REDISCOVERY AND REDESCRIPTION OF *Marmosops handleyi* (PINE, 1981) (DIDELPHIMORPHIA: DIDELPHIDAE), THE LEAST KNOWN ANDEAN SLENDER MOUSE OPOSSUM

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ABSTRACT: *Marmosops handleyi* was briefly described in 1981 based on two specimens collected in 1950 in the northern Andes of Colombia. Until now there have been no additional reported records for this species, and knowledge about its taxonomy, ecology, natural history and evolutionary relationships is deficient. Aiming to assess its current distribution, we searched for this species at four localities in the northern part of the Colombian Cordillera Central, where we collected the new material on which this report is based. Morphological comparisons with a sympatric congeneric species herein identified as *M. caucae*, revealed new external and craniodental characters that we use to redescribe *M. handleyi*. Our phylogenetic analysis groups *M. handleyi* as the sister taxon of a clade of small-bodied forms (*M. parvidens* + *M. pinheiroi*), and a basal polytomy includes *M. caucae* (a Colombian taxon currently synonymized with *M. impavidus*) and other large-bodied forms. Finally, a reassessment of *M. handleyi*'s current conservation status suggests that the species should be transferred from Critically Endangered (CR) to Endangered (EN) IUCN category based on our discovery of additional extant populations.

RESUMEN: Redescbrimiento y redescripción de *Marmosops handleyi* (Pine, 1981) (Didelphimorphia: Didelphidae), el marsupial más desconocido de los Andes. *Marmosops handleyi* fue descrito en 1981 basado en dos especímenes colectados en 1950 en el Norte de los Andes de Colombia. Hasta la fecha no existían registros adicionales de la especie y el conocimiento acerca de su taxonomía, ecología, historia natural y relaciones evolutivas era deficiente. Con el fin de evaluar su distribución actual, buscamos esta especie en cuatro localidades en el norte de la Cordillera Central de Colombia, en donde colectamos nuevo material en el cual basamos el presente trabajo. Comparaciones morfológicas con una especie congenérica distribuida simpátricamente, identificada como *M. caucae*, revelaron nuevos caracteres externos y craneodentales que utilizamos para redescribir la especie *M. handleyi*. Nuestros análisis filogenéticos agrupan a *M. handleyi* como el taxón hermano de un clado de especies de pequeño tamaño (*M. parvidens* + *M. pinheiroi*) y adicionalmente recuperamos una politomía basal en el género que incluye a *M. caucae* (un nombre de poblaciones de Colombia que actualmente es sinónimo de *M. impavidus*) y otras especies de gran tamaño. Finalmente, reevaluamos la categoría de amenaza de *M. handleyi* basados en la nueva información disponible y sugerimos que la especie sea transferida de la categoría Críticamente Amenazada (CR) a la categoría En Peligro (EN) de la UICN.

Key words. Colombia. Endangered species. Marsupial. Systematics. Taxonomy.

Palabras clave. Colombia. Especie amenazada. Marsupial. Sistemática. Taxonomía.

INTRODUCTION

Between 1948 and 1952 the North American mammalogist Philip Hershkovitz undertook several long expeditions to Colombia, where (among other places) he collected extensively in the northern part of the Cordillera Central (Central Andes; Hershkovitz, 1953; Patterson, 1987). Among the localities visited by Hershkovitz was a site 9 km south of Valdivia (in Antioquia department), where he collected two specimens of small didelphid marsupials that were subsequently described as a new species, *Marmosops handleyi* (Pine, 1981). This description was primarily based on three distinct characters: slightly woolly dorsal fur, gray-based ventral fur (hairs with dark bases and buffy tips), and the presence of rounded palatine fenestrae. Since the collection of the holotype and paratype, no additional material has been reported for the species (Gardner, 1993, 2005; Alberico et al., 2000; Cuartas-Calle and Muñoz-Arango, 2003a; Brown, 2004; Gardner and Creighton, 2008; but see "Ecogeographic Distribution and Natural History", below). Due to the absence of recent records and the accelerated deforestation of habitats near the type locality, *M. handleyi* was included in the Red List of Colombian mammals under the Critically Endangered category (Alberico, 2006).

To assess the current conservation status and taxonomic distinctness of *Marmosops handleyi*, we searched for new populations at other localities in the Cordillera Central of Antioquia department. Based on the new material we collected, a taxonomic redescription became necessary to summarize the myriad subtle differences we observed between *M. handleyi* and other congeneric forms. Although recent phylogenetic studies have shown *Marmosops* to be a monophyletic group (Jansa and Voss, 2000; Voss and Jansa, 2003, 2009; Jansa and Voss, 2005; Steiner et al., 2005; Flores, 2009), previous efforts to understand evolutionary relationships within the genus have been based on just a few species. Therefore, we performed a phylogenetic analysis by including morphological data from *M. handleyi* and

another sympatric species into the matrix of molecular and nonmolecular characters gathered for a large number of didelphid species (Voss and Jansa, 2009). Additionally, based on the newly available information regarding the geographic range of *M. handleyi*, we reassess its conservation status as codified by the IUCN system.

MATERIALS AND METHODS

Study area

Our selection of field sites was based on a priori knowledge of areas with dense forest cover in the Cordillera Central, not too far from the type locality of *Marmosops handleyi* and at approximately the same elevation. Four localities that fit these criteria were chosen, all in the department of Antioquia, at elevations ranging from 1700 to 1950 m (**Fig. 1**). The first two localities, in the municipalities of Amalfi (6°52'25.0''N, 75°05'56.7''W) and Anorí, (6º58'59.9''N, 75º08'01.0''W) are 45 and 48 km respectively from the original type locality of *M. handleyi*. The last two localities, in the municipality of Yarumal (Vereda El Rosario [07°05'0.9''N, 75°26'41.2''W] and Vereda Corcovado [07°04'21.7''N, 75°25'16.5''W]), are 2.6 km from each other and 2-3 km away from the type locality. Ecologically, these areas all fall within the transition between the "Wet Forest" and "Premontane Wet Forest" life zones of Holdridge (1967) and are characterized by relative humidity between 77-95%, and annual rainfall of 3500-4000 mm; the local dry season extends from December to February, and the wettest months include September, October and November (Cuervo, 2001).

These areas comprise secondary forests with trees approximately 15 meters high along the fragments margins, but taller trees (up to 30 m) occur in the forest interior and along stream banks (Cuervo et al., 2001). There is a high density of palms such as *Dyctiocarium lamarckianum, Wettinia* spp. and *Geonoma undata*, as well as several species of large ferns (Cuervo et al., 2001; Sánchez-Giraldo and Díaz-N., 2010). These forests, which are drained by many small streams, also support abundant epiphytes and dense understory vegetation that includes numerous species of the families Araceae and Piperaceae. The landscape is a mosaic of secondary forest fragments (mainly on steep slopes with difficult access) surrounded by cattle pastures and agricultural fields (Gómez, 1994; Cuervo, 2001).
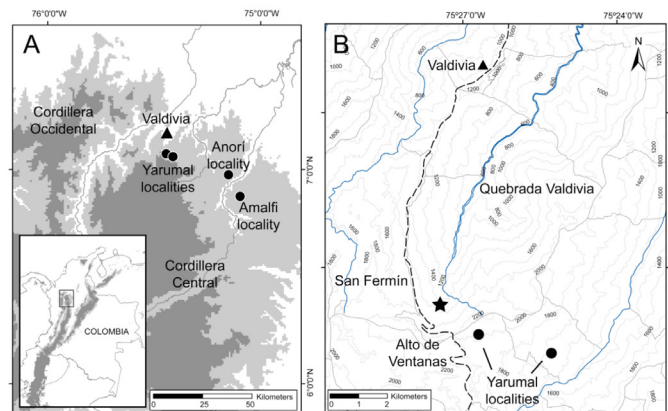
Fig. 1. Fieldwork localities and the town of Valdivia (**A**). Field sites at Yarumal and the inferred type locality (star) of *Marmosops handleyi* (9 km south of Valdivia) based on the inspection of Philip Hershkovitz's field notes (**B**). The broken line corresponds to the highway that Philip Heshkovtiz used to get to his camp (currently known as: "Carretera vía al Mar, Tramo Yarumal-Valdivia") where he collected the type material of *M. handleyi* (P. Hershkovitz field notes). Light-gray shaded regions are localities between 1000-2000 m and dark-gray shaded regions are localities above 2000 m.

Field work

Six surveys of approximately one week each were carried out between February 2004 and January 2006, during both wet and dry seasons and transitional periods. Captures were made using Sherman folding live traps (extra large [ca. 10 x 11 x 38 cm], large [ca. 8 x 9 x 23] and small [ca. 5 x 5 x 23 cm]), snap traps, and pitfall traps (10-liter plastic buckets sunk flush with the soil surface, without a drift fence) (**Table 1**). Traps were placed both in the forest interior and along the forest edge. Inside the forest, traps were placed in the understory and 2-12 m above the ground on tree branches with significant connections to higher canopy levels. Strips of Velcro® were used in order to hold arboreal Sherman traps and snap traps to tree branches (**Fig. 2**). Traps were usually baited every morning with a mixture of rolled oats, banana, and vanilla essence, but we sometimes used only a single slice of banana. Every captured individual was measured and its reproductive condition recorded following Hall (1962); ectoparasites and tissue samples (liver) associated with each specimen were preserved in 96% ethanol. The collected material was preserved as fluid (body preserved in ethanol with the skull extracted) and dry (traditional dry skin and skull, and carcass preserved in ethanol) specimens, which were subsequently deposited in the Colección Teriológica Universidad de Antioquia, Medellín (CTUA) and the Instituto de Ciencias Naturales, Bogotá (ICN).

We constructed species accumulation curves in order to assess the relative efficacy of our sampling among field sites (**Fig. 3**). We use the number of captured individuals as a measure of sampling effort given the differences in number of trap-nights and methodologies implemented among localities. We include only the species and individuals captured with traps in our surveys; therefore the individual of *Marmosops handleyi* CTUA 433 from Amalfi

Table 1

Capture effort measured as the number of traps-night per sampling methods (rows) in each of the surveyed localities (columns). Data from separate trapping sites near Yarumal are summarized in a single column.

Trapping method	Amalfi	Anori	Yarumal	Total
Sherman	992	451	571	2014
Snap	538	282	330	1150
Pit-fall	0	0	57	57
Total	1530	733	958	3221

Fig. 2. Sherman trap in the subcanopy (ca. 12 m) fastened to a branch using Velcro®. (Picture by CSG).
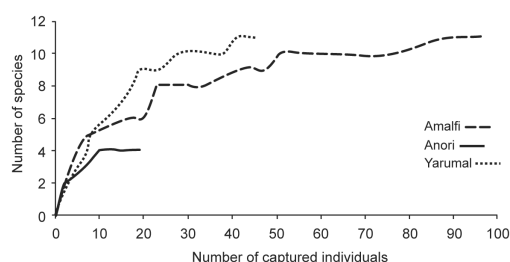

Fig. 3. Species accumulation curves for three localities surveyed in the present study (data for the localities at Yarumal are summarized in a single curve).

(captured in an independent fieldwork) and the specimens of *Marmosa* (*Micoureus*) *regina* captured manually in Yarumal were not taken into account for this analysis.

Taxonomy

Collected specimens were identified to species level using the literature (e.g., Thomas, 1900; Tate, 1933; Pine, 1981; Patton et al., 2000; Voss et al., 2001; Voss and Jansa, 2003, 2009; Voss et al., 2004; Gardner and Creighton, 2008) and by examining relevant comparative material (including types) at the Field Museum of Natural History (FMNH) and the American Museum of Natural History (AMNH). Our morphological descriptions of most external and craniodental characters follows the terminology defined by Voss and Jansa (2003, 2009), but for other characters (not discussed by those authors) we use the terminology described by Osborn (1907), Brown and Yalden (1973), Wible (1990), and Voss et al. (2004).

External measurements (recorded to the nearest millimeter, mm) were taken directly from the specimens in the field, and 10 additional craniodental measurements (described by Voss et al., 2004) were recorded to the nearest 0.01 mm using digital calipers. Measurements are abbreviated as follows: Total Length (TL), Length of Tail (LT), Head-and-Body Length (HB), Length of Hind Foot (HF), Length of Ear (Ear) and Weight, Condylobasal Length (CBL), Nasal Breadth (NB), Least Interorbital Breadth (LIB), Zygomatic Breadth (ZB), Palatal Length (PL), Palatal Breadth (PB), Maxillary Toothrow Length (MTR), Length of Molars (LM), Length of M1-M3 (M1-M3), and Width of M4 (WM4).

Dental age classes were recorded for every specimen examined following Tribe's description of molar eruption (Tribe, 1990). Morphological qualitative characters and measurements were observed and described only from adult specimens (Tribe's dental age classes 6-7) unless otherwise mentioned. Dental age classes 5 and 1-4 were considered to be subadults and juveniles respectively.

Phylogenetic analysis

We scored 125 external and craniodental characters described by Voss and Jansa (2009) from *Marmosops handleyi* and from a sympatric taxon that we provisionally identify as *M. caucae* (Thomas, 1900; see below). Two characters (12 and 13 of Voss and Jansa, 2009) were coded as missing data ("?") for *M. caucae* due to the absence of adult males for coding carpal tubercle morphology. In addition, four karyotypic characters were coded as missing data due to the absence of cytological information for both species. These data were included in the combined molecular and nonmolecular matrix of Voss and Jansa (2009). Because we are primarily interested in the relationships among species of *Marmosops,* we restricted our analysis to the tribe Thylamyini as described by Voss and Jansa (2009). These authors excluded *Chacodelphis formosa* in part of their analyses because of the complete absence of molecular data for that species; however, because our matrix includes two other species that lack DNA data, we do not have a clear justification for excluding *C. formosa.* Our designated outgroup was the same as that defined by those authors, which includes representatives of the non-didelphimorph marsupial orders Dasyuromorphia, Microbiotheria, Paucituberculata and Peramelemorphia. We used PAUP* 4.0b10 (Swofford, 2002) to perform a heuristic maximum-parsimony (MP) analysis with 100 000 replicates and tree-bisection-reconnection (TBR) branch swapping. We calculated a strict

consensus from the equally most parsimonious trees, and we assessed nodal support by bootstrap analyses with 1000 replicates and a heuristic search using 10 replicates of TBR branch swapping. Because of the amount of incomplete molecular data, we defer the implementation of model-based analyses (i.e. maximum likelihood and Bayesian inference) to future studies when further molecular data are available.

Conservation status

We assessed the current conservation status of *Marmosops handleyi* (see Alberico, 2006; Weksler et al., 2008) following the categories and criteria of the IUCN Red List (IUCN, 2001). We included in our evaluation relevant information such as our newly recorded localities for the species (presence-absence), natural history information, extent of occurrence, and known area of occupancy.

RESULTS AND DISCUSSION

A total of 16 *Marmosops* specimens representing two distinct species were captured. These include seven specimens (four adult females, a single juvenile female, and two juvenile males) of *M. handleyi* and nine specimens (four adult females, one subadult male, one juvenile female, and three juvenile males) of a species that we provisionally identify as *M. caucae* (sensu Tate, 1933; currently treated as a synonym of *M. impavidus,* see below). An adult male of *M. handleyi* (CTUA 433) was subsequently collected during independent fieldwork at the Amalfi locality, for a total of eight new specimens of this species.

Marmosops handleyi was successfully captured at every sampled locality except Anorí (**Fig. 1**). The locality at Anorí is ecologically similar to the other surveyed areas, and it is geographically intermediate to other localities where *M. handleyi* was found, but there was less effective sampling effort at this site (**Fig. 3**). Therefore, it seems premature to conclude that *M. handleyi* is really absent at Anorí until future fieldwork is done in the area.

Based on our material and other examined specimens (listed below), we redescribe *M. handleyi* and comment on the identification of the specimens that we refer to *M. caucae* in the following accounts. Except as noted otherwise, both species conform to the generic

diagnosis of *Marmosops* in Voss and Jansa (2009). Therefore, only characters that are useful for distinguishing these species from other congeneric forms are mentioned in these accounts.

Redescription of *Marmosops handleyi*

This species is of intermediate size within the genus, with external and craniodental measurements that fall between those of *M. noctivagus* (amongst the largest known species—see Patton et al., 2000; Voss et al., 2004) and *M. parvidens* (amongst the smallest—see Voss et al., 2001). The dorsal fur has dark-gray hair bases (ca. 7/8) with the tips (ca. 1/8) of the hairs ranging from dark brown to chestnut-brown. The flanks retain the same bicolor pattern, but slightly paler. The dorsal and lateral fur has a slightly woolly appearance (as originally described by Pine, 1981); however, this character has little taxonomic value because other sympatric small didelphids (i.e. *M. caucae* and *Marmosa* (*Micoureus*) *regina*) also have more-or-less woolly fur. The midrostral region (between the blackish ocular masks) is slightly paler than the crown of the head and the rest of the dorsum. The ventral fur is gray-based with whitish or buffy hair tips from chin to anus; self-colored (unicolored) white or buffy hairs are present only at the tip of the chin (at the base of submental vibrissae), on the scrotum, and in the inguinal mammary region. The single exception is CTUA 415, a subadult male (dental age class 5), which has a small longitudinal stripe (15x5 mm) of self-white hairs between scrotum and sternum. The eyes are surrounded by distinct black facial masks that contrast with the color of the head. At their anterior edge, the masks do not reach the mystacial vibrissae, and posteriorly they do not reach the ear base. Most mystacial, genal, and supercilliary vibrissae are black, but a few vibrissae are paler, and others seem to be completely transparent (e.g. the mental and submental vibrissae). When laid back alongside the head, the mystacial vibrissae do not reach the distal edge of the ear. All examined specimens, including adult males and females, seem to lack a gular gland. The ears are white

or light gray basally, becoming darker distally (towards the edge of the pinnae). The dorsal skin of the metacarpals and digits is white, but the metacarpal surface appears darker due to a covering of small grayish hairs. The manual digits are covered with short white hairs (only seen under magnification) that contrast with those over the metacarpals. The metatarsals and digits have pale skin, but the proximal metatarsal region (just distal to the ankle) is covered dorsally with grayish hairs that contrast with the white color of the hairs and skin over the distal metatarsal region and the digits. A few small unpigmented hairs are present at the base of claws, although these tufts do not cover the claws and can be only observed under magnification. Lateral carpal tubercles are conspicuously present in both examined adult males (CTUA 433 and FMNH 69823) and are consistently absent in females. Medial carpal tubercles are absent in both sexes. Ventrally the manus has four subequal interdigital plantar pads and two carpal pads (thenar and hypothenar). Although interdigital pad 1 and the thenar pad of the manus are close to one another, there is always a complete separation of both pads, so their dermatoglyph-bearing surfaces are not fused. The dermatoglyph-bearing surfaces of the hypothenar and interdigital pad 4 are conspicuously separated by a "valley" of tubercular plantar epithelium. The hindfeet have four interdigital plantar pads, the first of which is larger than the three remaining pads, which are subequal in size. The first interdigital pad and the thenar pad of the hind foot are in partial contact, but their dermatoglyph-bearing surfaces are not fused (**Fig. 4B**). Interdigital pad 4 and the hypothenar pad are clearly separated by tubercular plantar epithelium (**Fig. 4B**).

Brown and Yalden (1973) describe three different kinds of forelimb vibrissae, "anconeal" (near the elbow), "medial antebrachial" (forearm), and "ulnar carpal" (proximal to the wrist). We consistently observed two lateral unpigmented vibrissae in the forearm mid-region (medial antebrachial): a distal and a proximal one (**Fig. 5B**). The scrotal epithelium and the hairs covering it are both white. Lactating females have a rusty-reddish mammary area
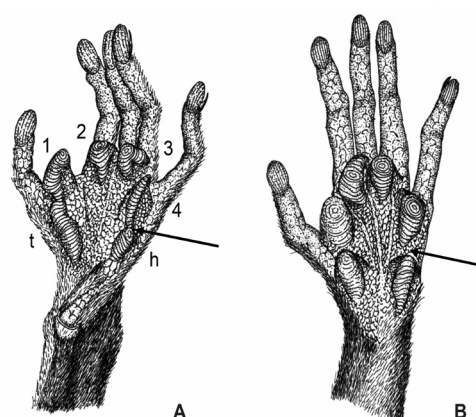

Fig. 4. Plantar view of the left hind feet of *Marmosops caucae* (A, [CTUA 427 – female, age class 6]) and *M. handleyi* (B, [CTUA 416 female, age class 6]). Although the hypothenar pad (h) and interdigital pad 4 are not fused in *M. caucae*, they are basally in contact, and no tubercular plantar epithelium can be observed between these pads. On the contrary, the hypothenar pad and interdigital pad 4 are conspicuously separated by tubercular plantar epithelium in *M. handleyi* (see arrows). Other abbreviations: Interdigital plantar pads, 1, 2, 3, 4; and t, thenar pad.

with seven nipples (3-1-3) restricted to the abdominal region (based on the analyses of specimens CTUA 413, 414, 416). The tail has rhomboidal scales arranged spirally; however, some rounded or oval scales can occasionally be observed. As for the remaining members of the genus, each scale has three hairs on its posterior margin; the central one is petiolate, longer and darker than the lateral hairs. The tail is bicolored, dark gray dorsally, lighter ventrally and slightly paler distally, but never distinctly particolored.

Cranially, the nasals of *Marmosops handleyi* extend anteriorly to the incisors, hiding the nasal fossa in dorsal view; the lateral margins of the nasals are nearly parallel until they reach the maxillo-frontal suture where they are expanded laterally. The interorbital region is broad relative to zygomatic breadth (LIB/ZB = 0.4, N = 4). Although the frontal bones have rounded dorsolateral margins, adult specimens tend to develop a weak beading that runs posteriorly onto the braincase as faint temporal crests. The incisive foramina extend
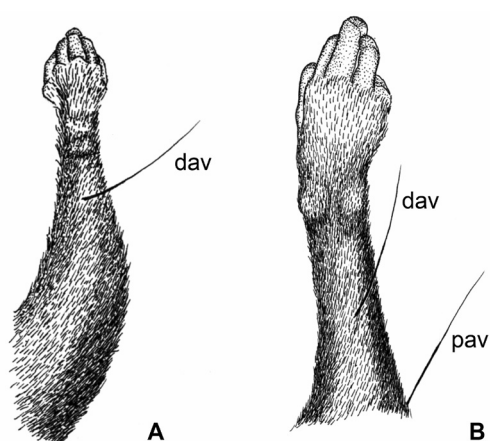
Fig. 5. Dorsal view of right forelimb vibrissae of *Marmosops caucae* (A, [CTUA 426]) and *M. handleyi* (B, [CTUA 416]). *Marmosops caucae* has a single distal medial antebrachial vibrissa (dav), while *M. handleyi* has two vibrissae, a distal medial antebrachial vibrissa (dav) and a proximal medial antebrachial vibrissa (pav).

Maxillary fenestrae are absent except as rare unilateral variants. The small posterolateral palatal foramina are posterior to the M4 metacone. Although the lacrimal foramina are usually located within the orbits and therefore cannot be observed in lateral view, some individuals have these foramina slightly exposed laterally. The petrosal is exposed on the lateral surface of the posterior braincase through a fenestra between the squamosal and parietal bones. The subsquamosal foramen is anteroposteriorly elongated; therefore, a large area (relative to other species, see below) of the petrosal bone (including the sulcus of the prootic sinus) is exposed (**Fig. 6B**). However, the sulcus of the prootic sinus is not visible in ventral view (as it is in related species; **Fig. 7B**). The auditory bullae conform to what has been described for the genus in detail by other authors (Voss et al., 2004; Voss and Jansa, 2009).

Dentally, the upper canines (C1) of the five adult females examined (including the holotype) have well-developed anterior and posterior accessory cusps (**Fig. 8B**), whereas the four males (including two juveniles and two adults such as CTUA 433 and FMNH 69823) have only a posterior accessory cusp. Although sexual dimorphism has previously been recorded for didelphids in traits such as size (Gardner, 1973; López-Fuster et al., 2000; Tague, 2003; Patterson and Mead, 2008), scent

from about I2 or I3 to the posterior edge of C1. Long maxillopalatine fenestrae are present, extending from the anterior margin of P3 to the anterior edge of M3. The palatine fenestrae extend from the M3 protocone to the M4 protocone (occasionally some specimens have highly fenestrated palatines and small additional fenestration is present posteriorly).
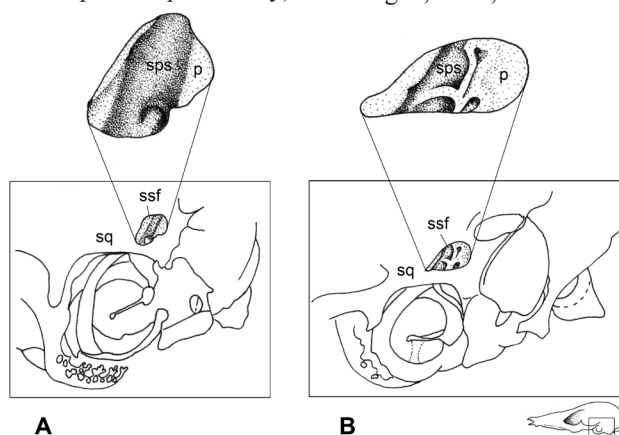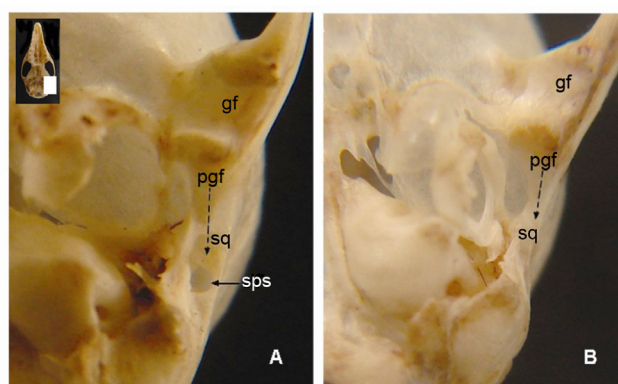

Fig. 6. Left lateral view of the posterior braincase of *Marmosops caucae* (A, [CTUA 426]) and *M. handleyi* (B, [CTUA 411]). The subsquamosal foramen (ssf) of *M. caucae*, is antero-posteriorly constricted; therefore, the only visible area of the petrosal bone (p) is the sulcus of prootic sinus (sps). In contrast, *M. handleyi* has an antero-posteriorly elongated subsquamosal foramen that exposes a much larger area of the petrosal bone (not only the sps). Other abbreviation: sq, squamosal.

Fig. 7. Ventral view of left basicranial region of *Marmosops caucae* (A, [CTUA 426]) and *M. handleyi* (B, [CTUA 411]). In *M. caucae* the postglenoid foramen (pgf) runs anteroposteriorly (broken arrow) and the sulcus of the prootic sinus (sps) is ventrally exposed. By contrast, in *M. handleyi* the postglenoid foramen is posteromedially oriented and the sulcus of the prootic sinus is not exposed. Other abbreviations: gf, glenoid fossa; sq, squamosal.

glands (Fadem and Schwartz, 1986) and bony structures (Lunde and Schutt Jr., 1999), to our knowledge no discrete dental feature has previously been reported to differentiate sexes
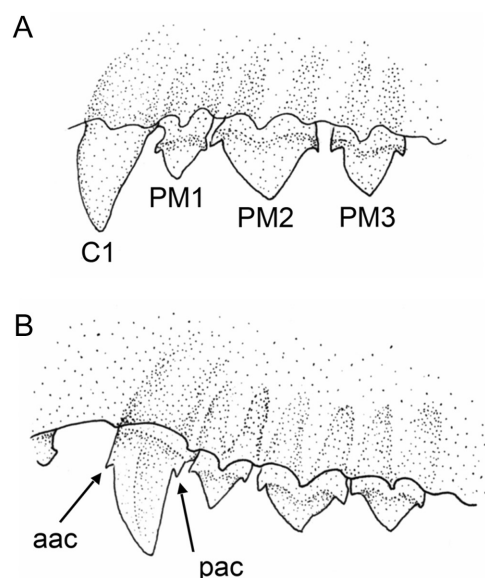

Fig. 8. Lateral view of left upper canine (C1) and upper premolars (PM1, PM2, PM3) of *Marmosops caucae* (A, [CTUA 419] and a female specimen of *M. handleyi* (B, [CTUA 411]). Both sexes of *M. caucae* lack canine accessory cusps, whereas accessory canine cusps are sexually dimorphic in *M. handleyi*: females have both an anterior accessory cusp (aac) and a posterior accessory cusp (pac), but males have only the posterior accessory cusp.

in this taxonomic group. Due to the consistent presence of this morphological difference between males and females, even among several distinct age classes, we believe that this is the first record of a qualitative dental character that is sexually dimorphic in didelphids (see below comparisons with other *Marmosops* species [*M. handleyi* vs. *M. fuscatus*]). The lower canines (c1) have a subtle but conspicuous anterior accessory cusp formed by a mesial projection of the anterior edge of the tooth (**Fig. 9B**). The
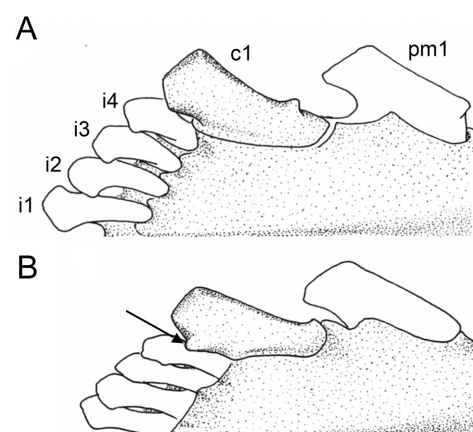

Fig. 9. Dorsal view of right anterior mandibular dentition of *Marmosops caucae* (A, [CTUA 419]) and *M. handleyi* (B, [CTUA 411]. The former species has a flat and smooth lingual surface of its lower canine (c1), whereas the later species has an anteromesial accessory cusp on its c1 (arrow).

first upper premolar (P1) is half the size of P2 and the P2 is subequal to P3 (P2>P3—**Fig. 8B**). The preprotocrista of M1-M3 ends at the paracone, so it is not continuous with the anterolabial cingulum. Adults have the basal first half of P3 with an anterior cutting edge, but the remaining distal half (to the apex) is rounded anteriorly. Juvenile individuals have the dP3 metastyle poorly developed or absent, and dp3 has a well-developed anterior cingulid.

Comparisons with sympatric congeners

Differences in size are evident between *M. handleyi* and *M. caucae*, as shown in **Table 2**. Females of the former species are consistently smaller as measured by mean size in TL, LT, and every cranial dimension. Additionally for females, four cranial measurements (NB, ZB, PL, and PB) exhibit no overlap between species (**Table 2**). Ventrally, *M. handleyi* has gray-based hairs (dark bases and white or buff tips) as opposed to the self-colored band of white or buff hairs present in *M. caucae* (**Table 3**). Interdigital plantar pad 4 and meta-tarsal hypothenar pad are fully separated by

tubercular plantar epithelium on the hind foot of *M. handleyi*, whereas in *M. caucae*, the bases of the dermatoglyph-bearing surfaces of the interdigital pad 4 and hypothenar pad are in contact basally, so that no tubercular plantar epithelium is observed between them (**Fig. 4**). *M. handleyi* has both distal and proximal medial-antebrachial vibrissae, whereas *M. caucae* has only the distal vibrissa (**Fig. 5**).

On the posterolateral braincase of *M. handleyi*, a large surface of the petrosal bone (including the sulcus of the prootic sinus) is exposed through the anteroposteriorly elongated subsquamosal foramen. By contrast, the subsquamosal foramen of *M. caucae* is constricted anteroposteriorly; therefore, only the sulcus of the prootic sinus can be observed (**Fig. 6**). In *M. caucae* the postglenoid foramen runs anteroposteriorly and the sulcus of prootic sinus is ventrally exposed. By contrast, in *M. handleyi* the postglenoid foramen is postero-medially oriented and the sulcus of the prootic sinus is not exposed in ventral view (**Fig. 7**).

Dentally, the upper canine of female *M. handleyi* has both anterior and posterior ac-

Table 2

External and craniodental measurements of adult specimens of *Marmosops handleyi* and *M. caucae*. All measurements are in millimeters and weight in grams. Numbers in parentheses are the observed range (minimum-maximum) for each measurement. For abbreviations of measurements see text.

| | *M. handleyi* | | *M. caucae* |
Sex	Female (N=5)	Male (N=2)	Female (N=4)
TL	240.125 (233 - 253)	259 - 271	251.75 (243 - 260)
LT	132.75 (129 - 141)	149	146.75 (142 - 157)
HB	107.375 (104 - 113)	110 - 122	105 (100 - 112)
HF	17.525 (17 - 18.5)	18.6 - 20	15.64 (13 - 16.85)
Ear	19.95 (19 - 20.5)	20 - 21.22	18.13 (17.2 - 18.7)
CBL	29.71 (29.37 - 30.7)	30.5	30.60 (30.01 - 31.16)
NB	3.405 (3.27 - 3.66)	3.51	3.78 (3.77 - 3.81)
LIB	5.93 (5.86 - 6.21)	6.04	6.05 (5.82 - 6.32)
ZB	15.11 (14.51 - 15.47)	15.54	15.69 (15.49 - 15.88)
PL	16.645 (16.3 - 17.02)	16.98	17.73 (17.4 - 18.2)
PB	8.975 (8.88 - 9.36)	9.54	9.59 (9.52 - 9.63)
MTR	12.32 (11.99 - 12.9)	12.5 - 12.58	12.89 (12.7 - 13.17)
LM	6.155 (5.93 - 6.56)	6.28 - 6.38	6.55 (6.5 - 6.57)
M1-M3	5.31 (5.18 - 5.6)	5.46 - 5.48	5.61 (5.56 - 5.68)
WM4	2.065 (1.97 - 2.25)	2.13 - 2.16	2.20 (2.16 - 2.22)
Weight	27 (21 - 31)	29.5	22.25 (17 - 24)

Table 3

Morphological comparisons among *Marmosops* species known from the Colombian Andes.

Character	*M. fuscatus*	*M. handleyi*	*M. caucae*	*M. parvidens*
Ventral color	Gray-based with white or buff tips	Gray-based with white or buff tips	Self-colored band of white or buff hairs	Self-colored band of white hairs
Interdigital pad 4 and hypothenar pad of hind foot	?	Clearly separated by tubercular plantar epithelium	Pads in contact basally, no tubercular plantar epithelium is visible between these pads.	?
Medial antebrachial vibrissae	Proximal and distal vibrissae	Proximal and distal vibrissae	Distal vibrissa	Proximal and distal vibrissae
Nasals at maxilofrontal suture	Not expanded	Expanded	Expanded	Expanded
Palatine fenestrae	Absent or reduced	Present	Present	Usually absent
Subsquamosal foramen	Enlarged anteroposteriorly	Enlarged anteroposteriorly	Constricted anteroposteriorly	Enlarged anteroposteriorly
Accessory cusps of C1	Males without accessory cusps; Females with posterior accessory cusp	Males with posterior cusp; females with anterior and posterior accessory cusps	Absence of accessory cusps	Males and females with posterior accessory cusps
Anterolabial margin of tooth crown of M3	Not continuous shelf	Not continuous shelf	Continuous shelf	Continuous shelf
TL	285 (Female, N=1) 284.5 (Male, N=2)	240.13 (Female, N=5) 271 (Male, N=1)	251.75 (Female, N=4)	226 (Female, N=3) 232.33 (Male, N=3)
CBL	34.3 (Male, N=2)	29.71 (Female, N=5) 30.5 (Male, N=1)	30.60 (Female, N=4)	26.99 (Female, N=2)

cessory cusps, whereas males have only a posterior accessory cusp. By contrast, no examined specimen of *M. caucae* has any trace of an accessory cusp on C1 (**Fig. 8**). Whereas a mesial anterior accessory cusp is present on the lower canine (c1) of *M. handleyi*, *M. caucae* does not exhibit this structure (although some individuals have an indistinct swelling on the anterior mesial margin of c1; see **Fig. 9**). Additionally, the upper third premolar (P3) of *M. handleyi* has a blade-like anterior basal margin and the remaining distal edge has a rounded margin. By contrast, the P3 of *M. caucae* has a completely rounded anterior

margin from base to tip. Whereas the prepro-tocrista of M1-M3 of *M. handleyi* terminates lingually on the paracone, the preprotocrista of *M. caucae* extends along the anterior surface of the paracone to join with the anterolabial cingulum, forming a continuous shelf. Juvenile individuals of *M. handleyi* have the anterior cingulid of dp3 well developed anterolabially, whereas *M. caucae* juveniles have a reduced anterior cingulid.

Comparisons with other *Marmosops* species

Two other congeneric species (besides *M. caucae*) are known to occur in the Colombian Andes and merit comparison with *M. handleyi* (**Table 3**).

   Marmosops fuscatus and *M. handleyi* are the only two montane Colombian species that have gray-based ventral hairs, both species possess two kinds of antebrachial vibrissae (distal and proximal), their petrosal bones have a large area exposed through the anteroposteriorly elongated subsquamosal foramen, and the anterolabial margin of M3 lacks a continuous shelf. However, these species differ in certain other respects. *Marmosops fuscatus* is larger on average (e.g., in TL and CBL; **Table 3**), and its nasals have nearly parallel lateral margins with hardly any trace of lateral expansion at the maxillo-frontal suture (by contrast, *M. handleyi* is smaller and has laterally expanded nasals at the suture of maxillary and frontal bones). Palatine fenestrae are reduced or ab-sent in *M. fuscatus*, as opposed to the large fenestrae present in *M. handleyi*. Although additional individuals should be examined, the inspection of two adult males and one adult female specimens of *M. fuscatus* (AMNH 31531, 276509, FMNH 22174) suggest sexual dimorphism of the accessory upper canine cusps. Although *M. handleyi* and *M. fucatus* share this trait, the details of sexual dimorphism in canine morphology differ between them. Namely, males of *M. fuscatus* lack accessory cusps completely, whereas the one female we examined had a single posterior accessory cusp (males of *M. handleyi* have only a posterior cusp and females have both anterior and pos-terior cusps) (**Table 3**).

Marmosops parvidens and *M. handleyi* have two antebrachial vibrissae (distal and proximal), the nasals are laterally expanded at the maxillo-frontal suture and the subsqua-mosal foramen is anteroposteriorly elongated. However, *M. parvidens* (as represented by our Colombian material) is smaller (**Table 3**), has a band of self-white ventral hairs, the palatine fenestrae are usually absent, both males and females have a single posterior accessory cusp on C1, and M3 has a continuous shelf along its anterolabial margin. By contrast, *M. handleyi* is larger, has completely gray-based ventral fur, conspicuous palatine fenestrae, a sexually dimorphic C1, and the anterolabial margins of M3 do not show a continuous shelf.

Ecogeographic distribution and natural history of *Marmosops handleyi*

As far as is known, *M. handleyi* is endemic to Wet Forest and Premontane Wet Forest in the northern part of the Cordillera Central of the Colombian Andes (**Figs. 1, 10**), where it has been collected at four localities between 1400 and 1950 m. Although Cuartas-Calle and Muñoz-Arango (2003b) reported four localities for the species in the north of the Cordillera Central, they provided no supporting reference to associated voucher material. Therefore, the only localities definitely known for the species include the type locality and the three additional sites recorded in the present work.

   Our capture results suggest that this species inhabits the interior of small and mid-sized fragments of secondary forest that have a high degree of epiphytism and great abundance of individuals of Arecaceae, Araceae and Pipera-ceae families. We did not record the presence of the species in early-successional vegetation, clearings or forest edges. The species was successfully caught in traps that were placed where aerial roots, trees, or small branches with reduced diameter created a connection between the understory and mid-canopy. All of our captures were in traps set on the ground; among these, one individual was captured in a pitfall trap. These facts suggest that the spe-cies has a strong tendency to use the ground and lower understory stratum as previously
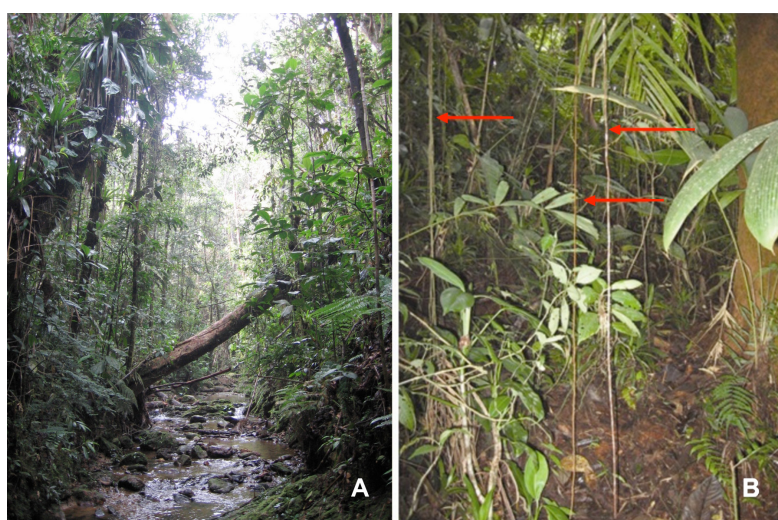
Fig. 10. Habitat of the species *Marmosops handleyi* and *M. caucae* captured in the present study. Riparian Premontane Wet Forest along a stream bank in Amalfi (**A**). Capture site of *M. handleyi* at Yarumal (**B**) showing the abundance of aerial roots (arrows).

reported by Passamani (1995), Cunha and Vieira (2002), and Loreto and Vieira (2008) for other congeneric species.

Three lactating adult females were found in October 2005 and January 2006 at the Yarumal locality (CTUA 413, 414, 416). Until a detailed multi-seasonal population ecology study is developed, these results suggest that this species is reproductively active during the rainy season (September-November) with a weaning period that may last until the dry season (December-February).

Marmosops handleyi was one of 11 species of small mammals collected at Amalfi and one of 12 species at Yarumal. At both localities, the species was sympatric with two other small opossums, *M. caucae* and *Marmosa (Micoureus) regina*. At the Amalfi locality, seven sympatric species of sigmodontine rodents and one heteromyine were also trapped; at Yarumal, seven sigmodontines, one heteromyine and one shrew were recorded along with *M. handleyi* (**Table 4**).

Phylogenetic analysis

Our analyzed matrix contains 7449 characters, of which 1451 are parsimony-informative. Ten equally most parsimonious trees of 3190 steps

were found, the strict consensus of which is presented in **Fig. 11**. Major relationships within the tribe Thylamyini recovered in our analysis do not differ significantly from those found by Voss and Jansa (2009, figure 36). All four polytypic member genera were recovered as monophyletic groups with bootstrap values greater than 90%. The monophyly of *Cryptonanus+Gracilinanus* is only weakly supported, and relationships among *Thylamys* species are unresolved. Although the present topology recovers *Chacodelphys formosa* as the most basal lineage in the tribe (as opposed to the polytomy found by Voss and Jansa, 2009), the bootstrap value supporting this relationship is weak. The genus *Marmosops* was still recovered as a monophyletic group after adding the two new taxa, and the four large-bodied taxa of *Marmosops* included in this study form a basal polytomy (**Fig. 11**). Although we do not recover much phylogenetic resolution among species of *Marmosops* based on this matrix, two interesting results merit comment.

First, although relevant nodal support is weak, *M. handleyi* was recovered as the sister taxon of two small-bodied species, *M. parvidens* and *M. pinheiroi*. These three species share the following three morphological
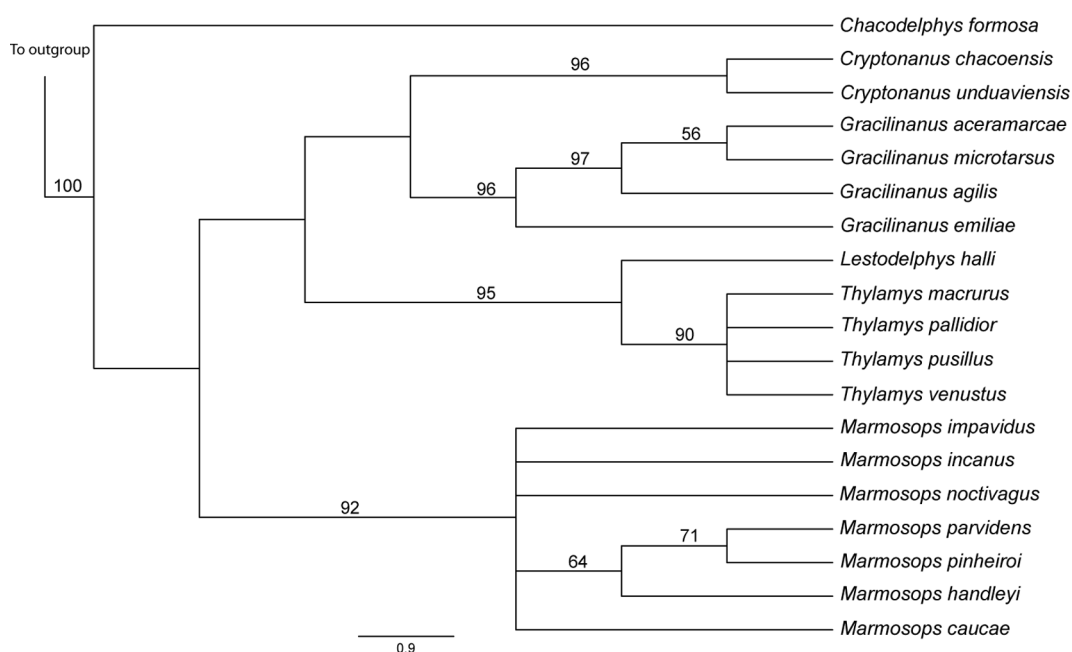
Fig. 11. Strict consensus of 10 equally most parsimonious trees recovered by a heuristic search of the Tribe Thylamyini (see text). Numbers above branches indicate bootstrap support values. Bootstrap values below 50% are not shown.

Table 4

Small non-volant mammals captured at the surveyed localities. The results from the two sites at Yarumal are summarized in a single column.

	Amalfi	Anori	Yarumal
DIDELPHIMORPHIA			
Marmosops handleyi	X		X
Marmosops caucae	X		X
Marmosa (Micoureus) regina	X		X
SORICOMORPHA			
Cryptotis colombiana			X
RODENTIA			
Chilomys instans	X		
Heteromys australis	X	X	X
Handleyomys intectus	X		X
Melanomys caliginosus	X		X
Microryzomys minutus	X		X
Neacomys tenuipes	X		X
Nephelomys albigularis	X	X	X
Rhipidomys latimanus	X	X	X
Thomasomys sp.		X	X

traits that have yet to be analyzed in a broad phylogenetic context: 1) at least in males, all three species have both anterior and posterior accessory cusps on their upper canines; 2) the subsquamosal foramen is anteroposteriorly elongated, exposing a large area of the petrosal bone behind the sulcus of the prootic sinus; and 3) the postglenoid foramen runs posteromedially so that the sulcus of the prootic sinus is not exposed in ventral view. Even though the presence of accessory cusps in the upper canines might be a variable character (Voss and Jansa, 2009), the last two mentioned traits appear to be consistent in these taxa as well as in other examined species such as *M. bishopi* (FMNH 84251, 203328, 203509) and *M. fuscatus* (AMNH 31531, 144832, FMNH 22174). Although these and other characters might optimize as synapomorphies for a clade comprising these species (and perhaps others not yet examined), we currently lack the taxon sampling to support such a diagnosis.

The second result to be highlighted from our phylogenetic analysis is the lack of support for a sister-taxon relationship between *Marmosops impavidus* (sensu Voss and Jansa, 2009) and the *impavidus*-like Colombian form included in this study (*M. caucae caucae* sensu Tate, 1933). Among the nonmolecular characters that we were able to score for this study, these two taxa differ in the morphology of the preprotocrista and anterolabial cingulum (character 105 of Voss and Jansa, 2009), which are fused to form a continuous shelf in *M. caucae* but not in *M. impavidus*. Given this difference and the lack of any support for a close relationship between Colombian and Peruvian populations currently referred to *M. impavidus*, we feel justified in using the name *M. caucae* for the Colombian form.

Conservation status

In order to assign a species into one of the IUCN Red List categories it is mandatory that the species meets some of the criteria established for that purpose (IUCN, 2001). It is necessary then, to evaluate each category, criterion and subcriterion to determine whether

Marmosops handleyi merits its current ranking as a Critically Endangered (CR) taxon.

Criteria A, C, D, and E each require information about population size, which is not currently available for *M. handleyi*. To meet criterion "CR B1" (Geographic range in the form of extent of occurrence) the species' estimated extent of occurrence must be less than 100 km^2. It is unlikely that *M. handleyi* meets this criterion. The distance between the two most distant capture localities is 48 km, and it seems probable that the species is not restricted to a 2-km wide strip connecting these points. The subcategory "B1a" does not apply to *M. handleyi,* because the species is known to occur at more than a single locality, and the subcategories "B1 b and c" cannot be evaluated, because they are based on information about population decline and habitat reduction that is lacking for the species. *Marmosops handleyi* does not meet criterion "CR B2" (Area of occupancy estimated to be less than 10 km^2) because, at least at the Amalfi site, it occurs in a forest fragment with an area greater than the required minimum (Cuervo, 2002). Therefore, the available information suggests that *M. handleyi* does not meet the required criteria for a Critically Endangered taxon.

Nevertheless, the available information is consistent with categorizing *M. handleyi* as a threatened species. To be formally categorized as Endangered (EN), the estimated extent of occurrence of a species should be less than 5000 km^2, no more than five localities should be known for the species, and the species area of occupancy should be less than 500 km^2. *Marmosops handleyi* meets all three of these criteria. Therefore, we propose that the species be transferred to the Endangered (EN) category based on its extent of occurrence and area of occupancy (criteria EN B1ab(ii) + 2ab(ii)).

ACKNOWLEDGMENTS

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APPENDIX

Specimens examined

Marmosops handleyi: COLOMBIA, Antioquia Department: **Municipio Amalfi**, Vereda Guayabito, Finca Costa Rica, Bosque Caracolí [6°52'25.0''N, 75°05'56.7''W], 1840 m CTUA 410 male, 02 November 2004; CTUA 411 female, 02 February 2005; CTUA 412 female, 06 July 2005; CTUA 433 male, 14 February 2008. **Municipio Valdivia**, 9km south (= Municipio Valdivia, Vereda San Fermín) [7°5'45''N, 75°27'57''W] FMNH 69838 (Holotype), 69823 (Paratype). **Municipio Yarumal**, Corregimiento El Cedro, Vereda Corcovado, Finca El Bosque, Bosque San Andrés [07°04'21.7''N, 75°25'16.5''W], 1760 m CTUA 413 female, 02 October 2005; CTUA 414 female, 01 October 2005. **Municipio Yarumal**, Vereda El Rosario, sitio Alto de Ventanas, Finca Villa Nueva [07°05'0.9''N, 75°26'41.2''W], 1950 m CTUA 415 male, 09 January 2006; CTUA 416 female, 11 January 2006.

Marmosops caucae: COLOMBIA, Antioquia Department: **Municipio Amalfi**, Vereda Guayabito, Finca Costa Rica, Bosque Caracolí [6°52'25.0''N, 75°05'56.7''W], 1840 m CTUA 417 male, 02 November 2004; CTUA 418 male, 02 November 2004; CTUA 419 female, 04 November 2004; CTUA 420 male 01 November 2005; CTUA 421 female, 02 February 2005; CTUA 422 male, 06 July 2005; ICN 17022 female, 12 February 2004. **Municipio Yarumal**, Corregimiento El Cedro, Vereda Corcovado, Finca El Bosque, Bosque San Andrés [07°04'21.7''N, 75°25'16.5''W], 1760 m CTUA 426 female, 03 October 2005; CTUA 427 female, 03 October 2005.

Marmosops parvidens: COLOMBIA, Antioquia Department: **Municipio Valdivia**, 9 km South (= Municipio Valdivia, Vereda San Fermín), 1400 m FMNH 69822. La Cabaña FMNH 69825. Quebrada Valdivia, 900 m FMNH 69826. **Municipio Uraba**, Villa Arteaga, 130 m FMNH 69837. Huila Department: **Municipio acevedo**, San Adolfo, 1400 m FMNH 70927. San Adolfo, 1700 m FMNH 70928.

Marmosops fuscatus: VENEZUELA, Mérida: **La Azulita** FMNH 22174. Carabobo: **Valencia**, La Cumbre de Valencia AMNH 31531. Aragua: **Girardot**, Rancho Grande AMNH 144832.

Marmosops bishopi: PERU, Cuzco: **Cosñipata**, Villa Carmen FMNH 84251. San Martin: **Rioja**, Pardo Miguel, Naranjos, Caserio El Diamante FMNH 203328, 203509.