southern Ecuador, perhaps during Pleistocene interglacials.

TABLE 5. Geographic relationships among six species of *Marmosa* in northwestern Amazonia^a

	<i>germana</i>	<i>jansae</i>	<i>lepida</i>	<i>rubra</i>	<i>rutteri</i>	<i>waterhousei</i>
<i>germana</i>	—					
<i>jansae</i>	sympatric	—				
<i>lepida</i>	sympatric	?	—			
<i>rubra</i>	sympatric	sympatric	sympatric	—		
<i>rutteri</i>	sympatric	?	sympatric	sympatric	—	
<i>waterhousei</i>	sympatric	sympatric	sympatric	sympatric	sympatric	—

^a Table entries are based on collection data summarized in appendix 2.

Lastly, the description of a new *Marmosa* from western Amazonia, a region already rich in congeneric species (Voss et al., 2014), raises interesting questions about how so many closely related taxa can coexist in the region. The geographic range of *Marmosa jansae* overlaps those of five other congeners, and most pairwise combinations of these six species have been observed in sympatry (table 5). However, no more than four species seem to have been documented at any one locality for reasons that remain obscure (appendix 2). Are these lists of locally co-occurring species incomplete, or are some species habitat specialists that do not occur at ecologically unfavorable sites? How is local species richness partitioned within and among habitats? How do syntopic congeners partition their shared habitat(s)? Only sustained fieldwork by researchers alert to the potential importance of accurate habitat and microhabitat information seems likely to provide convincing answers to these and other ecological questions about this uniquely diverse regional fauna of mouse opossums.

ACKNOWLEDGMENTS

We are grateful to the curators and collection support staff of numerous museums who hosted our visits or loaned us specimens over the many years that our revisionary work on the subgenus *Micoureus* has extended, including Roberto Portela (at the BMNH); Bruce Patterson, Adam Ferguson, and John Phelps (FMNH); Robert M. Timm and Maria Eifler (KU); Jake Esselstyn and Steve Cardiff (LSUMZ); Victor Pacheco and Judith Carrasco (MUSM); Mark Engstrom, Burton Lim, and Jacqui Miller (ROM); Robert Bradley and Heath Garner (TTU); Priscilla Tucker and Cody Thompson (UMMZ); and Alfred Gardner and Darrin Lunde (USNM).

We thank Victor Pacheco for compiling habitat information and photographs from MUSM field research at Quebrada Faical; Maria Eifler for searching out old field notes at KU; Neal Woodman for information about specimens he collected in Peru many years ago; Linda Barkley for kindly allowing us to use the photographs in figures 5 and 8; and Keith Barker for permission to use his photograph of Sharon Jansa. The skin photographs in figure 3 are the work of Denis Finnin, and the skull photographs in figure 4 were taken by Nicole Wong. Sharon Jansa prepared our map (fig. 2) under false pretenses, for which we simultaneously apologize and thank her. Suggestions by Silvia Pavan and Juan Díaz-Nieto improved an early draft of our manuscript.

REFERENCES

- Anthony, H.E. 1922. Preliminary report on Ecuadorean mammals. No. 2. American Museum Novitates 32: 1–6, map.
- Cabrera, A. 1919. Genera mammalium: Monotremata, Marsupialia. Madrid: Museo Nacional de Ciencias Naturales.
- Cabrera, A. 1958 (“1957”). Catálogo de los mamíferos de América del Sur [part 1]. Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Ciencias Zoológicas) 4 (1): i–iv, 1–307.
- Cadena, C.D., C.A. Pedraza, and R.T. Brumfield. 2016. Climate, habitat associations, and the potential distributions of Neotropical birds: implications for diversification across the Andes. Revista de la Academia Colombiana de Ciencias Físicas, Exactas, y Naturales 40: 275–287.
- Chapman, F.M. 1926. The distribution of bird-life in Ecuador: a contribution to a study of the origin of Andean bird-life. Bulletin of the American Museum of Natural History 55: frontispiece, i–xiv, 1–784, folding map.
- Duellman, W.E. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities. In W.E. Duellman (editor), The South American herpetofauna: its origin, evolution, and dispersal (Monograph of the Museum of Natural History, University of Kansas 7): 371–459. Lawrence, KS: University of Kansas.
- Duellman, W.E., and J.R. Mendelson III. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. University of Kansas Science Bulletin 55: 329–376.
- Emmons, L.H. 1997. Neotropical rainforest mammals, a field guide (2nd ed.). Chicago: University of Chicago Press.
- Ferrer-Paris, J.F., et al. 2018. An ecosystem risk assessment of temperate and tropical forests of the Americas with an outlook on future conservation strategies. Conservation Letters 12: e12623.
- Gardner, A.L. 1993. Order Didelphimorphia. In D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, 2nd ed.: 15–23. Washington, DC: Smithsonian Institution Press.
- Gardner, A.L. 2005. Order Didelphimorphia. In D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, a taxonomic and geographic reference, 3rd ed.: 3–18. Baltimore: Johns Hopkins University Press.
- Gardner, A.L., and G.K. Creighton. 2008 (“2007”). Genus *Micoureus* Lesson, 1842. In A.L. Gardner (editor), Mammals of South America, vol. 1. (Marsupials, xenarthrans, shrews, and bats): 74–82. Chicago: Chicago University Press.
- Giarla, T.C., and R.S. Voss. 2020. On the identity of Victoria’s mouse opossum, *Marmosa regina* Thomas, 1898. American Museum Novitates 3960: 1–13.
- Hershkovitz, P. 1977. Living New World monkeys (Platyrrhini), with an introduction to primates. Vol. 1. Chicago: University of Chicago Press.
- Hershkovitz, P. 1987. The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): a preliminary report and critical review with the description of a new species and a new subspecies. American Journal of Primatology 12: 387–468.
- Hice, C.L., and P.M. Velazco. 2012. The non-volant small mammals of the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru. Special Publications of the Museum of Texas Tech University 60: [i–ii], 1–135.
- Hurtado, N., and V. Pacheco. 2017. Revision of *Neacomys spinosus* (Thomas, 1882) (Rodentia: Cricetidae) with emphasis on Peruvian populations and the description of a new species. Zootaxa 4242 (3): 401–440.

- Lankester, E.R. (editor). 1904. Handbook of instructions for collectors, issued by the British Museum (Natural History), 2nd ed. London: Trustees of the British Museum.
- Linares-Palomino, R., L.P. Kvist, Z. Aguirre-Mendoza, and C. Gonzales-Inca. 2010. Diversity and endemism of woody plant species in the Equatorial Pacific seasonally dry forests. *Biodiversity and Conservation* 19: 169–185.
- Pacheco, V., R. Cadenillas, S. Velazco, E. Salas, and U. Fajardo. 2007. Noteworthy bat records from the Pacific Tropical rainforest region and adjacent dry forest in northwestern Peru. *Acta Chiropterologica* 9: 409–422.
- Parker, T.A., III, T.S. Schulenberg, M. Kessler, and W.H. Wust. 1995. Natural history and conservation of the endemic avifauna in north-west Peru. *Bird Conservation International* 5: 201–231.
- Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244: 1–306.
- Patton, J.L., U.F.J. Pardiñas, and G. D'Elia. 2015. Mammals of South America, vol. 2: rodents. Chicago: University of Chicago Press.
- Paynter, R.A., Jr. 1993. Ornithological gazetteer of Ecuador, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).
- Paynter, R.A., Jr. 1997. Ornithological gazetteer of Colombia, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).
- Ridgway, R. 1912. Color standards and color nomenclature. Washington, DC: Published by the author.
- Rivas, C.A., R.M. Navarro-Cerillo, J.C. Johnson, and J. Guerrero-Casado. 2020. Dry forest is more threatened but less protected than evergreen forest in Ecuador's coastal region. *Environmental Conservation* 47: 79–83.
- Robbins, M.B., and R.S. Ridgely. 1990. The avifauna of an upper tropical cloud forest in southwestern Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 142: 59–71.
- Rossi, R.V., R.S. Voss, and D.P. Lunde. 2010. A revision of the didelphid marsupial genus *Marmosa*. Part 1. The species in Tate's "Mexicana" and "Mitis" sections and other closely related forms. *Bulletin of the American Museum of Natural History* 334: 1–83.
- Solari, S., et al. 2001. The small mammal community of the lower Urubamba region, Peru. In A. Alonso, F. Dallmeier, and P. Campbell (editors), *Urubamba: the biodiversity of a Peruvian rainforest* (SI/MAB Series 7): 171–181. Washington, DC: SI/MAB Biodiversity Program.
- Tate, G.H.H. 1933. A systematic revision of the marsupial genus *Marmosa* with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). *Bulletin of the American Museum of Natural History* 66 (1): 1–250 + 26 pls.
- Thomas, O. 1898. Descriptions of new mammals from South America. *Annals and Magazine of Natural History* (ser. 7) 2: 265–275.
- Thomas, O. 1904. Two new mammals from South America. *Annals and Magazine of Natural History* (ser. 7) 13: 142–144.
- Torres-Porras, J., M.E. Cobos, J.M. Seoane, and N. Aguirre. 2017. Large and medium-sized mammals of Buenaventura Reserve. *Check List* 13 (4): 35–45.
- Vane-Wright, R.I. 1991. A portrait of Clarence Buckley, zoologist. *Linnean* 7 (3): 30–33.
- Voss, R.S., and T.C. Giarla. 2020. Case 3831—*Marmosa isthmica* Goldman, 1912 (Mammalia, Didelphimorphia, Didelphidae): proposal to conserve current usage by suppressing its senior synonym, *Marmosa regina* Thomas, 1898. *Bulletin of Zoological Nomenclature* 77: 139–142.

- Voss, R.S., and S.A. Jansa. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. *Bulletin of the American Museum of Natural History* 276: 1–82.
- Voss, R.S., and S.A. Jansa. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. *Bulletin of the American Museum of Natural History* 322: 1–177.
- Voss, R.S., E.E. Gutiérrez, S. Solari, R.V. Rossi, and S.A. Jansa. 2014. Phylogenetic relationships of mouse opossums (Didelphidae, *Marmosa*) with a revised subgeneric classification and notes on sympatric diversity. *American Museum Novitates* 3817: 1–27.
- Voss, R.S., D.W. Fleck, and S.A. Jansa. 2019. Mammalian diversity and Matses ethnomammalogy in Amazonian Peru. Part 3: Marsupials (Didelphimorphia). *Bulletin of the American Museum of Natural History* 432: 1–87.
- Voss, R.S., T.C. Giarla, J.F. Díaz-Nieto, and S.A. Jansa. 2020. A revision of the didelphid marsupial genus *Marmosa*. Part 2. Species of the Rapposa Group (subgenus *Micoureus*). *Bulletin of the American Museum of Natural History* 439: 1–60.
- Watsa, M., G.A. Erkenwick, J.A. Rehg, R.L. Pitman. 2012. Distribution and new sightings of Goeldi's monkey (*Callimico goeldii*) in Amazonian Peru. *International Journal of Primatology* 33: 1477–1502.
- Wiedenfeld, D.A., T.S. Schulenberg, and M.B. Robbins. 1985. Birds of a tropical deciduous forest in extreme northwestern Peru. In P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely, and F.G. Buckley (editors), *Neotropical ornithology* (Ornithological Monographs 36), 305–315. Washington, DC: American Ornithologists' Union.
- Wiley, R.H. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. *Bulletin of the American Museum of Natural History* 343: 1–68.

APPENDIX 1

GAZETTEER OF EXAMINED SPECIMENS

This gazetteer includes all localities from which we personally examined specimens of *Marmosa* (*Micoureus*) for this report. Italicized place names are those of currently recognized departments, provinces, or states; boldface identifies collection localities as they appear in the text. Unless recorded by the collector, geographic coordinates and elevation above sea level are provided in square brackets with a cited secondary source for these data. The name(s) of species collected at each locality are separated from the locality name and geographic data by a colon, followed by the name(s) of the collector(s) and date(s) of collection in parentheses. Localities with known geographic coordinates are mapped in figure 2.

COLOMBIA

1. *Caquetá*, La Tagua, **Tres Troncos**, 185 m [0.13°N, 74.68°W; Hershkovitz, 1977]: *Marmosa germana* (P. Hershkovitz, 3 February 1952).
2. *Putumayo*, **Mocoa** [1.15°N, 76.62°W, 579 m; Paynter, 1997]: *Marmosa jansae* (A. Pazos, 14 June 1966, 29 November 1967).
3. *Putumayo*, **Río Mecaya**, 185 m [0.65°N, 75.33°W; Hershkovitz, 1977]: *Marmosa jansae* (P. Hershkovitz, 16–22 February 1952).

ECUADOR

4. *El Oro*, **Piñas** [3.70°S, 79.70°W; Paynter, 1993], 3600 ft, near Río Tumbez: *Marmosa perplexa* (G.H.H. Tate, 12–13 September 1921).
5. *Loja*, **Guainche** [exact coordinates unknown], 3200 ft: *Marmosa perplexa* (G.H.H. Tate, 29 August 1921). According to Paynter (1993), Guainche is somewhere between Alamor (4.03°S, 80.03°W) and Celica (4.12°S, 79.65°W), so we mapped it at 4.07°S, 79.84°W.
6. *Loja*, **12 km E by road Portovelo** [ca. 3.72°S, 79.53°W], 2600 ft: *Marmosa perplexa* (A.L. Gardner, 8 August 1976).
7. *Loja*, Zaruma-Loja trail, near **Punta Santa Ana** [3.83°S, 79.55°W; Paynter, 1993], 3650 ft [1113 m]: *Marmosa perplexa* (H.E. Anthony, 21 December 1920).
8. *Orellana*, **Cerro Guataraco** [not located]: *Marmosa jansae* (W. Clarke-MacIntyre, 3 September 1937). “Guataraco” is probably a misspelling of Huataraco, which applies to a stream that drains the southeastern slopes of Volcán Sumaco, but it is not clear what landscape feature might correspond to the mountain or hill so designated.
9. *Orellana*, Parque Nacional Yasuní, **35 km S Pompeya Sur** (0.63°S, 76.47°W): *Marmosa germana* (ROM team, 9 February 1996).
10. *Orellana*, Parque Nacional Yasuní, **42 km S and 1 km E Pompeya Sur** (0.68°S, 76.43°W): *Marmosa jansae* (ROM team, 29 May 2006).
11. *Orellana*, **Río Suno Abajo** [not located]: *Marmosa jansae* (Olalla y Hijos, 24 March 1924). The Olallas’ collecting sites along the Río Suno, which drains the southeastern slopes of Volcán Sumaco, are problematic, but according to Chapman’s (1926: 21) itinerary, they

were collecting somewhere below San José de Sumaco (= San José Nuevo at 0.43°S, 77.33°W, ca. 500 m?; Paynter, 1993) on 24 March 1924. Paynter (1993) places this locality and the next in Napo province, but they are unambiguously within the modern (post-1998) borders of Orellana province.

12. Orellana, **Río Suno Arriba** [not located]: *Marmosa jansae* (Olalla y Hijos, 8 April 1923). See “Río Suno Abajo” (above). According to Chapman (1926: 21), the Olallas collected somewhere above Ávila (0.63°S, 77.42°W, 600 m; Paynter, 1993) throughout the month of April 1923.⁷
13. Orellana, **Tiputini Biodiversity Station** [0.63°S, 76.15°W; Google Earth]: *Marmosa jansae* (ROM team, 29 June 1996).
14. Pastaza, Río Bobonaza, **Canelos** [1.58°S, 77.75°W, 530 m; Paynter, 1993]: *Marmosa jansae* (M.G. Palmer, 8 May 1910).
15. Pastaza, **Río Copotaza**, 650 m [2.12°S, 77.45°W]: *Marmosa jansae* (R. Olalla, 5 April 1939).
16. Pastaza, **Río Pastaza**, 2500 ft [762 m; not located]: *Marmosa germana* (C.S. Webb, 3 August 1937) and *M. jansae* (C.S. Webb, 8 August 1937).
17. Pastaza, **Río Pindo Yacu** [exact coordinates unknown]: *Marmosa germana* (R. Olalla, 15 October 1935).
18. Pastaza, **Sarayacu** [1.73°S, 77.48°W, 700 m; Paynter, 1993]: *Marmosa germana* (C. Buckley, 1877–1878; G.H.H. Tate, 17 March 1924). See text for a discussion of Buckley’s dates.
19. Sucumbíos, **Marian** (0.05°S, 76.32°W): *Marmosa germana* (R.M. Timm, 6 October 1983).

PERU

20. Cajamarca, San Ignacio, Tabaconas, **Cerro La Viuda** (ca. 5.25°S, 79.35°W), 1897 m: *Marmosa perplexa* (L. Luna W., 20 July 2006).
21. Loreto, Río Pucacuro, **Collpa Salvador** [2.63°S, 75.15°W; Watsa et al., 2012]: *Marmosa germana* (L. Arias, 24 June 2001).
22. Loreto, **25 km S Iquitos**, Allpahuayo Reserve [3.97°S, 73.42°W, ca. 110–180 m; Hice and Velazco, 2012]: *Marmosa germana* (C.L. Hice, 17 January–22 October 1998) and *M. jansae* (C.L. Hice, 25–26 September 1998).
23. Loreto, **52 km S Iquitos**, La Habana (ca. 4.20°S, 73.48°W; Hurtado and Pacheco, 2017): *Marmosa jansae* (C.L. Hice, 4 November 2002).
24. Loreto, **Quebrada Orán**, ca. 5 km N Rio Amazonas [3.48°S, 72.52°W; Patton et al., 2015]: *Marmosa germana* (J.M. Chupasko, 30 June 1984).
25. Loreto, **San Jacinto** [2.32°S, 75.87°W, 180 m; Duellman and Mendelson, 1995]: *Marmosa germana* (R.M. Timm, 8 July 1993).
26. Loreto, Río Nanay, **Santa Luisa** [3.58°S, 74.50°W; Hershkovitz, 1987]: *Marmosa germana* (C. Kalinowski, 1 October 1956).

⁷ According to Wiley (2010: 9), Ávila is on the Río Suno, but his map (Wiley, 2010: fig. 1) shows it on the Río Cotapino. Satellite imagery suggests that Ávila is on a ridge dividing the watersheds of these obscure streams on the southeastern slopes of Sumaco, but this does little to clarify where, exactly, the Olallas were collecting in 1923.

27. Loreto, **Teniente López** [2.60°S, 76.12°W, 200 m; Duellman and Mendelson, 1995], including sublocality “1.5 km N Teniente López” [2.58°S, 76.12°W, 333 m]: *Marmosa germana* (N. Woodman, 19 July 1993) and *M. jansae* (R.M. Timm, 25–26 July 1993). The sublocality “1.5 km N Teniente López” corresponds to the “Teniente López Study Zone” as mapped by Duellman and Mendelson (1995: fig. 3), but the coordinates they provide in the accompanying text (Duellman and Mendelson, 1995: 335) cannot be correct; our coordinates are based on their map.
28. Tumbes, **Quebrada Faical**, 350 m [3.67°S, 80.26°W; Pacheco et al., 2007]: *Marmosa perplexa* (R. Cadenillas, 18–23 October 2007; L. Huamani, 19 October 2007).

APPENDIX 2

LOCALITIES IN NORTHWESTERN AMAZONIA WHERE TWO OR MORE SPECIES OF *Marmosa* ARE SYMPATRIC

Locality ^a	Species	Specimens ^b
Colombia: Caquetá, Tres Troncos	<i>M. germana</i> , <i>M. rutteri</i>	FMNH
Colombia: Putumayo, Río Mecaya	<i>M. jansae</i> , <i>M. waterhousei</i>	FMNH
Ecuador: Napo, “near the river Napo”	<i>M. rubra</i> , <i>M. rutteri</i> , <i>M. waterhousei</i>	BMNH
Ecuador: Orellana, San José de Payamino	<i>M. rubra</i> , <i>M. rutteri</i>	FMNH
Ecuador: Pastaza, Río Copotaza	<i>M. jansae</i> , <i>M. rubra</i>	FMNH
Ecuador: Pastaza, Río Pindo Yacu	<i>M. germana</i> , <i>M. waterhousei</i>	FMNH
Ecuador: Pastaza, Sarayacu	<i>M. germana</i> , <i>M. lepida</i>	AMNH
Ecuador: Sucumbíos, Marian	<i>M. germana</i> , <i>M. rubra</i>	FMNH
Peru: Amazonas, Huampami	<i>M. lepida</i> , <i>M. rubra</i> , <i>M. rutteri</i> , <i>M. waterhousei</i>	MVZ
Peru: Loreto, Boca Río Curaray	<i>M. rubra</i> , <i>M. rutteri</i> , <i>M. waterhousei</i>	AMNH
Peru: Loreto, 25 km S Iquitos	<i>M. germana</i> , <i>M. jansae</i> , <i>M. waterhousei</i>	TTU
Peru: Loreto, Teniente López	<i>M. germana</i> , <i>M. jansae</i>	KU

^a See appendix 1 of this report and gazetteers in Rossi et al. (2010) and Voss et al. (2019, 2020) for geographic coordinates and other relevant information.

^b Museum where relevant material is preserved (see Materials and Methods for abbreviations).

All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:
<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>
or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024