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A New Species of *Marmosops* (Marsupialia: Didelphidae) from the Pakaraima Highlands of Guyana, with Remarks on the Origin of the Endemic Pantepui Mammal Fauna

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ABSTRACT

A new species of the didelphid marsupial genus *Marmosops* is described from the Pakaraima Highlands of western Guyana and from two highland sites in eastern Venezuela. All known specimens were collected on sandstone table mountains (eroded fragments of the Roraima Formation) in the eastern subregion of Pantepui. The new species, *M. pakaraimae*, is one of only seven mammals known to be endemic to Pantepui, and phylogenetic analyses of cytochrome-*b* sequence data indicate that its sister taxon is *M. parvidens*, a geographically adjacent lowland species. Our results, together with those from phylogenetic studies of other Pantepui endemic mammals, suggest that at least some of these highland taxa evolved from lowland species in the late Cenozoic and are neither ancient relicts of tepui vicariance nor the descendents of long-distance-dispersing Andean progenitors.

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INTRODUCTION

The Pakaraima Highlands of western Guyana, including Mount Roraima (2810 m), Mount Ayanganna (2080 m), and Mount Wokomung (1585 m), are among the easternmost outliers of the Roraima Formation, remnants of an ancient plateau of Precambrian sandstone that are scattered like islands across hundreds of thousands of square kilometers in southern Venezuela (Mayr and Phelps, 1967; Huber, 1995a). The characteristic landforms of the Roraima Formation are steep-sided table mountains that rise dramatically from the surrounding lowlands. Known as *tepuis* in Venezuela, these iconic "lost worlds" harbor an extraordinarily rich endemic flora, the discovery and description of which were among the epic accomplishments of 20th-century Neotropical botany (Maguire, 1970; Huber, 1995b; Berry et al., 1995; Berry and Riina, 2005).

Collectively known as Pantepui, this geological archipelago also supports an endemic vertebrate fauna, of which the birds are relatively well known (Chapman, 1931; Mayr and Phelps, 1967; Cook, 1974). The dim outlines of an endemic Pantepui herpetofauna were perceived by Hoogmoed (1979), but only in the last few decades has the remarkable anuran and squamate endemism in this region become apparent (MacCulloch and Lathrop, 2002; McDiarmid and Donnelly, 2005; MacCulloch et al., 2006). By contrast with these groups, each of which includes dozens of tepui-restricted species, mammalian endemism in the region is unimpressive.

To date, only two didelphid marsupials (*Marmosa tyleriana*, *Monodelphis reigi*), one bat (*Platyrrhinus aurarius*), and three cricetid rodents (*Podoxomys roraimae*, *Rhipidomys macconnelli, R. wetzeli*) are known to be restricted to one or more tepuis and their skirting talus slopes (Tate, 1939; Handley, 1976; Gardner, 1989; Lim et al., 2005, 2010; Lim, 2012). To this short list can now be added a new species of the didelphid marsupial genus *Marmosops*, which we name and describe below. This species was recently collected on Royal Ontario Museum expeditions to the above-named peaks in the Pakaraima Highlands of western Guyana, but we subsequently identified two other specimens that had been collected many years ago in eastern Venezuela. Phylogenetic analyses that include DNA sequence data from our new species, together with analytic results from previous studies that included other Pantepui endemic mammals, shed new light on the historical origins of this small but zoogeographically distinctive fauna.

Materials and Methods

Morphology: The morphological specimens we examined and others mentioned below are preserved in the American Museum of Natural History (AMNH, New York), the Carnegie Museum (CM, Pittsburgh), the Field Museum (FMNH, Chicago), the Institut des Sciences de l'Evolution de Montpellier (ISEM, Montpellier), the Museum of Vertebrate Zoology (MVZ, Berkeley), the Museu de Zoologia da Universidade do São Paulo (MZUSP, São Paulo), the Royal Ontario Museum (ROM, Toronto), and the National Museum of Natural History (USNM, Washington).

We transcribed total length (nose to fleshy tail-tip, TL), length of tail (basal flexure to fleshy tip, LT), 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. We computed head-and-body length (HBL) by subtracting LT from TL, and we often remeasured HF on dried skins and fluid-preserved

TABLE 1. Primers used to amplify cytochrome *b.*

Name[a]	Sequence
CYTB-F1-Didelphidae	5′-TAACCTATGGCATGAAAAACCATTGTTG
CYTB-R1-Didelphidae	5′-CCTTCATTGCTGGCTTACAAGGC
CYTB-R2-Didelphidae	5′-GGACTAACACCCTACCATCAACACCCA
CYTB-400F-*Marmosops*	5′-CCATGAGGACAAATATCATTCTGAGG
CYTB-420F-*Marmosops*	5′-TGAGGACAGATATCATTTTGAG
CYTB-610R-*Marmosops*	5′-GTCCACCTCTTATTCCTCCATGAAAC
CYTB-620R-*Marmosops*	5′-TATTCCTACATGAAACAGGATC
CYTB-670R-*Marmosops*	5′-GACAAAATCCCATTCCATCCTTACTA
CYTB-421F-*parvidens*	5′-GAGGGGCTACAGTTATTACCAACC
CYTB-566F-*parvidens*	5′-CTAAGCCTTAGTCATCGTTCACC
CYTB-421R-*parvidens*	5′-GAGGGGCTACAGTTATTACCAACC

[a] Naming conventions follow Giarla et al. (2010: appendix 2).

specimens to check the accuracy of values recorded by the collector (using 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 as specimens were viewed at low magnification (6× to 12×) under a binocular microscope. We recorded craniodental measurements and computed sample statistics to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm (the smallest unit that can be repeatably obtained with calipers). The following dimensions were recorded as illustrated by Giarla et al. (2010: fig. 2): condylo-basal length (CBL), measured from the occipital condyles to the anteriormost point of the premaxillae; nasal length (NL), the greatest anteroposterior dimension of either bone; nasal breadth (NB), measured between the triple-point sutures of the nasal, frontal, and maxillary bones on each side; least interorbital breadth (LIB), measured at the narrowest point across the frontals between the orbits; least postorbital breadth (LPB), measured at the narrowest point across the frontals between the temporal fossae[4]; zygomatic breadth (ZB), measured at the widest point across both zygomatic arches; palatal length (PL), measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present); palatal breadth (PB), measured across the labial margins of the M4 crowns, at or near the stylar A position; maxillary toothrow length (MTR), measured from the anterior margin of C1 to the posterior margin of M4; length of 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

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[4] In effect, LPB (not illustrated by Giarla et al., 2010) is the width of the posteriormost of two frontal constrictions that sometimes exist simultaneously between the orbitotemporal fossae of small didelphids.

TABLE 2. Specimens of *Marmosops* sequenced for this report.

Species	Tissue[a]	Voucher[b]	Locality[c]	bp[d]
Ingroup				
pakaraimae	F46739	ROM 115129[e]	Guyana: Cuyuni-Mazaruni (14)	1149
pakaraimae	F47080	ROM 115841[e]	Guyana: Potaro-Siparuni (20)	1149
pakaraimae	F46454	ROM 114698[e]	Guyana: Potaro-Siparuni (19)	1149
parvidens	LHE 1161	AMNH 267817[e]	French Guiana (11)	1149
parvidens	ISEM T-3832	ISEM V-1633[e]	French Guiana (10)	645
parvidens	FN33439	ROM 97938[e, f]	Guyana: Upper Takutu-Upper Essequibo (21)	645
parvidens	F41219	ROM 114144[e]	Surinam: Brokopondo (22)	1149
parvidens	F54669	ROM 117348[e]	Surinam: Sipaliwini (27)	1149
pinheiroi		USNM 545543[e]	Brazil: Pará (5)	421
pinheiroi	MDC589	USNM 549294[e]	Brazil: Pará (4)	1149
pinheiroi	F43900	ROM 108920[e]	Guyana: Potaro-Siparuni (17)	1149
pinheiroi	TK10169	CM 63506[e]	Surinam: Nickerie (25)	1149
pinheiroi	F54337	ROM 116974[e]	Surinam: Sipaliwini (26)	1149
Outgroups				
incanus	MAM 186	MZUSP 29173[e]	Brazil: Rio de Janeiro (8)	1149
paulensis	JLP 16216	MVZ 183243	Brazil: São Paulo (9)	1149

[a] Sequences amplified from skins lack entries in this column.

[b] See Materials and Methods for explanation of museum acronyms.

[c] Numbers in parentheses refer to localities mapped in figure 1 and listed in the gazetteer (appendix).

[d] Number of base pairs sequenced.

[e] Examined by the authors.

[f] A partial cytochrome-*b* sequence from this specimen (accessioned as AJ606424.1 in GenBank) was published by Steiner and Catzeflis (2004), who incorrectly associated it with field number FN33449 (= ROM 97948, a phyllostomid bat).

lingual apex of the protocone. In addition, we measured height of upper canine (HC), from the posterior accessory cusp to the apex of this tooth using an ocular micrometer.

Following Voss et al. (2001), a specimen was judged to be juvenile if the deciduous third upper premolar (dP3) is still in place; subadult if dP3 has been shed but P3 is still incompletely erupted; and adult if the permanent dentition is complete. Except as noted otherwise below, 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 (Tate, 1933). 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, cream, or buffy. Capitalized color terminology is from Ridgway (1912).

Molecular methods: The methods we used to extract DNA from preserved tissues and museum skins were described by Voss and Jansa (2009) and Giarla et al. (2010), respectively. Whenever possible, we amplified the entire mitochondrial cytochrome-*b* gene (CYTB) in two

TABLE 3. *Marmosops* sequences downloaded from GenBank.[a]

Species	GenBank #	Voucher	Locality	bp
parvidens	AJ606425.1	ISEM V-1399	French Guiana (11)	800
parvidens	AJ606426.1	ISEM V-1581	French Guiana (11)	800
parvidens	AJ606423.1	MNHN 1998-1830	French Guiana (13)	800
parvidens	AJ606429.2	ROM 114299[b]	Surinam: Brokopondo (22)	755
parvidens	AJ606427.1	ROM 114322[b]	Surinam: Brokopondo (22)	773
pinheiroi	AJ606430.1	ISEM V-955	French Guiana (10)	800
pinheiroi	AJ606433.1	ROM 111558[b]	Guyana: Potaro-Siparuni (18)	799
pinheiroi	AJ606432.1	ROM 114318[b]	Surinam: Brokopondo (22)	800

[a] Deposited by Steiner and Catzeflis (2004), who used field numbers (prefixed by F or FN) as specimen identifiers for all of the ROM-vouchered sequences they obtained.

[b] Examined by the authors.

overlapping fragments using the primers listed in table 1. For two specimens we were able to amplify only the first half of CYTB (645 bp); in one case—where we extracted poor-quality DNA from a skin sample (USNM 545543)—we obtained only a short fragment of 421 bp. The amplification and sequencing methods we used have been described elsewhere (Gutiérrez et al., 2010), with the only difference that our four-stage touchdown protocol during amplifications had annealing temperatures of 61, 59, 57 and 55° C. Sequences were edited and compiled using Sequencher v4.8 (Gene Codes Corporation, 2007); only those with unambiguous base calls and open reading frames were used for phylogenetic analyses. The 15 new sequences obtained for this study (table 2) have been deposited in GenBank (with accession numbers KC954758–KC954772), from which we downloaded an additional eight sequences that we also used in the analyses reported below (table 3).

Phylogenetic assumptions: We assume the monophyly of an ingroup comprising *Marmosops parvidens*, *M. pinheiroi*, and our new species based on uniquely shared morphological characters (see below) and on unpublished phylogenetic analyses of mitochondrial and nuclear DNA sequences from a much larger revisionary study of the genus *Marmosops* (Díaz-N. et al., in preparation). Based on those analyses, we selected exemplar sequences of two southeastern Brazilian species (*M. incanus* and *M. paulensis*) to serve as outgroups for the current study.

Phylogenetic analyses: DNA sequences were aligned with MUSCLE in Geneious® Pro 5.6.3 (available from http://www.geneious.com/). The resulting matrix was analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Missing bases were coded as unknown characters in all analyses. We implemented MP analyses in PAUP* 4.0 (Swofford, 2002) using branch-and-bound (bandb) searches with default settings, and nodal support was assessed by bootstrap analysis of 1000 pseudoreplicated datasets under "bandb" search. For the model-based analyses (ML and BI), GTR+Γ+I was the best-fit model as determined by the Akaike Information Criterion in jModelTest (Posada, 2008). We conducted ML analyses in GARLI 2.0 (Zwickl, 2006) with the default options suggested for small data sets (i.e., attachmentspertaxon = 50, genthreshfortopoterm

= 5000, numberofprecreductions = 5). To ensure that the program found a stable topology and stable lnL value we performed five independent searches. For the ML analysis, nodal support was also evaluated based on bootstrap analyses of 1000 pseudoreplicated datasets with the same search parameters as the original ML search. Bayesian analyses were implemented in MrBayes v3.2.1 (Ronquist and Huelsenbeck, 2003) by running two independent Markov Chain Monte Carlo (MCMC) analyses for 1×10^6 generations each, sampling every 100 generations and including one cold chain and three heated chains. The results of the MCMC runs were inspected in Tracer v1.5 (Rambaut and Drummond, 2009) and AWTY (Nylander et al., 2008) to ensure convergence of the parameters. We discarded the first 50% of trees from each run and combined the remaining samples (10,000 trees) to estimate tree topology, mean lnL value, and posterior probabilities. We used MEGA5 (Tamura et al., 2011) to calculate average uncorrected *p*-distances and model-corrected K2P distances (the latter were computed for comparisons with previous molecular systematic work on *Marmosops*; e.g., Mustrangi and Patton, 1997).

RESULTS

Marmosops pakaraimae, new species

Figures 2–6

Holotype: The holotype (ROM 115129; original number F46739) consists of the skin, skull, postcranial skeleton, and preserved tissues of an adult male collected by Burton K. Lim and Deirdre M. Jafferally on 26 February 2003 at “Second Camp” (5°17′N, 60°45′W, 800 m above sea level) on Mount Roraima, Cuyuni-Mazaruni Region, Guyana.

Distribution: Known from five localities, of which three are in the Pakaraima Highlands of western Guyana and two are in the adjacent highlands of eastern Venezuela (fig. 1). Recorded elevations at these localities range from 800 to about 1500 m above sea level.

Description: A small species of *Marmosops* (measurements in table 4) with all the diagnostic qualitative traits of the genus (Voss and Jansa, 2009: 134–137). Body pelage dark brown (near Dark Umber) middorsally but indistinctly paler laterally; superficially whitish ventrally (the ventral coloration contrasting abruptly with the brownish flanks), but hairs of throat, chest, and abdomen uniformly gray-based (only the apex of the chin, the oral margins, and the scrotum have self-white fur). Gular gland apparently absent. Manus covered dorsally with pale hairs in some specimens (e.g., ROM 114698), but metacarpals distinctly darker than digits in others (e.g., ROM 115129); lateral carpal tubercles large and spoon shaped (Voss et al., 2001: fig. 20) in all examined adult males; forearm with both proximal and distal antebrachial vibrissae (Díaz-N. et al., 2011: fig. 5b). Mammary formula unknown (no female specimens examined). Scrotal epithelium unpigmented and covered with short self-white hairs. Hind foot covered dorsally with pale hairs; hypothenar and fourth interdigital plantar pads separate (with discontinuous dermatoglyphs; Díaz-N. et al., 2011: fig. 4B). Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 150%), dorsal surface dark (probably grayish in life) from base to tip, but ventral surface indistinctly paler (especially near the base).

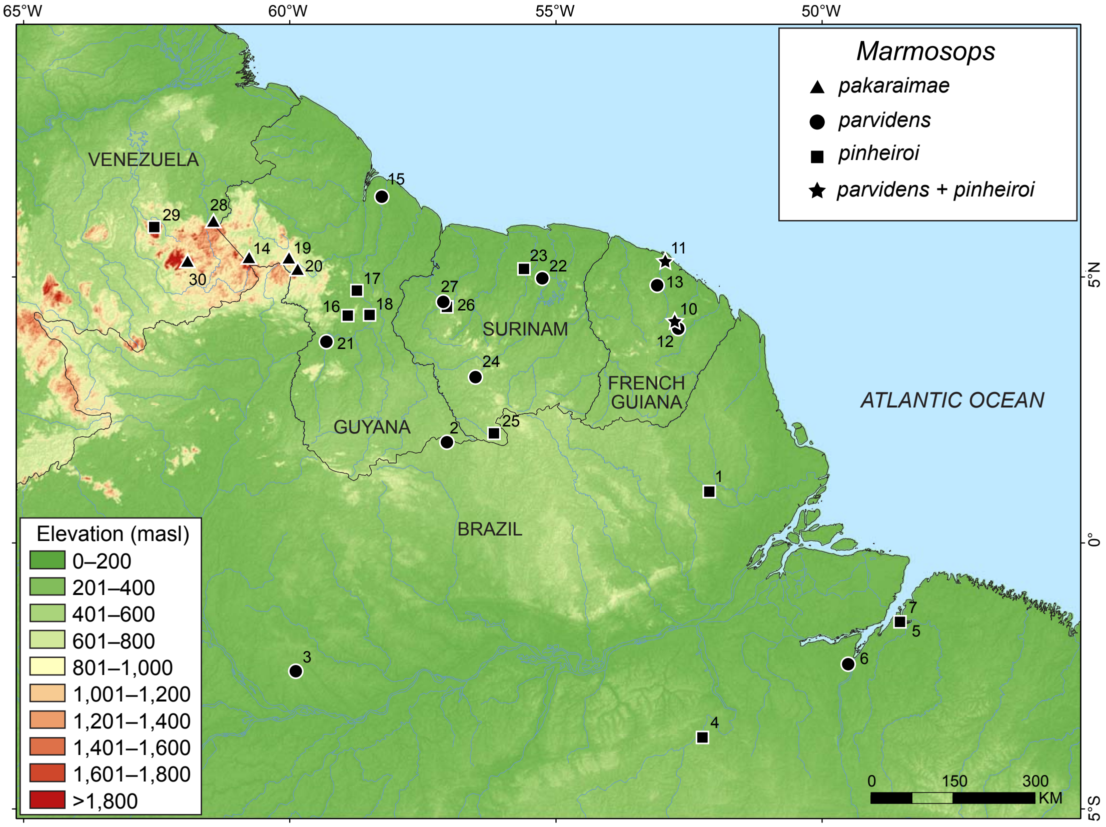

FIG. 1. Collecting localities of examined specimens of *Marmosops pakaraimae*, *M. parvidens*, and *M. pinheiroi*. Numbers are keyed to entries in the gazetteer (appendix).

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly. Interorbital region very broad, the supraorbital margins rounded (without distinct beads); postorbital processes absent. Lacrimal foramina concealed from lateral view inside anterior orbital margin; fenestra in squamosal-parietal suture consistently present and large; subsquamosal foramen anteroposteriorly elongated (exposing the petrosal well behind the sulcus for the prootic sinus; Díaz-N. et al., 2011: fig. 6B). Premaxillary rostral process long and well developed; incisive foramina short, not extending posteriorly behind canines; palatine fenestrae absent.

Upper canine (C1) short, with both anterior and posterior accessory cusps. Second upper premolar (P2) slightly but consistently taller than third upper premolar (P3); P3 oblique (not in line with C1–P2, its anterior base lingual to the posterior base of P2). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to lower first premolar (p1); anterolingual accessory cusp (Díaz-N. et al., 2011: fig. 9B) absent. Unworn fourth lower molar (m4) talonid with three distinct cusps (hypoconid, hypoconulid, and entoconid).

TABLE 4. Measurements (mm) and weights (g) of adult specimens of *Marmosops pakaraimae.*

	Guyana[a]						Venezuela[b]
	114698♂	115129♂	115148♂	115254♂	115841♂	115845♂	385046♂
HBL	107	110	112	116	105	104	112
LT	163	164	163	167	151	169	152
HF	18	18	19	19	17	18	19
Ear	22	22	22	23	22	22	23
CBL	30.5	31.2	31.9	31.7	29.8	30.3	30.1
NL	15.2	—	—	—	14.3	14.7	14.2
NB	3.7	3.8	3.9	4.0	3.5	3.8	3.8
LIB	6.1	6.1	6.1	6.2	5.8	6.0	6.1
LPB	6.0	6.0	6.1	6.4	6.2	6.4	6.6
ZB	15.2	15.5	15.3	15.7	14.8	14.9	15.0
PL	17.3	17.6	17.9	17.6	16.5	17.2	17.2
PB	9.0	9.4	9.0	9.3	8.2	8.8	8.7
MTR	12.0	12.3	12.5	12.6	12.0	12.1	11.9
LM	6.0	6.0	6.0	6.3	6.0	6.2	6.0
M1–3	5.3	5.2	5.2	5.4	5.2	5.3	5.2
WM3	2.1	2.1	2.0	2.0	2.0	2.0	2.0
HC	1.2	1.3	1.2	1.2	1.3	1.3	—
Weight	30	33	30	32	25	31	—

[a] All Guyanese specimens are at the ROM.

[b] At the USNM.

Morphological comparisons: *Marmosops pakaraimae* closely resembles *M. parvidens* and *M. pinheiroi*, both of which also occur in the Guiana Region (north of the Amazon and east of the Orinoco-Rio Negro; Voss et al., 2001: fig. 98). These three species share many qualitative morphological traits including (1) small size, (2) spoon-shaped lateral carpal tubercles in adult males, (3) two antebrachial vibrissae, (4) an anteroposteriorly elongated subsquamosal foramen, (5) no palatine fenestrae, (6) upper canines with both anterior and posterior accessory cusps, (7) P2 slightly but consistently larger than P3, and (7) a premolariform c1 that is subequal in height to p1. Although some of these traits occur in other congeneric species (Voss et al., 2001; Voss and Jansa, 2009; Díaz-N. et al., 2011), no extralimital (non-Guianan) species of *Marmosops* exhibits all of them, and spoon-shaped lateral carpal tubercles seem to occur uniquely in these three taxa. Additionally, we recovered this species triplet as a strongly supported monophyletic group in a multigene phylogenetic analysis of the entire genus (Díaz-Nieto et al., in prep.), so diagnostic morphological comparisons (summarized in tables 5 and 6) are appropriately restricted to just these forms.

Marmosops pakaraimae averages larger than *M. parvidens* in all measured external dimensions except ear length (table 5), and the two species differ strikingly in dorsal pelage coloration

FIG. 2. Dorsal views of skins. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (ROM 114144), *M. pinheiroi* (ROM 111558). Approximately life size.

(dark brown in *pakaraimae* versus a paler, somewhat dusty reddish-brown in *parvidens*; fig. 2). The difference in ventral pelage coloration (fig. 3) is even more striking: whereas *pakaraimae* has almost completely gray-based ventral fur, all examined specimens of *parvidens* have a continuous streak of self-whitish fur that extends from chin to groin. *Marmosops pakaraimae* is consistently larger than *M. parvidens* in all measured craniodental dimensions, especially in five variables (CBL, LIB, LPB, MTR, LM) that exhibit nonoverlapping variation between our all-male samples of these species (no female specimens of *pakaraimae* are known). Side-by-side comparisons of representative skulls (figs. 4–6) reveal that *pakaraimae* has a visibly broader interorbital region but relatively smaller orbits than *parvidens*. In qualitative aspects of craniodental morphology, however, these species are notably similar, both having lacrimal foramina that are mostly concealed from lateral view inside the anterior orbital margin (Voss et al., 2001:

FIG. 3. Ventral views of skins. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (ROM 114144), *M. pinheiroi* (ROM 111558). Approximately life size.

fig. 25A), short upper canines, upper third molars with narrowly complete anterior cingula, and tricuspid m4 talonids.

Marmosops pakaraimae also averages larger than *M. pinheiroi* in external dimensions (except ear length), and the two species differ in dorsal pelage color (dark brown in *pakaraimae* versus paler brownish-gray in *pinheiroi*). The ventral fur of *pakaraimae* is also more extensively gray-based than the ventral fur of *pinheiroi*, which usually includes a narrow, discontinuous midventral streak of self-white hairs. *Marmosops pakaraimae* is also larger on average than *M. pinheiroi* in craniodental measurements, especially in three dimensions (LIB, LPB, and LM) that exhibit nonoverlapping variation in our samples. Visual comparisons of representative skulls (figs. 4–6) reveal similar proportional differences between *pakaraimae* and *pinheiroi* to those previously noted between *pakaraimae* and *parvidens*, namely that *pakaraimae* has a

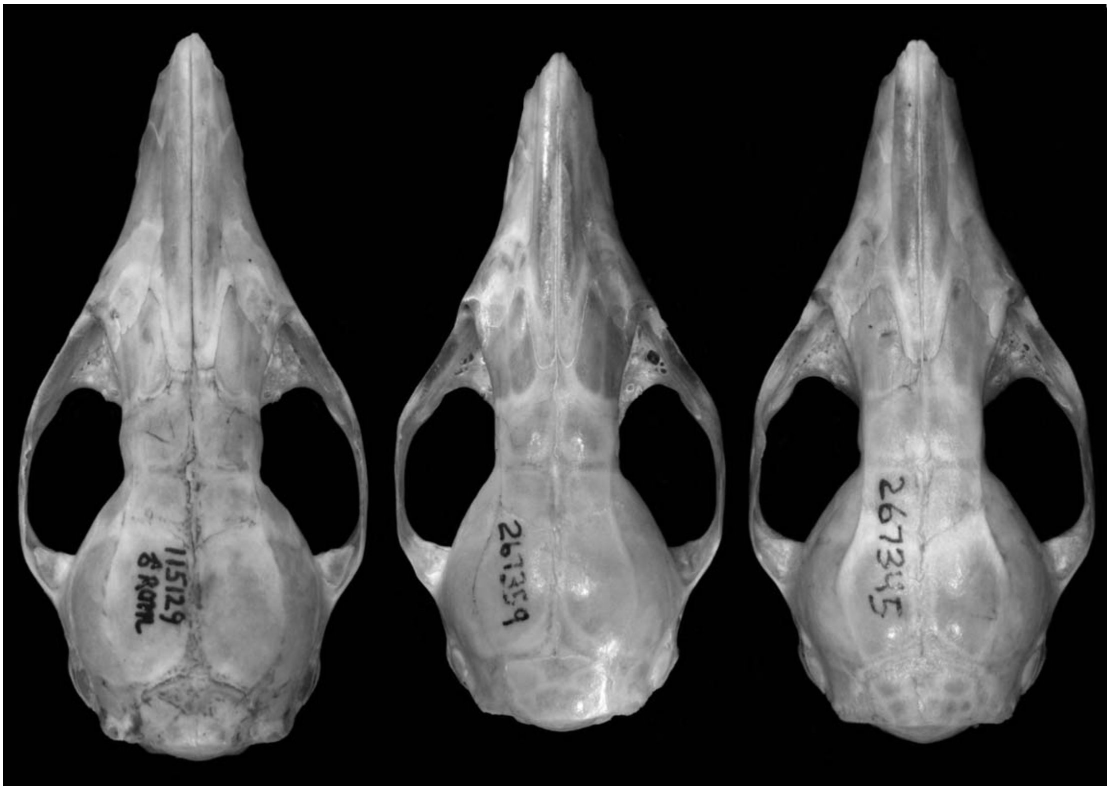

FIG. 4. Dorsal views of skulls. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

broader interorbit but smaller orbits. Unlike *pakaraimae* and *parvidens*, the lacrimal foramina are more prominently exposed laterally (Voss et al., 2001: fig. 25B), C1 is taller, M3 never has a complete anterior cingulum, and m4 usually has a bicuspid talonid in *pinheiroi*.

Remarks: Of the six Venezuelan specimens that Voss et al (2001: 50) identified as *Marmosops pinheiroi*, two can confidently be reidentified as *M. pakaraimae* based on the diagnostic criteria explained above; one of these is AMNH 176353 (from ca. 1500 m on Churi-tepui) and the other is USNM 385046 (from 1032 m in the Sierra de Lema). Two other specimens appear to be good examples of *M. pinheiroi*; both of these (AMNH 130568, 130570) are from 460 m at the base of Auyán-tepui. The remaining specimens (AMNH 130521, from 1100 m on Auyán-tepui; and AMNH 176352, apparently from the lower slopes of Churi-tepui) might be *M. pakaraimae* but have slightly shorter molar rows and somewhat narrower interorbits than our Guyanese material, and we are not confident of this identification.

Pine (1981: 62) reported two specimens that he identified as *Marmosa parvidens pinheiroi* from 85 km SSE El Dorado, Bolívar, Venezuela. One of these is USNM 385046, a paratype of *Marmosops pakaraimae*, but we were not able to examine the other specimen (USNM 385045), which has been returned to Venezuela and is now in the Museo de la Estación Biológica de Rancho Grande in Maracay (where it has been recataloged as EBRG 3945). Although we

TABLE 5. Summary statistics for measurements (mm) and weights (g) of adult male specimens of three *Marmosops* species.

	M. pakaraimae[a]	*M. parvidens*[b]	*M. pinheiroi*[c]
HBL	109 (104–116) 7	100 (93–107) 10	101 (85–121) 12
LT	161 (151–169) 7	150 (142–160) 10	150 (142–160) 12
HF	18 (17–19) 7	16 (15–17) 10	17 (16–18) 12
Ear	22 (22–23) 7	22 (21–24) 9	22 (20–25) 12
CBL	30.8 (29.8–31.9) 7	28.3 (27.3–29.1) 9	29.1 (28.4–29.8) 12
NL	14.6 (14.2–15.2) 4	13.7 (12.7–14.4) 9	14.1 (13.2–14.7) 11
NB	3.8 (3.5–4.0) 7	3.4 (2.9–3.6) 12	3.7 (3.1–4.2) 12
LIB	6.0 (5.8–6.2) 7	5.3 (4.9–5.5) 11	5.4 (5.2–5.7) 12
LPB	6.2 (6.0–6.6) 7	5.5 (5.2–5.7) 11	5.6 (5.2–5.9) 11
ZB	15.2 (14.8–15.7) 7	14.5 (13.9–15.0) 10	15.1 (14.6–16.0) 12
PL	17.3 (16.5–17.9) 7	16.00 (15.00–16.8) 10	16.3 (16.0–16.7) 11
PB	8.9 (8.2–9.4) 7	8.3 (8.0–8.7) 12	8.6 (8.2–8.9) 12
MTR	12.2 (11.9–12.6) 7	11.2 (11.0–11.6) 11	11.6 (11.3–12.0) 12
LM	6.1 (6.0–6.3) 7	5.5 (5.3–5.7) 12	5.7 (5.6–5.9) 12
M1–3	5.2 (5.2–5.4) 7	4.8 (4.6–5.2) 12	5.0 (4.8–5.2) 12
WM3	2.0 (2.0–2.1) 7	1.9 (1.8–2.0) 12	1.9 (1.8–2.0) 12
HC	1.2 (1.2–1.3) 6	1.2 (1.1–1.3) 11	1.4 (1.3–1.4) 9
Weight	30 (25–33) 6	25 (21–31) 9	27 (22–33) 12

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the type series (ROM 114698, 115129, 115148, 115254, 115841, 115845; USNM 385046).

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 93970, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-930, 1995-933; ROM 114144, 117348; and USNM 579989.

[c] The mean, the standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 266423, 267341, 267342, 267345, 267346, 267349, 267352, 267357; CM 63506; FMNH 95320; MNHN 1995-931, 1995-932; ROM 108920, 111558, 111663; USNM 461459, 461460, and 461462–461465.

assume that USNM 385045 is another example of *M. pakaraimae*, we are not currently able to confirm this identification personally.

Natural history: All of our Guyanese specimens of *Marmosops pakaraimae* were live-trapped at or near (< 2 m above) ground level in primary evergreen premontane forest. In the physiognomically defined classification of Grubb (1977), the dominant vegetation at these capture sites shares characteristics with both Lowland Rain Forest and Lower Montane Rain Forest (fig. 7): most (but not all) trees were unbuttressed, vascular epiphytes were sometimes (but not always) abundant, and thick-stemmed woody climbers (lianas) were infrequent but not completely absent. An abundant leaf litter was present, and tree trunks, roots, and boulders were often covered with moss. Soils were waterlogged at some sites and the canopy was more open

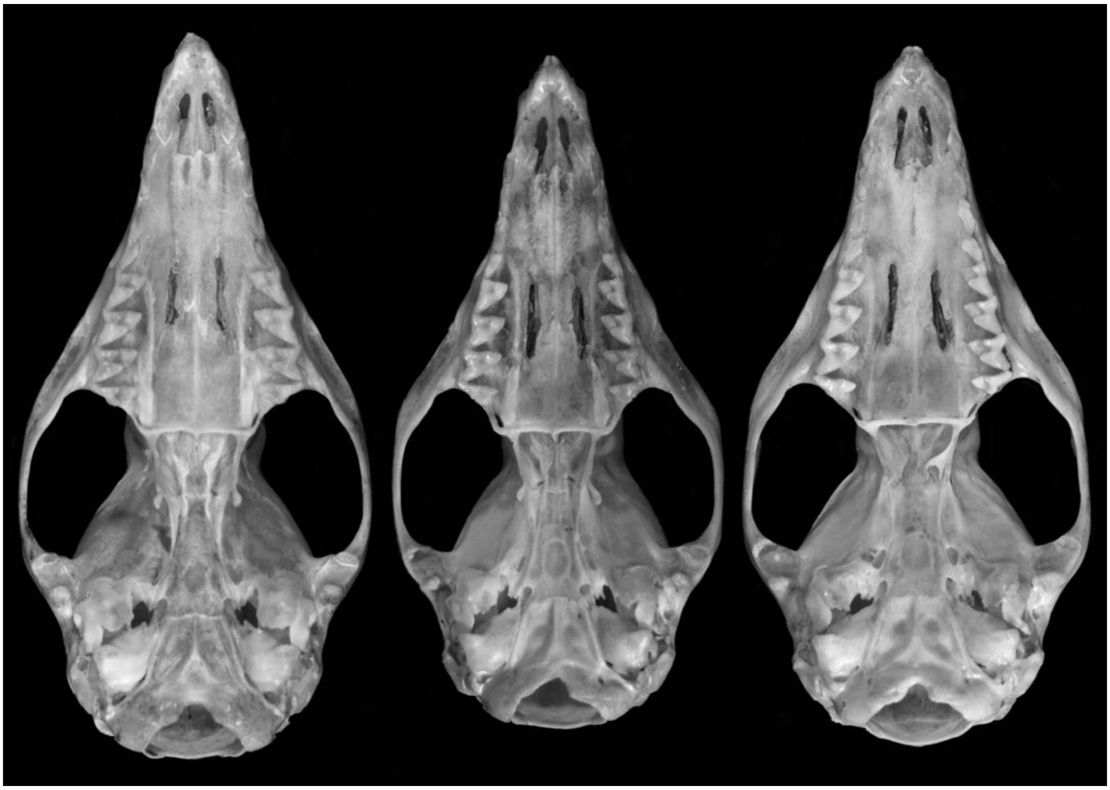

FIG. 5. Ventral views of skulls. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

than is commonly the case in primary forest at lower elevations; most of the trees were of moderate height (ca. 20 m tall). One specimen of *M. pakaraimae* was taken on the inclined trunk of a tree, but the rest were trapped on more or less horizontal surfaces.

According to Handley (1976: 74–75), the natural vegetation at 85 km SSE El Dorado (in the Sierra de Lema of eastern Venezuela) was "[d]ense, moist, luxuriant [premontane] forest (12–24 m high) ... festooned with orchids, ferns, mosses, and other epiphytes." The ground at this locality was described as wet and rocky, "with little cover except for abundant moss-covered boulders and fallen trees." The specimen tag attached to the skin of USNM 385046 bears the inscription "Live trap in forest on ground." No habitat information accompanies the specimen from Churi-tepui.

SPECIMENS EXAMINED: *Marmosops pakaraimae* (*N* = 8): **Guyana**—*Cuyuni-Mazaruni,* Mt. Roraima (ROM 115129, 115148, 115254); *Potaro-Siparuni,* Mt. Ayanganna (ROM 114698), Mt. Wokomung (ROM 115841, 115845). **Venezuela**—*Bolívar,* 85 km SSE El Dorado (USNM 385046), Churi-tepui (AMNH 176353).

Marmosops parvidens (*N* = 24): **Brazil**—*Amazonas,* Boca Rio Paratucu (AMNH 93970), 80 km N Manaus (USNM 579985–579989); *Pará,* Ilha do Taiuna (AMNH 97333). **French Guiana**—Paracou (AMNH 267344, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-933, 1995-939), River Arataye (USNM 548439). **Guyana**— *Demerara-Mahaica,* Hyde

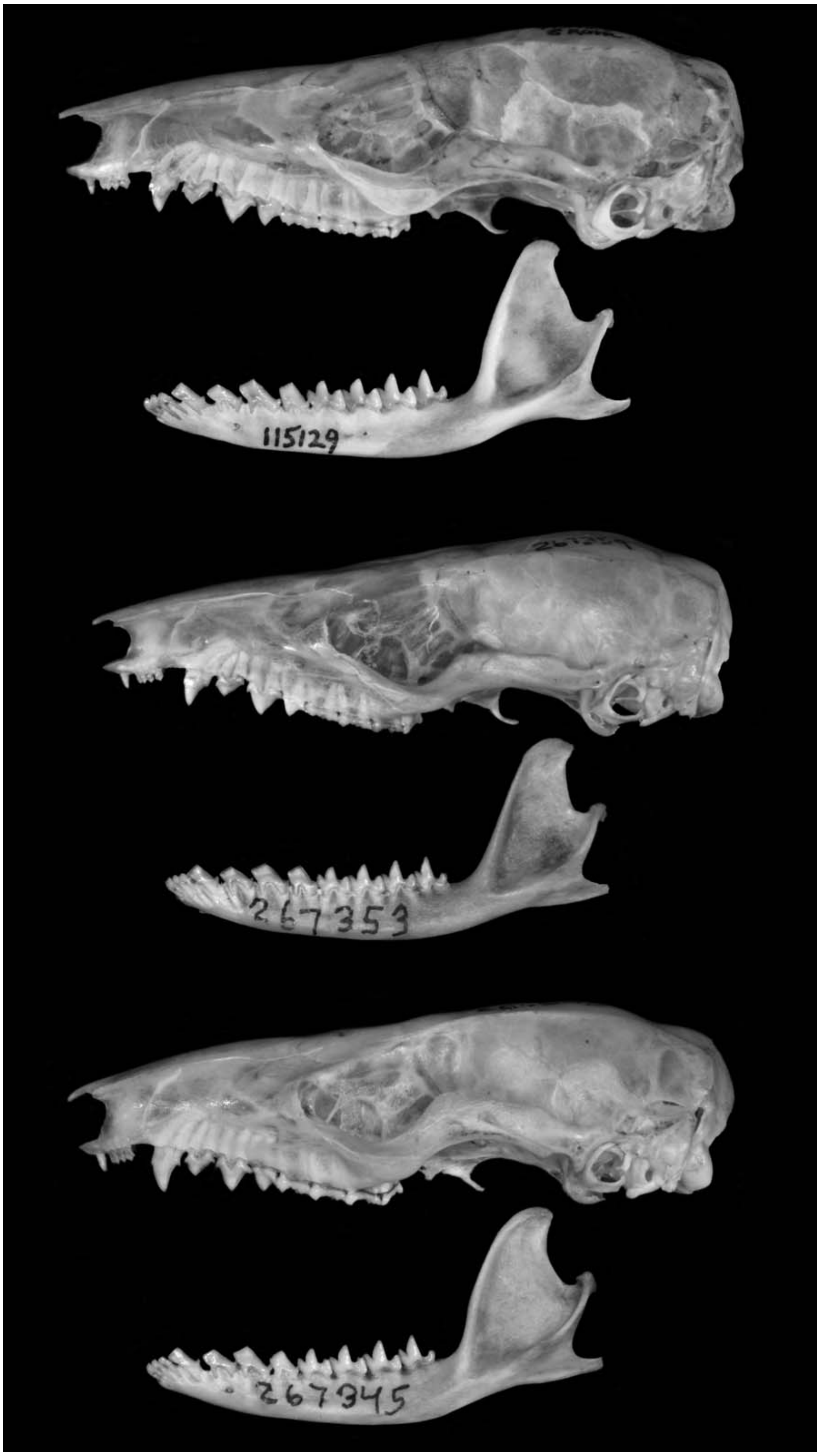
115129
267353
267345

FIG. 7. Forest vegetation at three Guyanese capture sites of *Marmosops pakaraimae*. **Top**, Mount Roraima, Third Camp (1000 m); **bottom left**, Mount Roraima, Second Camp (800 m); **bottom right**, Mount Ayanganna, First Plateau Camp (1100 m). Photos by Francis X. Faigal (Royal Ontario Museum).

(LEFT) FIG. 6. Lateral views of skulls. Top to bottom: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359 [skull], 267353 [mandible]), and *M. pinheiroi* (AMNH 267345). All views about ×3.

TABLE 6. Diagnostic morphological comparisons among three species of *Marmosops.*

Character	*pakaraimae*	*parvidens*	*pinheiroi*
Dorsal fur color	dark brown	paler, usually reddish brown	paler, usually grayish brown
Ventral fur	gray-based	mostly self-white (or -cream)	mostly gray-based, but variable
Lacrimal foramina	concealed inside orbit	concealed inside orbit	laterally exposed anterior to orbit
M3 anterior cingulum	narrowly complete	narrowly complete	incomplete
m4 talonid	tricuspid	tricuspid	often bicuspid

Park (FMNH 18545 [holotype]), *Upper Takutu-Upper Essequibo,* Karanambo (ROM 97938). **Surinam**—*Brokopondo,* Brownsberg Nature Park (ROM 113997, 114009, 114144); *Nickerie,* Kayser Gebergte Airstrip (FMNH 93169); *Sipaliwini,* Bakhuis Transect 13 (ROM 117348).

Marmosops pinheiroi (*N* = 32): **Brazil**—*Amapá,* Serra do Navio (USNM 461459 [holotype], 461460, 461462–461465); *Pará,* 52 km SSW Altamira (USNM 549294), Belém (USNM 545543), Utinga (USNM 393529–393532, 393534). **French Guiana**—Paracou (AMNH 266423, 267341, 267342, 267345, 267346, 267349, 267352, 267357; MNHN 1995-931, 1995-932). **Guyana**—*Potaro-Siparuni,* Canopy Walkway (ROM 119852), 10 km NW Kurupukari (ROM 108920), Kabukalli Landing (ROM 111558, 111663). **Surinam**—*Brokopondo,* Finisanti (FMNH 95320); *Nickerie,* Sipaliwini Airstrip (CM 63506); *Sipaliwini,* Bakhuis Transect 9 (ROM 116974). **Venezuela—***Bolívar,* Auyántepui (AMNH 130568, 130570).

Phylogenetic Analysis

We aligned 21 ingroup and 2 outgroup cytochrome-*b* sequences ranging in length from 421 to 1149 bp, resulting in a data matrix that contained 17.9% missing entries. There is no significant departure from base-compositional stationarity among individuals in these data ($\chi^2 = 36.764$, $df = 66$, $P = 0.999$). The five maximum-likelihood replicates produced identical topologies and lnL values (-4100.189), maximum-parsimony analysis produced 312 equally short trees (each of 579 steps), and Bayesian analysis produced a posterior distribution that converged on a single optimum topology (as evidenced by the "compare" plot of AWTY) with mean lnL value of -4133.336. All of these analyses yielded congruent topologies, of which we present the Bayesian maximum-credibility tree (fig. 8) with accompanying nodal support statistics from all three methods.

All three species of *Marmosops* recognized on the basis of morphology in this report were recovered as robustly supported clades, and a sister-group relationship between *M. pakaraimae* and *M. parvidens* was also strongly supported. Uncorrected mean sequence divergence within each of these species ranges from 0.1% (in *M. pakaraimae*) to 3.3% (in *M. pinheiroi*), whereas uncorrected mean interspecific distances range from 6.9% (between *M. pakaraimae* and *M. parvidens*) to 12.1% (between *M. parvidens* and *M. pinheiroi*; table 7). Some relatively shallow and weakly supported phylogeographic structure can be seen within *M. pakaraimae* and *M.*

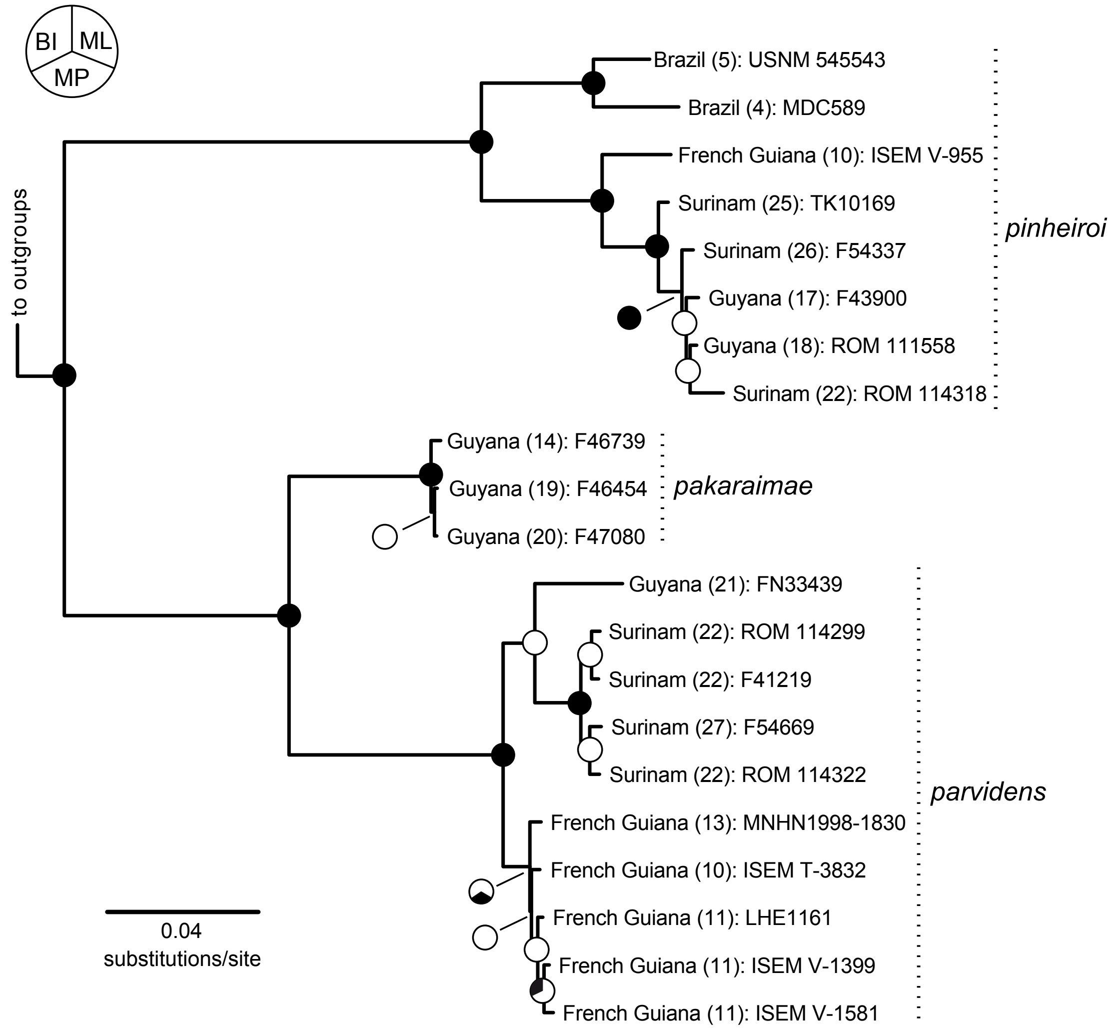

FIG. 8. Bayesian phylogeny of ingroup terminals (maximum-likelihood and parsimony analyses resulted in congruent topologies). Pie diagrams at internal nodes represent support from BI, ML, and MP analyses, with filled wedges corresponding to high support (posterior probabilities ≥ 0.95, bootstrap ≥ 0.75%). Each terminal is identified by country of origin and an alphanumeric specimen identifier (from tables 2 or 3). Numbers in parentheses refer to localities mapped in figure 1 and listed in the gazetteer (appendix).

parvidens, but analyzed sequences of *M. pinheiroi* were recovered as strongly supported haplotype groups representing samples collected north and south of the lower Amazon.

DISCUSSION

All known specimens of *Marmosops pakaraimae* are associated with premontane or montane habitats on eroded fragments of the Roraima Formation. These include the three Guyanese massifs mentioned in the Introduction (Mt. Ayanganna, Mt. Roraima, Mt. Wokomung)

TABLE 7. Matrix of genetic distances within and among three species of *Marmosops*.[a]

	pakaraimae	*parvidens*	*pinheiroi*
pakaraimae	**0.1**	7.5	12.6
parvidens	6.9	**1.6**	13.9
pinheiroi	11.2	12.1	**3.3**

[a] Average uncorrected (*p*-) distances (percent sequence divergence) among conspecific sequences are along the diagonal, interspecific *p*-distances are below the diagonal, and Kimura two-parameter (K2P) distances are above the diagonal.

together with two others (Sierra de Lema and Churi-tepui) in Venezuela. All belong to the eastern subdivision of Pantepui, comprising those highlands that occur east of the Río Caroní (Mayr and Phelps, 1967: 287, map 1). Of the other six mammalian species known to be endemic to Pantepui (table 8), none is known to have the same distribution as *M. pakaraimae*, although *Monodelphis reigi* and *Podoxomys roraimae* are similarly restricted to highlands of the eastern subdivision.

Mayr and Phelps (1967) considered several possible explanations for the spatiotemporal origin of tepui-restricted birds including (1) the Plateau (or "Lost World") Theory, which holds that Pantepui species are ancient relicts of a formerly continuous plateau biota now isolated on tepuis by geological vicariance; (2) the Cool Climate Theory, which postulates that widespread cold-adapted Pleistocene faunas were isolated on tepui summits and speciated there during warm interglacials; (3) the Habitat Shift Theory, which holds that Pantepui highland species evolved in situ from adjacent lowland taxa by adapting to upland habitats; and (4) the Distance Dispersal Theory, which holds that the ancestors of tepui endemics arrived by long-distance dispersal from the Andes. Although other biogeographic scenarios have been discussed in the context of tepui endemism (e.g., by Rull, 2005), none appear to represent real conceptual advances beyond this set of causal alternatives.

The Plateau Theory is implausible as a general explanation for biotic endemism in Pantepui because the highlands are much older than the fauna and flora that inhabit them. Whereas geological vicariance of the Roraima Formation (by erosion) is thought to have occurred in the Mesozoic, estimated dates for speciation events among endemic frogs and bromeliads are in the latter half of the Cenozoic (Salerno et al., 2012), and avian endemism in the region is also thought to be of geologically recent origin (Mayr and Phelps, 1967). All known endemic Pantepui rodents belong to the cricetid subfamily Sigmodontinae, an immigrant clade that probably entered South America from North America in the Miocene (Pardiñas et al., 2002), and the crown clades of marsupial genera with Pantepui-endemic species appear to be no older than about 10 million years (Jansa et al., in review). In effect, no mammalian taxon endemic to Pantepui appears to be an ancient relict.

The hypothetical role of Pleistocene climatic fluctuations (e.g., as in the Cool Climate Theory) in promoting Neotropical speciation and endemism was once popular (Prance, 1982; Whitmore and Prance, 1987), but now seems less appealing with the discovery that many

TABLE 8. Pantepui endemic mammals and their known geographic distributions.

	Elevational range	Known distribution	Reference
Marmosa tyleriana	1300–2100 m	Auyán-tepui, Duida, Meseta de Jaua	Creighton & Gardner (2008)
Marmosops pakaraimae	800–1130 m	Pakaraimas[a], Churi-tepui, Sierra de Lema	This report
Monodelphis reigi	1100–2050 m	Ayanganna, Sierra de Lema	Lim et al. (2010)
Platyrrhinus aurarius	700–2100 m	Widespread in Pantepui[b]	Gardner (2008)
Podoxomys roraimae	2620–2630 m	Roraima	Pérez-Zapata et al. (1992)
Rhipidomys macconnelli	750–2600 m	Widespread in Pantepui	Tribe (1996)
Rhipidomys wetzeli	1400–2200 m	Churi-tepui, Duida, Neblina, Sierra de Lema	Gardner (1989)

[a] Mount Ayanganna, Mount Roraima, Mount Wokomung.

[b] An apparently isolated population also occurs on the Tafelberg, a sandstone table mountain in central Surinam (Williams et al., 1983).

Neotropical species and associated patterns of taxic endemism are much older than the Pleistocene (Moritz et al., 2000). Although speciation dates are not currently available for Pantepui-endemic mammals, molecular (cytochrome-*b*) distances between three endemic species and their non-Pantepui sister taxa are substantial—approximately 7% to 11% (Gutiérrez et al., 2010; Lim et al., 2010; this report). Whether or not such divergence is consistent with a Pleistocene origin for tepui-endemic lineages remains to be determined.

The Habitat Shift and Distance Dispersal theories concern the spatial rather than the temporal origin of Pantepui endemics and make different phylogenetic predictions. According to the former theory, the sister taxa of Pantepui endemics should be adjacent lowland taxa, whereas the latter would predict them to be Andean species. To date, relevant phylogenetic information is available for only four tepui-endemic mammals (table 9). Of these, three (*Marmosa tyleriana*, *Marmosops pakaraimae*, and *Platyrrhinus aurarius*) have lowland sister taxa,[5] but it is noteworthy that only for *Marmosops pakaraimae* is the sister taxon currently known to occur adjacent to the tepuis. The fourth taxon (*Monodelphis reigi*) is sister to a clade that includes both Andean and lowland species.

Formal biogeographic analyses of mammalian lineages with Pantepui endemics would be useful for evaluating the Habitat Shift versus Distance Dispersal scenarios, but only one has been published to date. In Velazco and Patterson's (2008) parsimony- and likelihood-based biogeographic analyses of *Platyrrhinus*, the Pantepui endemic species *P. aurarius* was reconstructed as descended from a widespread ancestral species distributed across the Amazonian lowlands and the Guiana Shield, consistent with the Habitat Shift theory. However, none of the nodes adjacent to *P. aurarius* in Velazco and Patterson's phylogeny are strongly supported, so

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[5] Like many other western Amazonian lowland mammals, *Marmosa waterhousei* (the sister taxon of *M. tyleriana*) and *Platyrrhinus infuscus* (the sister taxon of *P. aurarius*) also occur on the lower slopes of the Andes (Gutiérrez et al., 2011; Velazco, 2005), where lowland rain forest extends to higher elevations than it does on isolated peaks due to the Massenerhebung effect (Richards, 1952; Grubb, 1977).

TABLE 9. Phylogenetic relationships of endemic pantepui mammals.

Pantepui endemic	Sister species	Geographic range of sister species	Reference(s)
Marmosa tyleriana	*Marmosa waterhousei*[a]	NW Amazonian lowlands	Gutiérrez et al. (2010)
Marmosops pakaraimae	*Marmosops parvidens*	NE & SE Amazonian lowlands	This report
Monodelphis reigi	*Monodelphis* spp.[a, b]	Andes and W Amazonian lowlands	Lim et al. (2010)
Platyrrhinus aurarius	*Platyrrhinus infuscus*[a]	W Amazonian lowlands	Velazco and Patterson (2008)
Podoxomys roraimae	unknown[c]		
Rhipidomys macconnelli	unknown[d]		
Rhipidomys wetzeli	unknown[d]		

[a] Key nodes are fully resolved but weakly supported.

[b] *Monodelphis reigi* was recovered as sister to a clade composed of *M. handleyi*, *M. osgoodi*, and *M. peruviana.*

[c] Not yet included in any phylogenetic analysis.

[d] Relationships to other congeners not resolved by available sequence data (Costa et al., 2011).

almost equally likely alternative topologies for their Clade C—which, in addition to *P. aurarius* and *P. infuscus*, also includes several Andean taxa—might support different biogeographic scenarios consistent with long-distance dispersal by montane taxa.

Recently, Lim (2012) suggested that parsimony optimization of geographic range information for *Monodelphis* would recover the Pantepui endemic species *M. reigi* as descended from an Andean ancestor (consistent with the Distance Dispersal theory), but his assessment was based on Solari's (2010: 325) statement that members of the *M. adusta* group (to which *M. reigi* belongs) are "associated with the Andean cordillera." This statement is somewhat misleading, however, because only one member species (*M. osgoodi*) is endemic to the Andes; by contrast, *M. handleyi* and *M. ronaldi* are known only from Amazonian lowland sites (Solari, 2004, 2007), and two other species that do occur in the Andes (*M. adusta* and *M. peruviana*) are also known to occur at Amazonian localities hundreds of kilometers to the east (e.g., at Allpahuayo, < 200 m above sea level; Hice and Velazco, 2012). A formal biogeographic analysis of the *M. adusta* group using accurate range descriptors is clearly needed to convincingly resolve the biogeographic ancestry of *M. reigi*.

Although there currently appears to be no compelling phylogenetic support for the hypothesis that tepui-endemic mammals are directly descended from Andean ancestors, some mammalogists have noted morphological resemblances between tepui endemics and Andean species that seem to suggest a close relationship. Pérez-Zapata et al. (1992), for example, emphasized cranial similarities between *Podoxymys roraimae* and *Akodon bogotensis* (formerly *Microxus bogotensis*, a northern Andean species), but neither *P. roraimae* nor *A. bogotensis* has yet been included in any phylogenetic analysis of akodont relationships (e.g., D'Elía, 2003), so it is not known whether or not they are sister taxa. Previously, Gardner (1989) discussed several tepui mammals that appeared to have Andean "affinities," but some of these (e.g., *Platyrrhinus aurarius*; see above) are now thought to be more closely related to lowland Amazonian than to Andean taxa, one (*Marmosops neblina*) has subsequently been reported to occur at lowland sites (Patton et al., 2000), and the phylogenetic relationships of others (e.g., *Rhipidomys macconnelli* and *R. wetzeli*) have yet to be resolved.

In summary, available evidence concerning the biogeographic origin of highland mammals endemic to Pantepui is less than ideal and has been variously interpreted. However, in the only case in which the sister taxon of a tepui endemic can be identified with reasonable certainty (*Marmosops pakaraimae*), the sister taxon still exists in lowland forests adjacent to Pantepui. Whether or not this pattern will be repeated as relevant phylogenetic information becomes available for other Pantepui endemics is an interesting question for future research.

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APPENDIX

Gazetteer

This gazetteer includes all localities from which we examined specimens or analyzed sequences of *Marmosops* for this study. Italicized place names are those of the largest administrative units (states, departments, etc.) within each country (but note that "French Guiana" is an overseas department of France); 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. Elevations are provided verbatim, in meters (m) or feet (ft). The name(s) of the 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. Collection localities of ingroup taxa are mapped in figure 1.

BRAZIL

1. *Amapá,* **Serra do Navio** (including sublocalities "Rio Amapari" and "Km 190 EFA" [ca. 0°59′N, 52°03′W, 100 m; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (F. de P. Pinheiro, 16 September 1969–8 May 1970).
2. *Amazonas,* Faro, **Boca Rio Paratucu** [= Rio Piratucu, mouth at 1°59′N, 56°58′W; Paynter and Traylor, 1991]: *Marmosops parvidens* (A.M. Olalla, 21 December 1930).
3. *Amazonas,* MCSE Reserves, **80 km N Manaus** (2°25′S, 59°50′W): *Marmosops parvidens* (J.R. Malcolm, 7 October 1983–4 September 1985).
4. *Pará,* **52 km SSW Altamira** (3°39′S, 52°22′W), east bank Rio Xingu: *Marmosops pinheiroi* (M.D. Carleton, 15 September 1986).
5. *Pará,* **Belém** [1°27′S, 48°29′W; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (collector unknown, 25 May 1970).
6. *Pará,* Rio Tocantins, **Ilha do Taiuna** [ca. 2°15′S, 49°30′W]: *Marmosa parvidens* (A.M. Olalla, 2 November 1931).
7. *Pará,* **Utinga** [near Belém, ca. 1°27′S, 48°29′W (see above); including sublocalities "Agua Preta", "Nova Area Experimental", and "Trapping Area 1"]: *Marmosops pinheiroi* (R.H. Pine, 10–14 June 1968; A.P. Souza, 18 February–25 June 1965 and 3 August 1967).

8. *Rio de Janeiro,* **Ibicuí** (22°57′S, 44°02′W, 50 m; Mustrangi and Patton, 1997), Município de Mangaratiba: *Marmosops incanus* (M.A. Mustrangi, 28 September 1993).
9. *São Paulo,* Base do Carmo, **Fazenda Intervales** [24°20′S, 48°25′W; Mustrangi and Patton, 1997), Município de Capão Bonito: *Marmosops paulensis* (J.L. Patton, 16 July 1994).

FRENCH GUIANA

10. **Les Nouragues** [4°05′N, 52°40′W, 210 m; Voss and Emmons, 1996]: *Marmosops parvidens* (F. Catzeflis, 3 August 2002) and *M. pinheiroi* (J.-F. Mauffrey, 15 May 1999).
11. **Paracou** [5°17′N, 52°55′W, ca. 45 m; Simmons and Voss, 1998], near Sinnamary: *Marmosops parvidens* and *M. pinheiroi* (L.H. Emmons, R.W. Kays, D.P. Lunde, and R.S. Voss, 1991–1994).
12. **River Aratayе** (4°00′N, 52°40′W, 30 m): *Marmosops parvidens* (L.H. Emmons, 2 October 1984).
13. **Saint-Eugène** [4°51′N, 53°04′W; Cosson et al., 1999]: *Marmosops parvidens* (S. Ringuet, 14 April 1996).

GUYANA

14. *Cuyuni-Mazaruni,* **Mount Roraima** (including “Second Camp” at 5°17′N, 60°45′W, 800 m; and “Third Camp” at 5°16′N, 60°44′W, 1000 m): *Marmosops pakaraimae* (B.K. Lim and D.M. Jafferally, 26 February–8 March 2003).
15. *Demerara-Mahaica,* **Hyde Park**, 30 mi [up the] Demerara R[iver] [6°30′N, 58°16′W, ca. 100 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (S.B. Warren, 8 September 1906).
16. *Potaro-Siparuni,* Iwokrama Forest, **Canopy Walkway** (4°15′N, 58°55′W, 70 m): *Marmosops pinheiroi* (B.K. Lim et al., 19 August 2008).
17. *Potaro-Siparuni,* Iwokrama Forest, Turtle Mountain, **10 km NW Kurupukari** (4°44′N, 58°43′W, 50 m): *Marmosops pinheiroi* (B.K. Lim et al., 31 October 1997).
18. *Potaro-Siparuni,* Iwokrama Forest, **Kabukalli Landing** (4°17′N, 58°31′W): *Marmosops pinheiroi* (B.K. Lim et al., 13–18 October 1999).
19. *Potaro-Siparuni,* **Mount Ayanganna**, First Plateau Camp (5°20′N, 59°57′W, 1100 m; Lim et al., 2010): *Marmosops pakaraimae* (B.K. Lim, 27 October 2002).
20. *Potaro-Siparuni,* **Mount Wokomung**, First Plateau Camp (5°07′N, 59°49′W, 1130 m): *Marmosops pakaraimae* (B.K. Lim and W.P. Kilburn, 19–20 February 2003).
21. *Upper Takutu-Upper Essequibo,* **Karanambo** [3°45′N, 59°18′W; Lim et al., 2008]: *Marmosops parvidens* (M.D. Engstrom et al., 1 October 1990).

SURINAM

22. *Brokopondo,* **Brownsberg Nature Park**, Jeep Trail (4°56′N, 55°12′W, 500 m): *Marmosops parvidens* (M.D. Engstrom et al., 13–19 April 2002).
23. *Brokopondo,* **Finisanti** [5°08′N, 55°29′W; Voss, 1991], Saramacca River: *Marmosops pinheiroi* (P. Hershkovitz, 31 December 1961).
24. *Nickerie,* **Kayser Gebergte Airstrip**, E of Zuid River [ca. 3°07′N, 56°27′W, ca. 278 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (H.A. Beatty, 30 December 1960).
25. *Nickerie,* **Sipaliwini Airstrip** (2°02′N, 56°08′W): *Marmosops pinheiroi* (S.L. Williams, 20 August 1979).
26. *Sipaliwini,* **Bakhuis Transect 9** (4°29′N, 57°02′W, 170 m): *Marmosops pinheiroi* (B.K. Lim and S.L. Peters, 3 November 2005).

27. *Sipaliwini,* **Bakhuis Transect 13** (4°33′N, 57°04′W, 175 m): *Marmosops parvidens* (B.K. Lim and A.V. Borisenko, 19 January 2006).

VENEZUELA

28. *Bolívar,* **85 km SSE El Dorado**, Km 121 [= "Km 125" at 6°02′N, 61°22′W, 1032 m (Gardner, 2008); in the Sierra de Lema]: *Marmosops pakaraimae* (M.D. Tuttle, 9 May 1966).
29. *Bolívar,* **Auyán-tepui** [ca. 5°55′N, 62°32′W; Paynter, 1982], 460 m: *Marmosops pinheiroi* (G.H.H. Tate, 9 March 1938). Based on the recorded elevation and dates of collection, the two AMNH specimens from this locality were either taken at the Phelps Expedition's "Urullén camp" or at the nearby airstrip in the "Urullén savanna." According to Tate (1938: 474), only the former locality included forest habitats, making it the more likely collection site for *M. pinheiroi*. Both places are at the base of the southeastern escarpment of Auyán-tepui (op. cit.: fig. 5).
30. *Bolívar,* **Churi-tepui** [ca. 5°13′N, 61°54′W; McDiarmid and Donnelly, 2005], Camp 5 (4900 ft): *Marmosops pakaraimae* (E. McGuire, 13 January 1953). Churi-tepui is not labeled on most published maps of Pantepui (e.g., those in Mayr and Phelps, 1967; McDiarmid and Donnelly, 2005) because it is part of the Chimantá massif (Huber, 1995a: fig. 1-27).

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