



Rediscovery and redescription of *Marmosa (Stegomarmosa) andersoni* Pine (Mammalia: Didelphimorphia: Didelphidae), an endemic Peruvian mouse opossum, with a reassessment of its affinities

SERGIO SOLARI^{1,3} & RONALD H. PINE²

¹Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, U.S.A.

²Natural History Museum and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, U.S.A.; and Field Museum, Chicago, IL 60605, U.S.A. E-mail: ronpine@mac.com

³Current address: Instituto de Biología, Universidad de Antioquia, Calle 67 No. 53-108, AA 1226, Medellín, Colombia. E-mail: ssolari@matematicas.udea.edu.co

Abstract

Mouse opossums of the genus *Marmosa* Gray (Didelphidae) represent a complex of taxa with poorly understood affinities. Species now placed within this genus are mostly the leftovers from previous taxonomic arrangements. Even the most recent and complete revisions have not fully resolved the relationships among *Marmosa* and the many taxa previously included in *Marmosa* or listed as synonyms of it. Herein, we review and discuss one of these taxa, *Stegomarmosa*, based on new specimens that significantly increase our knowledge of the morphological diversification of the group. Until recently, this genus/subgenus has been known only from a single specimen taken more than 50 years ago in south-eastern Peru. In 1997-1998, six additional specimens were collected at two little-separated localities almost 200 km NW of the type locality. We include a detailed diagnosis of the genus-group *Stegomarmosa* and its type species, *M. andersoni*, and update the distribution for and provide new information on the natural history of the latter. We also discuss published claims, concerning geographic range, that may be inaccurate and misleading. Finally, we scored the morphological characters used in the most recent phylogenetic analyses of the didelphids, in order to explore the affinities of *M. andersoni* and to determine the distinctiveness of the taxon *Stegomarmosa*.

Key words: Distribution, new data, systematics, taxonomy, Peru

Resumen

Las raposas del género *Marmosa* Gray (Didelphidae) representan un grupo de taxa de afinidades poco resueltas. La mayoría de especies en el género son los remanentes de previas revisiones taxonómicas. Incluso las revisiones más recientes y más completas no han podido resolver las relaciones entre *Marmosa* y los taxa previamente sinonimizados con ella. En este trabajo discutimos uno de estos taxa, *Stegomarmosa*, en base a especímenes adicionales que incrementan significativamente el conocimiento de la diversificación morfológica del grupo. Hasta hace poco, este género o subgénero era conocido de un único ejemplar colectado en el sureste de Perú, hace más de 50 años. Entre 1997-1998, seis especímenes adicionales fueron colectados en dos localidades cercanas, distantes cerca de 200 km al noroeste de la localidad tipo. Incluimos una diagnosis detallada del taxon *Stegomarmosa* y su especie tipo, *M. andersoni*, actualizamos su distribución y proveemos nueva información de su historia natural. También discutimos reportes sobre rangos geográficos que pueden resultar inexactos y confusos. Finalmente, codificamos los caracteres morfológicos usados en los más recientes análisis filogenéticos de los didélfidos, para explorar las afinidades de *M. andersoni* y determinar la distinción del taxon *Stegomarmosa*.

Palabras clave: Distribución, nueva información, sistemática, taxonomía, Perú

Introduction

The genus *Marmosa* Gray was restricted by Gardner and Creighton (1989) to include, basically, only the *murina* species group of Tate (1933); however, the genus as so restricted has never been revised. Most of the currently recognized species of *Marmosa* were included in Tate's (1933) classical review. The ones not included are *M. andersoni* Pine (1972) and *M. xerophila* Handley and Gordon (1979). *Marmosa lepida* (Thomas) was assigned to the "microtarsus group" by Tate in 1933, but Cabrera (1958) placed it under *Marmosa* sensu stricto. *Marmosa*, as now constituted, consists of the leftovers remaining since *Marmosa*, in the sense of Tate, has had various of its constituents removed as separate genera, e.g., *Thylamys* and *Micoureus*—see Marshall (1981) and Reig *et al.* (1985), *Marmosops* and *Gracilinanus*—see Gardner & Creighton (1989), *Tlacuatzin*—see Voss and Jansa (2003), *Chacodelphys*—see Voss *et al.* (2004), and *Cryptonanus*—see Voss *et al.* (2005).

Pine (1972) named *Marmosa andersoni* and erected the subgenus *Stegomarmosa* for it alone, stating, on the basis of skull characters, that his new subgenus was probably most closely related to the subgenus *Marmosa*, as then constituted, as opposed to its having affinity with the subgenus *Thylamys*, as then constituted. Tate (1933) had recognized no subgenera, but Cabrera (1919, 1958) had divided *Marmosa* (sensu lato) into these two subgenera, as had Gilmore (1941). Anticipating future developments, Pine (1972) wrote: "Future studies of the genus *Marmosa* may result in its being split into two or more genera." The subgenus *Marmosa*, as then constituted, contained the current *Marmosa*, *Marmosops*, *Micoureus*, and *Tlacuatzin*, while the then subgenus *Thylamys* contained the current *Thylamys*, *Gracilinanus*, *Cryptonanus*, and *Chacodelphys*. Pine (1972) cited, as subgeneric characters for *Stegomarmosa*, the exceptionally flared postorbital processes of the skull, the strongly constricted interorbital area, and the long, pale, tail bristles which form a fringe along each side of the naked grasping surface. Since Pine's description of the new subgenus, authors have been divided on whether to recognize it. Pine and Collins (1973), owing to a *lapsus*, omitted any mention of *Marmosa* (*Stegomarmosa*) *andersoni* and Marshall (1981) also failed to discuss it, as did Emmons and Feer (1990, 1997)—see Pine (1999). Creighton (1984) stated that *M. andersoni* agreed in almost every respect with the "murina group" of the subgenus *Marmosa* as defined by him, and thus he assigned *andersoni* to this "group." Gardner (1993, 2005) followed Creighton's view of this matter, placing *andersoni* in *Marmosa* in the strict sense and recognizing no subgenera. However, certain authors, e.g. Kirsch and Calaby (1977), Reig *et al.* (1985), and Nowak (1999) gave *Stegomarmosa* subgeneric status within a restricted genus *Marmosa* (including *Marmosops* Matschie, in the case of Kirsch and Calaby [1977] and Reig *et al.* [1985]). Voss and Jansa (2003) were noncommittal concerning this issue, while Solari *et al.* (2001) treated *Stegomarmosa* as a full genus.

The type and, for many years, the only known specimen of *Marmosa* (*Stegomarmosa*) *andersoni* is of an adult male taken at Hacienda Villa Carmen, Cosñipata [Valley], Cusco (12°52' S, 71°15' W; 600 m; Fig. 1), southeastern Peru, by C. Kalinowski in 1954 (see also Pacheco *et al.* 1993; Solari *et al.* 2006). Until now, no additional specimens have been reported in the literature (but see Cuartas-Calle & Muñoz A. 2003; discussed below), aside from a brief mention by Solari *et al.* (2001) of the new records discussed in depth below.

The new records, resulting from field work in southeastern Peru, extend the known geographic range and allow additional description of the species' morphology, including a phylogenetic analysis to clarify its systematic position in regard to other mouse opossums, including species of *Marmosa*.

Methods

Between 1997 and 1998, during a biodiversity assessment carried out by researchers of the United States National Museum (USNM), Smithsonian Institution, and the Museo de Historia Natural (MUSM), Universidad Nacional Mayor de San Marcos, small mammals were collected in the Lower Urubamba River (LUR)

Valley, La Convención Province, Cusco, southeastern Perú. The LUR Valley is located between Manu National Park and the Apurimac Reserve Zone at the base of the eastern foothills of the Andes. Four exploratory well-sites for natural gas were surveyed within the area known as the “Camisea region” (see Alonso *et al.* 2001). Traps used included Victor snap-traps, Sherman and Tomahawk live-traps, and pitfall traps. On a few occasions, opossums were caught by hand during night walks, or in “sticky-traps” which were being used for herpetological inventories. Mouse opossum specimens were prepared as skin with skull or skin with skeleton or skin with skinned carcass in 10% formalin to then be transferred to 70% ethanol. Some entire animals were also preserved in fluid in this way.

Standard external measurements in millimeters (Total length [TL], length of tail [LT], length of hind foot [HF], length of ear [E]), and weight (W) in grams were taken directly in the field; head-plus-body length [HBL] was obtained by subtracting LT from TL. We used ten craniodental measurements (Table 1); most of them are as defined by Voss *et al.* (2001), including: CBL—condylobasal length; LIB—least interorbital breadth; ZB—zygomatic breadth; PB—palatal breadth; MTR—maxillary toothrow; LM—molar length. Other measurements are as defined by Patton *et al.* (2000; PL: palatal length) or by Pine (1981; M1–M3: length of first three upper molars, M3–M3: maximum breadth between third upper molars, MDTL: mandibular toothrow length, from the front of the first lower incisor to the back of the last lower molar). Morphological characters were scored based on the dataset of Voss and Jansa (2003); phylogenetic relationships were inferred by Maximum Parsimony analyses as implemented in PAUP* (test version 4.0b; Swofford 2002), under full heuristic search with 100 random taxon addition, and tree-bisection-reconnection branch swapping. A majority-rule consensus tree was calculated from the sample of most parsimonious trees (MPTs). Reliability of clades was evaluated by bootstrap analyses (Felsenstein 1985) with 200 replicates.

Specimens examined are housed in the Field Museum of Natural History (FMNH), Chicago; Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Perú; and United States National Museum (USNM), Washington, D.C.

TABLE 1. External and cranial measurements (mm), and weight (g) for the three adult specimens of *Marmosa (Stegomarmosa) andersoni*. The museums represented are: Field Museum, Chicago (FMNH), and Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). Measurements follow those of Voss *et al.*, 2001 (except PL, from Patton *et al.*, 2000; and M1–M3, M3–M3, MDTL, from Pine 1981).

	FMNH 84252	MUSM 14154	MUSM 14155
TL	--	317	300
LT	181	193	175
HBL	--	124	125
HF	20.3	20	22
E	16.9	20	20
W	--	28	38
CBL	32.9	33.5	33.8
LIB	4.3	3.6	4.2
ZB	18.7	18.3	18.9
PL	18.8	17.9	18.1
PB	10.3	10.0	10.4
MTR	13.1	13.0	13.3
LM	6.7	6.5	6.7
M1–M3	5.6	5.5	5.7
M3–M3	9.9	9.7	10.0
MDTL	15.0	15.0	15.1

Rediscovery of *Marmosa (Stegomarmosa) andersoni*

Four juvenile opossums (MUSM 14151–14153, USNM 582777) were collected, by hand, on the night of 27 November 1997, in a large stand of bamboo at Cashiriari 3 well-site (11°52' S, 72°39' W; 694 m). Ranges of external measurements were: TL, 182–195; LT, 105–110; HF, 15–18; E, 14–16; W, 9 g. Although immature (MUSM 14151 falls into age class 2 of Pine *et al.* 1985a), their external characters (warm brownish coloration, black eye-rings, long distal caudal hairs) suggested membership in the genus *Gracilinanus*, and, accordingly, they were reported as *G. agilis* (Burmeister) (see Solari *et al.* 1998). The following year, two adult (of age class 5 of Pine *et al.* 1985a) female mouse opossums of similar appearance to each other, but unlike any known species in the area, were secured at two localities, Cashiriari 3 and San Martín 3 well-sites. One of these, MUSM 14154, carrying five attached young = 11 mm crown-rump, was taken on 31 August 1998 from a sticky-trap set around a branch of a medium-sized tree near the forest edge, by the herpetological team, at the Cashiriari 3 well-site. The other one, MUSM 14155, was caught inside a bamboo cane (*Guadua* sp.) by a native guide, on 9 November 1998, at the San Martín 3 well-site (11°47' S, 72°42' W; 474 m). Both of the new localities (Fig. 1) are within an area ecologically similar to the Cosñipata Valley, which contains the type locality.

All four juveniles were found climbing around in a single bamboo thicket, probably close to their nest. At the Cashiriari 3 well-site, other mouse opossums (*Marmosa quichua* Thomas, *Marmosops noctivagus* [Tschudi], and *Micoureus demerarae* [Thomas]) were collected in bamboo thickets, where they nested using dead leaves. None of our *M. andersoni* specimens was observed or caught more than 3 m above the ground.

Skull and external characters of the adults matched those given by Pine (1972) in his description of *Marmosa (Stegomarmosa) andersoni*. Although the type specimen (FMNH 84252) is of an adult male, the two adult female specimens resemble it in most essential details, such as the enormous postorbital processes, the strongly constricted interorbital area (Fig. 2), the presence of a conspicuous fringe of relatively long silvery bristles on each side of the naked caudal prehensile surface, and an obvious gular gland. Sexual dimorphism is evident, however, in that the male holotype, but not the females, possesses the lateral carpal tubercle (see Lunde & Schutt 1999). The three adults are remarkably similar in their dimensions (Table 1). After the adults were identified as *M. andersoni*, the four juveniles were re-identified as belonging to the same taxon (see Solari *et al.* 2001). Differences between the juveniles and the adults are no more than would be expected within a single species but involving animals of different ages. Diagnostic features used in assigning the juveniles to *M. andersoni* include various of those seen in adults, such as the skull profile, large orbits, the color pattern (although juvenile MUSM 14151, at least, shows somewhat browner, less reddish dorsal coloration), the incipient and beaded postorbital processes (highly unusual for such young animals), and the characteristic silvery bristle fringes on each side of the caudal prehensile surface. The six new specimens extend the geographic range of this rare and apparently endemic opossum by almost 200 km to the northwest of the type locality (Fig. 1).

At the type locality, Villa Carmen, three other species of mouse opossums were also reported by Pine (1972): *Marmosa rubra* Tate, *Marmosops impavidus* (Tschudi), and *Marmosops* cf. *parvidens* (Tate)—this last specimen actually represents *M. bishopi* (Pine) as defined by Voss *et al.* (2001). Didelphid species sympatric with *M. andersoni* at the two new localities include: *Didelphis marsupialis* Linnaeus, *Gracilinanus* cf. *agilis*, *Hyladelphys kalinowskii* (HersHKovitz), *Marmosa quichua*, *Marmosops noctivagus*, *Metachirus nudicaudatus* (É Geoffroy), *Micoureus demerarae*, *Monodelphis emiliae* (Thomas), and *Monodelphis peruviana* (Osgood). In the LUR Valley, which includes the aforementioned two well-sites plus two others (Cashiriari 2 and Pagoreni, see Alonso *et al.* 2001), 17 species of didelphids were recorded (Solari *et al.* 2001), thus giving this area one of the most diverse marsupial faunas in the Neotropics.

The predominant vegetation of the region was lowland tropical rainforest; descriptions of the vegetation at each well-site have been provided by Comiskey *et al.* (2001) and are summarized here. The terra firme forests

were characterized by a relatively low abundance of trees ≥ 10 cm dbh (diameter at breast height), but a high canopy, ascending to > 30 m. These primary forests were dominated by *Iriartea deltoidea* (Arecaceae) and *Matisia cordata* (Bombacaceae). Other important terra firme forest species included *Chimarrhis* sp. and *Pentagonia parvifolia* (both Rubiaceae). The most defining feature of the secondary forests was the overwhelming dominance of *Senefeldera inclinata* (Euphorbiaceae), which occurred under no other conditions. These secondary forests were characterized by a high abundance of trees ≥ 10 cm dbh and a low canopy. The mixed upland forests were structurally and compositionally intermediate as compared to the primary and secondary forests; however, they had the lowest stature of all the sites. The arborescent bamboo, *Guadua sarcocarpa*, was abundant at San Martín 3, and at Cashiriari 3, while it was absent from the Cashiriari 2 and Pagoreni well-sites. Important species at Cashiriari 3 included *Iriartea deltoidea* (Arecaceae), *Miconia triplinervis* (Melastomataceae), and *Pseudolmedia laevis* (Moraceae). In general, human disturbance was negligible throughout the study area. Temperatures across this area were typically warm and showed little annual variation. Mean temperatures ranged from 23.5 to 24.5 °C and relative humidity normally exceeded 80%. The region experienced distinct wet and dry seasons. Mean annual rainfall ranged between 3,000 and 3,500 mm and occurred mostly from the beginning of October through the end of April (Alonso & Dallmeier 1998).

According to NWMSG (1996), *M. andersoni* is “critically endangered” on the basis of being: “Severely endangered or known to exist at only a single location” and “Continuing decline, observed, inferred or projected, in...area, extent and/or quality of habitat.” Our new information has increased the known localities from one to three, but has not appreciably changed the extent of our knowledge concerning these criteria *vis-a-vis* *M. andersoni*. Only one adult was taken at each new locality, and the 4 juveniles were caught together. All the localities are within a narrow strip along the base of the Andes, in very similar pre-montane forests below 1000 m. However, the actual distribution and abundance of this animal may be quite different than the limited information currently available would seem to indicate. The actual conservation status of this species, like that of so many known from very few specimens, is unknown.

Redescription of *Marmosa (Stegomarmosa) andersoni*

Characters which may be taken as distinctive as compared to those of other mouse opossums, and at the sub-generic or generic level, for *Stegomarmosa* include the relatively enormous postorbital process of the frontal, in shape somewhat like that of *Caluromys* J. A. Allen, the strongly constricted interorbital area, and the exceptionally large orbits (see Pine 1972). In addition, the first lower premolar is normally in broad contact, above the level of the alveoli, with the lower canine (Fig. 2). On the right side of MUSM 14154, however, this contact misses by less than a hair's width. The lower canine is procumbent and apically laterally flattened, as characterized by Voss and Jansa (2003). The ascending ramus of the dentary forms an unusually obtuse angle with the horizontal body of the dentary (Fig. 2). Most of the ventral surface of the tail is covered distally with unusually long silvery bristles that form a well-developed and characteristic fringe on each side of the mid-ventral friction pad (see Pine 1972).

The species *Marmosa (Stegomarmosa) andersoni* is a medium-sized mouse opossum (28-38 g.). The throat gland is apparent in both adult males and adult females and in at least one immature male (MUSM 14151) of age class 2 as defined by Pine *et al.* (1985a). The apparent mammary formula is 4-1-4 with all teats being abdominal-inguinal (based on MUSM 14154). Black eye-rings are prominent, widest anterior to eyes but not prolonged into area where muzzle vibrissae originate; hair on cheeks and chin cream-colored to base; a pale buffy patch on top of muzzle just posterior to rhinarium; dorsal fur relatively long, lax, not kinky, plumbeous for most of its length but tipped with a color near Snuff Brown of Ridgway (1912); ventral surface cream-buff, with hairs plumbeous at base. Fur of mammary region short, white, and woolly. Ultraviolet-induced fluorescence (presumably fugitive; see Pine *et al.* 1985b) is bright rose on venter of (longer-prepared)

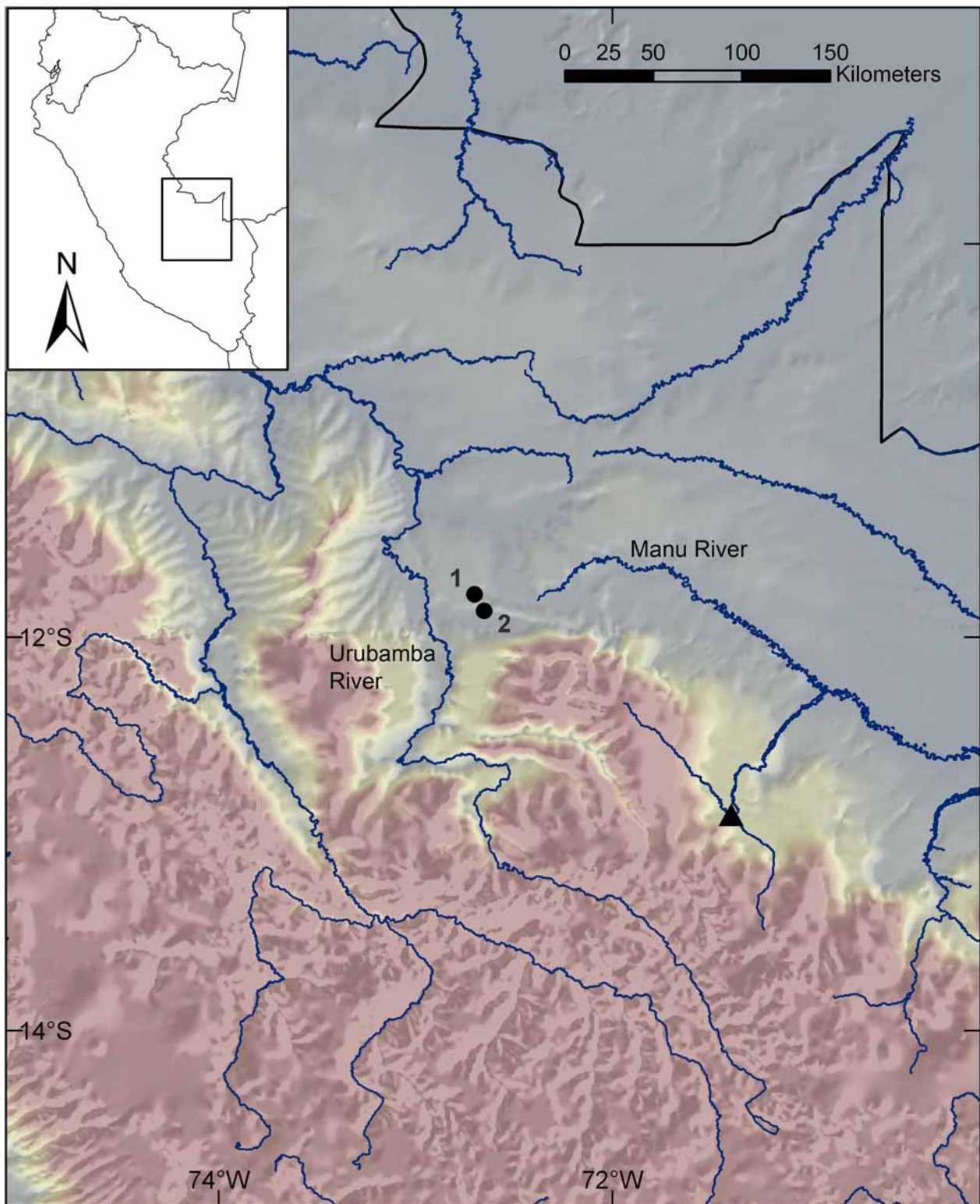


FIGURE 1. Map of southeastern Peru, showing the type locality of *Marmosa (Stegomarmosa) andersoni* (Hacienda Villa Carmen = black triangle), and the two new localities in the Lower Urubamba Region (black dots: 1 = San Martín 3, and 2 = Cashiriari 3 well-sites). Two major rivers near the collecting localities are named. Inset: Outline map of Peru, indicating the boundaries of the area shown in color.



FIGURE 2. Dorsal (above, left) and ventral (above, right) view of the skull and lower jaw (below) of MUSM 14154, a female specimen of *M. andersoni* reported in the text. Some of the distinctive traits of the species are shown, including the development of the postorbital processes and the first lower premolar's filling in the space between the lower canine and the second lower premolar. Scale bars = 5 mm.

juvenile MUSM 14151, less manifest in (more recently prepared) adults, as is often the case in didelphids. Dorsally, UV light elicits a maroon-chestnut shade in these animals. Facial vibrissae mostly black, but some are white near tips. Minor vibrissae along upper lip at least sometimes white; vibrissae on wrist and throat also white. Pinnae translucent and gray-brown, appearing naked but sprinkled externally with small shiny brown hairs visible under magnification; internally, pinnae with similar but mostly whitish hairs. Tail bicolored and longer than head plus body, with no evidence of incrassation; soft-furred only at base both dorsally and ventrally (on stuffed MUSM 14154 extends onto tail until about 20 mm from anus) and then with short blackish-brown spindle-shaped spines dorsally, becoming more elongate distally; ventral surface with proximal dark spindle-shaped bristles mixed with paler bristles, bristles becoming longer, slenderer, and whitish to silvery distally, longer and denser than in mouse opossums generally. Pattern of scalation of tail largely obscured by tail bristles except where skin of tail stretched by excess stuffing, apparently ranging from annular to spiral, depending on location (regarded as “in spiral series” by Voss & Jansa 2003, and scored as such by us). Scale shape is roughly circular, in some regions with distal margin flattened (see Tate 1933, who figured this condition for other mouse opossums). Interdigital pads 2 and 3 are subequal in size, a condition deemed by Creighton (1984) to be indicative of less arboreal habits.

As noted by Voss and Jansa (2003) for *andersoni* and other *Marmosa* species, the premaxillary rostral process is prominent. The rostrum is narrow and the braincase inflated. Rear margin of flaring postorbital process continuous with the low lambdoidal crest. Palatal fenestration in holotype appears to consist of elongated maxillopalatine fenestrae extending from level of anterior border of P3 to level of middle of M3; palatine fenestrae lie at level of M4. The normal condition of the palate may be completely without fenestration, however. MUSM 14154 has the left side of the palate completely imperforate, although there is a very thin area of bone extending from the hind margin of P2 to the level of the M3. Some portions of this thin region are thinner than others and in zones corresponding to reported fenestration in the holotype. Openings in the right side of the palate appear to be artifacts of specimen preparation. An originally imperforate palate appears to also be the case in MUSM 14151 and MUSM 14155. The postorbital process of jugal is very well developed, apparently indicating a very large eye. No anteromedial bony strut of the tympanic wing of the alisphenoid present, a secondary foramen ovale is absent. Incisors 2–5 increase in size toward rear; deciduous premolars fairly large and molariform. Exposed portion of upper canine about three times as long as exposed P1 and laterally compressed. Voss and Jansa (2003) wrote (pp. 64–65): “*Tlacuatzin canescens* resembles *Marmosa andersoni* (the type species of *Stegomarmosa* Pine 1972) in having large postorbital processes (Pine 1972: fig. 1), but these taxa are otherwise dissimilar. Based on our examination of the Peruvian type specimen (FMNH 84252), *M. andersoni* differs from *T. canescens* by having tail scales in spiral series; a long rostral process of the premaxillae; large palatine fenestrae; no maxillary fenestrae; upper incisor crowns that increase in breadth from I2 to I5; and a procumbent, apically flattened c1...we concur with the current treatment of *Stegomarmosa* as a synonym or subgenus of *Marmosa*.”

Other characters as given for the subgenus/genus.

Phylogenetic analysis based on morphology

The most recent splitting off of new genera of mouse opossums, e.g., *Hyladelphys* Voss *et al.* (2001), *Chaco-delphys* Voss *et al.* (2004), *Cryptonanus* Voss *et al.* (2005) from *Gracilinanus*; *Tlacuatzin* Voss and Jansa (2003), from *Marmosa*, is indicative of the current wave of increased activity and improvement in didelphid systematics. For *M. andersoni*, we scored most of the 71 nonmolecular characters used by Voss and Jansa (2003) to define and restrict the aforementioned genera; only two morphological characters (13: presence of medial carpal tubercle, and 61: eruption sequences of upper teeth) were scored as missing, owing to unavailability of suitable material. Character 18 was scored as inapplicable (“-”), as is done for other pouchless spe-

cies. The four characters (68-71) describing chromosomal fission/fusion events were scored as missing because no karyotype has been ascertained for this species. Our scoring is as follows: (1-10): 00100 10001; (11-20): 01?20 00-00; (21-30): 20201 00010; (31-40): 00010 00210; (41-50): 01010 00000; (51-60): 00001 11210; (61-70): ?0020 00??; (71): ?. We add *M. andersoni* to the available dataset matrix as recently updated (see Jansa and Voss, 2005: appendix I) and ran a maximum parsimony analysis following their restriction criteria for polarity of character states.

For this updated dataset (Jansa & Voss 2005), the parsimony analysis identified 67 informative characters that resulted in more than 56,000 most-parsimonious trees (179.5 steps; CI=0.50; RI=0.84) from two tree-islands [island 1=7,725 trees; island 2=48,714 trees]. To facilitate the discussion in regard to resolved nodes, we show the majority consensus tree for the >56,000 trees (Fig. 3) but remark on differences between consensus trees for each island. The consensus of Island 1 trees shows *Tlacuatzin* outside of the unresolved *Marmosa* plus *Micoureus* group of taxa, and sister to the remainder of the “didelphine” clade. The consensus of Island 2 trees is identical to Jansa & Voss’s (2005) topology, with the addition of *M. andersoni* to the ‘outsiders’ *M. robinsoni* Bangs and *M. mexicana* Merriam; these three taxa separate from the other murine opossums and basally join the most resolved part of the topology. Their positions as well as their relationships to each other are unresolved. However, the majority consensus of all trees (Island 1 + Island 2) is similar to that of Jansa and Voss (2005: fig. 1C) in that *Hyladelphys* is sister to the didelphine clade to the exclusion of the caluromyine clade, but the relationships among *Tlacuatzin* and all the *Marmosa* and *Micoureus* species are unresolved. The relative position of *M. andersoni*, *M. mexicana*, and *M. robinsoni* in island 2’s consensus suggests their distinctiveness from the other “*Marmosa*” (Fig. 3). None of the topologies recovered either a monophyletic *Marmosa* (sensu lato) or a monophyletic *Micoureus*.

Although none of the mentioned relationships had enough statistical support in the bootstrap analyses (Fig. 3) to validate generic status for *Stegomarmosa*, it is evident that it does not cluster with *murina* (type species of *Marmosa*) or other species in *Marmosa* (sensu lato). In our opinion, the inclusion of *andersoni* and *murina* in a single genus-level taxon would make it paraphyletic. However, no clades with two or more species of *Marmosa* or *Micoureus* appear in this tree. From the updated dataset of Jansa and Voss (2005), we identified only seven variable characters within the murine opossums of the genera *Tlacuatzin*, *Micoureus*, and *Marmosa*, and they do not consistently group species. Jansa and Voss’s (2005) nonmolecular topology puts *M. robinsoni* and *M. mexicana* outside *Marmosa*, but when combined with molecular data, *M. rubra* joined those two species in a separate clade (Gruber *et al.* 2007; fig. 2). It is possible that further analyses of molecular data will place *M. andersoni* with these species or as an independent lineage.

An explanation for the low resolution of the nonmolecular phylogenies is that many of the morphological characters supporting the separation of *M. andersoni* from the remainder of *Marmosa* are autapomorphies in the present phylogenetic context, but may become synapomorphies in a denser taxon sampling. Also, additional characters could be utilized which might eventually clarify the relationships of this enigmatic taxon. The present degree of divergence is similar to that between *Marmosa* and *Micoureus*, so if *Stegomarmosa* is not recognized as a genus, then neither should *Micoureus* (an arrangement already suggested by Voss & Jansa 2003). If future combined analyses of molecular and nonmolecular data find that the distinctiveness of *M. andersoni* is great enough as to justify its being regarded as representing a genus-level taxon separate from *Marmosa*, then the name *Stegomarmosa* Pine would be available for that taxon.

Unverified records of *Marmosa (Stegomarmosa) andersoni*

Cuartas-Calle and Muñoz A. (2003) listed *Marmosa andersoni* as a member of the Colombian fauna and provided a range map showing two localities in extreme northern Peru, along with two additional ones in nearby southern Colombia. A colored drawing is provided of the head and shoulders of an opossum identified as

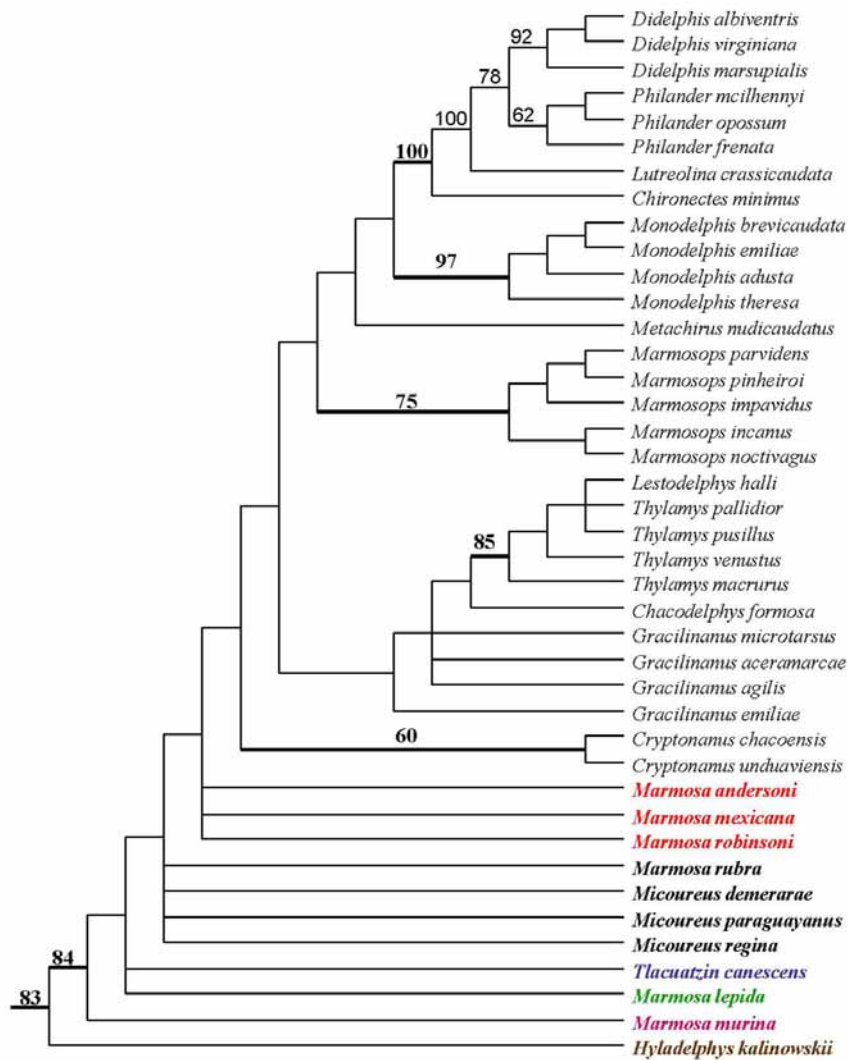


FIGURE 3. Majority-rule consensus of > 56,000 equally most-parsimonious trees obtained through a heuristic parsimony analysis of nonmolecular characters described by Jansa and Voss (2005), updated by inclusion of *M. andersoni*. The “caluromyine” outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, and *C. philander*) are not shown. Statistical support values, above branches, based on 200 bootstrap replicates and indicated only for those above 50%.

M. andersoni. The females are described as not possessing a pouch but developing lateral folds for protecting the young. Such folds are also stated to be characteristic of all six species of *Marmosa* that Cuartas-Calle and Muñoz A. (2003) list for Colombia. To our knowledge, such folds have not been claimed to exist by other contemporary authors nor have we ever observed such a condition in females of any species of *Marmosa*, with or without attached young. In addition, Cuartas-Calle and Muñoz A. (2003) stated that the penis is bifid in *M. andersoni*, which implies that they have examined at least one male. Of the six references that they give which supposedly concern this species, only two actually do so, and none record it from Colombia. The Colombian range of *M. andersoni* was given as “...las regiones de la Amazonia y la Orinoquia, en limites con Perú [=...Amazon and Orinoco basins on the border with Peru].” The habitat was given as “...tierras bajas y zonas calientes húmedas... asociada a lugares boscosos, densos y húmedos, en bosques primarios y secundarios [=...hot and humid lowlands...associated with densely forested humid areas in primary and secondary forests].” These places are hundreds of kilometers to the north of the Peruvian localities discussed by us. No specimens or localities are mentioned in their text. To our knowledge, no such records exist for northern Peru,

neither have such been cited in previous taxonomic lists for Colombia. In view of the many uncertainties concerning the claims of Cuartas-Calle and Muñoz A. (2003), we do not regard the presence of *M. andersoni* in northern Peru and in Colombia as having been, in any way, established. However, we do not maintain that this species might not have a more extensive geographic range than presently known.

Specimens examined

Marmosa (Stegomarmosa) andersoni (7): PERU: Cusco, Cosñipata Valley, Hacienda Villa Carmen, 600 m (FMNH 84252, holotype, adult male); Cusco, La Convención, Camisea, Cashiriari 3 well-site (MUSM 14151–14153, USNM 582777, juveniles; MUSM 14154, adult female); Cusco, La Convención, Camisea, San Martín 3 well-site (MUSM 14155, adult female).

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