

A Revision of the Didelphid Marsupial Genus *Marmosa* Part 4. Species of the Alstoni Group (Subgenus *Micoureus*)

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ABSTRACT

In this report, the fourth of a revisionary series on mouse opossums (*Marmosa*), we treat the members of a monophyletic group of trans-Andean taxa that include *M. alstoni* (Allen, 1900); *M. nicaraguae* Thomas, 1905; and *M. adleri*, a new species. Although cytochrome *b* sequence divergence values among these species are substantially lower than distances commonly observed among other congeners, members of the Alstoni Group are strikingly unlike one another in morphological traits. We conjecture that rapid phenotypic divergence accompanied the Pleistocene radiation of an ancestral lineage that entered Central America as a late participant in the Great American Biotic Interchange. Additional undescribed species of the Alstoni Group seem likely to exist based on the evidence at hand, and we emphasize the need for renewed collecting in Central America, which has long been neglected by mammalian biodiversity researchers.

INTRODUCTION

Most of the species of *Marmosa* Gray, 1821, are endemic to South America, and biogeographic reconstructions suggest that the genus evolved on that continent while it was still separated from North America by a marine water barrier (Jansa et al., 2014; Castro et al., 2021). Only a few species of *Marmosa* now belong to the North American fauna, but these include

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members of two subgenera. Whereas four North American species belong to the subgenus *Exulomarmosa*, only one is currently recognized in the subgenus *Micoureus* (Rossi et al., 2010; Voss et al., 2014; Voss et al., 2020).

Marmosa (Micoureus) alstoni was originally described by Allen (1900) from Costa Rican type material, but the epithet has subsequently been applied to specimens from Belize, Honduras, Nicaragua, Panama, Colombia, and Ecuador (e.g., by Tate, 1933; Hall, 1981; Patton et al., 2000; Gardner and Creighton, 2008; Voss et al., 2020). In this report we diagnose *M. alstoni* based on morphological and genetic criteria, distinguish it from another taxon long considered to be its junior synonym, and describe a new species belonging to the same clade. The Alstoni Group is almost certainly more diverse than the three species recognized herein, but the absence of molecular data for problematic specimens from northern Central America and the absence of adequate phenotypic data for specimens with divergent sequences from trans-Andean South America are obstacles that only future collecting in those regions will overcome.

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 (Chicago); KU, University of Kansas Biodiversity Research Center (Lawrence); LSUMZ, Louisiana State University Museum of Natural Science (Baton Rouge); NRM, Naturhistoriska Riksmuseet (Stockholm); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); and USNM, National Museum of Natural History (Washington, DC).

MEASUREMENTS: Except as noted otherwise, external measurements are those taken in the field by collectors using the standard 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 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 skins and fluid-preserved specimens to check the accuracy of values recorded by collectors, and we used our values whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm (the smallest decimal fraction of a millimeter 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 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 narrow-

est 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.

MORPHOLOGICAL TERMINOLOGY: The morphological terms used in our descriptions and comparisons of species are those defined or referenced by Voss and Jansa (2003, 2009) and by Voss et al. (2020). The latter publication explained and illustrated several morphological characters that are particularly useful for distinguishing species of the subgenus *Micoureus*, including ventral fur coloration, caudal pelage and pigmentation, palatal fenestration, and molar morphology.

AGE DETERMINATION: Except as noted below, we obtained all analyzed morphological data from adult specimens as determined by dental criteria. The third upper and lower premolars (P3/p3) are the last teeth to erupt in *Marmosa*, and we used the maxillary locus to define age classes: a specimen was judged to be *juvenile* if the deciduous third premolar (dP3) was still in place; *subadult* if dP3 had been shed but P3 was still incompletely erupted; and *adult* if the permanent upper dentition was complete. In effect, specimens that we judged to be adult by these criteria correspond to age classes 6–9 of Rossi et al. (2010). Although we acknowledge that our adult material exhibits substantial ontogenetic variation in many cranial dimensions (as evidenced by the tendency for specimens with more heavily worn teeth to have larger measurement values for most dimensions than specimens with unworn teeth), we were unable to consistently distinguish toothwear-defined age classes in our material.

TAXONOMIC ACCOUNTS

The cytochrome *b* sequences that Voss et al. (2020) associated with the binomen *Marmosa alstoni* included a robustly supported clade from the highlands of Costa Rica, a clade from lowland Panama, one divergent sequence from the lowlands of eastern Nicaragua, and a pair of divergent sequences from the Chocó region of trans-Andean South America (fig. 1, table 1). Although these mtDNA lineages were not designated as putative species according to the coalescent criterion adopted by the authors of that report, the associated phenotypes are distinct and provide compelling evidence of nuclear-gene divergence. We hypothesize that these forms correspond to recently evolved taxa, and for the purpose of future research on this small trans-Andean radiation of *Micoureus*, we formally recognize three species in the accounts that follow.

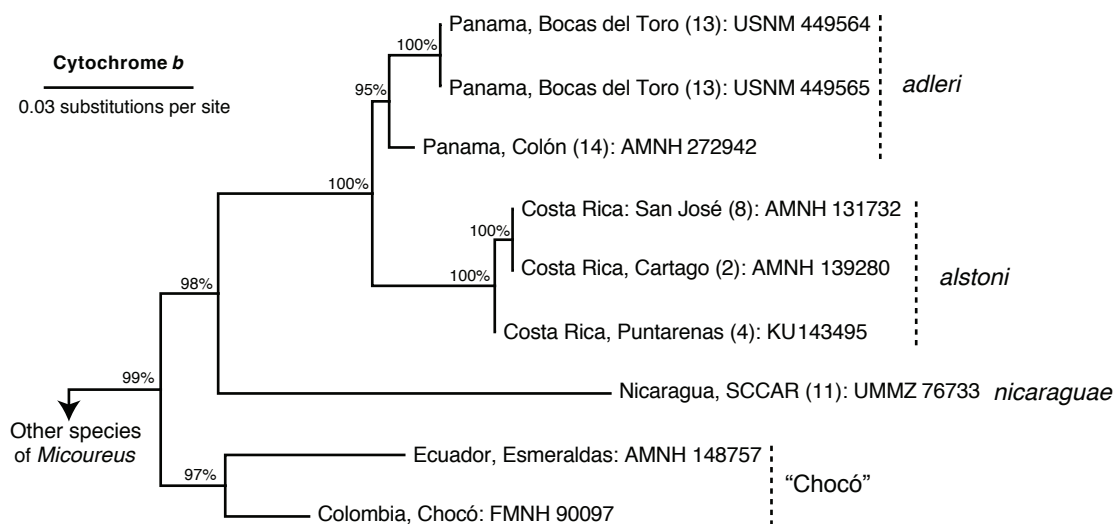


FIG. 1. Maximum-likelihood cytochrome *b* gene tree for members of the Alstoni Group of *Marmosa*. Each terminal is labeled by country of origin, province/department, a numerical geographic identifier (in parentheses) keyed to entries in our gazetteer (appendix 1), and the museum catalog number of the associated morphological voucher specimen. Numbers above branches are bootstrap support values. This subtree shows the full details of the clade cartooned as *M. alstoni* by Voss et al. (2020: fig. 5), who listed GenBank accession numbers and other relevant specimen information.

Marmosa (Micoureus) alstoni (Allen, 1900)

Caluromys alstoni Allen, 1900: 189 (original description).

Didelphys (Marmosa) alstoni: Trouessart, 1905: 855 (name combination).

Marmosa cinerea alstoni: Thomas, 1905: 313 (name combination).

Didelphis (Caluromys) alstoni: Matschie, 1916: 269 (name combination).

Marmosa alstoni alstoni: Tate, 1933: 67 (name combination).

Micoureus alstoni: Gardner and Creighton, 1989: 4 (name combination).

Marmosa (Micoureus) alstoni: Voss and Jansa, 2009: 101 (first use of current name combination).

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation; AMNH 11790/16210) consists of the skin and skull of an adult male collected at Tres Ríos, Cartago Province, Costa Rica, by G.K. Cherrie on 17 August 1893. Topotypical paratypes include one adult female (AMNH 11789/10059) and four juveniles.

DISTRIBUTION AND SYMPATRY: All the specimens that we refer to *Marmosa alstoni* are from the central highlands of Costa Rica, where they have been collected or photographed at elevations from about 700 to 1750 m above sea level (fig. 2). These highlands consist of several more or less contiguous ranges, of which *M. alstoni* has been collected in the Cordillera de Tilarán and in the Cordillera Central; we have not seen specimens from the Cordillera de Guanacaste, nor from the Cordillera de Talamanca. *Marmosa alstoni* is not known to co-occur with any other species of the subgenus *Micoureus*, but it has been collected sym-

TABLE 1. Mean uncorrected pairwise sequence divergence (%) at the cytochrome *b* locus within and among members of the Alstoni Group of *Marmosa*.

	<i>alstoni</i>	<i>nicaraguae</i>	<i>adleri</i>	“Chocó”
<i>alstoni</i>	0.20			
<i>nicaraguae</i>	7.97	—		
<i>adleri</i>	2.99	6.83	0.70	
“Chocó”	7.05	8.72	5.87	4.00

patrically with species of the subgenus *Exulomarmosa* at Escazú (appendix 1: locality 5) and Monteverde (locality 4) based on material examined by Rossi et al. (2010).

DESCRIPTION: The dorsal pelage of *Marmosa alstoni* is uniformly dull grayish brown—near Ridgway’s (1912) Clove Brown—from the crown of the head to the rump (fig. 3), but the midrostral fur (between the blackish facial masks) is much paler, as are the cheeks (below the masks). Measured at midback on 12 adult skins, the dorsal fur ranges in length from 11 to 15 mm (average = 13 mm) and appears distinctly fluffy. The ventral fur is almost entirely gray-based buffy in most specimens, with self-buffy fur restricted to the chin and inguinal regions; although some specimens have a median streak of self-buffy fur (broadest in AMNH 136863), this is discontinuous (not extending completely from chin to groin) because the fur of the upper chest and lower throat is always gray-based. On all of the specimens at hand, the inner (medial) surfaces of the forelimbs are also covered with gray-based fur.

The ears are dark (translucent-brownish in life), and in all specimens accompanied by measurement data they are shorter than the hind feet (table 2).⁴ As in other species of the subgenus *Micoureus* (Voss et al., 2014) gular glands are absent, and large adult males have both lateral and medial carpal tubercles. The dorsal surfaces of the hind feet are covered with short, pale hairs in most specimens, as are the digits of the forefeet, but the metacarpal fur is usually darker. Close examination of the skin of one lactating female (KU 165556) suggests that at least 4–1–4 = 9 mammae are present.

The tail is about 145% of head-and-body length, on average, and the base of the tail is densely furred for about 40 to 60 mm. This furry tail base is densely clothed with soft hairs that are about 20 mm long on average (range = 16 to 22 mm), and the caudal fur stands out from the long axis of the tail, giving the base of that organ a distinctly fluffy appearance. The naked, scaly part of the tail is particolored: dark (brownish in life) basally and unpigmented (whitish in life) distally. In most specimens only the basal ¼ or less of the naked caudal epithelium is dark; the remaining ¾ or more is whitish, a prominent marking that is useful for field identification.

Skulls of *Marmosa alstoni* are among the largest we have measured in the subgenus *Micoureus*, but they are otherwise unremarkable in dorsal aspect (resembling those of many other large congeners) with short, wide rostrums; broadly flaring zygomatic arches; and well-developed, broadly triangular postorbital processes (fig. 4A, D). The maxillopalatine fenestrae are narrow and usually extend from the level of M1 to a point opposite M3; palatine fenestrae are consistently

⁴ Measurements of the hind foot and ear are obviously transposed on the skin tag of KU 26922).

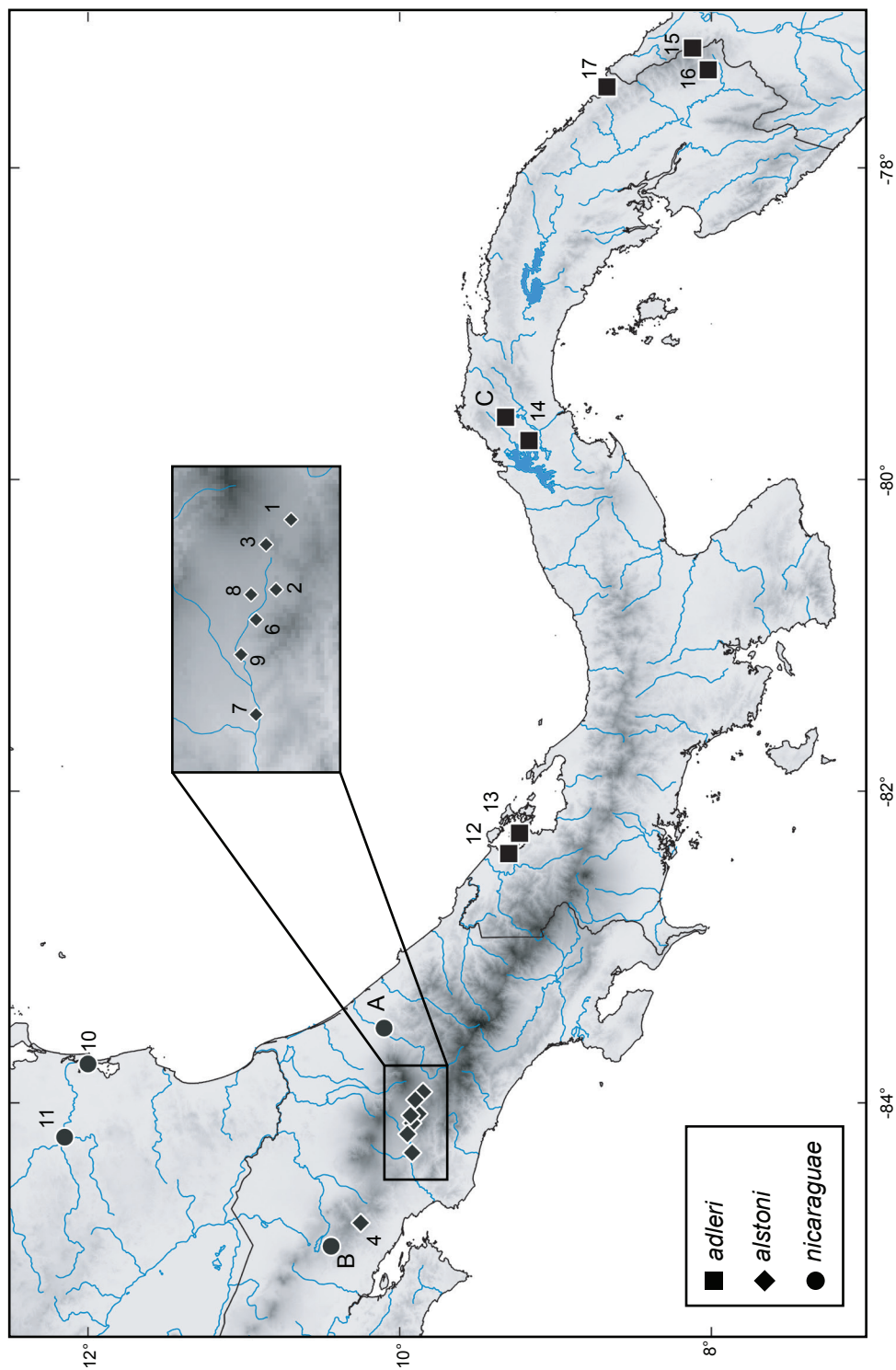


FIG. 2. Distribution of species of the Alstoni Group of *Marmosa* recognized as valid in this report. Numbers are keyed to entries in the gazetteer (appendix 1). Lettered localities correspond to material examined by other authors or vouchered only by photographs (see text): A, Siquirres (10.10° N, 83.52° W); B, La Chiripa de Tilarán (10.44° N, 84.92° W); C, Salamanca Hydrographic Station (9.32° N, 79.60° W).



FIG. 3. Dorsal and ventral views of skins of species in the Alstoni Group of *Marmosa*. From left to right in each panel: *M. alstoni* (KU 143495), *M. nicaraguae* (UMMZ 76732), and *M. adleri* (AMNH 272942).

absent. The auditory bullae (alisphenoid tympanic processes) are always small but variable in shape: whereas some are rounded ventrally (“globular”), others are provided with a bluntly conical ventral process. The ectoflexus (a labial indentation of the styler shelf) is shallow on M1–M3, where one or two distinct styler cusps usually occupy the “C” position (fig. 5A). The second upper premolar (P2) has an incomplete lingual cingulum, the postprotocrista of M3 is short (terminating at or near the base of the metacone), and m1–3 lack posterior cingulids.

COMPARISONS: Morphological comparisons between *Marmosa alstoni* and other members of the Alstoni Group are provided in the following accounts.

REMARKS: The name *Marmosa alstoni* has long been used for specimens of mouse opossums from Colombia, but we doubt that any are conspecific with material from the central highlands of Costa Rica. Tate (1933: 68) identified several Colombian specimens

TABLE 2. Measurements (mm) and weights (g) of *Marmosa alstoni*.

	Males ^a	Females ^b
HBL	186 ± 5 (180–192) 4	192 ± 4 (189–195) 2
LT	264 ± 14 (244–273) 4	272 ± 3 (270–274) 2
HF	32 ± 2 (30–35) 5	30 ± 1 (29–31) 4
Ear	26 ± 3 (23–30) 5	25 ± 0 (25–26) 4
CBL	44.2 ± 0.8 (43.8–45.6) 5	43.8 ± 2.4 (40.9–46.5) 5
NL	20.0 ± 0.9 (19.0–20.9) 6	20.1 ± 1.0 (19.0–21.1) 5
NB	6.8 ± 0.7 (5.6–7.5) 7	6.8 ± 0.6 (6.1–7.8) 5
LIB	8.8 ± 0.4 (8.3–9.3) 8	8.6 ± 0.5 (8.0–9.2) 5
LPB	8.2 ± 0.4 (7.7–8.7) 8	8.2 ± 0.5 (7.5–8.9) 5
ZB	25.2 ± 0.5 (24.5–26.1) 6	25.3 ± 1.3 (23.5–27.1) 5
PL	25.0 ± 0.6 (24.4–25.9) 7	24.9 ± 1.6 (23.2–26.6) 5
PB	14.9 ± 0.4 (14.4–15.5) 7	15.0 ± 0.4 (14.5–15.7) 5
MTR	18.1 ± 0.3 (17.7–18.9) 8	18.0 ± 0.5 (17.4–18.5) 5
LM	9.3 ± 0.2 (9.0–9.6) 10	9.3 ± 0.2 (9.1–9.6) 5
M1–3	7.7 ± 0.1 (7.4–7.8) 9	7.8 ± 0.3 (7.6–8.2) 5
WM3	3.0 ± 0.1 (2.9–3.1) 10	3.0 ± 0.1 (2.9–3.2) 5
Weight	126 ± 26 (100–153) 3	152 (150–155) 2

^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: AMNH 11789/10059, 11790/16210 (holotype), 139280, 140379; BMNH 98.10.9.11, 98.10.9.12; KU 26922, 143302; LSUMZ 12636. Statistics for LM and WM3 additionally include measurements from AMNH 137999, a subadult with completely erupted molars.

^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: AMNH 131732, 136863, 137288; KU 143495, 165556.

as *M. alstoni*, of which we have only been able to examine two. One, AMNH 61578 from Jericó (5.78° N, 75.78° W, 1967 m; Paynter, 1997) in Antioquia department, consists of cranial fragments and the skin of a juvenile individual; judging from the size of its erupted molar dentition, it would have grown to be an adult in the size range of *M. alstoni*; the tail is at least half-white, but features of the adult pelage cannot be inferred from the immature skin. The other specimen, AMNH 62796 from Calarcá (4.52° N, 75.63° W, ca. 1500 m) in Quindío department, consists of the skin of a large adult male unaccompanied by cranial material; consistent with Tate's identification, the skin has a long, fluffy-furred tail base, and almost two-thirds of the naked caudal epithelium is unpigmented distally. Despite their incompleteness, these specimens are sufficient to indicate that a species resembling *M. alstoni* in size and external traits is present in the mountains of northern Colombia. In fact, we have seen other Colombian examples of this phenotype, including FMNH 69863–69865 (from San Jerónimo at 6.45° N, 75.75° W in Antioquia department) and FMNH 69866 (from Sonsón, at 5.70° N, 75.30° W, also in Antioquia). However, the cytochrome *b* sequences that Voss et al. (2020) obtained from these specimens belong to the putative species that those authors called *M. phaea*, which differs from members of the *Alstoni*



FIG. 4. Dorsal and ventral cranial views ($\times 1.75$) of *Marmosa alstoni* (A, D; KU 143495), *M. nicaraguae* (B, E; UMMZ 76732), and *M. adleri* (C, F; AMNH 272942).

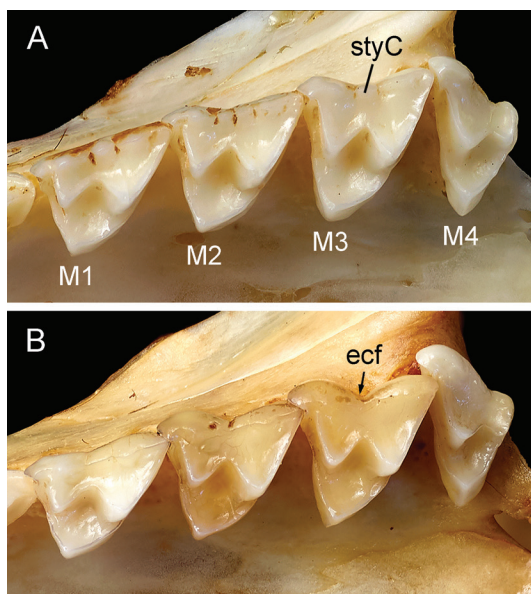


FIG. 5. Left upper molar toothrows of **A**, *Marmosa alstoni* (AMNH 137999) and **B**, *M. nicaraguae* (UMMZ 76733). Whereas the upper third molar (M3) of *M. alstoni* has one or two large stylar cusps in the “C” position (**styC**) and a shallow ectoflexus, *M. nicaraguae* lacks any stylar cusp in the “C” position and has a deep ectoflexus (**ecf**).

problematic. The USNM specimens that Tate (1933: 68) referred to this species from Nicaragua and Honduras, for example, are fragmentary and/or immature; none, in our opinion, are unambiguously identifiable as *M. alstoni*. We have not seen the Berlin specimen that Tate reported from Nicaragua. Remarkably, no other specimens of the subgenus *Micoureus* have been collected in either country for more than 50 years.

Another questionable record is based on a large mouse opossum live-trapped and subsequently released during an ecological study in the lowlands of central Panama. This animal was identified as *Marmosa alstoni* because of its large size (150 g) and a long (30 cm) furry tail base (Lambert et al., 2011); unfortunately, no tissue sample was obtained, and no photographs were taken (T.D. Lambert, personal commun.). Although Lambert et al.’s identification is not completely implausible, their central Panamanian capture site is several hundred kilometers east of the nearest confirmed locality for *M. alstoni* (in the highlands of central Costa Rica; see above), and the reported morphological traits are insufficiently diagnostic to support confident taxonomic inference. Clearly, however, it could not have been any of the species of mouse opossums previously known from central Panama—*M. adleri*, *M. isthmica*, or *M. robinsoni* (see Rossi et al. [2010] and this report)—all of which are substantially smaller and lack conspicuously furry tail bases. We suspect that Lambert et al.’s mouse opossum may have belonged to the *M. phaea* com-

Group by about 10%, on average, in uncorrected pairwise sequence comparisons.

The essential problem here is that the phenotype in question—large mouse opossums with particolored, fluffy-based tails—is shared among several distantly related species in the subgenus *Micoureus* (e.g., *Marmosa alstoni*, *M. paraguayana*, and some local populations of *M. constantiae*, *M. demerarae*, and *M. phaea*). Whether these traits have evolved convergently, or whether they have been retained as plesiomorphies from a common ancestor remains to be tested by character optimization, but if the phylogenetic results of Voss et al. (2020) are accurate, it is clear that such resemblances are an unreliable basis for taxonomic inference. Although we are aware that other Colombian specimens resembling *M. alstoni* (e.g., those mentioned by Díaz-Nieto and Gómez-Laverde, 2007) remain to be sequenced, the molecular results now in hand suggest that this species is unlikely to occur in South America.

Other specimens and observations previously identified as *Marmosa alstoni* are also

plex (sensu Voss et al., 2020), some examples of which are strikingly similar to *M. alstoni* in size and caudal pelage (see above); however, no specimen assignable to the *M. phaea* complex has previously been reported from Panama.

HABITATS: Although it is a small country, Costa Rica is topographically complex and has a corresponding diversity of vegetation types (Kappelle, 2016). At Monteverde, a biologically well-known locality in the Cordillera Tilarán, the natural vegetation at elevations where *M. alstoni* is known to occur (ca. 1300–1400 m) is premontane moist forest (fig. 6); this formation is characterized by an open understory of shrubs, treelets, and seedlings beneath a closed canopy of tall (25–40 m), mostly evergreen trees (Haber, 2000). Some specimens of *M. alstoni* collected at Monteverde, however, have been taken around buildings (R.M. Timm, personal commun.), so the species doubtless enters local gardens and secondary vegetation.

Marmosa alstoni also occurs at higher elevations and in wetter forests than those in which it has been collected at Monteverde. An animal that is unambiguously identifiable as *M. alstoni* (fig. 7A) was photographed by Victor J. Acosta-Chaves on 3 December 2012 at about 1750 m on the grounds of the Río Macho Biological Station (9.77° N, 83.85° W) in Cartago province. The natural vegetation at this site in the Cordillera Central is cloud forest (lower montane rain forest), but this individual was observed in secondary growth that was known to be only 17 years old. Photographs of local habitats (including the secondary vegetation in which the sighting occurred) are in Acosta-Chaves et al. (2015).

SPECIMENS EXAMINED ($N = 30$): COSTA RICA—*Cartago*, Agua Caliente (KU 26922), Paso Ancho (AMNH 139280), Tres Ríos (AMNH 11789/10059, 11790/16210 [holotype], 11791/10060, 11792/10061, 11793/10062); *Puntarenas*, Monteverde (KU 143302, 143495, 165556); *San José*, Escazú (AMNH 131737, 136863–136866, 137288, 137289, 137999, 140379, 140380; BMNH 98.10.9.11, 98.10.9.12), Los Higuerones (AMNH 137997, 137998), Piedras Negras (AMNH 139780), San José (AMNH 131732, 131736), ca. 2 km NW Santa Ana (LSUMZ 12636, 12638, 12639).

Marmosa (Micoureus) nicaraguae Thomas, 1905

Marmosa cinerea nicaraguae Thomas, 1905: 313 (original description).

Didelphis (Caluromys) nicaraguae: Matschie, 1916: 269 (name combination).

Marmosa alstoni nicaraguae: Tate, 1933: 69 (name combination).

Micoureus alstoni: Gardner, 2005: 12 (part, *nicaraguae* treated as a synonym).

Marmosa (Micoureus) alstoni: Voss and Jansa, 2009: 101 (part, *nicaraguae* treated as a synonym).

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation, BMNH 5.10.31.5) consists of the skin and skull of an adult male collected by Mervyn G. Palmer⁵ on 9 January 1905 at Bluefields, South Caribbean Autonomous Region (Región Autónoma de la Costa Caribe Sur), Nicaragua.

⁵ Both Thomas (1905: 313) and Jenkins and Knutson (1983) gave the collector's name as "G. Palmer," but the label attached to the type skin says "M.G. Palmer," and the individual in question is undoubtedly Mervyn G. Palmer, who described capturing the holotype in his memoirs (Palmer, 1945).



FIG. 6. Premontane moist forest at 1350 m near Monteverde, Puntarenas, Costa Rica. This is the natural vegetation at elevations where *Marmosa alstoni* has been collected in the Cordillera Tilarán (photo by Robert Lawton).

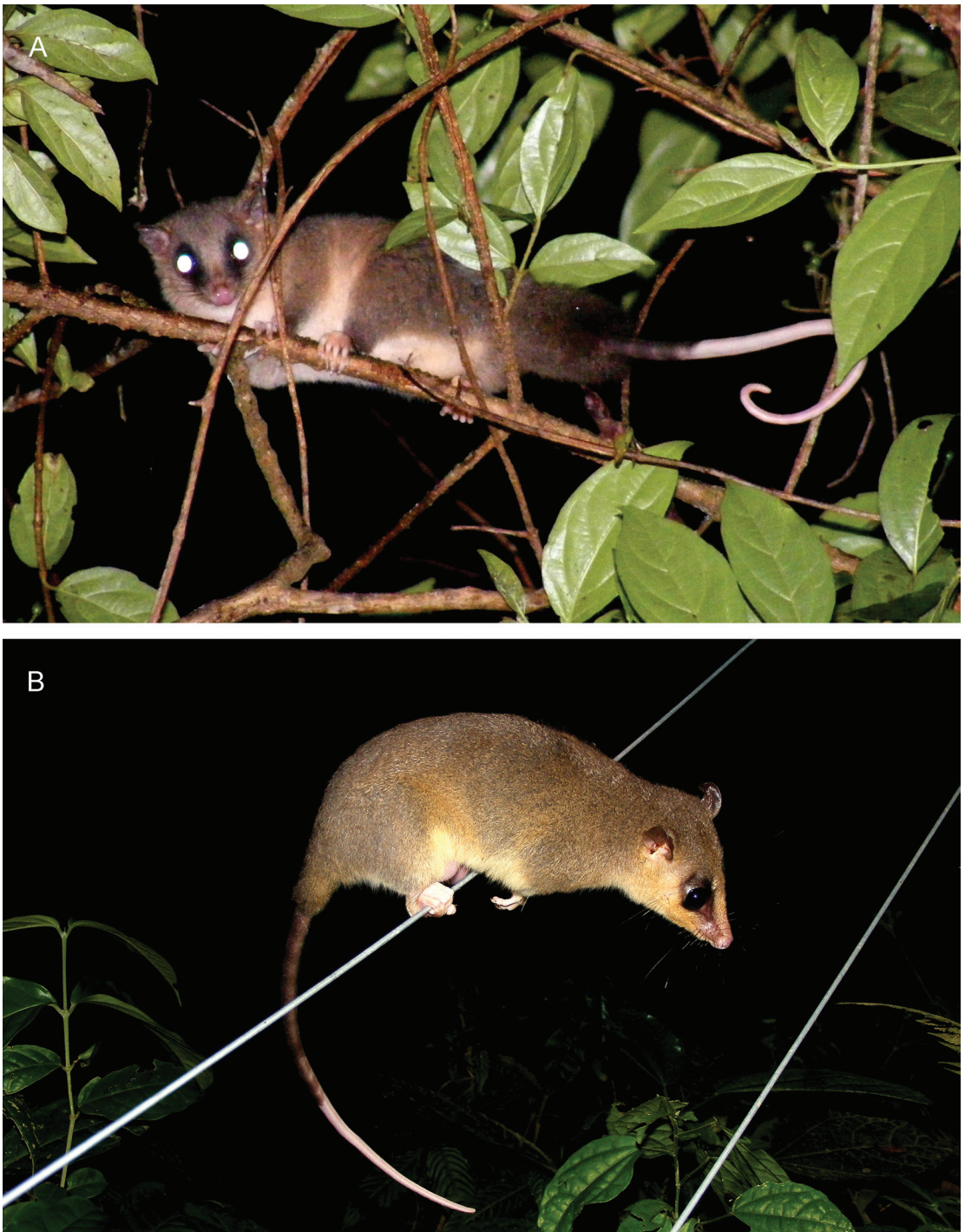


FIG. 7. Unvouchered field photographs of **A**, *Marmosa alstoni* (from Río Macho de Oro, Cartago, Costa Rica; ca. 1750 m) and **B**, *M. nicaraguae* (from La Chiripa de Tilarán, Guanacaste, Costa Rica; ca. 1000 m). Both photos courtesy of Victor Acosta.

DISTRIBUTION AND SYMPATRY: The three known collection localities of *Marmosa nicaraguae* are all in the Caribbean coastal lowlands of Nicaragua and Costa Rica, but if we have correctly identified an animal photographed in Guanacaste province Costa Rica (see Remarks, below), then *M. nicaraguae* may also occur in dry (deciduous or semideciduous) forests of the Pacific lowlands. *Marmosa nicaraguae* is not known to occur with other members of the subgenus *Micoureus*, but it probably occurs with *M. (Exulomarmosa) zeledoni*, which is definitely known from the Atlantic lowlands (Rossi et al., 2010), and it could also occur with *M. (E.) mexicana* on the Pacific side.

DESCRIPTION: The dorsal pelage of *Marmosa nicaraguae* is uniformly grayish brown—close to Ridgway's (1912) Hair Brown—from crown to rump on the single fully adult skin at hand (UMMZ 76732; fig. 3), but the fur is noticeably paler midrostrally and on the cheeks.⁶ Measured at midback on three adult skins, the dorsal fur is only 8–9 mm long, and it is closely applied to the body outline, appearing rather more sleek than woolly. The ventral pelage is gray-based buffy on each side between the fore- and hind legs, but there is a midventral streak of self-buffy fur that extends continuously from the groin to the chin, and the entire chest and the insides of the forelimbs are covered in self-buffy fur.

The ears are dark (probably translucent brownish in life), and they appear to be as long as or perhaps a bit longer than the hind feet, but neither of the adult specimens we examined is accompanied by complete measurement data obtained by the American method (table 3). No gular gland is present in the two adult males we examined, both of which, however, have medial and lateral carpal tubercles. The dorsal surfaces of the hind feet and the forefeet are covered with short, pale hairs and lack any darker markings. No lactating female specimen is available to determine the mammary complement.

The single adult male accompanied by American measurements (UMMZ 76732) has a tail that is 153% of head-and-body length. The furry tail base is only about 30–35 mm long, and the caudal fur is short (about 10 mm long) and appressed, not forming a conspicuously fluffy segment. The naked, scaly caudal epidermis is particolored: brownish basally and unpigmented (whitish in life) distally.⁷ In the two fully adult specimens at hand, only ½ to ⅓ of the distal part of the naked tail is unpigmented (whitish).

The skull of *Marmosa nicaraguae* resembles those of most other species in the subgenus *Micoureus*, with a short, broad rostrum; broadly flaring zygomatic arches; and well-developed, broadly triangular postorbital processes (fig. 4). The nasal bones seem to be narrower in proportion to their length in the single specimen from which both dimensions can be measured (UMMZ 76732) than in most other species of *Micoureus*, but this could be an individual peculiarity. In both adult skulls we examined, the maxillopalatine fenestrae extend from M1 to M3, and palatine fenestrae are absent. The auditory bullae are very small, and they are conical (rather than smoothly hemispherical) due to a blunt process on the ventral apex that appears

⁶ Thomas (1905) compared the dorsal fur to Ridgway's Sepia, and Tate compared it to Mummy Brown, but the former color seems too dark and the latter much too brownish.

⁷ Thomas (1905: 313) described the dark caudal skin of *Marmosa nicaraguae* as "blackish," but members of the tribe Didelphini (i.e., species of *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*) are the only opossums with blackish caudal skin (Voss and Jansa, 2003: char. 22).

TABLE 3. Measurements (mm) of *Marmosa nicaraguae*.

	BMNH 5.10.31.5 ^a	UMMZ 76732	UMMZ 76733
Age	adult	adult	subadult
Sex	male	male	male
HBL	167 ^b	178	160
LT	281 ^b	272	240
HF	28 ^c	28 ^c	27
Ear	29 ^b	—	—
CBL	44.4	45.2	—
NL	—	20.9	—
NB	6.3	6.4	5.7
LIB	8.3	8.5	7.4
LPB	7.2	7.6	7.7
ZB	24.7	25.1	22.9
PL	24.8	25.8	23.0
PB	14.3	14.3	14.1
MTR	18.0	18.3	17.1 ^c
LM	9.0	9.1	8.9 ^c
M1–3	7.6	7.6	7.4
WM3	3.0	3.0	2.8

^a Holotype.

^b Measured by the British method.

^c Estimated value.

to contain a vascular sinus. As in other members of the Alstoni Group, P2 has an incomplete lingual cingulum, the postprotocrista of M3 is short (terminating at or near the base of the metacone), and the lower molars lack posterior cingulids. However, M3 has a deep ectoflexus and lacks a distinct stylar cusp in the “C” position (fig. 5B).

COMPARISONS: Measurement data and visual comparisons of skins suggest that adults of *Marmosa nicaraguae* have absolutely and relatively longer tails and larger ears than *M. alstoni*, but with so few available specimens it is hard to be certain that these are consistent differences. However, *M. nicaraguae* also has much shorter dorsal fur than *M. alstoni*, a continuous streak of self-colored midventral fur that extends from chin to groin, and a much shorter furry tail base. Although most craniodental measurements of adult *M. nicaraguae* overlap the range of variation seen in same-sex adult specimens of *M. alstoni*, values for two dimensions (LPB and PB) suggest that *M. nicaraguae* may have narrower postorbital constrictions and narrower palates. Lastly, all three specimens of *M. nicaraguae* have a deep ectoflexus on M3, which lacks a distinct stylar cusp in the “C” position (fig. 5B), whereas in *M. alstoni* the M3 ectoflexus is shallower and at least one distinct stylar cusp is present in the “C” position on unworn teeth (fig. 5A). In the aggregate, these differences (table 4) would seem to provide an adequate basis for specimen identification.

TABLE 4. Selected morphological comparisons among species of the Alstoni Group of *Marmosa*.

	<i>M. alstoni</i>	<i>M. nicaraguae</i>	<i>M. adleri</i>
Ear (pinna)	shorter than hind foot	unknown ^a	longer than hind foot
Dorsal pelage (length) ^b	11–15 mm	8–9 mm	7–9 mm
Self-colored ventral fur	discontinuous	continuous	discontinuous
Furry tail base	long and fluffy	short, not fluffy	short, not fluffy
Tail	particolored (whitish distally)	particolored (whitish distally)	usually all-dark
M3 ectoflexus	shallow	deep	deep
StyC on M3 ^c	usually distinct	indistinct or absent	indistinct or absent
Head-and-body length (HBL) ^b	180–195 mm	167–178 mm	120–150 mm
Condylbasal length (CBL) ^b	40.9–46.5 mm	44.4–45.2 mm	34.8–38.0 mm
Length of molars (LM) ^b	9.0–9.6 mm	9.0–9.1 mm	7.3–8.0 mm

^a Insufficient measurement data available.

^b Table entries are the observed range (minimum–maximum) of each measurement for both sexes (including specimens of unknown sex, if any).

^c StyC = styler cusp(s) in the “C” position.

Comparisons with our new species, *Marmosa adleri*, are provided in the next account.

REMARKS: Tate (1933: 69) reported a male specimen of *Marmosa alstoni nicaraguae* from Siquirres (10.10° N, 83.52° W; DMA, 1983) in the Atlantic lowlands of Limón province, Costa Rica. This specimen was said to be in the “Stockholm Collection” with catalog number 39, and a footnote to Tate’s table of measurements indicates that it was a flat skin. According to Daniela Kalthoff at the Naturhistoriska Riksmuseet, this specimen, now cataloged as NRM 580721, was collected on 28 September 1882 by the Swedish polymath Carl Bovallius. Features that can clearly be seen in photographs of NRM 580721 (sent to us on 21 September 2020) support Tate’s identification,⁸ and his measurements of the hind foot (27.5 mm) and middorsal fur length (9 mm) are within the range of measurements that we obtained from the holotype and other Nicaraguan material.

Another plausible record of *Marmosa nicaraguae* from Costa Rica is based on photographs taken by Victor J. Acosta-Chaves of an animal that he observed on 19 September 2013 at La Chiripa de Tilarán in Guanacaste Province (fig. 7B). This locality (at 10.44° N, 84.92° S) is about 1000 m above sea level in a zone of transition between tropical dry forest and cloud forest (premontane moist forest). Both the local avifauna and the local herpetofauna include species typical of the dry forests that occur at lower elevations on the Pacific side of the Cordillera Tilarán and other species that typically occur in cloud forest at higher elevations (V.J. Acosta-Chaves, in litt., 16 September 2020). Because specimens of *Marmosa alstoni* are known from cloud forest at Monteverde (appendix 1: locality 4), which is only about 27 km to the SE and

⁸ The naked part of the tail is only about ½ white, the tail base is short furred, and the fur along the ventral midline appears to have been broadly self-buffy.

about 400 m higher than La Chiripa, we infer that *M. nicaraguae* probably belongs to the dry-forest fauna at this locality and might be widespread in the Guanacaste lowlands.

By contrast with these plausible records, the specimen that Hershkovitz (1951) identified as *Marmosa alstoni nicaraguae* from Belize does not closely match the phenotype that we attribute to *M. nicaraguae*. The specimen in question (FMNH 63889) consists of the faded skin and damaged skull of a large subadult male. Although it does resemble *M. nicaraguae* in having a narrowly continuous midventral streak of self-colored fur, and in having a deep ectoflexus on M3, it has somewhat longer (10 mm) dorsal fur, a distinctly fluffy-furred tail base, a broader postorbital constriction, and a broader palate than the typical Nicaraguan material we examined. Absent any sequence data, we are reluctant to commit to any species-level identification of this specimen.

HABITATS: The Caribbean lowlands of Nicaragua and Costa Rica are among the wettest regions in Central America, with annual rainfall well in excess of 3000 mm in most places (e.g., at Siquirres; Wernstedt, 1972). The climax vegetation along the Caribbean coast is lowland rainforest, but drier conditions occur in the Pacific lowlands of Guanacaste, where deciduous and semideciduous forests predominate (Jiménez et al., 2016). Therefore, if *Marmosa nicaraguae* really occurs in both areas, its geographic range likely encompasses a diversity of climax vegetation types.

The only information about the circumstances in which specimens of *Marmosa nicaraguae* were captured is a notation on the skin tag of the holotype, which says “caught at hotel chicken house.” The collector’s memoirs (Palmer, 1945: 13–14) provide additional context.

During the few days of waiting [for transportation] in Bluefields I was, of course, constantly on the look-out for additions to my collections and was rewarded by the capture of an opossum, no bigger than a rat ... I caught it by hand in the hotel as it was chasing some rats along the rafters.

Evidently, *M. nicaraguae* (like other congeners) is not restricted to pristine habitats, but also occurs in and around human habitations, or at least those of simple pole-and-thatch construction surrounded by gardens and secondary vegetation.

SPECIMENS EXAMINED ($N = 3$): NICARAGUA—*South Caribbean Autonomous Region*, Bluefields (BMNH 5.10.31.5), Río Siquia (UMMZ 76732, 76733).

Marmosa (Micoureus) adleri, new species

TYPE MATERIAL AND TYPE LOCALITY: The holotype (AMNH 272942; field number 1469) consists of the skin and skull of an adult female collected 1 km north of the Río Mendoza on Pipeline Road in Parque Nacional Soberanía, Colón province, Panama, by Gregory H. Adler and Alejandra Carvajal on 14 January 2001. A short (475 bp) fragment of the mitochondrial gene cytochrome *b* was obtained from this specimen and deposited in GenBank with accession number MN978602 (Voss et al., 2020: table 2).

DISTRIBUTION AND SYMPATRY: *Marmosa adleri* is only known from Panama, but it is widely distributed within that country, from near the border with Costa Rica to the Colombian frontier, and from near sea level to almost 1500 m (fig. 2). Although *M. adleri* is not known to

occur with other species in the subgenus *Micoureus*, it may often be sympatric with *M. isthmica* and *M. zeledoni*, two species of the subgenus *Exulomarmosa* that have broadly overlapping geographic ranges and occupy similar habitats (Rossi et al., 2010).

DESCRIPTION: The dorsal pelage of *Marmosa adleri* is uniformly dull grayish brown—near Ridgway's (1912) Olive Brown in most specimens—from crown to rump, but the midrostral fur (between the blackish facial masks) is abruptly paler, and the cheeks are distinctly buffy (Light Ochraceous Buff). Measured at mid-back on nine adult skins, the dorsal fur is only 7–9 mm long, and it seems sleek (closely applied to the body surface) rather than fluffy. The ventral fur is almost entirely gray-based buffy, with self-buffy fur only on the chin and in the inguinal region; the fur on the insides of the forelimbs is also gray-based. None of the specimens we examined has a midventral streak of self-colored fur.

The ears are dark (probably translucent-brownish in life) and, in all specimens accompanied by credible measurement data, they are longer than the hind feet (table 5).⁹ Gular glands are consistently absent, and large adult males (e.g., USNM 337963) have well-developed lateral and medial carpal tubercles. Complete mammary counts could not be obtained from any of the female skins we examined, but field notes (in the USNM Mammals archive) indicate that USNM 335029 had nine “pouch young,” so the mammary complement of this specimen must have been at least 4–1–4. The tail is very long—about 160% of head-and-body length, on average—and only about 10–15 mm at the base of the tail is covered with short (<5mm long) fur. The naked, scaly part of the tail is entirely dark (probably grayish or brownish in life) in most specimens, although some have indistinct pale mottling near the tip. In two specimens (USNM 335029, 449565), however, the terminal 25–30 mm of the tail is unpigmented (probably whitish in life). The hind feet and the digits of the forefeet are covered dorsally with uniformly short, pale hairs, but the hairs over the metacarpals are often indistinctly darker.

Skulls of *Marmosa adleri* are among the smallest we have measured in the subgenus *Micoureus*, but they are otherwise unremarkable dorsally with short, broad rostrums; wide zygomatic arches; and well-developed postorbital processes (fig. 4C, F). The maxillopalatine fenestrae are narrow and, in most specimens, extend from the level of M1 to a point opposite M3; palatine fenestrae are consistently absent. The auditory bullae are very small, and most are smoothly rounded ventrally (“globular”); only one specimen (USNM 315008) has “conical” bullae with well-developed ventral processes. The ectoflexus is consistently deep on M3, which lacks a distinct stylar cusp in the “C” position. The second upper premolar (P2) has an incomplete lingual cingulum, the postprotocrista of M3 is short (terminating at or near the base of the metacone), and m1–m3 lack posterior cingulids.

COMPARISONS: In side-by-side morphological comparisons, *Marmosa adleri* could never be confused with its sister taxon, *M. alstoni*. The size difference alone is striking; in fact, there is no overlap among most measurements of these species (tables 2, 5), and the average body weight of *M. adleri* (58 g) is less than half that of *M. alstoni* (137 g). *Marmosa adleri* is also longer tailed (mean LT/HBL \times 100 = 161%) than *M. alstoni* (mean LT/HBL

⁹ One specimen (USNM 339018) has a recorded hind-foot measurement of 33 mm, an obvious error (our estimate based on the dried skin is about 23 mm).

TABLE 5. Measurements (mm) and weights (g) of *Marmosa (Micoureus) adleri*.

	USNM 337963	USNM 449564	USNM 449565	AMNH 272942 ^a	USNM 309264	USNM 335029	USNM 335030	USNM 315008
Sex	male	male	male	female	female	female	female	female
HBL	138	143	143	120 ^b	150	137	138	121
LT	226	215	225	215 ^b	218	236	214	224
HF	23	22	20	22 ^b	22	22	22	23
Ear	25	23	24	22 ^b	25	25	24	24
CBL	37.6	36.5	36.9	34.8	38.0	37.1	36.2	35.2
NL	—	17.5	17.3	15.9	17.2	16.9	16.6	16.3
NB	4.9	5.2	5.8	4.7	5.3	4.9	4.6	4.8
LIB	6.6	6.8	7.3	6.2	6.8	6.4	6.3	6.3
LPB	6.8	6.6	6.9	6.6	6.5	6.6	6.7	6.2
ZB	20.5	21.7	21.7	20.2	21.6	20.1	20.8	20.7
PL	20.9	21.0	21.1	19.5	21.8	20.9	20.1	19.5
PB	11.6	11.6	11.6	11.6	12.2	11.7	11.5	12.1
MTR	15.3	14.4	14.5	14.3	15.4	15.2	14.4	14.4
LM	8.0	7.3	7.3	7.3	7.8	7.8	7.5	7.6
M1–3	6.8	6.2	6.1	6.2	6.5	6.5	6.4	6.4
WM3	2.6	2.4	2.4	2.5	2.6	2.6	2.6	2.5
Weight	—	63	68	40	—	54	67	—

^a Holotype.^a Measured on dry skin.

× 100 = 145%), and it has proportionately larger ears (whereas the pinnae of *M. adleri* are consistently longer than its hind feet, the pinnae of *M. alstoni* are consistently shorter than its hind feet). Additionally, the tail of *M. adleri* has a short furry base, and the unfurred (scaly) part of the tail is almost completely dark, whereas *M. alstoni* has a long, fluffy-furred tail base, and >50% of the naked part of the tail is white. However, these species are craniodentally similar (except in size); the only qualitative trait in which they differ seemingly consists in the morphology of M3, which has a deep extoflexus and lacks a distinct stylar cusp in the “C” position in *M. adleri*, whereas M3 has a shallow ectoflexus and a large cusp (or cusps) in the “C” position in *M. alstoni*.

Marmosa adleri is likewise much smaller than *M. nicaraguae*, from which it also differs externally by lacking a continuous midventral streak of self-colored fur and by having a mostly all-dark tail. Except in size, these species are craniodentally similar.

The material that we refer to *Marmosa adleri* was said by Handley (1966; see Remarks, below) to resemble *Marmosa phaea* Thomas, 1899, a species originally described from the Andes of southwestern Colombia. However, phylogenetic analyses of mtDNA sequence data suggest that *M. phaea* is not closely related to any member of the Alstoni Group (Voss et al.,

2020). Furthermore, the material that we refer to *M. phaea* from southwestern Colombia (in Nariño and Huila departments, including the holotype) averages larger than *M. adleri* in all dimensions and has longer dorsal fur, tails that are usually at least half white, multiple palatine fenestrae, a complete lingual cingulum on P2, and long postprotocristae.¹⁰

REMARKS: To the best of our knowledge, this species was first mentioned by Handley (1966: 755) as an unidentified taxon “resembling *Marmosa phaea* Thomas,” and the epithet *phaea* (in binomial combinations either with *Marmosa* or *Micoureus*) appeared on USNM specimen labels, catalogs, and databases for many years. Field guides that reported *Mic. phaea* from Panama (e.g., Emmons, 1997) were doubtless based on this USNM material. Subsequently, however, Patton et al. (2000) analyzed a cytochrome *b* sequence from USNM 449565, which they identified as *Mic. alstoni*.

Although massive faunal survey efforts followed U.S. annexation of the Canal Zone in the early 20th century, no specimens of *Marmosa adleri* were collected at the time; the species was clearly unknown to Goldman (1920) and Tate (1933). Apparently, the first specimen of *M. adleri* was collected in 1959 at Tacarcuna Casita Camp (appendix 1: locality 16) near the Colombian frontier, still a remote and roadless region, but more material was obtained at widely dispersed and more accessible localities over the next several years. Among the material we have not yet seen are one or more specimens from “Salamanca Hydrographic Station” (Handley, 1966: 755)¹¹ and a topotype from Pipeline Road; the latter specimen (with field number 1422) was prepared as a skin and skull and deposited in the zoological collection of the Universidad de Panamá (G.H. Adler, personal commun.).

HABITATS: Central Panama receives abundant rainfall (ca. 2600 mm annually; Dietrich et al., 1996), but there is a prolonged dry season in the vicinity of Pipeline Road (the type locality) and nearby Barro Colorado Island, where the local climax vegetation is usually described as semievergreen moist forest (e.g., by Croate, 1978). However, only a small number of trees are even facultatively deciduous, so the canopy as a whole remains closed and densely leafy throughout the year (Foster and Brokaw, 1996). Pipeline Road—an unpaved jeep track built in the mid-1900s to service a never-used oil pipeline—threads its way across hilly terrain ranging from 30 m to 200 m above sea level (Karr, 1990; Robinson et al., 2000), all of which is now protected within Parque Nacional Soberanía; local habitats include old-growth forest and old secondary vegetation (figs. 7, 8). A total of 10 individuals of *Marmosa adleri* were live-trapped in 2001 and 2002 by G.H. Adler and A. Carvajal at several locations along Pipeline Road, including four individuals taken in mature ridge-top forest just north of the Río Mendoza and six others that were taken in secondary growth or mixed (secondary and old-growth) forest elsewhere (G.H. Adler in litt., 5 October 2020). Most recorded captures of *M. adleri* (eight of nine accompanied by location data) were in traps set from 1.7 to 2.0 m above the ground on lianas or in trees, but one individual was trapped on the ground. By comparison, the same transect-trapping study captured 103 individuals identified in the field as *M. robinsoni* (prob-

¹⁰ Note, however, that these traits are not shared by all the sequenced material that Voss et al. (2020) referred to the putative species *Marmosa phaea*, which might represent a species complex.

¹¹ Salamanca Hydrographic Station (9.32° N, 79.60° W, 100 m; Siegel and Olson, 2008) is on the NW shore of Lago Alajuela about 23 km NE of the type locality (fig. 1, locality C).



FIG. 8. The forest along Pipeline Road at the Río Mendoza (photo by Katja Schulz). The holotype of *Marmosa adleri* was collected in mature ridge-top forest about 1 km north of this site.

ably *M. isthmica*; Rossi et al., 2010), which would appear to be either more abundant or more easily trapped than *M. adleri*.

The Caribbean coastal lowlands are substantially wetter than the isthmian interior of central Panama (Santiago and Mulkey, 2005), so the dominant climax vegetation on well-drained soils at collecting localities for *Marmosa adleri* in the provinces of Bocas del Toro and San Blas (appendix 1) is evergreen rainforest. However, at least some of the natural vegetation was apparently cleared for agriculture when these places were visited by USNM personnel. According to sources cited by Siegel and Olson (2008), the vegetation surrounding Almirante (in Bocas del Toro) at the time of Handley and Rhymer's visit in 1960 included banana and cacao groves and secondary growth in addition to rainforest, but a note on the skin tag of the single specimen trapped at this locality (USNM 315008) indicates only that it was caught in "forest." At Bocatorito (on Isla San Cristobal, also in Bocas del Toro), local habitats at the time of Greenwell's visit in 1989 included cacao plantations and secondary forest (Siegel and Olson, 2008); Greenwell's field catalog (also in the USNM Division of Mammals archives) indicates that both specimens from this locality were taken in banana-baited traps, one on a fallen tree in "patchy forest" with heliconias, and another on the ground in a "cacao patch." At Quebrada Venado (in



FIG. 9. Understory vegetation with lianas in old secondary growth along Pipeline Road (photo by Christian Ziegler). Trapping results suggest that lianas are the favored substrate of *Marmosa adleri* in the forest understory.

San Blas province), local habitats at the time of Handley and Greenwell's visit in 1963 included recent clearings, old cacao plantations, and "heavy forest" (Siegel and Olson, 2008: 416); one of Handley's specimens from this locality (USNM 335029) was trapped in a cacao tree, whereas the other (USNM 335030) was shot in a tree in the forest.

Annual rainfall is exceptionally high in eastern Panama, probably exceeding 4000 mm along the rugged Colombian frontier (Portig, 1965). Based on Anthony's (1916) description of local habitats, the predominant natural vegetation in the hills near Tacarcuna Casita¹² was tall evergreen rainforest, but a note on the skin tag of USNM 309264 says "caught by hand on rafter in camp kitchen." According to Siegel and Olson (2008: 257), USNM collectors camping near the summit of Cerro Malí in the 1960s worked in cloud forest and "more open, gallery type forest." Of the two specimens taken at this locality, USNM 339018 is not accompanied by ecological information, whereas the skin tag of 337963 indicates that it was trapped at the base of a tree in cloud forest. The vegetation at about the same elevation where this specimen was trapped on Cerro Malí was described by W.E. Duellman in a passage quoted by Myers (1969).

The forest contains many small trees, including palms, reaching heights of [about] 12 meters. Larger trees up to [about] 30 meters are scattered through the forest. There is an understory of bushes and ferns. Most of the trees have a thin covering of moss on the trunks. There is a thick mulch layer on the ground and many rotting logs. Many bromeliads and a few orchids present; few tree ferns.

In summary, *Marmosa adleri* seems to occur in a range of habitats including climax vegetation, secondary growth, and orchards in a diversity of humid-forested lowland and lower-montane landscapes. Because none of these habitats are distinctively Panamanian, it would be reasonable to expect that the species occurs well outside its currently known range, probably including the Caribbean coast of eastern Costa Rica as well as northwestern Colombia.

ETYMOLOGY: For Gregory H. Adler, who trapped the holotype during his ecological fieldwork, recognized it as something new, and had it prepared as a voucher specimen. Adler's many publications include important contributions to knowledge of seed dispersal, habitat use, community ecology, and demography of Neotropical small mammals based on several decades of trapping studies in Panama and northern South America.

SPECIMENS EXAMINED ($N = 9$): PANAMA—*Bocas del Toro*, Almirante (USNM 315008), Bocatorito (USNM 449564, 449565); *Colón*, Pipeline Road (AMNH 272942); *Darién*, Cerro Malí (USNM 337963), Cerro Malí Camp (USNM 339018), Tacarcuna Casita Camp (USNM 309264); *San Blas*, Quebrada Venado (USNM 335029, 335030).

Unidentified Material

The three taxa formally recognized in this report are probably not the only valid species of the Alstoni Group, but we are currently unable to properly assess the taxonomic status of two

¹² According to Siegel and Olson (2008), this locality is very close to Anthony's (1916) camp at Tacarcuna, a semiabandoned Amerindian settlement.

specimens from the trans-Andean “Chocó” lowlands of northwestern South America. The first is FMNH 90097, an adult female collected by Kjell von Sneider on 2 October 1958 at or near the confluence of the Río Sandó and the Río Baudó (5.11° N, 76.95° W; 160 m above sea level) in the Colombian department of Chocó (Voss et al., 2020: fig. 1, locality 66). The second is AMNH 148757, an adult female that arrived at New York on 2 May 1952 in a shipment of bananas from Esmeraldas (0.98° N, 79.70° W), a port city in the eponymous Ecuadorean province (Voss et al., 2020: fig. 1, locality 73).¹³ In our maximum-likelihood phylogenetic analysis, cytochrome *b* fragments that we obtained from these specimens form a clade that is sister to all other Alstoni Group sequences, from which they are notably divergent in uncorrected pairwise comparisons (fig. 1, table 1).

FMNH 90097 and AMNH 148757 are morphologically similar and somewhat resemble the phenotype described above for *Marmosa adleri*. Both are small mouse opossums (table 6) with very long, all-dark tails (LT/HBL \times 100 = 150%–161%). The grayish-brown dorsal pelage is short (ca. 7–9 mm), and the ventral pelage (including the insides of the forelimbs) is entirely gray-based buffy. Both specimens have well-developed postorbital processes, short maxillopalatine fenestrae, and lack palatine fenestrae. Both specimens have a deep ectoflexus and a short postprotocrista on M3. However, AMNH 148757 has small but distinct posterior cingulids on m1–m3 that are not present on FMNH 90097, whereas the latter specimen has a long white tail tip that is not present on AMNH 148757. In effect, it is not clear whether these specimens represent one or two new taxa, so it seems prudent to await the collection of fresh material accompanied by properly preserved tissues to assess phenotypic character variation and genetic divergence.

DISCUSSION

It is remarkable that one of the largest species of the subgenus *Micoureus* should have one of the smallest species as its sister taxon, and that taxa so morphologically disparate in both size and qualitative traits should be so similar in mtDNA sequence comparisons. The latter phenomenon suggests recency of common ancestry, whereas the former might be explained by strong ecological selection for divergent phenotypes. This, of course, is pure speculation, but the implied scenario would be consistent with the initial stages of adaptive radiation of an ancestral lineage in a formerly unoccupied region, as commonly hypothesized by evolutionary biologists (e.g., Glor, 2010; Stroud and Losos, 2016; Gillespie et al., 2020).

Biogeographic reconstructions suggest that the subgenus *Micoureus* evolved in South America when that continent was separated from Central America by a marine water barrier (Jansa et al., 2014; Castro et al., 2021), and geological evidence suggests that some form of marine barrier persisted until about three million years ago, when a definitive land bridge was formed (O’Dea et al., 2016). Pairwise cytochrome *b* distances among Central American members of the Alstoni Group (ca. 3%–8%; table 1) are consistent with a post-land-bridge radiation,

¹³ This specimen was received at the Bronx Zoo on 2 May 1952, where it died three days later.

but in the absence of any real evidence for the ecological significance of size and other phenotypic traits that distinguish the species treated in this report, there is not much more to be said on the topic of adaptive radiation.

New species of mammals are routinely described from South America, especially from remote localities in Amazonia and the Andes but, clearly, much remains to be learned about mammalian diversity in Central America. Seemingly authoritative faunal monographs for several Central American countries (e.g., Goldman, 1920; Goodwin, 1942, 1946) and the availability of an excellent field guide to the region (e.g., Reid, 1997) have perhaps contributed to the notion that Central American mammals are well known. However, recent discoveries in Panama, a country with a long history of mammalogical exploration (Handley, 1972), are compelling evidence that this is not true. The description of a new bat—*Lophostoma kalkoae* (see Velazco and Gardner, 2012)—captured just a few kilometers from Barro Colorado Island, perhaps the most thoroughly studied tropical field station on the planet, is one example. Our description of *Marmosa*

adleri from a nearby locality in central Panama is another. Similar examples of recent mammalogical discoveries (e.g., Gardner and Carleton, 2009; Ramírez-Fernández et al., 2020) can be cited for Costa Rica, which also has a long history of mammalogical fieldwork.

If mammalogical knowledge of Costa Rica and Panama is still incomplete, knowledge of mammalian diversity in Belize, Honduras, and Nicaragua can only be described as rudimentary. In particular, there have been no sustained attempts to inventory the small nonvolant mammal fauna of the rainforested lowlands of those countries for over half a century. As a result, although we know for a fact that mouse opossums resembling *Marmosa alstoni* and/or *M. nicaraguae* occur there, all we have at hand are a few fragmentary or immature specimens collected many years ago.

Whereas biological collecting throughout the Neotropics was once carried out primarily by European or North American researchers, or by professional collectors employed by European and North American museums, most biological inventory work in South America is now carried out—professionally and competently—by dedicated communities of in-country researchers supported by well-developed national university systems. By contrast, many Central American countries have neglected in-country mammalogical inventory initiatives, perhaps on the assumption

TABLE 6. Measurements (mm) of two specimens of *Marmosa* from the Chocó region of northwestern South America.

	FMNH 90097	AMNH 148757
Age	adult	adult
Sex	female	male
HBL	161	127
LT	242	205
HF	26	23
Ear	23	—
CBL	40.4	—
NL	17.7	—
NB	5.3	—
LIB	6.7	6.2
LPB	7.2	7.4
ZB	22.1	—
PL	22.7	19.3
PB	12.7	11.2
MTR	16.7	—
LM	8.2	7.6
M1–3	6.9	6.2
WM3	2.6	2.2

that there is nothing new left to discover in the region. It would be gratifying if our description of *Marmosa adleri* were to encourage a new generation of Central American mammalogists to question that assumption and to renew interest in local inventory fieldwork.

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REFERENCES

- Acosta-Chaves, V.J., G. Chaves, J.G. Abarca, A. García Rodríguez, and F. Bolaños. 2015. A checklist of the amphibians and reptiles of Río Macho Biological Station, Provincia de Cartago, Costa Rica. *Check List* 11 (6): 1–10.
- Allen, J.A. 1900. Note on the generic names *Didelphis* and *Philander*. *Bulletin of the American Museum of Natural History* 13 (15): 185–190.
- Anthony, H.E. 1916. Panama mammals collected in 1914–1915. *Bulletin of the American Museum of Natural History* 35 (20): 357–376.
- Castro, M.C., M.J. Dahur, and G.S. Ferreira. 2021. Amazonia as the origin and diversification area of Didelphidae (Mammalia: Metatheria), and a review of the fossil record of the clade. *Journal of Mammalian Evolution*. [doi.org/10.1007/s10914-021-09548-7]
- Clark, K.L., R.O. Lawton, and P.R. Butler. 2000. The physical environment. In N.M. Nadkarni and N.T. Wheelwright (eds.), *Monteverde: ecology and conservation of a tropical cloud forest*: 15–38. New York: Oxford University Press.
- Croate, T.B. 1978. *Flora of Barro Colorado Island*. Stanford: Stanford University Press.
- Díaz-Nieto, J.F., and M. Gómez-Laverde. 2007. Comentarios sobre el primer registro de *Micoureus alstoni* (Allen, 1900) (Didelphimorphia, Didelphidae) para Colombia. *Actualidades Biológicas* 29: 235–240.
- Dietrich, W.E., D.M. Windsor, and T. Dunne. 1996. Geology, climate, and hydrology of Barro Colorado Island. In E.G. Leigh, Jr., A.S. Rand, and D.M. Windsor (eds.), *The ecology of a tropical forest, seasonal rhythms and long-term changes*, 2nd ed.: 21–46. Washington DC: Smithsonian Institution.
- DMA. 1983. *Gazetteer of Costa Rica*, 2nd ed. Washington, DC: Defense Mapping Agency.
- DMA. 1985. *Gazetteer of Nicaragua*, 3rd ed. Washington, DC: Defense Mapping Agency.

- Emmons, L.H. 1997. Neotropical rainforest mammals, a field guide, 2nd ed. Chicago: University of Chicago Press.
- Foster, R.B., and N.V.L. Brokaw. 1996. Structure and history of the vegetation of Barro Colorado Island. In E.G. Leigh, A.S. Rand, and D.M. Windsor (eds.), *The ecology of a tropical forest*, 2nd ed.: 67–81. Washington, DC: Smithsonian Institution Press.
- Gardner, A.L. 2005. Order Didelphimorphia. In D.E. Wilson and D.M. Reeder (eds.), *Mammal species of the world, a taxonomic and geographic reference*, 3rd ed.: 3–18. Baltimore: Johns Hopkins University Press.
- Gardner, A.L., and M.D. Carleton. 2009. A new species of *Reithrodontomys*, subgenus *Aporodon* (Cricetidae: Neotominae), from the highlands of Costa Rica, with comments on Costa Rican and Panamanian *Reithrodontomys*. In R.S. Voss and M.D. Carleton (editors), *Systematic mammalogy: contributions in honor of Guy G. Musser*. *Bulletin of the American Museum of Natural History* 331: 157–181.
- Gardner, A.L., and G.K. Creighton. 1989. A new generic name for Tate's (1933) *microtarsus* group of South American mouse opossums (Marsupialia: Didelphidae). *Proceedings of the Biological Society of Washington* 102: 3–7.
- Gardner, A.L., and G.K. Creighton. 2008 ("2007"). Genus *Micoureus* Lesson, 1842. In A.L. Gardner (ed.), *Mammals of South America*, vol. 1. (Marsupials, xenarthrans, shrews, and bats): 74–82. Chicago: Chicago University Press.
- Gardner, A.L., R.K. LaVal, and D.E. Wilson. 1970. The distributional status of some Costa Rican bats. *Journal of Mammalogy* 51: 712–729.
- Gillespie, R.G., et al. [21 additional coauthors]. 2020. Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* 111: 1–20.
- Glor, R.E. 2010. Phylogenetic insights on adaptive radiations. *Annual Review of Ecology and Systematics* 41: 251–270.
- Goldman, E.A. 1920. Mammals of Panama. *Smithsonian Miscellaneous Collections* 69 (5): 1–309.
- Goodwin, G.G. 1942. Mammals of Honduras. *Bulletin of the American Museum of Natural History* 79: 107–195.
- Goodwin, G.G. 1946. Mammals of Costa Rica. *Bulletin of the American Museum of Natural History* 87: 271–474.
- Haber, W.A. 2000. Plants and vegetation. In N.M. Nadkarni and N.T. Wheelwright (eds.), *Monteverde: ecology and conservation of a tropical cloud forest*: 39–70. New York: Oxford University Press.
- Hall, E.R. 1962. Collecting and preparing study specimens of vertebrates. *Miscellaneous Publications of the University of Kansas Museum of Natural History* 30: 1–46.
- Hall, E.R. 1981. *Mammals of North America*, 2nd ed., 2 vols. New York: John Wiley and Sons.
- Handley, C.O., Jr. 1966. Checklist of the mammals of Panama. In R.L. Wenzel and V.J. Tipton (eds.), *Ectoparasites of Panama*: 753–795. Chicago: Field Museum of Natural History.
- Handley, C.O., Jr. 1972. Mammalogy in Panama. In M.L. Jones (ed.), *The Panamic biota, some observations prior to a sea-level canal* (*Bulletin of the Biological Society of Washington* 2): 217–227. Washington DC: Biological Society of Washington.
- Hershkovitz, P. 1951. Mammals from British Honduras, Mexico, Jamaica, and Haiti. *Fieldiana Zoology* 31: 547–569.
- Jansa, S.A., F.K. Barker, and R.S. Voss. 2014. The early diversification history of didelphid marsupials: a window into South America's "splendid isolation." *Evolution* 68: 684–695.

- Jenkins, P.D., and L. Knutson. 1983. A catalogue of the type specimens of Monotremata and Marsupialia in the British Museum (Natural History). London: British Museum (Natural History).
- Jiménez, Q., E. Carrillo, and M. Kappelle. 2016. The northern Pacific lowland seasonal dry forests of Guanacaste and the Nicoya Peninsula. In M. Kappelle (ed.), *Costa Rican ecosystems*: 247–289. Chicago: University of Chicago Press.
- Kappelle, M. 2016. *Costa Rican ecosystems*. Chicago: University of Chicago Press.
- Karr, J.R. 1990. The avifauna of Barro Colorado Island and the Pipeline Road, Panama. In A.H. Gentry (ed.), *Four Neotropical rainforests*: 183–198. New Haven: Yale University Press.
- Lambert, T.D., et al. 2011. First record of Alston's woolly mouse opossum (*Micoureus alstoni*) from the canal area of central Panama. *Mammalia* 75: 107–109.
- Matschie, P. 1916. Bemerkungen über die Gattung *Didelphis* L. *Sitzungsberichte der Gesellschaft Naturforschender Freunde (Berlin)*: 259–272.
- Myers, C.W. 1969. The ecological geography of cloud forest in Panama. *American Museum Novitates* 2396: 1–52.
- O'Dea, A., et al. [34 additional co-authors]. 2016. Formation of the Isthmus of Panama. *Science Advances* 2 (8): e1600883.
- Palmer, M.G. 1945. *Through unknown Nicaragua. The adventures of a naturalist on a wild-goose chase*. London: Jarrolds & Sons.
- 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.
- Paynter, R.A., Jr. 1997. *Ornithological gazetteer of Colombia*, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).
- Portig, W.H. 1965. Central American rainfall. *Geographical Review* 55: 68–90.
- Ramírez-Fernández, J.D., F.J. Durán, and M. Fernández-Vargas. 2020. First record of Tweedy's crab-eating rat, *Ichthyomys tweedii* Anthony, 1921 (Rodentia, Cricetidae, Sigmodontinae), for Costa Rica. *Check List* 16 (2): 435–440.
- Reid, F.A. 1997. *A field guide to the mammals of Central America and southeastern Mexico*. New York: Oxford University Press.
- Ridgway, R. 1912. *Color standards and color nomenclature*. Washington DC: Published by the author.
- Robinson, W.D., J.D. Brawn, and S.K. Robinson. 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs* 70: 209–235.
- 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.
- Santiago, L.S., and S.S. Mulkey. 2005. Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem. *Trees* 19: 349–356.
- Siegel, D.C., and S.L. Olson. 2008. *The birds of the Republic of Panama. Part 5. Ornithological gazetteer and bibliography*. Shipman, VA: Buteo Books.
- Stroud, J.T., and J.B. Losos. 2016. Ecological opportunity and adaptive radiation. *Annual Review of Ecology and Systematics* 47: 507–532.
- 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, folding tables.

- Thomas, O. 1905. New Neotropical *Chrotopterus*, *Sciurus*, *Neacomys*, *Coendou*, *Proechimys*, and *Marmosa*. *Annals and Magazine of Natural History* (ser. 7) 16: 308–314.
- Trouessart, E.-L. 1905. *Catalogus mammalium tam viventium quam fossilium*. Quinquennale supplementum (1899–1904). Cetacea, Edentata, Marsupialia, Allotheria, Monotremata. Berolini: R. Friedländer & Sohn.
- Velazco, P.M., and A.L. Gardner. 2012. A new species of *Lophostoma* d'Orbigny, 1836 (Chiroptera: Phyllostomidae) from Panama. *Journal of Mammalogy* 93: 605–614.
- Vencl, F.V., X. Luan, X. Fu, and L.S. Maroja. 2017. A day-flashing *Photinus* firefly (Coleoptera: Lampyridae) from central Panama: an emergent shift to predator-free space? *Insect Systematics and Evolution*. [doi 10.1163/1876312X-48022162]
- Voss, R.S., and S.A. Jansa. 2003. Phylogenetic studies of 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., 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.
- Wernstedt, F.L. 1972. *World climatic data*. Lemont, PA: Climatic Data Press.

APPENDIX 1

GAZETTEER OF EXAMINED SPECIMENS

This gazetteer includes all localities from which we personally examined specimens of the Alstoni Group of *Marmosa* (subgenus *Micoureus*). Italicized place names are those of currently recognized departments, provinces, or states; boldface identifies collection localities as they appear in the text of this report. 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. Numbers identify locality symbols plotted on our map (fig. 2).

COSTA RICA

1. *Cartago*, **Agua Caliente** [9.85° N, 83.93° W; VertNet database]: *Marmosa alstoni* (R. Torres, 15 December 1946).
2. *Cartago*, **Paso Ancho** [9.88° N, 84.07° W; DMA, 1983], ca. 4800 ft [1463 m]: *Marmosa alstoni* (C.F. Underwood, 23 December 1940).
3. *Cartago*, **Tres Ríos** [9.90° N, 83.98° W; DMA, 1983], 4000 ft [1219 m]: *Marmosa alstoni* (G.K. Cherrie, 17 August 1893).
4. *Puntarenas*, **Monteverde** [10.25° N, 84.77° W; Clark et al., 2000], 1300–1420 m: *Marmosa alstoni* (C.A. Langtimm, 15 February–1 December 1989; R.M. Timm, 11 May 2005).
5. *San José*, **Escazú** [9.92° N, 84.13° W; DMA, 1983], 3713 ft [1132 m]: *Marmosa alstoni* (C.F. Underwood, 26 July 1938–27 December 1941).
6. *San José*, **Los Higuerones** [not located, but said to be above Escazú; Goodwin, 1946], 4500 ft [1372 m]: *Marmosa alstoni* (C.F. Underwood, 20–22 October 1940).
7. *San José*, **Piedras Negras** [9.92° N, 84.32° W; DMA, 1983], 2056 ft [627 m]: *Marmosa alstoni* (C.F. Underwood, 6 October 1941).
8. *San José*, **San José** [9.93° N, 84.08° W; DMA, 1983], 3100 ft [945 m]: *Marmosa alstoni* (G.K. Cherrie, 15 October 1890; C.F. Underwood, 13 June 1938).
9. *San José*, **ca. 2 km NW Santa Ana** [9.95° N, 84.20° W; GBIF database], ca. 820 m (Gardner et al., 1970): *Marmosa alstoni* (A.L. Gardner, 6 June–8 August 1967).

NICARAGUA

10. *South Caribbean Coast Autonomous Region*, **Bluefields** [12.00° N, 83.75° W, at sea level; DMA, 1985]: *Marmosa nicaraguae* (M.G. Palmer, 9 January 1905).
11. *South Caribbean Coast Autonomous Region*, **Río Siquia** [presumably the stream near Rama at 12.15° N, 84.22° W, probably near sea level; DMA, 1985]: *Marmosa nicaraguae* (M.J. Allen, 7–14 September 1935).

PANAMA

12. *Bocas del Toro*, **Almirante** [9.30° N, 82.40° W, at sea level; Siegel and Olson, 2008]: *Marmosa adleri* (C.O. Handley, Jr., and D.I. Rhymer, 12 February 1960).

13. *Bocas del Toro*, Isla San Cristobal, **Bocatorito** [9.23° N, 82.27° W, at sea level; Siegel and Olson, 2008]: *Marmosa adleri* (F.M. Greenwell, 10–12 February 1989). Patton et al. (2000: fig. 51) mapped this locality in eastern Panama, approximately 500 km ESE of its true position.
14. *Colón*, Parque Nacional Soberanía, **Pipeline Road**, 1 km N Río Mendoza [9.17° N, 79.75° W, 120 m; Vencl et al., 2017]: *Marmosa adleri* (G.H. Adler and A. Carvahal, 14 January 2001).
15. *Darién*, **Cerro Malí** [8.12°N, 77.23°W; Siegel and Olson, 2008], including “Cerro Mali Camp,” 4700–4800 ft [1433–1463 m]: *Marmosa adleri* (R. Hinds, P. Galindo, and G.W. Barrett, 30 April 1963; C.O. Handley, Jr., 16 February 1964).
16. *Darién*, **Tacarcuna Casita Camp** [8.02°N, 77.37°W; Siegel and Olson, 2008], 2700 ft [823 m]: *Marmosa adleri* (C.O. Handley, Jr., and B.R. Feinstein, 26 January 1959).
17. *San Blas*, Armila, **Quebrada Venado** [ca. 8.67°N, 77.48°W, 30 m; Siegel and Olson, 2008]: *Marmosa adleri* (C.O. Handley, Jr., and F.M. Greenwell, 19–21 March 1963).

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