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## An Introduction to *Marmosops* (Marsupialia: Didelphidae), with the Description of a New Species from Bolivia and Notes on the Taxonomy and Distribution of Other Bolivian Forms

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## ABSTRACT

In order to facilitate much-needed revisionary research on *Marmosops*, we summarize the currently accepted species-level taxonomy, provide full bibliographic citations for original descriptions of all 36 included nominal taxa, map their type localities, and list their type material (if known). We rediagnose the genus *Marmosops*, compare it with three other didelphid genera to which misidentified specimens of *Marmosops* have often been referred, and review the phylogenetic evidence that *Marmosops* is monophyletic. After describing a new species from the eastern-slope montane forests of Bolivia, we review the taxonomy of other Bolivian congeners based on morphological characters and published cytochrome-*b* gene sequences. Among our taxonomic results, we synonymize *albiventris* Tate (1931), *dorothea* Thomas (1911), and *yungasensis* Tate (1931) with *M. noctivagus* (Tschudi, 1845). By contrast, *M. ocellatus* (Tate, 1931), currently considered a synonym of *dorothea*, appears to be a valid species. Whereas published range maps of Bolivian species of *Marmosops* are demonstrably based on misidentified material and show little correspondence with known environmental factors, locality records based on specimens examined for this report make much more eco-geographic sense.

## INTRODUCTION

Didelphid marsupials represent the only substantially intact radiation of metatherian mammals in the New World, where they constitute a distinctive component of terrestrial vertebrate faunas in many tropical and subtropical habitats. Although certain aspects of didelphid classification have remained stable for many years, notably the generic taxonomy of the larger opossums, recent discoveries have underscored our still very incomplete knowledge of phylogenetic diversity and relationships among the smaller forms, especially the so-called “marmosines” (formerly classified as, or allied with, *Marmosa* Gray, 1821). Such discoveries include highly divergent new clades (Voss et al., 2001; Voss and Jansa, 2003; Voss et al., 2004) and unsuspected species-level diversity concealed by traditional synonymies (Mustringi and Patton, 1997; Voss et al., 2001; Patton and Costa, 2003). Both phenomena suggest that the current classification of small didelphids requires critical attention.

The didelphid marsupial genus *Marmosops* was originally named by Matschie (1916) to contain 11 species, of which *M. incanus* (Lund, 1840) was designated as the type. Although Tate (1933) treated *Marmosops* as a junior synonym of *Marmosa*, he acknowledged that Matschie’s taxon corresponded to a diagnosable cluster of species (the “*Noctivaga* Group”) that could logically be recognized as a subgenus. In the decades that followed, however, *Marmosops* contin-

ued to be treated as a junior synonym of *Marmosa*, even in classifications that used subgeneric categories (e.g., Cabrera, 1958; Reig et al., 1985). The current recognition of *Marmosops* as a distinct taxon dates from Gardner and Creighton (1989), who raised all of Tate’s species groups of *Marmosa* to generic rank.

As currently recognized in the systematic literature, *Marmosops* includes 36 nominal taxa, of which 14 are considered to be valid species and 22 to be subspecies or junior synonyms (table 1). The geographic dispersion of type localities (fig. 1) approximates the distribution of the genus itself, which ranges from Panama to southeastern Brazil. Species of *Marmosops* occur in lowland rain forests, lowland dry forests, and in montane (“cloud”) forests to about 3000 m above sea level. Trapping studies suggest that these small (20–120 g) opossums are predominantly understory species that are often taken on the ground or a few meters above the ground (e.g., on logs, branches, and lianas), but apparently never in the canopy (Malcolm, 1991; Patton et al., 2000; Voss et al., 2001; Cunha and Vieira, 2002; Vieira and Monteiro-Filho, 2003). Although alleged to be insectivorous or omnivorous (Emmons, 1997; Mustringi and Patton, 1997; Cordero, 2001; Voss et al., 2001), no analyses of relevant dietary data have been published. In fact, the natural history of *Marmosops* remains almost completely unstudied despite the local abundance of some species in relatively accessible habitats.

TABLE 1  
Valid Species and Synonyms Currently Referred to the Genus *Marmosops*<sup>a</sup>

Taxa	Types <sup>b</sup>
<i>M. bishopi</i> (Pine, 1981) <sup>c</sup>	USNM 393535
<i>M. cracens</i> (Handley and Gordon, 1979)	USNM 418503
<i>M. dorothea</i> (Thomas, 1911) <sup>d</sup>	BMNH 1.6.7.79
Synonyms: <i>ocellatus</i> (Tate, 1931) <sup>e</sup>	BMNH 26.1.5.25
<i>yungasensis</i> (Tate, 1931) <sup>d</sup>	AMNH 72558
<i>M. fuscatus</i> (Thomas, 1896)	BMNH 96.11.1.6
Synonyms: <i>carri</i> (J. A. Allen and Chapman, 1897)	AMNH 7314/5922
<i>perfuscus</i> (Thomas, 1924)	BMNH 23.11.13.18
<i>M. handleyi</i> (Pine, 1981)	FMNH 69838
<i>M. impavidus</i> (Tschudi, 1845)	Not known to exist
Synonyms: <i>albiventris</i> (Tate, 1931) <sup>d</sup>	USNM 194378
<i>caucae</i> (Thomas, 1900)	BMNH 99.9.6.51
<i>celicae</i> (Anthony, 1922)	AMNH 47182
<i>madescens</i> (Osgood, 1913)	FMNH 19689
<i>oroensis</i> (Anthony, 1922)	AMNH 47180
<i>sobrinus</i> (Thomas, 1913)	BMNH 13.10.24.70
<i>ucayalensis</i> (Tate, 1931)	AMNH 78952
<i>M. incanus</i> (Lund, 1840)	[ZMUC 223, 224; L.14, L.15] <sup>f</sup>
Synonyms: <i>bahiensis</i> (Tate, 1931)	BMNH 3.9.5.137
<i>scapulatus</i> (Burmeister, 1856)	ZMB 2330
<i>M. invictus</i> (Goldman, 1912)	USNM 178708
<i>M. juninensis</i> (Tate, 1931) <sup>c</sup>	AMNH 63864
<i>M. neblina</i> Gardner, 1990 <sup>g</sup>	USNM 560735
<i>M. noctivagus</i> (Tschudi, 1845)	ZMB 3375 <sup>h</sup>
Synonyms: <i>collega</i> (Thomas, 1920)	BMNH 20.7.14.40
<i>keaysi</i> (J. A. Allen, 1900)	AMNH 16068
<i>leucastrus</i> (Thomas, 1927b)	BMNH 26.4.1.102
<i>lugendus</i> (Thomas, 1927a)	BMNH 27.1.1.178
<i>neglectus</i> (Osgood, 1915)	FMNH 19636
<i>politus</i> (Cabrera, 1913)	MNCN 797
<i>purui</i> (Miller, 1913)	USNM 105543
<i>stollei</i> (Miranda-Ribeiro, 1936)	MNRJ 1267 <sup>i</sup>
<i>M. paulensis</i> (Tate, 1931) <sup>j</sup>	FMNH 26576
<i>M. parvidens</i> (Tate, 1931)	FMNH 18545
<i>M. pinheiroi</i> (Pine, 1981) <sup>c</sup>	USNM 461459
Synonym: <i>woodalli</i> (Pine, 1981)	USNM 393532

<sup>a</sup>Synonyms (including "subspecies") are listed under each species recognized as valid by Gardner (1993) except as noted otherwise below. Full bibliographic information for all original descriptions is provided in the References section.

<sup>b</sup>Holotypes by original designation unless noted otherwise.

<sup>c</sup>Listed as a synonym of *M. parvidens* by Gardner (1993) but recognized as a valid species by Voss et al. (2001).

<sup>d</sup>Synonymized with *M. noctivagus* in this report.

<sup>e</sup>Considered to be a valid species in this report.

<sup>f</sup>Syntypes. Tate (1933: 164–165) claimed that only two specimens in Copenhagen (ZMUC 223 and 224) were actually collected by Lund and are therefore eligible to be "co-types" (= syntypes), but two uncataloged skulls (labelled L.14 and L.15) are also part of Lund's original material and therefore have the same nomenclatural status. Because ZMUC 224 is the only specimen that consists of both a skin and cranial material (223 is a skin only), it would be a logical choice for lectotype.

<sup>g</sup>Listed as a synonym of *M. impavidus* by Gardner (1993) but recognized as a valid species by Patton et al. (2000).

<sup>h</sup>A "co-type" (= syntype) according to Tate (1933: 153).

<sup>i</sup>See Langguth et al. (1997).

<sup>j</sup>Listed as a synonym of *M. incanus* by Gardner (1993) but recognized as a valid species by Musturangi and Patton (1997).

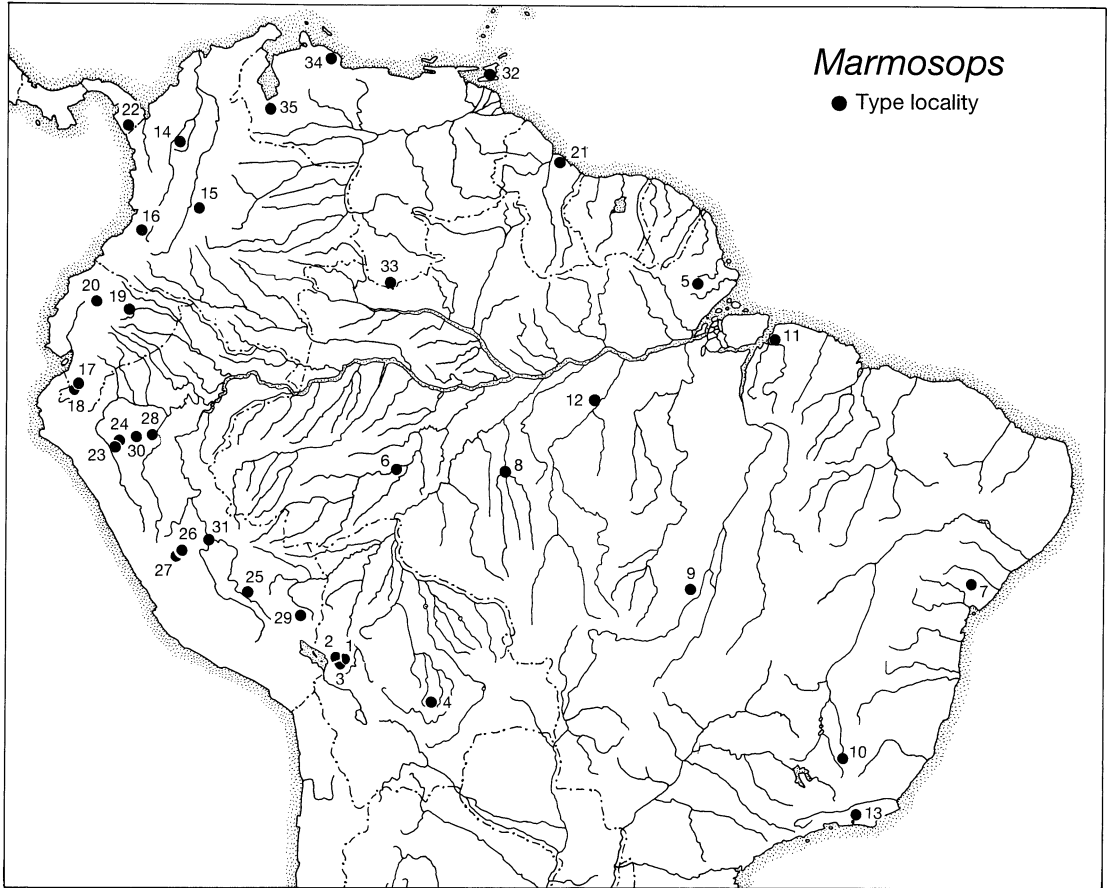


Fig. 1. Type localities of nominal species referred to the genus *Marmosops*. Numbers are keyed to gazetteer entries in appendix 1.

Museum specimens of *Marmosops* are frequently misidentified due to the absence of any comprehensive current reference for identifications. Although progress has been made in sorting out the taxonomy of *Marmosops* in southeastern Brazil (Mustringi and Patton, 1997), western Amazonia (Patton et al., 2000), and the Guiana region (Voss et al., 2001), no revisionary literature has addressed the species-level systematics of the genus in other parts of its enormous geographic range, especially along the Andes. Even a superficial familiarity with the large collections that have accumulated since Tate's (1933) revision suggests the urgent need for testing traditionally accepted species concepts with newly available material.

Herein we formally rediagnose *Marmo-*

*sops* to facilitate its recognition as a distinct clade and to provide a foundation for subsequent revisionary work. We next describe a new species from Bolivia and summarize what little is known about its ecogeographic distribution on the eastern slopes of the Andes. Lastly, we review the taxonomy and distribution of other Bolivian congeners in order to assess the regional diversity of the genus based on museum specimens examined in the course of this study.

#### MATERIALS AND METHODS

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); CBF, Colección Boliviana de Fauna (La Paz); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus); MNCN, Museo Nacional de Ciencias Naturales (Madrid); MNRJ, Museu Nacional (Rio de Janeiro); MSB, Museum of Southwestern Biology (University of New Mexico, Albuquerque); MVZ, Museum of Vertebrate Zoology (University of California, Berkeley); ROM, Royal Ontario Museum (Toronto); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History (Washington, D.C.); ZMB, Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin); and ZMUC, Zoological Museum of the University of Copenhagen (Copenhagen). In addition, we examined a small number of uncataloged specimens (cited by field number: LHE, Louise H. Emmons; MJS, Matthew J. Swarner) that will eventually be transferred to the USNM.

We transcribed total length (nose to fleshy tail-tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen labels or field notes, but we sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by the collector, and we used our values whenever large discrepancies were found. All external measurements are reported to the nearest millimeter, and all weights are reported to the nearest gram.

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm. The following were measured as illustrated in figure 2:

Condylal-Basal 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, even when the postorbital constriction (between the temporal fossae) is narrower.

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 Tooththrow 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 M4 (WM4): Measured from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

Except as noted below, all analyzed character data were obtained from adult specimens as determined by dental criteria. Following Voss et al. (2001), a specimen was judged to be *juvenile* if dP3 is still in place; *subadult* if dP3 has been shed but P3 and/or M4 are still incompletely erupted; and *adult* if the permanent dentition is complete. Qualitative character variation is described herein using terminology that is explained or referenced by Voss and Jansa (2003) and Wible (2003). An exception (not defined by those authors) is the prefix “self-” as used in combination with descriptors of ventral pelage color, such as self-white or self-cream. This usage applies to hairs that have the same coloration from base to tip, as opposed to hairs that are basally gray and distally white or cream (for example).

## TAXONOMIC ACCOUNTS

### *Marmosops* Matschie, 1916

TYPE SPECIES: *Marmosops incanus* (Lund, 1840) by original designation.

DIAGNOSIS: Species of *Marmosops* can be distinguished from other small didelphid marsupials by the following combination of character states: eye surrounded by mask of blackish fur contrasting in color with paler fur of crown and cheeks; dorsal pelage uni-

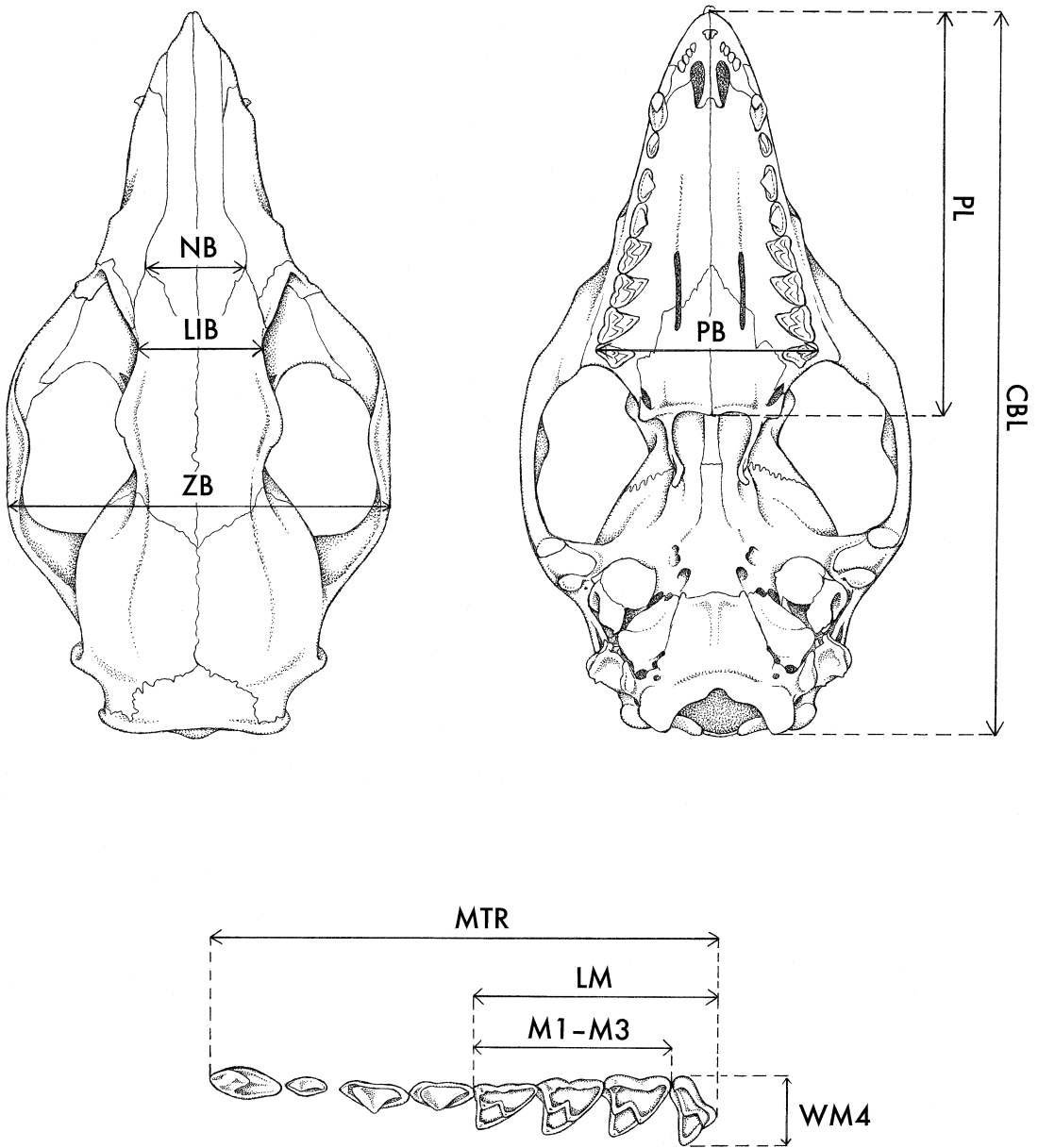


Fig. 2. Dorsal and ventral views of the skull, and occlusal view of the maxillary dentition of *Marmosa murina*, showing the anatomical limits of craniodental measurements defined in the text.

formly colored, unpatterned; manus mesaxonic (digit III longer than adjacent digits II and IV); manual claws small, not exceeding fleshy apical pads in length; central palmar surface of manus smooth (not densely tuberculate); digit IV of pes longer than adjacent digit III; caudal scales in spiral series; middle

hair of each caudal-scale triplet petiolate (narrower basally than at midlength), thicker, and usually more heavily pigmented than lateral hairs; tail longer than the combined length of head and body, not incrassate; ventral surface of tail-tip modified for prehension; premaxillary rostral process usually

well developed; postorbital processes usually absent; petrosal usually exposed on lateral surface of braincase through fenestra between squamosal and parietal bones; maxillary fenestrae absent; posterolateral palatal foramina small, not extending lingual to M4 protocones; maxillary and alisphenoid not in contact on floor of orbit; extracranial course of mandibular nerve ( $V^3$ ) enclosed by anteromedial strut of alisphenoid bulla (secondary foramen ovale present); fenestra cochleae exposed laterally (not enclosed in a bony sinus); I2–I5 with approximately symmetrical rhomboidal crowns increasing in breadth from front to back; P2 and P3 subequal in height; molar dentition highly carnassialized; centrocrista strongly V-shaped, its apex high above trigon basin; lower canine (c1) procumbent and premolariform (always with a flattened, bladeliike apex and usually with a small posterior accessory cusp); p2 taller than p3; dp3 fully molariform; m3 hypoconid labially salient; entoconid large and well developed on m1–m3.

**COMPARISONS WITH *MARMOSA*:** Species of *Marmosops* have long been confused with *Marmosa*, which they superficially resemble in size and external appearance, but these taxa are only distantly related (Jansa and Voss, 2000; Voss and Jansa, 2003) and can readily be distinguished by qualitative integumental and craniodental characters (table 2). In the field, two external characters are useful for generic identification. Whereas the manus of *Marmosops* is mesaxonic, with digit (d) III distinctly longer than the adjacent digits (dII and dIV; fig. 3A), the manus of *Marmosa* is paraxonic, with dIII and dIV subequal in length (fig. 3B). Easily determined from live specimens (or properly fluid-preserved material) with elastic phalangeal joints that can be manipulated to align and straighten adjacent digits for relative length comparisons, this character is often hard to score from dried skins with hard, bent, twisted, or otherwise distorted fingers (see Voss and Jansa, 2003: character 10). A second distinguishing external trait is the morphology of the caudal pelage, of which the central hair in each caudal-scale triplet is petiolate (narrower basally than at mid-length), thicker, and usually more darkly pigmented than the lateral hairs in *Marmosops*; by contrast,

the three hairs of each caudal-scale triplet are subequal in thickness and similarly shaped and pigmented in *Marmosa* (Voss and Jansa, 2003: character 27).

In dorsal cranial comparisons, these taxa are distinguished by the usual absence of distinct postorbital processes of the frontal bones in *Marmosops* (fig. 4B) versus the usual presence of distinct postorbital processes in adults of most species of *Marmosa* (fig. 4A). In lateral cranial view, the petrosal capsule that encloses the paraflacculus and semicircular canals (= pars canalicularis or pars mastoideus) is usually exposed through a fenestra between the squamosal and parietal bones in *Marmosops* (fig. 5A), but there is no such lateral petrosal exposure in *Marmosa* (fig. 5B). In ventral cranial view, *Marmosops* is distinguished by the invariant presence of a secondary foramen ovale (fig. 6B), which is just as consistently absent in *Marmosa* (fig. 6A).

*Marmosops* and *Marmosa* are similar in most dental traits, but the morphology of the deciduous lower third premolar (dp3) appears to provide a consistent difference. In all examined juvenile specimens of *Marmosops* (fig. 7, upper panel) this tooth is fully molariform because the trigonid includes a distinct paraconid, protoconid, and metaconid. By contrast, the dp3 of juvenile *Marmosa* (fig. 7, lower panel) is not fully molariform because the bicuspid trigonid lacks a distinct metaconid.

**COMPARISONS WITH *GRACILINANUS*:** Museum specimens of *Marmosops* are sometimes misidentified as *Gracilinanus*, apparently the result of using inaccurate published keys.<sup>5</sup> Despite such confusion, the two genera can be distinguished unambiguously by several external morphological differences (table 2). Unlike *Marmosops*, which has a mesaxonic manus with dIII longer than the other digits, *Gracilinanus* (like *Marmosa*) has a paraxonic manus with dIII and dIV subequal in length. Also, whereas *Marmosops* has spirally arranged caudal scales, the caudal scales of *Gracilinanus* are arranged in predominantly

<sup>5</sup> Among other characters erroneously used in relevant key couplets by Hershkovitz (1992: 6) and Anderson (1997: 30), presence/absence of gular glands, plantar pad morphology, nasal proportions, and presence/absence of postorbital processes do not reliably distinguish species of *Marmosops* from *Gracilinanus*.

TABLE 2  
 Diagnostic Morphological Comparisons among *Marmosops*, *Marmosa*, *Gracilinanus*, and *Thylamys*<sup>a</sup>

<i>Marmosops</i>	<i>Marmosa</i> <sup>b</sup>	<i>Gracilinanus</i> <sup>c</sup>	<i>Thylamys</i>
<i>Dorsal body pelage</i> uniformly colored, unpatterned	<i>Dorsal body pelage</i> uniformly colored, unpatterned	<i>Dorsal body pelage</i> uniformly colored, unpatterned	<i>Dorsal body pelage</i> distinctly darker medially than along flanks
<i>Manus</i> mesaxonic (dIII > dIV)	<i>Manus</i> paraxonic (dIII = dIV)	<i>Manus</i> paraxonic (dIII = dIV)	<i>Manus</i> mesaxonic (dIII > dIV)
<i>Central palmar surface of manus</i> smooth	<i>Central palmar surface of manus</i> smooth	<i>Central palmar surface of manus</i> smooth	<i>Central palmar surface of manus</i> densely tuberculate
<i>Lateral carpal tubercles</i> present in adult males	<i>Lateral carpal tubercles</i> present or absent in adult males	<i>Lateral carpal tubercles</i> present in adult males	<i>Lateral carpal tubercles</i> absent in both sexes
<i>Plantar surface of tarsus</i> naked or partially covered with microscopic hairs	<i>Plantar surface of tarsus</i> naked	<i>Plantar surface of tarsus</i> naked	<i>Plantar surface of tarsus</i> densely furred
<i>Tail</i> slender, not incrassate	<i>Tail</i> slender, not incrassate	<i>Tail</i> slender, not incrassate	<i>Tail</i> swollen, incrassate
<i>Caudal scales</i> in spiral series	<i>Caudal scales</i> in spiral series	<i>Caudal scales</i> in annular series	<i>Caudal scales</i> in annular series
<i>Central hair of each caudal-scale triplet</i> thicker and darker than lateral hairs	<i>Central hair of each caudal-scale triplet</i> subequal to lateral hairs in thickness and similarly colored	<i>Central hair of each caudal-scale triplet</i> subequal to lateral hairs in thickness and similarly colored	<i>Central hair of each caudal-scale triplet</i> subequal to lateral hairs in thickness and similarly colored
<i>Rostral process of premaxillae</i> usually well developed	<i>Rostral process of premaxillae</i> well developed	<i>Rostral process of premaxillae</i> well developed	<i>Rostral process of premaxillae</i> absent
<i>Nasals</i> conspicuously widened posteriorly in most species <sup>d</sup>	<i>Nasals</i> conspicuously widened posteriorly	<i>Nasals</i> conspicuously widened posteriorly	<i>Nasals</i> uniformly narrow, with subparallel lateral margins
<i>Postorbital processes</i> usually absent (sometimes weakly developed in old adult specimens)	<i>Postorbital processes</i> usually present in adult specimens (often absent in juveniles and subadults)	<i>Postorbital processes</i> usually absent (sometimes weakly developed in old adults)	<i>Postorbital processes</i> usually absent (sometimes weakly developed in old adults)



TABLE 2  
(Continued)

<i>Marmosops</i>	<i>Marmosab</i>	<i>Gracilinanus<sup>c</sup></i>	<i>Thylamys</i>
<i>Petrosal</i> usually exposed through fenestra between squamosal and parietal on lateral braincase	<i>Petrosal</i> never exposed between squamosal and parietal on lateral braincase	<i>Petrosal</i> usually exposed through fenestra between squamosal and parietal on lateral braincase	<i>Petrosal</i> usually exposed through fenestra between squamosal and parietal on lateral braincase
<i>Maxillary palatal fenestrae</i> absent	<i>Maxillary palatal fenestrae</i> absent	<i>Maxillary palatal fenestrae</i> present	<i>Maxillary palatal fenestrae</i> present or absent
<i>Posterolateral palatal foramina</i> small, not extending lingual to M4 protocones	<i>Posterolateral palatal foramina</i> small, not extending lingual to M4 protocones	<i>Posterolateral palatal foramina</i> small, not extending lingual to M4 protocones	<i>Posterolateral palatal foramina</i> large, usually extending lingual to M4 protocones
<i>Secondary foramen ovale</i> present	<i>Secondary foramen ovale</i> absent	<i>Secondary foramen ovale</i> present	<i>Secondary foramen ovale</i> present
<i>Fenestra cochleae</i> laterally exposed	<i>Fenestra cochleae</i> laterally exposed	<i>Fenestra cochleae</i> laterally exposed	<i>Fenestra cochleae</i> laterally concealed in a bony sinus
<i>Second upper premolar</i> subequal to P3	<i>Second upper premolar</i> subequal to P3	<i>Second upper premolar</i> subequal to P3	<i>Second upper premolar</i> shorter than P3
<i>Deciduous lower premolar (dp3)</i> fully molariform, with tricuspid trigonid	<i>Deciduous lower premolar (dp3)</i> incompletely molariform, with bicuspid or unicuspid trigonid	<i>Deciduous lower premolar (dp3)</i> incompletely molariform, with bicuspid trigonid (but only three specimens examined)	<i>Deciduous lower premolar (dp3)</i> incompletely molariform, with bicuspid trigonid in most examined specimens

<sup>a</sup>See text and Voss and Jansa (2003) for more complete character descriptions.

<sup>b</sup>Including *Micoureus*, but excluding *Tlacuatzin canescens* (see Voss and Jansa, 2003).

<sup>c</sup>As construed herein, *Gracilinanus* (sensu stricto) comprises the following species, all of which conform to Gardner and Creighton's (1989) original generic diagnosis: *aceramarcae* Tate, *agilis* Burmeister (including *beatrix* Thomas, *buenavistae* Tate, and *peruanus* Thomas), *emiliae* Thomas (including *longicaudus* Hershkovitz), *marica* Thomas (including *perijae* Hershkovitz), and *microtarsus* Wagner. Explicitly excluded from our concept of *Gracilinanus* (sensu stricto) are five nominal taxa (currently treated as synonyms of *agilis*, *emiliae*, or *microtarsus*; see Gardner, 1993) that belong to an unnamed clade to be described in a manuscript currently in preparation. These include *agricolai* Moonjen; *chaensis* Tate; *guahybae* Tate; *ignitus* Diaz, Flores, and Barquez; and *undaviensis* Tate. We have not examined material of three nominal taxa (*blaseri*, *rondoni*, and *herhardi*) originally described by Miranda-Ribeiro (1936) and currently assigned to *Gracilinanus* (sensu Gardner, 1993); their membership in one or the other of the groups mentioned above seems probable but remains to be determined.

<sup>d</sup>All known Bolivian species of *Marmosops* have nasals that are conspicuously wider posteriorly than anteriorly.

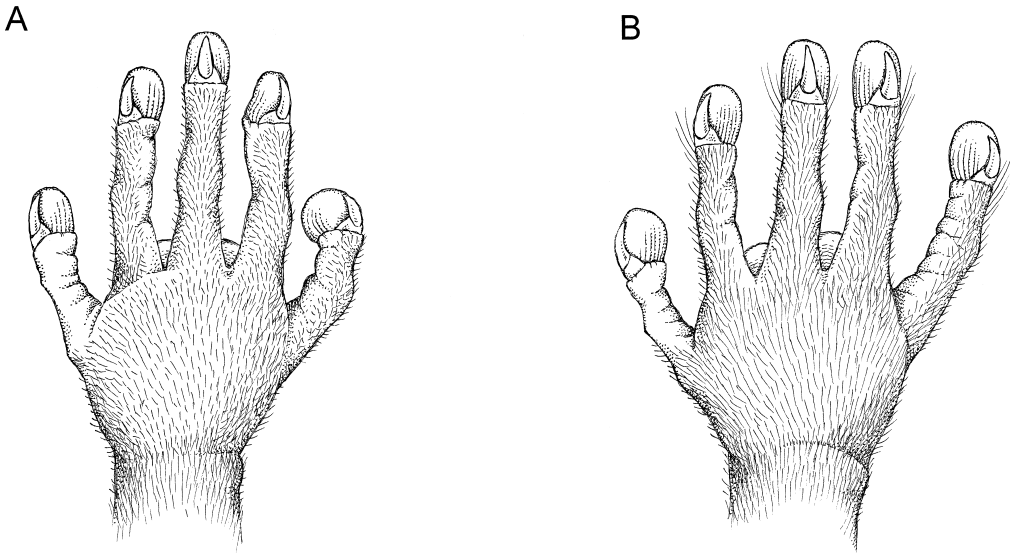


Fig. 3. Dorsal views of right forefeet of *Marmosops incanus* (A, MVZ 197629) and *Marmosa robinsoni* (B, AMNH 259983) illustrating generic differences in digital proportions. Species of *Marmosops* have mesaxonic forefeet in which digit III is longer than all of the other manual digits and digit V is short (about equal in length to digit I). By contrast, species of *Marmosa* (and *Gracilinanus*) have paraxonic forefeet in which digits III and IV are subequal and digit V is long.

annular series (Voss and Jansa, 2003: character 23). Lastly, the central hair of each caudal-scale triplet is petiolate, thicker, and usually more heavily pigmented than the lateral hairs in *Marmosops*, whereas the central hair is not conspicuously differentiated from the lateral hairs in *Gracilinanus* (Voss and Jansa, 2003: character 27).

Cranially, *Marmosops* consistently lacks maxillary fenestrae, palatal openings that are consistently present in *Gracilinanus* on each side of the maxillopalatine openings near the M1/M2 commissure (fig. 8). The morphology of the deciduous lower premolar (dp3) might also distinguish these taxa, but we have examined so few juvenile *Gracilinanus* (two specimens of *G. agilis* and one *G. emiliae*, all with incomplete trigonids) that the diagnostic value of this trait is unclear.

COMPARISONS WITH *THYLAMYS*: Specimens of *Marmosops* have occasionally been misidentified as *Thylamys* despite the large number of consistent differences that distinguish these very dissimilar taxa. Whereas the dorsal body pelage of *Marmosops* is uniformly colored and unpatterned, the middorsum of *Thylamys* is distinctly darker than the flanks,

with a more-or-less sharp line of transition between the two colors on either side (Voss and Jansa, 2003: character 7). Additional external differences (table 2) include the morphology of the central palmar surface of the manus (Voss and Jansa, 2003: character 11), the occurrence of lateral carpal tubercles (Voss and Jansa, 2003: character 12), occurrence of plantar pelage on the tarsus (Voss and Jansa, 2003: character 16), caudal hair morphology (Voss and Jansa, 2003: character 27), and caudal incassation (Voss and Jansa, 2003: character 28). Craniodental differences between these genera are likewise numerous, including the presence/absence of a rostral premaxillary process (Voss and Jansa, 2003: character 29), shape of the nasal bones (Voss and Jansa, 2003: character 33), size and extent of the posterolateral palatal foramina (Voss and Jansa, 2003: character 41), lateral exposure of the fenestra cochleae (Voss and Jansa, 2003: character 47), and upper premolar proportions (Voss and Jansa, 2003: character 55).

PHYLOGENETIC STATUS AND RELATIONSHIPS: Although distinguished from certain other “marmosines” by a relatively small number

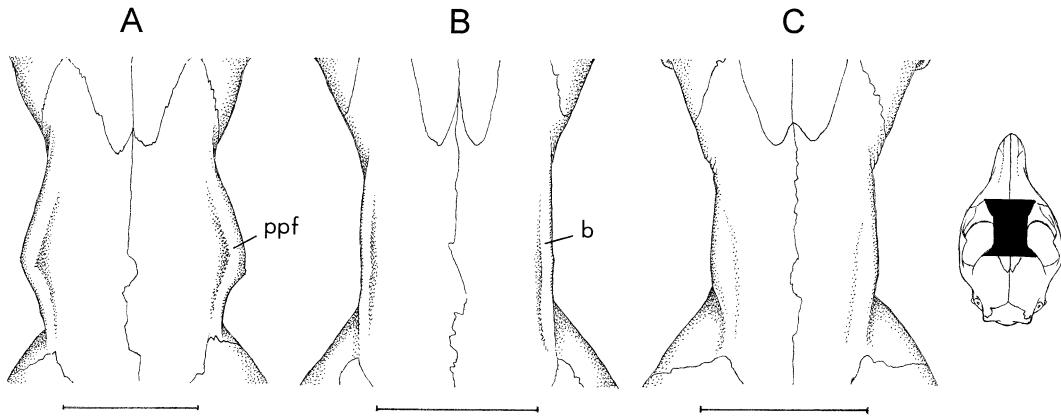


Fig. 4. Dorsal views of the interorbital region in *Marmosa murina* (A, AMNH 267368), *Marmosops noctivagus* (B, AMNH 262402), and *Gracilinanus agilis* (C, MVZ 197439) illustrating generic differences in the development of postorbital processes. Distinct postorbital processes of the frontals (**ppf**) are normally present in fully adult specimens of most *Marmosa* species, but they are usually absent in *Marmosops* and *Gracilinanus* (indistinct processes are sometimes developed in old adults). Supraorbital beads (**b**), consisting of upturned dorsally-grooved ridges, are present in some but not all species of *Marmosops*. Scale bars equal 5 mm.

of morphological characters, *Marmosops* appears to be a natural group based on recent phylogenetic analyses in which generic monophyly was tested rather than assumed (Jansa and Voss, 2000; Voss and Jansa, 2003). The most taxonomically complete analysis to date (Voss and Jansa, 2003) included only five species of *Marmosops*, but among these were members of the diminutive *M. parvidens* complex as well as large Amazonian and southeastern Brazilian forms; generic monophyly was supported in separate parsimony analyses of both non-molecular (morphological + karyotypic) characters and sequences from exon 1 of the nuclear gene encoding the Interphotoreceptor Retinoid Binding Protein (IRBP), in a likelihood analysis of the IRBP data, and in a parsimony analysis of a combined-data (non-molecular + IRBP) supermatrix. The only discrepant result concerning generic monophyly, Kirsch and Palma's (1995) report that *Gracilinanus agilis* and *Marmosops dorothea* are almost indistinguishable by thermal elution of scnDNA heteroduplexes, is now known to be an artifact of specimen misidentification (see Voss and Jansa, 2003: 57).

Several phylogenetic analyses of molecular data (e.g., Kirsch and Palma, 1995; Jansa and Voss, 2000; Voss and Jansa, 2003) sug-

gest that *Marmosops* belongs to a didelphine clade that also includes *Gracilinanus*, *Les-todelphys*, and *Thylamys*. The recently described genus *Chacodelphys* may also belong to this group (Voss et al., 2004). Although Patton et al. (1996) recovered *Marmosops* as the sister taxon of *Caluromys*, the cytochrome-*b* sequences they analyzed appear to be substitution-saturated at this level of taxonomic comparison (Jansa and Voss, 2000: fig. 12), and the relationship in question (*Marmosops* + *Caluromys*) had only trivial bootstrap support in their parsimony results. Palma and Spotorno's (1999) report of a sister-group relationship between *Marmosops* and *Metachirus* (supported by very large bootstrap values in their neighbor-joining and parsimony trees) is an unexplained anomaly that is not consistent with any other analytic results or character data of which we are aware.

*Marmosops creightoni*, new species  
Figure 9

HOLOTYPE: An adult male specimen in the Colección Boliviana de Fauna (CBF 6552) collected by Eric Yensen (original number 1705) on 5 August 1999 near the Saynani hydroelectric generating station (ca. 16°07'S,

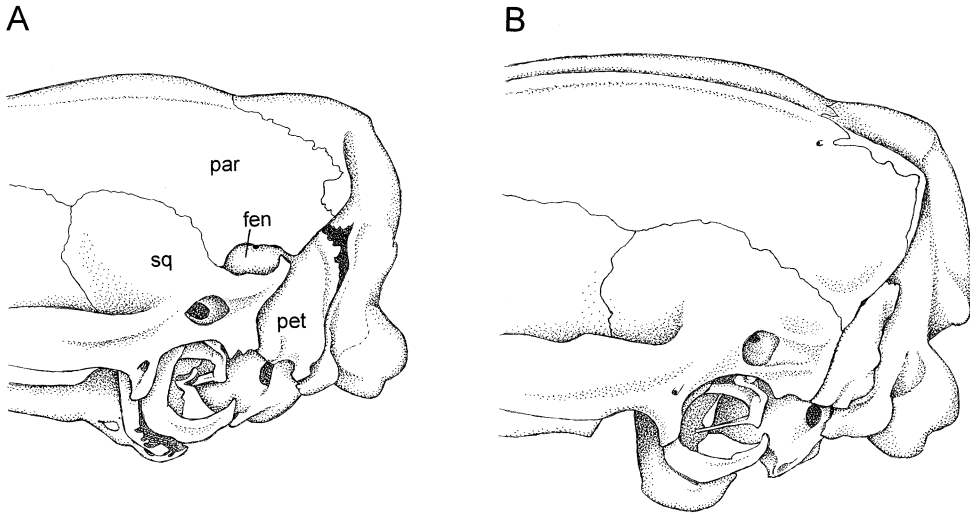


Fig. 5. Lateral view of posterior braincase in *Marmosops impavidus* (A, AMNH 272709) and *Marmosa murina* (B, AMNH 272816) illustrating the presence of a fenestra (fen) that exposes the petrosal (pet) between the parietal (par) and squamosal (sq) in the former taxon. The petrosal is not laterally exposed by a fenestra between the parietal and squamosal in *Marmosa*.

68°05'W; 2500 m above sea level) in the valley of the Río Zongo, Departamento La Paz, Bolivia. The holotype is a whole (unskinned) fluid-preserved specimen with an extracted skull and mandibles.

**PARATYPES:** Five additional specimens (listed as unidentified “*Marmosa*” by Anderson, 1997: 151) were collected by G.K. Creighton in 1979 at two adjacent localities in the valley of the Río Zongo, Departamento La Paz, Bolivia. Two of these (UMMZ 155999, 156000) were taken above the type locality near the Cuticucho hydroelectric generating station (ca. 16°08'S, 68°07'W) at a recorded elevation of 2967 m, whereas three others (UMMZ 156001–156003) were trapped below the type locality at a recorded elevation of 2000 m. All five paratypes are adult animals preserved as whole (unskinned) fluids with extracted skulls and mandibles.

**DISTRIBUTION:** Known only from wet montane forest in the valley of the Río Zongo, Departamento La Paz, Bolivia, between 2000 and 3000 m above sea level (fig. 10).

**ETYMOLOGY:** For G. Ken Creighton, collector of the first known specimens of this species and author of the first modern analysis of didelphid phylogeny based on morphological characters (Creighton, 1984).

**DESCRIPTION:** *Marmosops creightoni* is a medium-sized species (see table 3 for measurements and weights), much larger than members of the *M. parvidens* group (ca. 20–35 g adult weight; Voss et al., 2001: tables 9, 10) but substantially smaller than some lowland forms like *M. incanus* (adults of which can weigh as much as 120 g; Lorini et al., 1994). The body pelage is almost entirely dark, the colors probably somewhat faded in our fluid-preserved specimens, but still a rich chocolate-brown dorsally on the holotype (collected in 1999) and only a little more bleached on the 24-year-old paratypes. The ventral body coloration is slightly paler brown, but there is no sharp distinction between dorsal and ventral color zones, and all of the thoracic and abdominal fur is gray-based. The chin is self-white in all of the material at hand, and white fur extends posteriorly onto the throat of one paratype (UMMZ 155601). The blackish mask that surrounds the eye on each side of the head does not extend anteriorly to include the mystacial pads (which are covered with short brownish fur) or posteriorly to the base of the ears. The mystacial and genal vibrissae are blackish, whereas the submental and interramal hairs are white. The pinnae are uniformly dark and appear naked (a sparse au-

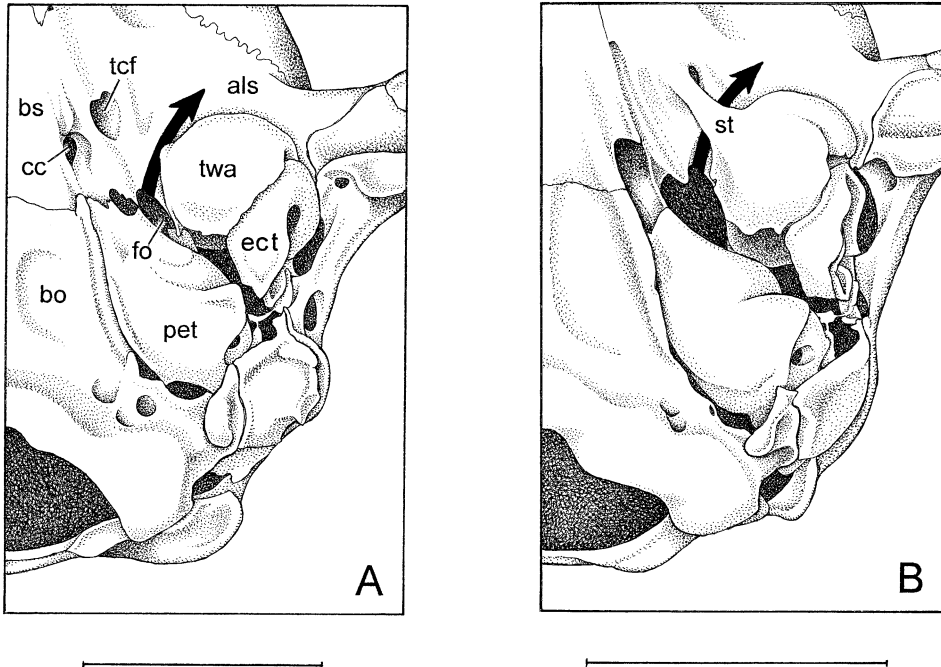


Fig. 6. Ventral view of left ear region in *Marmosa murina* (A, AMNH 267368) and *Marmosops pinheiroi* (B, AMNH 267346) illustrating generic differences in the presence/absence of a secondary foramen ovale. In *Marmosa*, the mandibular branch of the trigeminal nerve ( $V^3$ , reconstructed course shown by heavy arrow) emerges from the endocranial lumen via the foramen ovale (fo), which is bordered by the alisphenoid (als) and the petrosal (pet); the extracranial course of the nerve is unenclosed in this taxon. In *Marmosops*, however, the extracranial course of  $V^3$  is partially enclosed by a bony strut (st) that extends from the anteromedial surface of the tympanic wing of the alisphenoid (twa) across the transverse canal foramen (tcf); the nerve then emerges from a so-called secondary foramen ovale. Other abbreviations: bs, basisphenoid; bo, basioccipital; cc, carotid canal; ect, ectotympanic.

ricular pelage is only microscopically visible). Laid back alongside the head, the short mystacial vibrissae do not extend to the tips of the pinnae. A small patch of almost-naked skin on the midline of the throat suggests the presence of a weakly developed gular gland in all of the male specimens examined. The metacarpals and metatarsals are covered with dark (brownish) hairs, but the digits of both manus and pes are abruptly whitish. All of the males we examined have a knob-like glabrous tubercle on the lateral aspect of the wrist that is absent in both females. The scrotal epithelium is pigmented (mottled-grayish in preservative) and sparsely covered by brownish fur. Both female specimens have 4-1-4 = 9 abdominal-inguinal mammae. Body fur extends onto a short (ca. 1 cm) segment of the tail base, but the remainder (>90%) of the tail is virtually naked and

covered by epidermal scales in predominantly spiral series. Under high magnification (25-50 $\times$ ), each caudal scale is seen to have three hairs projecting from its posterior margin; the central hair is visibly thicker than the lateral hairs, but perhaps not quite twice as wide. On the dorsal surface of the tail, these hairs are no more than one to two scale rows long, but they are longer (three to four scale rows) on the ventral caudal surface. The exposed caudal epithelium is dark (grayish) above and below basally, but it is indistinctly bicolored (dark above, pale below) for at least half the length of that organ, and the tail-tip is entirely white for the last 1-3 cm.

In dorsal view the skull is distinctively proportioned with small orbits, narrow zygomatic arches, and a very broad interorbital region. The nasal bones are long and conspicuously widened posteriorly near the max-

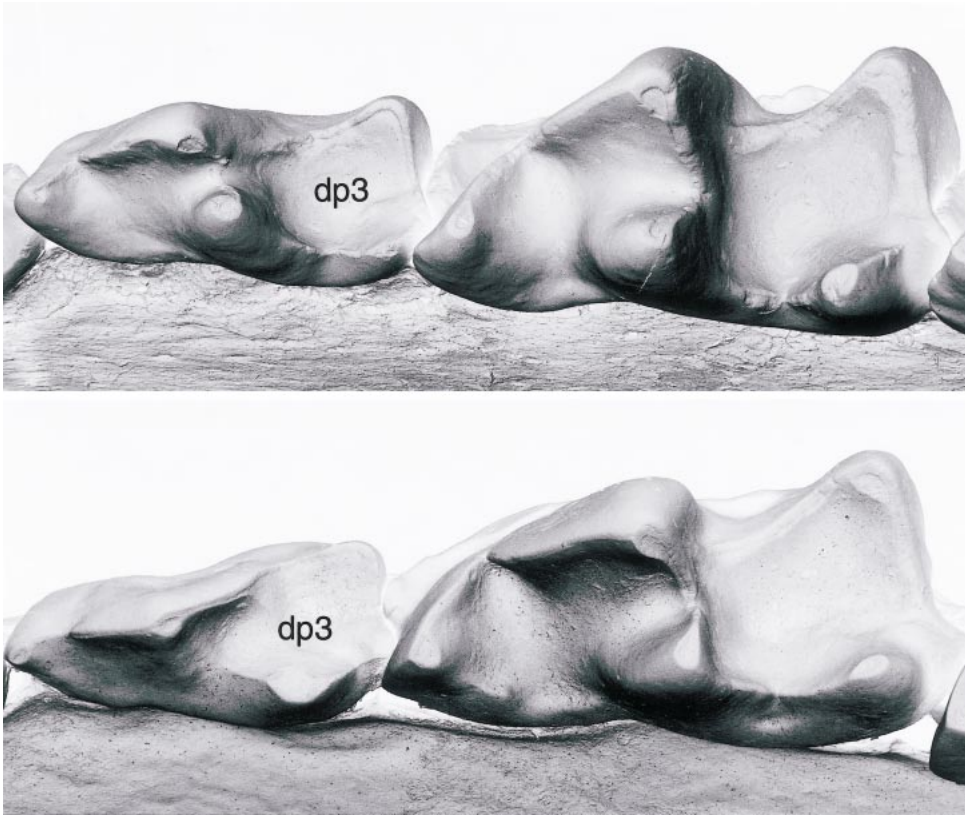


Fig. 7. Occlusal views of right dp3 and m1 illustrating the generic difference in trigonid morphology of the deciduous tooth. **Top**, *Marmosops impavidus* (MUSM 13286) with a complete (tricuspid) dp3 trigonid. **Bottom**, *Marmosa murina* (MUSM 15297) with an incomplete (bicuspid) dp3 trigonid. Note that whereas taxonomic variation in this trait was correctly described by Voss and Jansa (2003: character 64), the accompanying plate (Voss and Jansa, 2003: fig. 15) was mislabeled.

illary/premaxillary suture. The broad inter-orbital region is due to the considerable inflation of the cranial capsule that encloses the olfactory bulb, behind which there is a shallow postorbital constriction; the supraorbital margins are rounded, with only indistinct beading even in the largest male specimen examined.<sup>6</sup> The braincase is inflated and smooth, without conspicuous temporal scars. In lateral cranial view the premaxillary/maxillary suture is lateral to (rather than behind)

<sup>6</sup> The terms “bead” and “beading” as traditionally used by systematic mammalogists to describe the dorsally-grooved supraorbital ridges developed in some marsupials and rodents (fig. 4B) are derived by analogy from the upturned rims used to strengthen sheet metal or other flat surfaces in manufacture (i.e., the last of four definitions listed for the noun “bead” in *Webster’s Seventh New Collegiate Dictionary*, 1963).

the alveolus of I5 in most examined specimens (the suture is anterior to the alveolus on the left side of UMMZ 155999, and it is behind the alveolus on the right side of UMMZ 156000). The infraorbital foramen is very large (its anterior opening approximately as high as P3 is tall), and the ventral deflection of the zygomatic arch beneath the orbit is shallow. The lacrimal foramina are contained within the anterior orbital margin. The petrosal is laterally exposed through a fenestra between the squamosal and parietal bones. In ventral cranial view the incisive foramina extend between (but not behind) the canine alveoli. The maxillopalatine fenestrae are long and narrow, extending on each side from a point opposite P3 to M3 or to the M3/M4 commissure. The palatine fenestrae are

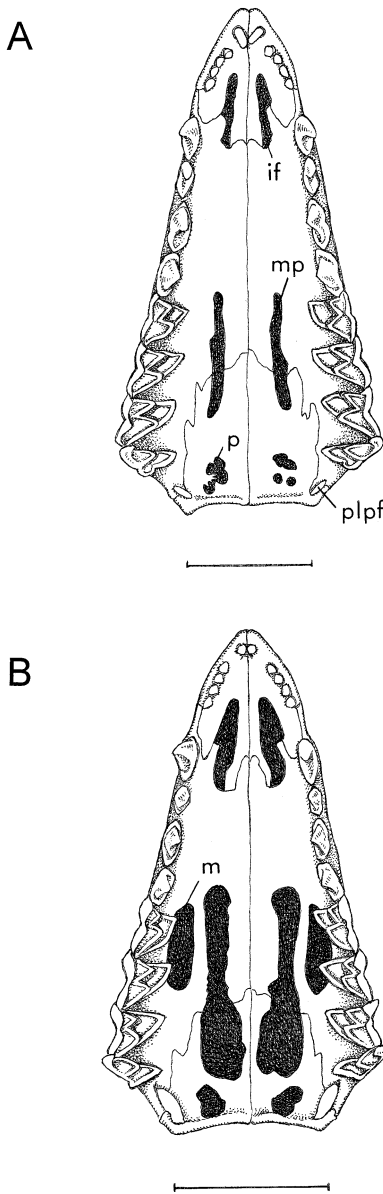


Fig. 8. Palatal morphology in *Marmosops noctivagus* (A, AMNH 262403) and *Gracilinanus agilis* (B, MVZ 197437) illustrating generic differences in patterns of fenestration. Both *Marmosops* and *Gracilinanus* have incisive foramina (if), posterolateral palatal foramina (plpf), and maxillopalatine fenestrae (mp); in addition, some species of *Marmosops* and all *Gracilinanus* have palatine fenestrae (p). Maxillary fenestrae (m), however, are present only in *Gracilinanus*. Scale bars equal 5 mm.

present as a cluster of larger and smaller openings between the maxillopalatine fenestrae and the postpalatine torus. The alisphenoid tympanic wings (auditory bullae) are large, almost hemispherical capsules without ventral processes or lateral constrictions. The upper canine lacks accessory cusps, and the last upper molar is not much wider (transverse dimension) than M3 and is approximately triangular in outline.

**MORPHOLOGICAL COMPARISONS:** *Marmosops creightoni* is the only known brownish-furred species of the genus to lack whitish thoracic or abdominal markings; all others have at least some white or cream-colored midventral fur that contrasts abruptly with the darker color of the dorsum and flanks.<sup>7</sup> In many species, whitish midventral fur (which may be either self-colored or gray-based) extends continuously from chin to anus, but in a few Amazonian and northern Andean forms (e.g., *M. neblina*; see Gardner, 1990: fig. 2) whitish midventral markings are narrow and sometimes discontinuous. Although narrow whitish midventral markings might occur polymorphically in larger samples of *M. creightoni*, the six examples at hand suggest that most individuals have completely dark venters.

Qualitative and morphometric comparisons with other Bolivian congeners (the identification and taxonomy of which are discussed below) reveal many additional differences (table 4). *Marmosops bishopi*, for example, is much smaller than *M. creightoni*, has dull reddish- or grayish-brown (versus rich chocolate-brown) dorsal fur, has pale-furred metapodials that do not contrast in color with the digits (versus dark-furred metapodials contrasting with whitish digits), does not have a pale tail-tip (versus pale tail-tip present), lacks palatine fenestrae (versus palatine fenestrae present), and has a small posterior accessory cusp on the upper canine (versus upper canine without accessory cusps). Also, adult males of *M. bishopi* usually lack a gular gland (versus gular gland weakly developed), have large bladelikey (versus knobby) lateral carpal tubercles, and

<sup>7</sup> *Marmosops invictus*, a small Panamanian species with blackish-gray fur, has dark underparts that are only superficially washed with white.

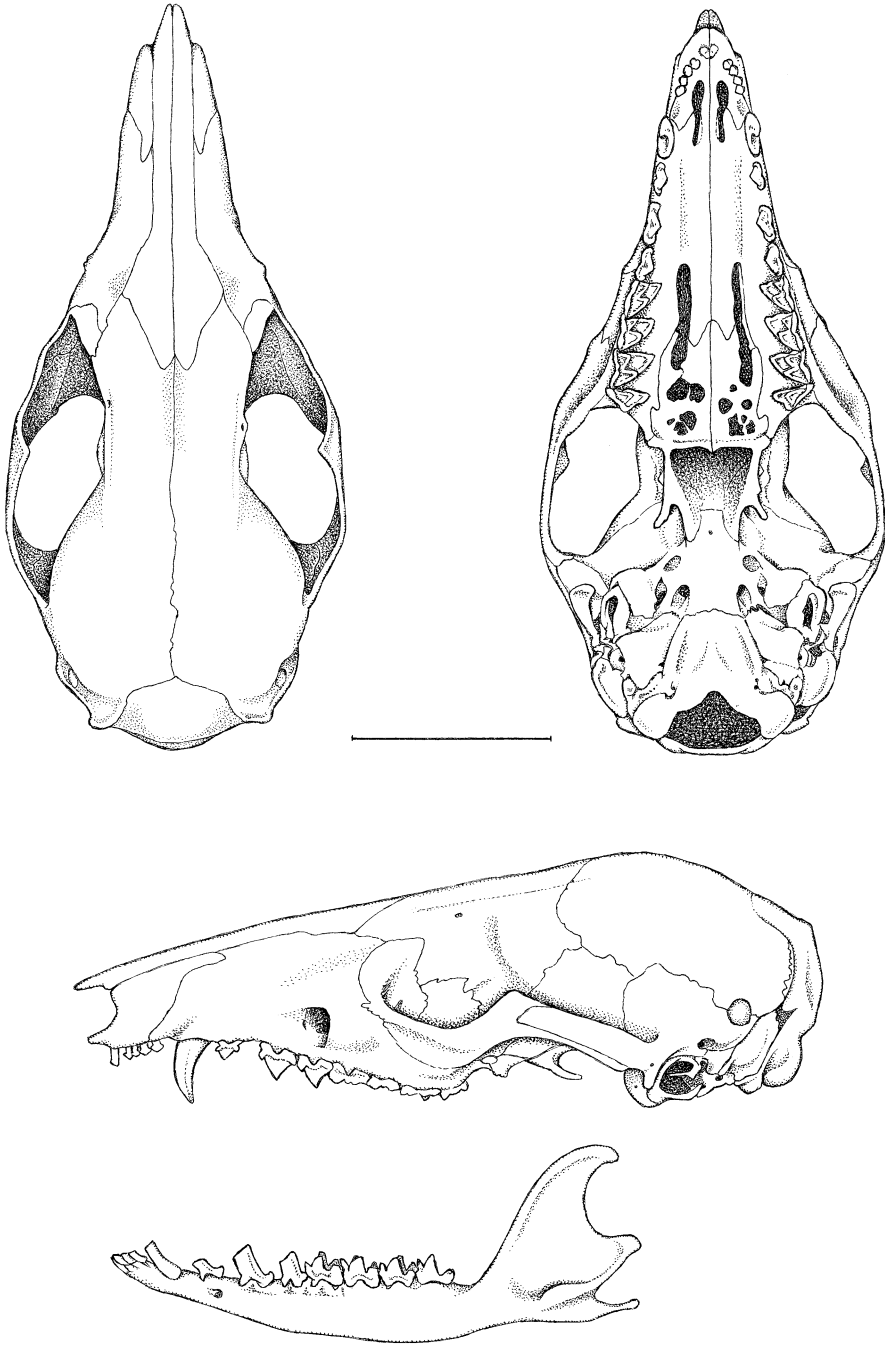


Fig. 9. Dorsal, ventral, and lateral views of the skull, and lateral view of the left hemimandible of the holotype of *Marmosops creightoni* (CBF 6552); however, some missing details (e.g., the nasal tips, broken in the holotype) are reconstructed from UMMZ 155999 (a paratype). Note that the illustrated left hemimandible of CBF 6552 is unusual in possessing only a single mental foramen; the right hemimandible has two foramina, as do both hemimandibles of all five paratypes. Scale bar equals 10 mm.



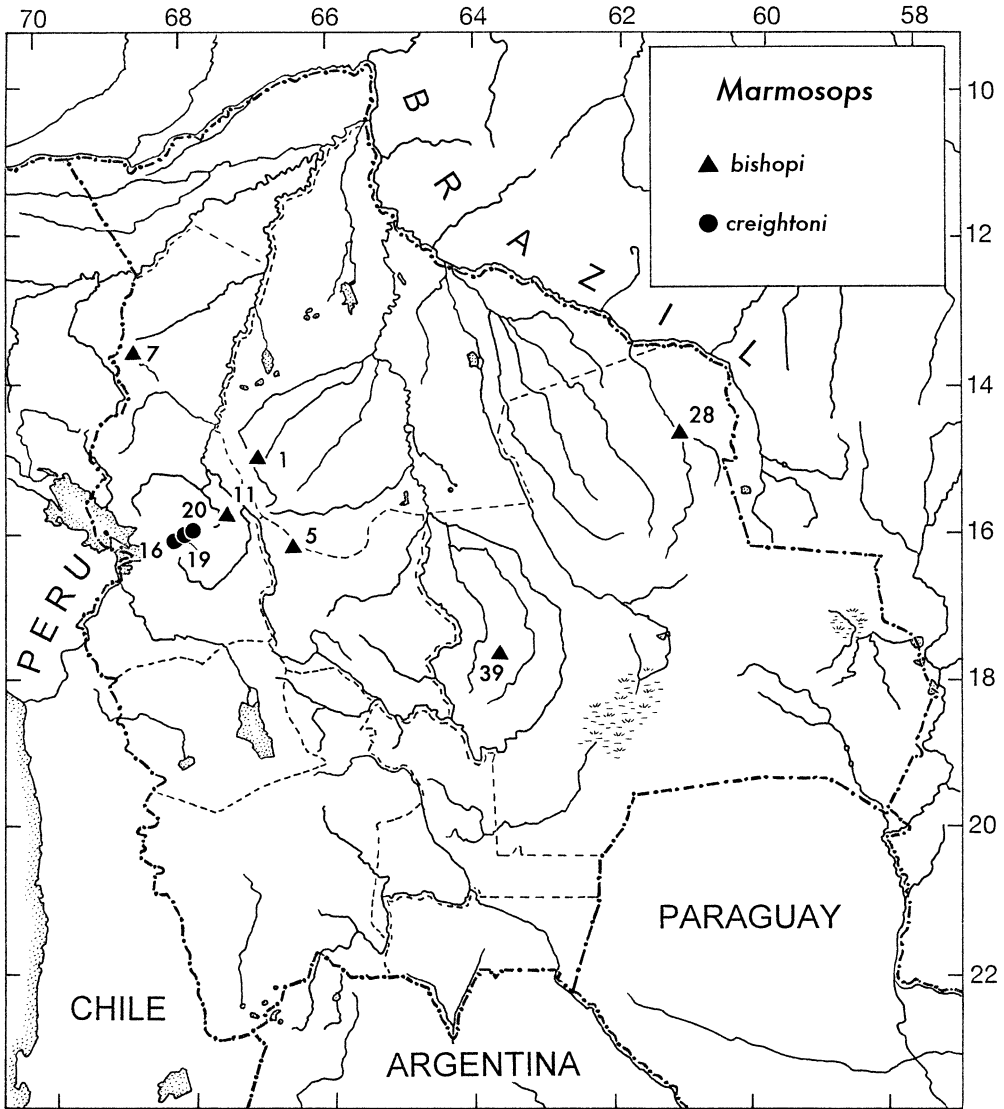


Fig. 10. Collection localities of *Marmosops bishopi* and *M. creightoni* in Bolivia. Numbers are keyed to gazetteer entries in appendix 2.

have a pale scrotum with white fur and unpigmented skin (versus scrotum dark with brown fur and mottled-grayish skin).

*Marmosops impavidus*, another Bolivian species, overlaps with *M. creightoni* in many measurements, although it averages smaller in most dimensions. However, *M. impavidus* has dull grayish- or reddish-brown (versus rich chocolate-brown) dorsal fur; pale-furred metapodials that do not contrast in color with

the digits (versus dark-furred metapodials contrasting with whitish digits); a much narrower interorbital region (LIB = 5.6–6.3 versus 6.6–7.2 mm); and much smaller bullae. In addition, adult males of *M. impavidus* appear to have no trace of a gular gland (versus gular gland weakly developed), and they have a pale scrotum with white fur and unpigmented skin (versus scrotum dark with brownish fur and mottled-grayish skin).

TABLE 3  
Measurements (mm) and Weights (g) of *Marmosops creightoni*

	CBF 6552 <sup>a</sup>	UMMZ 155999 <sup>b</sup>	UMMZ 156000 <sup>b</sup>	UMMZ 156001 <sup>b</sup>	UMMZ 156002 <sup>b</sup>	UMMZ 156003 <sup>b</sup>
Sex	male	male	male	male	female	female
HBL	132	127	140	129	120	114
LT	177	153	162	173	150	174
HF	20	18	20	19 <sup>c</sup>	18 <sup>c</sup>	18
Ear	23	23	25	23	21	21
CBL	35.6	33.3	35.5	35.0	32.7	32.6
NB	4.8	4.4	4.8	4.9	4.2	4.4
LIB	7.2	6.8	7.2	7.2	7.0	6.6
ZB	17.2	16.8	—	16.8	16.4	15.7
PL	21.2	19.7	—	20.3	19.3	19.2
PB	10.1	9.6	—	10.1	9.7	9.3
MTR	14.8	13.4	14.4	13.8	13.4	13.2
LM	6.8	6.5	7.0	6.6	6.7	6.5
M1–M3	5.7	5.6	6.1	5.7	5.8	5.6
WM4	2.2	2.1	2.3	2.2	2.0	2.0
Weight	48	36	54	43	32	35

<sup>a</sup>The holotype.

<sup>b</sup>Paratype.

<sup>c</sup>Remeasured from fluid-preserved specimen.

Bolivian specimens of *Marmosops noctivagus* overlap broadly with *M. creightoni* in most measured dimensions, but they usually have dull reddish-brown (versus rich chocolate-brown) dorsal fur; pale-furred metapodials that do not contrast in color with the digits (versus dark-furred metapodials contrasting with whitish digits); distinct supra-orbital beads that conceal the postorbital constriction from dorsal view (versus supra-orbital beads absent or indistinct and postorbital constriction visible dorsally); and smaller, conical or flask-shaped bullae (versus bullae larger and hemispherical). In addition, adult males of *M. noctivagus* have a pale scrotum with white fur and unpigmented skin (versus scrotum dark with brownish fur and mottled-grayish skin), and adult females have 5–1–5 = 11 mammae, of which the anteriormost pair is pectoral (versus 4–1–4 = 9 abdominal-inguinal teats).

*Marmosops ocellatus* also overlaps broadly with *M. creightoni* in most measured dimensions, but it has much paler grayish-brown (versus rich chocolate-brown) dorsal fur; pale-furred metapodials that do not contrast in color with the digits (versus dark-furred metapodials contrasting with whitish

digits); distinctly bi- and particolored tails, with the terminal one-third or more completely pale (versus tail indistinctly bicolored and only the tip completely pale); a much narrower interorbital region (LIB = 5.5–6.3 mm versus 6.6–7.2 mm); and proportionately wider zygomatic arches (ZB/CBL × 100 = 53–54% versus 48–50%). In addition, most adult males of *M. ocellatus* lack a gular gland (versus gular gland weakly developed), and adult females have 6–1–6 = 13 mammae, of which the anteriormost two pairs are pectoral (versus 4–1–4 = 9 abdominal-inguinal mammae).

Although we examined representative material of every species of *Marmosops* listed as valid in table 1, additional pairwise comparisons are unnecessary because other currently recognized species exhibit no special similarity with *M. creightoni*. Indeed, most extralimital (nonBolivian) species have strikingly divergent traits. *Marmosops cracens*, *M. fuscatus*, and *M. incanus*, for example, have uniformly narrow nasals with subparallel lateral margins (quite unlike the posteriorly expanded nasals of Bolivian forms); *M. pinheiroi* has lacrimal foramina that are laterally exposed anterior to the orbit (the

lacrimal foramina of Bolivian species are usually concealed from lateral view inside the orbit); and *M. paulensis* has very long incisive foramina that extend posteriorly behind the canine alveoli (the incisive foramina are substantially shorter in all Bolivian taxa). These and other taxonomically informative characters merit uniform scoring for phylogenetic analysis in any comprehensive attempt to revise the contents of *Marmosops*, but such exercises are beyond the scope of this preliminary report.

**MOLECULAR COMPARISONS:** The first 680 base-pairs of the mitochondrial cytochrome-*b* gene were sequenced from the holotype of *Marmosops creightoni* by J.L. Patton, whose generosity in sharing these data allowed us to make preliminary comparisons with homologous didelphid sequences previously obtained by his laboratory (Patton et al., 1996; Mustrangi and Patton, 1997; Patton et al., 2000). In order to assess the relationships of *M. creightoni* with other congeneric forms, we assembled a small dataset representing nine species of *Marmosops*, and we included *Gracilinanus microtarsus* as an outgroup (table 5). We selected exemplar haplotypes based on sequence length (the longest available sequence for each species was chosen), previous representation in published reports (Patton et al., 1996; Mustrangi and Patton, 1997; Patton et al., 2000), and accessibility of cataloged morphological voucher material in museums. Most species are represented by single haplotypes in our analysis, but we included three sequences from geographically divergent samples of *M. noctivagus* to assess molecular variation within a geographically widespread taxon.

As quantified by pairwise uncorrected sequence divergence (table 6), *Marmosops creightoni* is phenetically most similar to *M. noctivagus*, from which it differs on average by about 9.7%. Interestingly, of the three analyzed haplotypes of the latter species, *M. creightoni* is most divergent (10.9%) from the geographically proximal Bolivian sample and least divergent (9.2%) from each of the Peruvian and Brazilian specimens. All other pairwise interspecific comparisons in these results are >10% divergent, with the exception of a relatively small value (5.7%) between *M. impavidus* and *M. ocellatus*.

A branch-and-bound parsimony analysis of the nucleotide sequence data (implemented with PAUP 4.0b10; Swofford, 1998) recovered a single minimum-length tree with two main clades (fig. 11), one of which consists of *Marmosops creightoni*, *M. impavidus*, *M. noctivagus*, and *M. ocellatus* in the sequence (*noctivagus* (*creightoni* (*impavidus* + *ocellatus*))). The other clade contains members of the *parvidens* complex (*M. bishopi* and *M. parvidens*), two southeastern Brazilian forms (*M. incanus* and *M. paulensis*), and the Amazonian species *M. neblina*. Unfortunately, there is only weak Bremer and bootstrap support for several branches in this topology, notably including all of those that resolve the relationships of *creightoni* with other congeneric forms.

**NATURAL HISTORY:** All of our material of *Marmosops creightoni* was collected in the valley of the Río Zongo, one of the principal headwaters of the Río Beni on the eastern slopes of the Cordillera Real. The Valle de Zongo descends precipitously from 4800 to <900 m above sea level, with flanking slopes that are often in excess of 60°. The climate is very humid, with clouds and mist each morning and afternoon for most of the year. Between 2000 and 3000 m above sea level—the known elevational range of *M. creightoni*—the natural vegetation of the Valle de Zongo is humid montane (“cloud”) forest.<sup>8</sup> Habitat information associated with specimens of *M. creightoni* taken at three localities in the Valle de Zongo is summarized below, in order of their collection dates.

The five paratypes that G.K. Creighton collected in 1979 were taken at two localities along a road that descends the valley and provides access to a series of hydroelectric generating stations, power lines, and support facilities. His first collecting site was at Cu-

<sup>8</sup> We use the nontechnical term “cloud forest” for montane rainforests generally, including the formations that Grubb (1977) usefully defined as Lower Montane Rain Forest, Upper Montane Rain Forest, and Subalpine Rain Forest. Synonyms used by Bolivian botanists include “Ceja de Monte de Yungas” (corresponding to Subalpine Rainforest; e.g., at Cuticucho) and “Bosque Húmedo Montañoso de Yungas” (corresponding to Upper Montane Rainforest; e.g., at Saynani). For a critical review of “cloud forest” and its technical synonyms from a field zoologist’s point of view, see Myers (1969); for another (botanical) perspective, see Webster (1995).

TABLE 4  
Diagnostic Morphological Comparisons Among Five Bolivian Species of *Marmosops*<sup>a</sup>

<i>M. bishopi</i>	<i>M. creightoni</i>	<i>M. impanidus</i>	<i>M. noctivagus</i>	<i>M. ocellatus</i>
<p><i>Size</i> smallb HBL = 90–105 mm CBL = 26.2–27.3 mm LM = 5.4–5.8 mm Weight = 17–22 g</p> <p><i>Dorsal pelage</i> variable in coloration, dull reddish- to grayish-brown</p> <p><i>Ventral pelage</i> self-cream or self-white, with or without distinct lateral zones of gray-based hairs</p> <p><i>Gular gland</i> usually absent in both sexes</p> <p><i>Metacarpals and metatarsals</i> usually pale, not contrasting abruptly in color with digits</p> <p><i>Lateral carpal tubercles</i> present as large flattened blades in adult males</p> <p><i>Mammæ</i> unknown</p>	<p><i>Size</i> medium<sup>c</sup> HBL = 114–140 mm CBL = 32.6–35.6 mm LM = 6.5–7.0 mm Weight = 32–54 g</p> <p><i>Dorsal pelage</i> rich chocolate-brown</p> <p><i>Ventral pelage</i> (except for chin) entirely gray-based brown</p> <p><i>Gular gland</i> weakly developed in adult males</p> <p><i>Metacarpals and metatarsals</i> dark brown, contrasting abruptly with whitish digits</p> <p><i>Lateral carpal tubercles</i> present as small rounded knobs in adult males</p> <p><i>Mammæ</i> 4-1-4 = 9, all abdominal-inguinal</p>	<p><i>Size</i> medium<sup>d</sup> HBL = 109–130 mm CBL = 30.5–34.3 mm LM = 6.4–6.8 mm Weight = 25–34 g</p> <p><i>Dorsal pelage</i> grayish- to dull reddish-brown</p> <p><i>Ventral pelage</i> self-cream, usually with distinct lateral zones of gray-based hairs</p> <p><i>Gular gland</i> absent in both sexes</p> <p><i>Metacarpals and metatarsals</i> usually pale, not contrasting abruptly in color with digits</p> <p><i>Lateral carpal tubercles</i> present as small rounded knobs in adult males</p> <p><i>Mammæ</i> 3-1-3 = 7 or 4-1-4 = 9, all abdominal-inguinal<sup>g</sup></p>	<p><i>Size</i> medium to large<sup>e</sup> HBL = 120–151 mm CBL = 34.1–39.5 mm LM = 6.3–7.8 mm Weight = 39–55 g</p> <p><i>Dorsal pelage</i> variable in coloration, but usually some shade of dull reddish-brown</p> <p><i>Ventral pelage</i> self-cream, usually without distinct lateral zones of gray-based hairs</p> <p><i>Gular gland</i> always present in adult males</p> <p><i>Metacarpals and metatarsals</i> usually pale, not contrasting abruptly in color with digits</p> <p><i>Lateral carpal tubercles</i> present as small rounded knobs in adult males</p> <p><i>Mammæ</i> 5-1-5 = 11, of which the anteriormost pair is pectoral, the rest abdominal-inguinal<sup>g</sup></p>	<p><i>Size</i> medium<sup>f</sup> HBL = 104–140 mm CBL = 30.3–36.8 mm LM = 6.4–7.0 mm Weight = 24–39 g</p> <p><i>Dorsal pelage</i> uniformly pale grayish-brown</p> <p><i>Ventral pelage</i> self-cream, without distinct lateral zones of gray-based hairs</p> <p><i>Gular gland</i> usually absent in both sexes</p> <p><i>Metacarpals and metatarsals</i> usually pale, not contrasting abruptly in color with digits</p> <p><i>Lateral carpal tubercles</i> present as small rounded knobs in adult males</p> <p><i>Mammæ</i> 6-1-6 = 13, of which the two anteriormost pairs are pectoral, the rest abdominal-inguinal</p>

TABLE 4  
(Continued)

<i>M. bishopi</i>	<i>M. creightoni</i>	<i>M. impavidus</i>	<i>M. noctivagus</i>	<i>M. ocellatus</i>
<i>Scrotum</i> pale, with white fur and unpigmented skin	<i>Scrotum</i> dark, with brown fur and pigmented skin	<i>Scrotum</i> pale, with white fur and unpigmented skin	<i>Scrotum</i> pale, with white fur and unpigmented skin	<i>Scrotum</i> pale, with white fur and unpigmented skin
<i>Tail</i> unicolored (all dark) or indistinctly bicolored (dark above, pale below) above, pale below	<i>Tail</i> indistinctly bicolored (dark above, pale below) and particolored (all pale) near tip	<i>Tail</i> unicolored or indistinctly bicolored and particolored	<i>Tail</i> unicolored (all dark) in lowland populations, but indistinctly bicolored and particolored in the highlands	<i>Tail</i> distinctly bicolored and particolored, with the posterior half usually all pale
<i>Supraorbital margins</i> always rounded, apparently never with distinct beads	<i>Supraorbital margins</i> rounded in young adults, with indistinct beads in older individuals	<i>Supraorbital margins</i> rounded, usually without distinct beads	<i>Supraorbital margins</i> usually distinctly beaded in adults	<i>Supraorbital margins</i> rounded, apparently never with distinct beads
<i>Postorbital constriction</i> visible in dorsal view	<i>Postorbital constriction</i> usually visible in dorsal view	<i>Postorbital constriction</i> visible in dorsal view	<i>Postorbital constriction</i> usually concealed from dorsal view by supraorbital beads	<i>Postorbital constriction</i> visible in dorsal view
<i>Palatine fenestrae</i> absent	<i>Palatine fenestrae</i> present	<i>Palatine fenestrae</i> present	<i>Palatine fenestrae</i> present	<i>Palatine fenestrae</i> present
<i>Upper canine</i> with small posterior accessory cusp	<i>Upper canine</i> without accessory cusps	<i>Upper canine</i> without accessory cusps	<i>Upper canine</i> without accessory cusps	<i>Upper canine</i> without accessory cusps

<sup>a</sup>See text for more detailed character descriptions.

<sup>b</sup>Measurement and weight data from holotype and referred Bolivian material (table 7).

<sup>c</sup>Measurement and weight data from type series (table 3).

<sup>d</sup>Measurement and weight data from Peruvian and Bolivian material (table 8).

<sup>e</sup>Measurement and weight data from Peruvian and Bolivian material (tables 9, 10).

<sup>f</sup>Measurement and weight data from holotype and other referred Bolivian material (table 11).

<sup>g</sup>Mammary counts from Peruvian material only.

TABLE 5  
Exemplar Specimens Included in Molecular Analysis

Species	Voucher	Tissue	BP <sup>a</sup>	Geographic origin
<i>Gracilinanus microtarsus</i>	MVZ 197436	LPC 823	801	BRAZIL: <i>São Paulo</i> , Floresta Nacional de Ipanema
<i>Marmosops bishopi</i> <sup>b</sup>	AMNH 268938	NK 25679	801	BOLIVIA: <i>La Paz</i> , La Reserva
<i>Marmosops creightoni</i>	CBF 6552	EY 1705	680	BOLIVIA: <i>La Paz</i> , Saynani
<i>Marmosops impavidus</i>	MVZ 190268	MNFS 760	792	BRAZIL: <i>Amazonas</i> , Barro Vermelho, Rio Juruá
<i>Marmosops incanus</i>	MVZ 182771	MAM 204	801	BRAZIL: <i>Minas Gerais</i> , Estação Biológica de Caratinga
<i>Marmosops neblina</i>	USNM 560732	ALG 14410	801	VENEZUELA: <i>Amazonas</i> , Cerro de la Neblina
<i>Marmosops noctivagus</i>	AMNH 268936	NK 25272	801	BOLIVIA: <i>La Paz</i> , Chijchijpa
<i>Marmosops noctivagus</i>	INPA 2931	MNFS 381	792	BRAZIL: <i>Amazonas</i> , Penedo, Rio Juruá
<i>Marmosops noctivagus</i> <sup>c</sup>	MVZ 171408	JLP 11895	1149	PERU: <i>Cusco</i> , 72 km NE Paucartambo
<i>Marmosops ocellatus</i> <sup>d</sup>	MSB 58511	NK 15126	775	BOLIVIA: <i>Santa Cruz</i> , Tita
<i>Marmosops parvidens</i>	ROM 97938	FN 33439	666	GUYANA: <i>Upper Takutu–Upper Essequibo</i> , Karanambo
<i>Marmosops paulensis</i>	MNRJ 31369	ML 30	792	BRAZIL: <i>Rio de Janeiro</i> , Bonsucesso

<sup>a</sup>Base pairs of cytochrome *b* sequenced by J. L. Patton and his colleagues.

<sup>b</sup>Identified as *Marmosops parvidens* in analyses previously reported by Mustrangi and Patton (1997) and Patton et al. (2000).

<sup>c</sup>Identified as *Marmosops albiventris* in analyses previously reported by Mustrangi and Patton (1997).

<sup>d</sup>Identified as *Marmosops dorothea* or *M. impavidus* in analyses previously reported by Mustrangi and Patton (1997) and Patton et al. (2000).

ticucho (= Cuti Khuchu on recent topographic maps), which he recorded as having an elevation of 2967 m above sea level (but see appendix 2: locality 16). The site is described in his fieldnotes as follows:

Since our arrival [six days ago] we have not seen the sun for more than an hour a day. Clouds move up the valley in the morning at around 8:30AM and form just below our camp. Intermittent rain and mist are the order of the day. The temperature here stays relatively constant, between 55 and 65° F [13–18° C]. The forest here is *very damp*—many lichens, moss and ferns on branches of trees. We have trapped in three habitats here: cloud forest (relatively undisturbed), 2nd growth forest—with much bamboo; and

artificial clearings under power lines . . . We are very near treeline here; as one looks up the valley the trees thin out and disappear at a fairly distinct “line” about 300 m above camp. Looking down the valley the trees get noticeably higher . . . [3 October 1979]

Both specimens of *Marmosops creightoni* from Cuticucho were taken in the cloud forest with snap traps: one (UMMZ 155999) at the base of a tree and the second (UMMZ 156000) on a low branch. Creighton also collected five species of sigmodontine rodents at this site, of which *Akodon mimus*, *Oxymycterus nigrifrons*, and two undescribed forms of *Thomasomys* (“sp. 1” and “sp. 3”

TABLE 6  
Uncorrected Percent Sequence Divergence Among Cytochrome-*b* Haplotypes from Nine Species of *Marmosops*

<i>creightoni</i>	16.8							
<i>impavidus</i>	15.9	10.6						
<i>incanus</i>	18.0	14.5	15.2					
<i>neblina</i>	18.4	13.2	12.6	16.4				
<i>noctivagus</i>	18.7 <sup>a</sup>	9.7 <sup>a</sup>	11.6 <sup>a</sup>	15.2 <sup>a</sup>	15.1 <sup>a</sup>			
<i>ocellatus</i>	17.8	11.8	5.7	16.8	14.3	12.3 <sup>a</sup>		
<i>parvidens</i>	16.4	17.0	17.5	15.6	18.4	17.3 <sup>a</sup>	17.7	
<i>paulensis</i>	17.9	15.6	13.9	15.5	16.5	16.3 <sup>a</sup>	14.8	18.7
	<i>bishopi</i>	<i>creightoni</i>	<i>impavidus</i>	<i>incanus</i>	<i>neblina</i>	<i>noctivagus</i>	<i>ocellatus</i>	<i>parvidens</i>

<sup>a</sup>Average value of distances to all three *M. noctivagus* haplotypes included in the analysis (see table 5).

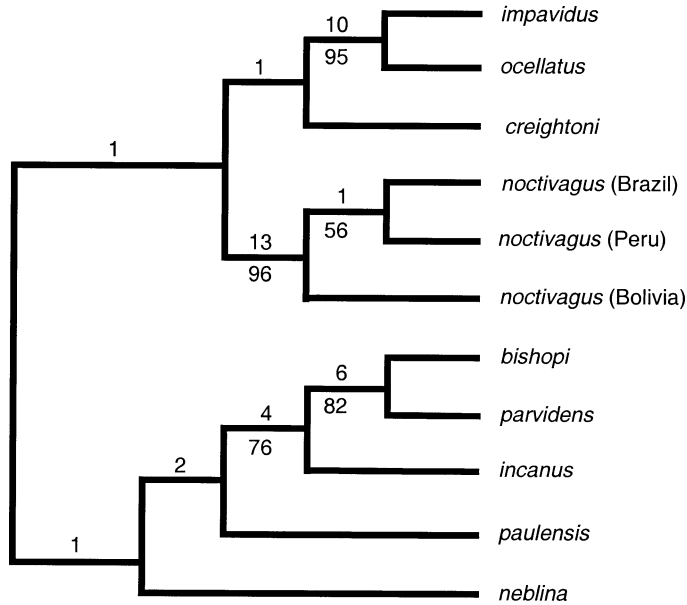


Fig. 11. The unique minimum-length tree recovered by a branch-and-bound parsimony analysis of cytochrome-*b* nucleotide sequences representing 11 ingroup haplotypes from 9 *Marmosops* species and 1 outgroup haplotype from *Gracilinanus microtarsus* (used to root the tree, not shown). Bremer support and bootstrap values (>50%) are provided above and below each branch, respectively. The bootstrap values were obtained from branch-and-bound analyses of 1000 pseudoreplicated datasets. Tree length (including autapomorphies) = 689 steps, consistency index (excluding autapomorphies) = 0.48, retention index = 0.44.

of Pacheco, 2003) were trapped in the cloud forest; *Oryzomys levipes* was trapped in nearby secondary growth. Additional species of small mammals subsequently trapped near Cuticucho by other researchers include *Gracilinanus aceramarcae* (see Salazar-Bravo et al., 2002), *Akodon* cf. *boliviensis*, and an undescribed form of *Oligoryzomys* ("sp. B" of the *flavescens* group; Carleton and Musser, 1989).

Farther down the valley G.K. Creighton described his camp at a locality he called "Cement Mine" (not identifiable on our topographic maps), with a recorded elevation of 2000 m, as being much warmer than at Cuticucho and with taller forest. However,

Much of the forest has been cut or burned at one time or another in the past 30 years, hence most . . . is 2nd growth except in the higher valleys intersecting this one at more or less right angles. Lichens & moss on trees are solid in places but not as "lush" as near Cuticucho. There are more broadleaf trees and "papaya-like" trees here. Also large (~10 m) tree ferns. Bamboo undergrowth is extensive and very dense

near artificial clearings. Little undergrowth beneath the bamboo except for a few ferns. [6 October 1979]

The first four nights of trapping (5–8 October) at this site yielded only rodents (the same species as those found in the cloud forest near Cuticucho plus *Microryzomys minutus* and *Thomasomys* cf. *oreas*), but two specimens of *Marmosops creightoni* were taken on 9 October and another on 10 October. Creighton's notes for these dates indicate that the marsupials were trapped in "humid, dark, mossy forest" on horizontal branches near large trees "covered with moss, ferns, bromeliads & vines". Apparently, they were "not caught coming to the bait but, rather, blundering into the traps as they tiptoe along their accustomed routes." The area where all three *Marmosops* were trapped included "about the only places where high, undisturbed natural forest is accessible enough to set a trapline", the only other primary forest being restricted to very steep slopes above the cultivated valley floor.

The holotype of *Marmosops creightoni* was collected by EY near the Saynani hydroelectric generating station at 2500 m on the southeastern side of the valley. The obviously disturbed forest at this site consisted of patches with a closed canopy but also open areas with isolated trees. The trees were laden with epiphytes, and the ground cover consisted of vines, small bamboo, grasses, moss, and ferns. The holotype was taken on the ground, in a snap trap set in dense grass under a small tree. All of the other small mammals trapped at Saynani by EY and other researchers are sigmodontine rodents, including *Akodon mimus*, *Chibchanomys* sp., *Microroryzomys minutus*, *Oryzomys levipes*, *Oxymycterus nigrifrons*, and the same undescribed forms of *Oligoryzomys* and *Thomomys* that occur at Cuticucho.

In summary, *Marmosops creightoni* has been collected in both primary cloud forest and disturbed vegetation in the Valle de Zongo, where it occurs sympatrically with *Gracilinanus aceramarcae* and several species of sigmodontine rodents between 2000 and 3000 m above sea level. A different species of *Marmosops*, however, inhabits lower elevations in the Zongo valley. Two specimens, one from El Vertigo at 1800 m (CBF 4003) and another from Kahua at 1150 m (CBF 3880), are both referable to *M. noctivagus* as we recognize that species below. Future collecting in the elevational interval between 2000 and 1000 m would be helpful in pinpointing just where these congeneric species occur sympatrically or parapatrically along the forested eastern slopes of the Cordillera Real.

#### NOTES ON THE TAXONOMY AND DISTRIBUTION OF OTHER BOLIVIAN FORMS

In the course of searching museum collections for additional examples of *Marmosops creightoni*, we examined many other Bolivian specimens of *Marmosops* and sorted them into phenotypically distinctive groups that we provisionally recognize as species. The following accounts summarize our conclusions about the taxonomy and distribution of these forms based on currently available information. For each species recognized be-

TABLE 7  
Measurements (mm) and Weights (g)  
of the Brazilian Holotype and Referred  
Bolivian Material of *Marmosops bishopi*

	Brazil		Bolivia		
	USNM 393535 <sup>a</sup>	AMNH 268938	CBF 7531	MSB 55843	LHE 1541 <sup>b</sup>
Sex	female	female	male	male	male
HBL	102	90	105	93	96
LT	116	120	130	137	126
HF	15	15	15	17	15
Ear	21	21	22	21	19
CBL	26.6	26.2	27.3	26.9	26.7
NB	3.3	3.5	3.4	3.3	3.5
LIB	5.4	5.2	5.5	5.4	5.1
ZB	14.5	13.4	14.1	13.7	14.2
PL	14.7	14.8	15.2	14.9	15.0
PB	8.8	8.4	8.2	8.3	8.0
MTR	11.0	11.2	10.8	10.9	10.6
LM	5.6	5.8	5.6	5.7	5.4
M1-M3	4.8	5.0	5.0	5.1	4.8
WM4	2.1	2.0	1.8	2.0	1.8
Weight	—	17	22	18	18

<sup>a</sup>The holotype, from Mato Grosso, Brazil.

<sup>b</sup>To be cataloged in the USNM collections.

low, we explain the morphological and other criteria that were used to assign names, and we note conflicting identifications of the same material reported by Anderson (1997), the most authoritative available reference on Bolivian mammalogy.<sup>9</sup>

#### *Marmosops bishopi*

This appears to be the appropriate name for Bolivian specimens of the *Marmosops parvidens* group, of which we have examined eight examples from widely scattered localities in Beni, Cochabamba, La Paz, and Santa Cruz (fig. 10). These are all very small animals (table 7) with much shorter molar series (LM  $\leq$  5.8 mm) than any other Bolivian congener. The skulls have rounded supraorbital margins that lack distinct beading, shallow postorbital constrictions are dorsally visible, there are no palatine fenestrae, and

<sup>9</sup> Because Anderson (1997) seldom cited museum catalog numbers, we consulted his card file of examined specimens (preserved in the AMNH Department of Mammalogy archives) to determine the empirical basis for mapped collection localities of Bolivian *Marmosops* (Anderson, 1997: figs. 493–495).



the upper canines have small posterior accessory cusps. Although one adult male (MSB 55843) has an almost-naked patch of skin and a streak of red-stained fur on the midline of the throat, two others (CBF 7531, LHE 1541) have no trace of a gular gland. All three adult males have well-developed, blade-like lateral carpal tubercles, and the scrotum is pale, with white fur and unpigmented skin. None of the females we examined had well-developed mammae, so it is not known whether or not this taxon has pectoral teats.

There is noteworthy pelage color variation among the material at hand. All of the specimens we examined from Beni, Cochabamba, La Paz, and western Santa Cruz have dull reddish-brown dorsal fur, self-whitish ventral fur bordered by more-or-less distinct lateral zones of gray-based hairs, and unicolored tails. By contrast, the single available skin from eastern Santa Cruz (LHE 1541)<sup>10</sup> has pale grayish-brown dorsal fur, self-cream ventral fur (without well-defined lateral zones of gray-based hairs), and an indistinctly bicolored tail. Despite these pigmental differences, specimens from eastern Santa Cruz do not differ from the rest of our Bolivian material in other respects (e.g., measurements and qualitative craniodental traits), and partial cytochrome-*b* sequences from representative exemplars (LHE 1541 and AMNH 268938) differ by only about 3.8% (J.L. Patton, personal commun.).

Specimens that we identify as *Marmosops bishopi* were included among the material that Anderson (1997) reported as *M. impavidus* (e.g., UMMZ 156014), *M. noctivagus keaysi* (USNM 579249), and *M. parvidens* (AMNH 268938).

BOLIVIAN SPECIMENS EXAMINED: *Beni*, 1 km E La Embocada (UMMZ 156014); *Cochabamba*, Cordillera de Mosetenes (CBF 7531); *La Paz*, Alto Río Madidi (USNM 579249), La Reserva (AMNH 268938); *Santa Cruz*, El Refugio (LHE 1541, 1553, 1556), San Rafael de Amboró (MSB 55843).

<sup>10</sup> Unfortunately, both of the other specimens we examined from eastern Santa Cruz (LHE 1553, 1556) consist of skulls extracted from rotted specimens found in pitfall traps.

### *Marmosops impavidus*

The application of the name *impavidus* is problematic because no type material is known to exist, and because Tschudi's (1845) original description is diagnostically inadequate (Tate, 1933: 25, 182). Current usage dates from Cabrera (1958), who used the binomen *M. impavidus* for the taxon that Tate (1933) recognized as *M. cauae*. Although the lost type material is assumed to have been collected in the eastern foothills of the Peruvian Andes, no exact location was explicitly stated in the original description. For the purposes of this report, we assume that a small series of specimens (AMNH 230017, 230018, 230020, 230022–230027) collected near San Pablo (ca. 10°27'S, 74°52'W; 275 m above sea level) in the Peruvian department of Pasco represents the typical morphology.

This a medium-size species (table 8), larger than *Marmosops bishopi* but averaging smaller than typical specimens of *M. noctivagus* (see Patton et al. [2000] and below). The dorsal pelage is dull grayish-brown to reddish-brown, with drab (grayish) hues predominating among younger specimens and warmer (reddish) tones predominating among older adults. The ventral pelage of most Peruvian and western Brazilian specimens consists of a median strip of self-white or cream-colored fur from chin to anus, bordered by lateral zones of gray-based fur between the fore- and hindlimbs. However, in the Peruvian material at hand (which includes specimens from Ucayali and Loreto in addition to the Pasco sample mentioned above) the relative widths of the median self-colored and lateral gray-based zones exhibit considerable variation. The metapodials are covered with pale fur that does not contrast abruptly in color with the digits. Tails are sometimes indistinctly bicolored (paler below than above; e.g., AMNH 230017) and particolored (paler distally than proximally; e.g., AMNH 230027), but other individuals have almost unicolored tails (e.g., AMNH 76531). Adult males have knob-like lateral carpal tubercles, but none that we examined has a gular gland; the scrotal fur is white and the scrotal epithelium is unpigmented. One lactating female from Loreto (AMNH

TABLE 8

Measurements (mm) and Weights (g) of Peruvian and Bolivian Specimens of *Marmosops impavidus*

	Peru					Bolivia
	AMNH 230017	AMNH 230020	AMNH 230025	AMNH 230027	AMNH 230026	MSB 57002
Sex	female	female	male	male	unknown	male
HBL	124	109	130	115	—	110
LT	141	—	150	132	—	147
HF	18	—	19	18	—	17
Ear	18	—	20	19	—	20
CBL	31.1	30.5	33.0	30.6	34.3	31.4
NB	4.1	3.7	4.3	4.2	4.4	3.7
LIB	5.8	5.8	5.8	5.7	6.3	5.6
ZB	—	16.0	16.6	16.6	—	16.3
PL	17.8	17.4	18.9	17.4	19.7	18.1
PB	10.6	9.9	9.8	10.2	10.7	9.7
MTR	13.0	13.8	14.0	12.7	14.0	12.7
LM	6.6	6.7	6.6	6.4	6.8	6.4
M1-M3	5.7	5.7	5.6	5.6	5.8	5.4
WM4	2.5	2.3	2.3	2.5	2.4	2.4
Weight	34	—	—	49	—	25

272709) has 3-1-3 = 7 mammae, but another from the same locality (AMNH 273151) has 4-1-4 = 9; all of the teats in both individuals are abdominal/inguinal.

In craniodental morphology, *Marmosops impavidus* can be distinguished from other Bolivian congeners by the absence of supra-orbital beads (usually distinct in *M. noctivagus*); presence of a shallow but usually distinct postorbital constriction (usually absent in *M. noctivagus*); presence of palatine fenestrae (absent in *M. bishopi*); absence of accessory upper canine cusps (present in *M. bishopi*); and very small, usually conical bullae.

The sole Bolivian specimen that we identify as *Marmosops impavidus* is MSB 57002, which was collected sympatrically with *M. noctivagus* at Palmira in the lowlands of Pando department (fig. 12). This specimen has redder dorsal fur and narrower nasals than do most Peruvian specimens, but its morphology is otherwise a good match with topotypical (Peruvian) material. Other Bolivian specimens previously referred to this species, however, appear to represent different taxa.

Anderson (1997: 153) reported two specimens identified as *Marmosops impavidus* from Incachaca in Cochabamba department, but cited only one by catalog number (AMNH 38718); the specimen in question is

a juvenile whose broken skull (originally miscataloged as 38711) exhibits incipient supra-orbital beading, very short canines, and small molars (LM = 6.3 mm), traits that closely match Tate's (1933) description of *yungasensis*—a taxon that we consider to be a junior synonym of *M. noctivagus* (see below). Two other Bolivian specimens explicitly identified by Anderson as *M. impavidus* are UMMZ 126680 (from 20 km NNE Caranavi, in La Paz department) and UMMZ 156014 (from 1 km E La Embocada, in Beni department). The former is a subadult whose lack of supra-orbital beading is possibly due to immaturity, but whose lack of a postorbital constriction more closely resembles the material we refer to *M. noctivagus* (see below). UMMZ 156014, however, is an example of *M. bishopi* (see above). The only additional material that Anderson referred to *M. impavidus* consists of MSB 57000 (from Independencia in Pando department) and MSB 58508 (from 2 km S Caranda in Santa Cruz department); both are examples of "*Gracilinanus*" *unduaviensis*, a taxon that is currently treated (e.g., by Gardner, 1993) as a junior synonym of *G. agilis*.

BOLIVIAN SPECIMENS EXAMINED: *Pando*, Palmira (MSB 57002).

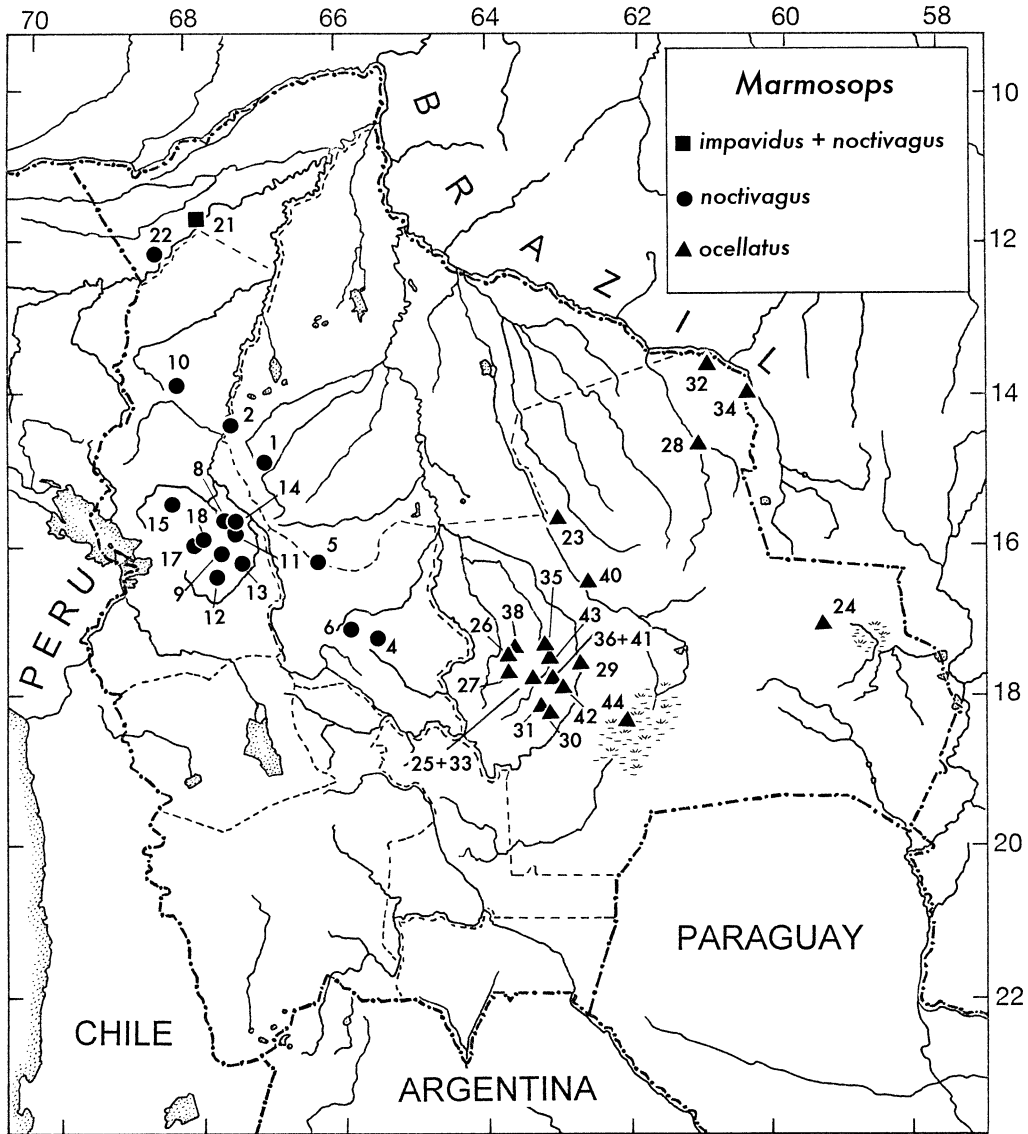


Fig. 12. Collection localities of *Marmosops impavidus*, *M. noctivagus*, and *M. ocellatus* in Bolivia. Numbers are keyed to gazetteer entries in appendix 2.

#### *Marmosops noctivagus*

This appears to be the appropriate name for the most-frequently collected species of *Marmosops* in north-central Bolivia (fig. 12); we consider *albiventris*, *dorothea*, *keaysi*, and *yungasensis* to be synonyms, as explained below. The name *noctivagus* is based on Peruvian type material that we have not examined, but a series of AMNH specimens from the Andean piedmont (<1000 m) near

Tarma in the department of Junín are more-or-less topotypical, and we have a large series of very similar specimens from Loreto. One Bolivian specimen from La Paz (USNM 579250) and three from Pando (AMNH 262402–262404) closely resemble this lowland Peruvian material and could be referred to the nominotypical subspecies (*M. n. noctivagus*) if a trinomial nomenclature were needed. This material comprises relatively

TABLE 9  
**Measurements (mm) and Weights (g) of Lowland Specimens of *Marmosops noctivagus*  
 from Peru and Bolivia**

	Peru: Junín <sup>a</sup>				Bolivia: La Paz and Pando			
	AMNH 230005	AMNH 230010	AMNH 230013	AMNH 230012	USNM 579250	AMNH 262404	AMNH 262402	AMNH 262403
Sex	female	female	female	male	female	female	male	male
HBL	141	124	[140] <sup>b</sup>	126	141	126	120	123
LT	170	156	165	189	173	164	184	167
HF	19	17	[19] <sup>b</sup>	21	19	20	20	20
Ear	25	20	18	24	23	20	22	21
CBL	—	34.8	36.3	38.7	35.9	34.7	36.1	35.0
NB	4.5	4.2	4.1	4.0	4.0	3.8	3.9	3.8
LIB	6.6	6.3	6.2	6.7	6.5	6.2	6.1	6.0
ZB	18.2	17.1	18.4	18.8	19.3	18.3	18.3	18.3
PL	20.5	20.0	21.0	22.4	21.0	20.2	21.2	20.2
PB	11.5	11.0	11.0	11.2	11.3	11.5	10.8	11.0
MTR	15.1	15.0	15.0	16.4	15.2	15.1	15.6	14.8
LM	7.5	7.5	7.4	7.6	7.8	7.4	7.4	7.4
M1–M3	6.4	6.4	6.4	6.5	6.7	6.3	6.4	6.4
WM4	2.9	2.6	2.7	2.7	2.9	2.8	2.6	2.6
Weight	48	—	59	58	42	37	36	35

<sup>a</sup>The external measurements of this series were taken by several different individuals, some of whom were inexperienced undergraduate students, and exhibit more variation than is usual in otherwise homogeneous samples of small didelphids.

<sup>b</sup>Two measurements recorded by the collector of this specimen are anatomically impossible. We assume that the true value for TL was 305 rather than the recorded value of 205 mm (resulting in a computed value for HBL of 140 versus 40 mm), and that the true value for HF was 19 rather than the recorded value of 9 mm.

large specimens (table 9) with dull reddish-brown dorsal fur, mostly self-whitish ventral fur, pale-furred metapodials that do not contrast abruptly in color with the digits, and more-or-less unicolored (all-dark) tails. All of the adult males we examined have well-developed gular glands, knobby (not blade-like) lateral carpal tubercles, and pale scrotums with whitish fur and unpigmented skin. Although we have not seen fluid-preserved parous adult females from Bolivia, two Peruvian specimens (AMNH 272782, 273051) each have 5–1–5 = 11 mammae, of which the anteriormost pair is pectoral. Associated skulls have distinct supraorbital beads (best developed in fully adult individuals; fig. 4B) and lack dorsally visible postorbital constrictions; palatine fenestrae are present, and the auditory bullae are small and conical. The upper canine lacks accessory cusps, and M4 is very wide.

The remaining Bolivian material that we refer to *Marmosops noctivagus* is from the foothills and lower montane regions of Beni,

Cochabamba, and La Paz. The specimens in question include the type material of *dorothea* and *yungasensis*, but an older name for the same phenotype is *keaysi* (from southern Peru; appendix 1).<sup>11</sup> Measurements of representative examples (including relevant type material; table 10) indicate that these highland specimens are about the same size as typical (lowland) *noctivagus*, but they have (on average) slightly broader interorbital regions, shorter molar rows, and narrower fourth upper molars. In addition, the dorsal fur tends to be slightly longer, the palatal fenestrae to be somewhat larger, and the bullae to be more inflated in highland examples than in lowland specimens. Also, whereas

<sup>11</sup> Although Anderson (1997: 152–154) reported “*Marmosops dorothea*” and “*Marmosops noctivagus keaysi*” as co-occurring at Chijchijpa in the department of La Paz, all of the specimens in question (at AMNH and MSB) are taxonomically indistinguishable. Anderson’s records of these taxa from Chijchijpa therefore represent alternative identifications (apparently copied from skin labels), not sympatry.

most lowland specimens have more-or-less unicolored (all dark) tails, tails of highland specimens are usually indistinctly bicolored (dark above, pale below) and particolored (paler distally than basally). Despite such elevation-correlated phenotypic variation, cytochrome-*b* sequences analyzed by Mustrangi and Patton (1997) and by Patton et al. (2000) indicate only minor divergence (about 3%) among lowland and highland haplotypes of *noctivagus*-like *Marmosops*, including specimens from the Amazonian lowlands of western Brazil (e.g., INPA 2931), the Andean slopes of southeastern Peru (e.g., MVZ 171408), and northern Bolivia (e.g., AMNH 268936). The nominal taxon that Tate (1931) described as *albiventris*, currently synonymized with *M. impavidus*, is morphologically indistinguishable from *M. noctivagus* and has similar mtDNA sequences (Mustrangi and Patton, 1997).<sup>12</sup>

Traditional taxonomic distinctions among forms that we consider conspecific with *Marmosops noctivagus* are almost entirely based on coat color. Tate (1933: 153–161), for example, described the dorsal fur as “varying from natal brown . . . to Mars brown” in typical *noctivagus*, by contrast with “bone brown . . . or warm sepia” in *keaysi* and “pecan brown” in *dorothea*. These chromatic differences are real, but similarities among these nominal taxa in other morphological characters, the existence of intermediate pelage hues in larger series of *noctivagus*-like eastern-slope specimens obtained in recent years, and the modest range of mtDNA variation among geographically widespread samples suggest that such color contrasts are not taxonomically significant.

Paradoxically, several holotypes in this complex exhibit atypical craniodental measurements, a factor that may have contributed to the traditional view that these specimens represent distinct taxa. For example, the ho-

lotype of *keaysi* is an exceptionally large male with a very broad interorbit that is not matched by any paratype or topotype that we examined. By contrast, the holotype of *dorothea* has an unusually narrow interorbit, and the holotype of *yungasensis* has a conspicuously short molar toothrow. Unfortunately, there are no large series from any locality to serve as a relevant standard by which such morphometric variation might be assessed. Just among the 11 specimens of “*yungasensis*” from Pitiguaya, however, interorbital breadth varies from 5.6 to 6.4 mm, and length of the molar series varies from 6.3 to 7.1 mm. Therefore, none of the exceptional values for these dimensions in table 10 would appear inconsistent with the hypothesis that the taxa represent one geographically variable species.

Most of the specimens that we refer to *Marmosops noctivagus* were identified by Anderson (1997) as *M. dorothea* or *M. noctivagus keaysi*, but some were identified as *M. impavidus* as explained in the preceding account, and three others (UMMZ 155829, 156006, 156007) were identified as *Gracilnanus agilis unduaviensis*.

BOLIVIAN SPECIMENS EXAMINED: *Beni*, 1 km E La Embocada (UMMZ 156008, 156013), Rurrenabaque (AMNH 247651); *Cochabamba*, Incachaca (AMNH 38718), Cordillera de Mosetenes (CBF 7527, 7560, 7573, 7577), Tablas Monte (AMNH 275451–275458; MSB 70276–70280, 87080); *La Paz*, 20 km NNE Caranavi (UMMZ 126680), Chijchijpa (AMNH 268936, 268937, 275459; MSB 57004, 68333, 68334, 87092, 87110), El Vertigo (CBF 4003), 13 km SW Ixiamas (USNM 579250), Kahua (CBF 3880), La Reserva (MSB 68335), Pitiguaya (AMNH 72550, 72558–72562, 72564, 72566; UMMZ 155829, 156006, 156007), Río Solacama (BMNH 1.2.1.36, 1.6.7.79), Serranía Bella Vista (AMNH 275460), Ticunhuaya (AMNH 72567); *Pando*, Palmira (AMNH 262402, 262403), Santa Rosa (AMNH 262404).

### *Marmosops ocellatus*

Judging from the large numbers of specimens in museum collections, *Marmosops ocellatus* is the commonest (or most frequently trapped) small marsupial throughout most of Santa Cruz department, from the base of the Andes to the Brazilian frontier (fig. 12). Currently considered to be a junior

<sup>12</sup> We examined the holotype of *Marmosa caucae albiventris* (USNM 194378) and the specimens that Mustrangi and Patton (1997) identified as *Marmosops albiventris* (MVZ 171408, 173930–173935). All of this material fits our working diagnosis of *M. noctivagus* (table 4) and exhibits no close similarity with *M. impavidus*. In particular, the ventral fur is mostly self-white, the supraorbital margins are distinctly beaded in mature adults, and all of the adult male skins exhibit well-developed gular glands.

TABLE 10  
 Measurements (mm) and Weights (g) of Highland Specimens of *Marmosops noctivagus*,  
 Including the Type Material of Nominal Taxa Originally Described as *keaysi*, *dorothea*, and *yungasensis*

	Peru: Puno				Bolivia: La Paz			
	AMNH 16069 <sup>a</sup>	AMNH 16472 <sup>b</sup>	AMNH 16473 <sup>b</sup>	AMNH 16068 <sup>c</sup>	BMNH 1.6.7.79 <sup>d</sup>	AMNH 72558 <sup>e</sup>	AMNH 268936 <sup>f</sup>	AMNH 268937 <sup>f</sup>
Sex	female	female	male	male	female	female	male	male
HBL	132	127	143	151	130	136	130	124
LT	185	178	175	204	158	169	168	163
HF	17	19	22	22	17	17	19	19
Ear	—	—	—	—	25	—	24	24
CBL	35.7	—	35.1	39.5	34.2	35.6	34.1	34.5
NB	4.4	3.9	4.8	4.6	4.3	4.7	4.1	4.2
LIB	6.8	6.5	7.2	7.5	5.9	6.6	6.4	6.3
ZB	17.7	17.3	18.6	20.0	17.5	18.3	17.5	17.6
PL	20.7	20.0	20.5	22.7	19.2	20.5	19.6	20.0
PB	10.7	10.8	10.9	11.6	10.9	10.6	10.4	10.6
MTR	14.5	14.6	14.2	16.0	13.9	13.6	13.8	14.4
LM	6.9	7.2	6.7	7.2	6.7	6.3	6.7	6.9
M1–3	5.9	6.1	5.8	6.2	5.8	5.6	5.8	5.8
WM4	2.3	2.5	2.4	2.6	2.4	2.2	2.5	2.5
Weight	—	—	—	—	—	—	37	37

<sup>a</sup>Paratype of *keaysi*.

<sup>b</sup>Topotype of *keaysi*.

<sup>c</sup>Holotype of *keaysi*.

<sup>d</sup>Holotype of *dorothea*.

<sup>e</sup>Holotype of *yungasensis*.

<sup>f</sup>From Chijchijpa; AMNH 268936 was sequenced by Mustrangi and Patton (1997).

synonym of *dorothea* (= *M. noctivagus* in our usage; see above), *M. ocellatus* is an unambiguously diagnosable taxon that more closely resembles *M. impavidus* in morphology and mtDNA sequences (tables 4, 6).

Externally, *Marmosops ocellatus* is distinctively paler than other Bolivian species, with sandy grayish-brown dorsal fur and self-cream underparts that lack distinct lateral zones of gray-based hairs. The metapodials are covered dorsally with pale (whitish) hairs that do not contrast abruptly in color with the digits. The tail is distinctly bicolored (dark above, pale below) and particolored (paler distally than proximally), such that the distal one-third or more of the organ is completely pale in most specimens. Most examined males have no trace of a gular gland, the only exception being the holotype (an unusually large specimen; table 11), in which the gland appears to be present. The lateral carpal tubercles of adult males are bulbous or knoblike, and the scrotum is pale (with

whitish fur and unpigmented skin). Three parous adult female specimens prepared in the field by L.H. Emmons (LHE 1468, 1596, 1808) each had 6–1–6 = 13 mammae, of which the anteriormost two pairs appear to be pectoral in digital images that we examined. The supraorbital margins of the skull are rounded, lacking distinct beads even in the largest specimens, and a shallow postorbital constriction is dorsally visible. Palatine fenestrae are consistently present, the upper canine lacks accessory cusps, and the auditory bullae are moderately large.

*Marmosops ocellatus* differs from *M. impavidus* by its paler and grayer dorsal coloration, absence of distinct lateral zones of gray-based ventral hairs, possession of pectoral mammae, and more distinctly bi- and particolored tail. In addition, the palate is more extensively fenestrated and the auditory bullae are much larger in *M. ocellatus* than in *M. impavidus*. Although the difference between exemplar sequences of these

TABLE 11  
 Measurements (mm) and Weights (g) of Selected Specimens of *Marmosops ocellatus*<sup>a</sup>

	AMNH 260027	AMNH 261267	MSB 58512	MSB 58513	BMNH 26.1.5.25 <sup>b</sup>	AMNH 260026	AMNH 261266	AMNH 263549 <sup>c</sup>
Sex	female	female	female	female	male	male	male	male
HBL	104	111	117	[137] <sup>d</sup>	140	117	132	126
LT	146	146	160	[133] <sup>d</sup>	186	161	170	166
HF	16	17	15	[12] <sup>d</sup>	20	18	19	19
Ear	25	25	23	22	25	25	21	24
CBL	30.3	30.6	31.8	31.3	36.8	32.5	34.5	34.0
NB	3.6	3.4	3.9	3.7	4.2	4.0	4.2	3.2
LIB	5.7	5.5	5.5	5.8	6.3	5.9	6.0	5.9
ZB	16.5	16.5	16.8	17.0	19.8	17.5	18.2	17.9
PL	17.0	17.4	18.3	17.8	20.7	18.5	19.2	19.4
PB	10.0	10.6	10.3	10.4	11.0	10.7	10.9	10.9
MTR	12.7	12.9	13.2	13.2	14.7	13.6	14.1	14.2
LM	6.4	6.7	6.8	6.8	6.8	7.0	6.8	6.8
M1–M3	5.6	5.9	5.9	5.9	5.8	6.0	5.9	5.8
WM4	2.4	2.6	2.6	2.5	2.6	2.7	2.6	2.6
Weight	30	24	28	28	—	39	38	36

<sup>a</sup>All specimens are from the Bolivian department of Santa Cruz; see text for other locality information.

<sup>b</sup>Holotype.

<sup>c</sup>Misidentified by Anderson (1997: 163) as *Thylamys macrurus*.

<sup>d</sup>The collector's recorded values for these dimensions are unusually large (HBL) or small (LT, HF) and may have resulted from mismeasurements.

taxa (about 5.7%; table 6) is not as large as the differences observed among other species recognized by us, the phenotypic distinctiveness of *M. ocellatus* and its apparently discrete geographic distribution suggest that it represents a unique evolutionary lineage that should be known by its own name.

Most of the material that we refer to *Marmosops ocellatus* was identified by Anderson (1997) as *M. dorothea*, but two specimens (MSB 67020, 87094) were identified as *Gracilinanus agilis buenavistae*, and another (AMNH 263549) was identified as *Thylamys macrurus*.

BOLIVIAN SPECIMENS EXAMINED: Santa Cruz, 6 km by road W Ascención (AMNH 261265), Aserradero Pontons (CBF 6163), Ayacucho (USNM 390571, 390572), Buenavista (BMNH 26.1.5.25 [holotype], 28.2.9.87, 28.2.9.90), 4.5 km N and 1.5 km E Cerro Amboró (MSB 55844), El Refugio (LHE 1569, 1573, 1577, 1596), 3.5 km W Estación El Pailon (AMNH 260026–260028; MSB 55070), Hacienda el Pelicano (AMNH 275462), 7 km E and 3 km N Ingeniero Mora (AMNH 247652), Lago Caimán (USNM 581979), 2 km SW Las Cruces (AMNH 263549; MSB 63274), Mangabalito (MJS 005), 3 km SE Montero (MSB 87094), Palmar (USNM 390569), San

Miguel Rincón (AMNH 260029), 10 km N San Ramón (AMNH 261266, 261267), 15 km S Santa Cruz (MSB 58510–58514, 59886, 67020), 27 km SE Santa Cruz (59884, 59885), Santa Rosita (USNM 390022), Tita (MSB 55071).

#### Unidentified *Marmosops*

Among the Bolivian specimens we examined are three that we are unable to confidently identify with any of the taxa recognized in this report. Two (AMNH 275461, MSB 67021) were collected 7 km SE Ariruma at an elevation of 1750 m on the lower Andean slopes of western Santa Cruz department. Unlike *Marmosops ocellatus*, which occurs in the adjacent lowlands of Santa Cruz, these specimens have darker dorsal fur, paler (self-white) underparts, and lack distinct postorbital constrictions. They differ from *M. impavidus* by their grayer dorsal fur, by lacking lateral zones of gray-based ventral fur, and by lacking distinct postorbital constrictions. They differ from all of the forms herein referred to *M. noctivagus* by lacking interorbital beads. They differ from *M. bishopi* by having grayer dorsal pelage, well-de-

TABLE 12  
 Geographic and Elevational Distribution of Small Nonvolant Cloud-Forest Mammals  
 Collected Sympatrically with *Marmosops creightoni*

	N <sup>a</sup>	Known distribution	Reference
<i>Gracilinanus aceramarcae</i>	5	N Bolivia to central Peru; 2530–3350 m	R. S. Voss (unpublished data)
<i>Akodon mimus</i>	14	Central Bolivia to SE Peru; 2000–3635 m	Myers et al. (1990)
<i>Microrhynchomys minutus</i>	131	Central Bolivia to Venezuela; 800–4265 m <sup>b</sup>	Carleton and Musser (1989)
<i>Oxymycterus nigrifrons</i>	10	N Bolivia to SE Peru; 2000–4200 m	Oliveira (1998)
<i>Thomasomys</i> “sp. 1”	7	N Bolivia to central Peru; 1880–3650 m	Pacheco (2003)
<i>Thomasomys</i> “sp. 3”	11	N Bolivia to SE Peru; 2000–3275 m	Pacheco (2003)

<sup>a</sup>Number of collection localities accompanied by elevational data.

<sup>b</sup>Most (>80%) collection localities for *Microrhynchomys minutus* are between 2000 and 3500 m (Carleton and Musser, 1989).

veloped palatine fenestrae, much larger teeth (LM = 6.7 mm), and by lacking accessory cusps on C1.

The other unidentified specimen is MSB 63275, a young adult female from the Río Limón at 1300 m on the lower Andean slopes of northeastern Chuquisaca. It has browner and somewhat paler dorsal fur than does the Río Ariruma material, and self-cream ventral fur with broad lateral bands of gray-based hairs (versus underparts entirely self-white). However, the crania of all three specimens are not dissimilar, and they differ from those of recognized Bolivian taxa by essentially the same characters.

## DISCUSSION

Bolivia encompasses a diversity of landscapes with different vegetation types that might be expected to support distinct faunas. As currently recognized in the literature, however, Bolivian species of *Marmosops* have broadly overlapping distributions that do not coincide with any obvious biogeographic regions or macrohabitats. Although we have not examined all of the material represented in published range maps, the specimens identified in this report suggest that some species have much more geographically restricted and ecologically comprehensible distributions than do those illustrated by Anderson (1997) and Brown (2004).

Specimens that fit our working diagnosis of *Marmosops noctivagus* (a total of 53 individuals from 17 localities) are from the lowland rain forests and lower-montane cloud forests of northern and central Bolivia, a region that approximately corresponds to

the Amazonian (“Acre y Madre de Dios”) and “Yungas” biogeographic provinces of Navarro and Maldonado (2002). This species is also widespread in eastern Peru and western Brazil, where it has been collected in similar habitats (Voss and Emmons, 1996; Patton et al., 2000). Future collecting in Bolivia will probably show that *M. noctivagus* occurs throughout Pando department, in the forested parts of La Paz up to about 2000 m on the eastern Andean slopes, along the forested Andean foothills of southernmost Beni, and on the Andean piedmont and lower-montane slopes of Cochabamba to at least 18°S.

The other Bolivian species for which we have examined enough material to characterize its ecogeographic distribution (a total of 37 individuals from 20 localities) is *Marmosops ocellatus*, which seems to be widespread in the “Cerrado” biogeographic province of Navarro and Maldonado (2002). Within this region, however, *M. ocellatus* has only been trapped in closed-canopy forests, not in the savanna woodlands or shrubby habitats that characterize Cerrado sensu stricto (L.H. Emmons, in litt.). We expect that future collecting will show that *M. ocellatus* occurs throughout those parts of Santa Cruz receiving about 1000–1500 mm of annual rainfall and in similar habitats of southwestern Brazil (Mato Grosso).

Although currently known from only three adjacent localities in La Paz, *Marmosops creightoni* is almost certainly more widespread. Based on the known geographic ranges of other small nonvolant cloud-forest mammals that occur in the same elevational interval in the Valle de Zongo (table 12), we



TABLE 13  
**Records of Sympatry Among Bolivian  
 Species of *Marmosops***  
 (Based on material examined for this report)

<i>creightoni</i>	no			
<i>impavidus</i>	no	no		
<i>noctivagus</i>	yes <sup>a</sup>	no	yes <sup>b</sup>	
<i>ocellatus</i>	yes <sup>c</sup>	no	no	no
	<i>bishopi</i>	<i>creightoni</i>	<i>impavidus</i>	<i>noctivagus</i>

<sup>a</sup>*Marmosops bishopi* and *M. noctivagus* were collected sympatrically at localities 1, 5, and 11 (see appendix 2).

<sup>b</sup>*Marmosops impavidus* and *M. noctivagus* were collected sympatrically at locality 21 (see appendix 2).

<sup>c</sup>*Marmosops bishopi* and *M. ocellatus* were collected sympatrically at locality 28 (see appendix 2).

predict that *M. creightoni* will eventually be found in wet montane forests from central Bolivia to southeastern Peru. Whether or not *M. creightoni* is really co-distributed with any of the taxa listed in table 12 remains to be demonstrated by more intensive collecting, but it is noteworthy that this assemblage of species is largely restricted to humid eastern-Andean slopes with few convenient points of access for inventory fieldwork except along roads where colonization has already caused extensive deforestation. Therefore, it may be a long time before significant range extensions of *M. creightoni* are reported.

The material that we refer to *Marmosops bishopi* (a total of eight individuals from six localities) is an interesting exception to the ecogeographically restricted distributions of other Bolivian forms. Instead, specimens of *M. bishopi* have been taken in a diversity of landscapes, where they account for most of the known examples of sympatry documented by congeneric material examined for this report (table 13). Because strikingly different macrohabitats can sometimes occur in close proximity, we consulted field notes associated with Bolivian specimens of *M. bishopi* seeking some common ecological circumstance in which they might have been taken, but we found none: captures have been recorded in primary lowland rainforest (UMMZ 156014, USNM 579249), lowland dry forest (LHE 1541), seasonally flooded evergreen gallery forest (LHE 1553, 1556), and cloud forest (CBF 7531). Either *M. bish-*

*opi* is an unusually eurytopic species, or the material that we consider conspecific may consist of two or more morphologically cryptic taxa.

Some of the obvious gaps in our distribution maps of Bolivian *Marmosops* are certainly artifactual, but others are probably not. Despite considerable collecting effort in the seasonally flooded savannas and gallery forests of central and northern Beni, for example, no specimens of *Marmosops* have been collected there. The genus is likewise unknown from substantial collections made in the arid thorn-scrub of southern Santa Cruz, eastern Chuquisaca, and eastern Tarija, nor have we seen any material among the many hundreds of small mammals collected in the altiplano habitats of southwestern Bolivia. By contrast, the eastern-slope lower-montane forests of Chuquisaca and Tarija remain very poorly sampled by mammalogists, and it is possible that the genus is more widely distributed there than current records suggest.

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Louise Emmons provided useful observations and digital images from her recent fieldwork in eastern Santa Cruz and allowed us to examine uncataloged material that she collected there. At the AMNH, Neil Duncan expertly extracted and cleaned skulls from

fluid-preserved specimens, and Pat Brunauer provided essential bibliographic support. Jim Patton set new standards for professional generosity in permitting us unrestricted access to the cytochrome-*b* sequences obtained by his lab, and Marcelo Weksler helped us analyze them. We gratefully acknowledge a familiar debt to Pat Wynne, whose artistic skills did so much to enhance our descriptions of didelphid morphology, and we thank Rob Anderson for his technical assistance in the production of figures 10 and 12. Our manuscript was substantially improved by helpful suggestions provided by Rob Anderson, Louise Emmons, David Flores, Al Gardner, and Rogerio Rossi, who generously read a preliminary draft when they had many other things to do: we thank them for their time, effort, and expertise.

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## APPENDIX 1

TYPE LOCALITIES OF NOMINAL SPECIES  
OF *MARMOSOPS*

Below we list the type localities of all nominal taxa currently referred to the genus *Marmosops*, including the new species described herein. Italicized place names are those of the largest political division (state/department/province) within each country. Unless reported by the original describer, geographic coordinates and elevation above sea level are provided in square brackets with a cited secondary source for these data. Numbered localities are mapped in figure 1.

## BOLIVIA

1. *La Paz*, Río Solacama [ca. 16°16'S, 67°24'W; 2300 m (Paynter, 1992)]. Type locality of *dorothea*. Thomas (1911: 517) misspelled the type locality “Solocame” and stated that the type was collected by P.O. Simons on 26 January 1901. The coordinates given above are those of Chocachaca on the Río Tamampaya, where Simons is known to have camped at 1200 m from 10 to 29 January 1901 (Chubb, 1919: 5). Presumably, Simons was running traplines from his base on the Tamampaya up the valley of the nearby Solacama, but no documentary evidence is apparently available to support this conjecture.
2. *La Paz*, Saynani hydroelectric plant (16°07'S, 68°05'W; 2500 m) on southeast side of the Zongo Valley. Type locality of *creightoni*.
3. *La Paz*, Río Unduavi, Pitiguaya, La Florida [ca. 16°21'S, 67°47'W; 1785 m (Anderson, 1997)]. Type locality of *yungasensis*.
4. *Santa Cruz*, Buenavista [17°27'S, 63°40'W; ca. 400 m (Paynter, 1992)]. Type locality of *ocellatus*.

## BRAZIL

5. *Amapá*, Rio Amapari, Serra do Navio [0°59'N, 52°03'W; ca. 100 m (Paynter and Traylor, 1991)]. Type locality of *pinheiroi*.
6. *Amazonas*, Huitanaã [7°40'S, 65°46'W; ca. 50 m (Paynter and Traylor, 1991)]. Type locality of *purui*, misspelled “Hyutana-ham” by Miller (1913).
7. *Bahia*, Lamarão [11°45'S, 38°55'W; 291 m (Paynter and Traylor, 1991)]. Type locality of *bahiensis*.
8. *Mato Grosso*, Aripuanan [7°35'S, 60°26'W; no elevation (Paynter and Traylor, 1991)]. Type locality of *stollei*. The coordinates are those at the confluence of the Rio Aripuanã and the Rio Roosevelt, where the collector of the holotype (E. Stolle) is known to have worked (Paynter and Traylor, 1991: 37).
9. *Mato Grosso*, 264 km N (by road) Xavantina, Serra do Roncador (12°51'S, 51°46'W; ca. 533 m). Type locality of *bishopi*.
10. *Minas Gerais*, Rio das Velhas, near Lagoa Santa [19°38'S, 43°53'W; 760 m (Paynter and Traylor, 1991)]. Type locality of *incanus*.
  - *Minas Gerais*,? Porto Alegre [not located]. Type locality of *scapulatus*. Burmeister (1856) only said that the type was collected in Minas Gerais, but Matschie (1916) gave the type locality as Porto Alegre, possibly a fazenda no longer in existence or too small to appear in maps and gazetteers.
11. *Pará*, Nova Area Experimental, Utinga, Belém [1°27'S, 48°29'W; ca. 10 m (Paynter and Traylor, 1991)]. Type locality of *woodalli*.
12. *Pará*, Rio Tapajos, Vila Braga [4°25'S, 56°17'W; ca. 100 m (Paynter and Traylor,

1991)]. Type locality of *collega*, misspelled "Villa Braga" by Thomas (1920: 281).

13. *Rio de Janeiro*, Teresópolis [22°26'S, 42°59'W; 902 m (Paynter and Traylor, 1991)]. Type locality of *paulensis*, spelled "Therezopolis" by Tate (1931: 8).

#### COLOMBIA

14. *Antioquia*, 9 km S Valdivia ([7°06'N, 75°28'W; Anderson, 1999], elev. 1400 m). Type locality of *handleyi*.
15. *Cundinamarca*, Fusagasugá [4°21'N, 74°22'W; 1746 m (Paynter, 1997)]. Type locality of *perfuscus*.
16. *Valle del Cauca*, Río Cauquita, near Cali ([3°27'N, 76°31'W; Paynter, 1997], 1000 m). Type locality of *caucaae*. Thomas (1900: 222) said the type was collected at "Rio Caqueta, a tributary of the Cauca, near Cali", but see Tate (1933: 178).

#### ECUADOR

17. *El Oro*, Portovelo ([3°43'S, 79°39'W; Paynter, 1993], 610 m). Type locality of *oroensis*.
18. *Loja*, Celica ([4°07'S, 79°59'W; Paynter, 1993], 2103 m). Type locality of *celicae*.
19. *Napo*, Coca [= Puerto Francisco de Orellana; 0°28'S, 76°58'W, ca. 260 m (Paynter, 1993)]. Type locality of *politus*.
20. *Pichincha*, Mindo ([0°02'S, 78°48'W; Paynter, 1993], 1280 m). Type locality of *sobrinus*.

#### GUYANA

21. *Demerara-Mahaica*, Hyde Park [6°30'N, 58°16'W; ca. 100 m (Stephens and Traylor, 1985)]. Type locality of *parvidens*.

#### PANAMA

22. *Darién*, Cana ([7°47'N, 77°42'W; Fairchild and Handley, 1966], 610 m). Type locality of *invictus*.

#### PERU

23. *Amazonas*, Tambo Carrizal ([ca. 6°47'S, 77°52'W; Stephens and Traylor, 1983], ca. 2743 m). Type locality of *leucastrus*.
24. *Amazonas*, Tambo Ventija ([6°11'S, 77°33'W; Stephens and Traylor, 1983], ca. 2743 m), 10 mi E Molinopampa. Type locality of *madescens*.

25. *Cusco*, Torontoy ([13°10'S, 72°30'W; Stephens and Traylor, 1983], 2438 m). Type locality of *albiventris*.

26. *Junín*, Montaña de Vitoc, near Chanchamayo [ca. 11°03'S, 75°19'W; no elevation, but presumably >500 m (Stephens and Traylor, 1983)]. Alleged type locality of *impavidus* and *noctivagus*. Although Tschudi (1845) did not state exactly where his material was collected, Tate (1933: 152–153) inferred that the type of *noctivagus* was collected here based on a published itinerary of Tschudi's collecting activities. Cabrera (1958: 16) assumed that the type of *impavidus* came from the same place.

27. *Junín*, Utcuyacu [ca. 11°12'S, 75°28'W; Stephens and Traylor, 1983], 1463 m). Type locality of *juninensis*.

28. *Loreto*, Yurimaguas ([5°54'S, 76°05'W; Stephens and Traylor, 1983], 183 m). Type locality of *neglectus*.

29. *Puno*, Inca Mines [ca. 13°51'S, 69°41'W; Stephens and Traylor, 1983], 1829 m). Type locality of *keaysi*. Allen (1900) stated that the type was collected at Juliaca, but later corrected himself (Allen, 1901).

30. *San Martín*, Yurac Yacu (ca. 762 m), about 20 miles WNW of Moyobamba [6°03'S, 76°58'W; Stephens and Traylor, 1983]. Type locality of *lugendus*.

31. *Ucayali*, Río Ucayali, Lagarto [10°40'S, 73°54'W; <500 m (Stephens and Traylor, 1983)]. Type locality of *ucayalensis*.

#### TRINIDAD AND TOBAGO

32. *Trinidad*, Caparo [10°27'N, 61°20'W; 46 m (Goodwin and Greenhall, 1961)]. Type locality of *carri*.

#### VENEZUELA

33. *Amazonas*, Camp VII (0°51'N, 65°58'W; 1800 m), Cerro de la Neblina. Type locality of *neblina*.

34. *Falcón*, 14 km ENE Mirimire, near La Pastora (11°12'N, 68°37'W; 150 m). Type locality of *cracens*.

35. *Mérida*, Río Albarregas ([probably near Mérida at 8°36'N, 71°08'W; Paynter, 1982], 1630 m). Type locality of *fuscatus*, misspelled "Abbarregas" by Thomas (1896: 314).

## APPENDIX 2

GAZETTEER OF EXAMINED SPECIMENS OF  
BOLIVIAN *MARMOSOPS*

This gazetteer includes all localities from which we personally examined Bolivian specimens of *Marmosops*. Italicized place names are those of currently recognized departments; boldface type 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 species name(s), name(s) of the collector(s), and date(s) of collection are separated from each locality entry by a colon. Numbered localities are plotted in figures 10 and 12.

1. **Beni, 1 km E La Embocada**, Estancia la Cabaña [15°03'S, 66°58'W; 600 m (Anderson, 1997)]: *Marmosops bishopi* and *M. noctivagus* (coll. G.K. Creighton, 10–13 November 1979).
2. **Beni, Rurrenabaque** (14°28'S, 67°34'W; 227 m): *Marmosops noctivagus* (coll. R.H. Pine, 1 September 1980).
3. **Chuquisaca, Río Limón** (19°33'S, 64°08'W; 1300 m): *Marmosops* sp. (coll. R.L. Cuellar, 5 August 1990).
4. **Cochabamba, Incachaca** [17°14'S, 65°41'W; 2347 m (Anderson, 1997)]: *Marmosops noctivagus* (coll. L.E. Miller and H.S. Boyle, 15 May 1915).
5. **Cochabamba, Cordillera de Mosetenes** (16°14'S, 66°25'W; 1300–1600 m): *Marmosops bishopi* (coll. E. Yensen, 3 September 2003) and *M. noctivagus* (coll. D. Embert, F. Guerra, and T. Tarifa, 2–13 September 2003).
6. **Cochabamba, Tablas Monte**, including 4.4 km by road N (17°04'S, 66°01'W; 1833–2100 m) and 9.5 km by road NE (17°02'S, 65°59'W; 1500 m): *Marmosops noctivagus* (coll. M.L. Campbell, S.L. Gardner, S.C. Peurach, and C.T. Seaton, 13–17 July 1993).
7. **La Paz, Iturraldi, Alto Río Madidi** [= "Moira Camp" or "Moire" in Iturralde province; 13°35'S, 68°46'W; 270 m (Anderson, 1997)]: *Marmosops bishopi* (coll. L.H. Emmons, 27 May 1990).
8. **La Paz, 20 km NNE Caranavi** [15°42'S, 67°35'W; 610 m (Anderson, 1997)]: *Marmosops noctivagus* (coll. G.K. Creighton, 8 May 1978).
9. **La Paz, Chijchijpa**, 20 km by road from Coroico (16°09'S, 67°45'W; 1114–1400 m): *Marmosops noctivagus* (coll. S. Anderson, H. Gomez, and R. Tejada, 6–8 July 1992).
10. **La Paz, 13 km SW Ixiamas** (13°53'S, 68°15'W; 400 m): *Marmosops noctivagus* (coll. L.H. Emmons, 2 June 1990).
11. **La Paz, La Reserva** (15°43'S, 67°31'W; 940 m): *Marmosops bishopi* (coll. T. Tiurina, 22 July 1992) and *M. noctivagus* (coll. AMNH/MSB party, 28 July 1992).
12. **La Paz, Río Unduavi, Pitiguaya**, La Florida [ca. 16°21'S, 67°47'W; 1785 m (Anderson, 1997)]: *Marmosops noctivagus* (coll. G.H.H. Tate, 9–14 May 1926; G.K. Creighton, 30 November 1979).
13. **La Paz, Río Solacama** [ca. 16°16'S, 67°24'W; 2300 m (Paynter, 1992)]: *Marmosops noctivagus* (coll. P.O. Simons, 26 June 1901). See appendix 1 for comments on this locality.
14. **La Paz, Serranía Bella Vista** [15°42'S, 67°29'W; 1300–1525 m (Anderson, 1997)]: *Marmosops noctivagus* (coll. S. Anderson, 24 July 1992).
15. **La Paz, Ticunhuaya** [15°28'S, 68°18'W; 1540 m (Anderson, 1997)]: *Marmosops noctivagus* (coll. G.H.H. Tate, 23 April 1926).
16. **La Paz, [Valle de Zongo,] Cuticucho** ([= Cuti Khuchu at 16°08'S, 68°07'W; IGM, 1967]; "2967 m"): *Marmosops creightoni* (coll. G.K. Creighton, 29 September–1 October 1979). There is some question about exactly where Creighton camped at Cuticucho. His field notes say 2967 m, but this is oddly similar to the posted elevation on road signs that now give the elevation of Cuticucho as 2697, so Creighton's figure might have resulted from an accidental transposition of two numerals. Modern topographic maps (IGM, 1967) give the elevation at the road adjacent to the Cuticucho power plant as 2800 m.
17. **La Paz, [Valle de Zongo,] El Vertigo** (16°05'S, 68°02'W, 1800 m): *Marmosops noctivagus* (coll. F. Guerra, 15 August 1993).
18. **La Paz, [Valle de Zongo,] Kahua** (ca. 16°02'S, 67°59'W, 1150 m): *Marmosops noctivagus* (coll. T. Tarifa and M. Tarifa, 23 January 1995). An alternative spelling on modern topographic maps is "Khaua".
19. **La Paz, [Valle de Zongo,] Saynani** (16°07'S, 68°05'W; 2500 m): *Marmosops creightoni* (coll. E. Yensen, 5 August 1999).
20. **La Paz, [Valle de Zongo,] Cement Mine**

- ([?ca. 16°05'S, 68°03'W], 2000 m): *Marmosops creightoni* (coll. G.K. Creighton, 4–11 October 1979).
21. *Pando, Palmira* (11°42'S, 67°56'W; 170 m): *Marmosops impavidus* and *M. noctivagus* (coll. L.A. Ruedas, 4 August 1986).
  22. *Pando, Santa Rosa* (12°13'S, 68°24'W; 180 m): *Marmosops noctivagus* (coll. L.A. Ruedas, 1 August 1986).
  23. *Santa Cruz, 6 km by road W Ascención* (15°43'S, 63°09'W; 240 m): *Marmosops ocellatus* (coll. I.D. Mercado T., August 1985).
  24. *Santa Cruz, Aserradero Pontons* (17°05'S, 59°34'W; no elevation): *Marmosops ocellatus* (coll. H. Aranibar and J. Vargas, 19 April 1999).
  25. *Santa Cruz, Ayacucho* [17°51'S, 63°20'W (Anderson, 1997); no elevation]: *Marmosops ocellatus* (coll. F. Bercerra and W.K. Kerr, 24 August 1966).
  26. *Santa Cruz, Buenavista* ([17°27'S, 63°40'W; Paynter, 1992], 450–500 m): *Marmosops ocellatus* (coll. J. Steinbach, 6 August 1924).
  27. *Santa Cruz, 4.5 km N and 1.5 km E Cerro Amboró*, Río Pitasama (17°44'S, 63°39'W; 620 m): *Marmosops ocellatus* (coll. B.R. Riddle, 15 August 1985).
  28. *Santa Cruz, El Refugio* (14°46'S, 61°02'W; ca. 200 m), Parque Nacional Noel Kempff Mercado: *Marmosops bishopi* (coll. L.H. Emmons, 6–15 November 1998) and *M. ocellatus* (coll. L.H. Emmons; 31 August–7 September 1999, 13 September 2000).
  29. *Santa Cruz, 3.5 km W Estación El Pailón* (17°39'S, 62°45'W; 300 m): *Marmosops ocellatus* (coll. S. Anderson, 22 September 1984).
  30. *Santa Cruz, Hacienda El Pelicano*, 3 km N Zanja Honda (18°16'S, 63°11'W; 500 m): *Marmosops ocellatus* (coll. M. Campbell, 4 July 1991).
  31. *Santa Cruz, 7 km E and 3 km N Ingeniero Mora* ([18°10'S, 63°16'W; Anderson, 1997] 488–579 m): *Marmosops ocellatus* (coll. P.A. Remsik, 10 August 1980).
  32. *Santa Cruz, Lago Caimán* [13°36'S, 60°55'W; ca. 200 m (Killeen and Schulenberg, 1998)], Parque Nacional Noel Kempff Mercado: *Marmosops ocellatus* (coll. E. Cuellar, 27 September 1995).
  33. *Santa Cruz, 2 km SW Las Cruces* (17°47'S, 63°22'W; 480 m): *Marmosops ocellatus* (coll. S. Anderson, 5 July 1990).
  34. *Santa Cruz, Mangabalito* [13°55'S, 60°30'W; ca. 200 m (DMA, 1992)], Parque Nacional Noel Kempff Mercado: *Marmosops ocellatus* (coll. M.J. Swarner, 4 October 2000). Spelled “Mangabalsinho” in DMA (1992); mapped by Killeen and Schulenberg (1998: fig. 1) closer to 13°50'S.
  35. *Santa Cruz, 3 km SE Montero*, 1 km N Villa Copacabana (17°23'S, 63°15'W; 250 m): *Marmosops ocellatus* (coll. AMNH/MSB party, 25 June 1991).
  36. *Santa Cruz, Palmar* [17°51'S, 63°09'W; no elevation (Anderson, 1997)]: *Marmosops ocellatus* (coll. D.R. Hadden, 13 August 1966).
  37. *Santa Cruz, Río Ariruma*, 7 km by road SE Ariruma (18°20'S, 64°13'W; 1750 m): *Marmosops* sp. (coll. J.A. Cook, 5 June 1991).
  38. *Santa Cruz, San Miguel Rincón* (17°23'S, 63°32'W; 300 m): *Marmosops ocellatus* (coll. N. Olds, 12 August 1984).
  39. *Santa Cruz, San Rafael de Amboró* (17°36'S, 63°36'W; 400 m): *Marmosops bishopi* (coll. B.R. Riddle, 31 July 1985).
  40. *Santa Cruz, 10 km N San Ramón* (16°36'S, 62°42'W; 250 m): *Marmosops ocellatus* (coll. S. Anderson and N. Olds, 7 August 1985).
  41. *Santa Cruz, 15 km S Santa Cruz* (17°53'S, 63°07'W; 400 m): *Marmosops ocellatus* (coll. MSB parties, 22–25 July 1987 and 16 June 1988; AMNH/MSB party, 16 June 1991).
  42. *Santa Cruz, 27 km SE Santa Cruz* (17°58'S, 63°03'W; 365 m): *Marmosops ocellatus* (coll. MSB party, 28 May 1988).
  43. *Santa Cruz, Santa Rosita* [17°31'S, 63°11'W; no elev. (Anderson, 1997)], 3 km S Warnes: *Marmosops ocellatus* (coll. M.L. Kuns, 29 July 1965).
  44. *Santa Cruz, Tita* (18°25'S, 62°10'W; 300m): *Marmosops ocellatus* (coll. AMNH/MSB party, 19 October 1984).