A REVISION OF THE DIDELPHID MARSUPIAL GENUS *MARMOSA*

PART 1. THE SPECIES IN TATE'S 'MEXICANA' AND 'MITIS' SECTIONS AND OTHER CLOSELY RELATED FORMS

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ABSTRACT

We revise the nominal species of mouse opossums currently synonymized with *Marmosa mexicana* Merriam, 1897, and *M. robinsoni* Bangs, 1898, which include all of the trans-Andean taxa currently assigned to the nominotypical subgenus of *Marmosa*. In addition, we redescribe two other species that appear to be closely related to *M. mexicana* and *M. robinsoni* based on morphological or molecular citeria: *M. rubra* Tate, 1931, and *M. xerophila* Handley and Gordon, 1979. Based on first-hand examination of holotypes and other material (about 1500 specimens in total), we additionally recognize *M. isthmica* Goldman, 1912, and *M. simonsi* Thomas, 1899 (both currently synonymized with *M. robinsoni*), and *M. zeledoni* Goldman, 1917 (currently synonymized with *M. mexicana*), as valid species. For each of the seven species recognized as valid herein (*M. mexicana*, *M. zeledoni*, *M. isthmica*, *M. robinsoni*, *M. xerophila*, *M. simonsi*, *M. rubra*), we describe and illustrate diagnostic external and craniodental characters, tabulate measurement data from adult specimens, list all known examples of sympatry, and map geographic ranges based on specimens examined. The species newly recognized as valid herein, all of which occur in Central America and/or northwestern South America, substantially increase the known diversity of trans-Andean mouse opossums, but it is not currently known whether or not these represent a distinct radiation within the genus *Marmosa*.

INTRODUCTION

Species of the genus *Marmosa*, commonly known as mouse opossums (fig. 1), are long-tailed, black-masked, pouchless didelphid marsupials that inhabit a wide range of tropical and subtropical habitats from Mexico to Argentina. *Marmosa* was last revised by Tate (1933), who recognized several species groups that have subsequently been elevated to generic rank (table 1). In the classification proposed by Gardner and Creighton (1989), the species in Tate's "Cinerea Group" were referred to the genus *Micoureus* Lesson, 1842; those in his "Murina Group" to *Marmosa* Gray, 1821; those in his "Noctivaga Group" to *Marmosops* Matschie, 1916; and those in his "Elegans Group" to *Thylamys* Gray, 1843. Most of the species in Tate's "Microtarsus Group" were placed in a new genus, *Gracilinanus* Gardner and Creighton, 1989.

Recent phylogenetic research based on molecular sequence data (e.g., Patton et al., 1996; Jansa and Voss, 2000; Steiner et al., 2005) has convincingly indicated that *Marmosa* (sensu Tate) was polyphyletic, and the same studies have consistently supported the monophyly of *Marmosops*, *Micoureus*, and *Thylamys* as those taxa were recognized by Gardner and Creighton (1989). However, a new genus was proposed for "*Marmosa*" *canescens* by Voss and Jansa (2003), and other new genera were later described for two clades formerly concealed by synonymies

within *Gracilinanus* (see Voss et al., 2004, 2005).

Despite these refinements, the taxonomic status of *Marmosa* remains problematic because all molecular phylogenies published to date indicate that the genus (as understood by Gardner and Creighton, 1989) is paraphyletic with respect to *Micoureus* (fig. 2). Obviously, several alternative classifications would be consistent with such results: either (1) *Micoureus* could be regarded as a junior synonym of *Marmosa*; or (2) *Micoureus* could be regarded as a valid subgenus of *Marmosa*; or (3) *Marmosa* could be restricted to *M. murina* (the type species). Of these, the first option would result in the loss of a useful and familiar name for a well-supported clade (*Micoureus*), whereas the second and third alternatives would require that additional subgenera or genera be resurrected from synonymy or described as needed to contain the other species currently referred to *Marmosa*.

The interim solution proposed by Voss and Jansa (2009), which we adopt herein, is to recognize *Micoureus* as a subgenus of *Marmosa*, and to refer all of the species formerly included in *Marmosa* to the nominotypical subgenus. In effect, this tactic simply moves the problem of paraphyly from the generic level (where it affects binomial usage) to the subgeneric level (where it does not). Although clearly suboptimal, no further progress in the classification of this complex

Fig. 1.   *Marmosa zeledoni*, photographed at La Selva Biological Station, Heredia province, Costa Rica, in August 2005 by Marco Tschapka. Zeledon's mouse opossum, formerly synonymized with *M. mexicana*, is resurrected as a valid species in this report. The local population at La Selva was previously reported as *M. mexicana* by Timm et al. (1989), Voss and Emmons (1996) and Sperr et al. (2009).

is possible until the phylogenetic relationships among all of the included species are worked out. To date, only five of the nine currently recognized species in the subgenus *Marmosa* are represented in published trees, and there is reason to believe that additional valid species may be concealed among the putative synonyms of several geographically widespread forms (table 2). Two of the latter are the primary focus of this report.

As currently recognized, *Marmosa robinsoni* includes 13 nominal taxa, of which Tate (1933) treated four as valid species belonging to his ''Mitis Section'': *M. chapmani, M.*

mitis, M. ruatanica, and *M. simonsi*. All of these were swept into synonymy by Hershkovitz (1951), who alleged that the diagnostic characters mentioned by Tate were artifacts of sexual dimorphism, age, imperfect preservation, or clinal variation. Although Hershkovitz provided no analyses of data to support these claims, his conclusions were accepted by subsequent compilers of influential checklists (e.g., Cabrera, 1958; Hall and Kelson, 1959). The nominal taxa of Tate's Mitis Section (for which *M. robinsoni* is the oldest available binomen; Cabrera, 1958) extend from Honduras southward to Pana-

TABLE 1
Tate's (1933) Groups and Sections of *Marmosa* and Their Current Classification[a]

Tate's name	Current name
Cinerea Group	*Marmosa* (*Micoureus*)
Murina Group	
Murina Section	*Marmosa* (*Marmosa*, part)
Mitis Section	*Marmosa* (*Marmosa*, part)
Mexicana Section	*Marmosa* (*Marmosa*, part)
Canescens Section	*Tlacuatzin*
Noctivaga Group	*Marmosops* (part)
Microtarsus Group	
Microtarsus Section	*Cryptonanus*, *Gracilinanus*
Lepida Section	*Marmosa* (*Marmosa*, part), *Marmosops* (part)
Elegans Group	*Chacodelphys*, *Thylamys*

[a] After Voss and Jansa (2009).

ma, Peru, Venezuela, and the Lesser Antilles (Hall, 1981; O'Connell, 1983; Creighton and Gardner, 2008).

According to recent phylogenetic results (fig. 2), *Marmosa mexicana* is closely related to *M. robinsoni*. Like the latter, it also includes several nominal taxa that are currently treated as synonyms or subspecies, but in this case the current taxonomy follows Tate's (1933) revision. The distribution of *M. mexicana* is less extensive than that of *M. robinsoni*, but it still extends over 2000 km, from Mexico to Panama (Hall, 1981).

Few nonvolant small mammals have geographic distributions in Central and South America as extensive as those currently attributed to *Marmosa robinsoni* and *M. mexicana*. The range of habitats occupied by each of these species is likewise remarkable, and even a superficial examination of allegedly conspecific skins and skulls reveals a surprising degree of morphological variation. Preliminary sorting of specimens at the American Museum of Natural History by D.P.L. during a recuration project in the early 1990s suggested that at least some of the species in Tate's (1933) Mitis Section were valid (contra Hershkovitz, 1951), and this conclusion was independently reached by R.V.R. after a much more extensive study of material in other museums.

This report, which is largely based on R.V.R.'s thesis research at the Universidade de São Paulo (Rossi, 2005), summarizes our conclusions regarding the taxonomy of species belonging to Tate's (1933) Mitis Section and his ''Mexicana Section.'' To this we append redescriptions of *Marmosa xerophila* Handley and Gordon, 1979, and *M. rubra* Tate, 1931. The former is a northern South American form that is morphologically similar to *M. robinsoni*, whereas the latter is a western Amazonian species that consistently appears as the sister taxon of *M. robinsoni* + *M. mexicana* in phylogenetic analyses of molecular sequence data (e.g., Voss and Jansa, 2003, 2009; Jansa et al., 2006; Jansa and Voss, 2005). Despite these indications, it is not our assumption that all of the species treated in this report form a natural group. Among other pertinent issues, the monophyly of Tate's ''sections'' has not been tested, but distinguishing the valid species that each contains is a necessary step toward a genuinely phylogenetic classification of mouse opossums.

Materials and Methods

SPECIMENS: We examined 1481 specimens for this report, most of which are preserved as skins and skulls in the following institutional collections: AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); FMNH, Field Museum of Natural History (Chicago); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); ROM, Royal Ontario Museum (Toronto); and USNM, National Museum of Natural History (Washington, D.C.).

ANATOMICAL TERMINOLOGY: Our names for external and craniodental structures of *Marmosa* follow Voss and Jansa (2009), whose anatomical descriptors are largely consistent with standard usage (Brown, 1971; Brown and Yalden, 1973; Bown and Kraus, 1979; Wible, 2003). Principal features of the skull are illustrated in figures 3 and 4. We follow Clemens (1966) in using positional criteria for naming cusps on the stylar shelf
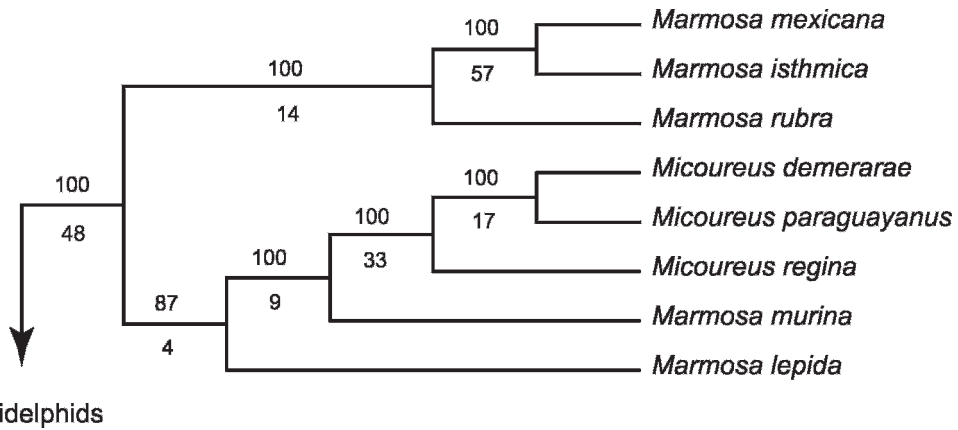
Fig. 2.   Phylogenetic relationships of *Marmosa* (sensu Gardner and Creighton, 1989) and *Micoureus* (treated as a subgenus of *Marmosa* in this report) based on a maximum-parsimony analysis of 7449 characters (including morphology, karyotypes, and sequence data from five nuclear genes; Voss and Jansa, 2009) scored for 43 species of Recent didelphids and seven nondidelphid outgroups. The numbers above and below each branch represent nonparametric bootstrap frequencies and Bremer support values, respectively. *Marmosa isthmica* (revalidated in this report) is the correct name for the terminal taxon labelled *Marmosa robinsoni* in previous analyses of these data. *Marmosa murina* is the type species of *Marmosa*.

of the upper molars (not treated in detail by Voss and Jansa, 2009) as follows:

Stylar cusp A (styA): A small cusp (often indistinct) at the anterior end of the stylar shelf anterolabial to the paracone, to which it is sometimes connected by the preparacrista (= ''parastyle'' of authors).

Stylar cusp B (styB): A much larger cusp (almost always distinct) posterior to styA (if present) and labial to the paracone, to which it is sometimes connected by the preparacrista (= ''stylocone'' of authors).

Stylar cusp(s) C (styC): One or two small cusps (sometimes indistinct or absent) posterolabial to the paracone and anterolabial to the metacone.

Stylar cusp D (styD): Usually single and sometimes indistinct in *Marmosa*, this cusp is posterolabial to the metacone, to which it is never directly connected.

Stylar cusp E (styE): A small cusp (often indistinct) at the posterior end of the stylar shelf posterolabial to the metacone, to which it is always connected by the postmetacrista (= ''metastyle,'' ''distostyle,'' ''metastylar spur,'' or ''metastylar corner'' of authors).

MEASUREMENTS: We recorded external measurements (in millimeters, mm) and weight (in grams, g) from specimen labels.

The former include total length (TL), length of tail (LT), length of hind foot (HF), and length of ear (Ear). Length of head-and-body (HBL) was calculated by subtracting LT from TL.

We measured the following 29 craniodental dimensions to the nearest 0.01 mm with digital calipers while specimens were viewed at low magnification under a stereomicroscope. Except as noted, anatomical endpoints are illustrated in figures 5 and 6.

Greatest Length of Skull (GLS): From the anteriormost point of the premaxillae to the posteriormost point of the braincase.

Condylobasal Length (CBL): From the occipital condyles to the anteriormost point of the premaxillae.

Rostral Length (RL): From the anteriormost point of the nasals to the ventralmost lacrimal foramen.

Nasal Length (NL): The greatest length of either the right or left nasal bone (whichever is longest).

Palatal Length (PL): From the anteriormost point of the premaxillae to the posterolateral corner of the postpalatine torus.

Length of Maxillary Tooth Row (MTR): From the anterior surface of the base of the upper canine to the posterior margin of M4.

TABLE 2
Currently Recognized Species of *Marmosa* (*Marmosa*)[a]

M. andersoni Pine, 1972

M. lepida (Thomas, 1888)

   Synonym: *grandis* Tate, 1931

M. mexicana Merriam, 1897

   Synonyms: *mayensis* Osgood, 1913
                   savannarum Goldman, 1917
                   zeledoni Goldman, 1917[b]

M. murina (Linnaeus, 1758)

   Synonyms: *bombascarae* Anthony, 1922
                   chloe Thomas, 1907
                   dorsigera (Linnaeus, 1758)
                   duidae Tate, 1931
                   guianensis (Kerr, 1792)
                   klagesi J.A. Allen, 1900
                   macrotarsus (Wagner, 1842)
                   madeirensis Cabrera, 1913
                   maranii Thomas, 1924
                   meridionalis Miranda-Ribeiro,
                     1936
                   moreiri Miranda-Ribeiro, 1936
                   muscula (Cabanis, 1848)
                   parata Thomas, 1911
                   roraimae Tate, 1931
                   tobagi Tate, 1931
                   waterhousei (Tomes, 1860)

M. quichua Thomas, 1899

   Synonym: *musicola* Osgood, 1913

M. robinsoni Bangs, 1898

   Synonyms: *casta* Thomas, 1911
                   chapmani J.A. Allen, 1900
                   fulviventer Bangs, 1901
                   grenadae Thomas, 1911
                   isthmica Goldman, 1912[b]
                   luridivolta Goodwin, 1961
                   mimetra Thomas, 1921[c]
                   mitis Bangs, 1898
                   nesaea Thomas, 1911
                   pallidiventris Osgood, 1912
                   ruatanica Goldman, 1911[d]
                   simonsi Thomas, 1899[b]

M. rubra Tate, 1931

M. tyleriana Tate, 1931

M. xerophila Handley and Gordon, 1979

  [a] After Gardner (2005); synonyms include "subspecies."
  [b] Recognized as a valid species in this report.
  [c] Synonymized with *M. isthmica* in this report.
  [d] Synonymized with *M. mexicana* in this report.

Length of Upper Molar Series (UMS): Crown length of the upper molars, from the anterolabial margin of M1 to the posterior margin of M4.

Length of M4 (LM4): Length (anteroposterior or mesiodistal dimension) of the fourth upper molar crown across the paracone and metacone.

Width of M2 (WM2): Greatest width (transverse dimension) of the second upper molar, from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

Width of M4 (WM4): Greatest width (transverse dimension) of the fourth upper molar, from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

Height of Upper Canine (HC): Height (vertical dimension) of C1, from the exposed labial base to the tip of the tooth.

Palatal Breadth (PB): Measured across the labial margins of the fourth molar (M4) roots.

Postpalatal Breadth (PPB): Least breadth across the anterior processes of the left and right alisphenoids (not illustrated).

Breadth of Basicranium (BB): The least distance between the anteromedial margins of the right and left alisphenoid tympanic processes.

Breadth across Tympanic Bullae (BTB): The greatest distance across the lateral margins of the right and left alisphenoid tympanic processes.

Length of Tympanic Bulla (LTB): From the anterior curvature of the alisphenoid tympanic process to the posteriormost point of the petrosal pars cochlearis.

Tympanic Bulla Opening (TBO): The distance between the alisphenoid tympanic process and the rostral tympanic process of the petrosal, measured across the medial margin of ectotympanic.

Width of Ectotympanic (WET): Greatest width of the ectotympanic (not illustrated).

Nasal Breadth (NB): Measured across the triple-point sutures of the nasal, frontal, and maxillary bones on each side.

Breadth of Rostrum across Canines (BRC): Measured across the labial bases of the upper canines.

Breadth of Rostrum between Jugals (BRJ): Measured across the triple-point sutures of
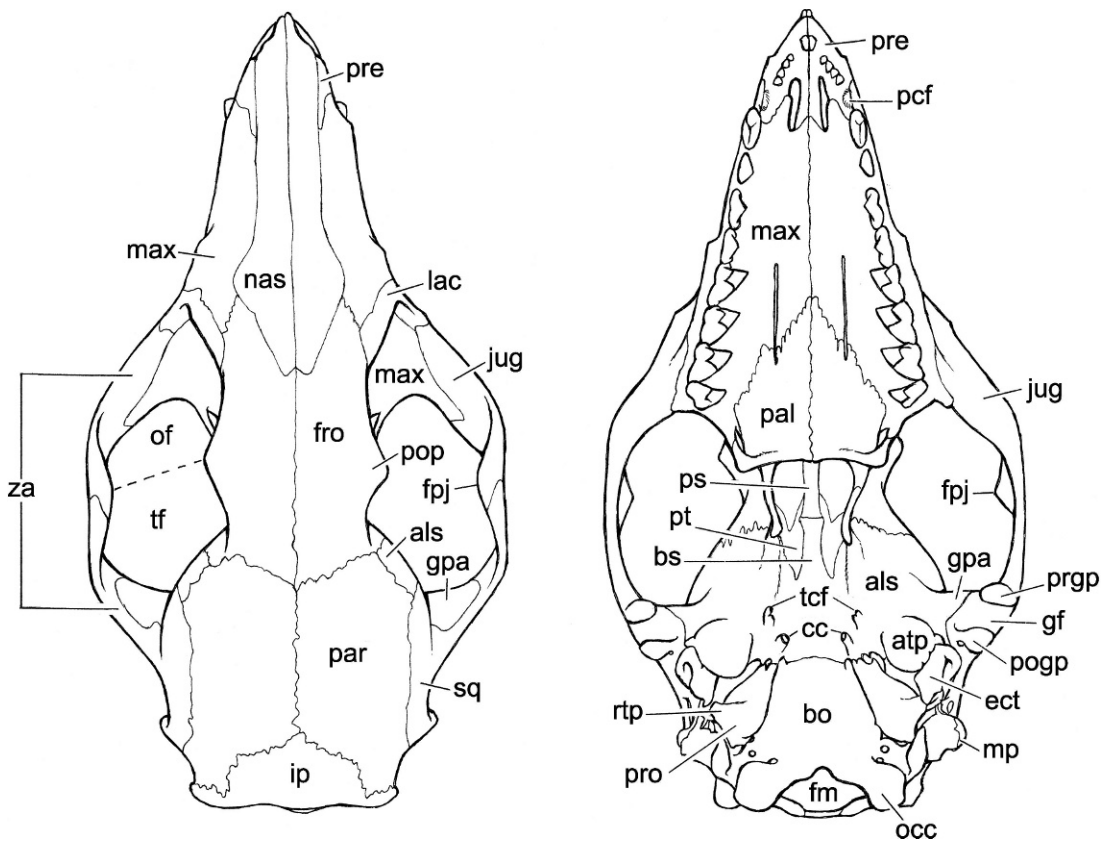
Fig. 3. Dorsal and ventral cranial views of *Marmosa murina* showing principal osteological features mentioned in the text. Abbreviations: **als**, alisphenoid; **atp**, alisphenoid tympanic process; **bo**, basioccipital; **bs**, basisphenoid; **cc**, carotid canal; **ect**, ectotympanic; **fm**, foramen magnum; **fpj**, frontal process of jugal; **fro**, frontal; **gf**, glenoid fossa; **gpa**, glenoid process of alisphenoid; **ip**, interparietal; **jug**, jugal; **lac**, lacrimal; **max**, maxillary; **mp**, mastoid process (of petrosal); **nas**, nasal; **occ**, occipital condyle (of exoccipital); **of**, orbital fossa; **pal**, palatine; **par**, parietal; **pcf**, paracanine fossa; **pogp**, postglenoid process (of squamosal); **pop**, postorbital process; **pre**, premaxillary; **prgp**, preglenoid process (of jugal); **pro**, promontorium (of petrosal); **ps**, presphenoid; **pt**, pterygoid; **rtp**, rostral tympanic process (of petrosal); **sq**, squamosal; **tcf**, transverse canal foramen; **tf**, temporal fossa; **za**, zygomatic arch.

the jugal, lacrimal, and maxillary bones on each side.

Least Interorbital Breadth (LIB): Measured at the narrowest point across the frontals between the orbits (anterior to the postorbital processes, if any).

Postorbital Constriction (POC): Measured at the narrowest point across the frontals between the temporal fossae (posterior to the postorbital processes, if present).

Breadth of Braincase (BBC): Measured immediately above the zygomatic process of the squamosal on each side.

Zygomatic Breath (ZB): Greatest breadth across the zygomatic arches.

Length of Mandible (LM): Measured from the anteriormost point of the mandible (medial to the alveolus of i1) to the posteriormost point of the angular process.

Length of Lower Molar Series (LMS): Crown length of the lower molars, from the anterolingual margin of m1 to the posterolingual margin of m4.

Length of m4 (Lm4): Length (anteroposterior or mesiodistal dimension) of m4, from the paraconid to the hypoconulid.

Fig. 4. Left lateral cranial and mandibular views of *Marmosa murina* showing principal osteological features mentioned in the text. Abbreviations: **als**, alisphenoid; **ap**, angular process; **atp**, alisphenoid tympanic process; **conp**, condylar process; **corp**, coronoid process; **ect**, ectotympanic; **exo**, exoccipital; **fpj**, frontal process of jugal; **fr**, foramen rotundum; **fro**, frontal; **hpp**, hamular process of pterygoid; **iof**, infraorbital foramen; **ip**, interparietal; **jug**, jugal; **lac**, lacrimal; **lc**, lambdoid crest; **lf**, lacrimal foramina; **maf**, masseteric fossa; **max**, maxillary; **mef**, mental foramina; **nas**, nasal; **pal**, palatine; **par**, parietal; **pc**, pars cochlearis (of petrosal); **pcf**, paracanine fossa; **pm**, pars mastoideus (of petrosal); **pop**, postorbital process; **pre**, premaxillary; **rmf**, retromolar fossa; **sq**, squamosal; **ssf**, subsquamosal foramen; **sup**, supraoccipital; **zps**, zygomatic process of squamosal.

Width of m2 (Wm2): Greatest width (transverse dimension) of m2, measured across the hypoconid and entoconid (not illustrated).

AGE CRITERIA: The age classification employed in this report is a refinement of that proposed by Tribe (1990), which was based on the pattern of tooth eruption that he observed in *Marmosops incanus* and other small didelphids (including *Marmosa*). In these taxa, the deciduous third upper premolar (dP3) is not replaced until M4 has erupted; therefore, P3 is the last upper tooth to erupt. Animals belonging to Tribe's age class 5 have a completely erupted upper molar dentition (M1–4), but dP3 is either unreplaced or P3 is just starting to erupt. Animals belonging to Tribe's age class 6 have shed dP3, P3 is almost completely erupted, and M4 is slightly worn; specimens in Tribe's age class 7 have P3 fully erupted, and M4 is considerably worn.

In the course of this study, we observed substantial ontogenetic variation among conspecific specimens assignable to Tribe's age classes 6 and 7. In order to take this variation into account for the purpose of taxonomic comparisons, we found it useful to redefine age classes 6 and 7 and to recognize two additional age classes as follows.

Age class 6: Labial cingulum of P3 emergent but slightly dorsal to labial cingulum of P2 (indicating the penultimate stage of P3 eruption); M3 and M4 cristae unworn or with very narrow and discontinuous strips of exposed dentine.

Age class 7: Labial cingulum of P3 aligned with or ventral to labial cingulum of P2 (indicating the complete eruption of P3); dentine narrowly exposed on all or most M3 and M4 cristae.

Age class 8: Labial cingulum of P3 aligned with or ventral to labial cingulum of P2; dentine broadly exposed along preparacrista
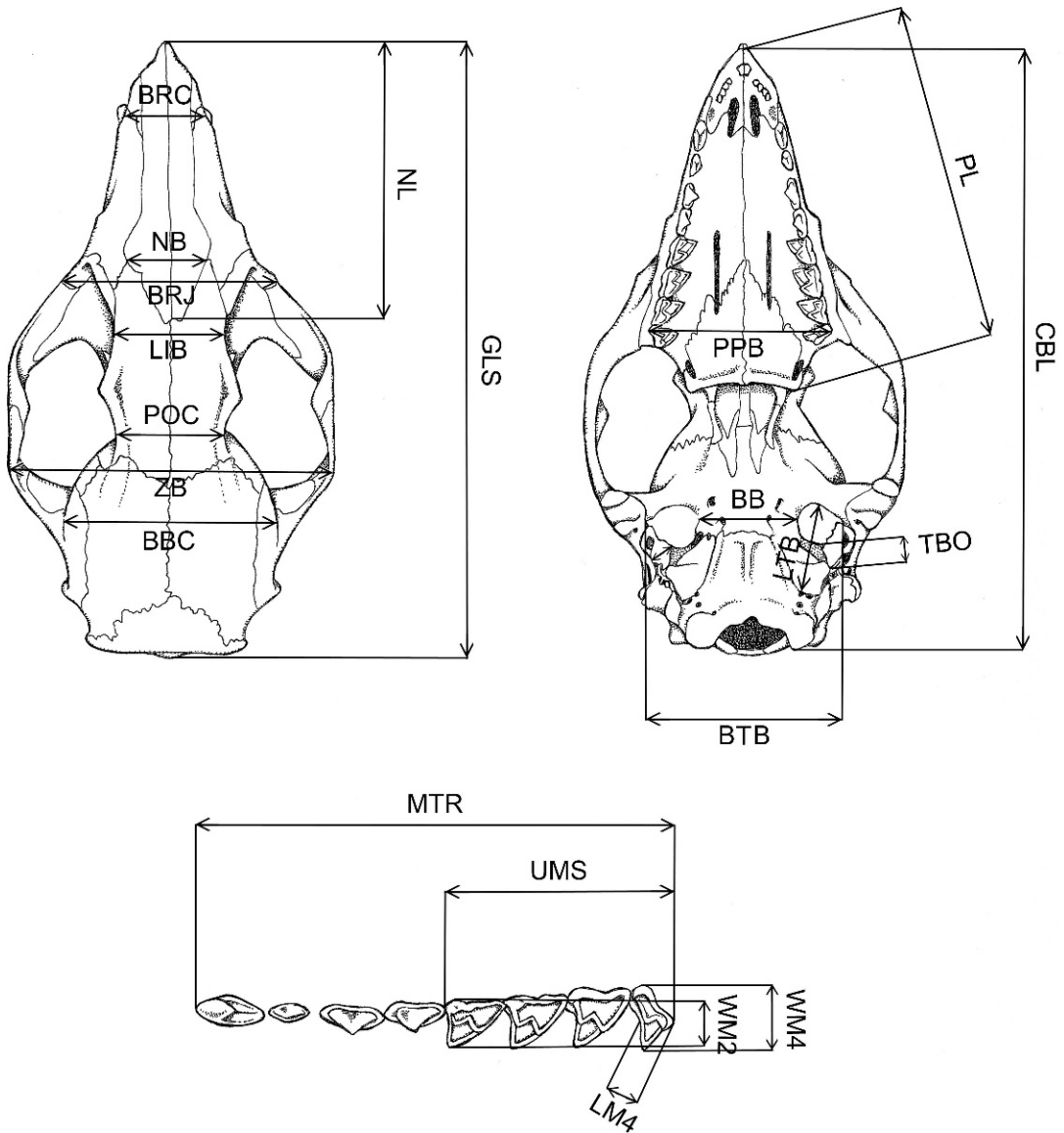
Fig. 5. Anatomical endpoints of 21 craniodental measurements of *Marmosa* defined in the text.

of M3 but narrowly and discontinuously exposed on at least some of the other cristae of M3 and M4.

Age class 9: Labial cingulum of P3 aligned with or ventral to labial cingulum of P2; dentine broadly and continuously exposed on most M3 and M4 cristae.

Hereafter, specimens belonging to age class 5 are called subadults, and specimens belonging to age classes 6 to 9 are called adults. We additionally distinguish "young adults" (specimens in age class 6) from "mature adults" (in age classes 7 to 9).

ONTOGENETIC VARIATION AND
SEXUAL DIMORPHISM

Like other didelphid marsupials (Gardner, 1973; Abdala et al., 2001; Flores et al., 2003), young mouse opossums are weaned long
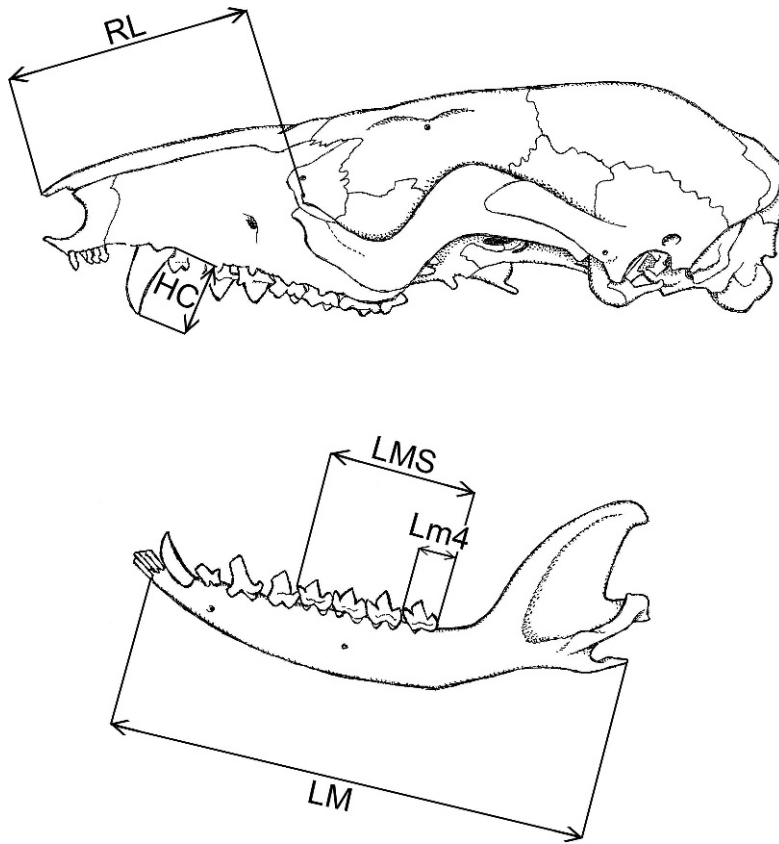
Fig. 6.   Anatomical endpoints of five additional craniodental measurements of *Marmosa* defined in the text.

before they are morphologically mature, with the result that mixed-age series of conspecific individuals often include specimens that differ conspicuously in size and size-correlated (allometric) proportions. Because immature (juvenile and subadult) individuals seldom exhibit all the diagnostic traits that allow confident taxonomic identifications of adults, careful attention to dental indicators of morphological maturity is important. However, substantial morphometric variation exists even among conspecific adults that differ in age and sex.

Statistical tests for age and sex effects on craniodental measurements of adult specimens reveal similar patterns of nongeographic variation in all species for which large samples were analyzed (Rossi, 2005). In particular, statistically significant age effects

were detected for most measured dimensions, with the usual exception of molar measurements (e.g., UMS, LM4, WM2, WM4, LMS, Lm4, Wm2) and measurements of auditory structures (e.g., LTB, TBO, WET). Almost all dimensions with significant age effects show progressive increases in measurement means from age class 6 to age class 9, indicating that older specimens are, on average, larger than younger specimens. (An exception is Postorbital Constriction [POC], which sometimes exhibits a statistically significant *decrease* in mean values with age.) In general, the largest age-correlated increases are seen in measurements spanning the rostrum (e.g., GLS, CBL, RL, PL, BRC, BRJ) and the zygomatic arches (ZB), but Least Interorbital Breadth (LIB), and Length of Mandible (LM) sometimes also exhibit

strong age effects. Height of Canine (HC) often exhibits a much stronger age effect in males than in females.

Statistical tests for sexual dimorphism are often significant when sample sizes are large (Rossi, 2005), but mean differences between conspecific males and females are minimal for molar and auditory dimensions, some basicranial measurements (e.g., PPB), and Postorbital Constriction (POC). Males are larger, on average, than females in all measurements that exhibit pronounced sexual dimorphism—which tend to be those that also show strong age effects—especially rostral dimensions, zygomatic breadth, and canine height.

The net result of ontogenetic variation and sexual dimorphism in mouse opossums is that valid taxonomic comparisons of affected craniodental dimensions must take age and sex into account. Although this is often true of other mammals, the magnitude of ontogenetic variation and sexual dimorphism in didelphids are sometimes large enough that conspecific samples differing in age and sex can have nonoverlapping ranges of variation. Condylobasal Length (CBL), for example, ranges from 32.1 to 38.6 mm in young adult (age class 6) female *Marmosa isthmica*, but the observed range in this dimension among old adult (age class 9) male *M. isthmica* is 39.8 to 43.6 mm. Additionally, because some dimensions are strongly affected by growth and sexual dimorphism while others are not, cranial proportions also vary among conspecific individuals. Thus, mature adult males tend to have proportionately smaller molars and auditory structures but much larger canines, longer rostrums, and more flaring zygomatic arches than young adult females.

Although multivariate statistical methods are available to adjust morphometric comparisons of species for age and sex effects, such methods are cumbersome for the purpose of identifying specimens. Instead, taxonomic identifications are more readily based on qualitative characters, which may vary with age and sex but do not require measurement or statistical analysis. In this report, measurement data play a secondary role because they are seldom necessary or sufficient for distinguishing the species of interest.

COMPARATIVE MORPHOLOGY

The qualitative external and craniodental characters analyzed in the course of this study are described below. To avoid unnecessary confusion, we refer to species of *Marmosa* as subsequently diagnosed herein (i.e., treating *M. isthmica*, *M. simonsi*, and *M. zeledoni* as valid binomials). Unrevised congeners, however, are referred to, when necessary, by their currently accepted names (as in table 2). Except as noted otherwise, all examined species of *Marmosa* conform to the morphological description of the genus provided by Voss and Jansa (2009), which should be consulted for information about taxonomically invariant external and craniodental features that are not mentioned in the following accounts.

External Characters

External morphology provides several useful characters for diagnosing species of the subgenus *Marmosa*. Although most details of pelage pigmentation are effectively preserved on dry skins, some colors that are vivid in life fade away and eventually disappear on museum specimens (Pine et al., 1985). Because this report is based largely on examination of museum specimens, we seldom had the opportunity to record such "fugitive" colors, which are not further considered here.

HEAD PELAGE: The middorsal fur of the rostrum (between the dark circumocular masks) is conspicuously paler than the fur of the crown of the head (between the ears) in some species of *Marmosa*. Among the species treated herein, this pigmental contrast is usually sharpest in *M. mexicana*, *M. robinsoni*, *M. simonsi*, and *M. rubra*. It is weakest and least often developed in *M. zeledoni*, and it is variably present or absent in *M. isthmica* and *M. xerophila*.

A dark median stripe that extends from the rhinarium to between the eyes—bisecting the pale midrostral fur—is consistently present in *M. rubra* (fig. 7, right). Somewhat resembling the median stripe of dark rostral fur described by Voss and Jansa (2003: character 2) for *Caluromys*, this trait is usually absent or inconspicuous in other species of *Marmosa* (e.g., *M. zeledoni*; fig. 7, left).

Fig. 7. Dorsal views of skins illustrating taxonomic variation in rostral pelage markings. A dark middorsal rostral stripe is absent in *Marmosa zeledoni* (left, FMNH 128398) but present in *M. rubra* (right, AMNH 68137). Scale bar = 1 cm.

The fur surrounding the eye is dark brown or blackish in all species of *Marmosa*, resulting in a masklike marking that contrasts abruptly with the paler (brownish, grayish, or whitish) coloration of the midrostrum, crown, and cheeks. In most examined specimens, this circumocular mask extends anteriorly among the bases of the mystacial vibrissae, where the dark fur gradually narrows and fades away, becoming less and less distinct toward the rhinarium. In some species, dark fur extends only a few millimeters behind the eye; in such forms (e.g., *M. isthmica*, *M. robinsoni*, *M. rubra*, *M. xerophila*), several millimeters of paler, brownish fur separate the mask from the base of the ear (fig. 8, bottom). In other species, however, dark fur extends much farther posteriorly, so that the mask reaches the base of the ear; among the species treated herein, this trait is best developed in *M. mexicana* (fig. 8, top), but it is also seen to a variable extent in *M. zeledoni* and *M. simonsi*.

BODY PELAGE: Although species of *Marmosa* (*Marmosa*) vary subtly in fur texture, perceived differences in pelage density and softness are somewhat subjective and do not provide a satisfactory basis for identification. Regardless of texture, the coat consists of cover hairs and guard hairs. The former are more abundant, wavy, and range from 7 to 11 mm in length. On the dorsal surface of the body, coat hairs are tricolored, with a basal gray band that makes up some 60% to 90% of the total length of each hair; a short buffy, yellowish, or reddish subterminal band; and a tiny dark-brown terminal band. Guard hairs are sparser and straighter than coat hairs, and range from 9 to 14 mm in length. Dorsal guard hairs are bicolored, grayish basally and paler near the tip.

Dorsal fur color is taxonomically variable in the subgenus *Marmosa*, but species differences are difficult to characterize by objective standards. Whereas much of the older literature made frequent reference to Ridgway's (1912) color standards, Ridgway's esoteric nomenclature—"Sayal Brown," "Hair Brown," "Mars Brown," "Pecan Brown," "Mikado Brown," "Natal Brown," "Sanford's Brown," and "Burnt Sienna" are examples of color names that Tate (1933) used to describe the dorsal pelage of *Marmosa*—is not helpful without a copy of this rare book in hand,[1] so more easily comprehensible vernacular descriptors (e.g., "reddish brown") are preferable in most circumstanc-

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[1] Without examining Ridgway's plates, for example, it is not clear that "Burnt Sienna" and "Sanford's Brown" are almost indistinguishably similar shades of reddish brown. The degree to which the color swatches in this book have faded in the ninety-odd years since it was published is unknown.
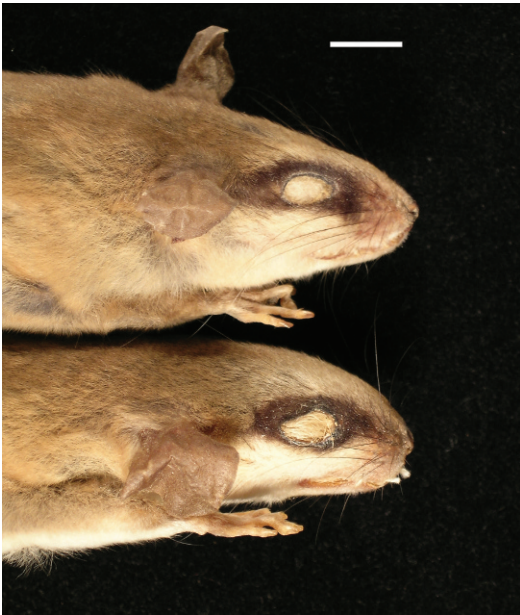
Fig. 8. Lateral views of skins illustrating taxonomic variation in facial markings. The dark circumocular mask extends posteriorly to the base of the ear in *Marmosa mexicana* (top, MVZ 130251), but not in *M. robinsoni* (bottom, AMNH 130579). Scale bar = 1 cm.

es. Taxonomic color differences are primarily useful in side-by-side comparisons, where they are sometimes decisive for identification.

Among the species treated in this report, *M. simonsi* has much grayer fur than the others, whereas most specimens of *M. mexicana*, *M. zeledoni*, and *M. rubra* are distinctly reddish. *Marmosa xerophila* could appropriately be described as pale grayish brown, *M. robinsoni* as yellowish brown, and *M. isthmica* as orangish brown. Typically, the dorsal fur is darker and more richly colored on the middle of the back than along the flanks, which tend to be slightly paler. Juvenile and subadult specimens usually have grayer and/or darker dorsal fur than adults. Young adults often have longer, softer, more brightly colored, and glossier coats than old adults, which often have dull and shabby-looking fur.

The ventral pelage of most species consists of both self-colored (unicolored) and gray-based (bicolored) fur. In most of the species treated in this report, self-colored fur—which may be orange, yellowish, or whitish—extends continuously along the ventral midline from the chin to the anus. Usually, however, the width of this pale self-colored median streak (when present) is narrowed by darker lateral zones of gray-based ventral hairs, the tips of which are either colored like the flanks or like the self-colored median streak. The lateral zones of gray-based ventral hairs may be restricted to the abdomen (as in *M. isthmica* and *M. xerophila*), or they may extend from the throat or chest to the inguinal region, including the ventral surfaces of the fore- and hind limbs (as in *M. mexicana*, *M. zeledoni*, *M. robinsoni*, and *M. rubra*). Indeed, the median streak of self-colored fur is sometimes discontinuous in *M. rubra* because it is interrupted by gray-based abdominal fur. By contrast, the entire ventral surface (except for the chin and throat) is covered with gray-based hairs in *M. simonsi*.

In reproductively active adult females, the fur of the inguinal-abdominal region becomes remarkably modified. Ordinary ventral fur in such animals is replaced by a distinctively short, thin, sparse, brownish mammary pelage. Although the color and extent of the mammary pelage varies among conspecific specimens, some taxonomic differences are also apparent (table 3).

EARS: The external ear or pinna is a prominent, membranous organ in *Marmosa*. Among the species treated herein, the ears are largest in *M. isthmica*, *M. robinsoni*, *M. simonsi*, and *M. xerophila* (averaging 25–26 mm in adult males; 24–25 mm in adult females; tables 4, 5) and smallest in *M. mexicana*, *M. zeledoni*, and *M. rubra* (22–23 mm in males, 20–22 mm in females). The internal and external surfaces of the ears are macroscopically naked, but a sparse covering of short hairs is visible under low magnification. The exposed auricular skin ranges in color from pale brown to dark brown, and it is usually more heavily pigmented distally than basally.

GULAR GLAND: In most species of *Marmosa* there is a distinct median patch of glandular (naked or sparsely haired) skin between the chest and the throat (Tate, 1933; Barnes, 1977). Although this gland is usually best developed in adult males, it is also visible in

TABLE 3
Reproductive Features of Female *Marmosa*[a]

	Mammae[b]	Litter size[c]	Color of mammary fur
M. mexicana	5–1–5 = 11 (2) 6–1–6 = 13 (1) 7–1–7 = 15 (1)	12	Intensely golden to reddish brown
M. zeledoni	4–1–4 = 9 (1) 5–1–5 = 11 (1)	—	—
M. isthmica	—	8.5 (6–12)	Light or dark reddish brown
M. robinsoni	6–1–6 = 13 (1)	11 (2–19)	Intensely golden to reddish brown
M. xerophila	5–1–5 = 11 (1)	9 (6–12)	Golden
M. simonsi	—	—	—
M. rubra	3–1–3 = 7 (1) 4–1–4 = 9 (1)	—	—

[a] Mammary formula as defined in the text.

[b] Data gathered from stuffed or fluid-preserved specimens. In parentheses, the number of specimens examined.

[c] Median (minimum–maximum) number of nursing young, recorded by collectors on specimen labels.

most subadult and female specimens. Among the species treated in this report, only *M. rubra* consistently lacks any external evidence of glandular activity in the gular region.

CARPAL TUBERCLES: Large tubercles, supported internally by carpal ossifications, project from the lateral and medial surfaces of the wrist in mature adult male specimens of all the *Marmosa* species treated in this report (other species, such as *M. murina*, lack carpal tubercles). The medial (or ''radial'') tubercle, which is supported internally by the prepollex (Lunde and Schutt, 1999), exhibits noteworthy taxonomic variation that can be recorded from suitably preserved dried skins. In *M. mexicana* (fig. 9A), the medial carpal tubercle is long, extending to the base of the pollex (manual digit I), and uniform in thickness (without distinguishable segments). By contrast, the long medial carpal tubercles of *M. zeledoni* (fig. 9B) and *M. isthmica* are divided by a shallow sulcus into similar but consistently recognizable proximal and distal parts. In the remaining species treated here— *M. robinsoni*, *M. simonsi* (fig. 9C), *M. xerophila*, and *M. rubra*—medial carpal tubercles can be long or short (not reaching the base of pollex), but they are more conspicuously segmented into globular proximal and comma-shaped distal parts.

MAMMAE: Because species of *Marmosa* are pouchless, the mammae of lactating females are exposed. Confined to the abdominal/inguinal region, these form a more or less circular abdominal/inguinal pattern that encloses an unpaired median teat (see Tate, 1933 [fig. 3] for an illustration of the mammae in *M. mexicana*). By convention, didelphid mammary complements are summarized by formulae representing the right-side (R), median (M), left-side (L), and total (T) teat counts in the format R–M–L = T. Mammary formulae vary taxonomically, but they also exhibit variation among conspecific individuals (table 3). In *M. mexicana*, from which we obtained mammary counts of four individuals, the number of teats ranges from 11 to 15, a range of variation that overlaps the teat numbers observed from most of the other species treated herein. Only *M. rubra* (with 7 to 9 mammae) seems like an outlier, but no definite conclusions are possible with such small sample sizes. Although we were not able to find any stuffed or fluid specimen of *M. isthmica* with countable mammae, a skin label recording 12 nursing young suggests a mammary count of at least 6–1–6 = 13 for this species. No information is available about mammary formulae or litter sizes for *M. simonsi*.

TAIL: A slender, muscular organ in *Marmosa*, the tail is always longer than the combined length of the head and body, but the ratio of tail length to head-and-body

TABLE 4
Summary Statistics[a] for External Measurements (mm) and Weights (g) of Adult Male Specimens of Seven Species of *Marmosa*

	mexicana	zeledoni	isthmica	robinsoni	xerophila	simonsi	rubra
HBL	133 ± 16 (42)	144 ± 14 (21)	161 ± 14 (177)	149 ± 17 (207)	133 ± 10 (37)	132 ± 13 (43)	153 ± 19 (11)
	110–168	120–162	115–200	111–218	105–159	107–156	128–200
LT	182 ± 18 (42)	184 ± 18 (21)	208 ± 17 (172)	179 ± 14 (203)	162 ± 10 (37)	160 ± 13 (43)	196 ± 10 (11)
	152–228	145–210	160–253	145–215	144–181	140–189	183–214
LT/HBL[b]	1.37 ± 0.13 (42)	1.28 ± 0.09 (21)	1.30 ± 0.12 (171)	1.21 ± 0.12 (201)	1.22 ± 0.10 (37)	1.21 ± 0.10 (43)	1.32 ± 0.11 (10)
	1.10–1.60	1.10–1.50	1.00–1.70	0.85–1.67	1.10–1.60	1.00–1.40	1.20–1.50
HF	22 ± 2 (45)	23 ± 2 (24)	26 ± 2 (179)	22 ± 2 (210)	19 ± 1 (37)	21 ± 2 (45)	23 ± 2 (12)
	19–25	18–27	20–33	19–30	17–22	17–26	20–26
Ear	22 ± 3 (34)	23 ± 2 (22)	26 ± 3 (144)	26 ± 3 (184)	26 ± 1 (36)	26 ± 3 (17)	22 ± 2 (13)
	14–26	19–26	14–34	20–32	24–28	16–30	18–25
Weight	63 ± 20 (21)	75 ± 16 (9)	99 ± 26 (35)	71 ± 15 (59)	58 ± 11 (36)	38 ± 11 (4)	77 (1)
	24–99	50–100	52–143	39–110	40–87	24–49	

[a] The sample mean plus or minus one standard deviation, the sample size (in parentheses), and the observed range.
[b] Ratio of tail length to head-and-body length.

length exhibits modest taxonomic variation among the species treated in this report (tables 4, 5), tending to be shortest in *M. simonsi*, *M. robinsoni*, and *M. xerophila* than in the other species treated herein (especially *M. mexicana* and *M. rubra*). The naked skin of the tail, brownish or grayish in life, is often slightly paler ventrally than dorsally, but the contrast is never abrupt. However, the distal one-third to one-half of the tail is unpigmented (whitish) in *M. simonsi*, a visually conspicuous and diagnostically useful marking.

The basal part of the tail, corresponding to less than 10% of the length of this organ (≤15 mm on stuffed skins), is covered by soft fur resembling the dorsal body pelage in texture and coloration. The rest of the tail is covered by epidermal scales that exhibit taxonomic variation in shape and arrangement. The caudal scales are distinctly rhomboidal (diamond-shaped) and arranged in consistently spiral series in *Marmosa rubra*, but the remaining species treated herein have caudal scales that vary in shape and exhibit no clear pattern of arrangement: both spiral and annular patterns can be found on the same individual, the former pattern usually on the dorsal surface of the tail and the latter on sides and ventral surface.

Of the three hairs that typically emerge from the posterior margin of each caudal scale, the central hair is usually slightly longer (by some 20%–50%) and thicker than the lateral hairs (fig. 10). Among the species treated in this report, these hairs are shortest in *Marmosa rubra* (in which the central hair of each caudal-scale triplet is only about as long as one caudal scale) and longest in *M. robinsoni*, *M. simonsi*, and *M. xerophila* (in which the central hair of each triplet is slightly longer than two caudal scales). The prehensile ventral surface of the distal part of the tail is scale- and hairless; it is marked by transverse pleats, a shallow median groove, and an apical pad bearing dermatoglyphs.

Craniodental Characters

The skull and dentition provide additional sources of useful diagnostic characters, but many of these are affected by age, which must be taken into account when making taxonomic identifications. In particular, diagnostic

TABLE 5
Summary Statistics[a] for External Measurements (mm) and Weights (g) of Adult Female Specimens of Seven Species of *Marmosa*

	mexicana	*zeledoni*	*isthmica*	*robinsoni*	*xerophila*	*simonsi*	*rubra*
HBL	121 ± 10 (17)	133 ± 8 (12)	140 ± 12 (139)	130 ± 14 (104)	121 ± 7 (47)	123 ± 12 (35)	143 ± 9 (7)
	94–133	119–145	105–182	83–155	101–133	98–145	130–156
LT	173 ± 22 (17)	176 ± 16 (12)	189 ± 13 (137)	163 ± 14 (102)	149 ± 8 (47)	148 ± 12 (35)	203 ± 10 (7)
	130–223	149–197	150–229	101–195	130–167	121–170	191–217
LT/HBL[b]	1.43 ± 0.14 (17)	1.33 ± 0.11 (12)	1.37 ± 0.11 (136)	1.27 ± 0.11 (102)	1.24 ± 0.09 (47)	1.21 ± 0.08 (35)	1.42 ± 0.10 (7)
	1.18–1.74	1.10–1.50	1.10–1.80	1.00–1.70	1.00–1.40	1.00–1.50	1.30–1.50
HF	20 ± 2 (17)	20 ± 2 (13)	22 ± 2 (144)	20 ± 2 (102)	17 ± 2 (44)	19 ± 1 (35)	22 ± 1 (9)
	15–24	16–24	16–29	16–25	16–27	17–23	20–24
Ear	22 ± 2 (12)	20 ± 3 (13)	24 ± 2 (123)	24 ± 2 (89)	24 ± 2 (44)	25 ± 3 (11)	22 ± 1 (7)
	19–25	15–24	19–28	18–30	16–28	17–28	21–23
Weight	46 ± 7 (8)	45 ± 18 (3)	59 ± 13 (26)	44 ± 12 (40)	39 ± 5 (48)	34 ± 5 (2)	69 ± 11 (3)
	35.4–56.7	28–64	40–93	16–72	29–57	30–37	59–81

[a] The sample mean plus or minus one standard deviation, the sample size (in parentheses), and the observed range.
[b] Ratio of tail length to head-and-body length.

bony structures are best developed in adult specimens, whereas some dental traits are only reliably preserved in young animals with unworn teeth. Although subtle species differences can be detected in many aspects of the cranium and dentition, the following accounts are focused on those that afford the clearest criteria for sorting specimens.

ROSTRAL PROCESS OF THE PREMAXILLAE: In many small didelphids, including most species of *Marmosa*, the premaxillae project anteriorly to form a more or less acutely pointed shelf-like process that extends the bony rostrum well beyond I1 and contains a distinct suture between the left and right bones. Among the species treated in this report, a rostral process of the premaxillae is absent only in *Marmosa xerophila*, which lacks any distinct bony projection anterior to the alveolar rim of I1. By contrast, most of the remaining species (*M. isthmica*, *M. mexicana*, *M. rubra*, and *M. zeledoni*) have long rostral processes that are typically about as long as I1 is tall (fig. 11A). An intermediate condition is seen in both *M. robinsoni* and *M. simonsi*, which have short rostral processes that are about half as long as I1 is tall (fig. 11B).

ORBITOSPHENOID SUTURE: The orbitosphenoid is a small bone that is wedged among the palatine, frontal, and alisphenoid bones in the posteromedial wall of the orbit; behind it is a large opening, the sphenorbital fissure. The length of the orbitosphenoid-alisphenoid suture relative to the height of the sphenorbital fissure exhibits noteworthy taxonomic variation in *Marmosa*. Whereas the suture is about twice as long as the fissure is high in *M. mexicana*, *M. zeledoni*, *M. isthmica*, and *M. simonsi*, the suture is visibly shorter in *M. robinsoni* and *M. xerophila*; in *M. rubra*, the suture is only about as long as the fissure is high.

INTERORBITAL REGION AND DORSAL BRAINCASE: The morphology of the dorsal surface of the frontal bones between the orbital fossae is taxonomically variable among small didelphids. All species of *Marmosa* have well-developed supraorbital ridges (or ''beads''), from which laterally projecting postorbital processes are sometimes developed. Behind the postorbital processes (when present), the supraorbital ridges are continu-
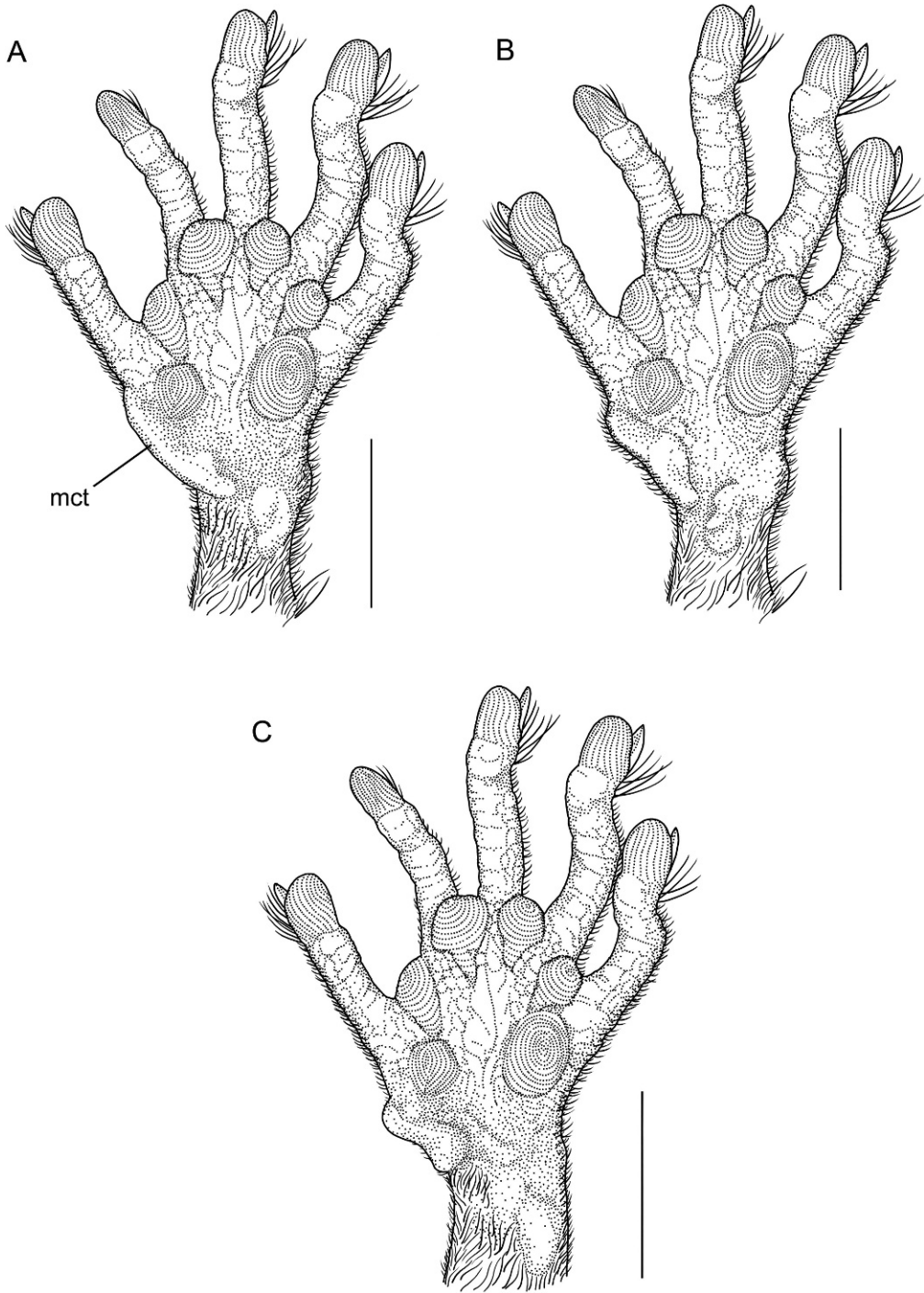
Fig. 9. Semidiagrammatic plantar views of the right manus and wrist, illustrating taxonomic differences in carpal tubercle morphology. The medial carpal tubercle (**mct**) is long (extending to the base of the pollex) and undifferentiated in *Marmosa mexicana* (**A**), but it is separated by a shallow sulcus into distinct proximal and distal segments in *M. zeledoni* (**B**). In *M. simonsi* (**C**), the medial carpal tubercle is short (not extending to the base of the pollex) and segmented. Scale bars = 5 mm.
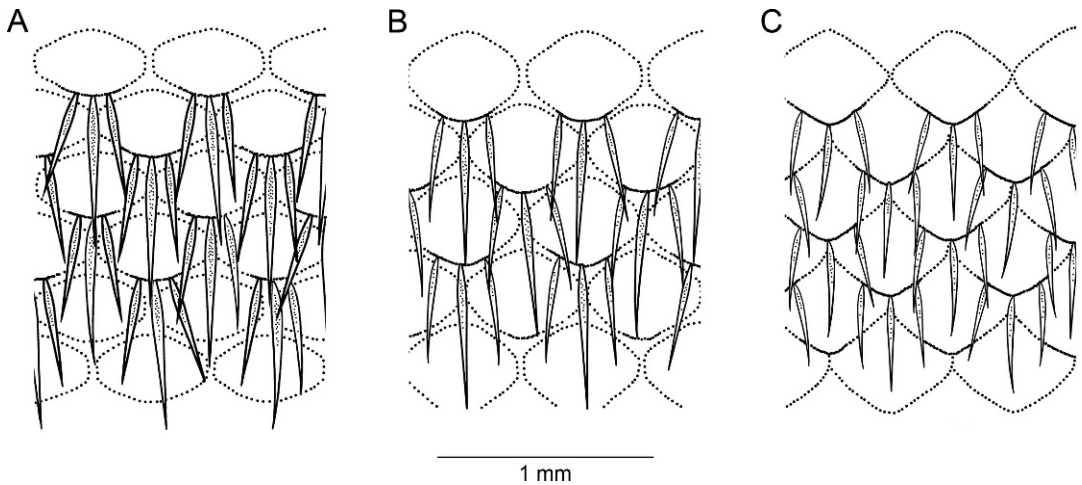
Fig. 10.   Semidiagrammatic views of caudal scales and scale-hairs in *Marmosa*. The central hair in each caudal-scale triplet is longer than two scales in *M. robinsoni* (**A**), about two scales long in *M. zeledoni* (**B**), and less than one scale long in *M. murina* (**C**).

ous with temporal ridges that mark the dorsalmost extension of the jaw adductor musculature onto the braincase. All of these bony structures are variously developed in relation to sex, age, and species. As a rule, they are better developed in males than in females, and they are better developed in mature adults than in juveniles, subadults, and young adults. Therefore, among large series of conspecific specimens, supraorbital ridges, postorbital processes (if any), and temporal ridges are almost always best developed in old adult males.

In mature adult specimens of *Marmosa zeledoni* (fig. 12B) and *M. rubra* (fig. 12G), the supraorbital ridges are typically slender, subparallel, and do not project laterally over the orbital fossae; postorbital processes in these taxa are usually absent or indistinct. By contrast, in mature adult specimens of *M. robinsoni* (fig. 12D) and *M. xerophila* (fig. 12E), the supraorbital ridges are thicker, more posteriorly divergent, and project slightly over the rear part of the orbital fossae; postorbital processes in these taxa are sometimes developed, but they are usually indistinct. In mature adult specimens of *M. mexicana* (fig. 12A) and *M. isthmica* (fig. 12C), the supraorbital ridges are usually thick, posteriorly divergent, and project laterally over the orbital fossae; postorbital processes are typically indistinct or small in

M. mexicana, but they are usually present in large specimens of *M. isthmica*. In mature adult specimens of *M. simonsi*, the supraorbital ridges are thick, strongly divergent and project laterally as they widen to form well-developed, acutely pointed postorbital processes (fig. 12F).

The left and right temporal ridges are widely separated on the dorsal surface of the braincase in most species of *Marmosa*. These muscle scars remain widely separated and subparallel throughout adult life in *M. rubra* and *M. zeledoni*, but they tend to converge posteriorly in large adult specimens of the other species treated in this report. Uniquely, some old adult specimens of *Marmosa robinsoni* and *M. xerophila* develop a weak sagittal crest where the left and right temporal ridges are joined along the dorsal midline of the parietal and interparietal bones (fig. 12E).

PALATAL PERFORATIONS: The bony palate in all species of *Marmosa* is perforated by paired incisive foramina (anteromedial to C1), maxillopalatine fenestrae (medial to M1–3), and posterolateral palatal foramina (posteromedial to M4; fig. 13). Although the posterolateral palatal foramina tend to be larger in *M. robinsoni*, *M. simonsi*, and *M. xerophila* than in the other species treated in this report, taxonomic differences are more readily apparent in other palatal features. Among these, the most striking interspecific
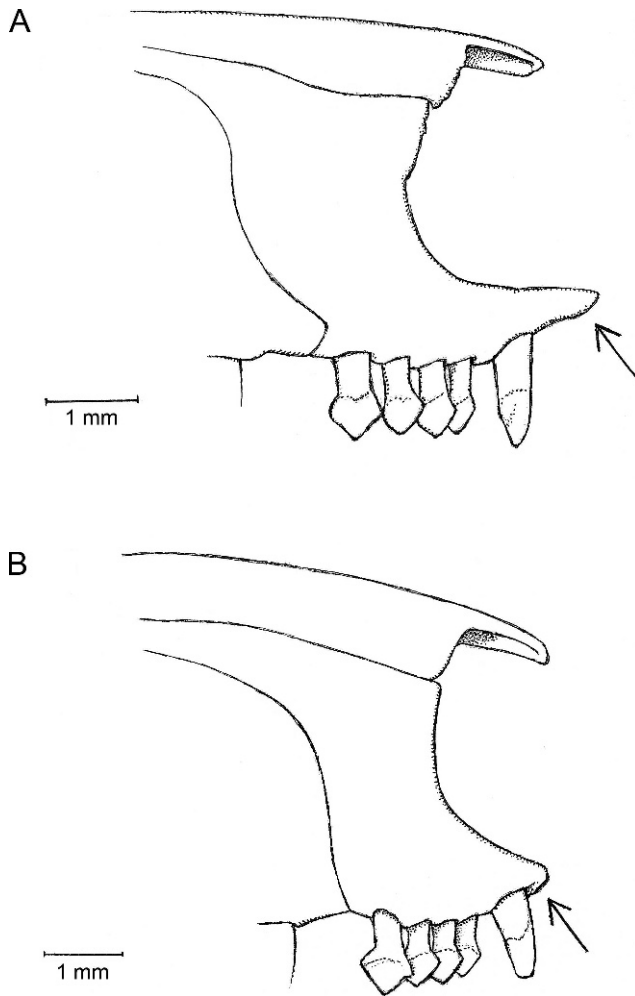
Fig. 11.   Lateral views of rostrum illustrating taxonomic variation in the development of a rostral process of the premaxillae (arrows). **A**, *Marmosa mexicana* (ROM 96090), with a long rostral process (about as long as I1 is tall). **B**, *Marmosa robinsoni* (AMNH 130584), with a short rostral process (about half as long as I1 is tall).

variation consists in the presence or absence of palatine fenestrae.

Palatine fenestrae, which consist of one or more distinct openings in each palatine bone behind the maxillopalatine fenestrae, are consistently absent in several species of *Marmosa*, including *M. zeledoni* (fig. 13B), *M. isthmica*, and *M. rubra*. In other congeneric species, palatine fenestrae vary in number, size, and shape. In *M. mexicana* (fig. 13A), palatine fenestrae sometimes consist of several irregular openings on each side, and in a few individuals these can be quite small. By contrast, In *M. robinsoni* (fig. 13C), *M. simonsi*, and *M. xerophila*, palatine fenestrae usually consist of a single large, rounded opening on each side.

EAR REGION: As in other didelphids, the anterior part of the middle ear in *Marmosa* is enclosed by the tympanic process (or ''wing'') of the alisphenoid, which exhibits subtle but useful taxonomic shape variation. In *M. mexicana* (fig. 14A), *M. zeledoni*, *M. isthmica*, and *M. rubra*, the tympanic process of the alisphenoid tends to be small and laterally compressed with a slightly to moderately
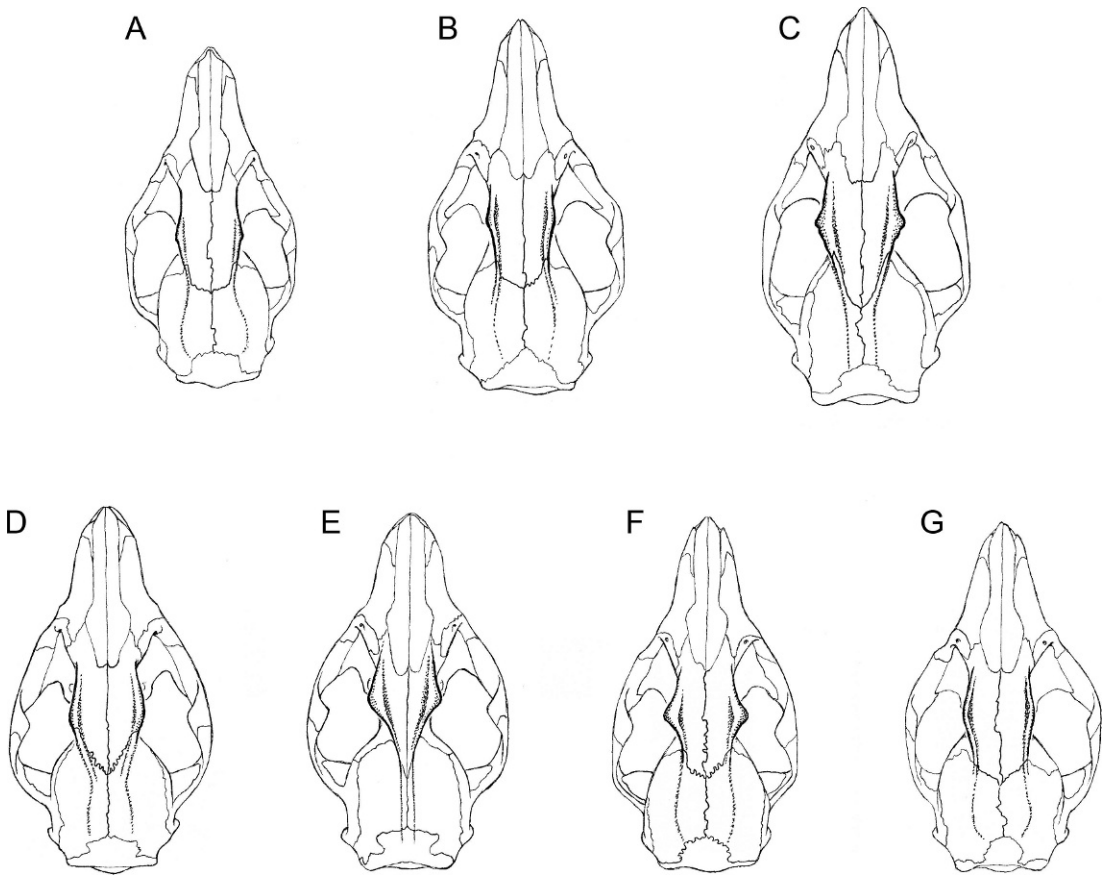
Fig. 12. Dorsal cranial views illustrating taxonomic differences in the morphology of supraorbital ridges, postorbital processes, and temporal ridges in mature adult male specimens. **A**, *M. mexicana* (ROM 99608); **B**, *Marmosa zeledoni* (AMNH 29542); **C**, *M. isthmica* (USNM 456815); **D**, *M. robinsoni* (AMNH 130583); **E**, *M. xerophila* (AMNH 276582); **F**, *M. simonsi* (AMNH 66883); **G**, *M. rubra* (MVZ 153280).

pointed or bluntly keeled ventral surface. By contrast, the alisphenoid tympanic process is larger and more or less globular (smoothly rounded) in *M. robinsoni* (fig. 14B), *M. simonsi*, and *M. xerophila*.

The ectotympanic exhibits correlated taxonomic variation. In species with small, laterally compressed alisphenoid bullae, the sulcus tympanicus (to which the tympanic membrane attaches) closely follows the inner border of the ectotympanic, which does not contribute significantly to the floor of the middle ear cavity. By contrast, in species with larger, more globular alisphenoid bullae, the ectotympanic is wider and contributes a small medial process to the floor of the middle ear.

DENTITION: All of the species of *Marmosa* treated in this report have the normal didelphid dental complement of 50 teeth (I5/4, C1/1, P3/3, M4/4), and they are undifferentiated with respect to both incisor and canine morphology: I1 is hypsodont, the crown of I2 is distinctly wider than its root, and C1 lacks any accessory cusps. By contrast, some congeneric South American forms differ by having a nonhypsodont I1 (*M. andersoni*), by usually lacking I1 as adults (*M. tyleriana*), by having a distinctively narrow-crowned I2 (*M. quichua*), or by having a small posterior accessory cusp on C1 (*M. lepida*). Distinguishing features of the upper premolars and of the lower dentition also seem wanting. Instead, the only qualitative dental traits
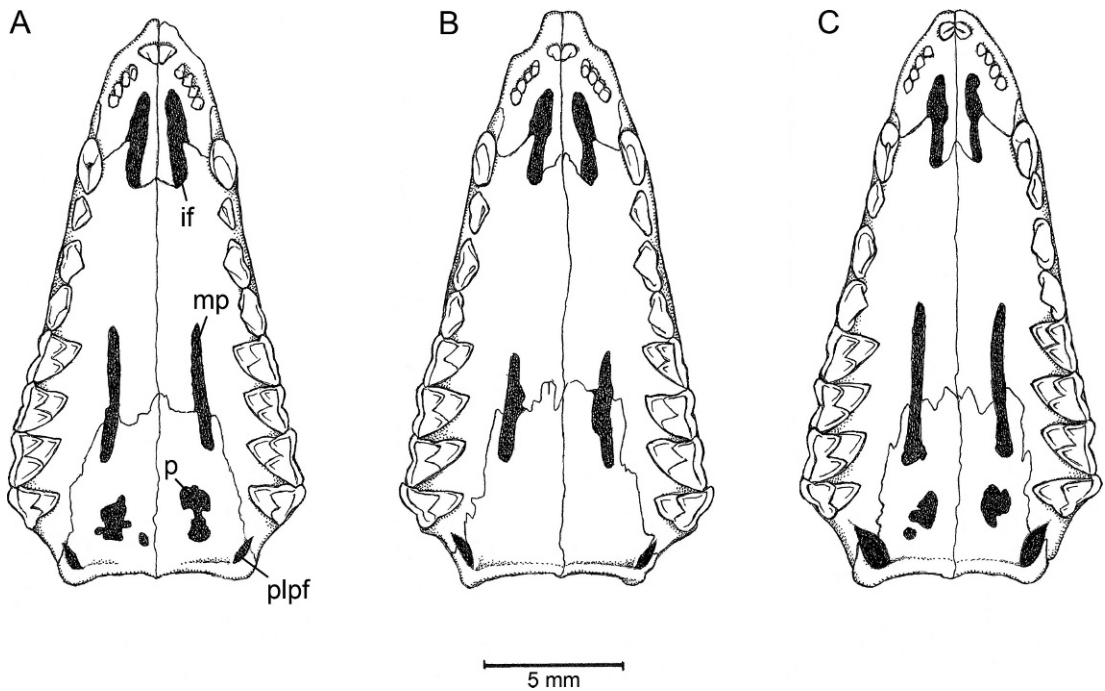
Fig. 13.   Palatal morphology of three species of *Marmosa*, illustrating diagnostic traits mentioned in this report. All species of *Marmosa* have incisive foramina (**if**), maxillopalatine fenestrae (**mp**), and posterolateral palatal foramina (**plpf**), but palatine fenestrae (**p**) are present in some species and absent in others. Additionally, posterolateral palatine foramina exhibit noteworthy taxonomic variation in size. In *M. mexicana* (**A**, ROM 96090) palatine fenestrae are present and posterolateral palatal foramina are small. In *M. zeledoni* (**B**, AMNH 29542) palatine fenestrae are absent and posterolateral palatal foramina are small. In *M. robinsoni* (**C**, AMNH 130584) palatine fenestrae are present and posterolateral palatal foramina are large.

that appear to be useful for identifying the species treated herein are those of the upper molar stylar cusps, for which minimally worn teeth must be examined.

As defined by positional criteria (after Clemens, 1966; see above), all five stylar cusps (A, B, C, D, and E) are usually present on M1 and M2 of *Marmosa*, but styD and styE are sometimes indistinctly separated (see below), and styC is often absent or indistinct on M3. Of the two cusps that sometimes occupy the C position, the one posterior to the ectoflexus is almost always larger. StyB, always the largest stylar cusp, is the labial terminus of the preparacrista in all species except *M. rubra*, in which the preparacrista usually terminates at styA.

Among the species treated in this report, we found noteworthy variation in the presence or absence of a distinct notch between stylar cusps D and E. This notch is usually present on unworn teeth, clearly separating styD from styE, in *Marmosa robinsoni*, *M. rubra*, *M. simonsi*, and *M. xerophila* (fig. 15A). However, no notch is present (with the result that styD and styE are indistinctly separated) in *M. isthmica*, *M. mexicana* (fig. 15B), and *M. zeledoni*.

Summary

The qualitative traits listed above provide an unambiguous basis for recognizing at least seven valid species among the nominal taxa treated in this report. In lieu of a key, we tabulate the most trenchant morphological and geographic comparisons to facilitate preliminary identifications (table 8). However, tabular summaries of diagnostic traits necessarily ignore many relevant complexities that may be taxonomically important. Those complexities, together with much additional
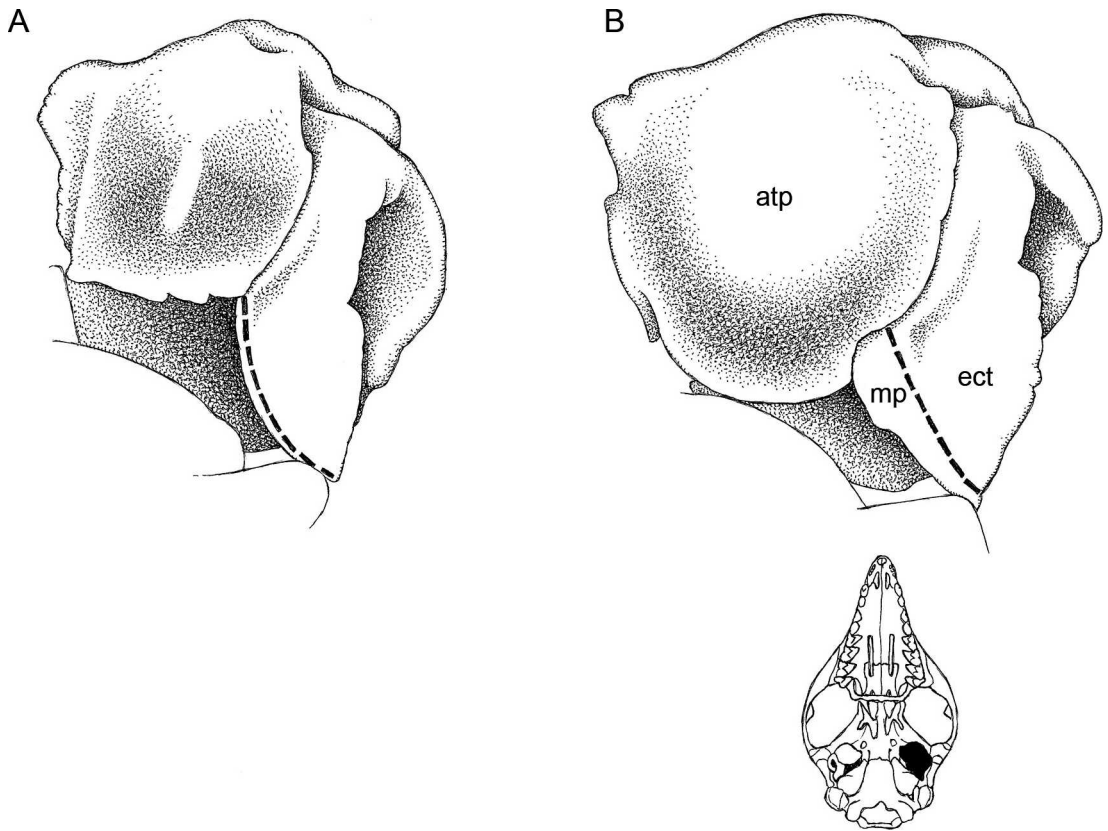
Fig. 14. Ventral view of the left ear region of *Marmosa mexicana* (**A**, AMNH 243700) and *M. robinsoni* (**B**, AMNH 266954) illustrating taxonomic differences in the morphology of the alisphenoid tympanic process (**atp**) and the ectotympanic (**ect**). The bold dashed line marks the course of the sulcus tympanicus, along which the tympanic membrane is attached on inner circumference of the ectotympanic. A small medial process of the ectotympanic (**mp**) contributes to the floor of the middle ear cavity in *M. robinsoni*.

information, are summarized in the following accounts.

SPECIES ACCOUNTS

Below we provide complete synonymies (after Gardner and Hayssen, 2004), information about type specimens and type localities, descriptions of diagnostic traits, comparisons with congeneric species, summaries of geographic distributions, descriptions of geographic variation (if any), comments on taxonomic history, and lists of specimens examined. Characters listed in the Morphological Diagnosis for each species are those described above, but additional features (e.g., morphometric traits) that are helpful for identification are mentioned under Compar-

isons. Holotypes of all of the nominal taxa included in these synonymies were examined by us and are listed together with other material at the conclusion of each account (under Specimens Examined).

Marmosa mexicana Merriam, 1897
Figure 16

Didelphys murina: Waterhouse, 1846: 508. Part, not *Didelphis murina* Linnaeus, 1758.

Didelphys murina: Alston, 1880: 200. ?Part, not *Didelphis murina* Linnaeus, 1758.

Didelphys murina: Thomas, 1882b: 372.

Didelphis (*Micoureus*) *murina*: Allen, 1890: 190. Name combination.

?*Didelphis* (*Micoureus*) *murina*: Allen, 1893: 240.

Didelphys [(*Micoureus*)] *murina*: Thomas, 1888: 343. Part, not *Didelphis murina* Linnaeus, 1758.
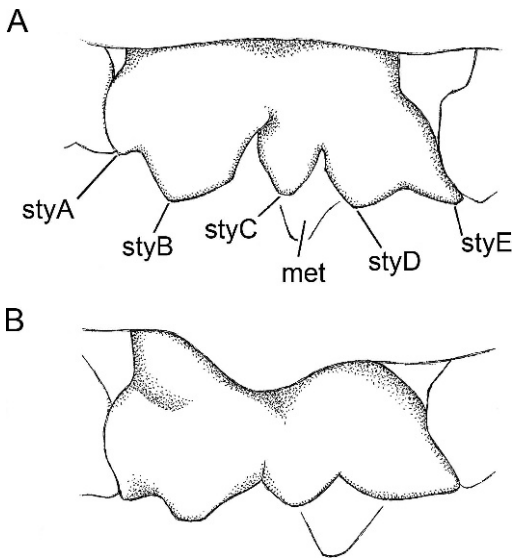
A

B

Fig. 15. Labial views of unworn second upper molars (M2) in *Marmosa xerophila* (**A**, USNM 443815) and *M. mexicana* (**B**, MVZ 159445). A distinct notch separates stylar cusp D (**styD**) from stylar cusp E (**styE**) in *M. xerophila*, but stylar cusps D and E are not separated by a notch in *M. mexicana*. Other abbreviations: **met**, metacone; **styA**, stylar cusp A; **styB**, stylar cusp B; **styC**, stylar cusp C.

?*Marmosa murina*: Thomas, 1895b: 58. Name combination.

?*Marmosa murina*: Allen, 1897: 44.

Marmosa murina mexicana Merriam, 1897: 44. Type locality "Juquila, Oaxaca."

Marmosa mexicana: Bangs, 1902: 19. Part; first use of current name combination.

[*Marmosa murina*] *mexicana*: Elliot, 1904: 6.

Marmosa murina mexicana: Elliot, 1905: 2.

Marmosa murina mexicana: Allen, 1908: 648.

?*Marmosa murina*: Allen, 1908: 648.

Marmosa murina mexicana: Allen, 1910: 92.

Marmosa murina: Allen, 1910: 92. Part, not *Didelphis murina* Linnaeus, 1758.

Marmosa ruatanica Goldman, 1911a: 237. Type locality "Ruatan Island, off the north coast of Honduras."

Marmosa mayensis Osgood, 1913: 176. Type locality "Izamal, Yucatan, Mexico."

[*Didelphis* (*Marmosa*)] *mexicana*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *mayensis*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *ruatanica*: Matschie, 1916: 270. Name combination.

Marmosa ruatanica: Elliot, 1917: 1.

Marmosa mayensis Elliot, 1917: 3.

Marmosa murina: Gaumer, 1917: 7.

Marmosa mexicana savannarum Goldman, 1917: 108. Type locality "Boqueron, Chiriqui, Panama."

[*Marmosa* (*Marmosa*)] *mexicana mayensis*: Cabrera, 1919: 37. Name combination.

[*Marmosa* (*Marmosa*)] *mexicana mexicana*: Cabrera, 1919: 37.

[*Marmosa* (*Marmosa*)] *mexicana savannarum*: Cabrera, 1919: 37.

[*Marmosa* (*Marmosa*)] *ruatanica*: Cabrera, 1919: 39.

Marmosa mexicana zeledoni: Peters et al., 1929: 129.

Marmosa ruatanica ruatanica: Tate, 1933: 124.

Marmosa mexicana mexicana: Tate, 1933: 132.

Marmosa mexicana mayensis: Tate, 1933: 132.

Marmosa mexicana mayensis: Hershkovitz, 1951: 551.

Marmosa mitis ruatanica: Hershkovitz, 1951: 551. Name combination.

Marmosa mexicana: Handley, 1966: 755.

Marmosa robinsoni ruatanica: Hall, 1981: 15. Name combination.

Marmosa mexicana mayensis: Hall, 1981: 15.

Marmosa mexicana mexicana: Hall, 1981: 15.

Marmosa mexicana savannarum: Hall, 1981: 16.

Marmosa mexicana: Honacki et al., 1982: 22.

Marmosa robinsoni: O'Connell, 1983: 1. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Alonso-Mejía and Medellín, 1992: 1. Part.

Marmosa mexicana savannarum: Villa-R. et al., 1993: 80.

Marmosa mexicana: Gardner, 1993: 18. Part.

Marmosa robinsoni: Gardner, 1993: 18. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Emmons, 1997: 26. Part.

Marmosa robinsoni: Emmons, 1997: 26. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Reid, 1997: 47. Part.

Marmosa robinsoni: Reid, 1997: 48. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Nowak, 1999: 21. Part.

Marmosa robinsoni: Nowak, 1999: 21. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Voss and Jansa, 2003: 75. Part.

Marmosa mexicana: Brown, 2004: 59. Part.

Marmosa robinsoni: Brown, 2004: 65. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Gardner, 2005: 9. Part.

[*Marmosa mexicana*] *mayensis*: Gardner, 2005: 9.

[*Marmosa mexicana*] *savannarum*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *ruatanica*: Gardner, 2005: 9.

Fig. 16.   Dorsal and ventral cranial views of *Marmosa mexicana* (USNM 77680, a mature adult male). Scale bar = 10 mm.

TYPE MATERIAL: The holotype (by original designation, USNM 71526) is a young adult (age class 6) male specimen consisting of a skin and skull. Although the skin is in good condition, the skull lacks most of the upper incisors, and the posterior palatal region is slightly damaged.

TYPE LOCALITY: The holotype was collected by E.W. Nelson and E.A. Goldman on 28 February 1895 at "Juquila" (= Santa Catarina Juquila, gazetteer entry 11; appendix), a town on the Pacific slopes of the Sierra Madre del Sur in southwestern Oaxaca, Mexico. According to Goldman (1951: 215), Juquila is at 5000 ft (1524 m) "near the frost line and just above the limits of coffee culture. The climate is cool and damp. Much fog and mist prevail, as shown by the moss on the trees on the north slopes of the adjacent hills and by the abundance of vegetation belonging to the temperate mountain flora."

MORPHOLOGICAL DIAGNOSIS: Midrostral fur pale, usually contrasting sharply with darker fur of crown; dark median rostral stripe absent or inconspicuous; dark facial mask usually extending posteriorly to contact base of ear; dorsal body pelage reddish brown; dorsal cover hairs 7–11 mm in length, guard hairs 9–14 mm; gray-based ventral pelage (covering the sides of chest, abdomen, and upper inguinal region, but sometimes also extending to the sides of neck and inner parts of arms and legs) with yellowish or orangish hair tips; self-colored ventral pelage (extending as a continuous median stripe of variable width from chin to anus) yellowish or orangish. Exposed skin of tail dark brown (indistinctly paler ventrally in some individuals), without any consistent pattern of scale arrangement (both spiral and annular patterns coexisting); 14–16 scales/cm on dorsal surface at caudal midlength; caudal scale-hairs reddish brown or light brown, detect-

able without magnification; central hair of each caudal-scale triplet as long as two scales (rarely 1.5 scales long). Gular gland present. Mammae 5–1–5 = 11 to 7–1–7 = 15. Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle in mature adult males long (reaching the base of the pollex) and unsegmented, without externally distinguishable proximal and distal segments.

Length of rostral process of premaxillae similar to I1 height. Orbitosphenoid-alisphenoid suture approximately twice as long as height of sphenorbital fissure in lateral view. Supraorbital ridges parallel or slightly divergent posteriorly, slender and dorsally reflected in some specimens but thicker and produced laterally in others; postorbital processes (when present) usually small but occasionally large (e.g., ROM 96090); temporal ridges usually converging posteriorly. Palatine fenestrae present, but often consisting of many irregular holes on each side (rather than a single large, rounded opening); posterolateral palatal foramina small, usually similar in length to M4 (measured across paracone-metacone). Tympanic wing of alisphenoid laterally compressed, with ventral surface slightly pointed or bluntly keeled; medial process of ectotympanic indistinct or absent. I1 hypsodont, normally present in adults; crown of I2 sharply defined in relation to root; C1 without accessory cusps; preparacrista connected to stylar cusp B on M1–M3; stylar cusps D and E confluent, not separated by a distinct notch on M2.

COMPARISONS: Marmosa mexicana merits close comparisons with three other species of Marmosa (Marmosa) that have overlapping geographic ranges in Central America, namely M. zeledoni, M. isthmica, and M. robinsoni. Specimens of these four taxa are often misidentified in museum collections, but each can be distinguished by a combination of morphometric and qualitative traits. For completeness, we also provide pairwise comparisons with allopatric congeners (M. xerophila, M. simonsi, M. rubra) that, although unlikely to be confused with M. mexicana geographically, may prove to be closely related.

Adult specimens of Marmosa mexicana average smaller than adult M. zeledoni in most external and craniodental measurements (tables 4–7), but there is broad overlap in all measurements, and none provides a satisfactory basis for identification. In qualitative features, M. mexicana is most readily distinguished from M. zeledoni by its brighter dorsal coloration (the dorsal pelage of M. zeledoni appears duller and darker in side-by-side comparisons); by the paler coloration of its midrostral fur, which contrasts sharply with the darker coloration of its crown fur (midrostral and crown fur are nearly the same color, seldom contrasting sharply, in M. zeledoni); by the posterior extension of its dark facial mask, which usually contacts the base of the ear (the mask of M. zeledoni seldom extends posteriorly to the ear base); by the more frequent presence of distinct postorbital processes (postorbital processes are usually absent or indistinct in M. zeledoni); and by the presence of palatine fenestrae (absent in M. zeledoni). Other differences include the coloration of the tips of the gray-based ventral hairs (yellowish or orangish in M. mexicana versus reddish or brownish in M. zeledoni), the morphology of the medial carpal tubercles of mature adult males (long and unsegmented in M. mexicana versus long but divided by a shallow sulcus into proximal and distal parts in M. zeledoni), caudal hair length (the central hair of each caudal-scale triplet is about two scales long in M. mexicana versus about one-and-a-half scales long in M. zeledoni), the size of the posterolateral palatal foramina (usually about as long as M4 measured across the paracone-metacone in M. mexicana versus usually shorter than M4 in M. zeledoni). In dorsal view, skulls of M. mexicana also have more laterally projecting and more posteriorly divergent supraorbital ridges, and temporal ridges that converge more strongly posteriorly, than skulls of like-aged M. zeledoni.

Adult specimens of Marmosa mexicana are distinctly smaller than adult M. isthmica in all measured external and craniodental dimensions (tables 4–7). Although no single measurement is sufficient for diagnosing these species, some of the observed overlap in external dimensions may be methodological artifacts; mean values for hind feet and ears are large enough to suggest that the size of these appendages might often be useful for field identification. It is also noteworthy that

morphometric overlap is minimal in several ontogenetically invariant molar dimensions (e.g., UMS; tables 6, 7). Among the qualitative external characters we studied, *M. mexicana* is most easily distinguished from *M. isthmica* by the posterior extension of its dark facial mask, which usually contacts the base of the ear (the dark facial mask of *M. isthmica* does not contact the ear base); by its more reddish- (versus orangish-) brown dorsal fur; by the more extensive distribution of gray-based ventral fur, which covers the sides of its chest, abdomen, and upper inguinal region, sometimes also extending to the sides of the neck and inner parts of the arms and legs (gray-based ventral fur is restricted to the sides of the abdomen in *M. isthmica*); and by the long, unsegmented medial carpal tubercles of mature adult males (the medial carpal tubercles of like-aged *M. isthmica* are divided by a shallow sulcus into subequal proximal and distal parts). In qualitative cranial characters, *M. mexicana* is most easily distinguished from *M. isthmica* by the presence of palatine fenestrae (absent in *M. isthmica*) and by the usual absence or small size of postorbital processes (postorbital processes are usually present and much larger in fully mature examples of *M. isthmica*).

Adult specimens of *Marmosa mexicana* are similar in size to adult *M. robinsoni*, although they average somewhat smaller in most dimensions (tables 4–7). On average, *M. mexicana* has a relatively longer tail than *M. robinsoni*, a difference that is noteworthy despite broad overlap in computed ratios (possibly another methodological artifact). In qualitative external characters, *M. mexicana* is most easily distinguished from *M. robinsoni* by the posterior extension of its dark facial mask, which usually contacts the base of the ear (the dark facial mask of *M. robinsoni* does not contact the ear base); by its more reddish- (versus yellowish-) brown dorsal fur; by its more conspicuous and more extensively distributed gray-based ventral fur, which covers the sides of its chest, abdomen, and upper inguinal region, sometimes also extending to the sides of the neck and inner parts of the arms and legs (gray-based ventral fur is often less conspicuous and is usually restricted to the sides of the abdomen in *M.*

robinsoni); and by the long, unsegmented medial carpal tubercles of mature adult males (the medial carpal tubercles of like-aged *M. robinsoni* are usually divided by a shallow sulcus into a globular proximal segment and a comma-shaped distal segment). In qualitative cranial traits, *M. mexicana* is most easily distinguished from *M. robinsoni* by its longer rostral process of the premaxillae, smaller and more irregularly shaped palatine fenestrae, smaller posterolateral palatal foramina, less inflated auditory bullae, and by the absence of a notch between styD and styE (a distinct notch is usually present in *M. robinsoni*). In addition, a low sagittal crest that is sometimes present on the skulls of old adult specimens of *M. robinsoni* is never seen in *M. mexicana*.

Marmosa mexicana differs from *M. xerophila* in all of the same traits that distinguish *M. mexicana* from *M. robinsoni*, except that the rostral process of the premaxillae (long in *M. mexicana*, short in *M. robinsoni*) is entirely absent in *M. xerophila*.

Marmosa mexicana is longer-tailed and smaller-eared, on average, than *M. simonsi*, but the two species are otherwise similar in univariate comparisons of measured external and craniodental dimensions (tables 4–7). In qualitative external traits, these taxa are most easily distinguished by their dorsal fur color (reddish brown in *M. mexicana*, distinctly grayish in *M. simonsi*), ventral fur color (a continuous median streak of self-colored fur is present in *M. mexicana* but absent in *M. simonsi*), and tail coloration (all-dark in *M. mexicana*, one-third to one-half white in *M. simonsi*). In qualitative cranial traits, they are most easily distinguished by the rostral process of the premaxillae (long in *M. mexicana*, short in *M. simonsi*), postorbital processes (usually indistinct or small in *M. mexicana*, consistently well developed in *M. simonsi*), and by the notch between stD and stE on unworn M2 (absent in *M. mexicana*, present in *M. simonsi*).

Marmosa mexicana is substantially smaller, on average, than *M. rubra* in most measured dimensions (tables 4–7), but only measurements of the upper molar series are diagnostic in same-sex univariate comparisons (UMS, tables 6, 7). In qualitative external traits, these species are most easily

TABLE 6
Summary Statistics[a] for Craniodental Measurements (mm) of Adult Male Specimens of Seven Species of *Marmosa*

	mexicana	*zeledoni*	*isthmica*	*robinsoni*	*xerophila*	*simonsi*	*rubra*
GLS	35.4 ± 2.1 (41) 31.3–39.5	37.4 ± 1.4 (21) 34.4–39.6	40.4 ± 2.1 (103) 36.0–45.0	37.6 ± 2.2 (142) 33.3–43.6	33.3 ± 1.2 (25) 31.2–36.3	36.0 ± 1.5 (24) 33.3–38.7	37.8 ± 1.0 (13) 36.7–40.3
CBL	34.7 ± 2.4 (39) 30.3–39.2	36.7 ± 1.4 (21) 33.6–38.9	39.8 ± 2.2 (99) 35.0–44.8	37.0 ± 2.3 (140) 32.6–43.3	32.8 ± 1.3 (24) 30.7–35.7	35.3 ± 1.8 (22) 32.8–38.4	37.3 ± 1.0 (13) 35.9–39.8
RL	12.6 ± 0.8 (40) 11.1–14.6	13.6 ± 0.6 (21) 12.5–14.5	14.4 ± 0.9 (106) 12.6–16.5	13.2 ± 1.0 (148) 11.4–16.1	11.1 ± 0.6 (25) 10.2–12.6	12.5 ± 0.7 (30) 11.1–14.0	13.4 ± 0.5 (16) 12.8–14.9
NL	15.6 ± 1.3 (42) 13.4–18.7	16.9 ± 1.0 (21) 15.0–18.2	17.9 ± 1.2 (106) 15.0–20.8	17.2 ± 1.2 (149) 14.5–20.4	14.9 ± 0.9 (25) 12.8–16.7	15.9 ± 1.0 (30) 14.3–18.2	16.6 ± 0.8 (16) 15.2–17.8
PL	19.9 ± 1.2 (44) 17.8–22.8	21.0 ± 0.8 (27) 19.0–22.4	22.8 ± 1.2 (110) 20.1–26.0	21.1 ± 1.2 (157) 18.7–24.5	18.4 ± 0.7 (26) 17.2–20.4	20.2 ± 1.0 (28) 18.7–22.2	21.2 ± 0.6 (13) 20.4–22.6
MTR	13.7 ± 0.6 (47) 12.6–15.6	14.5 ± 0.4 (28) 13.8–15.0	15.7 ± 0.6 (113) 14.2–17.6	15.0 ± 0.9 (164) 13.3–17.2	12.9 ± 0.4 (26) 12.3–13.7	14.2 ± 0.5 (29) 13.4–15.6	14.8 ± 0.3 (15) 14.3–15.2
UMS	6.7 ± 0.2 (47) 6.3–7.2	7.1 ± 0.2 (28) 6.7–7.4	7.6 ± 0.2 (113) 7.1–8.3	7.2 ± 0.4 (164) 6.6–8.0	6.4 ± 0.2 (27) 6.0–6.8	7.0 ± 0.2 (30) 6.7–7.7	7.4 ± 0.1 (16) 7.3–7.6
LM4	1.1 ± 0.1 (48) 0.9–1.2	1.2 ± 0.1 (28) 1.0–1.4	1.2 ± 0.1 (112) 1.0–1.4	1.2 ± 0.1 (164) 0.9–1.5	1.0 ± 0.0 (27) 0.9–1.1	1.1 ± 0.1 (30) 1.0–1.5	1.2 ± 0.1 (16) 1.1–1.3
WM2	1.9 ± 0.1 (48) 1.7–2.1	2.0 ± 0.1 (28) 1.8–2.2	2.2 ± 0.1 (112) 2.0–2.4	2.1 ± 0.1 (159) 1.8–2.5	1.8 ± 0.1 (26) 1.7–2.0	2.0 ± 0.1 (30) 1.9–2.2	2.1 ± 0.1 (15) 2.0–2.2
WM4	2.4 ± 0.1 (48) 2.1–2.6	2.5 ± 0.1 (27) 2.4–2.7	2.6 ± 0.1 (114) 2.3–3.0	2.6 ± 0.2 (167) 2.1–3.2	2.2 ± 0.1 (27) 2.0–2.4	2.5 ± 0.1 (29) 2.3–2.8	2.6 ± 0.1 (16) 2.4–2.8
HC	3.1 ± 0.3 (46) 2.3–3.7	3.2 ± 0.2 (27) 2.8–3.7	3.6 ± 0.3 (107) 2.8–4.5	3.3 ± 0.4 (152) 2.5–4.4	2.7 ± 0.2 (22) 2.4–3.1	3.6 ± 0.4 (30) 2.9–4.3	3.2 ± 0.2 (14) 2.9–3.7
PB	10.9 ± 0.6 (41) 9.8–12.4	11.5 ± 0.4 (27) 11.0–12.3	12.6 ± 0.6 (108) 11.3–14.0	12.1 ± 0.8 (160) 10.3–14.6	10.6 ± 0.5 (22) 9.8–11.7	11.2 ± 0.4 (26) 10.5–11.9	11.7 ± 0.4 (10) 11.1–12.2
PPB	3.5 ± 0.2 (42) 3.0–4.0	3.6 ± 0.2 (23) 3.2–3.9	3.6 ± 0.2 (109) 3.2–4.2	3.5 ± 0.2 (153) 3.1–4.0	3.3 ± 0.2 (27) 2.8–3.8	3.4 ± 0.2 (25) 3.0–3.7	3.6 ± 0.2 (13) 3.5–4.0
BB	6.8 ± 0.5 (32) 5.7–7.6	7.4 ± 0.4 (17) 6.8–7.9	7.8 ± 0.4 (71) 6.9–8.7	6.8 ± 0.5 (130) 5.7–7.9	6.3 ± 0.4 (27) 5.6–7.0	6.2 ± 0.3 (16) 5.7–6.8	7.2 ± 0.3 (14) 6.6–7.8
BTB	11.0 ± 0.5 (39) 10.1–12.1	11.6 ± 0.3 (22) 11.0–12.2	12.4 ± 0.6 (104) 11.0–13.8	12.2 ± 0.6 (146) 10.9–13.7	11.1 ± 0.5 (24) 10.3–12.2	11.5 ± 0.4 (22) 10.9–12.3	12.0 ± 0.4 (12) 11.5–12.8

TABLE 6
(*Continued*)

	mexicana	zeledoni	isthmica	robinsoni	xerophila	simonsi	rubra
LTB	5.4 ± 0.3 (41) 5.0–6.0	5.3 ± 0.2 (22) 4.8–5.6	5.7 ± 0.3 (98) 5.1–6.4	5.8 ± 0.3 (157) 5.1–6.6	5.4 ± 0.2 (24) 5.1–6.0	5.8 ± 0.2 (23) 5.4–6.2	5.4 ± 0.2 (14) 4.9–5.6
TBO	0.9 ± 0.2 (39) 0.6–1.4	1.0 ± 0.2 (24) 0.5–1.3	1.1 ± 0.2 (97) 0.4–1.8	1.2 ± 0.2 (139) 0.6–1.8	1.2 ± 0.2 (26) 0.8–1.6	1.4 ± 0.2 (23) 1.0–1.7	1.1 ± 0.2 (11) 0.8–1.3
WET	1.0 ± 0.1 (22) 0.8–1.1	—	1.1 ± 0.2 (12) 0.9–1.4	1.4 ± 0.2 (17) 1.1–1.7	1.5 (1)	1.4 ± 0.0 (2) 1.4–1.5	1.4 ± 0.1 (5) 1.2–1.5
NB	4.5 ± 0.5 (47) 3.5–5.8	4.5 ± 0.5 (28) 3.7–5.4	4.9 ± 0.4 (111) 4.1–6.0	4.7 ± 0.5 (165) 3.6–6.1	4.0 ± 0.4 (27) 3.2–4.7	4.3 ± 0.4 (30) 3.6–5.2	4.9 ± 0.5 (16) 4.1–5.6
BRC	5.9 ± 0.6 (44) 4.9–7.2	6.1 ± 0.3 (28) 5.5–6.8	6.8 ± 0.5 (108) 5.6–7.7	6.4 ± 0.6 (161) 5.2–7.9	5.8 ± 0.4 (24) 5.2–6.6	6.1 ± 0.4 (26) 5.2–6.9	6.1 ± 0.3 (14) 5.6–6.7
BRJ	10.1 ± 1.0 (43) 8.6–12.5	10.5 ± 0.8 (28) 8.2–12.6	11.7 ± 0.8 (111) 9.8–13.5	11.4 ± 1.0 (167) 9.0–14.2	9.8 ± 0.7 (26) 8.8–11.6	10.3 ± 0.7 (28) 9.1–11.8	11.0 ± 0.6 (14) 10.1–12.2
LIB	6.1 ± 0.5 (48) 5.3–7.4	6.4 ± 0.4 (28) 5.5–7.2	6.8 ± 0.5 (113) 5.7–8.2	6.0 ± 0.6 (167) 4.9–7.4	4.9 ± 0.4 (27) 4.3–5.8	5.6 ± 0.3 (30) 4.9–6.1	6.5 ± 0.3 (16) 5.9–7.2
POC	6.3 ± 0.4 (45) 5.3–7.2	6.5 ± 0.4 (28) 5.8–7.4	6.3 ± 0.4 (112) 5.3–7.4	5.7 ± 0.4 (163) 4.4–6.8	4.7 ± 0.3 (27) 4.2–5.1	5.8 ± 0.4 (29) 5.0–6.6	6.6 ± 0.6 (16) 5.1–7.4
BBC	13.3 ± 0.6 (41) 12.4–14.5	13.6 ± 0.4 (24) 12.4–14.4	14.7 ± 0.5 (106) 13.3–16.1	13.8 ± 0.6 (157) 12.5–15.4	12.5 ± 0.4 (25) 11.9–13.2	13.4 ± 0.4 (24) 12.4–14.1	14.5 ± 0.4 (15) 13.9–15.3
ZB	19.1 ± 1.8 (38) 16.1–22.8	19.8 ± 0.8 (23) 18.8–21.9	21.9 ± 1.2 (100) 19.3–25.2	20.9 ± 1.6 (147) 17.3–24.7	18.8 ± 1.0 (22) 17.0–21.2	19.6 ± 1.0 (23) 17.9–21.4	20.6 ± 0.6 (12) 19.5–21.9
LM	24.4 ± 1.7 (43) 21.2–27.8	26.0 ± 0.9 (22) 23.9–27.3	28.4 ± 1.6 (112) 25.0–32.7	27.0 ± 1.8 (157) 23.6–31.8	24.3 ± 1.3 (25) 22.4–27.6	25.8 ± 1.3 (30) 23.8–28.1	26.9 ± 1.1 (13) 24.5–29.0
LMS	7.4 ± 0.2 (47) 7.0–7.9	7.7 ± 0.2 (28) 7.4–8.2	8.3 ± 0.2 (114) 7.7–9.2	8.0 ± 0.4 (158) 7.2–8.9	7.1 ± 0.2 (27) 6.8–7.5	7.7 ± 0.2 (31) 7.1–8.3	8.1 ± 0.2 (15) 7.8–8.4
Lm4	2.0 ± 0.1 (47) 1.8–2.1	2.1 ± 0.1 (28) 2.0–2.3	2.3 ± 0.1 (114) 2.1–2.5	2.2 ± 0.1 (164) 1.9–2.5	2.0 ± 0.1 (27) 1.9–2.1	2.0 ± 0.1 (31) 1.9–2.3	2.2 ± 0.1 (15) 2.1–2.4
Wm2	1.1 ± 0.1 (47) 1.0–1.3	1.1 ± 0.0 (28) 1.1–1.3	1.2 ± 0.1 (113) 1.0–1.4	1.2 ± 0.1 (161) 1.0–1.4	1.1 ± 0.1 (27) 1.0–1.2	1.2 ± 0.0 (31) 1.1–1.3	1.2 ± 0.0 (15) 1.1–1.3

[a] The sample mean plus or minus one standard deviation, the sample size (in parentheses), and the observed range.

TABLE 7
Summary Statistics[a] for Craniodental Measurements (mm) of Adult Female Specimens of Seven Species of *Marmosa*

	mexicana	*zeledoni*	*isthmica*	*robinsoni*	*xerophila*	*simonsi*	*rubra*
GLS	33.5 ± 1.5 (12) 31.0–35.2	35.2 ± 1.1 (9) 33.4–37.6	37.0 ± 1.6 (84) 33.1–41.3	34.7 ± 1.7 (75) 31.4–40.3	31.0 ± 1.0 (28) 29.0–34.0	33.5 ± 1.4 (16) 30.5–35.6	36.5 ± 0.7 (13) 35.4–37.9
CBL	32.6 ± 1.7 (12) 29.9–34.7	34.2 ± 1.2 (9) 32.2–36.8	36.2 ± 1.7 (84) 32.1–40.4	34.0 ± 1.7 (80) 30.6–39.3	30.4 ± 1.0 (28) 28.5–33.8	32.9 ± 1.6 (16) 29.7–34.7	36.0 ± 0.9 (10) 34.8–37.3
RL	11.8 ± 0.6 (10) 10.6–12.6	12.7 ± 0.4 (11) 12.2–13.8	13.1 ± 0.8 (85) 11.3–15.1	12.1 ± 0.8 (78) 10.4–14.6	10.3 ± 0.4 (26) 9.7–11.3	11.4 ± 0.7 (19) 10.2–12.3	12.9 ± 0.4 (14) 11.8–13.6
NL	14.8 ± 1.0 (12) 13.1–17.0	15.4 ± 0.8 (11) 14.4–17.2	16.0 ± 1 (84) 13.5–19.0	15.6 ± 1.0 (77) 13.8–19.1	13.6 ± 0.7 (25) 12.3–15.4	14.4 ± 1.1 (20) 12.6–16.7	15.9 ± 0.5 (14) 14.6–16.4
PL	18.9 ± 1.0 (14) 17.2–20.0	19.9 ± 0.6 (10) 19.3–21.4	21.0 ± 0.9 (91) 18.8–23.4	19.6 ± 1.1 (83) 17.3–23.1	17.2 ± 0.6 (28) 16.2–19.1	18.8 ± 0.9 (20) 17.0–20.3	20.3 ± 0.5 (15) 19.3–21.1
MTR	12.9 ± 0.6 (17) 11.8–14.0	13.8 ± 0.2 (12) 13.5–14.4	14.7 ± 0.6 (95) 13.4–16.5	14.0 ± 0.7 (85) 12.9–16.1	12.2 ± 0.4 (28) 11.5–13.4	13.4 ± 0.5 (23) 12.4–14.4	14.2 ± 0.3 (17) 13.8–15.0
UMS	6.5 ± 0.2 (18) 6.1–6.8	7.0 ± 0.2 (12) 6.8–7.3	7.3 ± 0.3 (96) 6.8–8.1	7.0 ± 0.3 (85) 6.5–7.9	6.2 ± 0.2 (28) 5.9–6.5	6.8 ± 0.2 (23) 6.5–7.2	7.4 ± 0.2 (18) 7.1–7.5
LM4	1.0 ± 0.1 (18) 0.9–1.1	1.1 ± 0.0 (12) 1.0–1.2	1.1 ± 0.1 (95) 1.0–1.4	1.1 ± 0.1 (86) 0.9–1.3	1.0 ± 0.1 (28) 0.8–1.1	1.0 ± 0.1 (23) 0.8–1.1	1.2 ± 0.1 (18) 1.0–1.3
WM2	1.8 ± 0.1 (18) 1.7–2.0	1.9 ± 0.1 (12) 1.9–2.0	2.1 ± 0.1 (92) 1.8–2.5	2.1 ± 0.1 (84) 1.8–2.4	1.8 ± 0.1 (28) 1.6–1.9	2.0 ± 0.1 (23) 1.8–2.1	2.1 ± 0.1 (18) 1.9–2.2
WM4	2.2 ± 0.1 (18) 2.0–2.4	2.5 ± 0.1 (12) 2.3–2.6	2.5 ± 0.2 (95) 2.2–3.0	2.5 ± 0.2 (86) 2.2–2.9	2.1 ± 0.1 (28) 1.9–2.5	2.4 ± 0.1 (23) 2.2–2.7	2.5 ± 0.1 (18) 2.3–2.7
HC	2.6 ± 0.3 (15) 1.8–3.0	2.7 ± 0.2 (12) 2.4–3.0	2.9 ± 0.2 (91) 2.5–3.5	2.7 ± 0.2 (81) 2.2–3.3	2.2 ± 0.2 (27) 1.8–2.6	2.9 ± 0.2 (22) 2.4–3.3	2.7 ± 0.2 (16) 2.5–3.0
PB	10.4 ± 0.4 (16) 9.6–11.1	11.0 ± 0.4 (10) 10.5–11.6	11.8 ± 0.5 (89) 10.5–13.0	11.5 ± 0.6 (82) 10.2–13.1	10.0 ± 0.3 (28) 9.5–10.6	10.7 ± 0.4 (15) 10.0–11.3	11.7 ± 0.3 (15) 11.2–12.1
PPB	3.5 ± 0.2 (16) 3.1–4.1	3.5 ± 0.2 (10) 3.3–3.8	3.5 ± 0.2 (86) 3.1–4.0	3.4 ± 0.2 (81) 2.8–4.0	3.2 ± 0.1 (28) 3.0–3.5	3.3 ± 0.1 (16) 3.1–3.6	3.7 ± 0.3 (15) 3.3–4.7
BB	6.4 ± 0.3 (13) 5.7–6.7	7.0 ± 0.4 (6) 6.4–7.3	7.3 ± 0.4 (58) 6.5–8.1	6.2 ± 0.4 (69) 5.5–7.1	5.9 ± 0.3 (28) 5.4–6.4	6.0 ± 0.3 (5) 5.6–6.5	7.0 ± 0.4 (11) 6.4–7.7
BTB	10.6 ± 0.5 (13) 9.8–11.2	11.3 ± 0.5 (10) 10.4–12.2	11.6 ± 0.4 (82) 10.7–12.6	11.4 ± 0.5 (75) 10.4–12.8	10.5 ± 0.3 (26) 10.0–11.3	10.9 ± 0.4 (17) 10.1–11.4	11.8 ± 0.4 (13) 11.2–12.6

TABLE 7
(Continued)

	mexicana	*zeledoni*	*isthmica*	*robinsoni*	*xerophila*	*simonsi*	*rubra*
LTB	5.1 ± 0.2 (13) 4.7–5.4	5.1 ± 0.2 (10) 4.9–5.5	5.4 ± 0.2 (83) 4.9–5.8	5.5 ± 0.2 (79) 4.9–6.3	5.2 ± 0.3 (28) 4.8–6.2	5.7 ± 0.2 (17) 5.3–6.1	5.2 ± 0.2 (14) 4.9–5.5
TBO	0.8 ± 0.2 (14) 0.5–1.2	1.1 ± 0.3 (10) 0.6–1.6	1.1 ± 0.2 (83) 0.5–1.5	1.1 ± 0.2 (72) 0.7–1.6	1.1 ± 0.2 (27) 0.8–1.4	1.4 ± 0.1 (17) 1.1–1.6	0.9 ± 0.2 (15) 0.7–1.3
WET	0.9 ± 0.2 (6) 0.8–1.2	0.9 ± 0.1 (3) 0.8–1.0	1.0 ± 0.1 (10) 0.8–1.2	1.5 ± 0.2 (5) 1.4–1.8	—	1.5 ± 0.2 (6) 1.2–1.7	1.3 ± 0.1 (7) 1.2–1.4
NB	4.1 ± 0.3 (17) 3.5–4.6	4.2 ± 0.2 (11) 3.8–4.7	4.5 ± 0.4 (93) 3.6–5.8	4.4 ± 0.4 (85) 3.4–5.5	3.6 ± 0.2 (28) 3.1–3.9	3.9 ± 0.4 (21) 3.0–4.4	4.5 ± 0.3 (17) 4.1–5.4
BRC	5.6 ± 0.5 (14) 4.9–6.5	5.7 ± 0.4 (11) 5.2–6.6	6.1 ± 0.4 (93) 5.3–7.1	5.9 ± 0.4 (83) 5.0–7.3	5.3 ± 0.2 (28) 4.8–5.8	5.5 ± 0.4 (19) 4.9–6.5	6.0 ± 0.2 (16) 5.6–6.6
BRJ	9.4 ± 0.7 (17) 8.2–10.5	10.1 ± 0.6 (11) 9.4–11.4	10.5 ± 0.7 (93) 8.9–11.9	10.5 ± 0.8 (84) 8.8–12.0	9.0 ± 0.3 (28) 8.5–9.6	9.5 ± 0.7 (19) 8.6–10.5	10.8 ± 0.5 (16) 9.9–11.8
LIB	5.7 ± 0.3 (18) 5.2–6.2	6.1 ± 0.3 (12) 5.7–6.7	6.1 ± 0.4 (96) 5.4–7.2	5.6 ± 0.5 (83) 4.5–6.8	4.5 ± 0.2 (28) 4.2–5.0	5.2 ± 0.3 (20) 4.8–5.7	6.4 ± 0.3 (17) 6.0–6.8
POC	6.2 ± 0.4 (17) 5.7–6.9	6.6 ± 0.2 (12) 6.3–7.0	6.4 ± 0.4 (95) 5.6–7.9	5.8 ± 0.3 (84) 5.1–6.8	4.9 ± 0.3 (28) 4.3–5.7	5.9 ± 0.3 (20) 4.8–6.5	6.7 ± 0.6 (18) 5.6–7.8
BBC	12.9 ± 0.4 (15) 12.2–13.6	13.7 ± 0.5 (10) 12.7–14.7	14.0 ± 0.4 (87) 13.1–14.9	13.2 ± 0.5 (79) 12.2–14.2	12.1 ± 0.3 (28) 11.6–12.8	13.0 ± 0.4 (18) 12.3–14.0	14.1 ± 0.4 (15) 13.5–15.1
ZB	18.2 ± 1.0 (14) 16.4–19.6	18.9 ± 1.0 (10) 17.0–20.5	19.8 ± 1.0 (79) 17.5–22.6	19.4 ± 1.2 (73) 17.3–22.1	17.5 ± 0.5 (26) 16.7–18.9	18.5 ± 0.9 (12) 16.8–19.6	20.3 ± 0.7 (14) 19.2–21.3
LM	23.3 ± 1.5 (18) 20.5–25.8	24.4 ± 1.0 (12) 22.8–26.4	26.1 ± 1.3 (93) 22.9–29.5	25.0 ± 1.5 (83) 22.4–29.6	22.5 ± 0.9 (27) 20.7–25.3	23.9 ± 1.4 (21) 21.2–25.8	26.1 ± 0.6 (18) 24.9–27.1
LMS	7.1 ± 0.3 (18) 6.7–7.5	7.7 ± 0.2 (12) 7.4–7.9	8.2 ± 0.3 (95) 7.4–9.0	7.8 ± 0.4 (84) 7.1–8.7	6.9 ± 0.2 (27) 6.6–7.4	7.4 ± 0.3 (23) 6.9–7.9	8.0 ± 0.2 (17) 7.6–8.2
Lm4	2.0 ± 0.1 (18) 1.8–2.1	2.1 ± 0.0 (12) 2.0–2.2	2.2 ± 0.1 (96) 2.0–2.5	2.1 ± 0.1 (85) 1.9–2.3	1.9 ± 0.1 (27) 1.8–2.1	2.0 ± 0.1 (23) 1.8–2.2	2.2 ± 0.1 (18) 2.0–2.3
Wm2	1.1 ± 0.0 (18) 1.0–1.2	1.2 ± 0.1 (12) 1.1–1.2	1.2 ± 0.1 (96) 1.1–1.4	1.2 ± 0.1 (83) 1.1–1.4	1.1 ± 0.1 (27) 1.0–1.1	1.2 ± 0.1 (23) 1.1–1.3	1.2 ± 0.1 (17) 1.1–1.4

[a] The sample mean plus or minus one standard deviation, the sample size (in parentheses), and the observed range.

TABLE 8
Morphological and Geographic Comparisons among Seven Species of *Marmosa*[a]

	mexicana	*zeledoni*	*isthmica*
Midrostral and crown fur	sharp contrast	little or no contrast	sharp contrast
Dark median rostral stripe	absent	absent	absent
Facial mask contacts ear	yes	usually not	no
Dorsal pelage	reddish brown	reddish brown[b]	reddish brown
Self-colored ventral pelage	present	present	present
Gular gland	present	present	present
Medial carpal tubercle	long	long	long
Tail coloration	all-dark	all-dark	all-dark
Tail scale pattern	spiral & annular	spiral & annular	spiral & annular
Rostral process of premaxillae	long	long	long
Postorbital processes	small/indistinct	absent	often present
Sagittal crest	absent	absent	absent
Palatine fenestrae	present	absent	absent
Alisphenoid bullae	compressed	compressed	compressed
Medial process of ectotympanic	absent	absent	absent
Preparacrista connection	to stB	to stB	to stB
Notch between stD and stE	absent	absent	absent
Crown length M1–M4[g]	6.1–7.2 mm	6.7–7.4 mm	6.8–8.3 mm
Geographic distribution	Mexico–Panama	Nicaragua–Colombia[h]	Panama–Ecuador[h]

[a] Except as noted otherwise below, table entries for morphological characters describe modal traits of adult specimens examined.

[b] Usually darker than in sympatric *M. mexicana* and duller than in sympatric *M. isthmica*.

[c] Usually paler than in *M. robinsoni*.

[d] Except on chin and throat.

[e] Self-colored streak sometimes discontinuous on chest and/or abdomen, which may be entirely gray based.

[f] Short or long.

[g] The observed range of both sexes for measurements of the upper molar series (UMS; tables 6, 7).

[h] West of the Andes.

[i] Also on Trinidad and Tobago.

[j] East of the Andes.

distinguished by rostral markings (a dark median stripe is absent in *M. mexicana* but present in *M. rubra*), by the posterior extension of the dark facial mask (reaching the base of the ear in *M. mexicana* but not in *M. rubra*), by the presence or absence of a gular gland (present in *M. mexicana*, absent in *M. rubra*), by the arrangement of caudal scales (indeterminate in *M. mexicana*, distinctly spiral in *M. rubra*), and by the length of caudal-scale hairs (the central hair of each triplet is about two scales long in *M. mexicana*, but only about one scale long in *M. rubra*). In qualitative craniodental traits, these species are most readily distinguished by their palatal morphology (palatine fenestrae are present in *M. mexicana* but absent in *M. rubra*), by the stylar terminus of the preparacrista on M1–M3 (at styB in *M. mexicana*, at styA in *M. rubra*), and by the

presence or absence of a distinct notch between styD and styE on M2 (absent in *M. mexicana*, present in *M. rubra*).

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: *Marmosa mexicana* occurs in tropical and subtropical forests and shrubby habitats below 1600 m elevation from the Mexican states of Tamaulipas and San Luis Potosí southward to the eastern Panamanian province of Darién (fig. 17). It is also known from two offshore Caribbean islands, Isla de Roatán (Honduras; locality 53) and Isla del Maíz Grande (Nicaragua; locality 57).

In Mexico, this species occurs in both dry and moist forests that correspond to the Tropical Zone of Shelford (1926). However, *Marmosa mexicana* is also known from several localities (gazetteer entries 6, 10, and 11; appendix) where the Central American and Sierra Madre del Sur pine-oak forests are

TABLE 8
(*Extended*)

robinsoni	xerophila	simonsi	rubra
sharp contrast	sharp contrast	sharp contrast	sharp contrast
absent	absent	absent	present
no	no	sometimes	no
yellowish brown	yellowish brown[c]	grayish	reddish brown
present	present	absent[d]	variable[e]
present	present	present	absent
variable[f]	variable[f]	short	short
all-dark	all-dark	half-white	all-dark
spiral & annular	spiral & annular	spiral & annular	spiral
short	absent	short	long
usually indistinct	usually indistinct	well developed	absent
sometimes present	sometimes present	absent	absent
present	present	present	absent
globular	globular	globular	compressed
present	present	present	absent
to stB	to stB	to stB	to stA
present	present	present	present
6.5–8.0 mm	5.9–6.8 mm	6.5–7.7 mm	7.1–7.6 mm
Panama–Venezuela[i]	Colombia & Venezuela	Ecuador & Peru[h]	Colombia–Peru[j]

juxtaposed with Central American Pacific dry forests (as defined by Olson et al., 2001). In Central America, *M. mexicana* occurs in a wide variety of habitats that include dry and moist tropical forests, pine-oak forests, mangroves, and scrublands.

The range of *M. mexicana* overlaps that of *M. zeledoni* from northwestern Nicaragua to eastern Panama. The two species have been collected sympatrically at Río Coco (locality 60), Nicaragua; Finca Helechales (locality 79) and Monteverde (locality 80), Costa Rica; and Bugaba (locality 105), Panama. The range of *M. mexicana* also overlaps the known ranges of *M. isthmica* and *M. robinsoni* in Panama, although *M. mexicana* has apparently not been collected sympatrically with either of those species.

GEOGRAPHIC VARIATION: Available population samples of *Marmosa mexicana* exhibit variation in pelage color that is apparently related to habitat. Whereas specimens from pine-oak forests and moist forests tended to have rich reddish-brown dorsal fur and orangish ventral fur, specimens from dry forests and scrublands tend to be paler (with faded-reddish dorsal fur and yellowish buff or buff ventral fur). The palest specimens we examined were collected at Puerto El Triunfo

(El Salvador; locality 50) in the Northern Dry Pacific Coast Mangroves ecoregion of Olson et al. (2001). By contrast, we found no morphometric variation that could be unequivocally related to the geographic origin or habitat of the specimens analyzed.

TAXONOMIC HISTORY: The first literature reference to a specimen identifiable as *Marmosa mexicana* is in Waterhouse (1846), who identified a British Museum specimen from Mexico as *Didelphys murina*. Other 19th-century authors also used *murina* for specimens of *mexicana* (e.g., Alston, 1880; Thomas, 1882b, 1888, 1895; Allen 1893) and, indeed, Merriam (1897) originally described *mexicana* as a subspecies of *M. murina*. Although Merriam provided only a brief description of *mexicana*, based primarily on the pelage of two specimens from the Mexican states of Oaxaca and Chiapas, most subsequent authors (except Allen, 1908, 1910; and Gaumer, 1917) seem to have agreed that *mexicana* was a distinct taxon. Bangs (1902) provided additional details about the pelage color and cranial morphology of *mexicana*, which he considered to represent a valid species. However, his conclusion was not immediately accepted by other mammalogists (e.g., Elliot, 1904, 1905).
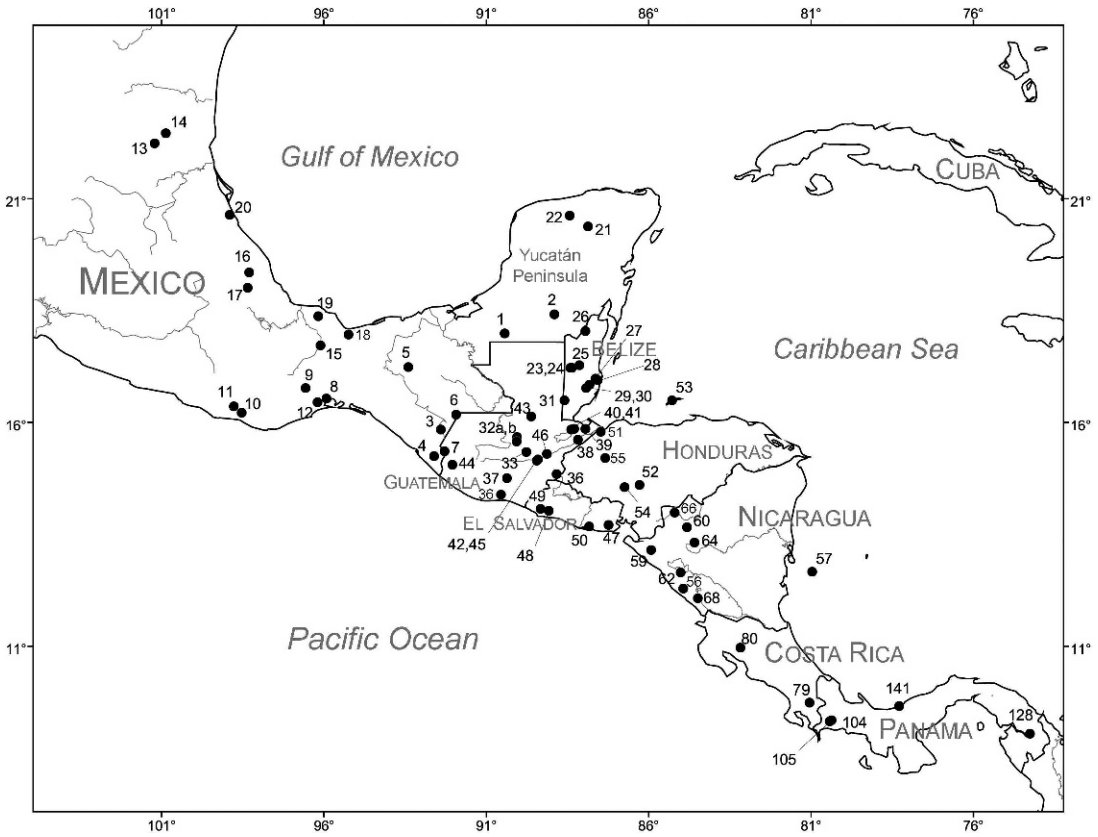
Fig. 17.   Geographic range of *Marmosa mexicana* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

Osgood (1913) described *Marmosa mayensis* based on a single specimen that he considered to represent the Yucatecan representative of *M. mexicana*. Later, Goldman (1917) described *Marmosa mexicana savannarum* based on five specimens from the Panamanian province of Chiriqui. In the same report, Goldman stated that "the continental Middle American forms now known [except for *Marmosa canescens* (= *Tlacuatzin canescens*)] may confidently be referred to a single species," thereby establishing a broad concept of *M. mexicana* that included not only *mayensis* and *savannarum*, but also *isthmica* and *zeledoni*.

Goldman's (1917) conclusions were adopted by Cabrera (1919), who listed *isthmica*, *mayensis*, *savannarum*, and *zeledoni* as subspecies of *Marmosa mexicana* in his influential checklist of marsupials. Tate (1933), however, recognized only *M. mexicana*

mayensis and *M. m. zeledoni* as valid subspecies, treating *savannarum* as synonym of *zeledoni*, and recognizing *M. isthmica* as a valid species. In Tate's classification, *M. mexicana* was referred to the monotypic Mexicana Section of the genus, whereas *M. isthmica* was referred to the Mitis Section. Tate's (1933) opinions about the validity of subspecific taxa in his Mexicana Section were accepted by Hershkovitz (1951), Hall (1981), and most subsequent authors.

REMARKS: Osgood (1913) described *mayensis* as paler than *mexicana*, and Tate (1933) used this character to maintain these taxa as valid subspecies. However, our examination of the holotypes of *mayensis* (FMNH 19994) and *mexicana* (USNM 71526) revealed no conspicuous differences in pelage color that could serve as an unambiguous basis for taxonomic diagnosis. Although the holotype skull of *mayensis* is damaged (with only

the rostral, palatal, and interorbital regions intact), the absence of any noteworthy qualitative or morphometric differences with the holotype skull of *mexicana* also support our opinion that *mayensis* and *mexicana* are conspecific.

Goldman (1917) described *savannarum* as smaller and paler than other Panamanian mouse opossums that he identified as "*M. mexicana zeledoni*" (= *M. zeledoni*) and "*M. m. isthmica*" (= *M. isthmica*). In fact, the differences in size and pelage color that he observed are marked, and they can be partially attributed to the specific status of the specimens he examined (*M. zeledoni* and *M. isthmica* are, indeed, larger and darker than *M. mexicana*). However, the holotype of *savannarum* (AMNH 18915) is a subadult with an incompletely erupted M4 (as noted by Tate, 1933), so its dimensions are not those of a fully mature individual. Our examination of the holotypes of *savannarum* and *mexicana* revealed no conspicuous differences other than the overall darker fur and broader gray-based lateral zones of ventral fur in the former specimen. Neither of these pelage differences exceeds the range of variation among other specimens that we refer to *M. mexicana*, however, and in the absence of qualitative osteological differences, we conclude that Goldman's and Merriam's taxa are conspecific.

Marmosa ruatanica was described by Goldman (1911) based on a single specimen (USNM 7785/37700 [skin/skull cataloged separately]) from Isla de Roatán, Honduras (locality 53). Tate (1933) also recognized *ruatanica* as a distinct species that included *isthmica* and *mimetra* as valid subspecies; these three nominal taxa were associated by virtue of their large size, well-developed postorbital processes, proportionately small alisphenoid tympanic processes, and minute or absent palatine fenestrae. By contrast, Hershkovitz (1951) considered *ruatanica* to be a subspecies of *M. mitis*, and *ruatanica* is currently regarded as a valid subspecies of *M. robinsoni* (e.g., by Hall, 1981; Gardner, 2005).

The large size of the holotype skull (fig. 18) is the principal characteristic that impelled several authors to compare *ruatanica* with the Trinidadian nominal taxon *chapmani* (= *M. robinsoni*) or to associate it

with *M. isthmica* (including *mimetra*). However, the type of *ruatanica* closely resembles *M. mexicana* in several qualitative traits, including the posterior extension of its dark facial mask (which contacts the base of the ear), by its medial carpal tubercle (which is long and unsegmented), and by the modest development of its temporal ridges (which tend to be much more strongly developed in other species). In fact, craniodental measurements of the holotype, an old adult male, are not much larger than other like-aged specimens of *M. mexicana*, some of which exhibit comparably developed postorbital processes and have small irregular holes in place of better-defined palatine fenestrae. Although additional material from Roatan Island (from which only the type is currently known) would be welcome, we are not convinced either that *ruatanica* is a distinct taxon or that its relationships are with geographically distant forms of mouse opossums. Instead, we provisionally regard it as an insular form of the adjacent mainland species.

SPECIMENS EXAMINED ($N = 131$): Without locality data (FMNH 34898, FMNH 49927; ROM 99608). **MEXICO—*Campeche***, 44 km S Constitución (ROM 95795), Xpujil (ROM 96090). ***Chiapas***, Chicharras (USNM 77680), Huehuetan (USNM 77681, 77682), Rayón (MVZ 159445, 159446), San José (MVZ 113483), Volcán Tacaná (MVZ 155505, 155506). ***Oaxaca***, Juchitán (AMNH 189209), Lachiguirí (AMNH 213754), San Gabriel Mixtepec (AMNH 189483–189485), Santa Catarina Juquila (= Juquila: USNM 71526 [holotype of *Marmosa murina mexicana* Merriam, 1897]), Tehuantepec (MVZ 149102–149107). ***San Luis Potosí***, El Salto Falls (USNM 329396). ***Tamaulipas***, Aserradero del Infernillo (AMNH 166059). ***Veracruz***, Achotal de Moreno (FMNH 13805, 13806), Jalapa Enríquez (BMNH 97.9.9.82, 97.9.9.83; AMNH 12453–12456/10762–10765), Mirador (USNM 62217–62219, 583340, A22019), Paso Nuevo (AMNH 17135, 17136), San Andrés Tuxtla (BMNH 7.1.1.186), Tuxpan de Rodríguez Cano (= Tuxpan: USNM 10719). ***Yucatán***, Chichén Itzá (AMNH 91192), Izamal (FMNH 19994 [holotype of *Marmosa mayensis* Osgood, 1913]). **BELIZE—*Cayo***, Central Farm (BMNH 64.2028, 64.2029, 65.3870; FMNH 106525; USNM

Fig. 18.   Dorsal and ventral cranial views of the holotype of *Marmosa ruatanica* (= *M. mexicana*, USNM 37700). Scale bar = 10 mm.

360468, 360469), Georgeville (BMNH 65.3866–69, 65.3873–65.3879, 66.2329–66. 2332), Roaring Creek (BMNH 63.626, 65.3871). ***Orange Walk***, Yo Creek (BMNH 65.3872). ***Stann Creek***, Bokowina Hill (= Bokowina: BMNH 84.369; FMNH 63887, 63888), Cockscomb Basin Wildlife Sanctuary (USNM 583001), Silk Grass (FMNH 63891). ***Toledo***, Double Fall (BMNH 84.370), Union Camp (USNM 583214, 583215). **GUATE-MALA**—no other locality data (AMNH 14248). ***Alta Verapaz***, Cobán (BMNH 75.2.27.15; FMNH 42040–42042), La Prima-vera (AMNH 79250). ***Baja Verapaz***, Chilascó (AMNH 14377), San Jerónimo (BMNH 65.5.18.67). ***Chiquimula***, Esquipulas (USNM 564594). ***Esquintla***, San Jose (USNM 275673). ***Guatemala***, Lago de Amatitlán (USNM 275672). ***Izabal***, Bobos (FMNH 41578, 41677), Escobas (FMNH 41577), La Esmer-alda (USNM 564588), Río Frío (USNM 564589). ***Progreso***, 5 km E San Cristóbal Acasaguastlán (ROM 99776), Puerta de Golpe (USNM 564591). ***San Marcos***, Nuevo Pro-greso (USNM 564592, 564593). ***Zacapa***, Ca-bañas (AMNH 265851), Río Hondo (= Finca El Chahuite: USNM 564590). **EL SALVA-DOR—*San Miguel***, Laguna Olomega (MVZ 98165). ***Sonsonate***, Chilata (= Hacienda Chi-lata: MVZ 98164, 130251), Sonsonate (AMNH 243700). ***Usulatán***, Puerto El Triunfo (MVZ 130252, 130253). **HONDURAS**—Department unknown (received in banana shipment: FMNH 43309). ***Cortés***, Catacombas (AMNH 123290). ***Francisco Morazán***, Monte Vásquez (= Cerro Vásquez: USNM 257078). ***Islas de la Bahía***, Isla de Roatán (= Ruatán Island: USNM 7785/37700 [holotype of *Marmosa ruatanica* Goldman, 1911]). ***La Paz***, Humuya (AMNH 126588–126590). **NICARAGUA—*Atlántico Sur***, Isla del Maíz Grande (= Great Corn Island: FMNH 34072, 34073). ***Chinan-dega***, Volcán San Cristóbal (= Volcán de Chinandega: AMNH 28314). ***Jinotega***, Río
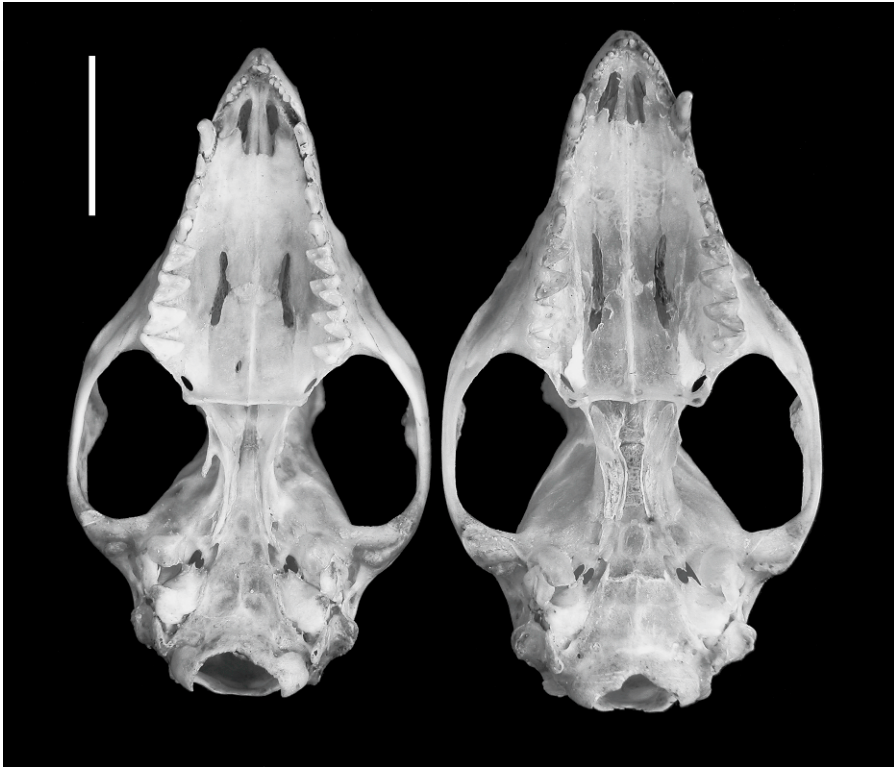
Fig. 19.   Dorsal cranial views of mature adult male *Marmosa zeledoni* (left, USNM 315005) and *Marmosa isthmica* (right, USNM 575395). Scale bar = 10 mm. Atypically, postorbital processes are present on this specimen of *M. zeledoni*; in most other examined conspecific specimens, postorbital processes are indistinct or absent.

Coco (AMNH 29270). ***Managua***, Managua (USNM 337503). ***Matagalpa***, Matagalpa (AMNH 29269). ***Nueva Segovia***, Ocotal (AMNH 28506). ***Rivas***, San Emilio (BMNH 97.4.7.12). ***Santa Barbara***, San Jose de Santa Barbara (AMNH 123291). **COSTA RICA—*Puntarenas***, Finca Helechales (USNM 547996, 548001, 548002), Monteverde (FMNH 126076). **PANAMA—*Chiriquí***, Bugaba (= Bogava: BMNH 0.7.11.90; USNM 248344), Boquerón (AMNH 18914, 18915 [holotype of *Marmosa mexicana savannarum* Goldman, 1917]). ***Darién***, Yaviza (MVZ 135833).

OTHER SPECIMENS: In addition to material positively identifiable as *Marmosa mexicana*, we examined five specimens that we provisionally refer to this species. Three are very young specimens preserved in fluid (USNM 297454–297456; from Diriamba [locality 58], Nicaragua), and two are skins unaccompanied by skulls (BM 94.11.1.7,

94.11.1.8; from Volcán San Cristóbal [locality 59], Nicaragua). Although the latter specimens exhibit some *mexicana*–like external traits (e.g., a dark circumocular mask extending to the base of the ear; long and unsegmented medial carpal tubercle), they seem to have shorter tails and yellower fur than is usual in the species.

Marmosa zeledoni Goldman, 1911
Figures 19, 20

?*Didelphys murina*: Alston, 1880: 200. Part, not *Didelphis murina* Linnaeus, 1758.

?*Didelphys* [(*Micoureus*)] *murina*: Thomas, 1888: 343. Part, not *Didelphis murina* Linnaeus, 1758.

Didelphys (*Micoureus*) *murina*: Allen, 1891: 218. Name combination.

?*Didelphis* (*Micoureus*) *murina*: Allen, 1893: 240.

?*Marmosa murina*: Thomas, 1895: 58. Name combination.

?*Marmosa murina*: Allen, 1897: 44.

Fig. 20. Ventral cranial views of mature adult male *Marmosa zeledoni* (left, USNM 315005) and *Marmosa isthmica* (right, USNM 575395). Scale bar = 10 mm.

Marmosa mexicana: Bangs, 1902: 19. Part, not *Marmosa murina mexicana* Merriam, 1897.

?*Marmosa murina*: Allen, 1908: 648.

Marmosa murina: Allen, 1910: 92. Part, not *Didelphis murina* Linnaeus, 1758.

Marmosa zeledoni Goldman, 1911: 238. Type locality "Navarro, Costa Rica."

?*Marmosa murina zeledoni*: Allen, 1912: 73. Part; name combination.

[*Didelphis* (*Marmosa*)] *zeledoni*: Matschie, 1916: 270. Name combination.

Marmosa zeledoni: Elliot, 1917: 2.

Marmosa mexicana zeledoni: Goldman, 1917: 108. Name combination.

[*Marmosa* (*Marmosa*)] *mexicana zeledoni*: Cabrera, 1919: 37.

Marmosa mexicana zeledoni: Tate, 1933: 135.

Marmosa mexicana zeledoni: Hall, 1981: 16. Part.

Marmosa mexicana: Honacki et al., 1982: 22. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Eisenberg, 1989: 37. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Alonso-Mejía and Medellín, 1992: 1. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Gardner, 1993: 18. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Emmons, 1997: 26. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Reid, 1997: 47. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Nowak, 1999: 21. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa mexicana: Voss and Jansa, 2003: 75. Part, not *Marmosa murina mexicana* Merriam, 1897.

Marmosa robinsoni: Voss and Jansa, 2003: 75. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa mexicana: Brown, 2004: 59. Part, not *Marmosa murina mexicana* Merriam, 1897.

[*Marmosa mexicana*] *savannarum*: Gardner, 2005: 9. Part, not *Marmosa mexicana savannarum* Goldman, 1917.

TYPE MATERIAL: The holotype (by original designation, USNM 12885) is a young adult (age class 6) male specimen prepared as a skin and skull; the skin is in good condition (except for a naked area on the left side), but the skull is partially damaged (missing the tips of both nasals, lacking most of the

basicranium, and with a loose supraoccipital).

TYPE LOCALITY: The holotype was collected by J. Cooper on 1 March 1878 at Navarro (gazetteer entry 71; appendix), ''[a] small village about 5 miles [8 km] south of Cartago on the Caribbean slopes of the Cordillera Central'' in Cartago province, Costa Rica (Goodwin, 1946: 456).

MORPHOLOGICAL DIAGNOSIS: Midrostral fur usually not contrasting sharply in color with fur of crown; dark median rostral stripe absent or inconspicuous; dark facial mask usually not extending posteriorly to contact base of ear; dorsal body pelage usually dull, dark, reddish brown; dorsal cover hairs 8–10 mm in length, guard hairs 10–12 mm; gray-based ventral pelage (covering the sides of chest, abdomen, and upper inguinal region, sometimes extending to the sides of neck, rarely to the inner parts of arms and legs) with reddish or brownish hair tips; self-colored ventral pelage (extending as a continuous median stripe of variable width from chin to anus) yellowish or orangish. Tail dark brown (indistinctly paler ventrally in some individuals), without any consistent pattern of scale arrangement (both spiral and annular patterns coexisting); 16–18 scales/cm on dorsal surface at caudal midlength; caudal scale hairs dark brown, usually detectable without magnification; central hair of each caudal-scale triplet as long as 1.5 scales (sometimes two scales) long. Gular gland present. Mammae 4–1–4 = 9 or 5–1–5 = 11. Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle long (reaching the base of the pollex), with subequal but recognizable proximal and distal segments divided by a shallow sulcus.

Length of rostral process of premaxillae similar to I1 height. Orbitosphenoid-alisphenoid suture approximately twice as long as height of sphenorbital fissure in lateral view. Supraorbital ridges subparallel, slender, and dorsally reflected; postorbital processes usually indistinct or absent; temporal ridges subparallel, never strongly convergent posteriorly. Palatine fenestrae absent (but tiny asymmetrical palatal perforations are sometimes present); posterolateral palatal foramina usually shorter than M4 (measured across paracone-metacone). Tympanic wing of alisphenoid laterally compressed, with ventral surface moderately pointed or bluntly keeled; medial process of ectotympanic usually indistinct or absent. I1 hypsodont, normally present in adults; crown of I2 sharply defined in relation to root; C1 without accessory cusps; preparacrista connected to stylar cusp B on M1–M3; stylar cusps D and E confluent, not separated by a distinct notch on M2.

COMPARISONS: Qualitative and morphometric comparisons between *Marmosa zeledoni* and *M. mexicana* were provided in the preceding account. In Central America, *M. zeledoni* overlaps geographically with two other congeners, *M. isthmica* and *M. robinsoni*, and it also co-occurs with the former species in western Colombia.

Marmosa zeledoni and *M. isthmica* overlap broadly in all measured dimensions (tables 4–7), and they are also externally similar in qualitative characters. On average, however, *M. isthmica* is the larger species, a difference that is best appreciated when size comparisons are made between specimens of the same age and sex, and there are subtle but diagnostically useful differences in some skin characters. In side-by-side comparisons, the midrostral fur of *zeledoni* is usually darker and contrasts less abruptly in coloration with the fur of the crown than in *isthmica* (which usually has much paler midrostral than coronal fur), and there is sometimes an indistinct posterior extension of the dark circumocular mask to the base of the ear in *zeledoni* that is not seen in *isthmica*. Although the body pelage is similarly pigmented in both forms, the dorsal fur of *zeledoni* is often a darker and duller hue of reddish brown than the somewhat brighter, orangish brown of *isthmica*. Additionally, the exposed skin of the tail is usually dark grayish brown above and below in *zeledoni*, whereas the tail is a lighter shade of brown and is often indistinctly paler below in *isthmica*. In dorsal cranial view, the supraorbital ridges of *zeledoni* are subparallel, slender, do not project laterally over the orbital fossae, and seldom form distinct postorbital processes; behind the orbits, the temporal ridges maintain this subparallel configuration onto the braincase. By contrast, the supraorbital ridges of *isthmica* are thicker and diverge more strongly posteriorly as they project

laterally over the orbital fossae; postorbital processes are usually well developed in mature adult male specimens, which have correspondingly better-defined postorbital constrictions, and whose temporal ridges often converge posteriorly on the braincase. In ventral cranial view, the posterolateral palatal foramina are usually smaller in *zeledoni* than they are in *isthmica*.

Marmosa zeledoni overlaps broadly in measured external dimensions with *M. robinsoni*, although it has visibly smaller ears. In side-by-side comparisons of skins, the midrostral fur color exhibits consistently less contrast with the color of the coronal fur in *zeledoni* than in *robinsoni*, and the dorsal body pelage of *zeledoni* is consistently redder than that of *robinsoni* (whose dorsal fur is usually some shade of yellowish or grayish brown). Whereas the medial carpal tubercles of mature adult male specimens of *zeledoni* are divided by a shallow sulcus into subequal and morphologically similar proximal and distal segments, the medial carpal tubercles of like-aged male *robinsoni* consist of a globular proximal segment and a comma-shaped distal segment. Under low magnification, the tail appears to be more sparsely haired in *zeledoni* than in *robinsoni*, a visual effect of the shorter caudal hairs in the former species. The rostral process of the premaxillae is long (about equal to the height of I1) in *zeledoni*, but this process is much shorter (about half as long as I1 is tall) in *robinsoni*. The supraorbital ridges (described above for *zeledoni*) are thicker and project laterally to a much greater extent in *robinsoni*, which sometimes develops distinct postorbital processes and has a more pronounced postorbital contriction (POC; tables 6, 7); the temporal ridges (which are subparallel in *zeledoni*) converge posteriorly in mature adult specimens of *robinsoni*, sometimes forming a low sagittal crest. The auditory bullae, which are small and laterally compressed in *zeledoni*, are much larger and smoothly globular in *robinsoni*. A distinct notch separates stylar cusps D and E on M2 in *robinsoni*, whereas this notch is absent in *zeledoni*.

Marmosa zeledoni differs from *M. xerophila* in the same characters that distinguish it from *M. robinsoni*, except that the rostral process of the premaxillae (long in *zeledoni*) is completely absent in *xerophila*.

Marmosa zeledoni is, on average, larger in most measured external dimensions than *M. simonsi*, but it has absolutely and relatively smaller ears (tables 4, 5). In external characters, the two species differ conspicuously in dorsal fur color, which is a rich reddish brown in *M. zeledoni* versus distinctly grayish in *M. simonsi*. Whereas a continuous streak of pale self-colored fur extends from the chin to the anus in *M. zeledoni*, almost all of the ventral pelage is gray based in *M. simonsi* (only the chin and throat are self-colored). Additionally, the tail is entirely dark in *M. zeledoni*, but the distal half of the tail is whitish in *M. simonsi*. Cranial differences between these dissimilar forms include the rostral process of the premaxillae (long in *zeledoni*, short in *simonsi*), postorbital processes (indistinct or absent in *zeledoni*, consistently well developed in *simonsi*), palatine fenestrae (absent in *zeledoni*, present in *simonsi*), and a distinct notch between stylar cusps D and E on M2 (absent in *zeledoni*, present in *simonsi*).

Marmosa zeledoni is externally similar in size and coloration to the western Amazonian species *M. rubra*, from which it principally differs by lacking a dark median rostral stripe (present in *rubra*), by possessing a gular gland (absent in *rubra*), and in caudal morphology (the caudal scales of *rubra* are arranged in unambiguously spiral series and the central hair of each triplet is only about one scale long). *Marmosa zeledoni* is smaller, on average, than *M. rubra* in most craniodental dimensions (tables 6, 7), but there is broad overlap in all measurements, none of which is sufficient for identification purposes. Instead, *M. zeledoni* differs from *M. rubra* by having a preparacrista that connects to stylar cusp B (the preparacrista connects to stylar cusp A in *rubra*), and by lacking a distinct notch between stylar cusps D and E (a distinct notch is present between these cusps in *rubra*).

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: Based on positively identified specimens, *Marmosa zeledoni* occurs from northern Nicaragua (Río Coco, locality 60; fig. 21) southward through Costa Rica and Panama to southwestern Colombia (Candelilla, local-
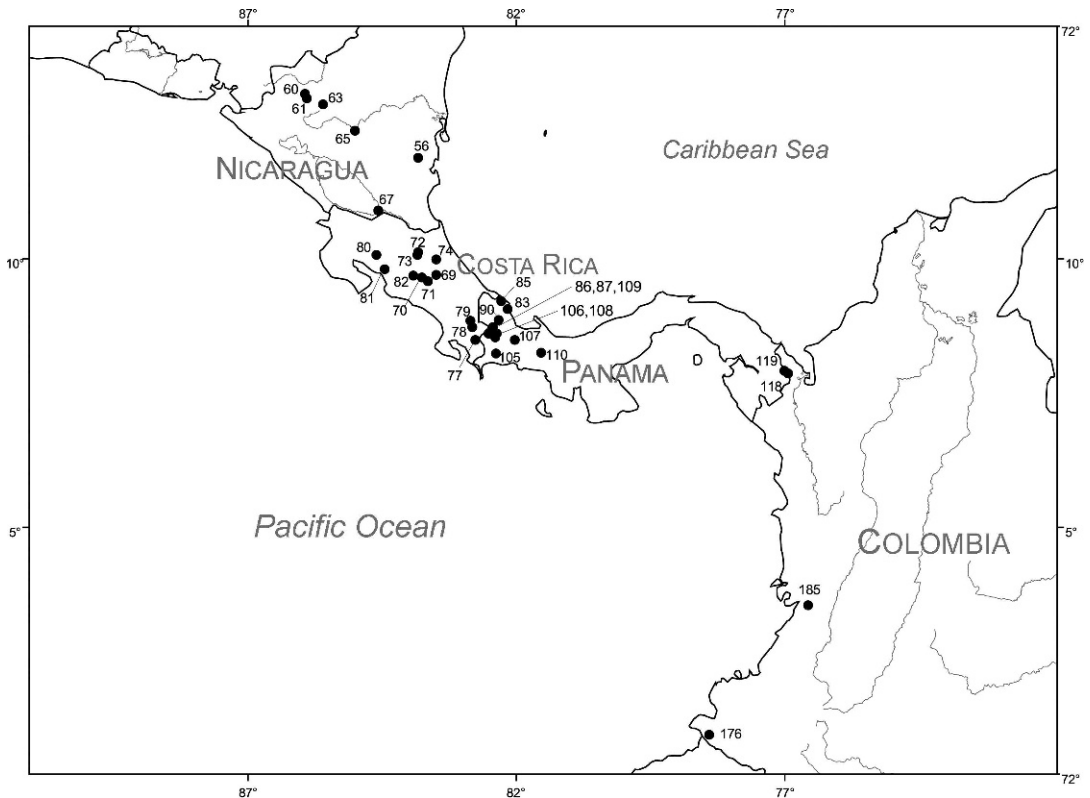
Fig. 21. Geographic range of *Marmosa zeledoni* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

ity 176). Incomplete and/or immature material that we tentatively identify as *M. zeledoni*, however, includes a skin (AMNH 46682) from Gualea (locality 218) in the Pacific foothills of western Ecuador.

Marmosa zeledoni has been collected between 100 m and 2200 m above sea level, but it is apparently more abundant in montane or submontane habitats than it is near sea level: 72% of the collecting localities for which there is altitude information are above 700 m, and 61% are above 1100 m. These upland localities are mainly in the Cordillera Central and Cordillera de Talamanca of Costa Rica, the Chiriquí highlands of western Panama, and the Serranía del Darién of eastern Panama. Vegetation maps suggest that most specimens of *Marmosa zeledoni* are associated with lowland or montane rain forests.

The range of *Marmosa zeledoni* partially overlaps that of *M. mexicana*, with which it sometimes occurs sympatrically as described

in the preceding account of that species. The range of *M. zeledoni* also overlaps the range of *M. isthmica* from western Panama to southwestern Colombia, but the two species have been collected sympatrically only at San José (locality 185) in western Colombia. The range of *M. zeledoni* additionally overlaps that of *M. robinsoni* in Panama, where the two species have been sympatrically collected at Finca Santa Clara (locality 109) and near Escopeta Camp (locality 110).

GEOGRAPHIC VARIATION: Examined specimens exhibit variation in pelage color that appears to be correlated with elevation. Thus, skins from montane habitats in Panama tend to have darker, brownish dorsal fur and darker and more broadly gray-based ventral fur (the latter extending to the inner sides of the arms and legs); in this material, the gray-based ventral fur is similar in color to the lateral body fur. By contrast, specimens from lowland habitats in Nicaragua, Costa Rica,

and Colombia tend to have redder dorsal fur and paler and more narrowly distributed gray-based ventral fur (the latter not extending to the inner side of the arms and legs); in this material, the gray-based ventral fur is substantially paler than the lateral body fur.

TAXONOMIC HISTORY: The first published reference to material that we identify as *Marmosa zeledoni* was by Allen (1891), who misidentified specimens of this mouse opossum as *Didelphys* (*Micoureus*) *murina*. Conspecific Central American material was also misidentified (as *M. murina* or *M. mexicana*) by subsequent authors, until Goldman (1911) described *M. zeledoni* based on five specimens from Navarro (Costa Rica) and Escondido River (Nicaragua). Allen (1912) treated *zeledoni* as a subspecies of *M. murina*, but Goldman (1917) allied *zeledoni* with *M. mexicana*, an opinion followed by most subsequent authors, including Tate (1933). Recent authors (e.g., Honacki et. al., 1982; Eisenberg, 1989; Alonso-Mejía and Medellín, 1992; Emmons, 1997; Reid, 1997; Nowak, 1999; Brown, 2004; Gardner, 2005) have consistently failed to recognize *zeledoni* as a valid taxon.

SPECIMENS EXAMINED (*N* = 77): **NICARAGUA**—Without other locality data (USNM 361203, 361204). *Atlántico Sur*, Escondido River (USNM 36348, 50882). *Jinotega*, Río Coco (AMNH 29271), San Rafael del Norte (AMNH 28285). *Matagalpa*, El Tuma (= Río Tuma: AMNH 29542), Vijagua (AMNH 29541). *Río San Juan*, San Carlos (= La Esperanza: USNM 361194–361202). **COSTA RICA**—*Cartago*, Aquiares (AMNH 63999), Cerro Carpintera (= La Carpintera: AMNH 3652), Navarro (USNM 12885 [holotype of *Marmosa zeledoni* Goldman, 1911]). *Heredia*, 11 km S and 4.5 km W Puerto Viejo (FMNH 128390, 128391, 128393, 128397, 128398), 11 km S and 11.5 km E San Miguel Angeles (FMNH 128400). *Limón*, Jiménez (AMNH 9593/7930). *Puntarenas*, Cerro Cañas Gordas (AMNH 142488, 142489), Coto Brus (= Costa Brus: USNM 516606), Finca Helechales (USNM 547941, 547995, 547997–548000, 548003), Monteverde (FMNH 123992), San Jerónimo (= San Geronomo: FMNH 35180). *San José*, Escazú (BMNH 3.2.1.10). **PANAMA**—*Bocas del Toro*, Almirante (USNM 315001, 315003), Changuinola (USNM 315005–3150007), E of Cerro Pando (USNM 516605), Fish Camp (USNM 520691), Río Changena Camp (USNM 319372). *Chiriquí*, Bugaba (= Bogava: BMNH 0.7.11.87–0.7.11.89, 0.7.11.91, 0.7.11.92, 3.3.3.107), Casa Tilley (USNM 314188–314190), Cerro Fortuna (= Reserva Florestal Fortuna: AMNH 269997), El Volcán (= Volcán: AMNH 147759, 147760), Finca Santa Clara (= Osta Clara: USNM 396509, 516603), Near Escopeta Camp (= 24 km NNE San Felix: USNM 541001, 541005, 541007, 541010, 541012, 541013, 541016, 541017). *Darién*, Cerro Malí (USNM 337954–337957), Cerro Tacarcuna (USNM 337958). **COLOMBIA**—*Nariño*, Candelilla (FMNH 89565). *Valle del Cauca*, San José (AMNH 31683).

OTHER SPECIMENS: In addition to material positively identifiable as *Marmosa zeledoni*, we examined 42 specimens that we provisionally refer to this species. Most of these are juveniles or subadults that have not developed all of the diagnostic traits that distinguish this species from *M. isthmica*, but a few are skins unaccompanied by skulls (e.g., AMNH 46682), and others are fluids from which skulls have yet to be extracted.

NICARAGUA—*Atlántico Sur*, Escondido River (USNM 36349). **COSTA RICA**—*Cartago*, Navarro (USNM 12884). *Heredia*, 11 km S and 4.5 km W Puerto Viejo (FMNH 128389, 128395, 128396, 128399). *Limón*, Pandora (USNM 284465). *Puntarenas*, Boruca (AMNH 11794/10063), Monteverde (FMNH 123993, 124100). **PANAMA**—*Bocas del Toro*, Almirante (USNM 315002), Boca del Drago (USNM 315004), N of El Volcán (USNM 516948). *Chiriquí*, Near Escopeta Camp (USNM 541003, 541004, 541006, 541008, 541009, 541011, 541014, 541015, 541018, 541325–541330, 541332, 541333), Finca Santa Clara (USNM 539832). **COLOMBIA**—*Cauca*, San José (AMNH 31694). **ECUADOR**—*Pichincha*, Gualea (AMNH 46682).

Marmosa isthmica Goldman, 1912
Figures 19, 20

Didelphys murina: Thomas, 1880: 403.
?*Didelphys murina*: Thomas, 1882b: 111.
?*Didelphys murina*: Alston, 1880: 200. Part, not *Didelphis murina* Linnaeus, 1758.

Didelphys [(*Micoureus*)] *murina*: Thomas, 1888: 343. Part, not *Didelphis murina* Linnaeus, 1758.

?*Marmosa murina zeledoni*: Allen, 1912: 73. Part, not *Marmosa zeledoni* Goldman, 1911.

Marmosa isthmica Goldman, 1912: 1. Type locality "Rio Indio, near Gatun, Canal Zone, Panama."

Marmosa isthmica: Anthony, 1916: 363.

[*Didelphis* (*Marmosa*)] *isthmica*: Matschie, 1916: 270. Name combination.

Marmosa isthmica: Elliot, 1917: 2.

Marmosa mexicana isthmica: Goldman, 1917: 108. Name combination.

[*Marmosa* (*Marmosa*)] *mexicana isthmica*: Cabrera, 1919: 37.

Marmosa mimetra Thomas, 1921: 521. Type locality "W. Ecuador … Santo Domingo, 0°13′S., 79°6′W. Alt. 1600′."

Marmosa ruatanica isthmica: Tate, 1933: 125. Name combination.

Marmosa ruatanica mimetra: Tate, 1933: 126. Name combination.

Marmosa mitis mimetra: Hershkovitz, 1951: 552. Name combination.

Marmosa mitis isthmica: Hershkovitz, 1951: 552. Name combination.

Marmosa [(*Marmosa*)] *robinsoni isthmica*: Cabrera, 1958: 24. Name combination.

Marmosa [(*Marmosa*)] *robinsoni mimetra*: Cabrera, 1958: 24. Name combination.

Marmosa robinsoni: Handley, 1966: 755. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni isthmica: Hall, 1981: 15.

Marmosa mexicana zeledoni: Hall, 1981: 16. Part, not *Marmosa zeledoni* Goldman, 1911.

Marmosa robinsoni: Honacki et al., 1982: 23. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: O'Connell, 1983: 1. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Eisenberg, 1989: 39. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Gardner, 1993: 18. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Reid, 1997: 48. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Emmons, 1997: 26. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Eisenberg and Redford, 1999: 62. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Nowak, 1999: 21. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Voss and Jansa, 2003: 75. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Brown, 2004: 65. Part, not *Marmosa robinsoni* Bangs, 1898.

[*Marmosa robinsoni*] *isthmica*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *simonsi*: Gardner, 2005: 9. Part, not *Marmosa simonsi* Thomas, 1899.

M[*armosa*]. *r*[*obinsoni*]. *isthmica*: Creighton and Gardner, 2008: 59.

M[*armosa*]. *r*[*obinsoni*]. *simonsi*: Creighton and Gardner, 2008: 59. Part, not *Marmosa simonsi* Thomas, 1899.

TYPE MATERIAL: The holotype (by original designation, USNM 170969) is a mature adult (age class 7) male specimen preserved as a skin and skull, both of which are in good condition.

TYPE LOCALITY: The holotype was collected by E.A. Goldman on 16 February 1911 on the Río Indio (gazetteer entry 103; appendix), a small tidal tributary of the lower Río Chagres, near the town of Gatun, Provincia Colón, Panama. According to Goldman (1912: 2), the type "was trapped in an old banana plantation only a few feet above sea level." A photograph of the type locality was subsequently published by Goldman (1920: pl. 3, fig. 1).

MORPHOLOGICAL DIAGNOSIS: Midrostral fur usually pale and contrasting sharply with darker fur of crown; dark median rostral stripe absent or inconspicuous; dark facial mask not extending posteriorly to contact base of ear; dorsal body pelage pale to dark orangish brown; dorsal cover hairs 8–12 mm in length, dorsal guard hairs 10–15 mm in length; gray-based ventral pelage conspicuous but usually restricted to the sides of the abdomen, with yellowish or orangish hair tips; self-colored ventral pelage (extending as a continuous median streak from chin to anus) yellowish or orangish. Exposed skin of tail brown, indistinctly bicolored (paler ventrally) in most large specimens, without any clear pattern of scale arrangement (both spiral and annular patterns coexisting); 16–18 scales/cm on dorsal surface at caudal midlength; caudal scale hairs light brown, usually detectable without magnification; central hair of each caudal-scale triplet usually about 1.5 (sometimes two) scales long. Gular gland present. Mammae 6–1–6 = 13 (Enders, 1935: 408). Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle long (reaching the base of the pollex), with subequal but recognizable proximal and distal segments separated by a shallow sulcus.

Length of rostral process of premaxillae similar to I1 height. Orbitosphenoid-alisphe-

noid suture usually about twice as long as height of sphenorbital fissure in lateral view. Supraorbital ridges slightly to moderately divergent posteriorly, slender and only slightly produced laterally in younger specimens and females (which usually have indistinct postorbital processes) but becoming much thicker and dorsolaterally produced in mature adult males (which usually have distinct postorbital processes); temporal ridges conspicuous and tending to become strongly convergent posteriorly (behind the postorbital constriction) in mature adult males. Palatine fenestrae absent (but tiny asymmetrical perforations are occasionally present); posterolateral foramina usually longer than M4 (measured across paracone-metacone). Tympanic wing of alisphenoid laterally compressed, with ventral surface globular or slightly pointed; medial process of ectotympanic usually indistinct or absent. I1 hypsodont, normally present in adults; crown of I2 sharply defined in relation to root; preparacrista connected to stylar cusp B on M1-M3; stylar cusps D and E confluent, not separated by a distinct notch on M2.

COMPARISONS: Qualitative and morphometric comparisons among *Marmosa isthmica*, *M. mexicana*, and *M. zeledoni*, all of which have overlapping geographic ranges, are provided in the preceding accounts. The geographic range of *M. isthmica* also overlaps with that of *M. robinsoni* in Panama, and it overlaps with that of *M. simonsi* in western Ecuador. Morphological comparisons with these and other species are provided below.

Marmosa isthmica is larger (on average) and has a relatively longer tail than *M. robinsoni*, but the two species overlap broadly in all external dimensions (tables 4, 5) and cannot be identified by measurement data alone. In side-by-side comparisons of skins, the two species are most readily distinguished by the more saturated, orangish-brown color of the dorsal pelage in *isthmica*, by contrast with the usually paler and more yellowish-brown pigmentation of the dorsal fur in *robinsoni*. Also, the tail appears more sparsely haired in *isthmica* (in which the central hair of each caudal-scale triplet is only about 1.5 scales long) than in *robinsoni* (in which the central hair is > 2 scales long). Additionally, the medial carpal tubercle of mature adult

male *isthmica* is long (reaching the base of the pollex) and divided by a shallow sulcus into subequal and morphologically similar proximal and distal segments, whereas the medial carpal tubercle of adult male *robinsoni* is either short (not reaching the base of the pollex) or (if long) consists of a bulbous proximal knob and a narrower, comma-shaped distal process.

Cranially, *Marmosa isthmica* and *M. robinsoni* differ in the length of the rostral process of the premaxillae (about equal in length to the height of I1 in *isthmica*, about half as long as I1 is tall in *robinsoni*), in the development of postorbital processes (usually distinct in large specimens of *isthmica*, usually indistinct in *robinsoni*), in the occurrence of palatine fenestrae (consistently absent in *isthmica*, consistently present in *robinsoni*), and in auditory morphology. Auditory differences between these species consist in the size and shape of the alisphenoid tympanic process, which is small, laterally compressed, and usually somewhat pointed ventrally in *isthmica* versus larger and globular (smoothly rounded ventrally) in *robinsoni*. Another auditory character is the medial process of the ectotympanic, which is indistinct or altogether absent in *isthmica*, but which is usually rather well developed in *robinsoni*.

Marmosa isthmica differs from *M. xerophila* in all the same characters by which it differs from *M. robinsoni*, but the contrast in rostral morphology is even more pronounced: the rostral process of the premaxillae (long in *isthmica*, short in *robinsoni*) is completely absent in *M. xerophila*.

Marmosa isthmica and *M. simonsi* are easily distinguished by visually obvious morphological differences. Although the two species overlap in all external dimensions (tables 4, 5), *isthmica* is much the larger species, on average, and it has a relatively longer tail than *simonsi*. In side-by-side comparisons of skins, the orangish-brown dorsal pelage of *isthmica* contrasts conspicuously with the grayish-brown fur of *simonsi*. Ventral pelage differences are also striking: there is always a continuous streak of self-colored fur that extends from chin to anus in *isthmica*, whereas almost the entire ventral surface of *simonsi* is covered by gray-based
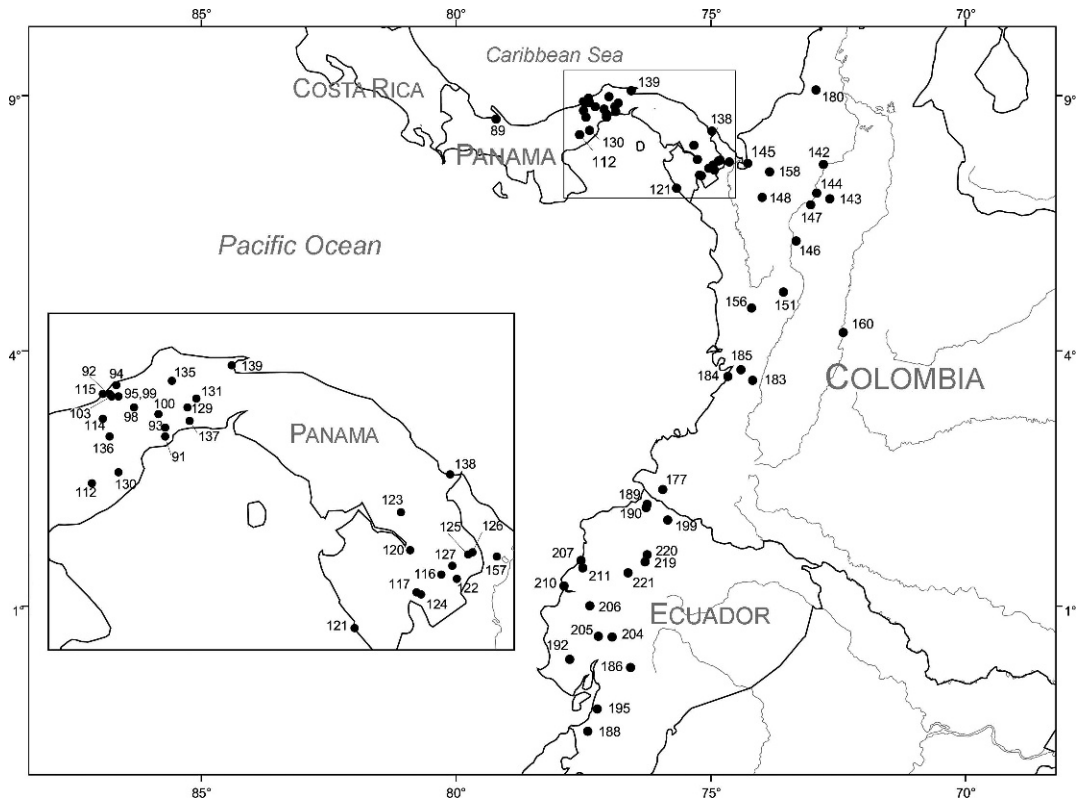
Fig. 22. Geographic range of *Marmosa isthmica* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

fur (usually only the fur of the chin, throat, and groin is self-colored). Whereas the medial carpal tubercle of adult male *isthmica* is long (reaching the base of the pollex), the medial carpal tubercle of *simonsi* is shorter and does not extend distally to the base of the pollex. The tail, which is entirely dark on its dorsal surface in *isthmica*, is completely unpigmented (whitish) distally in *simonsi*. Points of craniodental difference include the rostral process of the premaxillae (long in *isthmica*, short in *simonsi*), palatine fenestrae (absent in *isthmica*, present in *simonsi*), auditory bullae (small and compressed in *isthmica*, larger and globular in *simonsi*), and a notch between stylar cusps D and E (absent in *isthmica*, present in *simonsi*).

Marmosa isthmica is externally similar to *M. rubra*, but it usually lacks the dark midrostral streak that is usually present in *rubra*. Other external differences are apparent on close inspection: (1) the gular gland is consistently present in *isthmica* but absent in *rubra*; (2) the medial carpal tubercle of mature adult male specimens is long (extending distally to the base of the pollex) in *isthmica*, but this tubercle is much shorter and does not extend to the base of the pollex in *rubra*; (3) whereas the caudal scales of *isthmica* are arranged in both spiral and annular series, the caudal scales of *rubra* are consistently arranged in spiral series. Craniodental differences include the postorbital processes, which are often well developed in large specimens of *isthmica*, but which are absent or indistinct in all examined specimens of *rubra*; and the preparacrista of M1–M3, which is connected to stylar cusp B in *isthmica*, but which is usually connected to stylar cusp A in *rubra*.

GEOGRAPHIC DISTRIBUTION AND SYM-PATRY: The known distribution of *Marmosa isthmica* extends from Ñuri (locality 89; fig. 22) in the Panamanian province of Bocas

del Toro eastward across the isthmus and then southward along the Pacific coast of western Colombia to Santa Rosa (locality 188) in the Ecuadorean province of El Oro; *M. isthmica* also occurs in the Caribbean lowlands of northwestern Colombia, and it extends southward into the inter-Andean valleys of the Río Cauca and the Río Magdalena. Most collection localities are moist lowland and premontane forests below 1700 m elevation, but a few specimens have been collected in dry forests and mangroves, and one specimen has been recorded in the Guajira/Barranquilla Xeric Scrub of Olson et al. (2001).

The range of *Marmosa isthmica* partially overlaps the distributions of *M. mexicana* and *M. zeledoni*, with which it is known to occur sympatrically as described above. The range of *M. isthmica* also overlaps the distribution of *M. robinsoni* in Panama, where they have been collected sympatrically at Balboa (locality 91). Lastly, the range of *M. isthmica* overlaps the distribution of *M. simonsi* in western Ecuador, where the two species have been collected sympatrically at Santa Rosa (locality 188), Vinces (locality 205), and Río Briceño (locality 210).

GEOGRAPHIC VARIATION: Among the specimens we examined, geographic variation in morphological characters is apparent in pelage color and in the development of supraorbital and temporal ridges. In particular, specimens from Ecuador tend to have less developed supraorbital and temporal ridges by comparison with specimens from Colombia and Panama. Additionally, some specimens from the southern Ecuadorean provinces of Los Ríos and El Oro have intensely yellow-washed pelage in contrast to the darker orangish-brown or yellowish-brown pelage of specimens from northern Ecuador, Colombia, and Panama. As a result, every specimen with yellow-washed pelage has delicate supraorbital and temporal ridges, but not all specimens with delicate supraorbital and temporal ridges have yellowish fur. Neither of the cranial nor coat-color phenotypes we observed appears to be consistently associated with any of the several ecoregions (Olson et al., 2001) in which the species has been collected. Because coat color and cranial ornamentation are only partially

correlated, and in the absence of other phenotypic evidence of genetic divergence, we provisionally consider *M. isthmica* to be a monotypic species.

TAXONOMIC HISTORY: The first literature reference to a specimen of *Marmosa isthmica* is in Thomas (1880), who identified his material as *Didelphys murina*. Other specimens were subsequently identified by authors as either *murina* or *zeledoni* (e.g., by Alston, 1880; Thomas, 1882b, 1888; Allen, 1912). Shortly after Goldman (1912) described *Marmosa isthmica* based on a single specimen from the Canal Zone of central Panama, Anthony (1916) reported a large series from the eastern Panamanian province of Darién. Just one year later, however, Goldman (1917) treated *isthmica* as a subspecies of *M. mexicana*, as did Cabrera (1919).

In his monographic revision of *Marmosa*, Tate (1933) treated *isthmica* as a subspecies of *M. ruatanica* (a member of his Mitis Section, which also included *M. chapmani*, *M. mitis*, and *M. simonsi* as valid species). Hershkovitz (1951), however, regarded all of the nominal taxa in Tate's Mitis Section as conspecific, listing *M. mitis ruatanica* and *M. mitis isthmica* as separate subspecies. Cabrera (1958) accepted Hershkovitz's taxonomic conclusions, but he correctly pointed out that *robinsoni* was the oldest available name in Tate's Mitis Section, and he listed *M. robinsoni isthmica* as one of several valid South American forms. Most subsequent authors (e.g., Honacki et al., 1982; O'Connell, 1983; Eisenberg, 1989; Emmons, 1997; Nowak, 1999; Brown, 2004) have effectively treated *M. robinsoni* as monotypic, but Gardner (2005) listed *M. r. isthmica* as a valid subspecies.

REMARKS: Thomas (1921) described *Marmosa mimetra* based on four specimens from "Santo Domingo" (= Santo Domingo de los Colorados, Ecuador; locality 221). Although his description of *mimetra* strikingly resembles Goldman's description of *isthmica*, Thomas considered *mimetra* to be most similar to Allen's *chapmani* from Trinidad. Apparently, Tate (1933: 126) was the first to recognize the essential similarity between *isthmica* and *mimetra*—both of which he treated as subspecies of *M. ruatanica*— remarking that they are separable "only in

certain cases by the stronger cinnamon color of the ventral pelage and the smoother, more shiny tail scales of the latter'' and adding that "[s]pecimens from southwestern Colombia are probably transitional.'' Curiously, however, *mimetra* was recently included in the synonymy of *simonsi* by Gardner (2005) and Creighton and Gardner (2008).

We examined the holotypes of *isthmica* and *mimetra*, both of which are mature adult males. These specimens are remarkably similar in external and craniodental morphology, except for the slightly more yellow-washed fur of *mimetra*. Because the pelage color difference is not accompanied by other evidence of genetic divergence, we treat *mimetra* as a junior synonym of *isthmica*.

SPECIMENS EXAMINED (*N* = 408): **PANAMA—*Bocas del Toro***, Ñuri (USNM 575395, 575397–575400). ***Canal Zone***, Balboa (USNM 456810, 456811, 456816, 456819, 456823, 456824, 456827–456832, 456834–456841), Camp Piña (USNM 301377, 301378, 301546, 302631, 302635, 302636, 303048, 304634, 304636), Chiva Chiva (USNM 302326), Cristóbal (USNM 456842–456847, 456849–456866), Fort Davis (USNM 297874, 303044), Frijoles (USNM 503421), Gatún (AMNH 36724–36730), Madden Road (USNM 300331–300334, 301135–301140), Río Indio (USNM 170969 [holotype of *Marmosa isthmica* Goldman, 1912]). ***Coclé***, no other locality data (USNM 303407), El Valle (USNM 304710–304714). ***Colón***, Cuipo Point (= La Uyama: FMNH 124153), Piña (USNM 318315). ***Darién***, Boca de Río Paya (= Mouth of Río Paya: USNM 306406–306422; = Camp Mack: USNM 314553), Cana (FMNH 53996, 53997; USNM 178614–178616, 178620, 178703–178707, 178711, 178712, 178971), El Real (AMNH 37576–37579), Jaqué (= Junction of Ríos Jaque and Imamado: USNM 362318–362327), Paya Camp (USNM 314554, 314555), Río Chucunaque (USNM 306404, 306405), Río Setegantí (USNM 318120–318123), Tacarcuna Laguna Camp (USNM 309319–309327), Tacarcuna Village (USNM 309268–309318, 309328, 309329; = Mt. Tacarcuna: AMNH 37859; = Near G.M.L. Camp: USNM 512870, 512871; = Tacarcuna: AMNH 37859–37871, 37873, 37875–37888, 37891–37893), Tapalisa (AMNH 37889, 37890). ***Panamá***, Cerro Azul (USNM 302414–302416, 302418–302423, 302425–302428, 302630, 302632–302634, 302637, 302638, 303043, 303045–303047, 303050, 303052–303057, 303232, 303279, 303280, 304637, 306387–306392, 306397–306403, 314552), Cerro Campana (USNM 303406), Cerro Jefe (USNM 306393–306396), Río Pequeni (USNM 318336), Río Trinidad (AMNH 36731, 36732), Tocumen (USNM 304635). ***San Blas***, Armila (= Quebrada Venado: USNM 335031–335038), Mandinga (USNM 305147–305153). **COLOMBIA—*Antioquia***, Caucasia (USNM 499263), La Tirana (= 25 km S and 22 km W Zaragoza: USNM 499256–499262), Purí (FMNH 69858, 69859), Río Currulao (FMNH 69856, 69857), San Jerónimo (FMNH 69829–69832, 69836, 69852), Valdivia (= Quebrada Valdivia: FMNH 69828, 69851, 69861, 69862; = Quebrada de Oro: FMNH 69860), Villa Arteaga (FMNH 69833–69835, 69839, 69840, 69853, 69854). ***Caldas***, Samaná (FMNH 70978). ***Chocó***, Condoto (BMNH 13.8.10.15, 13.8.10.16, 14.5.28.29), Unguía (FMNH 69841–69848, 69855). ***Córdoba***, Socorré (FMNH 69316–69318). ***Cundinamarca***, W of Bogotá (BMNH 95.8.1.34). ***Nariño***, Guayacana (USNM 309046). ***Sucre***, Colosó (= Las Campañas: FMNH 69319). ***Valle del Cauca***, Lomitas (AMNH 32177), San José (AMNH 31682, 31718), Río Raposo (USNM 334679–334685). **ECUADOR**—No other locality data (BMNH 59.11.28.4). ***Chimborazo***, Puente de Chimbo (AMNH 62124, 62125). ***El Oro***, Santa Rosa (AMNH 61392). ***Esmeraldas***, Corondelet (= Carondelet: BMNH 1.6.5.20), San Javier (BMNH 1.3.19.48, 1.3.19.49; USNM 113319). ***Guayas***, Cerros de Colonche (= Cerro de Manglaralto: AMNH 64524), Huerta Negra (USNM 534287). ***Imbabura***, Hacienda Paramba (BMNH 1.6.5.19, 99.12.5.11, 99.12.5.12). ***Los Ríos***, Lima Pareja (USNM 534289), Vinces (= Near Puerto Nuevo: AMNH 63347–63349; USNM 534288, 534290). ***Manabí***, Cordillera de Balzar (= Balzar Mts: BMNH 80.5.6.89), Cuaque (= Coaque: AMNH 64534; FMNH 41248), Río Briceño (= Bahia de Caraquéz: AMNH 64527–64529), San José (FMNH 53354, 53355). ***Pichincha***, Mindo (BMNH 74.779, 13.10.24.67–13.10.24.69), Nanegal (BMNH 98.5.1.20), Santo Domingo de Los Colorados

Fig. 23.   Dorsal cranial views of mature adult male *Marmosa robinsoni* (left, USNM 443895) and *Marmosa xerophila* (right, USNM 443837). Scale bar = 10 mm.

(BMNH 15.1.1.53, 15.1.1.54 [holotype of *Marmosa mimetra* Thomas, 1921], 15.1.1.55, 15.1.1.57, 15.1.1.59, 15.1.1.60).

OTHER SPECIMENS: In addition to specimens positively identified as *Marmosa isthmica*, we examined 11 juvenile specimens that we provisionally refer to *M. isthmica* because they have not developed all of the diagnostic traits that distinguish this species from *M. zeledoni*.

PANAMA—*Canal Zone*, Camp Piña (USNM 301642, 301643, 304631), Fort Sherman (USNM 296190). *Coclé*, El Valle (USNM 304695). *Panamá*, Cerro Azul (USNM 302413, 302417, 302424, 303231, 304632), Tocumen (USNM 304630).

Marmosa robinsoni Bangs, 1898
Figures 23, 24

? *Didelphys murina*: Alston, 1880: 200. Part, not *Didelphis murina* Linnaeus, 1758.

Didelphis (*Micoureus*) *murina*: Allen and Chapman, 1893: 230. Name combination.

Marmosa murina: Thomas, 1896: 314. Name combination.

Marmosa murina: Allen and Chapman, 1897: 27.

Marmosa robinsoni Bangs, 1898a: 95. Type locality "Margarita Island, Venezuela."

Marmosa mitis Bangs, 1898b: 162. Type locality "Pueblo Viejo, Colombia, 8000 ft."

Marmosa chapmani Allen, 1900: 197. Type locality "Caura, Trinidad."

Marmosa fulviventer Bangs, 1901: 632. Type locality "San Miguel Island[, Panama]."

Marmosa mitis: Allen, 1904a: 337.

Marmosa mitis: Allen, 1904b: 417.

[*Marmosa*] *fulviventer*: Elliot, 1904: 5.

Marmosa fulviventer: Elliot, 1905: 3.

Marmosa grenadae Thomas, 1911: 514. Type locality "Annandale[, Island of Grenada, West Indies]."

Marmosa nesaea Thomas, 1911: 515. Type locality "Caparo[, Trinidad]."

Marmosa mitis casta Thomas, 1911: 516. Type locality "San Esteban, Carabobo, N. Venezuela."

Fig. 24. Ventral cranial views of mature adult male *Marmosa robinsoni* (left, USNM 443895) and *Marmosa xerophila* (right, USNM 443837). Scale bar = 10 mm.

Marmosa chapmani: Allen, 1911a: 194.

Marmosa mitis costa: Allen, 1911b: 245. Incorrect subsequent spelling of *Marmosa mitis casta* Thomas, 1911.

Marmosa mitis casta: Allen, 1911b: 246.

Marmosa mitis pallidiventris Osgood, 1912: 39. Type locality ''El Guayabal, 10 miles N. of Cucuta, Colombia.''

[*Marmosa*] *mitis*: Cabrera, 1913: 12.

[*Didelphis* (*Marmosa*)] *fulviventer*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *chapmanni*: Matschie, 1916: 270. Incorrect subsequent spelling of *Marmosa chapmani* Allen, 1900; name combination.

[*Didelphis* (*Marmosa*)] *grenadae*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *robinsoni*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *casta*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *pallidiventris*: Matschie, 1916: 270. Name combination.

[*Didelphis* (*Marmosa*)] *mitis*: Matschie, 1916: 270. Name combination.

[*Marmosa* (*Marmosa*)] *chapmani*: Cabrera, 1919: 36.

[*Marmosa* (*Marmosa*)] *fulviventer*: Cabrera, 1919: 36.

[*Marmosa* (*Marmosa*)] *mitis casta*: Cabrera, 1919: 38.

[*Marmosa* (*Marmosa*)] *mitis mitis*: Cabrera, 1919: 38.

[*Marmosa* (*Marmosa*)] *mitis pullidiventris*: Cabrera, 1919: 38. Incorrect subsequent spelling of *Marmosa mitis pallidiventris* Osgood, 1912.

[*Marmosa* (*Marmosa*)] *robinsoni*: Cabrera, 1919: 39.

Marmosa mitis mitis: Tate, 1933: 115.

Marmosa mitis casta: Tate, 1933: 116.

Marmosa mitis fulviventer: Tate, 1933: 117. Name combination.

Marmosa mitis robinsoni: Tate, 1933: 118. Name combination.

Marmosa chapmani: Tate, 1933: 119.

Marmosa mitis chapmani: Hershkovitz, 1951: 552. Name combination.

Marmosa [(*Marmosa*)] *robinsoni robinsoni*: Cabrera, 1958: 24. Name combination.

Marmosa mitis chapmani: Goodwin, 1961: 4.

Marmosa mitis luridavolta Goodwin, 1961: 5. Type locality ''Speyside, Tobago, the West Indies.''

Marmosa mitis grenadae: Goodwin, 1961: 8. Name combination.

Marmosa robinsoni robinsoni: Musso, 1962: 165.

Marmosa robinsoni: Handley, 1966: 755. Part.

Marmosa robinsoni: Handley, 1976: 7.

Marmosa robinsoni: Handley and Gordon, 1979: 68.

Marmosa robinsoni fulviventer: Hall, 1981: 14. Name combination.

Marmosa robinsoni grenadae: Hall, 1981: 14. Name combination.

Marmosa robinsoni: Honacki et al., 1982: 23. Part.

Marmosa robinsoni: O'Connell, 1983: 1. Part.

Marmosa robinsoni: Pérez-Hernández, 1985: 61.

Marmosa robinsoni robinsoni: Pérez-Hernández, 1989: 368.

Marmosa robinsoni: Eisenberg, 1989: 39. Part.

Marmosa robinsoni: Gardner, 1993: 18. Part.

Marmosa (Marmosa) robinsoni: Pérez-Hernández et al., 1994: 40.

Marmosa robinsoni: Reid, 1997: 48. Part.

Marmosa robinsoni: Emmons, 1997: 26. Part.

Marmosa robinsoni: Linares, 1998: 61.

Marmosa robinsoni: Nowak, 1999: 21. Part.

Marmosa robinsoni: López-Fuster et al., 2000: 829.

Marmosa robinsoni: Brown, 2004: 65. Part.

[*Marmosa robinsoni*] *chapmani*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *fulviventer*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *grenadae*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *luridavolta*: Gardner, 2005: 9.

[*Marmosa robinsoni*] *robinsoni*: Gardner, 2005: 9.

M[armosa]. r.[obinsoni]. chapmani: Creighton and Gardner, 2008: 59.

M[armosa]. r[obinsoni]. luridavolta: Creighton and Gardner, 2008: 59.

M[armosa]. r[obinsoni]. robinsoni: Creighton and Gardner, 2008: 59.

TYPE MATERIAL: The holotype (by original designation, MCZ B7749) is a mature adult (age class 8) male preserved as a skin and skull; although the skull lacks both ectotympanics, the specimen is otherwise in good condition.

TYPE LOCALITY: The holotype was collected by U.S. Army Lieutenant Wirt Robinson on 12 July 1895 on Isla Margarita, a large (ca. 1000 km^2) Caribbean island comprising the Venezuelan state of Nueva Esparta. Although the published type locality (''Margarita Island'') is imprecise, Robinson's published itinerary (Robinson and Richmond, 1896) states that he spent the week from 8 to14 July 1895 at El Valle de Espíritu Santo (10°59′N, 63°52′W, ca. 200 m above sea level; Paynter, 1982) on the lower slopes of Cerro Copey a few kilometers inland from Porlamar (10°57′N, 63°51′W) on the arid southeastern coast.

MORPHOLOGICAL DIAGNOSIS: Midrostral fur pale, usually contrasting sharply with darker fur of crown; dark median rostral stripe usually absent (an indistinct marking is occasionally present); dark facial mask usually not extending posteriorly to contact base of ear; dorsal body pelage variable but usually some shade of yellowish or grayish brown; dorsal cover hairs 8–11 mm in length, guard hairs 10–14 mm; gray-based ventral pelage conspicuous or not, usually restricted to sides of abdomen (but sometimes extending to the sides of lower chest, rarely to the inner parts of arms and legs), with yellowish hair tips; self-colored ventral pelage (extending as a continuous median strip of variable width from chin to anus) dark or light yellowish buff. Exposed skin of tail dark brown to yellowish brown, indistinctly bicolored (paler ventrally), without any consistent pattern of scale arrangement (both spiral and annular patterns coexisting); 14–22 scales/cm on dorsal surface at caudal midlength; caudal-scale hairs pale brown or whitish, detectable without magnification; central hair of each caudal-scale triplet as long as (or slightly longer) than two scales. Gular gland present. Mammae at least 6–1–6 = 13 (but perhaps sometimes as many as 9–1–9 = 19; see table 3). Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle long or short (reaching the base of the pollex or not), with globular proximal part and comma-shaped distal part.

Rostral process of premaxillae short, about half as long as I1 height. Orbitosphenoid-alisphenoid suture somewhat less than twice as long as sphenorbital fissure height in lateral view. Supraorbital ridges straight or slightly divergent posteriorly, tending to become thick and dorsally reflected in mature adults but seldom produced laterally to form distinct postorbital processes; temporal ridges usually conspicuous and converging posteriorly, sometimes forming a low sagittal crest in old adults. Palatine fenestrae consistently present and usually large (typically as a single rounded hole on each side); posterolateral palatal foramina large, usually similar in length to M3 (measured across paracone-metacone).

Tympanic wing of alisphenoid usually large and globular; medial process of ectotympanic usually well developed. I1 hypsodont; crown of I2 sharply defined in relation to root; C1 without accessory cusps; preparacrista connected to stylar cusp B on M1–M3; stylar cusps D and E usually separated by a distinct notch.

COMPARISONS: Morphological comparisons of *Marmosa robinsoni* with *M. mexicana*, *M. zeledoni*, and *M. isthmica* are provided in the preceding accounts. Comparisons of *M. robinsoni* with *M. xerophila*, *M. simonsi*, and *M. rubra* are provided below.

Marmosa robinsoni closely resembles *M. xerophila* in size and qualitative characters. Although *robinsoni* averages larger than *xerophila* in most external measurements (tables 4, 5), the two species overlap broadly in postcranial dimensions and cannot be identified on this basis alone. In side-by-side comparisons of skins, the dorsal pelage of *robinsoni* is usually darker and somewhat less grayish than that of *xerophila*, and the ventral pelage of *robinsoni* is usually yellowish ("cream-colored" sensu Handley and Gordon, 1979) whereas the ventral pelage of *xerophila* is usually whitish. Also, the lateral zones of gray-based ventral fur are more conspicuous in *robinsoni* than they are in *xerophila* because the pale hair tips are shorter (the longer pale hair tips of *xerophila* more effectively conceal the gray hair bases when the ventral fur is unruffled). *Marmosa robinsoni* averages larger than *M. xerophila* in almost all measured craniodental dimensions (tables 6, 7), with minimal overlap in observed ranges for Maxillary Tooth Row (MTR), Upper Molar Series (UMS), and Lower Molar Series (LMS).[2] Visual comparisons of skulls suggest that the rostrum is proportionately longer and more slender, and that the orbits are proportionately smaller in *robinsoni* than in *xerophila*. The qualitative cranial trait that differs most consistently between the species is the rostral process of the premaxillae, which, although small, is almost always distinct in *robinsoni*; by contrast, the rostral process seems to be

consistently absent in *xerophila*. Additionally, postorbital processes are less often distinct in *robinsoni* than they are in *xerophila*, and the temporal ridges are less strongly convergent posteriorly in *robinsoni* than they are in like-aged specimens of *xerophila*.

Marmosa robinsoni can be distinguished unambiguously from *M. simonsi* in numerous qualitative characters despite their similarity in external and craniodental measurements (tables 4–7). Whereas the dark facial mask of *robinsoni* seldom extends posteriorly to the base of the ear, the mask often extends continuously from the ear to the mystacial region in *simonsi*, some specimens of which closely resemble *mexicana* in this respect. Dorsal and ventral pelage coloration is also widely divergent in these species: the dorsal pelage is usually some shade of yellowish brown, and a broad streak of self-colored (usually yellowish) ventral fur invariably extends from chin to anus in *robinsoni*; by contrast, the dorsal pelage is distinctly grayish and the ventrum is almost entirely covered by gray-based fur in *simonsi* (only the chin and groin of which are self-colored). The tail, which is uniformly dark (brownish) in *robinsoni*, is boldly marked with white in *simonsi*. Postorbital processes are usually absent or indistinct in *robinsoni*, but they are consistently well developed and often large in *simonsi*. The temporal ridges are better developed and more strongly convergent posteriorly (sometimes forming a low saggital crest) in *robinsoni* than they are in like-aged specimens of *simonsi* (which never develops a saggital crest).

Marmosa robinsoni is unlikely ever to be confused with *M. rubra*, from which it differs externally by its relatively shorter tail and larger ears (tables, 4, 5), lack of a dark midrostral streak (usually present in *rubra*), yellowish- (versus reddish-) brown dorsal pelage, presence (versus absence) of a gular gland, inconsistent (versus spiral) caudal scale patterning, and much longer caudal-scale hairs. *Marmosa robinsoni* differs craniodentally from *M. rubra* by having a short (versus long) rostral process of the premaxillae; by having palatine fenestrae (which are absent in *rubra*); by having large, globular alisphenoid tympanic processes (the alisphenoid bullae are small and laterally com-

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[2] Despite such overlap, discriminant function analyses of craniodental measurements have already demonstrated that *robinsoni* and *xerophila* are morphometrically distinct (López-Fuster et al., 2002).

pressed in *rubra*); by having a small but usually distinct medial process of the ectotympanic (absent in *rubra*); and by the preparacrista connecting to stB on M1–3 (the preparacrista usually connects to stA in *rubra*).

Marmosa robinsoni also merits comparison with *M. murina*—a distantly related species not treated in this report—with which it occurs sympatrically in northern Colombia, northern Venezuela, and on the island of Tobago (see below). Among other characters, these species differ in caudal scale patterning (inconsistent in *robinsoni*, spiral in *murina*), carpal tubercles (present in mature adult male *robinsoni*, absent in *murina*), caudal-scale hairs (macroscopically visible in *robinsoni* but not in *murina*), the rostral process of the premaxillae (shorter in *robinsoni* than in *murina*), occurrence of palatine fenestrae (present in *robinsoni*, absent in mainland forms of *murina*), shape of the tympanic process of the alisphenoid (smoothly globular in *robinsoni*, laterally compressed and sometimes pointed ventrally in *murina*), medial process of the ectotympanic (well-developed in *robinsoni*, absent or indistinct in *murina*), and stylar cusps D and E (usually separated by a distinct notch in *robinsoni* but not in *murina*).

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: The known distribution of *Marmosa robinsoni* extends from Finca Santa Clara (locality 109; fig. 25) in the western Panamanian province of Chiriquí eastward across the isthmus to Colombia and northern Venezuela. Although most Venezuelan specimens are from north of the Orinoco River, we examined one specimen (AMNH 16132) from Ciudad Bolívar (locality 236) on the south (right) bank of the river in Bolívar state. The species is also known from several islands on the continental shelf of Central America (e.g., Isla del Rey, Isla Saboga) and South America (Isla Margarita, Trinidad, and Tobago), and from the Caribbean island of Grenada.

Marmosa robinsoni occurs in a wide variety of habitats from sea level to 2600 m elevation including lowland and montane moist forests, lowland dry forests, mangroves, savannas, and xeric shrublands. Among the collecting localities mapped in figure 25,

approximately 32% correspond to open habitats (llanos, xeric shrublands, etc) from which about 45% of the specimens examined were collected. Large numbers of museum specimens with the same locality data suggest that this species is often among the most abundant nonvolant small mammals in such environments (Handley and Gordon, 1979).

The range of *Marmosa robinsoni* partially overlaps the distributions of *M. mexicana*, *M. zeledoni*, and *M. isthmica* in Panama, as described above in the accounts of those species. The range of *M. robinsoni* also overlaps the distribution of *M. xerophila* in the arid and semiarid landscapes surrounding the Gulf of Venezuela in the Venezuelan states of Falcón and Zulia, and in the adjacent department of La Guajira, Colombia. However, there appear to be no collecting localities where both species have been taken sympatrically. The only other congeneric species with a distribution that overlaps the range of *M. robinsoni* is *M. murina*, which also occurs in northern Colombia, northern Venezuela, and on the island of Tobago (Goodwin, 1961; Handley, 1976; Pérez-Hernández, 1989; Linares, 1998). In Venezuela, *M. robinsoni* and *M. murina* have been collected sympatrically near Urama (locality 239), Ciudad Bolívar (locality 236), and San Augustín (locality 261); on the island of Tobago, these species have been collected together at Charlotteville (locality 294) and Speyside (locality 295).

GEOGRAPHIC VARIATION: Available population samples of *Marmosa robinsoni* exhibit noteworthy geographic variation in size and pelage color. Insular specimens—such as those from Trinidad (*chapmani*), Tobago (*luridavolta*), and Grenada (*grenadae*)—tend to be larger, on average, than specimens from the adjacent mainland regardless of the habitats in which they were collected. According to López-Fuster et al. (2000), however, mainland Venezuelan specimens from agricultural landscapes and disturbed forests exhibit larger craniodental dimensions than those from cloud forests and gallery forests. In general, specimens of *M. robinsoni* from humid habitats (including mangroves and high altitude cloud forests) tend to have darker pelage (grayish brown washed with orange or dark yellow dorsally, and orangish
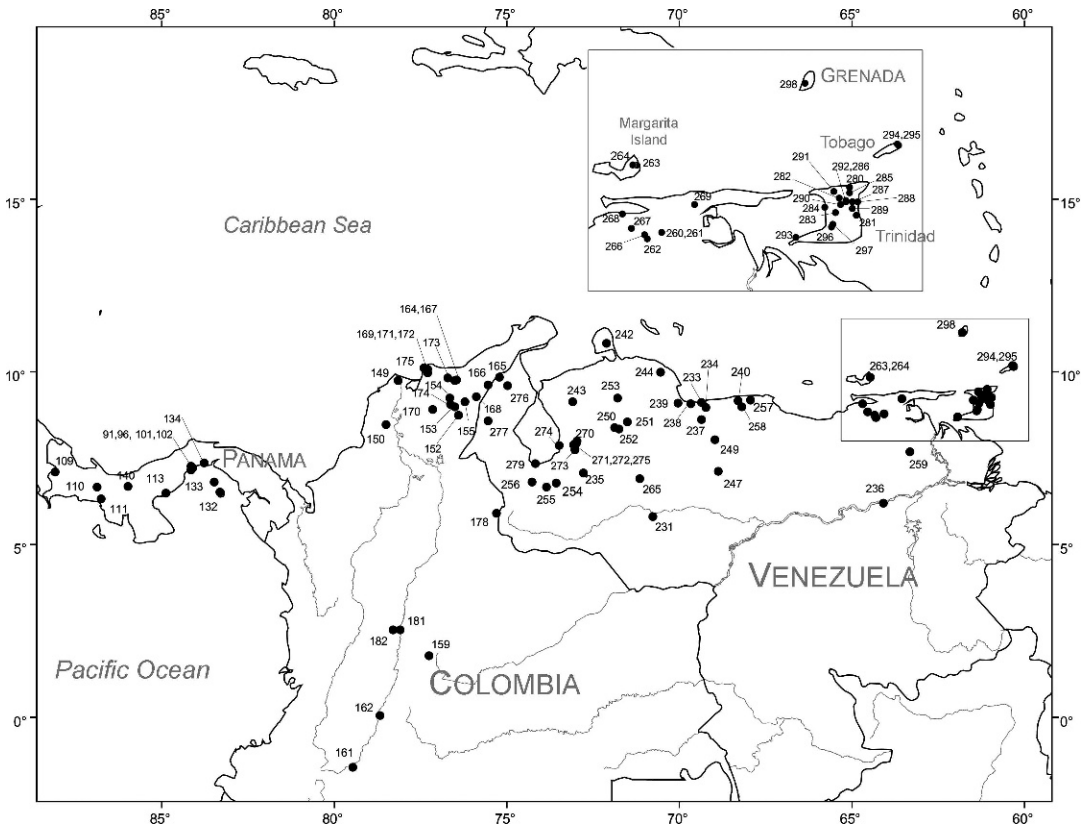
Fig. 25. Geographic range of *Marmosa robinsoni* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

buff or dark yellowish buff ventrally) as well as dark-brown ears, feet, and tail. By contrast, specimens from drier, more open habitats (e.g., dry forests, savannas, and xeric shrublands) tend to have paler pelage (light grayish brown washed with yellow dorsally, and yellowish buffy or cream buffy ventrally) and light-brown ears, feet, and tail (Tate, 1933; Handley and Gordon, 1979).

TAXONOMIC HISTORY: The first published reference to material identifiable as *Marmosa robinsoni* was Allen and Chapman's (1893) report of *Didelphis* (*Micoureus*) *murina* from Trinidad. Subsequently, Thomas (1896) and Allen and Chapman (1897) also misidentified specimens of *M. robinsoni* as *M. murina*.

Bangs (1898a) described *Marmosa robinsoni* based on three specimens from Isla Margarita (Venezuela). Later, and in the same volume of the *Proceedings of the*

Biological Society of Washington, Bangs (1898b) described *Marmosa mitis* based on 27 specimens from Pueblo Viejo (Colombia). Although the type series of *mitis* and *robinsoni* exhibit obvious external and cranial similarities, Bangs (1898b) provided comparisons only between *mitis* and *murina*. Because Bangs did not compare *mitis* with *robinsoni*, and because he provided only superficial descriptions of the cranial morphology of both taxa, several subsequent authors failed to recognize their close relationship to each other and to other related nominal taxa described in the years that followed.

Tate (1933) was the first author to recognize *robinsoni* and *mitis* as conspecific, treating them as valid subspecies along with *casta* (from mainland Venezuela) and *fulviventer* (from Isla del Rey, Panama). However, Tate erroneously used *mitis* as the senior name, and he recognized *chapmani* (from

Trinidad) as a separate valid species. Finally, Tate grouped *M. chapmani*, *M. mitis*, *M. ruatanica* (= *M. mexicana*), and *M. simonsi* as members of the Mitis Section of his Murina Group of *Marmosa* (table 1).

As explained in the introduction, Hershkovitz (1951) treated all of the species in Tate's (1933) Mitis Section, together with *isthmica* and *mimetra*, as subspecies of *Marmosa mitis*. This broad concept of *M. mitis* was subsequently endorsed by Cabrera (1958) who, however, correctly used *robinsoni* as the oldest available name. Cabrera's taxonomy was then adopted by Hall and Kelson (1959) and effectively persists (with minor modifications) to the present day (Gardner, 2005; Creighton and Gardner, 2008).

REMARKS: Despite the marked geographic variation in size and pelage color noted above, specimens that we refer to *Marmosa robinsoni* resemble one another closely and differ as a group from other valid species of *Marmosa* as diagnosed herein. Although molecular data would be welcome to assess the genetic distinctness of and phylogenetic relationships among the many named forms here treated as junior synonyms of *M. robinsoni* (including *casta*, *chapmani*, *fulviventer*, *grenadae*, *luridavolta*, *mitis*, *nesaea*, and *pallidiventris*), only morphological inferences are possible at present.

The larger body size of island populations of small nonvolant mammals by comparison with their mainland counterparts is a well-documented phenomenon for which a multitude of explanatory hypotheses have been proposed (Crowell, 1983; Lomolino, 1985; Adler and Levins, 1994; McNab, 1994). Several nominal taxa have been described for insular populations of *M. robinsoni*, including the nominotypical form (from Isla Margarita), *chapmani* and *nesaea* (Trinidad), *fulviventer* (Isla del Rey), *grenadae* (Grenada), and *luridavolta* (Tobago). Our examination of holotypes and other representative material of these taxa suggest that they are nothing more than large island forms with habitat-correlated coat color differences similar to those observed among many other widespread species of small mammals.

Most continental forms average smaller than typical (insular) *M. robinsoni*, but the young adult female holotype of *pallidiventris* (FMNH 18692) is exceptionally small by comparison with the mature adult male holotypes of *casta* (BMNH 11.5.25.184) and *mitis* (MCZ B-8123), a difference plausibly attributable to age and sexual dimorphism. Continental forms also differ from typical *robinsoni* in pelage color. The tropical moist forest ecoregions (Olson et al., 2001) where the holotypes of the former were collected plausibly explain their darker pelage when compared with the type material of *robinsoni* from the predominantly arid environments of Isla Margarita. Although the holotype of *mitis* has wider and more conspicuously gray-based ventral fur than the holotype of *casta*, comparable variation in ventral pelage markings is observable among other species of *Marmosa* and is not, in our opinion, a sufficient basis for taxonomic diagnosis.

SPECIMENS EXAMINED (*N* = 541): Without locality data (BMNH 95.3.9.6). **PANAMA**—No other locality data (USNM 303051). *Canal Zone*, no other locality data (USNM 318316), Balboa (USNM 456818, 456822), Fort Kobbe (USNM 298697, 298698, 300329, 300330, 301141, 303049), Miraflores (USNM 396415), Quarry Heights (USNM 303281–303283). *Chiriquí*, Near Escopeta Camp (= 23–25 km NNE San Felix: USNM 541000, 541002; = Colorado Camp: USNM 541324), Finca Santa Clara (USNM 520772), Tolé (USNM 331071). *Coclé*, Río Hato (USNM 331069). *Panamá*, Pacora (USNM 305146), Isla Saboga (= Saboga Island: MCZ 10809), Isla del Rey (= San Miguel Island: FMNH 34071; MCZ B8435 [holotype of *Marmosa fulviventer* Bangs, 1901], B8437, B8438). *Veraguas*, Santa Fé (= Río Santa Maria: USNM 304696–304709). **COLOMBIA**—*Atlántico*, Barranquilla (MVZ 135234–135243; = "Barranquilla", place of shipment: MVZ 183339; = Vicinity Barranquilla: MVZ 183334–183338). *Bolívar*, San Juan Nepomuceno (FMNH 69315). *Cesar*, El Salado (USNM 280814–280816), El Orinoco (= Río Cesar: USNM 280820, 280886–280888; = Río Guaimaral: USNM 280817, 280819), San Sebastián de Rábago (= San Sebastián: FMNH 69320, 69321), Valledupar (= Aguas Verdes: USNM 280818). *Cundinamarca*, Bogotá (AMNH 143521). *Huila*, Naranjal (= Valle de Suaza: USNM 541857–541861, 543120), Villavieja

(MVZ 113366, 113367, 113833–113835–113840). *La Guajira*, El Pueblito (= Pueblo Viejo: FMNH 18509; BMNH 9.4.15.18–9.4.15.20; MCZ B8117–B8122, B8123 [holotype of *Marmosa mitis* Bangs, 1898], B8125–B8127, B8132, B8143; USNM 85531, 85532; = Santa Marta: FMNH 18508), La Concepción (FMNH 18507), Las Marimondas (USNM 280876–280880, 280882, 280883, 280885), San Miguel (FMNH 18506), Villanueva (USNM 280853–280875; = Sierra Negra: USNM 280821–280852). *Magdalena*, Bonda (AMNH 14610, 14611, 15357–15361, 23273–23276, 23280, 23281, 23292, 23627), Colonia Agrícola de Caracolicito (USNM 280806), Mamatoco (AMNH 15362), Minca (AMNH 23293), Palomino (USNM 85533), Pueblo Bello (USNM 280807–280813), Santa Marta (AMNH 244887), Taganga (AMNH 15363). *Norte de Santander*, Cúcuta (FMNH 18692 [holotype of *Marmosa mitis pallidiventris* Osgood, 1912]). *Santa Marta*, no other locality data (AMNH 244887). *Tolima*, Honda (AMNH 34602–34604), Mariquita (AMNH 207766). **VENEZUELA—*Apure***, Hato El Frío (USNM 448524). *Aragua*, Camp Rangel (USNM 314171), Ocumare de La Costa (USNM 517271–517280), Rancho Grande (USNM 517262–517270). *Barinas*, Altamira (USNM 418540). *Bolívar*, Ciudad Bolívar (AMNH 16132). *Carabobo*, El Trompillo (BMNH 14.9.1.86–14.9.1.97), San Esteban (AMNH 31532; BMNH 11.5.25.178–11.5.25.183, 11.5.25.184 [holotype of *Marmosa mitis casta* Thomas, 1911], 11.5.25.185, 11.5.25.187; = San Esteban Valley: BMNH 11.5.25.186), Urama (USNM 372938–372940, 372942–372944, 372947). *Distrito Federal*, Caracas (AMNH 130586–130589). *Falcón*, Cerro Santa Ana (= 15 km SSW Pueblo Nuevo: USNM 442907; = 49 km N and 32 km W Coro: USNM 443870–443874, 443877, 443880–443888, 443890–443896), Hacienda Socopito (= 20 km S and 98 km E Maracaibo: USNM 443801; = 24 km S and 94 km E Maracaibo: USNM 418531, 418532), Mirimire (USNM 406953). *Guárico*, Estación Biológica de los Llanos (USNM 385052; = 9 km SE Calabozo: USNM 442908, 443906, 443908, 443910; = 7 km S and 5 km E Calabozo: USNM 443897, 443901–443905, 443911), Hato Las Palmitas (USNM 385053–385056, 418518, 418519, 443794, 443797,

443798, 443800). *Lara*, Caserio Boro (USNM 443913), Puerta Vieja (USNM 443914), La Concordia (USNM 443912), Río Tocuyo (AMNH 130577–130585, 130600). *Mérida*, Mérida (BMNH 2.3.4.8; = Cafetos de Chama: AMNH 24320, 24323, 24324, 33166; BMNH 5.1.1.6), Milla (= Cafetos de Milla: BMNH 98.7.1.21; USNM 149005), Pedregosa (BMNH 98.7.1.19). *Miranda*, Curupao (USNM 385057–385060), San Andrés (= 8 km SSE Caracas: USNM 385047–385049). *Monagas*, Hato Mata de Bejuco (= 47 km SE Maturin: USNM 385068–385072; = 54–55 km SE Maturín: USNM 443915–443917, 442720), Ipuré (BMNH 0.5.1.59), San Agustín (USNM 406951), San Antonio de Maturín (= San Antonio: AMNH 69939, 69940). *Nueva Esparta*, Isla Margarita (= Margarita Island: BMNH 99.11.12.1; MCZ B7749 [holotype of *Marmosa robinsoni* Bangs, 1898]; USNM 63209, 63210, 63212), Salamanca (USNM 388381, 388388–388397, 388399, 388400; = 3 km S La Asunción: USNM 388398). *Portuguesa*, Guanarito (AMNH 266951–266954). *Sucre*, Campo Alegre (BMNH 0.5.1.58), Cuchivano (AMNH 69938), Cumaná (USNM 388377–388379, 388385, 388386), Guaraúnos (AMNH 257208–257210). *Trujillo*, Isnotú (= Near Isnoto: USNM 370050), Agua Viva (USNM 371304), Agua Santa (USNM 370048, 370049), El Dividive (USNM 371305, 371315, 371316), La Ceiba (= Hacienda Valle Verde: USNM 371317), Valera (FMNH 22175). *Zulia*, Cerro Azul (= 17 km N and 55 km W Maracaibo: USNM 443807; = 18 km N and 56 km W Maracaibo: USNM 443802–443804; = 39 km NW La Paz: USNM 443805, 443806), Novito (= 3 km S and 19 km W Machiques: USNM 418529, 418530), Río Chama (BMNH 98.7.1.20). **TRINIDAD AND TOBAGO**—No other locality data (AMNH 6127; USNM 197042), El Cerro del Oropuche (= Orepouche Heights: AMNH 31229–31231), Bush Bush Forest (AMNH 188357, 189314–189316, 204855–204857, 206595–206597, 206761, 206762, 206764–206768). "Trinidad Island" (BMNH 95.3.9.7, 97.6.7.25, 97.6.7.26). *Arima*, Arima (= St. Patricks: AMNH 169671, 188355). *Caroni*, Caparo River (= Caparo Valley: BMNH 97.6.7.24 [holotype of *Marmosa nesaea* Thomas, 1911]), Caparo (AMNH 7426, 7429, 7660/

6046–7664/6050). **Saint Andrew**, no other locality data (AMNH 186440), Cumaca (AMNH 188354, 208996, 208999–209003, 212128–212130, 214425–214438, 214444, 234963–234970), Cumuto (AMNH 212303–212305), Sangre Grande (AMNH 173984, 173996, 174000, 174007, 174008, 174012, 174162, 188356; = El Reposo Rd.: AMNH 173990; = Maingot Estate: AMNH 173998), Turure Forest (AMNH 214440, 234972, 234976), Upper Fishing Pond (= Fishing Pond: AMNH 173997). **Saint George**, Brazil Village (AMNH 208997, 208998), Caura (AMNH 7665/6051, 7666/6052 [holotype of Marmosa chapmani Allen, 1900], 7667/6053–7670/6056, 7672/6058, 7674/6060–7676/6062; USNM 85556; = Caura Mts.: AMNH 7430). **Saint Patrick**, Aripo Savanna (= Aripo Valley: BMNH 35.2.10.1), Cedros Point (= Cedros: AMNH 234960, 234961; = Cedros Ward: AMNH 214424). **Tobago**, Charlotteville (AMNH 259973, 259983; USNM 537898, 537899, 538075–538078), Speyside (AMNH 184845, 184846, 184848 [holotype of Marmosa mitis luridavolta Goodwin, 1961], 184849). **Victoria**, Princestown (AMNH 4799–4802, 6046, 6049, 6121, 6123, 6045/4767, 6047/4768, 6048/47669, 6050/4770–6053/4773, 6055/4775, 6056/4776, 6058/4778), Savana Grande (BMNH 1939.3270). **GRENADA–Saint George**, Annandale (BMNH 87.6.30.5 [holotype of Marmosa grenadae Thomas, 1911]).

Marmosa xerophila Handley and Gordon, 1979
Figures 23, 24

Marmosa xerophila Handley and Gordon, 1979: 68. Type locality "La Isla, 15 m, near Cojoro, 37 km NNE Paraguaipoa, Dpto. Guajira, Colombia."
Marmosa xerophila: Honacki et al., 1982: 23.
Marmosa xerophila: Pérez-Hernández, 1989: 369.
Marmosa xerophila: Eisenberg, 1989: 41.
Marmosa xerophila: Gardner, 1993: 19.
Marmosa (Marmosa) xerophila: Pérez-Hernández et al., 1994: 41.
Marmosa xerophila: Linares, 1998: 65.
Marmosa xerophila: Nowak, 1999: 21.
Marmosa xerophila: López-Fuster, 2002: 201.
Marmosa xerophila: Brown, 2004: 69.
Marmosa xerophila: Gardner, 2005: 10.
Marmosa xerophila: Creighton and Gardner, 2008: 61.

TYPE MATERIAL: The holotype (by original designation, USNM 443819) is a mature adult (age class 7) male specimen preserved as a skin in good condition and a skull that is missing the left ectotympanic but is otherwise complete.

TYPE LOCALITY: The holotype was collected on 28 June 1968 at a locality called "La Isla" near Cojoro (gazetteer entry 163) in the Colombian department of La Guajira by a Smithsonian Venezuelan Project field team consisting of Norman E. Peterson, Fred P. Brown, Jr., and John O. Matson, whose field notes were the basis for Handley's (1976: 67) published description of coastal-desert habitats near Cojoro.

MORPHOLOGICAL DIAGNOSIS: Midrostral fur pale, usually contrasting sharply with darker fur of crown; dark median rostral stripe absent or inconspicuous; dark facial mask not extending posteriorly to contact base of ear; dorsal body pelage pale, usually some shade of faded yellowish brown or light grayish brown; dorsal cover hairs about 7 mm in length, guard hairs about 10 mm; gray-based ventral pelage restricted to the sides of abdomen, with whitish or yellowish hair tips; self-colored ventral pelage (extending as a wide median stripe from chin to anus) whitish or yellowish. Exposed skin of tail grayish brown, indistinctly bicolored (paler ventrally), without any clear pattern of scale arrangement (both spiral and annular patterns coexisting); 14–16 scales/cm on dorsal surface at caudal midlength; caudal-scale hairs usually whitish and detectable without magnification; central hair of each caudal-scale triplet as long as (or slightly longer than) two scales. Gular gland present. Mammae at least 5–1–5 = 11 (but perhaps as many as 6–1–6 = 13; see table 3). Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle long or short (reaching the base of pollex or not), with subequal but recognizable proximal and distal parts.

Rostral process of premaxillae absent. Orbitosphenoid-alisphenoid suture somewhat less than twice as long as sphenorbital fissure height in lateral view. Supraorbital ridges parallel or slightly divergent posteriorly, usually thick and dorsally reflected in mature adults, sometimes produced laterally
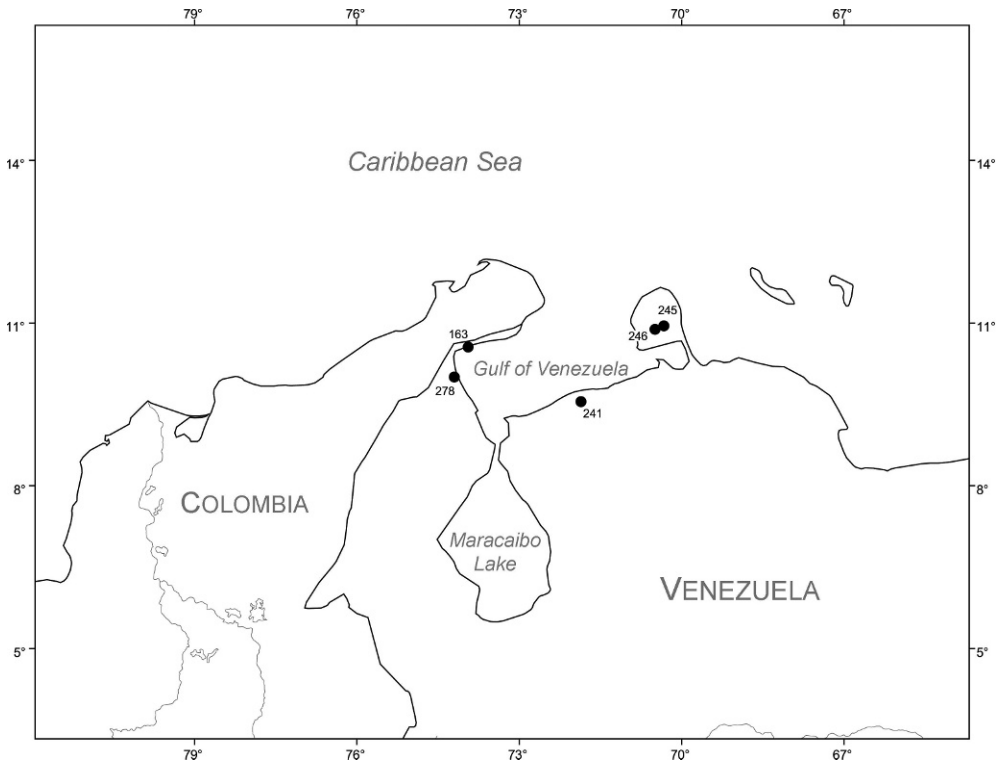
Fig. 26. Geographic range of *Marmosa xerophila* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

as more or less distinct postorbital processes; temporal ridges conspicuous, usually strongly convergent posteriorly and sometimes joining to form a low sagittal crest in old adults. Palatine fenestrae consistently present and well developed (typically as a single rounded hole on each side); posterolateral palatal foramina large, similar in length to M3 (measured across paracone-metacone) or even longer. Tympanic wing of alisphenoid usually large and globular; medial process of ectotympanic well developed. I1 hypsodont; crown of I2 sharply defined in relation to root; C1 without accessory cusps; preparacrista connected to stylar cusp B on M1–M3; stylar cusps D and E usually separated by a distinct notch.

COMPARISONS: Morphological comparisons of *Marmosa xerophila* with *M. mexicana*, *M. zeledoni*, *M. isthmica*, and *M. robinsoni* are provided in the preceding accounts. *Marmosa xerophila* differs from *M. simonsi*, *M. rubra*, and *M. murina* in all of the same characters by which *M. robinsoni* differs from those species, except that the rostral process of the premaxillae (short in *M. robinsoni*) is entirely lacking in *M. xerophila*.

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: The known geographic distribution of *Marmosa xerophila* is restricted to the coastal deserts surrounding the Golfo de Venezuela (including the Península de Paraguaná) in the Venezuelan states of Falcón and Zulia and in the Colombian department of La Guajira (fig. 26). The habitats in which specimens have been collected correspond to the "Paraguaná Xeric Scrub" and the "Guajira/Barranquilla Xeric Scrub" ecoregions of Olson et al. (2001). Although the species is not known from the Netherlands Antilles, it may once have occurred on the continental-shelf island of Aruba, where several other species of small mammals that now inhabit

arid or semiarid mainland habitats have been reported as subfossils (Hooijer, 1960, 1967).

Although the range of *Marmosa xerophila* is completely overlapped by the macrogeographic distribution of *M. robinsoni*, these species have yet to be recorded in sympatry. The range of *M. xerophila* is also contained within the macrogeographic distribution of *M. murina*, a rainforest species not treated in this report.

GEOGRAPHIC VARIATION: According to López-Fuster et al. (2002), *Marmosa xerophila* is a morphometrically homogeneous species that exhibits no noteworthy geographic differences in measured dimensions. Although our observations and data are broadly consistent with their assessment, we agree with Handley and Gordon (1979) that specimens from the west coast of the Golfo de Venezuela (in the Venezuelan state of Zulia and the Colombian department of La Guajira) have visibly smaller bullae than those on the east coast (in the Venezuelan state of Falcón).

TAXONOMIC HISTORY: Remarkably, no specimens of this locally abundant mouse opossum appear to have been collected prior to the Smithsonian Venezuelan Project expeditions to the northwestern coastal lowlands of Venezuela in 1968. Therefore, the brief taxonomic history of *Marmosa xerophila* effectively began with Handley and Gordon's (1979) original description, which was based on the Colombian holotype and 245 paratypes from the localities listed below. Despite a close resemblance to *M. robinsoni*, the distinctness of *M. xerophila* has not been questioned by subsequent researchers.

SPECIMENS EXAMINED (*N* = 105): **COLOMBIA**—*La Guajira*, Cojoro (= 37–55 km NNE Paraguaipoa: USNM 443812–443818, 443819 [holotype of *Marmosa xerophila* Handley and Gordon, 1979], 443820–443831). **VENEZUELA**—*Falcón*, Capatárida (USNM 442721–442727, 442729–442731, 442733–442735, 442744, 443918–443925, 443927–443929, 443931, 443936–443938, 443940–443942, 443946, 443947, 443951, 443952, 443955–443957, 443959, 443960, 443963–443972, 443974–443978; = 18 km WSW Capatárida: USNM 442728), Moruy (= 49 km N and 33 km W Coro: USNM 443834–443848, 443851), Yabuquiva

(= 25 km SW Pueblo Nuevo: USNM 442906; = 48 km N and 46 km W Coro: USNM 443852, 443854–443856, 443862, 443863, 443868–443869). **Zulia**, Paraguaipoa (= 114 km N and 32 km W Maracaibo: USNM 443810, 443811, 443832).

Marmosa simonsi Thomas, 1899
Figure 27

? *Didelphys murina*: Thomas, 1882a: 111.

Marmosa Simonsi Thomas, 1899: 287. Type locality "Puná, Puná Island, and Guayaquil."

[*Didelphis* (*Caluromys*)] *simonsi*: Matschie, 1916: 269. Name combination.

[*Marmosa* (*Marmosa*)] *simonsi*: Cabrera, 1919: 39.

Marmosa simonsi: Tate, 1933: 121.

Marmosa mitis simonsi: Hershkovitz, 1951: 552. Name combination.

Marmosa [(*Marmosa*)] *robinsoni simonsi*: Cabrera, 1958: 25. Name combination.

Marmosa robinsoni: Honacki et al., 1982: 23. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: O'Connell, 1983: 1. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Gardner, 1993: 18. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Emmons, 1997: 26. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Eisenberg and Redford, 1999: 62. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Nowak, 1999: 21. Part, not *Marmosa robinsoni* Bangs, 1898.

Marmosa robinsoni: Brown, 2004: 65. Part, not *Marmosa robinsoni* Bangs, 1898.

[*Marmosa robinsoni*] *simonsi*: Gardner, 2005: 9. Part.

M[*armosa*]. *r*[*obinsoni*]. *simonsi*: Creighton and Gardner, 2008: 50. Part.

TYPE MATERIAL: The holotype (by original designation, BMNH 99.8.1.20) is a young adult (age class 6) male, preserved as a skin and skull in good condition.

TYPE LOCALITY: The holotype was collected by P.O. Simons on 3 November 1898 at Puná (gazetteer entry 197; appendix), a village on the island of Puná in the Ecuadorean province of Guayas. The island of Puná (855 km^2) is covered with Ecuadorean dry forests and Gulf of Guayaquil/Tumbes mangroves (Olson et al., 2001).

MORPHOLOGICAL DIAGNOSIS: Midrostral fur pale, contrasting sharply with darker fur of crown; dark median rostral stripe absent; dark facial mask often extending posteriorly

Fig. 27.　Dorsal and ventral cranial views of *Marmosa simonsi* (USNM 461643, a mature adult male). Scale bar = 10 mm.

to contact base of ear; dorsal body pelage distinctly grayish; dorsal cover hairs 8–10 mm in length, guard hairs 10–11 mm in length; most of ventral surface (including chest, abdomen, and the inner parts of the fore- and hind limbs) covered by gray-based fur with yellowish hair tips; self-colored ventral pelage (present only on chin or as a narrow median stripe extending from chin to upper chest) yellowish buff. Exposed caudal skin brownish basally but abruptly whitish on distal ⅓ to ½ of tail; caudal scales without any clear pattern of arrangement (both spiral and annular patterns coexisting); about 14 scales/cm on dorsal surface at caudal mid-length; caudal-scale hairs usually whitish, detectable without magnification; central hair of each caudal-scale triplet slightly longer than two scales. Gular gland present. Mammary formula unknown. Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle short and

comma-shaped, not reaching base of pollex, and not segmented into distinguishable proximal and distal parts.

Rostral process of premaxillae short, usually a little less than half of I1 height. Orbitosphenoid-alisphenoid suture about twice as long as sphenorbital fissure height in lateral view. Supraorbital ridges moderately to strongly divergent posteriorly, tending to become thick and produced laterally over orbital fossae in adults; postorbital processes consistently present and distinct; temporal ridges weakly developed and moderately to strongly convergent posteriorly. Palatine fenestrae present (usually as a single well-developed rounded or irregular hole on each side); posterolateral palatal foramina large, typically about as long or longer than M3 (measured across paracone-metacone). Tympanic wing of alisphenoid globular; medial process of ectotympanic usually well developed. I1 hypsodont; crown of I2 sharply

defined in relation to root; C1 without accessory cusps; preparacrista connected to stylar cusp B on M1–M2; stylar cusps D and E usually separated by a distinct notch.

COMPARISONS: Comparisons of *Marmosa simonsi* with *M. mexicana*, *M. zeledoni*, *M. isthmica*, *M. robinsoni*, and *M. xerophila* are provided in the preceding accounts. *Marmosa simonsi* and *M. rubra* are compared below.

Marmosa simonsi is smaller than *M. rubra* in most measured external and craniodental dimensions (tables 4–7), with the notable exception of its relatively and absolutely larger ears, longer upper canines, and larger bullar dimensions. In qualitative external traits, *M. simonsi* is easily distinguished from *M. rubra* by its long facial mask (often extending posteriorly to the ear), distinctly grayish dorsal pelage, almost entirely gray-based ventral pelage, particolored (white-tipped) tail, annularly and spirally arranged caudal scales, and long caudal-scale hairs. By contrast, *M. rubra* has a short facial mask, reddish dorsal fur, more extensively self-colored ventral fur, an all-dark tail, spirally arranged caudal scales, and much shorter caudal-scale hairs. In addition, whereas *M. simonsi* lacks a dark midrostral stripe and possesses a gular gland, *M. rubra* possesses a dark midrostral stripe and lacks a gular gland.

In qualitative craniodental traits, these species are most readily distinguished by the rostral process of the premaxillae (shorter in *simonsi* than in *rubra*), postorbital processes (consistently well developed in *simonsi*, indistinct or absent in *rubra*), palatine fenestrae (present in *simonsi*, absent in *rubra*), tympanic wing of the alisphenoid (relatively more inflated and globular in *simonsi* than in *rubra*), medial process of the ectotympanic (better developed in *simonsi* than in *rubra*), and by the attachment of the preparacrista (to stylar cusp B in *simonsi*, to stylar cusp A in *rubra*).

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: The known distribution of *Marmosa simonsi* extends along the Pacific littoral zone and adjacent hilly country of western Ecuador (between sea level and 1600 m elevation) from Jama (locality 208; fig. 28) in Manabí province southward to Naranjito (locality 228) in the Peruvian department of Piura.

Although a wide range of terrestrial habitats occur in this region (e.g., mangroves, dry forests, lowland moist forests, and montane moist forests), most collection localities appear to be from mangroves or dry (deciduous) forests.

The geographic range of *Marmosa simonsi* partially overlaps that of *M. isthmica*. Geographic details about the extent of this overlap and the localities where these species occur sympatrically are described in the preceding account for *M. isthmica*.

GEOGRAPHIC VARIATION: We did not observe any noteworthy variation among geographic samples of this species.

TAXONOMIC HISTORY: *Marmosa simonsi* was briefly assigned to the genus *Caluromys* by Matschie (1916), an obvious mistake that was soon rectified by Cabrera (1919). Tate (1933) recognized *simonsi* as a valid species that he associated with *chapmani* and *mitis* (both treated as synonyms of *M. robinsoni* in this report) and with *ruatanica* (= *M. mexicana*) in his Mitis Section of *Marmosa*. Hershkovitz (1951), however, considered *simonsi* to be a subspecies of *mitis*, alleging that it grades into the darker *mimetra* (a taxon that he also regarded as a subspecies of *M. mitis*) in northern Ecuador. Hershkovitz's broad concept of *M. mitis* (= *M. robinsoni*) has been accepted by all subsequent authors (e.g., Cabrera, 1958; Honacki et al., 1982; Gardner, 2005; Creighton and Gardner, 2008).

SPECIMENS EXAMINED ($N = 117$): **ECUADOR**—***El Oro***, Río Puyango (MSB 87083–87087), Santa Rosa (AMNH 61195; USNM 513423). ***Guayas***, Cerro Bajo Verde (AMNH 63416), Chongoncito (AMNH 63012, 63401–63414), Guayaquil (BMNH 99.8.1.50–99.8.1.57, 99.9.9.140; USNM 121155, 121156, 121158), Isla Puná (AMNH 140232, 140233), Puná (BMNH 99.8.1.20 [holotype of *Marmosa simonsi* Thomas, 1899], 99.8.1.21–99.8.1.26), San Ramón (AMNH 66851–66868, 66870–66881, 66883–66885; = Hacienda San Ramon: FMNH 41402–41404). ***Loja***, Hacienda Casanga (= Casanga: AMNH 47181; = Río Casanga: AMNH 93797), Malacatos (FMNH 53356–53366), Zozoranga (USNM 461643). ***Los Ríos***, Vinces (= Hacienda Pijigual: AMNH 63343–63346, 63350). ***Manabí***, Jama (FMNH 53353), Los Pozos (AMNH 67282, 67283), Río Briceño (AMNH 64525, 64526,
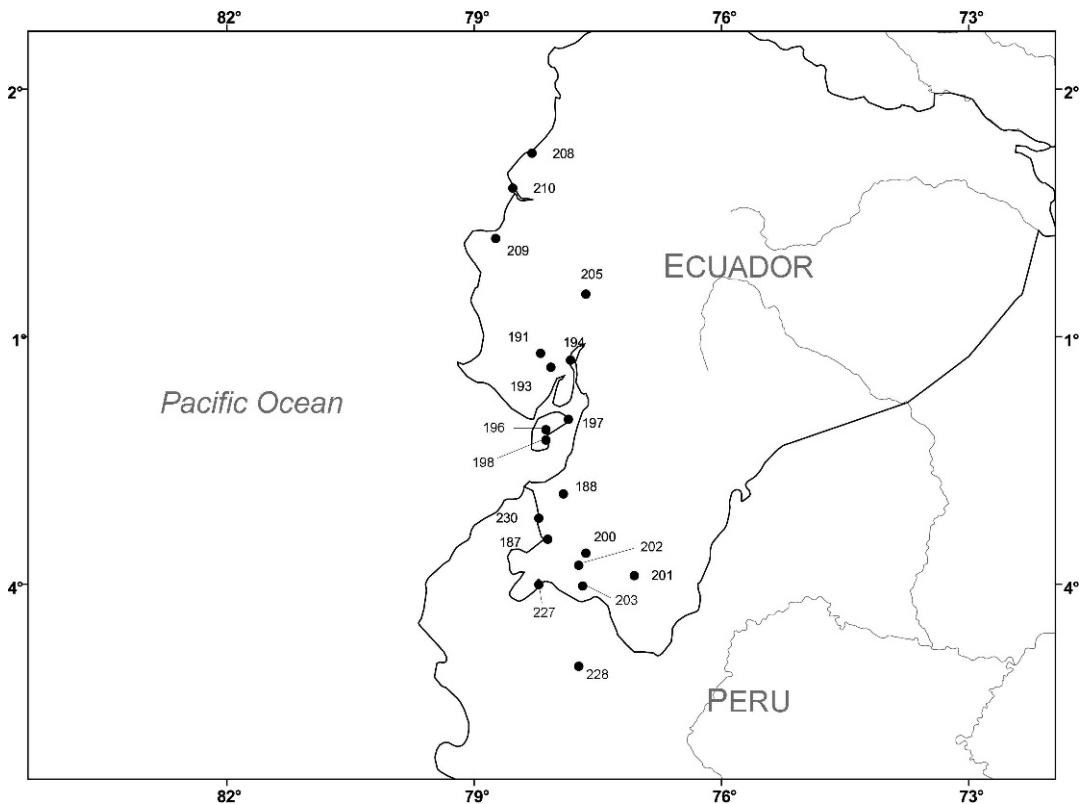
Fig. 28. Geographic range of *Marmosa simonsi* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

64530–64533, 64536). **PERU—*Piura***, Huásimo (FMNH 81448–81451), Naranjito (USNM 551640). ***Tumbes***, Matapalo (FMNH 81452–81455), Papayal (USNM 302980).

Marmosa rubra Tate, 1931
Figure 29

Marmosa rubra Tate, 1931: 6. Type locality "mouth of Rio Curaray, Province of Oriente, Ecuador" (this locality is actually in Departamento Loreto, Peru; see below).
Marmosa rubra: Tate, 1933: 105.
Marmosa [(*Marmosa*)] *rubra*: Cabrera, 1958: 25.
Marmosa rubra: Honacki et al., 1982: 23.
Marmosa rubra: Gardner, 1993: 19.
Marmosa rubra: Emmons, 1997: 25.
Marmosa rubra: Eisenberg and Redford, 1999: 62.
Marmosa rubra: Nowak, 1999: 21.
Marmosa rubra: Voss and Jansa, 2003: 75.
Marmosa rubra: Brown, 2004: 68.
Marmosa rubra: Gardner, 2005: 9.
Marmosa rubra: Creighton and Gardner, 2008: 60.

TYPE MATERIAL: The holotype (by original designation, AMNH 71973) is a mature adult (age class 8) female preserved as a skin and skull; although the skin is in good condition, the auditory region is damaged on the left side of the skull.

TYPE LOCALITY: The holotype of *Marmosa rubra* was collected by Carlos Olalla and Sons (an Ecuadorean family of professional collectors) on 7 December 1925 at a locality they called "Boca río Curaray" (gazetteer entry 226; appendix) in territory historically claimed by Ecuador. Tate's (1931: 6) verbatim type locality "mouth of Rio Curaray, Province of Oriente, Ecuador" reflects the Olallas' patriotism, but it is geographically inaccurate because the mouth of the Curaray—a right-bank tributary of the lower Napo—is (and was, de facto, in 1925) in the Peruvian department of Loreto. According to Wiley (in press), the Olallas' collections from "Boca río Curaray" proba-

Fig. 29.   Dorsal and ventral cranial views of *Marmosa rubra* (USNM 274577, mature adult male). Scale bar = 10 mm.

bly include material collected on both banks of the Curaray and the Napo within a radius of several kilometers around the confluence of those rivers. It is not known exactly where the holotype of *M. rubra* was taken in this general area.

MORPHOLOGICAL DIAGNOSIS: Midrostral fur pale, usually contrasting sharply with darker fur of crown; dark median rostral stripe present and usually distinct; dark facial mask not extending posteriorly to contact base of ear. Dorsal body pelage usually dull reddish brown (occasionally dark grayish brown washed with dark orange or red); dorsal cover hairs 8–10 mm in length, guard hairs 10–12 mm in length; gray-based ventral pelage conspicuous, usually covering sides of neck, chest, and abdomen (sometimes also extending to the inner parts of arms and legs), with orangish hair tips; self-colored ventral pelage (usually extending as a continuous median strip from chin to anus)

yellowish buff or orangish buff. Exposed skin of tail dark brown dorsally from base to tip, indistinctly paler ventrally; caudal scales arranged in spiral pattern; about 16 scales/cm on dorsal surface at caudal midlength; caudal-scale hairs dark brown and not apparent without magnification; central hair of each caudal-scale triplet about as long as one scale. Gular gland absent. Mammae 3–1–3 = 7 or 4–1–4 = 9. Lateral and medial carpal tubercles present in mature adult males; medial carpal tubercle short, robust, comma shaped, close to the base of pollex, and not bipartite.

Rostral process of premaxillae long, slightly greater than or equal to I1 height. Orbitosphenoid-alisphenoid suture variable, somewhat longer than or similar to sphenorbital fissure height in lateral view. Supraorbital ridges subparallel or slightly divergent posteriorly, slender, and dorsally reflected in mature adults, not projecting laterally over

orbital fossae; postorbital process absent or indistinct; temporal ridges conspicuous, parallel or slightly convergent posteriorly. Palatine fenestrae absent (but tiny asymmetrical palatine perforations occasionally present); posterolateral palatal foramina small, similar in length to M4 (measured at paracone-metacone). Tympanic wing of alisphenoid small and laterally compressed, often somewhat pointed ventrally; medial process of ectotympanic absent or indistinct. I1 hypsodont; crown of I2 usually sharply defined in relation to root; C1 without accessory cusps; preparacrista usually connected to stylar cusp A on M1–M3; stylar cusps D and E usually separated by a distinct notch on M2.

COMPARISONS: Morphological comparisons of *Marmosa rubra* with other congeneric species treated in this report are provided in the preceding accounts. Brief comparisons with other members of the subgenus *Marmosa* with which it overlaps geographically in western Amazonia are provided below.

Marmosa rubra is most readily distinguished from *M. andersoni* by having a dark median rostral streak (absent or indistinct in *andersoni*), by usually having a continuous median streak of self-colored ventral fur (absent in *andersoni*), by having spirally arranged caudal scales (the caudal scales are both spirally and annularly arranged in *andersoni*), by lacking distinct postorbital processes and palatine fenestrae (both present in *andersoni*), and by the preparacrista of M1–2 connecting to stylar cusp A (the preparacrista of these teeth connects to styB in *andersoni*).

Marmosa rubra is much larger than *M. lepida* in all measured dimensions (the length of the upper molar series, for example, is 7.1–7.6 mm in *rubra* but only 5.6–6.7 mm in *lepida*). Qualitative character differences that distinguish these species include the dark median rostral streak (present in *rubra*, absent in *lepida*), distinct postorbital processes (absent in *rubra*, present in *lepida*), a posterior accessory cusp on C1 (absent in *rubra*, present in *lepida*), and the connection of the preparacrista on M1–M2 (to styA in *rubra*, to styB in *lepida*).

Marmosa rubra can be distinguished from *M. murina* and *M. quichua* by having a dark median rostral streak (absent in *murina* and *quichua*), by having reddish-brown dorsal fur (the dorsal pelage is grayish brown in *murina* and *quichua*), by lacking a gular gland (present in *murina*), by the presence of carpal tubercles in mature adult males (absent in *murina* and *quichua*), by lacking postorbital processes (present in *murina* and *quichua*), by the preparacrista of M1–2 connecting to stylar cusp A (the preparacrista of these teeth connects to styB in *murina* and *quichua*), and by the usual presence of a distinct notch between stylar cusps D and E on M2 (usually absent in *murina* and *quichua*).

GEOGRAPHIC DISTRIBUTION AND SYMPATRY: The known distribution of *Marmosa rubra*, the only Amazonian species treated in this report, extends from the Río Mecaya (locality 179; fig. 30) in Departmento Putumayo, Colombia, southward along the eastern Andean piedmont and adjacent lowlands (between 180 m and 730 m elevation) to Hacienda Villa Carmen (locality 225) in Departmento Cusco, Peru. The natural vegetation throughout this region is either lowland or premontane rain forest.

Although the geographic range of *Marmosa rubra* does not overlap that of any other species reviewed herein, it does overlap the distributions of several distantly related congeners, including *M. andersoni*, *M. lepida*, *M. murina*, and *M. quichua*. The details of this overlap and lists of localities where *M. rubra* occurs sympatrically with other species of *Marmosa* (*Marmosa*) will be described in subsequent reports.

GEOGRAPHIC VARIATION: We did not observe any noteworthy variation among geographic samples of this species.

TAXONOMIC HISTORY: *Marmosa rubra* was originally described by Tate (1931) based on the holotype and 11 paratypes. Tate considered *M. rubra* to be closely related to *M. murina*, but provided no arguments to support that hypothesis. Later, based on perceived similarities in mammary formulae, inguinal pelage color, caudal features, and supraorbital morphology, Tate (1933) grouped *M. rubra*, *M. murina*, *M. quichua*, and *M. tyleriana* to form his Murina Section of the Murina Group of *Marmosa*. A close relationship between *M. rubra* and *M. murina*, however, is not supported by recent
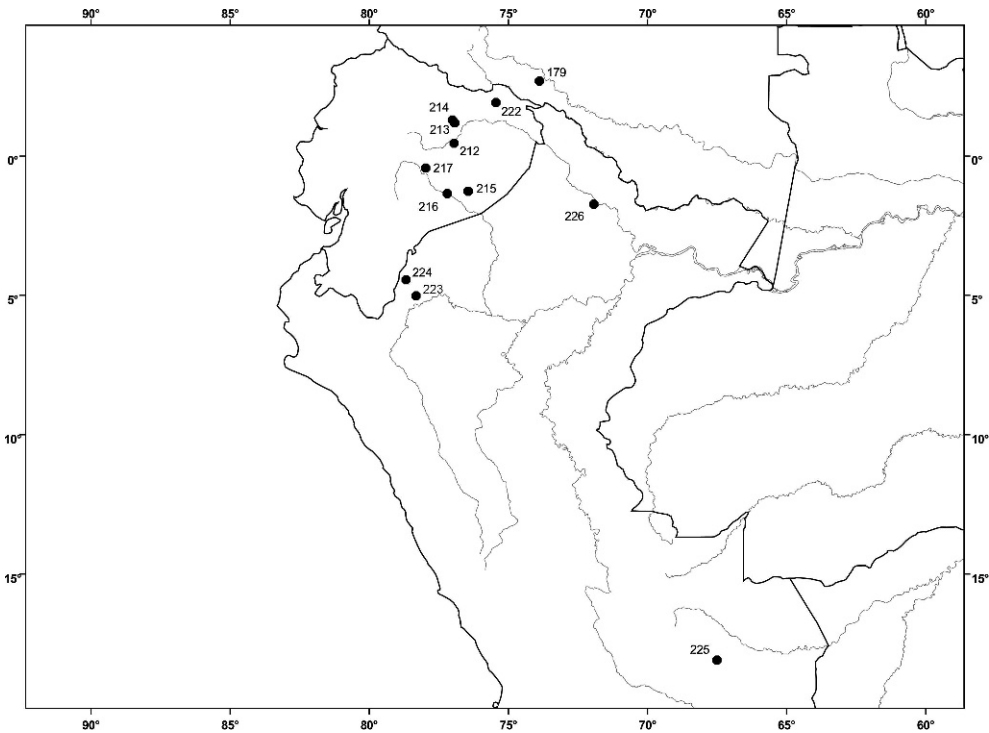
Fig. 30. Geographic range of *Marmosa rubra* based on specimens examined. Numbered points correspond to collection localities listed in the gazetteer (appendix).

analyses of molecular sequence data (e.g., Voss and Jansa, 2003, 2009; see fig. 2). To our knowledge, the validity of *Marmosa rubra* as a full species of mouse opossum has never been questioned.

SPECIMENS EXAMINED ($N = 44$): **CO-LOMBIA**—*Putumayo*, Río Mecaya (FMNH 70969–70977). **ECUADOR**—Province unknown, Huachi (BMNH 54.268). *Napo*, Puerto Napo (= Near the River Napo: BMNH 34.9.10.230–34.910.233). *Orellana*, San José Nuevo (= San José: AMNH 68128; = San José Abajo: AMNH 68129, 68137–68139), San José de Payamino (FMNH 124612). *Pastaza*, Montalvo (FMNH 41452–41454, USNM 274577), Río Copotaza (= Río Copataza: FMNH 53348, 53350), Río Pindo (= Rio Pindo Yaco: FMNH 43181–43183, USNM 274578). *Sucumbíos*, Marian (FMNH 124611). **PERU**—*Amazonas*, Huampami (= Headwaters of Río Huampami: MVZ 153283; = [Vicinity of] Huampami (MVZ 153280, 153282, 154759, 154765), Puesto Vigilancia Comaina (USNM 581941). *Cusco*, Hacienda Villa Carmen (FMNH 84253). *Loreto*, Boca del Río Curaray (AMNH 71950, 71952, 71953, 71972, 71973 [holotype of *Marmosa rubra* Tate, 1931], 71976).

DISCUSSION

Most Neotropical biogeographers recognize a basic dichotomy between lowland and lower-montane biotas separated by high elevations of the Andean cordilleras. Following the terminology suggested by Haffer (1967), landscapes east of the Andes are called cis-Andean, whereas those west of the Andes are trans-Andean. Trans-Andean biotas include those found in Central America, along the Pacific coast of Colombia and Ecuador, and in the Caribbean lowlands of northern Colombia and western Venezuela. The biotas most commonly referred to as cis-Andean include those of the eastern Andean piedmont, the Amazonian lowlands, and the Atlantic Forest of southeastern Brazil.

The seven species recognized as valid in this report include all of the trans-Andean taxa in the nominotypical subgenus of *Marmosa*. Four of these (*M. mexicana*, *M. zeledoni*, *M. isthmica*, and *M. simonsi*) are trans-Andean endemics, a fifth (*M. robinsoni*) occurs on both sides of the Andes, and a sixth (*M. xerophila*) is restricted to a transitional region flanked by separate spurs of the northern Andes. The seventh species (*M. rubra*) is cis-Andean, as are all of the other currently recognized species of the subgenus *Marmosa*: *M. andersoni*, *M. lepida*, *M. murina*, *M. quichua*, and *M. tyleriana*.

Phylogenetic relationships are crucial for evaluating alternative historical scenarios that might account for the current distribution of *Marmosa* species east and west of the Andes. Although *M. mexicana* and *M. isthmica* form a well-supported monophyletic group (fig. 2), the relationships of other trans-Andean congeners are effectively unknown. Obviously, relatively simple scenarios would be supported if all of the trans-Andean species were found to belong to a monophyletic group that did not include any cis-Andean taxa. No morphological traits seem to be unique to the trans-Andean species of *Marmosa*, however, and relevant molecular data are not yet available for analysis. Absent a meaningful phylogenetic context, most of the biogeographic implications of our taxonomic results are obscure.

Nevertheless, the trans-Andean didelphid fauna is evidently more speciose than was previously recognized, and we expect that even more trans-Andean species will be recognized when other opossum genera known to occur in the region are eventually revised. A probable outcome of such revisionary work will be the recognition of several trans-Andean centers of mammalian endemism that have long been obscured by traditional taxonomy. The geographic range of *Marmosa simonsi* in southwestern Ecuador and northwestern Peru, for example, is strikingly similar to that of *Sigmodon peruanus* (see Voss, 1992), whereas the distribution of *M. zeledoni* from Nicaragua to western Colombia strikingly resembles that of *Transandinomys bolivaris* (see Musser et al., 1998). Such distributional congruences suggest the existence of shared historical or ecological constraints that may have shaped the range limits of other organisms in the region and merit the attention of both zoogeographers and conservationists.

This report is not, of course, the last word about the taxonomy of the *Marmosa* species treated herein. In fact, molecular sequencing studies are currently underway to assess whether or not the species herein recognized on the basis of morphology are genetically distinct lineages, and we welcome such close scrutiny of our results. Morphology doubtless provides an incomplete record of evolved differences among populations and taxa: we have just scratched the surface by examining dried skins and skulls. Although we are confident that the species we recognize are valid, it seems plausible that other (genetically distinct but morphologically cryptic) species remain to be discovered within at least some of the geographically widespread forms diagnosed in this report (E. Gutiérrez, personal commun.). Should that prove to be the case, then another cycle of specimen examination informed by new analytic results will be in order.

ACKNOWLEDGMENTS

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APPENDIX

Gazetteer of Examined Specimens

This gazetteer includes all localities from which we personally examined specimens of *Marmosa* for this report. Numbers correspond to specimen records plotted on maps in the text. Countries are listed in geographic sequence from Mexico through Central America to South America. Italicized place names are those of the largest political divisions (state, department, province, etc) within each country. Boldface identifies collection localities as they appear in the text of this report. For each entry we provide geographic coordinates and elevation above sea level (in square brackets, if known), and the source from which we obtained the coordinate data. We also list verbatim place names (in double quotes) as they appear on specimen labels, followed by the name(s) of the collector(s), date(s) of collection, and the name of the species collected there. Some obsolete place names (e.g., the "Canal Zone" of central Panama) are retained to minimize confusion with well-established usage in the zoological literature.

MEXICO

1. *Campeche*, **44 km S Constitución** (18°15′N, 90°04′W; NGA, 2005; ITM, 1989). "44 km S Constitución, Campeche," M.D. Engstrom et al., 16 January 1989: *Marmosa mexicana*.
2. *Campeche*, **Xpujil** (18°30′N, 89°24′W; NGA, 2005). "25 km N Xpujil, Campeche," M.D. Engstrom et al., 5 February 1989: *Marmosa mexicana*.
3. *Chiapas*, **Chicharras** (15°06′N, 92°15′W; USBGN, 1956a). "Chicharras, Chiapas," E.W. Nelson and E.A. Goldman, 15 February 1896: *Marmosa mexicana*. See Goldman (1951) for an account of this locality, which is also known as "Las Chicharras."
4. *Chiapas*, **Huehuetan** (15°01′N, 92°22′W; NGA, 2005). "Huehuetan, Chiapas," E.W. Nelson and E.A. Goldman, 26 February–1 March 1896: *Marmosa mexicana*.
5. *Chiapas*, **Rayón** (17°12′N, 93°00′W [ca. 1000 m]; NGA, 2005). "3.5 mi SE (by road) Rayón, Chiapas," D.S. Rogers, 23 December 1980: *Marmosa mexicana*.
6. *Chiapas*, **San José** (16°02′N, 91°49′W [1493 m]; NGA, 2005). "San José, 28 mi ESE Comitán, Chiapas," C.B. Koford and W.J. Riemer, 8 April 1950: *Marmosa mexicana*.
7. *Chiapas*, **Volcán Tacaná** (15°08′N, 92°06′W [1300 m]; NGA, 2005). "Upper Unión Juárez, Volcán Tacaná, Chiapas," R.L. Seib, 31 July 1978: *Marmosa mexicana*.
8. *Oaxaca*, **Juchitán** (16°26′N, 95°01′W; NGA, 2005). "Río Negro, junction of río Porta Moneda, Juchitán, Oaxaca," T. MacDougall, 4 March 1962: *Marmosa mexicana*.
9. *Oaxaca*, **Lachiguirí** (16°41′N, 95°32′W; NGA, 2005). "Agua Sarco, Lachiguirí, Tehuantepec District, Oaxaca," T. MacDougall, 18 February 1967: *Marmosa mexicana*.
10. *Oaxaca*, **San Gabriel Mixtepec** (16°05′N, 97°06′W; NGA, 2005). Including "2 mi E San Gabriel Mistepec, Oaxaca" and "5 mi E San Gabriel Mistepec, Oaxaca," M.D. Tuttle, 25 July–1 August 1962: *Marmosa mexicana*.
11. *Oaxaca*, **Santa Catarina Juquila** (16°14′N, 97°18′W [1500 m]; NGA, 2005). "Juquila, Oaxaca," E.W. Nelson and E.A. Goldman, 28 February 1895: *Marmosa mexicana*.
12. *Oaxaca*, **Tehuantepec** (16°20′N, 95°14′W; NGA, 2005). "4 mi E Tehuantepec, via Hwy. 190, Oaxaca," R.D. Sage, 21 June 1965: *Marmosa mexicana*.
13. *San Luis Potosí*, **El Salto Falls** (ca. 22°36′N, 99°24′W; USBGN, 1956a). "El Salto Falls, San Luis Potosí," A.D. Stock, 24 February 1963: *Marmosa mexicana*. Kirkpatrick and Zimmerman (1975: fig. 1) plotted this locality at or near the town of Salto de Agua, which has the USBGN coordinates given here.
14. *Tamaulipas*, **Aserradero del Infernillo** (ca. 23°03′N, 99°09′W; USBGN, 1956a). "Aserradero del Infernillo cave, alt. 4400′, Tamaulipas," P.S. Martin, 5 June 1953: *Marmosa mexicana*. According to Goodwin (1954), Aserradero del Infernillo is 11 km west of Gómez Farías, which has the USBGN coordinates given here.
15. *Veracruz*, **Achotal de Moreno** (17°44′N, 95°10′W; NGA, 2005). "Achotal, Vera Cruz," E. Heller, 8 January–20 February 1904: *Marmosa mexicana*.
16. *Veracruz*, **Jalapa Enríquez** (19°32′N, 96°55′W [1341 m]; NGA, 2005). "Jalapa, Vera Cruz," F.M. Chapman, 1 April 1896, 4 April–29 June 1897, 29–31 March 1901: *Marmosa mexicana*.
17. *Veracruz*, **Mirador** (19°13′N, 96°51′W; USBGN, 1956a). "Mirador, Veracruz," [C.] Sartorius [no date]: *Marmosa mexicana*. According to Smith and Braestrup (1962), Mirador (also known as "El Mirador") was a farm belonging to C. Sartorius "situated 24 leagues west of Vera Cruz," for which the best USBGN match is given here.
18. *Veracruz*, **Paso Nuevo** (18°01′N, 94°27′W; USBGN, 1956a). "Pasa Nueva, Veracruz," A.E. Colburn, 3 October–3 November 1901: *Marmosa mexicana*. Wetmore's (1943: fig. 11) map of ornithological collecting stations in southern Veracruz convincingly associates Colburn's "Pasa Nueva" with the Paso Nuevo of modern gazetteers.
19. *Veracruz*, **San Andrés Tuxtla** (18°27′N, 95°13′W; NGA, 2005). "San Andre Tuxtla," Sallé, April 1857: *Marmosa mexicana*.
20. *Veracruz*, **Tuxpan de Rodríguez Cano** (20°57′N, 97°24′W; NGA, 2005). "Tuxpan, Vera Cruz," G. Lincecum [no date]: *Marmosa mexicana*.
21. *Yucatán*, **Chichén Itzá** (20°40′N, 88°34′W; NGA, 2005). "Chichén Itzá, Yucatán," Hatt, 21 October 1929: *Marmosa mexicana*.
22. *Yucatán*, **Izamal** (20°56′N, 89°01′W; NGA, 2005). "Izamal, Yucatán," G.F. Gaumer, March 1913: *Marmosa mexicana*.

BELIZE

23. *Cayo*, **Central Farm** (17°11′N, 89°00′W; NGA, 2005). "Central Farm, Cayo," R.H.L. Disney, 18 May–28 November 1964: *Marmosa mexicana*.

24. *Cayo*, **Georgeville** (17°11′N, 88°58′W; NGA, 2005). Including "About 10.5 miles along Chiquibul Road from San Diego (or Georgeville), Cayo District," "About 7 miles along Chiquibul Road from San Diego (or Georgeville), Cayo District," and "About 8 miles along Chiquibul Road from San Diego (or Georgeville), Cayo District," R.H.L. Disney, 28 January–31 December 1965: *Marmosa mexicana*.

25. *Cayo*, **Roaring Creek** (17°15′N, 88°47′W; NGA, 2005). Including "Roaring Creek (New Capital Site), Cayo District," R.H.L. Disney, 1964; and "5 miles on Humming Bird Highway from Roaring Creek to Stann Creek," P. Lainson [no date]: *Marmosa mexicana*.

26. *Orange Walk*, **Yo Creek** (18°05′N, 88°38′W; NGA, 2005). "Yo Creek, Orange Walk District," R.H.L. Disney, 26 August 1965: *Marmosa mexicana*.

27. *Stann Creek*, **Bokawina Hill** (16°55′N, 88°23′W; NGA, 2005). "Bokowina," I.T. Sanderson, 24 October–3 November 1939: *Marmosa mexicana*.

28. *Stann Creek*, **Cockscomb Basin Wildlife Sanctuary** (16°46′N, 88°32′W [80 m]; collector's label). "Cockscomb Basin Wildlife, at confluence of Cockscomb branch and Mexican branch, Stann Creek," J.F. Jacobs, 16 May 1995: *Marmosa mexicana*.

29. *Stann Creek*, **Silk Grass** (16°53′N, 88°20′W; NGA, 2005). "Silkgrass," I.T. Sanderson, 1 December 1939: *Marmosa* cf. *mexicana*.

30. *Toledo*, **Double Fall** (16°41′N, 88°37′W; NGA, 2005). "Double Falls," I.T. Sanderson, 17 December 1939: *Marmosa mexicana*.

31. *Toledo*, **Union Camp** (16°23′N, 89°09′W [700 m]; collector's label). "Union Camp, Columbia River Forest, Toledo," L.H. Emmons, 4–5 April 1992: *Marmosa mexicana*.

GUATEMALA

32a. *Alta Verapaz*, **Cobán** (15°29′N, 90°19′W; NGA, 2005). "Cobán, Alta Vera Paz," F.J.W. Schmidt, 24–28 March 1934: *Marmosa mexicana*.

32b. *Alta Verapaz*, **La Primavera** (ca. 15°20′N, 90°28′W [ca. 1100 m]; estimated by authors [see below]). "La Primavera," A.W. Anthony, 4 April 1928: *Marmosa mexicana*. According to Stuart (1948), La Primavera was a finca 21 km SW of Cobán (15°29′N, 90°19′W; NGA, 2005) at about 1100 m.

33. *Baja Verapaz*, **Chilascó** (15°07′N, 90°05′W; NGA, 2005). "Chilascó," A. Alfaro, May 1897: *Marmosa mexicana*.

34. *Baja Verapaz*, **San Jerónimo** (15°03′N, 90°12′W; USBGN, 1965). "San Geronimo," [O.] Salvin, November 1878: *Marmosa mexicana*. Based on Griscom's (1932) account of Salvin's collecting activities, it would appear that 1878 was the date

when the specimen was donated to the BMNH, not the date of collection.

35. *Chiquimula*, **Esquipulas** (14°34′N, 89°21′W; NGA, 2005). "Caserio El Chajal, Esquipulas," R.G. Mclean and S.R. Ubico, 14 April 1983: *Marmosa mexicana*.

36. *Esquintla*, **San José** (13°55′N 90°49′W; Hooper, 1952). "San Jose," C.O. Handley, Jr., 4 April 1947: *Marmosa mexicana*.

37. *Guatemala*, **Lago de Amatitlán** (14°28′N, 90°34′W [1280 m]; NGA, 2005). "Lake Amatitlán," C.O. Handley, Jr., 16 March 1947: *Marmosa mexicana*.

38. *Izabal*, **Bobos** (15°21′N, 88°48′W; USBGN, 1965). "Bobos, Izabal," F.J.W. Schmidt, 17–26 December 1933: *Marmosa mexicana*.

39. *Izabal*, **Escobas** (15°41′N, 88°38′W [183 m]; NGA, 2005). "Escobas, Izabal," F.J.W. Schmidt, 30 November 1933: *Marmosa mexicana*.

40. *Izabal*, **La Esmeralda** (15°40′N, 88°59′W; NGA, 2005). "10 km W La Esmeralda, Finca Santa Anita, Izabal," J. Garcia and H. Orellana, 7 August 1981: *Marmosa mexicana*.

41. *Izabal*, **Río Frío** (15°41′N 88°55′W; NGA, 2005). "Finca Río Frío, Izabal," R.G. Mclean and S.R. Ubico, 14 March 1984: *Marmosa mexicana*.

42. *Progreso*, **5 km E San Cristóbal Acasaguastlán** (14°54′N, 89°50′W [240 m]; collector's label). "5 km E San Cristóbal Acasaguastlán, Río Uyus, El Progreso," M.D. Engstrom et al., 2 January 1992: *Marmosa mexicana*.

43. *Progreso*, **Puerta de Golpe** (15°59′N, 89°58′W; NGA, 2005). "Aldea Puerta Golpe, 4.5 km N San Agustín, El Progreso," R.G. Mclean and S.R. Ubico, 24 February 1983: *Marmosa mexicana*.

44. *San Marcos*, **Nuevo Progreso** (14°48′N, 91°55′W; NGA, 2005). Including "Finca Eden, Nuevo Progreso, San Marcos" and "Finca Eden, 10 km N Nuevo Progreso, Nuevo Progreso, San Marcos," R.G. Mclean and S.R. Ubico, 19 April 1983: *Marmosa mexicana*.

45. *Zacapa*, **Cabañas** (14°56′N, 89°48′W; NGA, 2005). "Cabanas," G. Ibarra, July 1990: *Marmosa mexicana*.

46. *Zacapa*, **Río Hondo** (ca. 15°04′N, 89°35′W; NGA, 2005). "Finca El Chahuite, Sierra de las Minas, Zacapa," R.G. Mclean and S.R. Ubico, 17 May 1984: *Marmosa mexicana*. Finca El Chahuite is situated in Río Hondo municipality according to the USNM collection database.

EL SALVADOR

47. *San Miguel*, **Laguna Olomega** (13°19′N, 88°04′W [61 m]; NGA, 2005). "SW edge lake Olomega, Depto. San Miguel," M. Hildebrand and R.A. Stirton, 7 February 1942: *Marmosa mexicana*.

48. *Sonsonate*, **Chilata** (13°40′N, 89°32′W [610 m]; NGA, 2005). Including "Hacienda Chilata, Depto. Sonsonate" and "Hacienda Chilata [792 m], Finca Las Tablas, Depto. Sonsonate,"

R.A. Stirton, 22 April 1927 and 6 May 1942 (respectively): *Marmosa mexicana.*

49. *Sonsonate*, **Sonsonate** (13°43′N, 89°44′W; NGA, 2005). "9 mi ENE Sonsonate, Sonsonate Dept.," R.W. Dickerman, 8 July 1972: *Marmosa mexicana.*

50. *Usulatán*, **Puerto El Triunfo** (13°17′N, 88°33′W [0 m]; NGA, 2005). "Puerto del Triunfo, Depto. Usulatan," R.A. Stirton, 9–16 January 1926: *Marmosa mexicana.*

HONDURAS

51. *Cortés*, **Catacombas** (ca. 15°35′N, 88°20′W; estimated by authors [see below]). "Catacombas," C.F. Underwood, 28 March 1933: *Marmosa mexicana.* According to Goodwin (1942), Catacombas was a farm about 15 miles northwest of Cofradía (15 24′N, 88 09′W; USBGN, 1956c).

52. *Francisco Morazán*, **Monte Vásquez** (14°18′N, 87°18′W; NGA, 2005). "Cerro Vásquez," C.F. Underwood, 15 February 1932: *Marmosa mexicana.*

53. *Islas de la Bahía*, **Isla de Roatán** (16°23′N, 86°30′W; NGA, 2005). "Ruatán Island, Islas de La Bahía," J. Akhurst [no date]: *Marmosa mexicana.*

54. *La Paz*, **Humuya** (14°15′N, 87°40′W [670 m]; NGA, 2005; ITM, 1989). "Humuya, La Paz," C. F. Underwood, 20–24 February 1937: *Marmosa mexicana.*

55. *Santa Bárbara*, **San José de Santa Bárbara** (ca. 15°00′N, 88°13′W; USBGN, 1956c). "San Jose de Santa Barbara," C. F. Underwood, 13 April 1935: *Marmosa mexicana.* According to Goodwin (1942), San José de Santa Bárbara is a "hamlet east of Ilama," the coordinates of which are given above.

NICARAGUA

56. *Atlántico Sur*, **Escondido River** (ca. 12°05′N, 84°03′W; ITM, 1989). Including "Escondido River, 35 mi from Bluefields," J.C. Zeledon, 13 May 1892; and "Escondido River, 50 mi from Bluefields," J.C. Zeledon, 23 August 1892: *Marmosa zeledoni* and *M.* cf. *zeledoni.*

57. *Atlántico Sur*, **Isla del Maíz Grande** (12°10′N, 83°03′W; NGA, 2005). "Great Corn Island, Corn Islands," J. L. Peters, 16–18 December 1927: *Marmosa mexicana.*

58. *Carazo*, **Diriamba** (11°53′N, 86°15′W [610 m]; NGA, 2005). "Finca America, 30 mi S Managua, Managua," J.M. Boshell, Fall 1953: *Marmosa* cf. *mexicana.*

59. *Chinandega*, **Volcán San Cristóbal** (12°42′N, 87°01′W; NGA, 2005). "Volcán de Chinandega," W.B. Richardson, 9 May 1907: *Marmosa mexicana* and *M.* cf. *mexicana.*

60. *Jinotega*, **Río Coco** (13°27′N, 85°55′W; Howell, 1993). "Río Coco," W.B. Richardson, 11 November–1 December 1908: *Marmosa mexicana* and *M. zeledoni.* See Howell (1993) for a thoughtful discussion of this problematic local-

ity, which seems to correspond to the environs of the village of Santa Cruz, the coordinates of which are given above.

61. *Jinotega*, **San Rafael del Norte** (13°11′N, 86°06′W; NGA, 2005). "San Rafael del Norte," W.B. Richardson, 11 April 1907: *Marmosa zeledoni.*

62. *Managua*, **Managua** (12°09′N, 86°17′W; NGA, 2005). "13 km S Managua," G. Espinosa, 14 May 1963: *Marmosa mexicana.*

63. *Matagalpa*, **El Tuma** (13°04′N, 85°48′W; ITM, 1989). "Río Tuma, E Matagalpa," W.B. Richardson, 30 March 1929: *Marmosa zeledoni.* El Tuma is a village in NE Matagalpa, close to the Río Tuma.

64. *Matagalpa*, **Matagalpa** (12°53′N, 85°57′W; NGA, 2005). "Matagalpa," W.B. Richardson, 10 November 1908: *Marmosa mexicana.*

65. *Matagalpa*, **Vijagua** (12°35′N, 85°13′W; NGA, 2005). "Vijagua," W.B. Richardson, 21 March 1909: *Marmosa zeledoni.*

66. *Nueva Segovia*, **Ocotal** (13°38′N, 86°29′W; USBGN, 1956b). "Ocotal," W.B. Richardson, 5 September 1928: *Marmosa mexicana.*

67. *Río San Juan*, **San Carlos** (11°07′N, 84°47′W; NGA, 2005). "La Esperanza, 5 km S and 3.5 km E San Carlos," M.K. Clark, 30 January–7 May 1965: *Marmosa zeledoni.* The location of La Esperanza as "5 km S and 3.5 km E San Carlos" is provided by the USNM collection database.

68. *Rivas*, **San Emilio** (11°03′N, 85°26′W; Howell, 1964). "San Emilio," W.B. Richardson, 22 March 1896: *Marmosa mexicana.*

COSTA RICA

69. *Cartago*, **Aquiares** (9°56′N, 83°43′W [1219 m]; NGA, 2005). "Aquiares, Cartago," A.P. Smith, 14 April 1920: *Marmosa zeledoni.*

70. *Cartago*, **Cerro Carpintera** (9°53′N, 83°59′W; NGA, 2005). "La Carpintera," G.K. Cherrie, 15 December 1890: *Marmosa zeledoni.* "La Carpintera" is a mountain 8 miles east of San José (Allen, 1891).

71. *Cartago*, **Navarro** (9°49′N, 83°52′W; NGA, 2005). "Navarro, Cartago," J. Cooper, 1 March 1878: *Marmosa zeledoni* and *M.* cf. *zeledoni.*

72. *Heredia*, **11 km S and 4.5 km W Puerto Viejo** (10°21′N, 84°03′W [325 m]; NGS, 2004). "Parque Nacional Braulio Carrillo, 11 km S and 4.5 km W Puerto Viejo, Heredia," R.M. Timm, 28–31 March 1986: *Marmosa zeledoni* and *M.* cf. *zeledoni.*

73. *Heredia*, **11 km S and 11.5 km E San Miguel Ángeles** (10°18′N, 84°04′W [710 m]; NGS, 2004). "Parque Nacional Braulio Carrillo, 11 km S and 11.5 km E San Miguel, Heredia," R.M. Timm, 4 April 1986: *Marmosa zeledoni.*

74. *Limón*, **Jiménez** (10°13′N, 83°43′W; NGA, 2005). "Jiménez," G.K. Cherrie, August 1891: *Marmosa zeledoni.*

75. *Limón*, **Pandora** (9°45′N, 82°57′W; NGA, 2005). "3 mi S Pandora, Estrella Valley," H.W. Setzer, 20 April 1949: *Marmosa* cf. *zeledoni.*

76. *Puntarenas*, **Boruca** (9°00′N, 83°20′W; NGA, 2005). "Boruca," G.K. Cherrie, 30 November 1891: *Marmosa* cf. *zeledoni*.

77. *Puntarenas*, **Cerro Cañas Gordas** (8°44′N, 83°00′W; NGA, 2005). "Cañas Gordas," C.F. Underwood, 8 December 1942–5 January 1943: *Marmosa zeledoni*.

78. *Puntarenas*, **Coto Brus** (8°58′N, 83°03′W; NGS, 2004). "Costa Brus, Puntarenas," R.K. Enders, 11 March 1974: *Marmosa zeledoni*.

79. *Puntarenas*, **Finca Helechales** (ca. 9°05′N, 83°05′W [910–1550 m]; collectors′labels and fieldnotes). Including "Finca Helechales, Puntarenas," "2 km NE (by road) Finca Helechales, Puntarenas," "2.6 km (by road) NE Finca Helechales, Puntarenas," and "4.7 km (by road) NE Finca Helechales, Puntarenas," G.K. Creighton and R.S. Voss, 19–26 December 1984: *Marmosa mexicana* and *M. zeledoni*. Creighton and Voss collected from 910 m (at Finca Helechales) to 1550 m (at 4.7 km NE); *Marmosa mexicana* was collected only at the lowermost elevation, whereas *M. zeledoni* was collected at all sampled elevations.

80. *Puntarenas*, **Monteverde** (10°18′N, 84°49′W [1400 m]; NGA, 2005). Including "Monteverde, Puntarenas," R.K. LaVal, 9 December 1980, 5 February 1983; and "Alajuela, Monteverde," R.M. Timm, 3 June 1982: *Marmosa mexicana* and *M. zeledoni*.

81. *Puntarenas*, **San Jerónimo** (10°02′N, 84°40′W; NGA, 2005). "San Geronimo, Puntarenas," C.F. Underwood, 8 April 1931: *Marmosa zeledoni*.

82. *San José*, **Escazú** (9°55′N, 84°08′W; NGA, 2005). "Escazu," C.F. Underwood, 30 March 1901: *Marmosa zeledoni*.

PANAMA

83. *Bocas del Toro*, **Almirante** (9°18′N, 82°24′W; Fairchild and Handley, 1966). "Almirante, Bocas del Toro," C.O. Handley, Jr. and D.I. Rhymer, 19–21 January 1960: *Marmosa zeledoni* and *M.* cf. *zeledoni*.

84. *Bocas del Toro*, **Boca del Drago** (9°26′N, 82°20′W; Fairchild and Handley, 1966). "Boca del Drago, Bocas del Toro," C.O. Handley, Jr. and D. I. Rhymer, 22 February 1960: *Marmosa* cf. *zeledoni*.

85. *Bocas del Toro*, **Changuinola** (9°27′N, 82°31′W; Fairchild and Handley, 1966). "7 km SSW Changuinola, Bocas del Toro," C.O. Handley, Jr. and D.I. Rhymer, 3–10 March 1960: *Marmosa zeledoni*.

86. *Bocas del Toro*, **E of Cerro Pando** (8°55′N, 82°42′W [2200 m]; USNM collection database). "E of Cerro Pando, Bocas del Toro," G.K. Cherrie, 30 November 1891: *Marmosa zeledoni*.

87. *Bocas del Toro*, **Fish Camp** (8°58′N, 82°40′W [1493 m]; USNM collection database). "Fish Camp, Bocas del Toro," W.B. Richardson, 5 December 1910: *Marmosa zeledoni*.

88. *Bocas del Toro*, **N of El Volcán** (8°55′N, 82°38′W [1050 m]; Kevin Healey's Travel Map of Panamá [1:800,000]). "North El Volcán, Bocas del Toro," R.K. Enders, 31 March 1975: *Marmosa* cf. *zeledoni*.

89. *Bocas del Toro*, **Ñuri** (8°55′N, 81°49′W; NGA, 2005). "Ñuri, Bocas del Toro," F.M. Greenwell, 9–22 March 1993; C.O. Handley, Jr., 31 March–3 April 1993: *Marmosa isthmica*.

90. *Bocas del Toro*, **Río Changena Camp** (9°06′N, 82°34′W [762 m]; Fairchild and Handley, 1966). "Above Rain Forest, Rio Changena Camp, Bocas," W.B. Richardson, 3 December 1910: *Marmosa zeledoni*.

91. *Canal Zone*, **Balboa** (8°57′N, 79°35′W; Fairchild and Handley, 1966). "8 km W Balboa, Rodman Naval Ammo Depot, Canal Zone," T.H. Fleming, 11 June 1966–3 May 1967: *Marmosa isthmica* and *M. robinsoni*.

92. *Canal Zone*, **Camp Piña** (9°16′N, 80°00′W; Fairchild and Handley, 1966). "Camp Piña, Fort Sherman, Canal Zone," C.M. Keenan, 11–12 May 1955; collector unknown, 2 March–30 August 1956: *Marmosa isthmica* and *M.* cf. *isthmica*.

93. *Canal Zone*, **Chiva Chiva** (9°01′N, 79°35′W; Fairchild and Handley, 1966). "Chiva-Chiva, Canal Zone," C.M. Keenan, 12 September 1955: *Marmosa isthmica*.

94. *Canal Zone*, **Cristóbal** (9°20′N, 79°57′W; Fairchild and Handley, 1966). "6 km W, Fort Sherman, Cristóbal, Canal Zone," T.H. Fleming, 23 July 1966–14 May 1967: *Marmosa isthmica*.

95. *Canal Zone*, **Fort Davis** (9°15′N, 79°56′W; Fairchild and Handley, 1966). Including "Dock 45 Rd, Fort Davis, Canal Zone," C.M. Keenan, 24 September 1953; and "Fort Davis, Canal Zone," collector unknown, 16 March 1956: *Marmosa isthmica*.

96. *Canal Zone*, **Fort Kobbe** (8°54′N, 79°36′W; Fairchild and Handley, 1966). "Fort Kobbe, Canal Zone," C.M. Keenan, 2 September 1954–6 April 1955; collector unknown, 23 March 1956: *Marmosa robinsoni*.

97. *Canal Zone*, **Fort Sherman** (9°21′N, 79°57′W; Fairchild and Handley, 1966). "3 mi S Fort Sherman, Mohinga Valley, Canal Zone," H.W. Setzer, 17 January 1953: *Marmosa* cf. *isthmica*.

98. *Canal Zone*, **Frijoles** (9°10′N, 79°49′W; Fairchild and Handley, 1966). "1.75 km NNW Frijoles, Buena Vista Peninsula, Canal Zone," D.E. Wilson, 31 May 1972. *Marmosa isthmica*.

99. *Canal Zone*, **Gatún** (9°15′N, 79°56′W; Fairchild and Handley, 1966). "Gatún," H.E. Anthony, 26 February–3 March 1914; collector unknown, 16 March 1956: *Marmosa isthmica*.

100. *Canal Zone*, **Madden Road** (9°07′N, 79°38′W; Fairchild and Handley, 1966). "Madden Road, Canal Zone," C.M. Keenan, 25 January–8 March 1955: *Marmosa isthmica*.

101. *Canal Zone*, **Miraflores** (8°59′N, 79°36′W; Fairchild and Handley, 1966). "Miraflores, Canal Zone," C.M. Keenan, 20 December 1960: *Marmosa robinsoni*.

102. *Canal Zone*, **Quarry Heights** (8°57′N, 79°34′W; Fairchild and Handley, 1966). "Quarry Heights,

Canal Zone," collector unknown, 28 June–3 July 1956: *Marmosa robinsoni*.

103. *Canal Zone*, **Río Indio** (9°15′N, 79°59′W; Fairchild and Handley, 1966). "Río Indio, Near Gatún, Canal Zone," E.A. Goldman, 16 February 1911: *Marmosa isthmica*.

104. *Chiriquí*, **Boquerón** (8°31′N, 82°34′W; Fairchild and Handley, 1966). "Boquerón, Chiriquí," J.H. Batty, 6–31 October 1901: *Marmosa mexicana*.

105. *Chiriquí*, **Bugaba** (8°29′N, 82°37′W; Fairchild and Handley, 1966). "Bogava, Chiriquí," H.J. Watson, 2 September–9 November 1898, 2 Sep 1903: *Marmosa mexicana* and *M. zeledoni*.

106. *Chiriquí*, **Casa Tilley** (8°51′N, 82°36′W; Fairchild and Handley, 1966). "Casa Tilly, Cerro Punta, Chiriquí," C.M. Keenan, 23 January 1960: *Marmosa zeledoni*.

107. *Chiriquí*, **Cerro Fortuna** (8°44′N, 82°16′W [1100 m]; NGA, 2005). "Quebrada Honda, Reserva Florestal Fortuna," A. Carvajal, 16 October 2001: *Marmosa zeledoni*.

108. *Chiriquí*, **El Volcán** (8°47′N, 82°38′W [1249 m]; Fairchild and Handley, 1966). "Volcán, Chiriquí," F.A. Hartman, 16–17 March 1951: *Marmosa zeledoni*.

109. *Chiriquí*, **Finca Santa Clara** (8°51′N, 82°45′W; USNM collection database). "Finca Santa Clara, 14.5 km NW El Volcán, Chiriquí," R.K. Enders, 18 February 1971, 13 November 1973; "Osta Clara," R.K. Enders, 19 February 1973: *Marmosa zeledoni*, *M.* cf. *zeledoni*, and *M. robinsoni*.

110. *Chiriquí*, **Near Escopeta Camp** (8°30′N, 81°47′W [1275 m]; Kevin Healey's Travel Map of Panamá [1:800,000]). Including "Near Escopeta Camp, 24 km NNE San Felix, Chiriquí," "24.5 km NNE San Felix, Escopeta Camp, Chiriquí," "25 km NNE San Felix, Chiriquí," and "Colorado Camp, 1.25 km N Escopeta Camp, Chiriquí," R.J. Izor and R.H. Pine, 19 May–8 July 1980: *Marmosa zeledoni*, *M.* cf. *zeledoni*, and *M. robinsoni*.

111. *Chiriquí*, **Tolé** (8°14′N, 81°41′W [305 m]; Fairchild and Handley, 1966). "2 mi NE Tolé, Chiriquí," E.L. Tyson, 8 December 1961: *Marmosa robinsoni*.

112. *Coclé*, **El Valle** (8°36′N, 80°08′W [609–914 m]; Fairchild and Handley, 1966). "6 mi from El Valle, Coclé," R.K. Enders, 9–19 March 1957: *Marmosa isthmica* and *M.* cf. *isthmica*.

113. *Coclé*, **Río Hato** (8°22′N, 80°11′W; Fairchild and Handley, 1966). "2 mi E Rio Hato, Coclé," E.L. Tyson, 31 October 1961: *Marmosa robinsoni*.

114. *Colón*, **Cuipo Point** (9°05′N, 80°03′W; NGA, 2005). "La Uyama, Rio Ciri, Gatún Lake, between Quipo and Escobal, Canal Zone," Chapin, August 1923: *Marmosa isthmica*.

115. *Colón*, **Piña** (9°16′N, 80°03′W; Fairchild and Handley, 1966). "Piña, Colón," C.M. Keenan, 15 November 1960: *Marmosa isthmica*.

116. *Darién*, **Boca de Río Paya** (7°55′N, 77°31′W; Fairchild and Handley, 1966). Including "Camp Mack, Boca de Paya, Darién," R. Hinds, 28 March 1959; and "Mouth of Río Paya, Darién,"

C.O. Handley, Jr., 24 February–10 March 1958: *Marmosa isthmica*.

117. *Darién*, **Cana** (7°47′N, 77°42′W [549 m]; Fairchild and Handley, 1966). "Cana, Darién," E.A. Goldman, 10 March–5 April 1912: *Marmosa isthmica*.

118. *Darién*, **Cerro Malí** (8°07′N, 77°14′W [1432 m]; Fairchild and Handley, 1966). "Cerro Malí, Darién," C.O. Handley, Jr., 30 January–15 February 1964: *Marmosa zeledoni*.

119. *Darién*, **Cerro Tacarcuna** (8°10′N, 77°18′W [1249 m]; Fairchild and Handley, 1966). "Cerro Tacarcuna, Darién," C.O. Handley, Jr., 7 March 1964: *Marmosa zeledoni*.

120. *Darién*, **El Real** (8°06′N, 77°45′W; Fairchild and Handley, 1966). "El Real," W.B. Richardson, 23–24 December 1914: *Marmosa isthmica*.

121. *Darién*, **Jaqué** (7°31′N, 78°10′W; Fairchild and Handley, 1966). Including "8 mi SE Jaqué, Darién," "Junction of Ríos Jaque and Imamado, Jaqué, Darién," and "Jaqué," F.M. Greenwell and T.H. Fleming, 31 January–12 February 1966: *Marmosa isthmica*.

122. *Darién*, **Paya Camp** (7°53′N, 77°24′W; Fairchild and Handley, 1966). "Paya Camp, Darién," R. Hinds, 4–5 April 1959: *Marmosa isthmica*.

123. *Darién*, **Río Chucunaque** (8°23′N, 77°49′W; Fairchild and Handley, 1966). "Río Chucunaque, Darién," C.O. Handley, Jr., 19–20 February 1958: *Marmosa isthmica*.

124. *Darién*, **Río Seteganti** (7°46′N, 77°40′W [640 m]; Fairchild and Handley, 1966). "Near Río Seteganti, Darién"; C.M. Keenan, 31 January–7 February 1961: *Marmosa isthmica*.

125. *Darién*, **Tacarcuna Laguna Camp** (8°04′N, 77°19′W [1219 m]; Fairchild and Handley, 1966). "Tacarcuna Laguna Camp, Darién," C.O. Handley, Jr. and B.R. Feinstein, 9–11 March 1959: *Marmosa isthmica*.

126. *Darién*, **Tacarcuna Village** (8°05′N, 77°17′W [808 m]; Fairchild and Handley, 1966). Including "Mt. Tacarcuna," H.E. Anthony, 21 February–27 March 1915; "Tacarcuna," W.B. Richardson, 7–8 April 1915; "Near G.M.L. Camp, Tacarcuna Region, Darién," collector unknown, 17–18 July 1963; and "Tacarcuna Village Camp, Darién," C.O. Handley, Jr. and B.R. Feinstein, 1 February–15 March 1959: *Marmosa isthmica*.

127. *Darién*, **Tapalisa** (7°59′N, 77°26′W [305 m]; Fairchild and Handley, 1966). "Tapalisa, Darién," W.B. Richardson, 14 March and 3 December 1915: *Marmosa isthmica*.

128. *Darién*, **Yaviza** (8°11′N, 77°41′W; NGA, 2005). "Yaviza, Darién," C. Cavalier, 2 November 1967: *Marmosa mexicana*.

129. *Panamá*, **Cerro Azul** (9°10′N, 79°25′W; NGA, 2005). "Cerro Azul, Panamá," C.M. Keenan, 28 December 1955–9 February 1956; collector unknown, 16 February–14 August 1956, 26 January–1 February 1958; C.O. Handley, Jr., 22 January–7 February 1958; E. Mendez, 20 June 1959: *Marmosa isthmica* and *M.* cf. *isthmica*.

130. *Panamá*, **Cerro Campana** (8°41′N, 79°56′W; Fairchild and Handley, 1966). "Cerro Campana,

Panamá," R.K. Enders, 27 July 1955: *Marmosa isthmica*.

131. *Panamá*, **Cerro Jefe** (9°14′N, 79°21′W; Fairchild and Handley, 1966). "Cerro Jefe, Panamá," collector unknown, 5–7 February 1958: *Marmosa isthmica*.

132. *Panamá*, **Isla del Rey** (8°23′N, 78°56′W; Fairchild and Handley, 1966). "San Miguel Island," W.W. Brown, Jr., 4–8 May 1900; O. Bangs, 28 April 1900: *Marmosa robinsoni*.

133. *Panamá*, **Isla Saboga** (8°37′N, 79°04′W; NGA, 2005). "Saboga Island," W.W. Brown, Jr., 13 April 1904: *Marmosa robinsoni*.

134. *Panamá*, **Pacora** (9°04′N, 79°18′W; Fairchild and Handley, 1966). "4 mi E, 1 mi S Pacora, Panamá," C.B. Koford, 25 April 1957: *Marmosa robinsoni*.

135. *Panamá*, **Río Pequeni** (9°22′N, 79°32′W; Fairchild and Handley, 1966). "Río Pequeni, Candelaria Hydrographic Station," A. Wetmore, 4 March 1961: *Marmosa isthmica*.

136. *Panamá*, **Río Trinidad** (8°57′N, 80°00′W; Fairchild and Handley, 1966). "R. Trinidad, Maxim Ranch," H.E. Anthony, 9–10 March 1914: *Marmosa isthmica*.

137. *Panamá*, **Tocumen** (9°04′N, 79°24′W; Fairchild and Handley, 1966). "Tocumen, Cerro Azul, Panamá," collector unknown, 8 August 1956: *Marmosa isthmica* and *M.* cf. *isthmica*.

138. *San Blas*, **Armila** (8°40′N, 77°27′W; Fairchild and Handley, 1966). "Quebrada Venado, Armila, San Blas," C.O. Handley, Jr. and F.M. Greenwell, 10–28 March 1963: *Marmosa isthmica*.

139. *San Blas*, **Mandinga** (9°29′N, 79°05′W; Fairchild and Handley, 1966). "Mandinga, San Blas," P. Galindo, 29 May 1957; C.O. Handley, Jr., 16–29 May 1957: *Marmosa isthmica*.

140. *Veraguas*, **Santa Fé** (8°31′N, 81°04′W; Fairchild and Handley, 1966). "Río Santa Maria, Santa Fé, Veraguas," R.K. Enders, 17–26 February 1957: *Marmosa robinsoni*.

141. *Veraguas*, **Veraguas** (8°52′N, 80°54′W; NGA, 2005). "Veragua" [collector and date unknown]: *Marmosa mexicana*.

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142. *Antioquia*, **Caucasia** (8°00′N, 75°12′W [250 m]; Paynter, 1997). "12 km S Caucasia, at Hacienda Barro, Antioquia," N.E. Peterson, 11 October 1972: *Marmosa isthmica*.

143. *Antioquia*, **La Tirana** (7°18′N, 75°04′W [520 m]; NGA, 2005). "25 km S and 22 km W Zaragoza, at La Tirana, Antioquia," N.E. Peterson, 9 June 1970–11 November 1971: *Marmosa isthmica*.

144. *Antioquia*, **Purí** (7°25′N, 75°20′W [140 m]; Paynter, 1997). "Purí, above Cáceres, Antioquia," P. Hershkovitz, 24 July 1950: *Marmosa isthmica*.

145. *Antioquia*, **Río Currulao** (8°01′N, 76°44′W [50 m]; Paynter, 1997). "Río Currulao, 20 km SE Turbo, Urabá, Antioquia," P. Hershkovitz, 25 April 1950: *Marmosa isthmica*.

146. *Antioquia*, **San Jerónimo** (6°27′N, 75°45′W [720 m]; Paynter, 1997). "San Jerónimo, 35 km NW Medellín, Medellín, Antioquia," P. Hershkovitz, 19–30 December 1949, 30 December 1950: *Marmosa isthmica*.

147. *Antioquia*, **Valdivia** (7°11′N, 75°27′W [950 m]; Paynter, 1997). Including "Quebrada de Oro, 4 km S Valdivia, Antioquia," "Valdivia, Quebrada Valdivia, Antioquia," "10 km S Valdivia [1700 m], Antioquia," "9 km S Valdivia [1400 m], Antioquia," and "Valdivia, La Cabaña, Antioquia," P. Hershkovitz, 19 June–8 August 1950: *Marmosa isthmica*.

148. *Antioquia*, **Villa Arteaga** (7°20′N, 76°26′W [120 m]; Paynter, 1997). "Villa Arteaga, Urabá, Antioquia," P. Hershkovitz, 16 January–2 February 1950: *Marmosa isthmica*.

149. *Atlántico*, **Barranquilla** (10°58′N, 74°48′W [ca. 100m]; NGA, 2005; Paynter, 1997). Including "Barranquilla, Magdalena" and "Barranquilla," W.C. Russell, 1967; and "Vicinity Barranquilla," M. Hildebrand and R.D. Barnes, 19 May 1966: *Marmosa robinsoni*.

150. *Bolívar*, **San Juan Nepomuceno** (9°57′N, 75°05′W [167 m]; Paynter, 1997). "San Juan Nepomuceno, Bolívar," P. Hershkovitz, 25 January 1949: *Marmosa robinsoni*.

151. *Caldas*, **Samaná** (5°25′N, 76°00′W [1000 m]; NGA, 2005). "Rio Hondo, Samaná, Caldas," P. Hershkovitz, 2 March 1951: *Marmosa isthmica*. Samaná is close to Rio Honda, not to Rio Hondo (Paynter, 1997).

152. *Cesar*, **El Orinoco** (10°10′N, 73°24′W [158 m]; NGA, 2005; Hershkovitz, 1947). Including "Río Cesar, El Orinoco, Valledupar District, Magdalena," P. Hershkovitz, 23 October 1942, 7–12 April 1943; and "Rio Guaimaral, Valledupar District, Magdalena," P. Hershkovitz, 15–23 September 1942: *Marmosa robinsoni*.

153. *Cesar*, **El Salado** (10°22′N, 73°29′W [430 m]; Hershkovitz, 1947). "El Salado, Magdalena," P. Hershkovitz, 5–19 July 1942: *Marmosa robinsoni*.

154. *Cesar*, **San Sebastián de Rábago** (10°34′N, 73°36′W [1900–2000 m]; NGA, 2005; Paynter, 1997). "San Sebastián, Cesar," P. Hershkovitz, 10–14 September 1949: *Marmosa robinsoni*.

155. *Cesar*, **Valledupar** (10°29′N, 73°15′W [202 m]; NGA, 2005; Paynter, 1997). "Aguas Verdes, Valledupar District, Magdalena," P. Hershkovitz, 20 September 1942: *Marmosa robinsoni*.

156. *Chocó*, **Condoto** (5°06′N, 76°39′W [91 m]; NGA, 2005; Paynter, 1997). "Condoto," H.G.F. Spurrell, 20–27 May 1913, 11 March 1914: *Marmosa isthmica*.

157. *Chocó*, **Unguía** (8°03′N, 77°06′W [0 m]; NGA, 2005; Paynter, 1997). "Unguía, Choco," P. Hershkovitz, 8–27 March 1950: *Marmosa isthmica*.

158. *Córdoba*, **Socorré** (7°51′N, 76°17′W [100 m]; Paynter, 1997). "Socorré, upper Rio Sinú, Córdoba," P. Hershkovitz, 6 March–6 April 1949: *Marmosa isthmica*.

159. *Cundinamarca*, **Bogotá** (4°36′N, 74°05′W [2590 m]; NGA, 2005; Paynter, 1997). "Bogotá," M. Bates, 8 May 1944: *Marmosa robinsoni*.

160. *Cundinamarca*, **W of Bogotá** (ca. 4°36′N, 74°48′W; DMA). "Magdalena River, W Bogotá," 22 September 1894: *Marmosa isthmica*.

161. *Huila*, **Naranjal** (2°01′N, 75°51′W; NGA, 2005; DMA, 1986). "Valle de Suaza, Naranjal, Huila," C. del Aguila, 21 July–24 August 1971: *Marmosa robinsoni*.

162. *Huila*, **Villavieja** (3°13′N, 75°13′W [488 m]; NGA, 2005). Including "16 km NE Villavieja, Huila," O.P. Pearson, 12–13 July 1950; "5 km N Villavieja, Huila," A.H. Miller, 13–15 February 1949, 21–23 July 1950; and "7.5 km E Villavieja, Huila," O.P. Pearson, 26 June 1950: *Marmosa robinsoni*.

163. *La Guajira*, **Cojoro** (11°38′N, 71°50′W [15 m]; Handley, 1976). "37 km NNE Paraguaipoa, near Cojoro, La Guajira," N.E. Peterson et al., 28 June 1968; Smithsonian Venezuelan Project, 26–30 June 1968: *Marmosa xerophila*.

164. *La Guajira*, **El Pueblito** (10°59′N, 73°27′W [610 m]; Paynter, 1997). Including "Pueblo Viejo" and "Santa Marta, Pueblo Viejo, Magdalena," W.W. Brown, Jr., 24 March–18 May 1898: *Marmosa robinsoni*.

165. *La Guajira*, **La Concepción** (11°03′N, 72°27′W [ca. 800 m]; Paynter, 1997). "La Concepción," W.W. Brown, Jr., 29 March 1899: *Marmosa robinsoni*.

166. *La Guajira*, **Las Marimondas** (10°52′N, 72°43′W [ca. 1000 m]; Hershkovitz, 1947). "Las Marimondas, Fonseca District, Magdalena," P. Hershkovitz, 6–12 March 1943: *Marmosa robinsoni*.

167. *La Guajira*, **San Miguel** (10°58′N, 73°29′W [1700 m]; Paynter, 1997). "San Miguel," W.W. Brown, Jr., 8 June 1898: *Marmosa robinsoni*.

168. *La Guajira*, **Villanueva** (10°36′N, 72°59′W [274 m]; NGA, 2005; Hershkovitz, 1947). Including "Sierra Negra, Villanueva, Valledupar District, Magdalena," P. Hershkovitz, 30 November 1942–13 January 1943; and "Villanueva, Valledupar District, Magdalena," P. Hershkovitz, 22 January–26 February 1943: *Marmosa robinsoni*.

169. *Magdalena*, **Bonda** (11°14′N, 74°07′W [46 m]; NGA, 2005; Paynter, 1997). "Bonda," H.H. Smith, 1 March–21 September 1899, 2 August 1901; G.H. Hull, 25 August–5 September 1899: *Marmosa robinsoni*.

170. *Magdalena*, **Colonia Agrícola de Caracolicito** (10°18′N, 74°00′W [400 m]; Hershkovitz, 1947). "Colonia Agrícola de Caracolicito, Magdalena," P. Hershkovitz, 6 March 1942: *Marmosa robinsoni*.

171. *Magdalena*, **Mamatoco** (11°14′N, 74°10′W [ca. 25 m]; NGA, 2005; Paynter, 1997). "Mamatoco," H.H. Smith, 1 June 1899: *Marmosa robinsoni*.

172. *Magdalena*, **Minca** (11°09′N, 74°07′W [670 m]; NGA, 2005; Paynter, 1997). "Minca," H.H. Smith, June 1899: *Marmosa robinsoni*.

173. *Magdalena*, **Palomino** (11°02′N, 73°39′W [ca. 600 m]; Paynter, 1997). "Palomino," W.W. Brown, 2 May 1898: *Marmosa robinsoni*.

174. *Magdalena*, **Pueblo Bello** (10°25′N, 73°35′W [1067 m]; NGA, 2005; Hershkovitz, 1947). "Pueblo Bello, Magdalena," P. Hershkovitz, 11 May–2 June 1942: *Marmosa robinsoni*.

175. *Magdalena*, **Taganga** (11°16′N, 74°12′W [0 m]; NGA, 2005; Paynter, 1997). "Taganga," H.H. Smith, 25 June 1899: *Marmosa robinsoni*.

176. *Nariño*, **Candelilla** (1°28′N, 78°41′W [200 m]; NGA, 2005). "Candelilla, Nariño," K. Sneider, 15 March 1958: *Marmosa zeledoni*.

177. *Nariño*, **Guayacana** (1°26′N 78°27′W [250 m]; NGA, 2005). "La Guayacana, Nariño," M.A. Carriker, 2 May 1958: *Marmosa isthmica*.

178. *Norte de Santander*, **Cúcuta** (7°54′N, 72°31′W [215 m]; Paynter, 1997). "Cucuta, 10 mi N," W.H. Osgood and S.G. Jewett, Jr., 14 March 1911: *Marmosa robinsoni*.

179. *Putumayo*, **Río Mecaya** (0°28′N, 75°20′W [185 m]; Paynter, 1997). "Caquetá, Río Mecaya," P. Hershkovitz, 18 February–6 March 1952: *Marmosa rubra*.

180. *Sucre*, **Colosó** (9°30′N, 75°21′W [350 m]; Paynter, 1997). "Las Campañas, Colosó," P. Hershkovitz, 31 May 1949: *Marmosa isthmica*.

181. *Tolima*, **Honda** (5°12′N, 74°45′W [183 m]; Paynter, 1997). "Madalegna River, Honda," Chapman and Cherrie, 7–9 February 1913: *Marmosa robinsoni*.

182. *Tolima*, **Mariquita** (5°12′N, 74°55′W [535 m]; NGA, 2005; Paynter, 1997). "Mariquita, Tolima," J.R. Tamsitt, 18 June 1960: *Marmosa robinsoni*.

183. *Valle del Cauca*, **Lomitas** (3°38′N, 76°38′W [1524 m]; Paynter, 1997). "Las Lomitas, Cauca Valley," W.B. Richardson, 26 February 1911: *Marmosa isthmica*.

184. *Valle del Cauca*, **Río Raposo** (3°43′N, 77°08′W; Paynter, 1997). "Virology Field Camp, Río Raposo, Valle del Cauca," J. Duran, 6 May–26 July 1962: *Marmosa isthmica*.

185. *Valle del Cauca*, **San José** (3°51′N, 76°52′W [99 m]; Paynter, 1997). "San José, Cauca," H.H. Smith [no dates]; W.B. Richardson, 29 November–5 December 1910: *Marmosa zeledoni*, *M.* cf. *zeledoni*, and *M. isthmica*.

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186. *Chimborazo*, **Puente de Chimbo** (2°10′S, 79°06′W; Paynter, 1993). "Puente de Chimbo," H.E. Wickenheiser and G.H.H. Tate, 3 September 1922: *Marmosa isthmica*.

187. *El Oro*, **Río Puyango** (3°53′S, 80°07′W; collector's label). "Rio Puyango, 0353S, 8007W, El Oro," [collector and date unknown]: *Marmosa simonsi*.

188. *El Oro*, **Santa Rosa** (3°27′S, 79°58′W [ca. 100 m]; NGA, 2005; Paynter, 1993). "4 km SE Santa Rosa, El Oro," A.L. Gardner, 27 July 1976; "Santa Rosa, El Oro," G.H.H. Tate, 22–26 October 1921: *Marmosa isthmica* and *M. simonsi*.

189. *Esmeraldas*, **Corondelet** (1°08′N, 78°46′W [18 m]; NGA, 2005; Paynter, 1993). "Carondelet, NW

Ecuador,'' R. Miketta, 5 October 1900: *Marmosa isthmica*.

190. *Esmeraldas*, **San Javier** (1°04′N, 78°47′W [18 m]; Paynter, 1993). "St. Javier, NW Ecuador," G. Flemming, 20 May–19 August 1900: *Marmosa isthmica*.

191. *Guayas*, **Cerro Bajo Verde** (ca. 2°06′S, 80°11′W [152 m]; approximate coordinates based on Paynter, 1993). "Cerro Bajo Verde," G.H.H. Tate, 3 October 1922: *Marmosa simonsi*.

192. *Guayas*, **Cerros de Colonche** (2°00′S, 80°20′W; Paynter, 1993). "Cerro de Manglaralto," G.H.H. Tate, 30 May 1923: *Marmosa isthmica*. Cerros de Colonche is situated in Cerro de Manglaralto (Paynter, 1993).

193. *Guayas*, **Chongoncito** (2°14′S, 80°05′W [ca. 100 m]; Paynter, 1993). Including "Chongoncito, Guayas" and "Chongoncito," G.H.H. Tate and H.E. Wickenheiser, 29 September–12 October 1922: *Marmosa isthmica*.

194. *Guayas*, **Guayaquil** (2°10′S, 79°54′W [0–60 m]; NGA, 2005; Paynter, 1993). Including "Guayaquil, Guayas" and "Guayaquil," P.O. Simons, 26 November 1897, 1 September–2 December 1898: *Marmosa simonsi*.

195. *Guayas*, **Huerta Negra** (3°00′S, 79°46′W; Paynter, 1993). "Huerta Negra, ca. 20 Km ESE Balao, E of Tenguel, Guayas," R.G. Mclean: *Marmosa isthmica*.

196. *Guayas*, **Isla Puná** (2°50′S, 80°08′W; NGA, 2005). "Isla Puna, Guayaquil, Guayas," J. Wimpfheimer, 10 December 1941: *Marmosa simonsi*.

197. *Guayas*, **Puná** (2°44′S, 79°55′W [10 m]; NGA, 2005). "Puná, Gulf of Guayaquil, Puná Island," P.O. Simons, 3–11 November 1898: *Marmosa simonsi*.

198. *Guayas*, **San Ramón** (2°56′S, 80°08′W; NGA, 2005). "San Ramón, Puna Island" or "Hacienda San Ramon, Puna," G.H.H. Tate, 23–28 December 1923: *Marmosa simonsi*.

199. *Imbabura*, **Hacienda Paramba** (0°49′N, 78°21′W [1067 m]; NGA, 2005; Paynter, 1993). "Paramba, N Ecuador," R. Miketta, 20 December 1898, 15 January 1899, 27 June 1900: *Marmosa isthmica*.

200. *Loja*, **Hacienda Casanga** (4°01′S, 79°45′W; NGA, 2005). "Casanga, Prov. del Oro," H.E. Anthony, 19 September 1920: *Marmosa simonsi*.

201. *Loja*, **Malacatos** (4°14′S, 79°17′W [1600 m]; NGA, 2005; Paynter, 1993). "Malacatos, Loja," H. Cuesta and L. Ponce, 11–19 August 1939: *Marmosa simonsi*.

202. *Loja*, **Río Casanga** (4°08′S, 79°49′W [ca. 884 m]; Paynter, 1993). "Rio Casanga, Loja," Anthony and Cherrie, 1 September 1920: *Marmosa simonsi*.

203. *Loja*, **Zozoranga** (4°20′S, 79°47′W [ca. 1000 m]; NGA, 2005; Paynter, 1993). "Sozoranga, Zusuco," L. Perez, 5 June 1970: *Marmosa simonsi*.

204. *Los Ríos*, **Lima Pareja** (1°33′S, 79°28′W; collector's label). "Lima Pareja, 4 km SW Pueblo Viejo, Los Ríos," R.G. Mclean, 21 February 1975: *Marmosa isthmica*.

205. *Los Ríos*, **Vinces** (1°32′S, 79°45′W [ca. 15 m]; Paynter, 1993). Including "Vinces, near Puerto Nuevo" and "Vinces, Los Ríos," R.G. Mclean, 24 September 1975; "Puerto Nuevo, on Rio Nuevo, N of Vinces, Los Ríos," R.G. Mclean, 23 September 1976; and "Hacienda Pijigual, Vinces," H.E. Wickenheiser and G.H.H. Tate, 28 October–1 November 1922: *Marmosa isthmica* and *M. simonsi*.

206. *Manabí*, **Cordillera de Balzar** (0°55′S, 79°55′W [ca. 300 m]; NGA, 2005; Paynter, 1993). "Balzar Mts.," Illingworth [no date]: *Marmosa isthmica*.

207. *Manabí*, **Cuaque** (0°00′S, 80°06′W [90 m]; Paynter, 1993). "Coaque, El Destino, Manabí," G.H.H. Tate, 8 July 1923: *Marmosa isthmica*.

208. *Manabí*, **Jama** (0°11′S, 80°16′W [100 m]; Paynter, 1993). "Jama, Manabí," T. Mena, 22 April 1942: *Marmosa simonsi*.

209. *Manabí*, **Los Pozos** (1°00′S, 80°37′W; NGA, 2005). "Los Pozos," G.H.H. Tate, 28 April 1924: *Marmosa simonsi*.

210. *Manabí*, **Río Briceño** (0°31′S, 80°27′W; NGA, 2005). Including "Sea Level, Río Briseño, Bahia de Caráquez," "Sea Level, Bahia de Caráquez," and "Sea Level, Rio Briseño," G.H.H. Tate, 15 June–27 July 1923: *Marmosa isthmica* and *Marmosa simonsi*.

211. *Manabí*, **San José** (0°09′S, 80°04′W [85 m]; FMNH collection database). "San José, Manabí," L. Gomez, 10–16 June 1942: *Marmosa isthmica*.

212. *Napo*, **Puerto Napo** (1°03′S, 77°47′W [464 m]; Paynter, 1993). "Near the river Napo, Oriente," L. Söderstrom, March–September 1921: *Marmosa rubra*. Puerto Napo, where the old trail from Quito reached the Río Napo, seems like the best match for Söderstrom's historical locality, but Voss (1988: 477) thought that this locality might be near Tena (0°59′S, 77°49′W [518 m]), which is only a few kilometers to the north.

213. *Orellana*, **San José de Payamino** (0°30′S, 77°17′W [300 m]; NGA, 2005). "San José de Payamino, Napo," R.M. Timm, 16 November 1983: *Marmosa rubra*.

214. *Orellana*, **San José Nuevo** (0°26′S, 77°20′W [500–1000 m]; Paynter, 1993). Including "San José," "San José Abajo," and "San José Abajo, Napo," Olalla y Hijos, 28 March–8 April 1924: *Marmosa rubra*.

215. *Pastaza*, **Montalvo** (2°04′S, 76°58′W [314 m]; NGA, 2005; Paynter, 1993). "Montalvo, Rio Bonbonazo," R. Olalla, 3–6 February 1932: *Marmosa rubra*.

216. *Pastaza*, **Río Copotaza** (2°07′S, 77°27′W; NGA, 2005; Paynter, 1993). "Rio Copataza, Oriente," M. Olalla, 10–20 April 1939: *Marmosa rubra*.

217. *Pastaza*, **Río Pindo** (1°32′S, 77°57′W; FMNH collection database). "Rio Pindo Yaco, Oriente," R.E. Olalla, 12–16 October 1934: *Marmosa rubra*.

218. *Pichincha*, **Gualea** (0°07′N, 78°44′W [1523 m]; NGA, 2005). "Gualea," H.E. Anthony, 7 December 1913: *Marmosa* cf. *zeledoni*.

219. *Pichincha*, **Mindo** (0°02′S, 78°48′W [1284–1676 m]; NGA, 2005; Paynter, 1993). "Mindo," G. Hammond, 10 July 1913; "Near Mindo," A.J.E. Cave, June 1925: *Marmosa isthmica*.

220. *Pichincha*, **Nanegal** (0°07′N, 78°46′W [ca. 1400 m]; NGA, 2005; Paynter, 1993). "Nanegal," Söderstrom, September 1896: *Marmosa isthmica*.

221. *Pichincha*, **Santo Domingo de Los Colorados** (0°15′S, 79°09′W [489 m]; Paynter, 1993). Including "Santo Domingo, W Ecuador" and "Santo Domingo, 0013S, 7906W, Ecuador," G. Hammond, 29 June–22 July 1914: *Marmosa isthmica*.

222. *Sucumbíos*, **Marian** (0°02′S, 76°20′W; NGA, 2005). "Marian, Napo," R.M. Timm, 7 October 1983: *Marmosa rubra*.

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223. *Amazonas*, **Huampami** (4°28′S, 78°10′W; Patton et al., 1982). Including "Headwaters of Río Huampami, N of Huampami, Río Cenepa, Depto. Amazonas," "Huampami, Río Cenepa, Depto. Amazonas," "Vicinity of Huampami, Río Cenepa, Depto. Amazonas," "Vicinity of Huampami [Aguaruna Village], Río Cenepa, Depto. Amazonas," "Kayamas, Río Cenepa, Depto. Amazonas," and "ca. 0.5 mi W Huampami, Río Cenepa, Depto. Amazonas," J.L. Patton, 9 July–19 August 1977 and 10 July–18 August 1978: *Marmosa rubra*.

224. *Amazonas*, **Puesto Vigilancia Comaina** (4°06′S, 78°24′W [665 m]; collector's label). "Valle Rio Comaina, Puesto Vigilancia Comaina, West Bank of River, Cordillera del Condor," L.H. Emmons, 5 August 1994: *Marmosa rubra*.

225. *Cusco*, **Hacienda Villa Carmen** (12°50′S, 71°15′W [600 m]; Stephens and Traylor, 1983). "Hacienda Villa Carmen, Cosñipata, Cuzco," C. Kalinowski, 21–22 September 1954: *Marmosa rubra*.

226. *Loreto*, **Boca del Río Curaray** (ca. 2°22′S, 74°05′W; Stephens and Traylor, 1983). "Boca R. Curaray, Pastaza," Olalla y Hijos, 10 October–27 December 1925: *Marmosa rubra*. See Wiley (in press) for a discussion of this collecting locality.

227. *Piura*, **Huásimo** (4°19′S, 80°12′W [750 m]; Stephens and Traylor, 1983). "Huásimo, Tumbes," C. Kalinowski, 23–26 June 1954: *Marmosa simonsi*.

228. *Piura*, **Naranjito** (5°06′S, 79°49′W; NGA, 2005). "Naranjito, Chalaco District, Piura," Programa Control Peste, 16 August 1973: *Marmosa simonsi*.

229. *Tumbes*, **Matapalo** (3°41′S, 80°12′W [80 m]; Stephens and Traylor, 1983). "Matapalo, Tumbes," C. Kalinowski, 1–4 July 1954: *Marmosa simonsi*.

230. *Tumbes*, **Papayal** (3°34′S, 80°14′W; Stephens and Traylor, 1983). "Popayal," J.M. de la Barrera, 19 January 1956: *Marmosa simonsi*.

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231. *Apure*, **Hato El Frío** (7°49′N, 68°54′W; NGA, 2005). "Hato El Frío, Apure," P. Morales, 8 August 1986: *Marmosa robinsoni*.

232. *Aragua*, **Camp Rangel** (10°09′N, 67°09′W; Anderson and Gutiérrez, 2009). "Camp Rangel," J.M. de la Barrera, 24 October 1959: *Marmosa robinsoni*. The coordinates given above for this locality (also known as "Campamento Rafael Rangel") differ slightly from those provided by Voss (1992)

233. *Aragua*, **Ocumare de La Costa** (10°28′N, 67°46′W [183 m]; Paynter, 1982). "2 km NE Ocumare de La Costa, Aragua," C.O. Handley, Jr. and D.I. Rhymer, 7 April 1960: *Marmosa robinsoni*.

234. *Aragua*, **Rancho Grande** (10°21′N, 67°40′W [1050–1100 m]; Handley, 1976). "Rancho Grande, Aragua," C.O. Handley, Jr. and D.I. Rhymer, 23 March–7 April 1960: *Marmosa robinsoni*.

235. *Barinas*, **Altamira** (8°50′N, 70°30′W [697 m]; Handley, 1976). "La Quinta, 5 km SW Altamira," Smithsonian Venezuelan Project, 23 December 1967: *Marmosa robinsoni*.

236. *Bolívar*, **Ciudad Bolívar** (8°08′N, 63°33′W [ca. 100 m]; Paynter, 1982). "Ciudad Bolívar," S.M. Klages, 11 September 1898: *Marmosa robinsoni* and *M. murina*.

237. *Carabobo*, **El Trompillo** (10°04′N, 67°46′W [ca. 500 m]; Paynter, 1982). "El Trompillo, Carabobo," S.M. Klages, 25 April–8 May 1914: *Marmosa robinsoni*.

238. *Carabobo*, **San Esteban** (10°26′N, 68°01′W [ca. 200 m]; Paynter, 1982). Including "San Esteban," M.A. Carriker, Jr., 14 November 1910; and "San Esteban, N Venezuela," S.M. Klages, 20 January–11 February 1911: *Marmosa robinsoni*.

239. *Carabobo*, **Urama** (10°27′N, 68°19′W [25 m]; NGA, 2005). "El Central, 10 km NW Urama, Río Yaracuy," Smithsonian Venezuelan Project, 7–15 March 1966: *Marmosa robinsoni* and *M. murina*.

240. *Distrito Federal*, **Caracas** (10°30′N, 66°55′W [950 m]; NGA, 2005). "Caracas, Distrito Federal," J.R. Dillon, 2–5 April 1938: *Marmosa robinsoni*.

241. *Falcón*, **Capatárida** (11°07′N, 70°46′W [75 m]; NGA, 2005). "18 km WSW Capatárida, Capatárida, Falcón," Smithsonian Venezuelan Project, 26 March–26 June 1968: *Marmosa xerophila*.

242. *Falcón*, **Cerro Santa Ana** (11°50′N 69°58′W [575 m]; Paynter, 1982). Including "15 km SSW Pueblo Nuevo, Cerro Santa Ana, Peninsula de Paraguaná, Falcón" and "49 km N and 32 km W Coro (Cerro Santa Ana), Falcón," Smithsonian Venezuelan Project, 25 July–1 August 1968: *Marmosa robinsoni*.

243. *Falcón*, **Hacienda Socopito** (10°30′N, 70°44′W [470–480 m]; Handley, 1976). Including "20 km S and 98 km E Maracaibo (Hda. Socopito), Falcón" and "24 km S and 94 km E Maracaibo,

Falcón," Smithsonian Venezuelan Project, 13–27 May 1968: *Marmosa robinsoni*.

244. *Falcón*, **Mirimire** (11°10′N, 68°43′W [250 m]; NGA, 2005). "Nr. Mirimire, Falcón," Smithsonian Venezuelan Project, 19 August 1967: *Marmosa robinsoni*.

245. *Falcón*, **Moruy** (11°50′N, 69°59′W [90 m]; Paynter, 1982). "49 km N and 33 km W Coro (Moruy), Falcón," Smithsonian Venezuelan Project, 5–16 July 1968: *Marmosa xerophila*.

246. *Falcón*, **Yabuquiva** (11°48′N, 70°04′W [13 m]; NGA, 2005). Including "25 km SW Pueblo Nuevo, Yabuquiva, Peninsula de Paraguaná, Falcón" and "48 km N and 46 km W Coro (Yabuquiva), Falcón," Smithsonian Venezuelan Project, 17–20 July 1968: *Marmosa xerophila*.

247. *Guárico*, **Calabozo** (8°52′N, 67°23′W [100 m]; Paynter, 1982). "7 km S and 5 km E Calabozo, Guárico," Smithsonian Venezuelan Project, 16 August 1968: *Marmosa robinsoni*.

248. *Guárico*, **Estación Biológica de los Llanos** (8°52′N, 67°23′W [115 m]; Handley, 1976). Including "Estación Biológica de los Llanos, Guárico," "9 km SE Calabozo [100 m], Estación Biológica de los Llanos," and "7 km S and 5 km E Calabozo, Guárico," Smithsonian Venezuelan Project, 28 August 1966 and 16–20 August 1968: *Marmosa robinsoni*.

249. *Guárico*, **Hato Las Palmitas** (9°36′N, 67°27′W [181 m]; Handley, 1976). "34 km S and 12 km W San Juan de los Morros, Hto. Las Palmitas, Guárico," Smithsonian Venezuelan Project, 4 September 1966 and 5 January 1968: *Marmosa robinsoni*.

250. *Lara*, **Caserio Boro** (9°53′N, 69°47′W [528 m]; Handley, 1976). "10 km N El Tocuyo, Caserio Boro, Lara," Smithsonian Venezuelan Project, 23 July 1968: *Marmosa robinsoni*.

251. *Lara*, **La Concordia** (10°01′N, 69°29′W [592 m]; NGA, 2005). "8 km SW Barquisimeto, La Concordia, Lara," Smithsonian Venezuelan Project, 23 July 1968: *Marmosa robinsoni*.

252. *Lara*, **Puerta Vieja** (9°51′N, 69°41′W [616 m]; NGA, 2005). "14 km NE El Tocuyo, Puerta Vieja, Lara," Smithsonian Venezuelan Project, 24 July 1968: *Marmosa robinsoni*.

253. *Lara*, **Río Tucuyo** (10°16′N, 69°56′W [500 m]; Voss, 1991). Río Tucuyo; G.H.H. Tate, 23–27 March 1938: *Marmosa robinsoni*.

254. *Mérida*, **Mérida** (8°36′N, 71°08′W [1600 m]; Paynter, 1982). "Cafetos de Chama, Mérida," S. Briceño G., 14 December 1903 and 20 March 1907: *Marmosa robinsoni*.

255. *Mérida*, **Milla** (8°30′N, 71°22′W [ca. 1100 m]; NGA, 2005; Paynter, 1982). "Cafetos de Milla, Mérida," collector unknown, 8 June 1904; S. Briceño [no dates]: *Marmosa robinsoni*.

256. *Mérida*, **Pedregosa** (8°37′N, 71°42′W [1630 m]; NGA, 2005). "Pedregoza, Mérida," S. Briceño, 5 May 1896: *Marmosa robinsoni*.

257. *Miranda*, **Curupao** (10°31′N, 66°38′W [1160 m]; Handley, 1976). "19 km E Caracas, Curupao, Miranda," Smithsonian Venezuelan Project, 6–10 October 1966: *Marmosa robinsoni*.

258. *Miranda*, **San Andrés** (10°22′N, 66°50′W [1144 m]; Handley, 1976). "8 km SSE Caracas," Smithsonian Venezuelan Project, 10 August 1966: *Marmosa robinsoni*.

259. *Monagas*, **Hato Mata de Bejuco** (9°19′N, 62°56′W [18 m]; Handley, 1976). Including "47 km SE Maturín, Hato Santa Barbara, Monagas," "54 km SE Maturín, Monagas," and "55 km SSE Maturín, Hato Mata de Bejuco, Monagas," Smithsonian Venezuelan Project, 9 August 1966 and 4–5 June 1968: *Marmosa robinsoni*.

260. *Monagas*, **Ipuré** (10°07′ N, 63°45′ W; Google Earth). "Ipuré, Cumaná," F. Caracciolo, 9 March 1899: *Marmosa robinsoni*. This town, also known as "Laguna de Ipuré," is only a few kilometers west of San Antonio de Maturín (locality 262, below).

261. *Monagas*, **San Agustín** (10°12′N, 63°32′W [1150 m]; Handley, 1976). "5 km NW Caripe, San Agustín, Monagas," Smithsonian Venezuelan Project, 23 June–15 July 1967: *Marmosa robinsoni* and *M. murina*.

262. *Monagas*, **San Antonio de Maturín** (10°07′N, 63°43′W [549 m]; Paynter, 1982). "San Antonio," Tate and Clement, 20–23 April 1925: *Marmosa robinsoni*.

263. *Nueva Esparta*, **Isla Margarita** (11°03′N, 63°51′W; Handley, 1976). "Margarita Island," W. Robinson, 2–12 July 1895: *Marmosa robinsoni*.

264. *Nueva Esparta*, **Salamanca** (11°03′N, 63°52′W [38 m]; Handley, 1976). Including "2 km N and 1 km E La Assunción (Salamanca), Nueva Esparta" and "3 km S La Asunción, Isla Margarita, Nueva Esparta," Smithsonian Venezuelan Project, 6 January–8 February 1967: *Marmosa robinsoni*.

265. *Portuguesa*, **Guanarito** (8°42′N, 69°12′W; NGA, 2005). Including "Palmarito Curbeleno, near Guanarito, Portuguesa," "Near Guanarito, Portuguesa," "La Hoyada, near Guanarito, Portuguesa," and "La Arenosa, near Guanarito, Portuguesa," Wilson and Tesh, 1–16 February 1992: *Marmosa robinsoni*.

266. *Sucre*, **Campo Alegre** (10°10′N, 63°45′W [411 m]; Paynter, 1982). "Campo Alegre, Cumaná," F. Caracciolo, 31 January 1899: *Marmosa robinsoni*.

267. *Sucre*, **Cuchivano** (10°15′N, 63°55′W [213 m]; Paynter, 1982). "Cuchivano, Sucre," Tate and Clement, 1 March 1925: *Marmosa robinsoni*.

268. *Sucre*, **Cumaná** (10°26′N, 64°02′W [0 m]; Handley, 1976). "16 km E Cumaná (Quetepe), Sucre," Smithsonian Venezuelan Project, 21–23 December 1966: *Marmosa robinsoni*.

269. *Sucre*, **Guaraúnos** (10°33′N, 63°07′W [10 m]; NGA, 2005). "Finca Vuelta Larga, 9.7 km (by road) SE Guaraúnos, Sucre," H.G. Castellanos, 8–18 August 1987: *Marmosa robinsoni*.

270. *Trujillo*, **Agua Santa** (9°31′N, 70°40′W [90 m]; NGA, 2005). "23 km NW Valera, Nr. Agua Santa, Trujillo," Smithsonian Venezuelan Project, 23–26 August 1965: *Marmosa robinsoni*.

271. *Trujillo*, **Agua Viva** (9°34′N, 70°39′W [164 m]; NGA, 2005). "18 km N Valera, Nr. Agua Viva, Trujillo," Smithsonian Venezuelan Project, 8 September 1965: *Marmosa robinsoni*.

272. *Trujillo*, **El Dividive** (9°29′N, 70°44′W [90 m]; NGA, 2005). "30 km NW Valera, Nr. El Dividive, Trujillo," Smithsonian Venezuelan Project, 18 September–14 October 1965: *Marmosa robinsoni*.

273. *Trujillo*, **Isnotú** (9°22′N, 70°42′W [930 m]; NGA, 2005; Handley, 1976). "10 km WNW Valera, Nr. Isnoto, Trujilo," Smithsonian Venezuelan Project, 30 August 1965: *Marmosa robinsoni*.

274. *Trujillo*, **La Ceiba** (9°28′N, 71°04′W [29 m]; Handley, 1976). "Hda. Valle Verde, Trujillo," Smithsonian Venezuelan Project, 4 November 1965. *Marmosa robinsoni*.

275. *Trujillo*, **Valera** (9°32′N, 70°40′W [645 m]; Handley, 1976). "Valera, Trujillo," W.H. Osgood and H.B. Conover, 10 March 1920: *Marmosa robinsoni*.

276. *Zulia*, **Cerro Azul** (10°51′N, 72°16′W [80 m]; Handley, 1976). Including "39 km NW La Paz, Nr. Cerro Azul, Zulia," "17 km N and 55 km W Maracaibo (Hda. El Tigre), Zulia," and "18 km N and 56 km W Maracaibo (Hda. Rodeo), Zulia," Smithsonian Venezuelan Project, 9–14 June 1968: *Marmosa robinsoni*.

277. *Zulia*, **Novito** (10°02′N, 72°43′W [1132 m]; Handley, 1976). "3 km S and 19 km W Machiques, Zulia," Smithsonian Venezuelan Project, 27–28 April 1968: *Marmosa robinsoni*.

278. *Zulia*, **Paraguaipoa** (11°21′N, 71°55′W [15 m]; Handley, 1976). "114 km N and 32 km W Maracaibo (La Isla), Zulia," Smithsonian Venezuelan Project, 23 June–1 July 1968: *Marmosa xerophila*.

279. *Zulia*, **Río Chama** (9°03′N, 71°37′W; Paynter, 1982). "Río Chama," S. Briceño, 15 May 1896: *Marmosa robinsoni*.

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280. [Trinidad] **El Cerro del Oropuche** (10°46′N, 61°09′W; NGA, 2005). "Orepouche Heights, Trinidad," M.A. Carriker Jr., 18–22 July 1910: *Marmosa robinsoni*.

281. [Trinidad] **Bush Bush Forest** (10°24′N, 61°03′W; NGA, 2005). Including "Nariva Swamp, Bush Bush Forest, Trinidad" and "Bush Bush Forest, Trinidad," Trinidad Regional Virus Laboratory personnel (T.H.G. Aitken, W.G. Downs, etc.), 22 March 1961–12 February 1963: *Marmosa robinsoni*. See Downs et al. (1968) for more information about this locality.

282. *Arima* [Trinidad], **Arima** (10°38′N, 61°17′W. NGA, 2005). Including "St. Patricks, Arima," W.G. Downs, 15 October 1953; and "St. Patricks, Arima, Trinidad," C.R. Anderson, 10 January 1953: *Marmosa robinsoni*.

283. *Caroni* [Trinidad], **Caparo** (10°27′N, 61°20′W; NGA, 2005). "Caparo, Trinidad," F.M. Chapman, 21 March 1891 and 16–31 March 1894: *Marmosa robinsoni*.

284. *Caroni* [Trinidad], **Caparo River** (10°31′N, 61°28′W; NGA, 2005). "Caparo Valley, Trinidad," P. Rendall, 18 January 1897: *Marmosa robinsoni*. Geographic coordinates are those at the mouth of the Caparo River.

285. *Saint Andrew* [Trinidad], **Cumaca** (10°42′N, 61°09′W; NGA, 2005). Including "Valencia Ward, Cumaca, St. Andrew, Trinidad" and "Cumaca, Trinidad," Trinidad Regional Virus Laboratory personnel (W.G. Downs and unknown collectors), 6 November 1954, 21 July–26 September 1965, 30 March–27 May 1967, and 27 November 1968: *Marmosa robinsoni*.

286. *Saint Andrew* [Trinidad], **Cumuto** (10°35′N, 61°12′W; NGA, 2005). Including "Tamana Ward, Cumuto, St. Andrew, Trinidad," and "Valencia Ward, Cumuto, St. Andrew Co., Trinidad," Trinidad Regional Virus Laboratory personnel, 20 May–4 June 1964, 4 August 1965: *Marmosa robinsoni*.

287. *Saint Andrew* [Trinidad], **Sangre Grande** (10°35′N, 61°07′W; NGA, 2005). Including "Sangre Grande, Trinidad," "El Reposo Rd., Sangre Grande, Trinidad," and "Maingot Estate, 5 miles from Sangre Grande, Trinidad," W.G. Downs, 26 January–6 July 1955, 4 February 1959: *Marmosa robinsoni*.

288. *Saint Andrew* [Trinidad], **Upper Fishing Pond** (10°35′N, 61°03′W; NGA, 2005). "Fishing Pond, Trinidad," W.G. Downs, 24 May 1955: *Marmosa robinsoni*.

289. *Saint Andrew* [Trinidad], **Turure Forest** (ca. 10°35′N, 61°10′W; estimated by authors). "Turure Forest, Trinidad"; collector unknown, 23 Sep 1966; Trinidad Regional Virus laboratory personnel, 11 May and 18 December 1968: *Marmosa robinsoni*. According to Everard and Tikasingh (1973), Turure Forest is 3 km west of Sangre Grande (locality 287, above).

290. *Saint George* [Trinidad], **Brazil Village** (10°33′N, 61°16′W; NGA, 2005). "Brazil village, Trinidad," collector unknown, 13 August 1965: *Marmosa robinsoni*.

291. *Saint George* [Trinidad], **Caura** (10°43′N, 61°21′W; NGA, 2005). "Caura Mts., Trinidad," F.M. Chapman, 1–23 April and 24 September 1894: *Marmosa robinsoni*.

292. *Saint Patrick* [Trinidad], **Aripo Savanna** (10°36′N, 61°12′W; NGA, 2005). "Aripo Valley," collector unknown, 16 February 1935: *Marmosa robinsoni*.

293. *Saint Patrick* [Trinidad], **Cedros Point** (10°08′N, 61°50′W; NGA, 2005). Including "Cedros Ward, Cedros, St. Patrick Co., Trinidad," collector unknown, 2 December 1966; and "Cedros, Trinidad," Trinidad Regional Virus Laboratory personnel, 4 August 1966: *Marmosa robinsoni*.

294. *Tobago*, **Charlotteville** (11°19′N, 60°33′W; NGA, 2005). "1 km E Charlotteville," G.S. Morgan, 13–15 July 1979; "near Charlotteville, Tobago," R.S. Voss and M.E. Holden, 17–22 January 1989: *Marmosa robinsoni* and *M. murina*.

295. *Tobago*, **Speyside** (11°18′N, 60°32′W; NGA, 2005). "Speyside, Tobago," F. Thurab, 17–31 March 1960: *Marmosa robinsoni* and *M. murina*.
296. *Victoria* [Trinidad], **Princestown** (10°16′N, 61°23′W; NGA, 2005). "Princestown, Trinidad," F.M. Chapman, 4–25 March 1893: *Marmosa robinsoni*.
297. *Victoria* [Trinidad], **Savana Grande** (10°18′N, 61°22′W; NGA, 2005). "Savannah Grande, Trinidad," P. Rendall, 8 February 1897: *Marmosa robinsoni*.

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298. *Saint George*, **Annandale Estate** (12°05′N, 61°43′W; NGA, 2005). "Annandale," G.R.M. Murray, August 1886: *Marmosa robinsoni*.