

## **An Annotated Checklist of Recent Opossums (Mammalia: Didelphidae)**

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# AN ANNOTATED CHECKLIST OF RECENT OPOSSUMS (MAMMALIA: DIDELPHIDAE)

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## ABSTRACT

Living opossums (Didelphidae) comprise 125 species in 18 genera and 4 subfamilies. This synopsis lists all the didelphid taxa (subfamilies, tribes, genera, subgenera, and species) currently recognised as valid, summarizes information about typification, synonyms, and geographic distributions, remarks noteworthy recent changes in usage, and comments on still outstanding problems. A concluding discussion rejects the notion that the almost twofold increase in opossum species from 1993 to the present is “taxonomic inflation” and considers the impact of new kinds of data and new methods of data analysis on species delimitation.

## INTRODUCTION

The need for an up-to-date taxonomic synopsis of Recent opossums (Didelphidae) has long been apparent. The last complete technical checklist was Gardner’s (2005), although an important partial synopsis—restricted to the South American taxa—appeared just a few years later (Gardner, 2008). Both were major advances over earlier compilations, but these useful publications were immediately followed by a decade-long phase of revisionary research that substantially increased the number of species recognized as valid. Subsequent lists that appeared in volumes written for nonspecialist readers (Astúa, 2015; Voss and Jansa, 2021) necessarily omitted much relevant nomenclatural detail. Although no synopsis can plausibly claim to be the last word on the taxonomy of this diverse and geographically widespread group, most opossum genera have now received at least some critical scrutiny based on firsthand examination of type material and supporting analyses of morphological and molecular data. Therefore, a summary of taxonomic progress is timely.

Here I list all the didelphid subfamilies, tribes, genera, subgenera, and species currently regarded as valid. I provide information about typification and synonyms for each taxon and remark any nomenclatural issues not previously discussed by Gardner (2005, 2008). For supraspecific taxa, I additionally comment on published evidence for monophyly. For each species, I summarize information about geographic distribution and cite relevant analyses of genetic and phenotypic data

in the recent literature. A concluding discussion mentions some general trends in recent didelphid taxonomic research.

## Categories of Information

Several categories of technical information provided in this synopsis merit brief explanations. Readers unfamiliar with taxonomic terminology may also wish to consult the helpful glossary section of the International Code of Zoological Nomenclature (ICZN, 1999).<sup>1</sup>

**TYPE SPECIES:** Type species (of genera or subgenera) are nominal taxa, which are sometimes junior synonyms of species currently known by other names. In these accounts, type species are identified by their original binomial combinations, with a parenthetical explanation if any is needed. For example, the type species of *Monodelphis* is *Didelphis brachyuros* Schreber, 1777, which corresponds to the species currently known as *Monodelphis brevicaudata* (Erxleben, 1777). Type species may have been originally designated as such by the author of the genus-group name in question, or they may have been designated by the same author or by a different author at some later date.

**TYPE MATERIAL AND TYPE LOCALITY:** Except as noted, information provided under this heading is consistent with that provided by the original describer, although I have often updated the spelling of geographic place names and provided geographic coordinates if none

<sup>1</sup> Available online (<https://www.iczn.org/the-code/the-code-online/>).

were originally given. Geographic coordinates provided without cited references are usually consistent with gazetteer entries in Gardner (2008) or with standard references such as the ornithological gazetteers published by the Museum of Comparative Zoology (Harvard University) or those published by the U.S. government (e.g., by the U.S. Board on Geographic Names and the Defense Mapping Agency). However, comments with supporting references are provided if the type material or the type locality differs from what has previously been reported in the literature. Common misconceptions notwithstanding, the type locality is simply the place where the name-bearing specimen(s)—holotype, lectotype, neotype, or syntypes—was (or were) collected, so the type locality of a species based on material of unknown origin is unknown, regardless of any “restrictions” subsequently proposed by authors without definite knowledge of provenance.

**SYNONYMS:** Except as noted, only available names based on Recent type material are listed under this heading, including both objective synonyms (based on the same type material as the currently recognized valid name) and subjective synonyms (based on different type material). For conciseness, only the epithet (with author and date) is listed for species-group junior synonyms, which were often published in combination with different generic names. In the event that a species-group junior synonym was originally combined with a generic name that differed in gender from the generic name in current use, the gender of the epithet has been changed to agree with current usage. Although I acknowledge the potential usefulness of trinomial nomenclature in several accounts, I do not formally recognize subspecies in this report.

**DISTRIBUTION:** Information provided under this heading is concise if a published range map based on accurately identified material can be cited, or it may require a lengthy description if no such map is available.

**REMARKS:** All other relevant information is provided under this heading.

## Abbreviations

The following abbreviations are used for museum collections in which types and other specimens are preserved:

- AMNH, American Museum of Natural History (New York, NY)
- BMNH, Natural History Museum (London, UK)
- CBF, Colección Boliviana de Fauna (La Paz, Bolivia)
- CM, Carnegie Museum of Natural History (Pittsburgh, PA)
- CTUA, Colección Teriológica, Universidad de Antioquia (Medellín, Colombia)
- EBD, Estación Biológica Doñana (Sevilla, Spain)
- EBRG, Estación Biológica Rancho Grande (Maracay, Venezuela)
- ENCB, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (Ciudad de México, Mexico)
- FMNH, Field Museum (Chicago, IL)
- ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (Bogotá, Colombia)
- INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil)
- IZH, Institut für Zoologie der Universität Zoologische Sammlungen (Halle, Germany)
- LIVCM-D, World Museum (Liverpool, UK)
- LSUMZ, Louisiana State University Museum of Natural Science (Baton Rouge, LA)
- MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina)
- MBUCV, Museo de Biología, Universidad Central de Venezuela (Caracas, Venezuela)
- MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, MA)
- MHNLS, Museo de Historia Natural La Salle (Caracas, Venezuela)
- MHNN, Muséum d’Histoire Naturelle de Neuchâtel (Neuchâtel, Switzerland)
- MN, Museu Nacional (Rio de Janeiro, Brazil)
- MNCN, Museo Nacional de Historia Natural (Madrid, Spain)
- MNHN, Muséum National d’Histoire Naturelle (Paris, France)

MPEG, Museu Paraense Emilio Goeldi (Belém, Brazil)  
 MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima, Peru)  
 MVZ, Museum of Vertebrate Zoology, University of California (Berkeley, CA)  
 NMW, Naturhistorisches Museum Wien (Vienna, Austria)  
 RMNH, Naturalis Biodiversity Center (Leiden, the Netherlands)  
 ROM, Royal Ontario Museum (Toronto, Canada)  
 UFMT, Universidade Federal de Mato Grosso (Cuiabá, Brazil)  
 UFPA, Universidade Federal do Pará (Belém, Brazil)  
 UMMZ, University of Michigan Museum of Zoology (Ann Arbor, MI)  
 USNM, National Museum of Natural History (Washington DC)  
 ZMB, Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin, Germany)  
 ZMUC, Zoological Museum of the University of Copenhagen (Copenhagen, Denmark)

## SYSTEMATIC ACCOUNTS

Subfamily Caluromyinae Reig et al., 1987

TYPE GENUS: *Caluromys* J.A. Allen, 1900.

REMARKS: See Voss and Jansa (2009) for a morphological diagnosis. This subfamily includes only *Caluromys* and *Caluromysiops*. An alternative concept of Caluromyinae that once included *Glironia* (e.g., in Gardner, 2008) is not demonstrably monophyletic (Jansa and Voss, 2000; Voss and Jansa, 2009).

Genus *Caluromys* J.A. Allen, 1900

TYPE SPECIES: *Didelphis philander* Linnaeus, 1758, by original designation.<sup>2</sup>

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for an emended generic description. Generic monophyly is strongly supported by phylogenetic analyses of multilocus sequence data (e.g., Voss and Jansa, 2009; Amador and Giannini, 2016). Two subgenera are currently recognized.

Subgenus *Caluromys* J.A. Allen, 1900

TYPE SPECIES: As for the genus.

SYNONYMS: None.

REMARKS: This subgenus has long been thought to contain only one species (but see remarks under *Caluromys philander*, below).

*Caluromys (Caluromys) philander*  
 (Linnaeus, 1758)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 67.4.12.414, the holotype by monotypy, consists of the fluid-preserved carcass and extracted skull of an adult female (Thomas, 1892; Jenkins and Knutson, 1983). The type locality is unknown, but it is often assumed to be Surinam (after Thomas, 1911).

SYNONYMS: *affinis* Wagner, 1842; *cajopolin* Müller, 1776; *cayopollin* Schreber, 1777; *cayopolin* Kerr, 1792; *dichurus* Wagner, 1842; *flavescens* Brongniart, 1792; *leucurus* Thomas, 1904; *trinitatis* Thomas, 1894; *venezuelae* Thomas, 1903.

DISTRIBUTION: *Caluromys philander* occurs in lowland rainforest and dry forests in north-central and eastern Venezuela; the Guianas; northern, central, and southeastern Brazil; and eastern Bolivia (Gardner, 2008: map 2).

REMARKS: As currently recognized, *Caluromys philander* is unrevised and may represent a species complex, but published results are neither sufficient to distinguish valid taxa among the synonyms listed above nor among geographic populations currently lacking available names. Although López-Fuster et al. (2008) suggested that populations in Trinidad and northern Venezuela should be recognized as a distinct species, this inference was not supported by phylogenetic analyses of mtDNA sequence data reported by

<sup>2</sup> Voss and Jansa (2009: table 15) incorrectly attributed the type designation to Hershkovitz (1949).



Voss et al. (2019). By contrast, the latter authors discovered that mtDNA sequences from eastern Bolivia were highly divergent from sequences obtained elsewhere in the known range of *C. phillander*; unfortunately, voucher material from eastern Bolivia has yet to be examined for possibly diagnostic morphological traits.

Subgenus *Mallodelphys* Thomas, 1920

TYPE SPECIES: *Didelphis laniger* Desmarest, 1820 (= *Caluromys lanatus*; see below), by original designation.

SYNONYMS: None.

REMARKS: The monophyly of this subgenus was only weakly supported by the mtDNA sequence data analyzed by Voss et al. (2019). Two species are currently recognized.

*Caluromys (Mallodelphys) derbianus*  
(Waterhouse, 1841)

TYPE MATERIAL AND TYPE LOCALITY: LIVCM-D 194, the holotype by monotypy, is a female specimen of unstated age, originally mounted for exhibition, but subsequently remade as a study skin and skull (Thomas, 1913; Largen, 1985; Fisher, 2002). The type locality is unknown, but it has often been assumed to be somewhere in the Río Cauca watershed of northern Colombia (e.g., by Allen, 1904; Thomas, 1913).

SYNONYMS: *antioquiae* Matschie, 1917; *aztecus* Thomas, 1913; *canus* Matschie, 1917; *centralis* Hollister, 1914; *fervidus* Thomas, 1913; *guayanus* Thomas, 1899; *nauticus* Thomas, 1913; *pallidus* Thomas, 1899; *pictus* Thomas, 1913; *pulcher* Matschie, 1917; *pyrrhus* Thomas, 1901; *senex* Thomas, 1913.

DISTRIBUTION: *Caluromys derbianus* is a transAndean species that occurs in lowland rainforest, dry forest, and montane ("cloud") forest from Veracruz (Mexico) throughout most of Central America to northwestern South America (Bucher and Hoffmann, 1980: fig. 3). In South America, the species is known from the Pacific littoral and adjacent Andean foothills of western

Colombia and western Ecuador, but it is also known from the Caribbean lowlands of northwestern Colombia and from the interAndean valley of the Río Cauca (Gardner, 2008: map 2).<sup>3</sup>

REMARKS: Phylogenetic analyses of mtDNA sequence data suggest that *Caluromys derbianus* and *C. lanatus* are genetically divergent and reciprocally monophyletic species (Voss et al., 2019), but most 19th and early 20th century authors (e.g., Thomas, 1913) regarded these taxa as conspecific. Apparently, the first researcher to treat them as valid species was Gilmore (in Bugher et al., 1941), who mentioned ear color and differences in the extent of caudal pelage as distinguishing characters. However, because there is said to be some species overlap in caudal pelage traits (Gardner, 2008: 5), and because pelage markings said to distinguish these species appear to be similarly unreliable (Voss et al., 2019), only ear coloration seems to be diagnostically useful (the pinnae are unpigmented in *derbianus* versus blackish or purple in *lanatus*). Although Bucher and Hoffman (1980: 1) claimed that *C. derbianus* is the "largest species in the genus," measured series of *C. derbianus* and *C. lanatus* exhibit broad morphometric overlap (R.S.V., personal obs.). Recent landmark-based multivariate morphometric analyses of *Caluromys* have either failed to convincingly distinguish *C. derbianus* and *C. lanatus* from one another (López-Fuster et al., 2008) or have simply not addressed the problem (Fonseca and Astúa, 2015).

<sup>3</sup> Insofar as I am aware, *Caluromys derbianus* and *C. lanatus* are allopatric, but several problematic records of *C. derbianus* mapped by Fonseca and Astúa (2015: fig. 2) merit comment because they imply geographic range overlap. One such Colombian record (their locality 69) is based on USNM specimens from the Río Raposo, which is in the Cauca valley, not (as mapped) in the Cordillera Oriental. A second Colombian record (locality 68) is based on FMNH specimens from the upper Río Sinú, which drains the western slopes of the Cordillera Occidental, not (as mapped) the northeastern slopes of the Serranía de San Lucas. A third problematic record (locality 71), mapped in the Cordillera Oriental of Ecuador, is based on AMNH 10058, a specimen from Costa Rica. A fourth anomalous record, from Tingo Maria in eastern Peru (locality 75), is based on a specimen (LSUMZ 17681) that is almost certainly misidentified (*C. derbianus* is not known from Peru; Pacheco et al., 2020).



Some authors (e.g., Hall, 1981) have recognized valid subspecies of *Caluromys derbianus*, but there is a striking lack of mtDNA sequence variation among samples collected in Costa Rica, Panama, and Ecuador (Voss et al., 2019). Broader geographic sampling of genetic variation is needed to determine whether any of the nominal taxa herein treated as synonyms of *C. derbianus* represent evolutionarily significant units worthy of taxonomic recognition.

*Caluromys (Mallodelphys) lanatus* (Olfers, 1818)

TYPE MATERIAL AND TYPE LOCALITY: MNCN-M2630, the holotype by monotypy, consists of the skin and skull of a juvenile male collected at Caazapá (26.15° S, 56.40° W), Caazapá department, Paraguay (Voss et al., 2009).

SYNONYMS: *bartletti* Matschie, 1917; *cahyensis* Matschie, 1917; *cicur* Bangs, 1898; *hemiurus* Miranda-Ribeiro, 1936; *jivaro* Thomas, 1913; *juninensis* Matschie, 1917; *lanigera* Desmarest, 1820; *meridensis* Matschie, 1917; *modestus* Miranda-Ribeiro, 1936; *nattereri* Matschie, 1917; *ochropus* Wagner, 1842; *ornatus* Tschudi, 1845; *vitalinus* Miranda-Ribeiro, 1936.

DISTRIBUTION: *Caluromys lanatus* occurs in rainforest, dry forest, and premontane forest from northern Colombia to eastern Bolivia, eastern Paraguay, and southeastern Brazil (Fonseca and Astúa, 2015: fig. 3). Most records are from Amazonia, the Cerrado, and the lower slopes of the tropical Andes, but the species is also known to occur in the subtropical Paraguayan extension of the Atlantic Forest (Owen et al., 2018).

REMARKS: To date, mtDNA sequence data for *Caluromys lanatus* are available only from western Amazonian and Cerrado samples, which exhibit little genetic divergence and a striking absence of phylogeographic structure (Voss et al., 2019: fig. 7); these results clearly support Fonseca and Astúa's (2015) suggestion that just one taxon (for which *ochropus* is the oldest available name if any trinomial classification were warranted) occurs throughout these regions. Although specimens from eastern Paraguay and southeastern Brazil (representing the

nominotypical form) appear to differ morphologically from western Amazonian and Cerrado material (Fonseca and Astúa, 2015; Voss et al., 2019), the taxonomic significance of such comparisons is unclear in the absence of genetic data.

Genus *Caluromysiops* Sanborn, 1951

TYPE SPECIES: *Caluromysiops irrupta* Sanborn, 1951, by original designation.

SYNONYMS: None.

REMARKS: For an emended generic description, see Voss and Jansa (2009), who also discussed the status of *Caluromysiops* as a valid genus (distinct from *Caluromys*), a once controversial topic. Only a single species is currently recognized.

*Caluromysiops irrupta* Sanborn, 1951

TYPE MATERIAL AND TYPE LOCALITY: FMNH 68336, the holotype by original designation, consists of the skin and skull of a juvenile male collected at Quincemil (13.22° S, 70.70° W; 680 m), Cusco department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Caluromysiops irrupta* is restricted to lowland Amazonia, where it is known from scattered localities in Brazil (Mato Grosso, Rondônia), Colombia (Amazonas), and Peru (Loreto, Madre de Dios) (Santori et al., 2016: fig. 2).

REMARKS: See Voss and Jansa (2009) for illustrations, analyses of phylogenetic relationships and qualitative morphological descriptors. The only published morphometric data for *Caluromysiops irrupta* are still those in Izor and Pine (1987). Despite several reported sightings and one recent capture (summarized by Santori et al., 2016), no new morphological specimens or genetic samples have been obtained for several decades.

Subfamily Gliriniinae Voss and Jansa, 2009

TYPE GENUS: *Glironia* Thomas, 1912.

REMARKS: See Voss and Jansa (2009) for a morphological diagnosis. *Glironia* was formerly

placed in the subfamily Caluromyinae (e.g., by Gardner, 2008), but morphological and genetic support for Caluromyinae sensu lato is weak or nonexistent (Jansa and Voss, 2000; Voss and Jansa, 2009; Amador and Giannini, 2016).

#### Genus *Glironia* Thomas, 1912

TYPE SPECIES: *Glironia venusta* Thomas, 1912, by original designation.

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for a detailed morphological description of *Glironia*, which exhibits several morphological traits that are unknown among other opossums. Only a single species is currently recognized.

#### *Glironia venusta* Thomas, 1912

TYPE MATERIAL AND TYPE LOCALITY: BMNH 12.1.15.7, the holotype by original designation, consists of the skin and skull of an adult male collected at Pozuzo (10.07° S, 75.53° W; 800 m), Pasco department, Peru.

SYNONYMS: *aequatorialis* Anthony, 1926; *criniger* Anthony, 1926.

DISTRIBUTION: *Glironia venusta* has been collected or observed at widely scattered rainforest localities throughout much of Amazonia, but it is also known to occur in tropical dry forest in eastern Bolivia (Santa Cruz) and southwestern Brazil (Mato Grosso). Noteworthy recent extensions of the geographic range as mapped by Díaz and Willig (2004: fig. 1) include records from southeastern Colombia (Montenegro and Restrepo, 2018), eastern Brazil (Ardente et al., 2013), and French Guiana (Sant and Catzeflis, 2018). Formerly thought to be a lowland species, *G. venusta* is now known to occur at elevations >1500 m in the Andes (Argüero et al., 2017).

REMARKS: The only molecular data available to assess the taxonomic status of nominal taxa currently regarded as synonyms of *Glironia venusta* were analyzed by Voss et al. (2019), who reported a trivial sequence difference (0.2%, uncorrected) between fragments of cytochrome

*b* amplified from the holotypes of *aequatorialis* and *criniger* (from north of the Amazon in eastern Ecuador and northeastern Peru, respectively) but a much larger distance (ca. 6%) between those sequences and one from south of the Amazon in western Brazil. Unfortunately, no sequence data are currently available from eastern Amazonia. Measurements from five western Amazonian specimens were tabulated by Voss et al. (2019).

#### Subfamily Hyladelphinae Voss and Jansa, 2009

TYPE GENUS: *Hyladelphys* Voss et al., 2001.

REMARKS: See Voss and Jansa (2009) for a morphological diagnosis. This taxon represents a very long branch that is consistently recovered as the sister lineage of Didelphinae in phylogenetic analyses of multilocus sequence datasets (e.g., by Voss and Jansa, 2009; Amador and Giannini, 2016).

#### Genus *Hyladelphys* Voss et al., 2001

TYPE SPECIES: *Gracilinanus kalinowskii* Hershkovitz, 1992, by original designation.

SYNONYMS: None.

REMARKS: Emended morphological descriptions were provided by Jansa and Voss (2005) and Voss and Jansa (2009). Only one species is currently recognized.

#### *Hyladelphys kalinowskii* (Hershkovitz, 1992)

TYPE MATERIAL: FMNH 89991, the holotype by original designation, consists of the skin and skull of an adult female collected at Hacienda Cadena (13.33° S, 70.77° W; 890 m), Cusco department, Peru.

SYNONYMS: None.

DISTRIBUTION: As currently understood, *Hyladelphys kalinowskii* is known from eastern Peru (Cusco, Junín, Loreto), northern Brazil (Amazonas, near Manaus), southern Guyana, and French Guiana (Gardner 2008: map 18).

REMARKS: The possibility that multiple cryptic taxa might be represented among the material currently referred to this species was discussed

by Jansa and Voss (2005). Measurement data from recently collected specimens are in Catzefflis (2017) and Voss et al. (2019).

#### Subfamily Didelphinae Gray, 1821

TYPE GENUS: *Didelphis* Linnaeus, 1758.

SYNONYMS: Chironectinae Hershkovitz, 1997; Lutreolinae Hershkovitz, 1997.

REMARKS: See Voss and Jansa (2009: 100) for a morphological diagnosis. Monophyly of the nominotypical subfamily has been consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., Voss and Jansa, 2009; Amador and Giannini, 2016).

#### Tribe Marmosini Hershkovitz, 1992

TYPE GENUS: *Marmosa* Gray, 1821.

REMARKS: The monophyly of Marmosini as constituted herein—including *Marmosa*, *Monodelphis*, and *Tlacuatzin*, but not the other genera referred to “Marmosidae” by Hershkovitz (1992)—has been consistently and strongly supported by all relevant phylogenetic analyses of multilocus sequence datasets (e.g., Voss and Jansa, 2009; May-Collado et al., 2015; Vilela et al., 2015; Amador and Giannini, 2016). Recently, however, Beck and Taglioretti (2020) suggested that Marmosini be restricted to include just *Marmosa* and *Tlacuatzin* (or that Marmosini be restricted to include just *Marmosa* with a new tribe for *Tlacuatzin*), and that *Monodelphis* be placed in a separate tribe (Monodelphini). These proposed changes were prompted by phylogenetic analyses that recovered two highly specialized fossil taxa in a clade with *Monodelphis*. However, as explained elsewhere (appendix 1), Beck and Taglioretti’s phylogenetic results are sufficiently open to question that it seems unnecessary to disrupt the current classification. Restricting Marmosini as they propose would leave the robustly supported clade that includes *Marmosa*, *Tlacuatzin*, and *Monodelphis* without a name, and their alternative tribal usage lacks any compensatory advantage for communicating phylogenetic relationships among Recent taxa.

#### Genus *Marmosa* Gray, 1821

TYPE SPECIES: *Didelphis murina* Linnaeus, 1758, by monotypy.

SYNONYMS: *Asagis* Gloger, 1841; *Grymaeomys* Burmeister, 1854; *Cuica* Liais, 1872; *Grayium* Kretzoi and Kretzoi, 2000.

REMARKS: For an emended generic description see Voss et al. (2014), who additionally recognized the five subgenera listed below. Although *Micoureus* was formerly regarded as a separate genus (e.g., by Gardner and Creighton, 2008a), the monophyly of *Marmosa*—as recognized herein, including *Micoureus* as a subgenus—has been consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., by Voss and Jansa, 2009; Voss et al., 2014; Amador and Giannini, 2016).

#### Subgenus *Eomarmosa* Voss et al., 2014

TYPE SPECIES: *Marmosa rubra* Tate, 1931, by original designation.

SYNONYMS: None.

REMARKS: Only a single species is currently recognized.

#### *Marmosa* (*Eomarmosa*) *rubra* Tate, 1931

TYPE MATERIAL AND TYPE LOCALITY: AMNH 71973, the holotype by original designation, consists of the skin and skull of an adult female collected at the mouth of the Río Curaray (ca. 2.37° S, 74.08° W; ca. 200 m), Loreto, Peru. Tate (1931, 1933) thought that the type was collected in Ecuador, but “Boca Río Curaray” (as this locality was originally recorded by the collectors) is well within the internationally recognized borders of Peru (Wiley, 2010).

SYNONYMS: None.

DISTRIBUTION: *Marmosa rubra* is known from just a few localities in the Amazonian lowlands of southeastern Colombia (Putumayo), eastern Ecuador (Napo, Orellana, Pastaza, and Sucumbios), and eastern Peru (Loreto, and Madre de Dios) (Rossi et al., 2010: fig. 30). Addi-

tional Peruvian records were summarized by Pacheco et al. (2020).

REMARKS: See Rossi et al. (2010) for an emended morphological description, illustrations, measurement data, and comparisons with congeneric species.

Subgenus *Exulomarmosa* Voss et al., 2014

TYPE SPECIES: *Marmosa robinsoni* Bangs, 1898, by original designation.

SYNONYMS: None.

REMARKS: Subgeneric monophyly has been consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., by Voss et al., 2014; Amador and Giannini, 2016). Six species are currently recognized as valid.

*Marmosa (Exulomarmosa) isthmica*  
Goldman, 1912

TYPE MATERIAL AND TYPE LOCALITY: USNM 170969, the holotype by original designation, consists of the skin and skull of an adult male collected on the Río Indio (9.25° N, 79.98° W; at sea level), a tributary of the lower Río Chagres near Gatún, Colón province, Panama.

SYNONYMS: *mimetra* Thomas, 1921; *regina* Thomas, 1898 (suppressed; see Remarks).

DISTRIBUTION: *Marmosa isthmica* is known from humid lowland and lower-montane localities (usually below 1700 m) in Panama, western Colombia (including the interAndean Cauca and Magdalena valleys), and western Ecuador (Rossi et al., 2010: fig. 22).

REMARKS: Originally described as a full species, *Marmosa isthmica* was treated for many years as a subspecies or synonym of *M. robinsoni* (after Hershkovitz, 1951). Current usage follows Rossi et al. (2010), who demonstrated that *M. isthmica* and *M. robinsoni* are morphologically distinct, known to occur in sympatry, and usually occupy different habitats (*M. isthmica* in rainforest, *M. robinsoni* in dry forest). A subsequent mtDNA sequencing study (Gutiérrez et al.,

2010) provided compelling evidence that these are, in fact, genetically distinct species.

Although *Marmosa regina* is a senior synonym of *M. isthmica*, the former name has long been misapplied to species in the subgenus *Micoureus*. To preserve long-standing binomial usage of *M. isthmica*, Voss and Giarla (2020a) petitioned the International Commission on Zoological Nomenclature to suppress usage of *M. regina*. A ruling from the Commission is pending.

*Marmosa (Exulomarmosa) mexicana*  
Merriam, 1897

TYPE MATERIAL AND TYPE LOCALITY: USNM 71526, the holotype by original designation, consists of the skin and skull of an adult male collected at “Juquila” (= Santa Catarina Juquila: 16.23° N, 97.30° S; 1500 m), Oaxaca state, Mexico.

SYNONYMS: *mayensis* Osgood, 1913; *ruatanica* Goldman, 1911; *savannarum* Goldman, 1917.

DISTRIBUTION: As currently recognized (see Remarks), *Marmosa mexicana* is known from rainforested and dry-forested localities from northern Mexico (Tamaulipas) southward and eastward throughout Central America to eastern Panama (Rossi et al., 2010: fig. 17).

REMARKS: See Rossi et al. (2010) for an emended description, tabulated measurement data, and morphological comparisons with congeneric species. As reported by Gutiérrez et al. (2010), mtDNA sequences from specimens that fit the morphological description of *Marmosa mexicana* form two highly divergent haplogroups. Some authors (e.g., Ramírez-Pulido et al., 2014) now recognize *M. mayensis* as a distinct species—presumably based on Gutiérrez et al.’s sequencing results—but diagnostic morphological characters are elusive, and no sequence data are available from holotypes or topotypes to confidently assign names to either mtDNA clade. *Marmosa mexicana* was formerly thought to be conspecific with *M. zeledoni* (e.g., by Tate, 1933), but evidence that these are separate species was summarized by Rossi et al. (2010) and Gutiérrez et al. (2010).

*Marmosa (Exulomarmosa) robinsoni*  
Bangs, 1898

TYPE MATERIAL AND TYPE LOCALITY: MCZ B7749, the holotype by original designation, consists of the skin and skull of an adult male collected at El Valle de Espíritu Santo (10.98° N, 63.87° W; ca. 200 m) on Isla Margarita, Nueva Esparta state, Venezuela (Rossi et al., 2010).

SYNONYMS: *casta* Thomas, 1911; *chapmani* Allen, 1900; *fulviventer* Bangs, 1901; *grenadae* Thomas, 1911; *luridivolta* Goodwin, 1961; *mitis* Bangs, 1898; *nesaea* Thomas, 1911; *pallidiventris* Osgood, 1912.

DISTRIBUTION: *Marmosa robinsoni* occurs primarily in dry forests, but also occasionally in other habitats from western Panama to Colombia, northern Venezuela, and several adjacent continental-shelf islands (including Isla Margarita, Trinidad, and Tobago); the species is also known from Grenada, a Caribbean island that is not on the continental shelf (Rossi et al., 2010: fig. 25).

REMARKS: See Rossi et al. (2010) for an emended description, tabulated measurement data, and morphological comparisons with congeneric species. Several taxa that were formerly treated as subspecies or synonyms of *Marmosa robinsoni* (e.g., by Hershkovitz, 1951; Hall, 1981; Creighton and Gardner, 2008a) are now recognized as valid species (*M. isthmica*, *M. simonsi*) or have been relegated to the synonymies of other species. Even in its currently restricted sense (Rossi et al., 2010), however, *M. robinsoni* is a geographically and ecologically widespread species that includes numerous nominal taxa as subjective synonyms. Analyses of DNA sequence data (Gutiérrez et al., 2014a) have shown that geographic populations of this species sort out into two strongly supported phylogroups: an eastern clade for which the oldest available trinomen would be *M. robinsoni robinsoni*, and a western clade for which the oldest trinomen would be *M. r. mitis*. Unfortunately, these putative subspecies appear to be phenotypically indistinguishable,

such that specimens cannot be assigned to one or the other without DNA sequence data.

*Marmosa (Exulomarmosa) simonsi*  
Thomas, 1899

TYPE MATERIAL AND TYPE LOCALITY: BMNH 99.8.1.20, the holotype by original designation, consists of the skin and skull of an adult male collected at Puná (2.73° S, 79.92° W; near sea level), on Isla Puná, Guayas province, Ecuador.

SYNONYMS: None.

DISTRIBUTION: *Marmosa simonsi* occurs in mangroves and dry forests of the Pacific lowlands and Andean foothills of western Ecuador and northwestern Peru (Rossi et al., 2010: fig. 28).

REMARKS: See Rossi et al. (2010) for an emended description, tabulated measurement data, and morphological comparisons with congeneric species. *Marmosa simonsi* was long considered a synonym or subspecies of *M. robinsoni* (e.g., by Hershkovitz, 1951; Creighton and Gardner, 2008a), but Rossi et al. (2010) and Gutiérrez et al. (2010) showed that these taxa are morphologically and genetically distinct.

*Marmosa (Exulomarmosa) xerophila* Handley  
and Gordon, 1979

TYPE MATERIAL AND TYPE LOCALITY: USNM 443819, the holotype by original designation, consists of the skin and skull of an adult male collected at La Isla (ca. 11.63° N, 71.83° S; near sea level), Guajira department, Colombia.

SYNONYMS: None.

DISTRIBUTION: *Marmosa xerophila* occurs in desert thornscrub along the arid Caribbean coast of northeastern Colombia and northwestern Venezuela (Rossi et al., 2010: fig. 26). Additional specimen records and comments on the ecogeographic distribution of this species were provided by Gutiérrez et al. (2014b).

REMARKS: See Rossi et al. (2010) for an emended morphological description, tabulated measurement data, and morphological comparisons with congeneric species.



*Marmosa (Exulomarmosa) zeledoni*  
Goldman, 1911

TYPE MATERIAL AND TYPE LOCALITY: USNM 12885, the holotype by original designation, consists of the skin and skull of an adult male collected at Navarro (9.82° N, 83.87° S; ca. 840 m), Cartago province, Costa Rica.

SYNONYMS: None.

DISTRIBUTION: *Marmosa zeledoni* is known from widely scattered localities, mostly in pre-montane or montane rainforest (to 2200 m) but sometimes in very wet lowland forests, from north-central Nicaragua southward through Costa Rica and Panama to western Colombia and north-western Ecuador (Rossi et al., 2010: fig. 21).

REMARKS: See Rossi et al. (2010) for an emended description, tabulated measurement data, and morphological comparisons with congeneric species. *Marmosa zeledoni* was long regarded as a synonym or subspecies of *M. mexicana* (e.g., by Tate, 1933), but these are morphologically and genetically distinct taxa that are known to occur sympatrically at several localities (Rossi et al., 2010; Gutiérrez et al., 2010).

Subgenus *Marmosa* Gray, 1821

TYPE SPECIES: As for the genus.

SYNONYMS: As for the genus.

REMARKS: Monophyly of the nominotypical subgenus has been consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., by Voss et al., 2014; Amador and Giannini, 2016). Four species are currently recognized as valid.

*Marmosa (Marmosa) macrotarsus*  
(Wagner, 1842)

TYPE MATERIAL AND TYPE LOCALITY: No type was designated in the original description, although Wagner (1847) mentioned two specimens collected by Johann Natterer on the Rio Madeira that have subsequently been regarded as syntypes. Pelzeln (1883), however, listed only one

Natterer specimen of this species from the Rio Madeira. Tate (1933: 101) referred to this specimen as “Vienna 195,” and called it a “co-type.” It is now cataloged as NMW B-2610 and consists of the skin and skull of an adult male (F. Zachos, in litt., 2 December 2021).

SYNONYMS: *madeirensis* Cabrera, 1913 (an invalid replacement name; see Remarks); *musicola* Osgood, 1913; *quichua* Thomas, 1899.

DISTRIBUTION: As recognized by Rossi (2005; see Remarks), *Marmosa macrotarsus* is an Amazonian species that occurs south of the Amazon and west of the Tapajós; reported collection localities are in rainforested lowlands and foothills (below 1900 m) in Peru, Brazil, and Bolivia (Rossi, 2005: fig. 62).

REMARKS: *Marmosa macrotarsus* was ranked as a subspecies of *M. murina* by Tate (1933) who, however, used Cabrera’s (1913) replacement name for this taxon, and it was treated as a synonym of *M. murina* by Creighton and Gardner (2008a). Current recognition of *M. macrotarsus* as a valid species follows Rossi (2005), who provided a morphological description, tabulated measurement data, and carried out morphometric comparisons with other congeners. Subsequently, Gutiérrez et al. (2010) found that specimens geographically assignable to *M. macrotarsus* (sensu Rossi, 2005) are highly divergent from *M. murina* in cytochrome *b* sequence comparisons (>9%, uncorrected), and phylogenetic analyses of multilocus sequence data later showed that these species may not even be sister taxa (Voss et al., 2014). Nevertheless, the morphological criteria by which specimens of *M. macrotarsus* and *M. murina* can be distinguished remain to be convincingly documented. Voss et al. (2019) discussed morphological comparisons between *M. macrotarsus* and *M. waterhousei*, another taxon formerly ranked as a subspecies of *M. murina* (see below).

Cabrera (1913) believed that *Didelphys macrotarsus* Wagner, 1842, was preoccupied by *D. macrotarsos* Schreber, 1778 (a tarsier), and this opinion was endorsed by Creighton and Gardner (2008a). However, the one-letter difference in

spelling is sufficient to prevent homonymy (Rossi, 2005). Therefore, although Cabrera's replacement name is available in the sense of the Code (ICZN, 1999: Article 12.2.3), it is an objective junior synonym of Wagner's *macrotarsus* and therefore invalid.

*Marmosa (Marmosa) murina* (Linnaeus, 1758)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 67.4.12.542, the lectotype (designated by Husson, 1978), consists of a fluid-preserved female specimen from which the skull has been extracted and lost (Voss et al., 2001). Rossi (2005: 95) thought that BMNH 67.4.12.541 (a male) was the lectotype, citing Thomas (1892) as having so designated that specimen, but Thomas merely identified two probable syntypes without choosing either as the unique name-bearer. Jenkins and Knutson (1983) also appear to have been unaware of Husson's lectotype designation. The type locality is unknown, but it is often assumed to be Surinam (after Thomas, 1911).

SYNONYMS: *chloe* Thomas, 1907; *dorsigera* Linnaeus, 1758<sup>4</sup>; *duidae* Tate, 1931; *klagesi* J.A. Allen, 1900; *meridionalis* Miranda-Ribeiro, 1936; *moreirae* Miranda-Ribeiro, 1936; *musculus* Cabanis, 1848; *parata* Thomas, 1911; *roraimae* Tate, 1931; *tobagi* Thomas, 1911.

DISTRIBUTION: As currently understood (Voss et al., 2014), *Marmosa murina* is known from northwestern Venezuela and eastern Colombia eastward and southward throughout the Guianas to Brazil; in Brazil, the species is known from Amazonia (east of the Rio Negro and the Tapajós), the Cerrado, and the Atlantic Forest. *Marmosa murina* is also known from Tobago, but not from Trinidad. Rossi (2005: fig. 56) mapped the joint distribution of *M. murina* and *M. tobagi*, which he regarded as distinct species.

REMARKS: Analyses of cytochrome *b* sequence data (Faria et al., 2013a; Voss et al.,

2014) suggest that geographic populations currently recognized as *Marmosa murina* include four strongly supported phylogroups that might reasonably be recognized as subspecies: (1) mainland populations north of the Amazon, for which the oldest available trinomen would be *M. m. murina*; (2) an insular population on Tobago, which could be called *M. m. tobagi*; (3) populations in southeastern Amazonia (east of the Tapajós and south of the Amazon), for which *M. m. parata* would seem to be the appropriate trinomen; and (4) populations in the Atlantic Forest of southeastern Brazil, which could be referred to *M. m. moreirae*. Of these nominal taxa, however, only *tobagi* appears to be morphologically diagnosable from the others (Rossi, 2005). The logic of treating *tobagi* as a subspecies of *M. murina* rather than as a valid species was briefly discussed by Voss et al. (2014), whose phylogenetic results implied that this phenotypically divergent insular form is closely related to adjacent mainland populations.

*Marmosa (Marmosa) tyleriana* Tate, 1931

TYPE MATERIAL AND TYPE LOCALITY: AMNH 76983, the holotype by original designation, consists of the skin and skull of an adult female collected at an expeditionary locality known as Central Camp (ca. 3.38° N, 65.58° W; 1400 m) on the Mt. Duida massif, Amazonas state, Venezuela.

SYNONYMS: *phelpsi* Tate, 1939.

DISTRIBUTION: This species is known from just a few localities in the Guiana highlands of southern Venezuela at elevations from 1300 to 2100 m (Creighton and Gardner, 2008a: map 24).

REMARKS: *Marmosa tyleriana* is the sister taxon of a clade that contains all the other species in the subgenus *Marmosa* (Voss et al., 2014). Rossi (2005) provided a detailed morphological description and tabulated measurement data of the specimens he examined, but additional measurement data were reported by Ochoa (1985).

<sup>4</sup> For the priority of *murina* Linnaeus, 1758, over *dorsigera* Linnaeus, 1758, see Husson (1978: 22).



*Marmosa (Marmosa) waterhousei*  
(Tomes, 1860)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 7.1.1.215, the lectotype (designated by Thomas, 1921a), consists of a skull, said to be that of an adult female, collected at Gualaquiza (3.40° S, 78.55° W; 914 m), Morona-Santiago province, Ecuador. The rest of the specimen, originally preserved in fluid, has been lost.<sup>5</sup> Jenkins and Knutson (1983) referred to this specimen as the holotype, but Tomes' (1860) description was based on an adult and an unspecified number of young individuals, all of which were, in effect, syntypes.

SYNONYMS: *bombascarae* Anthony, 1922; *maranii* Thomas, 1924.

DISTRIBUTION: As currently recognized, *Marmosa waterhousei* occurs in the lowlands and adjacent Andean foothills of southeastern Colombia, eastern Ecuador, northeastern Peru (north of the Amazon), and a few scattered localities in the Andes of northern Colombia and western Venezuela (Gutiérrez et al., 2011: fig. 2). A recently published Peruvian record from south of the Amazon (in Junín department; Pacheco et al., 2020) merits phenotypic and genetic confirmation.

REMARKS: *Marmosa waterhousei* was ranked as a subspecies of *M. murina* by Tate (1933), and it was treated as a synonym of *M. murina* by Creighton and Gardner (2008a). Current recognition of *M. waterhousei* as a valid species follows Rossi (2005), who provided a morphological description, tabulated measurement data, and carried out morphometric comparisons with other congeners. Despite compelling support for currently recognized species limits in the subgenus *Marmosa* from phylogenetic analyses of

DNA sequence data (Gutiérrez et al., 2010; Voss et al., 2014), morphological distinctions between some pairs of species remain problematic. Apparently, only measurement data seem to consistently distinguish specimens of *M. waterhousei* from specimens of *M. macrotarsus* (see Voss et al., 2019).

This name was originally spelled *waterhousii*, but most subsequent authors have spelled it *waterhousei*. The latter spelling would appear to have been an incorrect subsequent spelling (in the special sense of the Code) when it was first adopted by Thomas (1888a), but *waterhousei* is the spelling in prevailing usage today and should be maintained (ICZN, 1999: Article 33.3.1).

Subgenus *Micoureus* Lesson, 1842

TYPE SPECIES: *Didelphis cinerea* Temminck, 1824 (= *Marmosa paraguayana*; see below), by subsequent designation (Thomas, 1888a)

SYNONYMS: None.

REMARKS: *Micoureus* was formerly ranked as a genus (e.g., by Gardner and Creighton, 2008a), but this clade has been consistently recovered nested within *Marmosa* by phylogenetic analyses of multilocus sequence datasets (Voss and Jansa, 2009; Voss et al., 2014; Amador and Giannini, 2016). Thirteen species are currently recognized, most of which can be sorted into one or another of several groups based on robustly supported phylogenetic relationships (table 1).

*Marmosa (Micoureus) adleri* Voss et al., 2021

TYPE MATERIAL AND TYPE LOCALITY: AMNH 272942, the holotype by original designation, consists of the skin and skull of an adult female collected 1 km north of the Río Mendoza on Pipeline Road (9.17° N, 79.75° W; 120 m), Parque Nacional Soberanía, Colón province, Panama.

SYNONYMS: None.

DISTRIBUTION: *Marmosa adleri* is currently known only from Panama, where it has been collected from near the Costa Rican border to the Colombian frontier (Voss et al., 2021: fig. 2).

<sup>5</sup> Tomes' (1860) assertion that the fluid-preserved type of *Marmosa waterhousei* had a pouch is impossible to reconcile with its skull, which clearly belongs to a species in the pouchless nominotypical subgenus of *Marmosa*. However, the application of this name can only be based on what remains of the specimen, and on the type locality (eastern Ecuador), where only a single species of the nominotypical subgenus is known to occur.

TABLE 1

**Species-group Assignments in the  
Subgenus *Micoureus* of *Marmosa***

|                             |
|-----------------------------|
| Alstoni Group <sup>a</sup>  |
| <i>M. adleri</i>            |
| <i>M. alstoni</i>           |
| <i>M. nicaraguae</i>        |
| Perplexa Group <sup>b</sup> |
| <i>M. jansae</i>            |
| <i>M. perplexa</i>          |
| Phaea Group <sup>b</sup>    |
| <i>M. constantiae</i>       |
| <i>M. demerarae</i>         |
| <i>M. phaea</i>             |
| Rapposa Group <sup>c</sup>  |
| <i>M. parda</i>             |
| <i>M. rapposa</i>           |
| <i>M. rutteri</i>           |
| Unaffiliated species        |
| <i>M. germana</i>           |
| <i>M. paraguayana</i>       |

<sup>a</sup> After Voss et al. (2021).

<sup>b</sup> New (see text).

<sup>c</sup> After Voss et al. (2020).

REMARKS: *Marmosa adleri* is the sister species of *M. alstoni* and a member of the Alstoni Group (Voss et al., 2021). Specimens of *M. adleri* were previously misidentified as *M. alstoni* (e.g., by Patton et al., 2000; Voss et al., 2020) or as *M. phaea* (e.g., by Handley, 1966; Emmons, 1997), but they are unmistakably distinct from both. Illustrations, a morphological description, measurement data, and comparisons with closely related congeners were provided by Voss et al. (2021).

*Marmosa (Micoureus) alstoni* (J.A. Allen, 1900)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 11790/16210, the holotype by original designation, consists of the skin and skull of an adult male collected at Tres Ríos (9.90° N, 83.98° W; 1219 m), Cartago province, Costa Rica.

SYNONYMS: None.

DISTRIBUTION: As currently understood (see Remarks, below), *Marmosa alstoni* is only known from a handful of localities in the central highlands of Costa Rica (Voss et al., 2021: fig. 2).

REMARKS: *Marmosa alstoni* was once thought to range from Belize to Colombia (Tate, 1933; Hall, 1981; Gardner and Creighton, 2008a) and to include *M. nicaraguae* as a synonym, but a recent revision of the Alstoni Group of *Marmosa* restricted the application of this name to specimens collected in the central highlands of Costa Rica (Voss et al., 2021).

*Marmosa (Micoureus) constantiae* Thomas, 1904

TYPE MATERIAL AND TYPE LOCALITY: BMNH 3.7.7.157, the holotype by original designation, consists of the skin and skull of an adult male collected at “Chapada” (= Santa Ana de Chapada: 15.43° S, 55.75° W; 800 m), Mato Grosso state, Brazil.

SYNONYMS: *domina* Thomas, 1920; *mapirien-sis* Tate, 1931.

DISTRIBUTION: As currently recognized (see Remarks), *Marmosa constantiae* occurs from the foothills of the Andes (below about 1100 m) in eastern Peru and eastern Bolivia eastward across Amazonia and the Cerrado to central Brazil; mtDNA sequencing results (see Remarks) suggest that the range of this species does not extend north of the Amazon nor east of the Xingu (Silva et al., 2019: fig. 5; Voss et al., 2020: fig. 2).

REMARKS: The name *Marmosa constantiae* has long been misapplied to a superficially similar congener, *M. rapposa*, that also occurs in Mato Grosso and eastern Bolivia (see below). Previous reports of *M. constantiae* from Argentina (Flores et al., 2007) and Paraguay (de la Sancha et al., 2012; Smith and Owen, 2015) likewise appear to have been based on specimens of *M. rapposa*. As recognized by Silva et al. (2019) and Voss et al. (2020), *M. constantiae* is geographically variable in coloration: whereas Cerrado populations have pale dorsal fur, broadly self-yellow underparts, and parti-

colored (white-tipped) tails, rainforest populations are darker dorsally and have mostly gray-based ventral fur and all-dark tails (Voss et al., 2019). The rainforest phenotype of *M. constantiae* is difficult to distinguish morphologically from *M. germana* (a distantly related congener that occurs north of the Amazon; Voss and Giarla, 2021), so currently recognized range limits are based, in part, on sequencing results rather than examined specimens. Phylogenetic analyses of multilocus sequence data recover *M. constantiae* and *M. demerarae* as sister taxa (Voss et al., 2020), and comparisons of sequenced specimens suggest that these taxa are morphologically diagnosable (Silva et al., 2019).

*Marmosa (Micoureus) demerarae* Thomas, 1905

TYPE MATERIAL AND TYPE LOCALITY: BMNH 5.11.1.25, the holotype by original designation, consists of the skin and skull of an adult female collected at “Comackka” (= Takama: 5.57° N, 57.92° W; ca. 100 m), East Demerara-West Coast Berbice, Guyana.

SYNONYMS: *arenticola* Tate, 1931; *esmeraldae* Tate, 1931; *limae* Thomas, 1920; *meridae* Tate, 1931; *pfrimeri* Miranda-Ribeiro, 1936.

DISTRIBUTION: As currently recognized (see Remarks), *Marmosa demerarae* occurs from eastern Venezuela eastward and southward throughout the Guianas to Brazil. In Brazil, this species occurs east of the Rio Negro on the north side of the Amazon; it occurs east of the Tapajós along the south bank of the Amazon, and it occurs as far south as Bahia along the Atlantic coast (Silva et al., 2019: fig. 5; Voss et al., 2020: fig. 2).

REMARKS: This concept of *Marmosa demerarae* follows Silva et al. (2019) and includes several cytochrome *b* haplogroups from south of the Amazon that Voss et al. (2020) recognized as putative species and associated with the name *limae*. However, the latter authors cautioned that their voucher specimens of *limae* might not be phenotypically distinguishable from *M. demerarae*, and subsequent examination of large series

of specimens from south of the Amazon has likewise failed to find compelling evidence that *limae* is a distinct species.

*Marmosa (Micoureus) germana* Thomas, 1904

TYPE MATERIAL AND TYPE LOCALITY: BMNH 80.5.6.77, the holotype by original designation, consists of the skin and skull of a subadult female collected at Sarayacu (1.73° S, 77.48° W; ca. 700 m) on the Río Bobonaza, Pastaza province, Ecuador.

SYNONYMS: None.

DISTRIBUTION: *Marmosa germana* has been collected at scattered localities in the Amazonian lowlands of southeastern Colombia (Caquetá), eastern Ecuador (Orellana, Pastaza), and northeastern Peru (Loreto, north of the Amazon) (Voss and Giarla, 2021: fig. 2).

REMARKS: This species was long considered a subspecies or synonym of *Marmosa regina* (e.g., by Gardner and Creighton, 2008a). Diagnostic morphological characters, taxonomic comparisons, and phylogenetic relationships were discussed by Voss and Giarla (2021). As currently recognized, this species contains at least two cytochrome *b* haplogroups that might represent distinct taxa (Voss et al., 2020), but too few specimens are available to assess the constancy of observed phenotypic differences.

*Marmosa (Micoureus) jansae*  
Voss and Giarla, 2021

TYPE MATERIAL AND TYPE LOCALITY: ROM 118880, the holotype by original designation, consists of the skin, skull, postcranial skeleton, and frozen tissues of an adult male collected 42 km south and 1 km east of Pompeya Sur (0.68° S, 76.47° W), Parque Nacional Yasuní, Orellana province, Ecuador.

SYNONYMS: None.

DISTRIBUTION: *Marmosa jansae* is currently known from the Amazonian lowlands of southeastern Colombia (Putumayo), eastern Ecuador (Orellana, Pastaza), and northeastern Peru

(Loreto, north of the Amazon) (Voss and Giarla, 2021: fig. 2).

REMARKS: Specimens of *Marmosa jansae* were identified by Tate (1933) as *M. germana germana* or as *M. g. rutteri*, and subsequently collected specimens have often been identified as *M. regina* (e.g., by Hice and Velazco, 2012). Voss and Giarla (2021) provided a morphological description, measurement data, taxonomic comparisons, and other relevant information about this species.

*Marmosa (Micoureus) nicaraguae* Thomas, 1905

TYPE MATERIAL AND TYPE LOCALITY: BMNH 5.10.31.5, the holotype by original designation, consists of the skin and skull of an adult male collected at Bluefields (12.00° N, 83.75° W; sea level), South Caribbean Autonomous Region, Nicaragua.

SYNONYMS: None.

DISTRIBUTION: Examined specimens of *Marmosa nicaraguae* are from just three localities in the Caribbean coastal lowlands of Nicaragua and Costa Rica, but a photographed individual from the Pacific foothills of the Cordillera Tilarán (in Costa Rica) suggests that the species may be more widely distributed (Voss et al., 2021: fig. 2).

REMARKS: *Marmosa nicaraguae* was formerly considered to be a subspecies of *M. alstoni* (e.g., by Tate, 1933; Hall, 1981), but evidence that these taxa are morphologically and genetically distinct was discussed by Voss et al. (2021).

*Marmosa (Micoureus) paraguayana* Tate, 1931

TYPE MATERIAL AND TYPE LOCALITY: BMNH 25.5.1.15, the holotype by original designation, consists of the skin and skull of an adult male collected at Villarica (25.75° S, 56.43° W), Guairá department, Paraguay.

SYNONYMS: *cinerea* Temminck, 1824 (preoccupied); *travassosi* Miranda-Ribeira, 1936.

DISTRIBUTION: *Marmosa paraguayana* is found in the Atlantic Forest of Brazil (south of

Bahia) and in the contiguous subtropical humid forests of northeastern Argentina (Misiones) and eastern Paraguay (Gardner and Creighton, 2008a: map 33).

REMARKS: The current assumption that *Didelphis cinerea* Temminck, 1824 (preoccupied by *Didelphis cinerea* Goldfuss, 1812; Gardner and Creighton, 2008a) is a synonym of *Marmosa paraguayana* merits some skepticism. The lectotype of Temminck's *cinerea* (AMNH 845; designated by Avila Pires, 1965) is a very old skin that does not preserve any convincingly diagnostic traits. Moreover, the type locality of *cinerea* (Morro d'Arara, at 18.10° S, 39.58° W) is in Bahia, where only *Marmosa demerarae*—externally indistinguishable from *M. paraguayana* according to Guimarães (2013)—is known to occur. Molecular sequence data from the lectotype of *cinerea* would help settle the question as to whether this name belongs in the synonymy of *M. paraguayana* or *M. demerarae*.

*Marmosa (Micoureus) parda* Tate, 1931

TYPE MATERIAL AND TYPE LOCALITY: FMNH 24140, the holotype by original designation, consists of the skin and skull of an adult male collected at Huachipa (ca. 9.50° S, 75.87° W; 855–1405 m), Huánuco department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Marmosa parda* is known from just a few localities on the cloud-forested eastern Andean slopes of central Peru.

REMARKS: *Marmosa parda* was long treated as a subspecies or synonym of *Marmosa germana* or *M. regina*, but it was recently validated and assigned to the Rapposa Group by Voss et al. (2020), who provided an emended morphological description, measurement data, and relevant taxonomic comparisons.

*Marmosa (Micoureus) perplexa* Anthony, 1922

TYPE MATERIAL AND TYPE LOCALITY: AMNH 47188, the holotype by original designation, con-

sists of the skin and skull of a young adult female collected at Punta Santa Ana (3.83° S, 79.55° W; 1113 m), Loja province, Ecuador.

SYNONYMS: None.

DISTRIBUTION: *Marmosa perplexa* is known from the Pacific lowlands and western Andean foothills of southwestern Ecuador (El Oro, Loja) and northwestern Peru (Cajamarca, Tumbes) (Voss and Giarla, 2021: fig. 2).

REMARKS: This species has long been treated as a synonym of *Marmosa phaea*, which it externally resembles. However, *M. perplexa* and *M. phaea* are not sister taxa, they have highly divergent mtDNA sequences, and they differ in several details of craniodental morphology (Voss and Giarla, 2021).

#### *Marmosa (Micoureus) phaea* Thomas, 1899

TYPE MATERIAL AND TYPE LOCALITY: BMNH 98.9.5.2, the holotype by original designation, consists of the skin and skull of a young adult female collected at San Pablo (1.10° N, 78.02° W; ca. 1500 m), Nariño department, Colombia.

SYNONYMS: None.

DISTRIBUTION: Specimens that resemble the type of *Marmosa phaea* are from Andean foothills and middle elevations (between ca. 1200 and 2800 m) in the Colombian departments of Cauca, Huila, and Nariño.

REMARKS: This species has not been critically evaluated since Tate (1933), and it badly needs revisionary attention. Voss et al. (2020) recovered a strongly supported haplogroup that they associated with the name *Marmosa phaea*, but some of the *phaea*-like sequences in their study came from specimens that differ in size and qualitative craniodental traits from typical material, and other specimens are from implausibly distant localities (e.g., in northern Venezuela and northwestern Brazil; Voss et al., 2020: fig. 2). Gardner and Creighton (2008a) listed *M. perplexa* as a synonym of *M. phaea*, but subsequent research has shown that these are unequivocally distinct species (Voss and Giarla, 2021).

#### *Marmosa (Micoureus) rapposa* Thomas, 1899

TYPE MATERIAL AND TYPE LOCALITY: BMNH 98.11.6.13, the holotype by original designation, consists of the skin and skull of an old adult female collected on the “Vilcanota River just north of Cuzco” (= Huadquiña: 13.12° S, 72.65° W; 1500 m), Cusco department, Peru (Voss et al., 2020).

SYNONYMS: *budini* Thomas, 1920.

DISTRIBUTION: *Marmosa rapposa* is known from cloud forests along the eastern slopes of the Andes below about 2500 m in southeastern Peru, Bolivia, and northwestern Argentina, and from the dry-forested lowlands of eastern Bolivia, Paraguay, and southwestern Brazil (Voss et al., 2020: fig. 12).

REMARKS: Although *Marmosa rapposa* was one of several valid species previously synonymized with *Marmosa regina* (sensu Gardner and Creighton, 2008a), specimens from Bolivia, Brazil, and Argentina were frequently identified as *M. constantiae* (e.g., by Anderson, 1997; Flores et al., 2007). Silva et al. (2019) were the first to distinguish this species—which they called *M. budini*—from *M. constantiae*, but *M. rapposa* is an older available name (Voss et al., 2020). *Marmosa rapposa* is closely related to *M. parda* and *M. rutteri*, which together comprise the Rapposa Group of the subgenus *Micoureus*.

#### *Marmosa (Micoureus) rutteri* Thomas, 1924

TYPE MATERIAL AND TYPE LOCALITY: BMNH 24.2.22.67, the holotype by original designation, consists of the skin and skull of an adult male collected at Tushemo (8.60° S, 74.32° W; 225 m) near Masisea, Ucayali department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Marmosa rutteri* occurs in lowland rainforest (below about 800 m) in southeastern Colombia, eastern Ecuador, eastern Peru, and western Brazil (Voss et al., 2020: fig. 17).

REMARKS: *Marmosa rutteri* was long treated as a synonym or subspecies of *M. germana* or *M. regina*, but it is morphologically and genetically



distinct from both (Voss et al., 2019). Voss et al. (2020) provided a description, tabulated morphometric variation, and discussed the phylogenetic relationships of this widespread species, which they assigned to the Rapposa Group.

#### Subgenus *Stegomarmosa* Pine, 1972

TYPE SPECIES: *Marmosa andersoni* Pine, 1972, by monotypy.

SYNONYMS: None.

REMARKS: The monophyly of *Stegomarmosa* as constituted herein is strongly supported by phylogenetic analyses of multilocus sequence data (Voss et al., 2014). Two species are currently recognized.

#### *Marmosa (Stegomarmosa) andersoni* Pine, 1972

TYPE MATERIAL AND TYPE LOCALITY: FMNH 84252, the holotype by original designation, consists of the skin and skull of a young adult male collected at Hacienda Villa Carmen (12.83° S, 71.25° W; 600 m) on the Río Cosñipata, Cusco department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Marmosa andersoni* is currently known from just four rainforested localities between 470 and 1100 m along the base of the eastern Andes in the Peruvian departments of Cusco and Pasco (Zeballos et al., 2019: fig. 1).

REMARKS: This morphologically distinctive species, originally known only from the holotype, is now represented by 13 specimens and has been redescribed by Solari and Pine (2008), Voss et al. (2014), and Zeballos et al. (2019). The last-named authors tabulated measurement data from four adults, the largest morphometric sample yet compiled for publication.

#### *Marmosa (Stegomarmosa) lepida* (Thomas, 1888)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 69.3.31.4, the holotype by original designation, consists of the skin and skull of an adult female

collected at Santa Cruz (5.55° S, 75.80° W; 150 m) on the Río Huallaga, Loreto, Peru.

SYNONYMS: *grandis* Tate, 1931 (but see Remarks).

DISTRIBUTION: *Marmosa lepida* probably occurs throughout Amazonia (Guimarães et al., 2018: fig. 1) and in contiguous premontane forests along the lower slopes of the eastern Andes (below about 1600 m; Brito and Pozo-Zamora, 2015). Although there are some notable gaps among the Amazonian collection localities mapped by Guimarães et al. (2018), one of them is filled by two overlooked records from southern Venezuela: the first is a specimen from the Río Caura reported by Ochoa et al. (2009), and the second is a previously unpublished specimen in the collection of the Estación Biológica Doñana.<sup>6</sup>

REMARKS: Rossi (2005) and Voss et al. (2019) provided morphological descriptions and illustrations of this species and tabulated measurement data. Additional phenotypic data are in Guimarães et al. (2018). The possibility that *grandis*, which differs from *M. lepida* in several morphological features, might be a distinct species was discussed by Voss et al. (2019).

#### Genus *Monodelphis* Burnett, 1830

TYPE SPECIES: *Didelphis brachyuros* Schreber, 1777 (= *Monodelphis breviceaudata*; see below), by subsequent designation (Matschie, 1916).

SYNONYMS: *Hemiurus* Gervais, 1855 (preoccupied); *Peramys* Lesson, 1842.

REMARKS: See Pavan and Voss (2016) for an emended morphological description of this highly distinctive genus. Generic monophyly is consistently supported by model-based phylogenetic

<sup>6</sup> The latter is EBD 11, collected by J. Castroviejo on 4 April 1973 at “El Platanal, alto Orinoco.” Many localities in Venezuela are known as “El Platanal,” but this one appears to be a village on the upper Orinoco upstream from the mouth of the Río Mavaca where EBD researchers worked in the early 1970s (R. Rodríguez, personal commun.). The USBGN gazetteer for Venezuela provides coordinates (2.42° N, 64.92° W) for a populated place called “Platanal” that fits this description.

analyses of multilocus sequence datasets (e.g., Voss and Jansa, 2003, 2009; Pavan et al., 2014; Vilela et al., 2015; Amador and Giannini, 2016). Five subgenera are currently recognized following Pavan and Voss (2016), who discussed synonymies and provided morphological diagnoses.

Subgenus *Microdelphys* Burmeister, 1856

TYPE SPECIES: *Didelphis tristriata* Illiger, 1815 (= *Monodelphis americana*; see below), by subsequent designation (Thomas, 1888a).

SYNONYMS: None.

REMARKS: See Pavan and Voss (2016) for a morphological diagnosis of this distinctive taxon. Monophyly of *Microdelphys* as recognized herein was consistently supported by parsimony, maximum-likelihood, and Bayesian analyses of multilocus sequence data reported by Pavan et al. (2014, 2016). Although subgeneric monophyly was not supported by maximum-likelihood and Bayesian analyses of a multigene dataset reported by Vilela et al. (2015), none of the conflicting nodes in Vilela et al.'s results were strongly supported. Four species are currently recognized.

*Monodelphis (Microdelphys) americana*  
(Müller, 1776)

TYPE MATERIAL AND TYPE LOCALITY: No type material is known to exist. *Monodelphis americana* is based on a 17th-century description of a species observed in Brazil by the Dutch naturalist Marcgraf (Pine and Handley, 2008), so the type locality is often assumed to be Recife, the main Dutch settlement in Brazil (Cabrera, 1958). Although the application of this name is not currently disputed, future taxonomic contingencies might require the designation of a neotype.

SYNONYMS: *brasiliensis* Erxleben, 1777; *brasiliensis* Daudin (in Lacépède, 1802); *rubida* Thomas, 1899; *trilineata* Lund, 1840; *tristriata* Illiger, 1815; *umbristriata* Miranda-Ribeiro, 1936.

DISTRIBUTION: *Monodelphis americana* is known from the right bank of the Tocantins in

eastern Pará southward along the rainforested (or formerly rainforested) Atlantic coast of Brazil to Santa Catarina; the range of this species also extends inland along gallery-forested rivers into the Cerrado (Pine and Handley, 2008: map 37).

REMARKS: See Duda and Costa (2015) for a morphological description, measurement data, and comparisons with *Monodelphis iheringi*, a superficially similar and closely related sympatric congener. The names *brasiliensis*, *trilineata*, and *tristriata* are all based, directly or indirectly, on the same 17th-century description authored by Marcgraf (Pine and Handley, 2008), so they are objective synonyms of *M. americana*. However, the names *rubida* and *umbristriata* are subjective synonyms based on specimens that exhibit ontogenetic pelage-color variants (Pavan et al., 2014; Duda and Costa, 2015). Northern and southern cytochrome *b* haplogroups of *M. americana* differ by an average uncorrected sequence distance of 8.2% (Pavan et al., 2014) and merit close taxonomic scrutiny.

*Monodelphis (Microdelphys) gardneri*  
Solari et al., 2012

TYPE MATERIAL AND TYPE LOCALITY: MUSM 24216, the holotype by original designation, consists of the skin, skull, and fluid-preserved carcass of an adult female collected at Abra Esperanza (11.93° S, 71.28° W; 2784 m), Pasco department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis gardneri* is currently known from several localities between 2000 and 3000 m in the eastern Andes of central Peru (Huánuco, Pasco, Junín, and Cusco departments; Solari et al., 2012: fig. 1).

REMARKS: This is the only member of the subgenus *Microdelphys* that does not occur in the Atlantic Forest of southeastern Brazil; for a discussion of its biogeographic significance, see Pavan et al. (2016). *Monodelphis gardneri* is the taxon that Pine and Handley (2008: 107) called "*Monodelphis* [species C]."



*Monodelphis (Microdelphys) iheringi*  
(Thomas, 1888)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 82.9.30.43, the lectotype (designated by Thomas, 1888a; see Remarks), consists of the fluid-preserved carcass and extracted skull of an adult male collected at Taquara (29.65° S, 50.78° W; 29 m), Rio Grande do Sul state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis iheringi* occurs in the Atlantic Forest of southeastern Brazil, from Espírito Santo to Rio Grande do Sul (Pine and Handley, 2008: map 40).

REMARKS: The original description of this species (Thomas, 1888b) was evidently based on several specimens, none of which was designated as the unique name-bearer, but the fluid-preserved male from Taquara was subsequently designated as such by Thomas (1888a). For descriptions, measurements, and morphological comparisons with sympatric congeners, see Duda and Costa (2015) and Abreu and Percequillo (2019). Pavan et al. (2014) reported that a specimen of *Monodelphis iheringi* from Rio de Janeiro differed from material collected in Espírito Santo and São Paulo by an average uncorrected sequence distance of 8.2% at the cytochrome *b* locus, a sufficiently large value to justify closer study of the corresponding voucher material.

*Monodelphis (Microdelphys) scalops*  
(Thomas, 1888)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 51.7.21.23, the lectotype (designated by Thomas, 1888a; see Remarks), consists of the skin and skull of an adult male from an unknown locality in Brazil. Vieira's (1950) "restriction" of the type locality to Teresópolis (in Rio de Janeiro) was not based on any information about where the lectotype was actually collected and, therefore, is irrelevant. Pavan and Voss (2016) incorrectly listed the type as having been collected at Teresópolis.

SYNONYMS: *theresa* Thomas, 1921.

DISTRIBUTION: *Monodelphis scalops* occurs in the Atlantic Forest of Brazil from Espírito Santo southward and from the contiguous subtropical forests of northeastern Argentina (Misiones). Pine and Handley's (2008) map approximated the distribution of this species in Brazil but omitted the unique Argentinian locality mentioned in their text; additional collection localities for *M. scalops* in Argentina were reported by Cirignoli et al. (2011) and Pavan and Voss (2016).

REMARKS: The original description of this species (Thomas, 1888b) was presumably based on the two specimens subsequently listed by Thomas (1888a), who designated the Brazilian male as type. *Monodelphis thesa* (recognized as a distinct species by Pine and Handley, 2008) was synonymized with *M. scalops* by Pavan et al. (2014), whose sequencing results confirmed Gomes' (1991) hypothesis that these taxa are conspecific (see also Vilela et al., 2015). Abreu and Percequillo (2019) provided a morphological description based on freshly collected material of this ontogenetically variable and sexually dimorphic species.

Subgenus *Monodelphiops* Matschie, 1916

TYPE SPECIES: *Microdelphys sorex* Hensel, 1872 (= *Monodelphis dimidiata*; see below), by original designation.

SYNONYMS: *Minuania* Cabrera, 1919.

REMARKS: See Pavan and Voss (2016) for a morphological diagnosis of this taxon. Subgeneric monophyly remains to be effectively tested due to the absence of molecular sequence data from *Monodelphis unistriata*, the taxonomic status of which also remains unclear (see below). Two species are currently recognized.

*Monodelphis (Monodelphiops) dimidiata*  
(Wagner, 1847)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 55.12.24.72, the holotype by monotypy, consists of the skin and skull of a very old adult male col-

lected at Maldonado (34.90° S, 54.95° W; at sea level), Maldonado department, Uruguay.

SYNONYMS: *brevicaudis* Olfers, 1818 (see Remarks, below); *fosteri* Thomas, 1924; *henseli* Thomas, 1888; *itaiyayae* Miranda-Ribeiro, 1936; *lundi* Matschie, 1916; *paulensis* Vieira, 1950; *sorex* Hensel, 1872.

DISTRIBUTION: *Monodelphis dimidiata* occurs in a variety of forested and open habitats in southeastern Brazil, eastern Paraguay, northeastern Argentina, and Uruguay (Vilela et al., 2010: fig. 2).

REMARKS: *Monodelphis dimidiata* and *M. sorex* were considered distinct species by Pine and Handley (2008), but Vilela et al. (2010) summarized molecular and morphometric evidence that they are conspecific. As discussed elsewhere (Voss et al., 2009a; Vilela et al., 2010), *brevicaudis* is probably a senior synonym, but it should not be used to replace either of these long-established names.

*Monodelphis (Monodelphiops) unistriata*  
(Wagner, 1842)

TYPE MATERIAL AND TYPE LOCALITY: NMW B-1063, the holotype by monotypy, consists only of the skin of a male specimen collected at “Ytararé” (= Itararé, at 24.12° S, 49.33° W; ca. 740 m), São Paulo state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis unistriata* is known from just two localities, one in southeastern Brazil (the type locality; see above) and another in northeastern Argentina (possibly Misiones province; Pine et al., 2013).

REMARKS: Alternative interpretations of the phylogenetic relationships of *Monodelphis unistriata* were discussed by Pine et al. (2013) and Pavan and Voss (2016). A third interpretation of the scant data at hand is that the two specimens currently identified as *M. unistriata* are nothing more than rare coat-color variants of *M. dimidiata*. Molecular sequence data, if any can be obtained from these specimens, could help resolve the status of this problematic taxon.

Subgenus *Monodelphis* Burnett, 1830

TYPE SPECIES: As for the genus.

SYNONYMS: As for the genus.

REMARKS: See Pavan and Voss (2016) for a morphological diagnosis of this taxon. Subgeneric monophyly is strongly supported by phylogenetic analyses of the multilocus sequence datasets reported by Pavan et al. (2014, 2016) and Vilela et al. (2015). Eight species are currently recognized.

*Monodelphis (Monodelphis) arlindoi*  
Pavan et al., 2012

TYPE MATERIAL AND TYPE LOCALITY: MPEG 38052, the holotype by original designation, consists of the skin, skull, and preserved tissues of an adult male collected at Platô Grieg (1.83° S, 56.42° W; 160 m), 43 km SW Porto Trombetas, Pará state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis arlindoi* occurs in lowland rainforest in central and southern Guyana and Brazil; in Brazil, it occurs north of the Amazon in southeastern Roraima, eastern Amazonas, and northern Pará (Pavan et al., 2012: fig. 6)

REMARKS: *Monodelphis arlindoi* is one of three species currently recognized within what was once considered to be *M. brevicaudata* (e.g., by Voss et al., 2001; Pine and Handley, 2008).

*Monodelphis (Monodelphis) brevicaudata*  
(Erxleben, 1777)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 67.4.12.540, the holotype by monotypy, consists of the fluid-preserved body and extracted skull of an adult female that was probably collected near Kartabo in northwestern Guyana (Voss et al., 2001: 57).

SYNONYMS: *brachyuros* Schreber, 1777; *dorsalis* Allen, 1904; *hunteri* Waterhouse, 1841; *orinoci* Thomas, 1899; *sebae* Gray, 1827.

**DISTRIBUTION:** *Monodelphis brevicaudata*, in the strict sense that this species is now understood, occurs in Venezuela (south and east of the Orinoco), northwestern Guyana, and northern Brazil (north of the Rio Negro and west of the Rio Branco; Pavan et al., 2012: fig 6).

**REMARKS:** Abreu et al. (2017) commented on the difficulty of phenotypically distinguishing *Monodelphis brevicaudata* from *M. arlindoi* along the lower Rio Jufari in Roraima, Brazil. Because the distinction between these species was largely based on mtDNA sequencing (Pavan et al., 2012), genetic evidence from nuclear markers would be welcome to test the hypothesis that these are distinct species.

*Monodelphis (Monodelphis) domestica*  
(Wagner, 1842)

**TYPE MATERIAL AND TYPE LOCALITY:** This species was based on an unknown number of specimens collected by Johann Natterer at “Cuyaba” (= Cuiabá: 15.58° S, 56.08° W; ca. 200 m), Mato Grosso state, Brazil. No type was designated in the original description, and none to my knowledge has been designated subsequently, so Natterer’s entire series must be considered syntypes. I have seen nine such specimens in Vienna (NMW B-2604–2608, -2611, -2612, -2617, -2625) plus two that were exchanged: one to London (BMNH 87.10.25.1) and another to Berlin (ZMB 3195). Additionally, Thomas (1888a: 359) mentioned “co-types” in Munich, so Wagner’s original material has been widely dispersed. Of the specimens I have personally examined, BMNH 87.10.25.1, an adult female, is the best preserved and retains Natterer’s original label with the notation “Cuyaba, Mto. Grosso.” However, no purpose is served by designating a lectotype at this time.

**SYNONYMS:** *concolor* Gervais, 1856.

**DISTRIBUTION:** *Monodelphis domestica* occurs throughout the Arid Diagonal of open vegetation (Chaco, Cerrado, and Caatinga) that extends from eastern Bolivia, northwestern Argentina, and western Paraguay across central Brazil to Ceará and Pernambuco (Pine and Handley, 2008:

map 40), and it is also known from the Pantanal (Antunes et al., 2021).

**REMARKS:** Phylogenetic analyses of mtDNA sequence data have shown that *Monodelphis domestica* consists of two robustly supported haplogroups, one in the Chaco, Cerrado, and Pantanal and another in the Caatinga (Caramaschi et al., 2011); according to Pavan et al. (2014), these haplogroups differ, on average, by about 5% (uncorrected) at the cytochrome *b* locus.

*Monodelphis (Monodelphis) glirina*  
(Wagner, 1842)

**TYPE MATERIAL AND TYPE LOCALITY:** NMW B-2626, the holotype by monotypy (Bezerra et al., 2018), consists of the skin and skull of a young adult male collected at “Mamore” (= Cachoeira do Pau Grande on the Rio Mamoré: 10.47° S, 65.40° W), Rondônia state, Brazil.

**SYNONYMS:** *maraxina* Thomas, 1923.

**DISTRIBUTION:** As currently recognized, *Monodelphis glirina* occurs from northeastern Bolivia (La Paz, Pando) and eastern Peru (Ucayali, Madre de Dios, Cusco) across southern Amazonian Brazil to eastern Pará (including Marajó Island) (Pavan, 2019: fig. 1).

**REMARKS:** For an emended description, illustrations, and tabulated measurement data, see Pavan, (2019). Although *Monodelphis glirina* and *M. maraxina* (with type locality on Marajó Island) were recognized as distinct species by Pine and Handley (2008), phylogenetic analyses of mtDNA sequence data reported by Pavan et al. (2014) recovered a topotype of *maraxina* nested within a clade comprised of mainland specimens with the phenotypic traits of *glirina*, so these taxa are currently regarded as conspecific. Nevertheless, *M. glirina* is known to include two highly divergent mtDNA haplogroups, one of which is in Bolivia and western Brazil, whereas the other is in central and eastern Brazil. As noted by Bezerra et al. (2018), the name *maraxina* is available for the latter haplogroup if these mtDNA clades were eventually shown to be taxonomically distinct, but neither coat-color nor

morphometric variation seems to correlate with haplogroup membership (Pavan, 2019).

*Monodelphis (Monodelphis) palliolata*  
(Osgood, 1914)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 20524, the holotype by original designation, consists of the skin and skull of an adult male collected at San Juan de Colón (8.03° N, 72.27° W; ca. 760 m), Táchira state, Venezuela.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis palliolata* occurs north and west of the Orinoco River in Venezuela, and it probably also occurs in eastern Colombia. Collection localities for this species include those recognized as such by Pine and Handley (2008: map 44) as well as those they attributed to “species A” (Pine and Handley, 2008: map 38). This species occurs in both rain-forest and savannas.

REMARKS: For an emended description of *Monodelphis palliolata* and morphological comparisons with closely related congeners, see Pavan et al. (2012). Specimens collected in the Llanos are paler than otherwise similar specimens collected in adjacent forested regions, and this pale savanna phenotype was formerly identified as *M. orinoci* by Venezuelan authors. However, *orinoci* is a synonym of *M. breviceaudata* sensu stricto (Voss et al., 2001; Pavan et al., 2012), so the savanna phenotype lacks a name. Pine and Handley (2008: 106) referred to this form as “*Monodelphis* [species A],” but examined specimens exhibit the distinctive caudal pelage traits and color pattern of *M. palliolata*, and phylogenetic analyses of cytochrome *b* sequence data suggest that “species A” is nothing more than an ecotype of the present species (Pavan et al., 2014).

*Monodelphis (Monodelphis) sanctaerosae*  
Voss et al., 2012

TYPE MATERIAL AND TYPE LOCALITY: AMNH 263548, the holotype by original designation, consists of the skin, skull, postcranial skeleton,

and frozen tissues of a young adult female collected at Santa Rosa de la Roca (15.83° S, 61.45° W; 250 m), Santa Cruz department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis sanctaerosae* is only known from the type locality (but see Remarks).

REMARKS: See Voss et al. (2012) and Pavan (2019) for morphological descriptions, illustrations, measurements, and comparisons with closely related congeners. Phylogenetic analyses of multilocus sequence data suggest that *Monodelphis sanctaerosae* is the sister species of *M. glirina*. This is the taxon that Pine and Handley (2008: 106) called “*Monodelphis* [species B].” A specimen identified as “*Monodelphis* cf. *sanctaerosae*” was recently reported from the Brazilian state of Mato Grosso by Brandão et al. (2019), but neither phenotypic nor genetic evidence for this tentative identification has yet been published.

*Monodelphis (Monodelphis) touan* (Shaw, 1800)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 21720, the neotype (designated by Voss et al., 2001), consists of the skin and skull of an adult male collected at Cayenne (4.93° N, 52.33° W; near sea level), French Guiana.

SYNONYMS: *touan* Bechstein, 1800; *touan* Daudin (in Lacépède, 1802); *tricolor* Geoffroy St.-Hilaire, 1803.

DISTRIBUTION: As currently recognized, *Monodelphis touan* is known from French Guiana, Amapá, and eastern Pará (south of the Amazon and east of the Xingu, including Marajó Island) (Pavan et al., 2012: fig. 6).

REMARKS: Although *Monodelphis touan* was treated as a subjective junior synonym of *M. breviceaudata* by Voss et al. (2001) and Pine and Handley (2008), these taxa were judged to be valid species by Pavan et al. (2012) based on coat-color differences and phylogenetic analyses of mtDNA sequence data. However, Husson (1978: 14) remarked on the difficulty of distinguishing *M. touan* from *M. breviceaudata*.

due to the phenotypic intermediacy of Surinamese specimens, which were not included in Pavan et al.'s (2012) study. The population of *M. touan* that is south of the Amazon differs in pelage traits from the population on the north bank and was called "*Monodelphis* [species D]" by Pine and Handley (2008), but representative sequences from these populations were not recovered as reciprocally monophyletic haplogroups by Pavan et al. (2012).

*Monodelphis (Monodelphis) vossi* Pavan, 2019

TYPE MATERIAL AND TYPE LOCALITY: MPEG 34837, the holotype by original designation, consists of the skin and skull of a young adult male collected at Surumu (4.18° N, 60.78° W) in the Serra do Mel, Roraima state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis vossi* is known from only two localities, both of which are in the savannas of the upper Rio Branco in the Brazilian state of Roraima (Pavan, 2019: fig. 1).

REMARKS: Phylogenetic analyses of multilocus sequence datasets reported by Pavan et al. (2014) recovered *Monodelphis vossi* ("species 3") as the sister lineage of a clade that includes *M. sanctaerosae* and *M. glirina*.

Subgenus *Mygalodelphys* Pavan and Voss, 2016

TYPE SPECIES: *Peramys adustus* Thomas, 1897, by original designation.

SYNONYMS: None.

REMARKS: See Pavan and Voss (2016) for a diagnosis of this morphologically distinctive taxon. Subgeneric monophyly is strongly supported by phylogenetic analyses of the multilocus sequence datasets reported by Pavan et al. (2014, 2016) and by Bayesian analysis of the dataset reported by Vilela et al. (2015). Nine species are currently recognized, but several of these are difficult to distinguish morphologically, and identifications of unsequenced specimens are correspondingly problematic.

*Monodelphis (Mygalodelphys) adusta*  
(Thomas, 1897)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 77.7.2.1, the holotype by original designation, consists of the skin and skull of an individual of unknown sex collected in "w.[est] Cundinamarca, in the low-lying hot regions" (Thomas, 1897: 220), presumably in the valley of the Río Magdalena west of Bogotá, Cundinamarca department, Colombia.

SYNONYMS: *melanops* Goldman, 1912.

DISTRIBUTION: As currently understood (see Remarks), *Monodelphis adusta* occurs in eastern Panama, in the humid transAndean lowlands of northwestern South America, in the eastern Andean foothills (below about 1000 m) of Colombia and Ecuador, and in northwestern Amazonia (north of the Amazon and west of the Rio Negro). No published map illustrates the geographic range of this species as currently restricted by authors (see Remarks).

REMARKS: There is no adequate morphological description of *Monodelphis adusta* in the literature, although measurements of specimens from the cis-Andean lowlands of Ecuador and Peru (north of the Amazon) were tabulated by Voss et al. (2019), and cranial photographs are in Pavan et al. (2017). This species has never received critical revisionary attention, and it seems unlikely that it will survive such scrutiny without a dramatic reduction in geographic range. The current concept of the species is largely based on mtDNA sequence analyses (e.g., Solari, 2007; Pavan et al., 2014), but no sequence data are available from the trans-Andean lowlands, which is where the type was collected. Therefore, it is quite possible that the cis-Andean sequences hitherto thought to represent *Monodelphis adusta* might eventually be shown to belong to a different taxon.

*Monodelphis peruviana* was formerly treated (e.g., by Pine and Handley, 2008) as a subspecies of *M. adusta*, but phylogenetic analyses of sequence datasets have conclusively shown that these are not sister taxa. Instead, *M. adusta* (as



represented by cis-Andean sequence data; see above) appears to be the sister species of *M. reigi*, whereas *M. peruviana* belongs to a clade that includes *M. handleyi*, *M. osgoodi*, *M. ronaldi*, and *M. saci* (see Pavan et al., 2014, 2016, 2017; Ruelas and Pacheco, 2022). Unfortunately, *M. adusta* and *M. peruviana* are not known to differ morphologically, so these names currently serve only as labels for genetically divergent but phenotypically similar specimens collected on opposite banks of the upper Amazon (Voss et al., 2019).

*Monodelphis (Mygalodelphys) handleyi*  
Solari, 2007

TYPE MATERIAL AND TYPE LOCALITY: MUSM 15991, the holotype by original designation, consists of the skin, skull, and preserved tissues of an adult male collected at the Centro de Investigaciones Jenaro Herrera (4.87° S, 73.65° W; 135 m) on the right bank of the lower Río Ucayali, Loreto department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Monodelphis handleyi* is currently known from two Peruvian localities—the type locality in Loreto and another in Pasco department.<sup>7</sup> A recent report of *M. handleyi* from western Brazil (Bezerra et al., 2019) appears to have been based on a subadult specimen of *M. ronaldi* (see Ruelas and Pacheco, 2022).

REMARKS: For descriptions, illustrations, measurements, and morphological comparisons with other congeners, see Solari (2007), Voss et al. (2019), and Ruelas and Pacheco (2022). Phylogenetic analyses of DNA sequence data indicate that *Monodelphis handleyi* belongs to a clade that includes *M. osgoodi*, *M. peruviana*, *M. ronaldi*, and *M. saci* (see Solari, 2007; Pavan et al., 2014, 2016, 2017; Ruelas and Pacheco, 2022).

<sup>7</sup> The Pasco locality, previously unreported in the literature, is vouchered by a single specimen (MUSM 24217) collected by Elena Vivar on the Río Pescado (10.38° S, 75.25° W; 500 m).

*Monodelphis (Mygalodelphys) kungsi* Pine, 1975

TYPE MATERIAL AND TYPE LOCALITY: USNM 461348, the holotype by original designation, consists of the skin and skull of an adult male collected at La Granja (13.30° S, 64.15° W; 200 m), on the west bank of the Río Itonamas, Beni department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: As currently recognized (see Remarks), *Monodelphis kungsi* is known from the Chaco, Cerrado, and Pantanal, including localities in eastern Bolivia (Beni, Santa Cruz, Tarija), northern Argentina (Salta), Paraguay (Canendeyú, Presidente Hayes), and Brazil (Distrito Federal, Goiás, Mato Grosso, Mato Grosso del Sur, Minas Gerais, São Paulo, Tocantins) (de la Sancha et al., 2007; Pavan et al., 2017; Antunes et al., 2021). The eastern Amazonian specimens (from Pará) reported by Gettinger et al. (2011) were reidentified by Pavan et al. (2017) as *M. saci*, and the western Amazonian locality (in Acre) mapped by Pine and Handley (2008) is almost certainly also based on a specimen of the latter species.

REMARKS: No emended description of *Monodelphis kungsi* that includes all the characters now known to be important for distinguishing species of the subgenus *Mygalodelphys* has yet been published. Compilations of measurement data are in de la Sancha et al. (2007) and Pavan (2015). Phylogenetic analyses of DNA sequence data (e.g., by Pavan et al., 2014, 2016) have consistently recovered *M. kungsi* as the sister taxon of *M. pinocchio*.

*Monodelphis (Mygalodelphys) osgoodi*  
Doutt, 1938

TYPE MATERIAL AND TYPE LOCALITY: CM 5242, the holotype by original designation, consists of the skin and skull of an adult male collected at Incachaca (17.23° S, 65.68° W; 2600 m), Cochabamba department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: Although specimens alleged to be *Monodelphis osgoodi* are known from cen-

tral Peru to central Bolivia (Pine and Handley, 2008: map 43), it is not clear that any, except Bolivian material from Cochabamba department and two specimens from La Paz (all sequenced by Pavan et al., 2014: SI, table 1) are correctly identified (see Remarks).

REMARKS: No emended description of *Monodelphis osgoodi* that mentions all the characters now known to distinguish species in the subgenus *Mygalodelphys* has been published. As a result, the morphological traits that diagnose this species from its sister taxon, *M. peruviana*, are poorly documented. The current recognition of *M. osgoodi* as a valid species is largely based on DNA sequence data (Solari, 2007, 2010; Pavan et al., 2014), an obviously unsatisfactory situation.

*Monodelphis (Mygalodelphys) peruviana*  
(Osgood, 1913)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 19362, the holotype by original designation, consists of the skin and skull of an adult male collected at Moyobamba (6.05° S, 76.97° W; 860 m), San Martín department, Peru.

SYNONYMS: None.

DISTRIBUTION: Specimens currently referred to *Monodelphis peruviana* (e.g., those examined by Pavan et al., 2016) are from northern Bolivia (La Paz) and eastern Peru (south of the Amazon) with recorded elevations from a few hundred meters in the Amazonian lowlands to 2600 m in the Andes. Pacheco et al. (2020) discussed the Peruvian distribution of this species.

REMARKS: No emended description of this species has been published; however, measurement data were tabulated by Voss et al. (2019), and cranial illustrations are in Pavan et al. (2017). As explained by Voss et al. (2019), *Monodelphis peruviana* does not appear to be morphologically distinguishable from the species on the north bank of the Amazon that is currently called *M. adusta*, even though these are not sister taxa (Pavan et al., 2014). Although *M. peruviana* has consistently been recovered as a strongly supported clade by phylogenetic

analyses of mtDNA sequence data, the same analyses have shown that this species includes three highly divergent and geographically disjunct haplogroups that merit closer study (Solari, 2007; Pavan et al., 2014; Ruelas and Pacheco, 2022).

*Monodelphis (Mygalodelphys) pinocchio*  
Pavan, 2015

TYPE MATERIAL AND TYPE LOCALITY: MN 78680, the holotype by original designation, consists of the skin, skull, and postcranial skeleton of an adult male collected at the Reserva Forestal do Morro Grande (23.06° S, 46.92° W), São Paulo state, Brazil.

SYNONYMS: None (but see Remarks for unavailable or informal names by which this species was previously known).

DISTRIBUTION: *Monodelphis pinocchio* occurs in montane forests from about 790 to 2400 m in southeastern Brazil, where it has been collected in the states of Espírito Santo, Rio de Janeiro, Minas Gerais, and São Paulo (Pavan, 2015: fig. 2).

REMARKS: See Pavan (2015) for illustrations, measurements, and morphological comparisons with other species in the subgenus *Mygalodelphys*. This is a morphologically distinctive species that was recognized as such long before it was formally described. It was previously called “*Monodelphis macae*” (an unavailable manuscript name) by Gomes (1991), “*Monodelphis* [species E]” by Pine and Handley (2008), and “*Monodelphis* species 1” by Pavan et al. (2014).

*Monodelphis (Mygalodelphys) reigi*  
Lew and Pérez-Hernández, 2004

TYPE MATERIAL AND TYPE LOCALITY: MBUCV I-2358, the holotype by original designation, consists of the skin and skull of an adult male collected at Kilometer 134 (5.90° N, 61.43° W; 1300 m) on the road from El Dorado to Santa Elena de Uairén, Bolívar state, Venezuela.

SYNONYMS: None.



**DISTRIBUTION:** *Monodelphis reigi* is known only from the type locality in eastern Venezuela and from nearby Mount Ayangana (5.33° N, 59.98° W; 1100 m), Potaro-Siparuni Region, Guyana (Lim et al., 2010).

**REMARKS:** See Lew and Pérez-Hernández (2004) for a description, illustrations, measurements of the holotype, and comparisons with other congeners. The two Guyanese specimens reported by Lim et al. (2010) are both juveniles, so the holotype is still the only known adult specimen. Phylogenetic analyses of multilocus sequence data (Pavan et al., 2014, 2016) have consistently recovered *Monodelphis reigi* as the sister taxon of *M. adusta*.

*Monodelphis (Mygalodelphys) ronaldi*  
Solari, 2004

**TYPE MATERIAL AND TYPE LOCALITY:** MUSM 17027, the holotype by original designation, consists of the skin and skull of an old adult male collected at Pakitza (11.93° S, 71.28° W; 356 m) on the left bank of the Río Manu, Madre de Dios department, Peru.

**SYNONYMS:** None.

**DISTRIBUTION:** *Monodelphis ronaldi* is currently known from only two localities in the Amazonian lowlands of eastern Peru (Madre de Dios, Ucayali) and one locality in western Brazil (Amazonas) (Ruelas and Pacheco, 2022).

**REMARKS:** For an emended description, illustrations, tabulated measurement data, and comparisons with closely related congeners see Ruelas and Pacheco (2022). The same authors reported phylogenetic analyses of mtDNA sequence data that convincingly resolved *Monodelphis ronaldi* as the sister taxon of *M. handleyi*, and they reidentified as *M. ronaldi* the western Brazilian specimen that Bezerra et al. (2019) had previously reported as *M. handleyi*.

*Monodelphis (Mygalodelphys) saci*  
Pavan et al., 2017

**TYPE MATERIAL AND TYPE LOCALITY:** UFPA 1422, the holotype by original designation, con-

sists of the skin, skull, postcranial skeleton, and preserved tissues of an adult male collected at Bom Jardim (5.61° S, 57.12° W) on the left bank of the Rio Tapajós, Pará state, Brazil.

**SYNONYMS:** None.

**DISTRIBUTION:** *Monodelphis saci* is known from scattered rainforest localities south of the Amazon in the Brazilian states of Acre, Rondônia, Mato Grosso, and Pará (Pavan et al., 2017: fig. 2).

**REMARKS:** For illustrations, description, measurement data, and morphological comparisons with closely related congeners, see Pavan et al. (2017). This is the taxon that Pavan et al. (2014, 2016) called “*Monodelphis* species 2,” and which they recovered in a clade with *M. handleyi*, *M. osgoodi*, and *M. peruviana*.

Subgenus *Pyrodelphys* Pavan and Voss, 2016

**TYPE SPECIES:** *Peramys emiliae* Thomas, 1912, by original designation.

**SYNONYMS:** None.

**REMARKS:** See Pavan and Voss (2016) for a morphological diagnosis of this distinctive taxon, which includes only a single currently recognized species.

*Monodelphis (Pyrodelphys) emiliae*  
(Thomas, 1912)

**TYPE MATERIAL AND TYPE LOCALITY:** BMNH 11.12.22.16, the holotype by original designation, consists of the skin and skull of an adult male collected at Boim (2.82° S, 55.17° W), on the left bank of the Rio Tapajós, Pará, Brazil.<sup>8</sup>

**SYNONYMS:** None.

**DISTRIBUTION:** *Monodelphis emiliae* occurs in lowland rainforest from eastern Peru (Loreto, Ucayali, Cusco, and Madre de Dios departments; Pacheco et al., 2020) and northern Bolivia (Pando department) eastward along the south

<sup>8</sup> Pine and Handley (1984) referred to this specimen as a subadult, but P3 is fully erupted.

bank of the Amazon to the left bank of the Tocantins in Pará state, Brazil (Pine and Handley, 2008: map 41).

REMARKS: See Pavan et al (2016) for an emended description and morphological comparisons with members of other subgenera. Measurement data from Peruvian specimens of *Monodelphis emiliae* were tabulated by Voss et al. (2019), who also remarked on postmortem pelage-color changes and unusual examples of cranial-character polymorphisms. As currently recognized, this species includes two cytochrome *b* haplogroups—one from eastern Amazonia and the other from western Amazonia—with a mean uncorrected sequence difference of 11.4% (Pavan et al., 2014), but comparisons of eastern and western Amazonian specimens have yet to reveal any consistent morphological differences (Voss et al., 2019).

#### Genus *Tlacuatzin* Voss and Jansa, 2003

TYPE SPECIES: *Didelphis (Micoureus) canescens* J.A. Allen, 1893, by original designation.

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for an emended generic description. The relationships of *Tlacuatzin* within the tribe Marmosini have yet to be satisfactorily resolved, although the largest concatenated-gene dataset yet analyzed (Amador and Giannini, 2016) suggests that it is the sister group to *Marmosa*.

Arcangeli et al. (2018) recognized five species of this Mexican endemic genus based on phylogenetic analyses of sequence data from one mitochondrial gene (cytochrome *b*) and one nuclear gene (IRBP). Unfortunately, only cytochrome *b* was taxonomically informative, and taxonomic differences in morphological traits were not convincingly documented. In the absence of compelling evidence for nuclear-gene divergence, the following taxa are perhaps nothing more than mtDNA haplogroups; alternatively, they might be treated as subspecies. However, until relevant phenotypic analyses or

additional genetic analyses are carried out, I list them here as valid species.

#### *Tlacuatzin balsasensis* Arcangeli et al., 2018

TYPE MATERIAL AND TYPE LOCALITY: ENCB 26195, the holotype by original designation, consists of the skin and skull of an adult male collected 14 km N and 11 km E Panindícuaro (20.12° N, 101.65° W), Michoacán state, Mexico.

SYNONYMS: None.

DISTRIBUTION: *Tlacuatzin balsasensis* occurs in the valley of the Río Balsas in south-central Mexico; Arcangeli et al. (2018) listed examined specimens from the states of Guerrero, México, Michoacán, Morelos, and Puebla, but the species is also said to occur in Jalisco and Oaxaca.

REMARKS: A very brief morphological diagnosis and tabulated measurement data were provided by Arcangeli et al. (2018). Their phylogenetic analyses of DNA sequence data suggest that *Tlacuatzin balsasensis* is the sister taxon of a clade that includes *T. canescens* and *T. gaumeri*.

#### *Tlacuatzin canescens* (J.A. Allen, 1893)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 3111/2433, the holotype by original designation, consists of the skin and skull of an adult male collected at Santo Domingo de Guzmán (16.82° N, 95.15° W; ca. 275 m)<sup>9</sup> on the Isthmus of Tehuantepec, Oaxaca state, Mexico.

SYNONYMS: *oaxacae* Merriam, 1897.

DISTRIBUTION: *Tlacuatzin canescens* occurs on the Isthmus of Tehuantepec and in the Valley of Oaxaca; Arcangeli et al. (2018) listed examined specimens from the states of Chiapas and Oaxaca.

REMARKS: A very brief morphological diagnosis and tabulated measurement data were provided by Arcangeli et al. (2018), whose phylogenetic analyses of DNA sequence data suggested that *Tlacuatzin canescens* is the sister taxon of *T. gaumeri*.

<sup>9</sup> Coordinates and elevation are for Santo Domingo Petapa, a synonym according to Goodwin (1969).

*Tlacuatzin gaumeri* (Osgood, 1913)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 19995, the holotype by original designation, consists of the skin and skull of a subadult (or very young adult) of unknown sex collected at Yaxcabá (20.53° N, 88.83° W), Yucatán state, Mexico.

SYNONYMS: None.

DISTRIBUTION: *Tlacuatzin gaumeri* is known from the Mexican states of Campeche and Yucatán, where its range seems to be disjunct from those of other congeners (Arcangeli et al., 2018: fig. 1).

REMARKS: A very brief morphological diagnosis and tabulated measurement data were provided by Arcangeli et al. (2018) whose phylogenetic analyses of DNA sequence data suggested that *Tlacuatzin gaumeri* is the sister taxon of *T. canescens*. Only five specimens of this uncommon taxon are known to exist.

*Tlacuatzin insularis* (Merriam, 1898)

TYPE MATERIAL AND TYPE LOCALITY: USNM 89215, the holotype by original designation, consists of the skin and skull of an adult male from Isla María Madre (21.58° N, 106.55° W), Nayarit state, Mexico.

SYNONYMS: None.

DISTRIBUTION: *Tlacuatzin insularis* occurs in the Islas Marias (also known as the Tres Marias Islands) off the Pacific coast of Mexico (Arcangeli et al., 2018: fig. 3).

REMARKS: A very brief morphological diagnosis and tabulated measurement data were provided by Arcangeli et al. (2018), whose phylogenetic analyses of DNA sequence data suggest that *Tlacuatzin insularis* is the sister taxon of *T. sinaloae*.

*Tlacuatzin sinaloae* (J.A. Allen, 1898)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 98.3.2.161, the holotype by original designation, consists of the skin and skull of an adult male

collected at Tatemaes (ca. 23.00° N, 105.52° W),<sup>10</sup> Sinaloa state, Mexico.

SYNONYMS: None.

DISTRIBUTION: *Tlacuatzin sinaloae* occurs along the Pacific coast of northern Mexico and in adjacent inland valleys. Arcangeli et al. (2018) examined specimens from the Mexican states of Colima, Jalisco, Nayarit, and Sinaloa, but they said the species also occurs in Durango and Zacatecas.

REMARKS: A very brief morphological diagnosis and tabulated measurement data were provided by Arcangeli et al. (2018).

## Tribe Metachirini Hershkovitz, 1992

TYPE GENUS: *Metachirus* Burmeister, 1854.

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009: 110) for the technical availability of this family-group name from Hershkovitz (1992). Only one genus is included.

Genus *Metachirus* Burmeister, 1854

TYPE SPECIES: *Didelphis nudicaudata* E. Geoffroy Saint-Hilaire, 1803, by subsequent designation (Thomas, 1888a).

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for an emended generic description. Gardner and Dagosto (2008) thought that the type species of *Metachirus* was *Didelphis myosuroides* Burmeister, 1854, but—as explained by Hershkovitz (1976)—the type species is unambiguously *D. nudicaudata* E. Geoffroy Saint-Hilaire, 1803. *Metachirus* was long thought to contain only a single species, but *M. myosuroides* was shown to be distinct from *M. nudicaudatus* by Voss et al. (2019), who also mentioned the possibility that specimens from the Tocantins-Xingu interfluvium might represent a third, undescribed species.

<sup>10</sup> Coordinates are for Rosario, which is near Tatemaes according to Birney and Jones (1971).

*Metachirus myosuros* (Temminck, 1824)

TYPE MATERIAL: NMW B-2589, the lectotype (designated by Pohle, 1927), consists of the skin and skull of a juvenile female collected at “Ypanema” (= Ipanema: 23.43° S, 47.60° W; 950 m), São Paulo state, Brazil.

SYNONYMS: *antioquiae* J.A. Allen, 1916; *bolivianus* J.A. Allen, 1901; *colombianus* J.A. Allen, 1900; *dentaneus* Goldman, 1912; *imbutus* Thomas, 1923; *infuscus* Thomas, 1923; *modestus* Thomas, 1923; *personatus* Miranda-Ribeiro, 1936; *phaeurus* Thomas, 1901; *tschudii* J.A. Allen, 1900.

DISTRIBUTION: As currently understood (Voss et al., 2019), *Metachirus myosuros* ranges from southern Mexico possibly throughout the humid lowlands of Central America to South America (Mérida and Cruz, 2015: fig. 2); however, there are curiously large gaps with no recorded specimens from some parts of Central America (e.g., the Atlantic lowlands of Costa Rica). In South America, specimens are known from the humid trans-Andean lowlands of western Colombia and western Ecuador and from most of the tropical and subtropical cis-Andean lowlands (except the northeastern quadrant of Amazonia and the Tocantins-Xingu interfluvium; see above and below) to Bolivia, eastern Paraguay, and northern Argentina. There are, unfortunately, no maps that adequately illustrate the South American distribution of this species: Gardner and Dagosto’s (2008) map does not distinguish records of *M. myosuros* from those of *M. nudicaudatus*, and Voss et al.’s (2019) map only shows collection localities for sequenced specimens.

REMARKS: See Voss et al. (2019) for illustrations, measurements, and morphological comparisons with *Metachirus nudicaudatus*. Phylogenetic analyses of cytochrome *b* sequence data suggest the existence of distinct haplogroups of *M. myosuros* in (1) Central America, (2) northwestern Amazonia, (3) southwestern Amazonia, and (4) the Atlantic Forest of southeastern Brazil (Voss et al., 2019). However, despite modestly

large sequence divergence among these populations (5.3%–7.6%, uncorrected), there appear to be no consistent phenotypic differences among representative specimens. Therefore, whether these haplogroups represent cryptic taxa or merely geographic variation in mtDNA among populations of a single widespread species remains to be determined.

*Metachirus nudicaudatus*  
(E. Geoffroy Saint-Hilaire, 1803)

TYPE MATERIAL AND TYPE LOCALITY: MNHN 1990-420, the holotype by monotypy, consists of the mounted skin and extracted skull of an adult female collected at Cayenne (4.75° N, 52.25° W; near sea level), French Guiana.

SYNONYMS: None.

DISTRIBUTION: As diagnosed by Voss et al. (2019), this species is only known from northeastern Amazonia (north of the lower Amazon and east of the Rio Negro), but whether *Metachirus nudicaudatus* occupies the whole of this region or just the part of it circumscribed by the collection localities of specimens they examined (from Guyana, Surinam, French Guiana, and the Brazilian state of Amapá) is unknown.

REMARKS: Jansa and Voss’s (2009) generic description was based on topotypical (French Guianan) material of *Metachirus nudicaudatus*. Morphological comparisons of this species with *M. myosuros* were reported by Voss et al. (2019), who also illustrated craniodental features and summarized measurement data.

## Tribe Didelphini Gray, 1821

TYPE GENUS: As for the subfamily.

SYNONYMS: As for the subfamily.

REMARKS: See Voss and Jansa (2009) for a tribal diagnosis. The monophyly of Didelphini is consistently supported by phylogenetic analyses of multilocus sequence datasets (e.g., Voss and Jansa, 2009; Amador and Giannini, 2016). Four Recent genera are currently recognized.

Genus *Chironectes* Illiger, 1811

TYPE SPECIES: *Lutra minima* Zimmermann, 1780, by monotypy.

SYNONYMS: *Gamba* Liais, 1872; *Memina* G. Fischer, 1814.

REMARKS: See Voss and Jansa (2009) for an emended generic description. This genus contains only a single species, the water opossum, *Chironectes minimus*. Although the results of morphometric analyses have sometimes been interpreted as evidence for multiple species of water opossums (Damasceno and Astúa, 2016; Cerqueira and Weber, 2017), the remarkable genetic similarity among specimens collected at widely scattered localities from Central America to southeastern Brazil suggests recent range expansion or widespread gene flow (Voss and Jansa, 2018).

*Chironectes minimus* (Zimmermann, 1780)

TYPE MATERIAL AND TYPE LOCALITY: No type material is known to exist. This species is based on Buffon's description of an animal from Cayenne (4.93° N, 52.33° W), French Guiana.

SYNONYMS: *argyrodites* Dickey, 1928; *bresslaui* Pohle, 1927; *cayennensis* Turton, 1800; *guianensis* Kerr, 1792; *gujanensis* Link, 1795; *langsдорffi* Boitard, 1842; *palmata* Daudin, 1802; *panamensis* Goldman, 1914; *paraguensis* Kerr, 1792; *sari-covienna* Shaw, 1800; *variegatus* Olfers, 1818; *yapock* Desmarest, 1820.

DISTRIBUTION: *Chironectes minimus* occurs from southern Mexico throughout most of the rainforested lowlands of Central America to South America; in South America it has been reported from most humid-tropical and -subtropical lowland biomes from Colombia southward to eastern Paraguay, northeastern Argentina (Misiones), and southern Brazil (Rio Grande do Sul). Recent collections from the Cerrado and the Pantanal were mapped by Brandão et al. (2015) and Antunes et al. (2021), respectively. Most range maps (e.g., Stein and Patton, 2008a: map 5) suggest that *C. minimus* does not occur

in central Amazonia, but several central Amazonian specimens and observations indicate that it probably occurs throughout the region (Voss et al., 2019).

REMARKS: The emended generic description provided by Voss and Jansa (2009) serves equally as a description of this species. Although several of the names listed above as synonyms have been recognized as valid subspecies by authors (e.g., Stein and Patton, 2008a), the absence of substantial genetic variation among geographic populations of water opossums (Voss and Jansa, 2018) suggests that a trinomial nomenclature is unnecessary.

Genus *Didelphis* Linnaeus, 1758

TYPE SPECIES: *Didelphis marsupialis* Linnaeus, 1758, by subsequent designation (Thomas, 1888a).

SYNONYMS: *Leucodidelphis* Ihering, 1914; *Opossum* Schmid, 1818; *Sarigua* Muirhead, 1819.

REMARKS: See Voss and Jansa (2009) for an emended generic description. Despite a voluminous literature, *Didelphis* has not been comprehensively revised since the early 20th century, and the species-level taxonomy is correspondingly problematic. Six species are currently recognized, of which the Virginia opossum (*D. virginiana*) is consistently recovered as the sister taxon to a Neotropical complex that includes three "white-eared" species (*D. albiventris*, *D. imperfecta*, *D. pernigra*) and two "black-eared" species (*D. aurita*, *D. marsupialis*) (Amador and Giannini, 2016; Dias and Perini, 2018; Dias et al., 2020). Whereas white-eared opossums are morphologically quite distinct from black-eared opossums and occur sympatrically with them in various combinations—for example, *D. marsupialis* with *D. imperfecta* in the Guianas, *D. aurita* with *D. albiventris* in southeastern Brazil—the nominal species within each of these groups are morphologically similar and, apparently, allopatric or parapatric. All six currently recognized species are listed as such below, but



there are good reasons to question the taxonomic status quo.

*Didelphis albiventris* Lund, 1840

TYPE MATERIAL AND TYPE LOCALITY: No specimens were mentioned in the original description, which was based on material obtained near Lagoa Santa (19.63° S, 43.82° W), Minas Gerais state, Brazil. However, a single specimen known to have been collected by Lund (ZMUC L4) can perhaps be considered the holotype by monotypy.

SYNONYMS: *bonariensis* Marelli, 1930; *dennleri* Marelli, 1930; *lechei* Ihering, 1892; *leucotis* Wagner, 1847; *paraguayensis* J.A. Allen, 1902; *poecilotis* Wagner, 1842; *poecilonota* Schinz, 1844.

DISTRIBUTION: As currently recognized (see Remarks), *Didelphis albiventris* occurs in more or less open habitats—savannas, dry forests, anthropogenic clearings, etc.—in Brazil (south of the Amazon), eastern Bolivia, Paraguay, Uruguay, and northern Argentina (Cerqueira and Tribe, 2008: map 6).

REMARKS: Species limits within the Neotropical white-eared opossum group (*Didelphis albiventris*, *D. imperfecta*, *D. pernigra*) remain to be convincingly documented. Among other uncertainties, there has been no geographically comprehensive survey of mtDNA variation in this complex, so it is not even known whether these taxa are convincingly resolvable as reciprocally monophyletic haplogroups.<sup>11</sup> Additionally, diagnostic morphological differences are elusive. *Didelphis imperfecta* and *D. albiventris*, in particular, have broadly overlapping measurements (Lemos and Cerqueira, 2002: appendix II) and are said to be phenotypically distin-

guishable only by the extent of white on the pinnae (Cerqueira and Tribe, 2008). Although white ear markings are potentially useful for identification, they are known to vary within other species (e.g., *D. virginiana*; Gardner, 1973), and the constancy of this difference between *D. imperfecta* and *D. albiventris* has never been quantified. The lack of unambiguously diagnostic morphological features in this complex and the consequent reliance on geographic criteria for species identification—as in Cerqueira and Tribe's (2008) key—makes it difficult to assign names to specimens that have been collected well outside the previously documented ranges of these taxa. The white-eared opossums that Díaz and Willig (2004) reported from the vicinity of Iquitos is a relevant example that was discussed inconclusively by Cerqueira and Tribe (2008: 22).

*Didelphis aurita* Wied-Neuwied, 1826

TYPE MATERIAL AND TYPE LOCALITY: AMNH 836, the lectotype (designated by Avila-Pires, 1965), consists of the skin and skull of an adult male collected at "Villa Viçosa" (= Nova Viçosa: 17.88° S, 39.37° W; near sea level) on the Rio Peruípe, Bahia state, Brazil.

SYNONYMS: *azarae* Temminck, 1824 (see Remarks); *koseritzi* Ihering, 1892; *longipilis* Miranda-Ribeiro, 1935; *melanoidis* Miranda-Ribeiro, 1935.

DISTRIBUTION: *Didelphis aurita* is said to occur in the Atlantic Forest of southeastern Brazil (from Paraíba to Rio Grande do Sul), and from contiguous humid-subtropical habitats in eastern Paraguay and northeastern Argentina (Misiones) (Cerqueira and Tribe, 2008: map 7).

REMARKS: The validity of *Didelphis aurita* as a species distinct from *D. marsupialis* is not well established. Although phylogenetic analyses have recovered mtDNA sequences from black-eared opossums collected in the Atlantic Forest on the one hand and Amazonia on the other as reciprocally monophyletic haplogroups, pairwise distances between Amazonian and Atlantic Forest

<sup>11</sup> Although Dias and Perini's (2018) phylogenetic analyses of COI sequences from white-eared opossums recovered distinct haplogroups that they interpreted as support for the three currently recognized species, their *albiventris* sequences were all from southeastern Brazil, their *imperfecta* sequences were all from the Guianas, and their *pernigra* sequences were all from Ecuador. With such widely separated geographic samples, intraspecific isolation by distance is a plausible alternative explanation for their results.

sequences are unimpressive (e.g., 2.9% K2P-corrected, on average; Patton et al., 2000), and no sequences of black-eared opossums from geographically intermediate biomes (e.g., the Cerrado) have yet been analyzed. Additionally, no qualitative morphological character seems to distinguish these nominal taxa, and statistically significant morphometric differences reported by Cerqueira and Lemos (2000) seem to be artifacts of very large sample sizes ( $df \geq 450$  in all the two-sample ANOVAs performed by those authors). In the key provided by Cerqueira and Tribe (2008), *D. aurita* and *D. marsupialis* are only distinguished geographically.

As explained by Cerqueira and Tribe (2008), *Didelphis azarae* Temminck, 1824, is an older name based on one or more specimens of black-eared opossums that were probably collected in the Atlantic Forest, but *D. azarae* was previously used for the white-eared species currently known as *D. albiventris* Lund, 1840. In the interest of stability, usage of Wied's name should be maintained, at least so long as the black-eared opossums of the Atlantic Forest are judged to be taxonomically distinct from *D. marsupialis*.

*Didelphis imperfecta*

Mondolfi and Pérez-Hernández, 1984

TYPE MATERIAL AND TYPE LOCALITY: MHNL 1751, the holotype by original designation, consists of the skin and skull of an adult female collected at Kilometer 125 (ca. 6.03° N, 68.65° W; 1100 m) on the road from El Dorado to Santa Elena de Uairén, Bolívar state, Venezuela.

SYNONYMS: None.

DISTRIBUTION: Specimens identified as *Didelphis imperfecta* have been reported from montane forest, lowland savannas, and lowland rainforest in the Guianas, eastern and southern Venezuela, eastern Colombia, and Brazil north of the Amazon (Caramaschi et al., 2013; González et al., 2020: fig. 1).

REMARKS: This taxon was originally named as a subspecies of *Didelphis albiventris*, but Voss and Emmons (1996) imprudently recognized it

as a valid species despite the absence of compelling phenotypic or genetic criteria for specimen identification (see Remarks for *D. albiventris*, above). Unfortunately, *D. imperfecta* now appears to be nothing more than a binomial convention for *D. albiventris*-like specimens collected north of the Amazon.

*Didelphis marsupialis* Linnaeus, 1758

TYPE MATERIAL AND TYPE LOCALITY: ROM 113908, the neotype (designated by Feijó and Voss, 2019), consists of the skin, skull, postcranial skeleton, and frozen tissues of an adult female collected at the Brownsburg Nature Park headquarters (4.95° N, 55.18° W; 500 m), Brokopondo District, Surinam.

SYNONYMS: *battyi* Thomas, 1902; *cancrivora* Gmelin, 1788; *caucae* J.A. Allen, 1900; *colombica* J.A. Allen, 1900; *etensis* J.A. Allen, 1902; *insularis* J.A. Allen, 1902; *karkinophaga* Zimmermann, 1780; *mesamericana* J.A. Allen, 1902; *particeps* Goldman, 1917; *richmondi* J.A. Allen, 1901; *tabascensis* J.A. Allen, 1901.

DISTRIBUTION: *Didelphis marsupialis* occurs from northeastern Mexico (Tamaulipas) southward throughout most of Central America (Gardner, 1973: fig. 12) to South America; in South America, this species occurs in the humid-forested tropical lowlands from Colombia southward to coastal Peru on the west side of the Andes and—by convention (see Remarks)—throughout Amazonia to eastern Bolivia and central Brazil on the east side of the Andes (Cerqueira and Tribe, 2008: map 7).

REMARKS: Feijó and Voss (2019) discussed nomenclatural issues that were definitively resolved by designating a neotype. *Didelphis marsupialis* has received no serious revisionary attention since Gardner's (1973) treatment of North American subspecies; the South American forms currently regarded as synonyms or subspecies have not been revised for over a century. The range of *D. marsupialis* is said to be disjunct from that of *D. aurita* (Cerqueira and Tribe, 2008), but this conventional view should be reevaluated in



the light of new collections from the Cerrado, as should the currently accepted notion that *D. aurita* is a valid species (see above).

*Didelphis pernigra* J.A. Allen, 1900

TYPE MATERIAL AND TYPE LOCALITY: AMNH 16071, the holotype by original designation, consists of the skin and skull of an adult female collected at "Juliaca" (= Santo Domingo: 13.85° S, 69.68° W; ca. 2130 m), Puno department, Peru.

SYNONYMS: *andina* J.A. Allen, 1902; *meriden-sis* J.A. Allen, 1902.

DISTRIBUTION: *Didelphis pernigra* is said to occur in montane forests from western Venezuela and northern Colombia southward along the Andes to Bolivia (Cerqueira and Tribe, 2008: map 8), but specimens identified as *D. pernigra* have also been reported from coastal deserts near sea level in western Peru (Pacheco et al., 2020). Reports of this species from northwestern Argentina are apparently unsupported by voucher specimens (Teta et al., 2018).

REMARKS: *Didelphis pernigra* would appear to be the most phenotypically distinct of the three currently recognized species of white-eared opossums (Lemos and Cerqueira, 2002; Dias et al., 2020), but there has been no assessment of the genetic integrity of this taxon, which ranges across several thousand kilometers of deeply dissected Andean terrain. Although Lemos and Cerqueira (2002) noted a seemingly abrupt transition between the *per-nigra* and *albiventris* phenotypes along an elevational transect in eastern Bolivia, a phenomenon that they reasonably interpreted as evidence for parapatry between reproductively isolated forms, their inference is another hypothesis that merits genetic investigation.

*Didelphis virginiana* Kerr, 1792

TYPE MATERIAL AND TYPE LOCALITY: No type material is known to exist. The original description was based on a specimen presumed to have come from Virginia.

SYNONYMS: *boreoamericana* J.A. Allen, 1902; *breviceps* Bennett, 1833; *californica* Bennett, 1833; *cozumelae* Merriam, 1901; *illinensium* Link, 1795; *pigra* Bangs, 1898; *pilosissima* Link, 1795; *pruinosa* Wagner, 1843; *texensis* J.A. Allen, 1901; *woapink* Barton, 1806; *yucatanensis* J.A. Allen, 1901.

DISTRIBUTION: *Didelphis virginiana* occurs from southern Canada throughout most of the eastern and midwestern United States (populations on the Pacific coast of the United States are descended from introductions), in Mexico, and in Central America as far south as Nicaragua (Gardner, 1973: fig. 14).

REMARKS: Gardner (1973) provided a careful analysis of phenotypic and karyological differences between *Didelphis virginiana* and *D. marsupialis* where they occur sympatrically in Mexico and Central America. In the same publication, Gardner commented on geographic variation in size, anatomical proportions, and coloration that he associated with several subspecies of *D. virginiana*. Three of those subspecies (*D. v. californica*, *D. v. virginiana*, and *D. v. yucatanensis*) were recovered as reciprocally monophyletic haplogroups in Cervantes et al.'s (2010) neighbor-joining analysis of mtDNA sequence data, a result that should be followed up with more geographically comprehensive phylogeographic analyses of this taxonomically neglected species.

Genus *Lutreolina* Thomas, 1910

TYPE SPECIES: *Didelphis crassicaudata* Desmarest, 1804, by monotypy.

SYNONYMS: None.

REMARKS: Voss and Jansa (2009) provided an emended generic description based on *Lutreolina crassicaudata*, but their morphometric descriptors did not include the substantially smaller dimensions of *L. massaia*, which was described several years later. Two species are currently recognized.

*Lutreolina crassicaudata* (Desmarest, 1804)

TYPE MATERIAL AND TYPE LOCALITY: No type material is known to exist. The species is based on Felix de Azara's description of two specimens that he examined from eastern Paraguay (Voss et al., 2009a).

SYNONYMS: *bonaria* Thomas, 1923; *crassicaudis* Olfers, 1818; *ferruginea* Larrañaga, 1923; *lutrilla* Thomas, 1923; *macroura* Desmoulins, 1824; *paranalis* Thomas, 1923; *travassosi* Miranda-Ribeiro, 1936; *turneri* Günther, 1879.

DISTRIBUTION: The distribution of *Lutreolina crassicaudata* is famously disjunct, with one population in the Llanos and adjacent savannas of northern South America (eastern Colombia, Venezuela, and Guyana) and a second in tropical and subtropical open habitats of eastern Bolivia, southern Brazil, Paraguay, Uruguay, and northern Argentina (Stein and Patton, 2008b: map 9).

REMARKS: Voss and Jansa's (2009) description of *Lutreolina* was based exclusively on *L. crassicaudata*, and so serves as a description of the species as well. By convention, the northern population (in Colombia, Guyana, and Venezuela) is known as *L. c. turneri*, whereas the southern population is referred to *L. c. crassicaudata*. Although other subspecies have been recognized based on specimens from southern Brazil and northern Argentina, analyses of cytochrome *b* sequence data (Martínez-Lanfranco et al., 2014) suggest remarkably little phylogeographic structure within what is currently considered the nominotypical form.

*Lutreolina massaia*

Martínez-Lanfranco et al., 2014

TYPE MATERIAL AND TYPE LOCALITY: MACN 25333, the holotype by original designation, consists of the skin, skull, postcranial skeleton, and preserved tissues of an adult female collected at the Reserva Provincial Santa Ana (27.43° S, 65.78° W; 455 m), Tucumán province, Argentina.

SYNONYMS: None.

DISTRIBUTION: *Lutreolina massaia* occurs in premontane and montane forests of the Yungas ecoregion in southeastern Bolivia and northwestern Argentina, from about 450 to 2000 m above sea level (Martínez-Lanfranco et al., 2014: fig. 1).

REMARKS: See Martínez-Lanfranco et al. (2014) for phylogenetic analyses of mtDNA sequence data, a morphological description, tabulated measurements, illustrations, and comparisons with *Lutreolina crassicaudata*.

Genus *Philander* Brisson, 1762

TYPE SPECIES: *Didelphis opossum* Linnaeus, 1758, by plenary action of the International Commission on Zoological Nomenclature (ICZN, 1998).

SYNONYMS: *Metachirops* Matschie, 1916; *Holothylax* Cabrera, 1919.

REMARKS: See Voss et al. (2018) for an emended generic description. Patton and da Silva (2008) summarized the protracted and now entirely irrelevant historical controversy concerning the application of this name, which was permanently settled by fiat (ICZN, 1998). Ten species are currently recognized, although problems of morphological diagnosis remain for some taxon pairs as discussed below.

*Philander andersoni* (Osgood, 1913)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 19655, the holotype by original designation, consists of the skin and skull of an adult male collected at Yurimaguas (5.90° S, 76.08° W), Loreto department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Philander andersoni* is found in northeastern Peru, eastern Ecuador, southeastern Colombia, southern Venezuela, and northwestern Brazil (north of the Amazon and west of the Rio Negro. Patton and da Silva's (2008) range map approximates this distribution but includes localities in east-central Peru (Junín

and Ayacucho) that were based on specimens of *P. nigratus*, a distinct species (see Remarks).

REMARKS: *Philander andersoni* and *P. mcilhennyi* resemble one another and are distinguished from other congeners by having clear (ungrizzled) blackish middorsal fur. Although Hershkovitz (1997) regarded *mcilhennyi* as a subspecies of *M. andersoni*, Patton and da Silva (2008) treated these taxa as valid species that were said to differ in several external morphological characters. Phylogenetic analyses of multilocus sequence data indicate that *P. andersoni* and *P. mcilhennyi* are not sister species (Voss et al., 2018). Nevertheless, examination of large series of specimens suggests that morphological diagnosis is problematic (Voss et al., 2019). *Philander nigratus*, treated as a synonym of *P. andersoni* by Patton and da Silva (2008), was subsequently revalidated by Voss and Giarla (2020b).

*Philander canus* (Osgood, 1913)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 19347, the holotype by original designation, consists of the skin and skull of an adult male collected at Moyobamba (6.05° S, 76.97° W; ca. 860 m), San Martín department, Peru.

SYNONYMS: *crucialis* Thomas, 1923; *mondolfi* Lew et al., 2006; *olrogii* Flores et al., 2008.

DISTRIBUTION: As currently understood, *Philander canus* seems to have a disjunct distribution, with one population in Venezuela and eastern Colombia and another that extends from eastern Peru and western Brazil southward to eastern Bolivia, Paraguay, and northern Argentina (Voss et al., 2018: fig. 9).

REMARKS: *Philander canus* was long treated as a synonym or subspecies of *P. opossum*, but these taxa are not closely related according to phylogenetic analyses reported by Voss et al. (2018), who also illustrated diagnostic traits, provided a morphological description, tabulated summary statistics of measurement data, discussed synonyms, and documented sympatry with congeneric species. Despite the wide and possibly disjunct distribution of this species, Voss et al.'s (2018)

analyses of mtDNA sequence data revealed little evidence of phylogeographic structure.

*Philander deltae* Lew et al., 2006

TYPE MATERIAL AND TYPE LOCALITY: MHNLS 10679, the holotype by original designation, consists of the skin, skull, and postcranial skeleton of an adult male collected “frente a Isla Venado” (10.00° N, 62.82° W; at sea level) in the Reserva Forestal Guarapiche, Monagas state, Venezuela.<sup>12</sup>

SYNONYMS: None.

DISTRIBUTION: *Philander deltae* is said to occur in seasonally flooded habitats in and around the Orinoco delta of northeastern Venezuela (Delta Amacuro and Monagas) (Lew et al., 2006: fig. 1).

REMARKS: As described by Lew et al. (2006), *Philander deltae* seems like a morphologically distinctive form, but genetic data from this taxon is needed to corroborate its taxonomic status and determine its relationships to other congeners.

*Philander mcilhennyi* Gardner and Patton, 1972

TYPE MATERIAL AND TYPE LOCALITY: LSUMZ 16395, the holotype by original designation, consists of the skin and skull of an adult female collected at Balta (10.13° S, 17.22° W; ca. 300 m) on the Río Curanja, Ucayali (formerly Loreto) department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Philander mcilhennyi* occurs south of the Amazon in eastern Peru (Huánuco, Loreto, Ucayali) and western Brazil (Acre, Amazonas) (Patton and da Silva, 2008: map 10).

REMARKS: *Philander mcilhennyi*, originally described as a valid species, was treated as a subspecies of *P. andersoni* by Hershkovitz (1997), but Patton and da Silva (2008) disagreed. Although *P. andersoni* and *P. mcilhennyi*

<sup>12</sup> The type locality of *Philander deltae* is described differently in Lew et al.'s (2006) text (p. 227) and in their appendix (p. 235). The latter description is more easily understood and corresponds to the version given here.

are not sister species, they are genuinely difficult to distinguish morphologically (Voss et al., 2018, 2019).

*Philander melanurus* (Thomas, 1899)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 97.11.7.61, the holotype by original designation, consists of the skin and skull of an adult male collected at Paramba (0.82° N, 78.35° W; 700 m), Imbabura province, Ecuador.

SYNONYMS: *fuscogriseus* J.A. Allen, 1900; *griseus* J.A. Allen, 1901; *melantho* Thomas, 1923.

DISTRIBUTION: Based on sequenced specimens, *Philander melanurus* occurs in western Ecuador, western and inter-Andean Colombia, and Panama (Voss et al., 2018: fig. 3), but it seems likely that the species's range also extends northward into Costa Rica, Nicaragua, and possibly Honduras.

REMARKS: Morphological traits that distinguish this species from other congeners formerly synonymized with *Philander opossum* remain to be adequately documented. Phylogenetic analyses of multilocus sequence data (Voss et al., 2018) suggest that this species is the sister taxon of *P. vossi*, another trans-Andean endemic.

*Philander nigratus* (Thomas, 1923)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 0.7.7.62, the holotype by original designation, consists of the skin and skull of an old adult female collected at Utcuyacu (11.20° S, 75.47° W; 1600 m), Junín department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Philander nigratus* is currently known from just six localities in the foothills of the eastern Andes (between 1000 and 1600 m) in the Peruvian departments of Ayacucho and Junín (Voss and Giarla, 2020b).

REMARKS: *Philander nigratus* has been variously treated as a subspecies or synonym of *P. andersoni*, *P. canus*, and *P. opossum*, but it is genetically and morphologically distinct from these and other congeneric forms. A morphological description, mea-

surement data, taxonomic comparisons, and analyses of mtDNA sequence data were provided by Voss and Giarla (2020b).

*Philander opossum* (Linnaeus, 1758)

TYPE MATERIAL AND TYPE LOCALITY: RMNH 25421a, the lectotype (designated by Hershkovitz, 1976), is a fluid-preserved adult female with pouch young collected in Surinam.

SYNONYMS: *frenatus* Olfers, 1818; *superciliaris* Olfers, 1818.

DISTRIBUTION: As currently recognized (see Remarks), *Philander opossum* occurs in eastern Amazonia, including the Guianas and northern Brazil; in Brazil, this species occurs in Amapá, Amazonas (north of the Amazon and east of the Rio Negro), Pará, and Roraima. No published range map accurately shows the range of this species as restricted by recent revisionary research.

REMARKS: Patton and da Silva's (2008) concept of *Philander opossum* included several taxa herein recognized as distinct species, including *P. canus*, *P. melanurus*, and *P. vossi* (formerly *P. pallidus*; see below). In fact, none of these taxa are closely related to *P. opossum*, which appears, instead, to belong to a monophyletic group that includes *P. andersoni* and *P. mcilhennyi* (see Voss et al., 2018). The identity of *frenatus* as a subjective synonym of *P. opossum* was discussed by Voss and Angermann (2018; in Voss et al., 2018). The identity of *superciliaris* as a subjective synonym was fixed by neotype selection (Voss et al., 2018).

*Philander pebas* Voss et al., 2018

TYPE MATERIAL AND TYPE LOCALITY: MVZ 190343, the holotype by original designation, consists of the skin, skull, and frozen tissues of an adult male collected at Igarapé Nova Empresa (6.80° S, 70.73° W) on the left bank of the Rio Juruá, Amazonas, Brazil.

SYNONYMS: None.

DISTRIBUTION: As currently documented by examined specimens, *Philander pebas* occurs in



eastern Ecuador (Orellana), eastern Peru (Loreto, Madre de Dios, Ucayali), and western Brazil (Acre, Amazonas), but Voss et al. (2018) speculated that the species might range throughout the *várzea* landscapes (seasonally inundated by white-water rivers) of western Amazonia, including those in southeastern Colombia, where it is still unknown.

REMARKS: A morphological description, illustrations, comparisons with congeneric species, summary statistics for external and craniodental measurements, and analyses of mtDNA sequence data were provided by Voss et al. (2018).

*Philander quica* (Temminck, 1824)

TYPE MATERIAL AND TYPE LOCALITY: The lectotype (designated by Hershkovitz, 1959) is a female specimen collected at “Sapitiba” (= Sepe-tiba: 22.97° S, 43.70° W; near sea level), Rio de Janeiro, Brazil. Although this specimen was formerly at the NMW, its current whereabouts are unknown (Voss et al., 2018).

SYNONYMS: *azaricus* Thomas, 1923.

DISTRIBUTION: *Philander quica* is known from tropical and subtropical landscapes in southeastern Brazil, northeastern Argentina (Misiones), and eastern Paraguay (Voss et al., 2018: fig. 9).

REMARKS: An emended morphological description, illustrations, comparisons with congeneric species, summary statistics for external and craniodental measurements, and analyses of mtDNA sequence data were provided by Voss et al. (2018). This species was previously widely known as *Philander frenatus*, but the type of *frenatus* is now known to have been collected in eastern Amazonia, and that name is currently regarded as a junior subjective synonym of *P. opossum* (see Voss et al., 2018).

*Philander vossi*

Gardner and Ramírez-Pulido, 2020

TYPE MATERIAL AND TYPE LOCALITY: USNM 58158, the holotype (by replacement of a preoc-

cupied name; ICZN, 1999: Article 72.7), consists of the skin and skull of an adult male collected at Orizaba (18.85° N, 97.10° W; 1280 m), Veracruz state, Mexico.

SYNONYMS: *pallidus* J.A. Allen, 1901 (preoccupied; see Remarks).

DISTRIBUTION: Sequenced specimens suggest that *Philander vossi* occurs in Mexico, Belize, and El Salvador (Voss et al., 2018: fig. 3), but it seems likely to also occur in Guatemala and perhaps other Central American countries.

REMARKS: Gardner and Ramírez-Pulido (2020) proposed *Philander vossi* as a replacement name for the species previously known as *P. pallidus*, which is preoccupied by *Philander laniger pallidus* Thomas, 1899 (= *Caluromys derbianus*; see above). Phylogenetic analyses of multilocus sequence data (Voss et al., 2018) suggest that *P. vossi* is the sister taxon of *P. melanurus*, but consistent morphological criteria for distinguishing these putative species have yet to be discovered.

Tribe Thylamyini Hershkovitz, 1992

TYPE GENUS: *Thylamys* Gray, 1843.

SYNONYMS: None.

REMARKS: Tribal monophyly is strongly and consistently supported by phylogenetic analyses of multilocus sequence datasets (Voss and Jansa, 2009; Amador and Giannini, 2016; Díaz-Nieto et al., 2016a), although only Díaz-Nieto et al.'s (2016a) analyses included species from all six member genera.

Genus *Chacodelphys* Voss et al., 2004

TYPE SPECIES: *Marmosa formosa* Shamel, 1930, by original designation.

SYNONYMS: None.

REMARKS: An emended morphological description was provided by Voss and Jansa (2009). Phylogenetic analyses of multilocus sequence data have recovered *Chacodelphys* as the sister taxon of *Cryptonanus* within a monophyletic group of thylamy-



ines that includes *Gracilinanus*, *Lestodelphys*, and *Thylamys*, but not *Marmosops* (Díaz-Nieto et al., 2016a; Fegies et al., 2021). Only a single species is currently recognized.

*Chacodelphys formosa* (Shamel, 1930)

TYPE MATERIAL AND TYPE LOCALITY: USNM 236330, the holotype by original designation, consists of the skin and skull of a young adult male collected at Estancia Linda Vista (25.22° S, 59.78° W; ca. 100 m) on the Riacho Pilagá, Formosa province, Argentina.

SYNONYMS: *muscula* Shamel, 1930 (preoccupied).

DISTRIBUTION: All known specimens of *Chacodelphys formosa* are from Chacoan landscapes in northern Argentina (Chaco, Formosa, and Misiones; Teta et al., 2006; Teta and Pardiñas, 2007)

REMARKS: *Chacodelphys formosa* is currently known from just a handful of specimens, most of which were recovered from owl vomitus.

Genus *Cryptonanus* Voss et al., 2005

TYPE SPECIES: *Marmosa agilis chacoensis* Tate, 1931, by original designation.

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for an emended generic description. Phylogenetic analyses of multilocus sequence datasets strongly support generic monophyly and convincingly recover *Cryptonanus* and *Chacodelphys* as sister taxa in a larger clade that includes *Gracilinanus*, *Lestodelphys*, and *Thylamys*, but not *Marmosops* (Díaz-Nieto et al., 2016a; Fegies et al., 2021). Of the five species originally referred to *Cryptonanus* by Voss et al. (2005), only four are now recognized as valid. Currently recognized species of *Cryptonanus* are all from south of the Amazon (in Brazil, Paraguay, Bolivia, Uruguay, and Argentina), but specimens of a possibly undescribed species have been reported from Amapá (Silva et al., 2013) and French Guiana (Baglan and Catzefflis, 2016).

*Cryptonanus agricolai* (Moojen, 1943)

TYPE MATERIAL AND TYPE LOCALITY: MN 1495, the holotype by original designation, consists of the skin and skull of an adult male collected at Crato (7.23° S, 39.38° W; 422 m), Ceará state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Cryptonanus agricolai* occurs in open habitats (including agricultural areas in formerly forested biomes) in northeastern, central, and southeastern Brazil (Fegies et al. (2021: fig. 1).

REMARKS: For an emended description see Voss et al. (2005), who also tabulated measurement data from eight referred specimens. Although subsequent phylogenetic analyses of multilocus sequence data suggest that specimens referable to *Cryptonanus agricolai* belong to three allopatric phylogroups that may have diverged in the Middle Pleistocene (Fegies et al., 2021), none of these putative species has yet been characterized morphologically.

*Cryptonanus chacoensis* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 4.1.5.48, the holotype by original designation, consists of the skin and skull of an adult male collected at “Sapucay” (= Sapucaí, at 25.67° S, 56.92° W; ca. 220 m), Paraguari province, Paraguay.

SYNONYMS: *ignitus* Díaz et al., 2002.

DISTRIBUTION: *Cryptonanus chacoensis* occurs in grasslands and dry forests from central Brazil to Paraguay and northern Argentina (Fegies et al., 2021: fig. 1); the species might also occur in Uruguay (see Remarks).

REMARKS: For an emended description see Voss et al. (2005), who also tabulated measurement data from nine specimens. DNA sequence data obtained from the holotype of *Cryptonanus ignitus* (originally described as a distinct species), together with new information about ontogenetic character variation in *C. chacoensis* provide compelling evidence that these taxa are conspecific (Teta and Díaz-Nieto, 2019). Phylogenetic analy-

ses of multilocus sequence data also suggest that specimens referable to *C. chacoensis* belong to four morphologically cryptic phylogroups that probably diverged in the Middle Pleistocene (Fegies et al., 2021). Two of these phylogroups are known to contact one another in central Brazil, but the taxonomic interpretation of sympatrically collected specimens is not clear due to mitochondrial discordance. The identity of the Uruguayan specimens reported by D'Elía and Martínez, 2006) has yet to be determined, but some of them could be *C. chacoensis*.

*Cryptonanus guahybae* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: ZMB 4306, the holotype by original designation, consists of the skin and skull of an adult male collected on the island of "Guahyba" (= Ilha Guaíba; ca. 30.10° S, 53.75° W; at sea level) near Pôrto Alegre, Rio Grande do Sul state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Cryptonanus guahybae* occurs in a variety of subtropical habitats—including grasslands, seasonally flooded forests, deciduous forests, Araucaria forest, and coastal scrub—in southern Brazil (Fegies et al., 2021: fig. 1) and possibly also in Uruguay (see Remarks).

REMARKS: For an emended description see Voss et al. (2005), Quintela et al. (2011), and Dias et al. (2016), all of whom also tabulated measurement data for this species. Phylogenetic analyses of multilocus sequence data suggest that specimens referable to *Cryptonanus guahybae* include members of two morphologically cryptic, allopatric phylogroups, one of which occupies the Atlantic coastal plain and the other the interior highlands of Rio Grande do Sul (Fegies et al., 2021). The identity of the Uruguayan specimens reported by D'Elía and Martínez, 2006) has yet to be determined, but some of them could be *C. guahybae*.

*Cryptonanus unduaviensis* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 72563, the holotype by original designation, con-

sists of the skin and skull of an adult male collected at Pitiguaya (ca. 16.35° S, 67.78° W; 1740 m), La Paz department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: *Cryptonanus unduaviensis* is known from savannas and other open habitats in southeastern Peru (Madre de Dios), eastern Bolivia, southwestern Brazil (Mato Grosso), and western Paraguay (Medina et al., 2016; Fegies et al., 2021: fig. 1).

REMARKS: For an emended description see Voss et al. (2005), who also tabulated measurement data from eight referred specimens. Phylogenetic analyses of DNA sequence datasets (e.g., Dias et al., 2016; Teta and Díaz-Nieto, 2019; Fegies et al., 2021) have consistently recovered *Cryptonanus unduaviensis* as the sister species to a clade that contains all the other species in this genus.

Genus *Gracilinanus*

Gardner and Creighton, 1989

TYPE SPECIES: *Didelphys microtarsus* Wagner, 1842, by original designation.

SYNONYMS: None.

REMARKS: See Voss and Jansa (2009) for an emended generic description. The monophyly of *Gracilinanus* (as recognized herein) is strongly supported by phylogenetic analyses of multilocus datasets (e.g., Voss and Jansa, 2009; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016). At least seven species are currently thought to be valid, but unpublished preliminary results suggest that more remain to be described.

*Gracilinanus aceramarcae* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 72568, the holotype by original designation, consists of the skin and skull of a young adult female collected on the Río Aceramarca (16.30° S, 67.88° W; 3292 m), a tributary of the Río Unduavi, in La Paz department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: *Gracilinanus aceramarcae* has been collected in montane forest at elevations above

2000 m in Peru and northern Bolivia (Creighton and Gardner, 2008b: map 16). In Peru, this species (or a complex of similar species) is said to be widely distributed, from the department of Piura in the north to Puno in the south (Pacheco et al., 2020).

REMARKS: See Voss et al. (2009b) and Semedo et al. (2015) for morphological comparisons with other congeneric species. The relationships of this species with other congeners are notably inconsistent as recovered by different phylogenetic analyses of DNA sequence data (e.g., Semedo et al., 2015, 2022; Díaz-Nieto et al., 2016a).

*Gracilinanus agilis* (Burmeister, 1854)

TYPE MATERIAL AND TYPE LOCALITY: IZH M-27, the holotype by monotypy, consists of the mounted skin and extracted skull of a young adult male collected at Lagoa Santa (19.63° S, 43.82° W), Minas Gerais state, Brazil.

SYNONYMS: *beatrice* Thomas, 1910; *blaseri* Miranda-Ribeiro, 1936; *rondoni* Miranda-Ribeiro, 1936.

DISTRIBUTION: *Gracilinanus agilis* occurs in gallery forests and other woody formations of the Cerrado and Caatinga in northeastern and central Brazil (Bahia, Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pernambuco, Piauí) and eastern Bolivia (Santa Cruz); it also occurs in subtropical forests in eastern Paraguay (Caazapá, Canindeyú, Cordillera, Paraguari). No published range map adequately represents the distribution of this species: Creighton and Gardner's (2008b) map includes records based on specimens now known to represent *G. peruanus*, whereas the maps in Costa et al. (2003), Faria et al. (2013b), and Semedo et al. (2015) only show collection localities of sequenced Brazilian material.

REMARKS: Illustrations, measurements, and morphological comparisons with other congeners are in Costa et al. (2003), Geise and Astúa (2009), Lóss et al. (2011), and Semedo et al. (2015). *Gracilinanus peruanus* was listed as a synonym of *G. agilis* by Creighton and Gardner (2008b), but these nonsister taxa are genetically

and morphologically distinct, and they are known to occur sympatrically (Semedo et al. 2015). Phylogenetic analysis of at least one taxon-dense multilocus dataset provides reasonably strong support for *G. agilis* as the sister taxon of *G. microtarsus* (Díaz-Nieto et al., 2016a).

*Gracilinanus dryas* (Thomas, 1898)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 98.5.15.2, the holotype by original designation, consists of the skin and skull of an adult male collected at "Culata" (= Páramo de la Culata in the Cordillera de Mérida: ca. 8.75° N, 71.08° W; 4000 m), Mérida state, Venezuela.

SYNONYMS: None.

DISTRIBUTION: *Gracilinanus dryas* has been reported from high elevations (>2200 m) in the Cordillera de Mérida and the Cordillera de Trujillo of western Venezuela and in the Cordillera Oriental (eastern Andes) of Colombia (Creighton and Gardner, 2008b: map 16).

REMARKS: This species has received no revisionary attention and is not represented in any published phylogenetic analysis of DNA sequence data. Although unpublished analyses of cytochrome *b* sequences (cited by Díaz-Nieto et al., 2016a) failed to resolve *Gracilinanus dryas* and *G. marica* as reciprocally monophyletic taxa, no careful review of relevant voucher identifications has yet been undertaken. Types and topotypes of these taxa from the Cordillera de Mérida certainly have the morphological aspect of distinct species (as noted by Thomas, 1898), so additional research is needed to resolve this apparent discrepancy. Tate (1933: 203) claimed that the auditory bullae of *G. dryas* lack "processes," but well-developed anteromedial processes of the alisphenoid tympanic wing are present in all the specimens I have examined for this trait ( $N = 10$ ), including the holotype.

*Gracilinanus emiliae* (Thomas, 1909)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 9.3.9.10, the holotype by original designation,

consists of the skin and skull of a subadult male collected at “Para” (= Belém: 1.45° S, 48.48° W), Pará state, Brazil.

SYNONYMS: *longicaudus* Hershkovitz, 1992.

DISTRIBUTION: *Gracilinanus emiliae* is known from fewer than 20 localities, but these are widely scattered across cis-Andean tropical South America, mostly in Amazonian rainforest, but also in northern Venezuela, at the northern margin of the Cerrado, and at the western edge of the Llanos (Brandão et al., 2014: fig. 3).

REMARKS: See Voss et al. (2001, 2009b) for emended descriptions, illustrations, measurements, and morphological comparisons with other congeners; additional illustrations, measurements, and morphological observations are in Brandão et al. (2014). Phylogenetic analyses of taxon-dense multilocus datasets suggest that *Gracilinanus emiliae* is the sister species of *G. marica*, and that this pair is the sister group of a larger clade that includes all the other species in the genus (Díaz-Nieto et al., 2016a; Teta and Díaz-Nieto, 2019).

*Gracilinanus marica* (Thomas, 1898)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 98.5.15.1, the holotype by original designation, consists of the skin and skull of an adult male collected on the “Rio Abbaregas” (= Río Albarregas: 8.58° N, 71.15° W; 1630 m), Mérida state, Venezuela.

SYNONYMS: *perijae* Hershkovitz, 1992.

DISTRIBUTION: As currently understood, *Gracilinanus marica* occurs in lower montane forests (between about 1400 and 2200 m) of the Venezuelan Andes, the Caribbean coastal cordilleras of northern Venezuela, the Serranía de Perijá of northeastern Colombia, and the Cordillera Oriental near Bogotá.

REMARKS: This species has received no substantive revisionary attention and its status with respect to *Gracilinanus dryas* is currently uncertain (see above). Phylogenetic analyses of multilocus sequence data suggest that *G. marica* and *G. emiliae* are sister species

(Díaz-Nieto et al., 2016a; Teta and Díaz-Nieto, 2019).

*Gracilinanus microtarsus* (Wagner, 1842)

TYPE MATERIAL AND TYPE LOCALITY: No type material was designated in Wagner’s original description, which was based on specimens collected at “Ypanema” (= Ipanema: 23.43° S, 47.60° W), São Paulo state, Brazil. As many as eight syntypes may have once been at the NMW (Pelzeln, 1883), but only four (NMW B-2601, -2615, -2602A, -2602B) now remain there according to a list kindly provided by the current NMW mammal curator, Frank Zachos. Hershkovitz (1992) believed that one of them was designated as the lectotype by Tate (1933: table 1, section 7), although it is not clear that Tate really intended to do so.

SYNONYMS: *erhardti* Miranda-Ribeiro, 1936.<sup>13</sup>

DISTRIBUTION: *Gracilinanus microtarsus* occurs in tropical and subtropical evergreen and semideciduous forests in southeastern Brazil (from Bahia southward to Rio Grande do Sul; Lóss et al., 2011: fig. 11), northeastern Argentina (Misiones; Teta et al., 2007), and possibly Uruguay (D’Elía and Martínez, 2006).

REMARKS: For an exemplary revision and redescription of this species, which exhibits substantial geographic variation in mtDNA sequences and morphology, see Lóss et al. (2011), who also provided illustrations and tabulated measurement data. There is reasonably strong support from phylogenetic analyses of at least one multilocus dataset that *Gracilinanus microtarsus* and *G. agilis* are sister species (Díaz-Nieto et al., 2016a; Teta and Díaz-Nieto, 2019).

*Gracilinanus peruanus* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 27.11.1.268, the holotype by original designation, consists of the skin and skull of an adult male

<sup>13</sup> See Lóss et al. (2011: 23) for comments on the correct spelling of this subjective synonym.

collected at Tingo María (9.30° S, 75.98° W; 600 m), Huánuco department, Peru.

SYNONYMS: *buenavistae* Tate, 1931 (see Remarks).

DISTRIBUTION: *Gracilinanus peruanus* occurs in west-central Brazil (Mato Grosso and Rondônia), eastern Bolivia (Santa Cruz), and eastern Peru (Semedo et al., 2022: fig. 4). In addition to the type locality (in Huánuco), *G. peruanus* is known from the Peruvian departments of Cusco, Madre de Dios, Pasco, and Ucayali (Voss et al., 2019).

REMARKS: *Gracilinanus peruanus* was considered a synonym of *G. agilis* by Creighton and Gardner (2008b), but Semedo et al. (2015) showed that these species are genetically divergent, morphologically diagnosable, occur sympatrically, and are probably not sister taxa. The relationships of this species with other congeners, however, have yet to be convincingly resolved (Díaz-Nieto et al., 2016a; Teta and Díaz-Nieto, 2019; Semedo et al., 2022). As first revisers in the sense of the Code (ICZN, 1999: Article 24.2), Semedo et al. (2015) determined the priority of *peruana* Tate, 1931, over *buenavistae* Tate, 1931 (both names having first appeared in the same publication).

#### Genus *Lestodelphys* Tate, 1934

TYPE SPECIES: *Notodelphys halli* Thomas, 1921, by original designation.

SYNONYMS: *Notodelphys* Thomas, 1921 (preoccupied).

REMARKS: See Voss and Jansa (2009) for an emended generic description. Only a single species is currently recognized.

#### *Lestodelphys halli* (Thomas, 1921)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 21.6.7.19, the holotype by original designation, consists of the skin, skull, and postcranial skeleton of an adult male collected at “Estancia Madujada” (= Estancia La Madrugada: 47.22° S, 66.45° W) near Puerto Deseado, Santa Cruz province, Argentina. Jenkins and Knutson (1983: 19) gave the type locality as “Cape Tres Puntas, SE Pata-

gonia” after Thomas (1921b), but Thomas (1929) subsequently corrected the type locality based on correspondence with the collector.

SYNONYMS: None.

DISTRIBUTION: *Lestodelphys halli* is found in the Monte Desert and Patagonian Steppe ecoregions of Argentina, including the provinces of Chubut, La Pampa, Mendoza, Neuquén, Río Negro, and Santa Cruz (Formoso et al., 2015: fig. 1).

REMARKS: Given the extensive geographic range of *Lestodelphys halli* and its uniquely austral distribution (approximately from 31° to 48° S), a phylogeographic analysis of mtDNA sequence data from this species would be of considerable interest. Morphological variation within a large series of specimens was described by Martin (2005), who also provided a craniodental diagnosis.

#### Genus *Marmosops* Matschie, 1916

TYPE SPECIES: *Didelphis incana* Lund, 1840, by original designation.

SYNONYMS: None.

REMARKS: Generic monophyly is consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., Voss and Jansa, 2009; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016). Two subgenera are currently recognized.

#### Subgenus *Marmosops* Matschie, 1916

TYPE SPECIES: As for the genus.

SYNONYMS: None.

REMARKS: Subgeneric monophyly is consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., Díaz-Nieto et al., 2016a, 2016b; Amador and Giannini, 2016). Two species are currently recognized from the Atlantic Forest of southeastern Brazil and another five from the Andes and Amazonia, but deep phylogeographic structure in several wide-ranging, unrevised species suggest the need for additional revisionary research (Díaz-Nieto et al., 2016b).



*Marmosops (Marmosops) cauae*  
(Thomas, 1900)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 99.9.6.51, the holotype by original designation, consists of the skin and skull of an old adult male that was probably collected at about 1000 m on the Río Cauquita near Cali (ca. 3.45° N, 76.52° W), Valle del Cauca department, Colombia.<sup>14</sup>

SYNONYMS: *celicae* Anthony, 1922; *madescens* Osgood, 1913; *neblina* Gardner, 1990; *oroensis* Anthony, 1922; *perfuscus* Thomas, 1924; *purui* Miller, 1913; *sobrinus* Thomas, 1913; *ucayaliensis* Tate, 1931).

DISTRIBUTION: As currently recognized (see below), *Marmosops cauae* ranges from eastern Panama southward along the Andes to northern Peru, and it also occurs in the adjacent western Amazonian lowlands as far south as Madre de Dios (in southeastern Peru); a possibly isolated population occurs on Cerro de la Neblina in southern Venezuela. No published range map accurately illustrates the distribution of this species (or species complex), although Díaz-Nieto et al. (2016b) mapped the localities of numerous sequenced specimens.

REMARKS: As recognized herein, *Marmosops cauae* includes *M. neblina*—recognized as a valid species by Gardner and Creighton (2008b)—as well as most of the nominal taxa that those authors referred to *M. impavidus* (Tschudi, 1845), a nomen dubium as explained by Tate (1933: 25) and Díaz-Nieto et al. (2016b: 931). Phylogenetic analyses of cytochrome *b* sequence data reported by Díaz-Nieto et al. (2016b) revealed that *M. cauae* includes at least three robustly supported haplogroups (including the haplogroup they called *ucayaliensis*), but none is known to be morphologically diagnosable. The nominal taxon *purui* Miller, 1913, was listed as a synonym of *M. noctivagus* by Voss and Jansa (2009), but the craniodental traits of the holotype and paratype (including smooth inter-orbital margins and a complete anterior cingu-

lum on M3) suggest that it belongs to the *M. cauae* complex.

*Marmosops (Marmosops) creightoni*  
Voss et al., 2004

TYPE MATERIAL AND TYPE LOCALITY: CBF 6552, the holotype by original designation, consists of the fluid-preserved body and extracted skull of an adult male collected at the Saynani electrical generating station (ca. 16.12° S, 68.08° W; 2500 m) in the valley of the Río Zongo, La Paz department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: *Marmosops creightoni* is known to occur only in montane forests above 2000 m on the eastern slopes of the Andes in La Paz department, Bolivia.

REMARKS: Phylogenetic analyses of multilocus sequence datasets (Díaz-Nieto et al., 2016a, 2016b) suggest that *Marmosops creightoni* is the sister species of *M. noctivagus*.

*Marmosops (Marmosops) incanus* (Lund, 1840)

TYPE MATERIAL AND TYPE LOCALITY: No type material was designated in the original description, but four specimens in the Zoological Museum of the University of Copenhagen known to have been collected by Lund are assumed to be syntypes. Of these, PVLund L14 and PVLund L15 consist only of skulls, whereas PVLund 223 consists only of a skin. The most anatomically complete is PVLund 224 (skin and skull), but no purpose is served by selecting a lectotype at this time.

SYNONYMS: *bahiensis* Tate, 1931; *scapulatus* Burmeister, 1856.

DISTRIBUTION: *Marmosops incanus* is found primarily in the Atlantic Forest biome of Brazil, from the state of Sergipe (Calazans and Bocchi-glieri, 2020) southward to Paraná (Mustringi and Patton, 1997: fig. 6).

REMARKS: Mustringi and Patton's (1997) analysis of mtDNA sequence data remains the only phylogeographic study of this species, which includes several impressively divergent

<sup>14</sup> See Tate (1933: 178) for comments on this problematic locality.

haplogroups. The same authors also illustrated and discussed morphological characters that distinguish *Marmosops incanus* from its broadly sympatric congener, *M. paulensis*. Phylogenetic analyses of multilocus sequence datasets either recover *M. incanus* as the sister taxon to all other members of the nominotypical subgenus (Díaz-Nieto et al., 2016a, 2016b) or as the sister taxon of *M. paulensis* (see Amador and Giannini, 2016).

*Marmosops (Marmosops) noctivagus*  
(Tschudi, 1845)

TYPE MATERIAL AND TYPE LOCALITY: No type material was designated in Tschudi's original description, but three syntypes are said to be at Neuchâtel (MHNN 94.1008A, 94.1008B, 94.1008C; Serrano-Villavicencio et al., 2020), and a fourth is in Berlin (ZMB 3375). The Berlin specimen (consisting of the skin and skull of an adult female) is the one upon which Tate (1933) based his concept of the species, and so would be a logical choice as lectotype. Tschudi's subsequently published travelogue and correspondence—cited by Tate (1933: 154–155) and Serrano-Villavicencio et al. (2020)—suggest that his type series was collected near “Vitoc” (= Pueblo Nuevo: ca. 11.17° S, 75.27° W; ca. 500 m), Junín department, Peru.

SYNONYMS: *albiventris* Tate, 1931; *collega* Thomas, 1920; *dorothea* Thomas, 1911; *keaysi* J.A. Allen, 1900; *leucastrus* Thomas, 1927; *lugendus* Thomas, 1927; *neglectus* Osgood, 1915; *politus* Cabrera, 1913; *stollei* Miranda-Ribeiro, 1936; and *yungasensis* Tate, 1931.

DISTRIBUTION: *Marmosops noctivagus* occurs in the Andes (usually below 2000 m) from Ecuador to Bolivia, and in the Amazonian lowlands as far eastward as the left bank of the Tapajós (Gardner and Creighton, 2008b: map 30).

REMARKS: *Marmosops noctivagus* includes several deeply divergent mtDNA haplogroups whose taxonomic status remains to be determined (Díaz-Nieto et al., 2016b). The nominal taxon *purui* Miller, 1913, was listed among the

putative synonyms of *M. noctivagus* by Voss and Jansa (2009), but craniodental traits of the type and paratype better match the morphology of *M. cauae* (see above).

*Marmosops (Marmosops) ocellatus* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 26.1.5.25, the holotype by original designation, consists of the skin and skull of an old adult male collected at Buenavista (17.45° S, 63.67° W; ca. 475 m), Santa Cruz department, Bolivia.

SYNONYMS: None.

DISTRIBUTION: *Marmosops ocellatus* is known from eastern Bolivia (Chuquisaca, Santa Cruz) and southwestern Brazil (Mato Grosso, Mato Grosso del Sur) (Semedo et al., 2013: fig. 1).

REMARKS: This species was formerly treated as a synonym of *Marmosops dorothea* (now recognized as a synonym of *M. noctivagus*; see above), but it was revalidated and redescribed by Voss et al. (2004a); illustrations and tabulated morphometric data are in Semedo et al. (2013). Phylogenetic analyses of multilocus sequence data reported by Díaz-Nieto et al. (2016b) recovered *Marmosops ocellatus* as a member of a strongly supported clade with two unnamed taxa, one of which (“Gálvez”) was subsequently described as *M. soinii* by Voss et al. (2019).

*Marmosops (Marmosops) paulensis* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 26576, the holotype by original designation, consists of the skin and skull of a young adult male collected at “Therezopolis” (= Teresópolis: 22.43° S, 42.98° W; ca. 870 m), Rio de Janeiro state, Brazil.

SYNONYMS: None.

DISTRIBUTION: *Marmosops paulensis* is restricted to premontane and montane tropical and subtropical forests (above about 800 m) in southeastern Brazil (Rio de Janeiro, Minas Gerais, São Paulo, Paraná) (Gardner and Creighton (2008b).

REMARKS: An emended description of *Marmosops paulensis* together with illustrations, measurement data, and morphological comparisons with sympatric *M. incanus* were provided by Mustrangi and Patton (1997), who also documented moderately deep divergence between a coastal haplogroup in Rio de Janeiro and São Paulo and an inland haplogroup in Minas Gerais. Phylogenetic analyses of multilocus sequence datasets either recover *M. paulensis* as the sister taxon to a clade that contains all the Amazonian and Andean members of the nominotypical subgenus (Díaz-Nieto et al., 2016a, 2016b) or as the sister taxon of *M. incanus* (see Amador and Giannini, 2016).

*Marmosops (Marmosops) soinii* Voss et al., 2019

TYPE MATERIAL AND TYPE LOCALITY: MUSM 13284, the holotype by original designation, consists of the fluid-preserved body, extracted skull, and frozen tissues of an adult male collected at Nuevo San Juan (5.25° S, 73.17° W), a Matses Indian village on the right bank of the Río Gálvez, Loreto department, Peru.

SYNONYMS: None.

DISTRIBUTION: *Marmosops soinii* is currently known from only three localities in the Yavari-Ucayali interfluvium of Loreto department, Peru.

REMARKS: DNA sequences from this species were identified as *Marmosops* “Gálvez” in the phylogenetic analyses reported by Díaz-Nieto et al. (2016b). The closest relatives of *M. soinii* are *M. ocellatus* and a still undescribed form from eastern Peru and western Brazil (*M. “Juruá”* sensu Díaz et al., 2016b). A morphological description, summary statistics of external and craniodental measurements, and morphological comparisons with closely related congeners are in Voss et al. (2019).

Subgenus *Sciophanes* Díaz-Nieto et al., 2016

TYPE SPECIES: *Marmosa parvidens* Tate, 1931, by original designation.

SYNONYMS: None.

REMARKS: Subgeneric monophyly is consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., Díaz-Nieto et al., 2016a, 2016b; Amador and Giannini, 2016). *Sciophanes* was revised by Díaz-Nieto and Voss (2016), who recognized 12 species that they sorted into several informally recognized groups. One subsequently described species and another species recently recognized as valid (Ferreira et al., 2020) can be accommodated in the same species-group arrangement (table 2).

*Marmosops (Sciophanes) bishopi* (Pine, 1981)

TYPE MATERIAL AND TYPE LOCALITY: USNM 393535, the holotype by original designation, consists of the skin and skull of an adult female collected at the base camp of the Royal Geographic Society’s Xavantina-Cachimbo Expedition (12.85° S, 51.77° W; 533 m), 264 km N Xavantina, Mato Grosso state, Brazil.

SYNONYMS: None.

DISTRIBUTION: As currently understood (see Remarks), *Marmosops bishopi* is known to occur in premontane and lowland rainforest from the eastern foothills of the Andes (below about 1300 m) in Ecuador, Peru, and Bolivia eastward across much of lowland Amazonia. North of the Amazon, the range of this species seems to extend at least as far eastward as the Rio Branco (Abreu et al., 2017: fig. 5); south of the Amazon, the easternmost known occurrence is the type locality in central Brazil (Díaz-Nieto and Voss, 2016: fig. 12).

REMARKS: For illustrations, an emended description, measurements, and morphological comparisons with closely related species, see Díaz-Nieto and Voss (2016), who associated *Marmosops bishopi* with other species of the Bishopi Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b). The latter authors recognized six morphologically cryptic, allopatric haplogroups within *Marmosops bishopi*, but whether these haplogroups are distinct lin-

eages that merit taxonomic recognition is currently unknown.

*Marmosops (Sciophanes) carri*  
(Allen and Chapman, 1897)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 7314/5922, the holotype by original designation, consists of the skin and skull of an adult male collected at Caparo (10.45° N, 61.33° W; ca. 80 m), Trinidad.

SYNONYMS: None.

DISTRIBUTION: *Marmosops carri* is known from lowland and premontane rainforest on Trinidad and Tobago, and from premontane and montane forest on the adjacent mainland of Venezuela. On the mainland, the species occurs along the Caribbean coastal cordilleras from Monagas westward to Carabobo, but it is also known from the interior Cordillera de Trujillo; recorded elevations range from near sea level to >2000 m (Díaz-Nieto and Voss, 2016: fig. 17).

REMARKS: For illustrations, an emended description, measurement data, and morphological comparisons with closely related species, see Díaz-Nieto and Voss (2016), who assigned *Marmosops carri* to the Fuscatus Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b). This species was formerly regarded as an insular subspecies of *M. fuscatus* (e.g., by Gardner and Creighton, 2008b), but analyses of mtDNA sequence data and morphometric comparisons suggest otherwise.

*Marmosops (Sciophanes) chucha*  
Díaz-Nieto and Voss, 2016

TYPE MATERIAL AND TYPE LOCALITY: CTUA 434, the holotype by original designation, consists of the skin, skull, fluid-preserved carcass, and frozen tissues of an adult female collected at Hacienda Vegas de La Clara (6.58° N, 75.20° W; 1120 m), Antioquia department, Colombia.

SYNONYMS: None.

TABLE 2

Species-group Assignments in the  
Subgenus *Sciophanes* of *Marmosops*

|                      |
|----------------------|
| Bishopi Group        |
| <i>M. bishopi</i>    |
| <i>M. chucha</i>     |
| <i>M. juninensis</i> |
| <i>M. magdalenae</i> |
| <i>M. ojestii</i>    |
| Fuscatus Group       |
| <i>M. carri</i>      |
| <i>M. fuscatus</i>   |
| <i>M. handleyi</i>   |
| <i>M. invictus</i>   |
| Parvidens Group      |
| <i>M. marina</i>     |
| <i>M. pakaraimae</i> |
| <i>M. parvidens</i>  |
| <i>M. pinheiroi</i>  |
| <i>M. woodalli</i>   |

DISTRIBUTION: *Marmosops chucha* occurs in the northern part of the Cordillera Occidental and the northern part of the Cordillera Central in Antioquia and Caldas departments, Colombia (Díaz-Nieto and Voss, 2016: fig. 28).

REMARKS: For illustrations, morphological description, measurement data, and morphological comparisons with closely related congeners, see Díaz-Nieto and Voss (2016), who assigned this species to the Bishopi Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) fuscatus*  
(Thomas, 1896)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 96.11.1.6, the holotype by original designation, consists of the skin and skull of an old adult female collected at 1630 m elevation along the Río “Abbaregas” (= Albarregas) near the city of

Mérida (8.60° N, 71.13° W), Mérida state, Venezuela.

SYNONYMS: *cracens* Handley and Gordon, 1979.

DISTRIBUTION: *Marmosops fuscatus* is known from just four localities from sea level to 1600 m in northwestern Venezuela, including two in the Cordillera de Mérida, one in the Cordillera de San Luís (in western Falcón), and another in the coastal lowlands of eastern Falcón (Díaz-Nieto and Voss, 2016: fig. 17). Most of the localities previously mapped for this species by Gardner and Creighton (2008b) were based on specimens that Díaz-Nieto and Voss (2016) reidentified as *M. carri*.

REMARKS: For illustrations, an emended description, measurement data, and morphological comparisons with closely related congeners, see Díaz-Nieto and Voss (2016), who assigned *Marmosops fuscatus* to the eponymous species group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b). The holotype of the nominal taxon *perfusca* Thomas, 1924, which Tate (1933) treated as a synonym of *M. fuscatus* and which Gardner and Creighton (2008b) treated as a valid subspecies, does not exhibit the diagnostic traits of the subgenus *Sciophanes*. Instead, Díaz-Nieto and Voss (2016) treated *perfusca* as a synonym of *M. caucae* (a species in the nominotypical subgenus), as it is also listed in this report (see above).

*Marmosops (Sciophanes) handleyi* (Pine, 1981)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 69838, the holotype by original designation, consists of the skin, skull, and postcranial skeleton of an adult female collected 9 km S Valdivia (7.10° N, 75.43° W; 1400 m), Antioquia department, Colombia.

SYNONYMS: None.

DISTRIBUTION: *Marmosops handleyi* is currently known only from the northern terminus of the Cordillera Central (central Andes) of Colombia at elevations from about 1400 to 1950 m (Díaz-Nieto and Voss, 2016: fig. 20).

REMARKS: For illustrations, an emended description, and measurement data, see Díaz-Nieto et al. (2011). Díaz-Nieto and Voss (2016) provided morphological comparisons with closely related congeners and assigned *Marmosops handleyi* to the Fuscatus Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) invictus*  
(Goldman, 1912)

TYPE MATERIAL AND TYPE LOCALITY: USNM 178708, the holotype by original designation, consists of the skin and skull of an adult male collected at “Cana” (= Santa Cruz de Cana: 7.78° N, 77.70° W; 610 m), Darién province, Panama.

SYNONYMS: None.

DISTRIBUTION: Specimens of *Marmosops invictus* examined by Díaz-Nieto and Voss (2016: fig. 20) were all from eastern and central Panama, where this species has been recorded from about 600 to 1500 m. Although Handley (1966) and Mangan and Adler (2000) reported *M. invictus* from western Panama (Bocas del Toro and Chiriquí), no voucher material from western Panama is known to exist.

REMARKS: For illustrations, an emended description, measurement data, morphological comparisons with closely related congeners, and comments about previously misidentified specimens, see Díaz-Nieto and Voss (2016), who assigned *Marmosops invictus* to the Fuscatus Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) juninensis* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: AMNH 63864, the holotype by original designation, consists of the skin and skull of a young adult female collected at Utcuyacu (ca. 11.20° S, 75.47° W; 1463 m), Junín department, Peru.

SYNONYMS: None.



**DISTRIBUTION:** *Marmosops juninensis* occurs in premontane and montane forests (between about 1300 and 2400 m) on the eastern slopes of the Andes in central Peru (Junín and Pasco; Díaz-Nieto and Voss, 2016).

**REMARKS:** For illustrations, an emended description, measurement data, and morphological comparisons with closely related congeners, see Díaz-Nieto and Voss (2016), who assigned *Marmosops juninensis* to the Bishopi Group based on phylogenetic analyses of mtDNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) magdalenae*  
Díaz-Nieto and Voss, 2016

**TYPE MATERIAL AND TYPE LOCALITY:** ICN 19924, the holotype by original designation, consists of the skin and skull of an adult female collected at the Reserva Biológica Cachalú (6.12° N, 73.13° W; 1940 m), Santander department, Colombia.

**SYNONYMS:** None.

**DISTRIBUTION:** *Marmosops magdalenae* is known from lowland and montane forests (from ca. 100 to 1900 m) in the valley of the Río Magdalena and in the Cordillera Oriental (eastern Andes) of Colombia (Díaz-Nieto and Voss, 2016: fig. 28).

**REMARKS:** For illustrations, description, measurement data, and morphological comparisons with closely related congeners, see Díaz-Nieto and Voss (2016), who assigned *Marmosops magdalenae* to the Bishopi Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) marina*  
Ferreira et al., 2020

**TYPE MATERIAL AND TYPE LOCALITY:** UFMT 4078, the holotype by original designation, consists of the skin and skull of an adult male collected at Fazenda São José (9.63° S, 56.08° W)

on the right bank of the Rio Teles Pires, Mato Grosso state, Brazil.

**SYNONYMS:** None.

**DISTRIBUTION:** *Marmosops marina* occurs south of the Amazon between the Rio Xingu and the Rio Madeira in the Brazilian states of Pará, Mato Grosso, and Rondônia (Ferreira et al., 2020: fig. 5).

**REMARKS:** Guimarães et al. (2021) applied species-delimitation algorithms to DNA sequence data from *Marmosops marina* collected on both banks of the Rio Tapajós and concluded that the population between the Tapajós and Madeira rivers is genetically distinct from that in the Xingu-Tapajós interfluvium (which includes the type locality); however, it is not clear that these populations are phenotypically distinguishable, and there seems to be no point in restricting the application of the name as they suggest. Morphological traits described by Ferreira et al. (2020) clearly place this species in the Parvidens Group of Díaz-Nieto and Voss (2016). Within the Parvidens Group, *M. marina* appears to be the sister species of a clade that includes *M. pinheiroi* and *M. woodalli* based on phylogenetic analyses of DNA sequence data reported by Guimarães et al. (2021).

*Marmosops (Sciophanes) ojasii*  
García et al., 2014

**TYPE MATERIAL AND TYPE LOCALITY:** EBRG 27474, the holotype by original designation, consists of the fluid-preserved body and extracted skull of an adult male collected on Pico Guacamaya (10.35° N, 67.67° W; 1850 m), Parque Nacional Henri Pittier, Aragua state, Venezuela.

**SYNONYMS:** None.

**DISTRIBUTION:** *Marmosops ojasii* occurs in the Cordillera de la Costa of northern Venezuela and in the Cordillera de Mérida in western Venezuela (García et al., 2014: fig. 1).

**REMARKS:** For illustrations, descriptions, measurement data, and morphological comparisons with closely related congeners, see García et al. (2014) and Díaz-Nieto and Voss (2016). The latter authors assigned *Marmosops ojasii* to the

Bishopi Group based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b). Those analyses additionally suggested that, within the Bishopi Group, *M. ojastii* is the sister species of a clade that includes *M. chucha* and *M. magdalenae*.

*Marmosops (Sciophanes) pakaraimae*  
Voss et al., 2013

TYPE MATERIAL AND TYPE LOCALITY: ROM 115129, the holotype by original designation, consists of the skin, skull, postcranial skeleton, and preserved tissues of an adult male collected at “Second Camp” (5.28° N, 60.75° W, 800 m), an expeditionary site on Mount Roraima, Cuyuni-Mazaruni Region, Guyana.

SYNONYMS: None.

DISTRIBUTION: *Marmosops pakaraimae* is definitely known from just five localities in the contiguous highlands of western Guyana and eastern Venezuela from 800 to about 1500 m above sea level (Voss et al., 2013: fig. 1). Silva et al.’s (2017) report of this species from the Rio Japurá—in the Amazonian lowlands of western Brazil, over 1100 km from the closest verified collection locality in eastern Venezuela—is almost certainly in error; the specimen in question (SISJAP-M-705, at INPA) should be reexamined to determine its correct identification.

REMARKS: For illustrations, description, measurement data, and morphological comparisons with closely related congeners, see Voss et al. (2013). This species was assigned to the Parvidens Group of the subgenus *Sciophanes* by Díaz-Nieto and Voss (2016) based on analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b). Within the Parvidens Group, *M. pakaraimae* is the sister species of *M. parvidens*.

*Marmosops (Sciophanes) parvidens* (Tate, 1931)

TYPE MATERIAL AND TYPE LOCALITY: FMNH 18545, the holotype by original designation, consists of the skin and skull of an adult female collected at Hyde Park (6.50° N, 58.27° W; near sea

level), on the Demerara River about 35 km S Georgetown, East Demerara–West Coast Berbice region, Guyana.

SYNONYMS: None.

DISTRIBUTION: *Marmosops parvidens* occurs throughout northeastern Amazonia (north of the lower Amazon and east of the Rio Negro-Orinoco), including Guyana, Surinam, French Guiana, and Brazil. In Brazil, this species is known from Amapá, northern Pará, and northeastern Amazonas. Díaz-Nieto and Voss’s (2016: fig. 10) map, unfortunately still the best available for this species, does not include the localities in Amapá reported by Silva et al. (2013) nor those from northern Pará reported by Rossi et al. (2016), and it includes an erroneous record from south of the Amazon (see Remarks).

REMARKS: See Díaz-Nieto and Voss (2016) for illustrations, an emended description, measurement data, and morphological comparisons with closely related species. Additional illustrations and comparisons of *Marmosops parvidens* are in Ferreira et al. (2020), but the small accessory cuspid between the metaconid and entocoid that they attribute to this species is not present in any material that I have seen. Ferreira et al. (2020) questioned the identification of a specimen that Voss et al. (2001) and Díaz-Nieto and Voss (2016) identified as *M. parvidens* from Ilha do Taiuna on the lower Rio Tocantins (south of the Amazon). I have since reexamined this specimen (AMNH 97333) and determined that it cannot be confidently distinguished from *M. woodalli*, which is the species expected to occur there based on Ferreira et al.’s (2020: fig. 5) range map.

*Marmosops (Sciophanes) pinheiroi* (Pine, 1981)

TYPE MATERIAL AND TYPE LOCALITY: USNM 461459, the holotype by original designation, consists of the skin and skull of an adult female collected at the Serra do Navio (0.98° N, 52.05° W) on the Rio Amapari, Amapá state, Brazil. According to Ferreira et al. (2020), Serra do Navio is on the left bank of the Rio Amapari.

SYNONYMS: None (see Remarks).

DISTRIBUTION: As currently understood (see Remarks), *Marmosops pinheiroi* is restricted to the Guiana Region (north of the lower Amazon and east of the Rio Negro-Orinoco, where it is known to occur in eastern Venezuela, Guyana, Surinam, French Guiana, and northern Brazil (Amapá, Roraima, and northern Pará). No published range map shows all the localities from which this species is now known, and some include erroneous records. Díaz-Nieto and Voss's (2016: fig. 10) map, for example lacks the localities in Amapá, Roraima, and northern Pará reported by Silva et al. (2013), Rossi et al. (2016), and Ferreira et al. (2020), and it includes several localities south of the Amazon that were based on specimens of *M. woodalli* (but see below). By contrast, Ferreira et al.'s (2020: fig. 5) map does not include any non-Brazilian localities.

REMARKS: Ferreira et al. (2020) provided an emended description of *Marmosops pinheiroi* as well as illustrations, measurement data, and morphological comparisons with closely related taxa (including *M. woodalli*, previously treated as a junior synonym; see below). *Marmosops pinheiroi* was assigned to the Parvidens Group by Díaz-Nieto and Voss (2016) based on phylogenetic analyses of DNA sequence data previously reported by Díaz-Nieto et al. (2016b).

*Marmosops (Sciophanes) woodalli* (Pine, 1981)

TYPE MATERIAL AND TYPE LOCALITY: USNM 393532, the holotype by original designation, consists of the skin and skull of an adult female collected at the Nova Área Experimental Utinga near Belém (1.45° S, 48.48° W), Pará state, Brazil.

SYNONYMS: None.

DISTRIBUTION: As currently recognized (see Remarks), *Marmosops woodalli* occurs in southeastern Amazonia from the right bank of the Rio Xingu eastward along the south bank of the Amazon and the Atlantic coast to Maranhão; it also ranges southward along the Tocantins and

Araguaia rivers into northern Tocantins (Ferreira et al., 2020: fig. 5).

REMARKS: *Marmosops woodalli* was treated as a synonym of *M. pinheiroi* by Díaz-Nieto and Voss (2016), but it has recently been treated as a distinct species by Brazilian authors. Although *M. pinheiroi* and *M. woodalli* are listed here as valid species in deference to my colleagues, these taxa exhibit broad morphometric overlap (Ferreira et al., 2020: tables 4, 5; fig. 1) and appear to lack unambiguously diagnostic qualitative traits (Ferreira et al., 2020: table 6). Additionally, inconsistent results have been obtained from relevant species-delimitation analyses (Guimarães et al., 2021). In effect, these allopatric forms seem dubiously distinct and merit critical evaluation when more material becomes available, especially from geographically intermediate localities such as Marajó Island.

#### Genus *Thylamys* Gray, 1843

TYPE SPECIES: *Didelphis elegans* Waterhouse, 1839, by monotypy.

SYNONYMS: None.

REMARKS: Generic monophyly has been consistently and strongly supported by phylogenetic analyses of multilocus sequence datasets (e.g., Díaz-Nieto et al., 2016a; Amador and Giannini, 2016). See Voss and Jansa (2009) for an emended generic description. Two subgenera are currently recognized (Giarla et al., 2010).

#### Subgenus *Thylamys* Gray, 1843

TYPE SPECIES: As for the genus.

SYNONYMS: As for the genus.

REMARKS: Monophyly of the nominotypical subgenus has been consistently and robustly supported by all relevant phylogenetic analyses of multilocus datasets (e.g., Giarla et al., 2010; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016). Seven species are recognized as valid in this report, of which five have been assigned to species groups based on the aforementioned phylogenetic analyses (table 3).

TABLE 3

**Species-group Assignments in the Nominotypical Subgenus of *Thylamys***

|                      |
|----------------------|
| Elegans Group        |
| <i>T. elegans</i>    |
| <i>T. pallidior</i>  |
| <i>T. tatei</i>      |
| Venustus Group       |
| <i>T. sponsorius</i> |
| <i>T. venustus</i>   |
| Unaffiliated species |
| <i>T. macrurus</i>   |
| <i>T. pusillus</i>   |

*Thylamys (Thylamys) elegans*  
(Waterhouse, 1839)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 53.8.29.18, the lectotype (designated by Thomas, 1888a), consists of the skin and skull of an adult male collected at Valparaíso (33.03° S, 71.63° W), Valparaíso region, Chile.

SYNONYMS: *coquimbensis* Tate, 1931; *soricinus* Philippi, 1894 (but see Remarks).

DISTRIBUTION: *Thylamys elegans* is endemic to Chile, where recent sequencing studies suggest that it ranges from about 21° S (in Tarapacá) to almost 36° S (in Maule), and from near sea level to about 1700 m (Palma et al., 2014; Boric-Bargetto et al., 2016). However, there are historical records of this species from as far south as Angol (37.80° S, 72.72° W) in the Araucanía region based on specimens seen by Tate (1933) and Greer (1965).

REMARKS: See Giarla et al. (2010) for an emended description and morphological comparisons of *Thylamys elegans* with congeneric taxa. Despite much taxonomic attention, this species remains problematic in several respects, some of which were discussed by Boric-Bargetto et al. (2016) and Giarla and Voss (2020b). A recent, geographically comprehensive analysis of mtDNA sequence data (Boric-Bargetto et al., 2021) suggests that the southernmost populations currently recognized as *T. elegans* might be

a distinct species, for which *T. soricinus* could be the appropriate binomen if the diagnostic pelage traits mentioned by Pine (1979) and Giarla et al. (2010) were confirmed by examination of sequenced specimens. In that event, and if Philippi's holotype—last seen by Osgood (1943)—cannot be found, then a neotype should be designated to fix the application of this name.

Phylogenetic analyses of multilocus sequence datasets have consistently recovered *Thylamys elegans* in a clade that also includes *T. pallidior* and *T. tatei* (see Giarla et al., 2010; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016).

*Thylamys (Thylamys) macrurus* (Olfers, 1818)

TYPE MATERIAL AND TYPE LOCALITY: UMMZ 125243, the neotype (designated by Voss et al., 2009a), consists of the skin and skull of an adult female collected 28 km SW Pedro Juan Caballero (22.63° S, 55.95° W), Amambay department, Paraguay.

SYNONYMS: *griseus* Desmarest, 1827.

DISTRIBUTION: *Thylamys macrurus* is only known from eastern Paraguay and from the adjacent Brazilian state of Mato Grosso do Sul (Cáceres et al., 2007: fig. 1; Voss et al., 2009a: fig. 3).

REMARKS: Morphological descriptions of *Thylamys macrurus*, together with measurement data and taxonomic comparisons are in Carmignotto and Monfort (2006), Voss et al. (2009a), and Giarla et al. (2010). Relevant nomenclatural issues were discussed by Voss et al. (2009a). Phylogenetic analyses of multilocus sequence datasets (e.g., Giarla et al., 2010; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016) have yet to convincingly resolve the relationships of this species within the nominotypical subgenus.

*Thylamys (Thylamys) pallidior* (Thomas, 1902)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 2.2.2.116, the holotype by original designation, consists of the skin and skull of an adult male collected at Challapata (18.90° S, 66.78° W; 3800 m), Oruro department, Bolivia.

SYNONYMS: *fenestrae* Marelli, 1932.

DISTRIBUTION: *Thylamys pallidior* occurs along the arid Pacific coast of southern Peru and northern Chile (from ca. 16° S to 20° S); in the Altiplano of Peru, Bolivia, and Chile (to ca. 3800 m); and in arid landscapes on the eastern side of the Andes as far south as Chubut province, Argentina (ca. 46° S). No published map illustrates the entire geographic distribution of this widespread species, but Giarla et al. (2010: fig. 5) and Palma et al. (2014: fig. 1) mapped the localities of their sequenced specimens, and Formoso et al. (2011: fig. 1) mapped collection localities in Patagonia.

REMARKS: See Giarla et al. (2010) for an emended morphological description, measurements, and comparisons with congeneric taxa. The nominal taxon *coquimbensis* Tate, 1931, which Giarla et al. (2010) synonymized with *Thylamys pallidior* based on morphological similarity, was returned to the synonymy of *T. elegans* by Giarla and Voss (2020b) based on phylogenetic analysis of a cytochrome *b* sequence obtained from the holotype.

*Thylamys (Thylamys) pusillus* (Desmarest, 1804)

TYPE MATERIAL AND TYPE LOCALITY: MVZ 144311, the neotype (designated by Voss et al., 2009a), consists of the skin and skull of an adult male collected on the Trans-Chaco Highway (Ruta Nacional 9) 460 km NW Villa Hayes (ca. 28.37° S, 60.20° W), Boquerón department, Paraguay.

SYNONYMS: *bruchi* Thomas, 1921; *citellus* Thomas, 1912; *nanus* Olfers, 1818; *pulchellus* Cabrera, 1934; *verax* Thomas, 1921.

DISTRIBUTION: As recognized herein (see Remarks), *Thylamys pusillus* occurs in southeastern Bolivia, western Paraguay, and northern Argentina, including the Dry Chaco, Humid Chaco, Mesopotamian Savanna, and Humid Pampas ecoregions (Teta et al., 2009: fig. 1).

REMARKS: Teta et al. (2009) recognized *Thylamys citellus* and *T. pulchellus* as valid species distinct from *T. pusillus*, but Giarla et al. (2010: 41–43) were unable to distinguish these allopatric taxa

morphologically and, therefore, treated them as synonyms. South American authors (e.g., Palma et al., 2014) have subsequently tended to follow Teta et al. (2009), so the binomina *T. citellus* and *T. pulchellus* remain in current use. Because geographic variation in morphology and isolation by distance remain plausible explanations for the reported phenotypic and genetic differences among these nominal taxa, it still seems an appropriately conservative option to treat them as conspecific.

*Thylamys (Thylamys) sponsorius* (Thomas, 1921)

TYPE MATERIAL AND TYPE LOCALITY: BMNH 21.1.1.85, the holotype by original designation, consists of the skin and skull of an adult male collected at Sunchal (23.57° S, 65.00° W; 1200 m) in the Sierra de Santa Barbara, Jujuy province, Argentina.

SYNONYMS: *janetta* Thomas, 1926.

DISTRIBUTION: *Thylamys sponsorius* occurs along the foothills and eastern slopes of the Andes at recorded elevations from about 500 m to over 3700 m in southern Bolivia (Tarija) and northwestern Argentina (Jujuy, Salta, Tucumán, Catamarca) (Giarla et al., 2010: fig. 9).

REMARKS: For an emended morphological description, measurement data, and comparisons with congeneric taxa, see Giarla et al. (2010). Phylogenetic analyses of multilocus sequence datasets (Giarla et al., 2010; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016) consistently recover *Thylamys sponsorius* and *T. venustus* as sister taxa. Morphological analyses of sequenced specimens suggest that these closely related species are primarily distinguished by size, although no single measurement is diagnostic (Giarla et al., 2010).

*Thylamys (Thylamys) tatei* (Handley, 1957)

TYPE MATERIAL AND TYPE LOCALITY: USNM 302915, the holotype by original designation, consists of the skin and skull of an adult male collected at Chasquitambo (10.32° S, 77.62° W; 710 m), Ancash department, Peru.

SYNONYMS: None.



**DISTRIBUTION:** *Thylamys tatei* is only known from western Peru in the departments of Ancash and Lima (Creighton and Gardner, 2008c: map 49).

**REMARKS:** See Giarla et al. (2010) for an emended description, measurement data, and comparisons with closely related taxa. Phylogenetic analyses of multilocus sequence datasets (e.g., Giarla et al., 2010) have recovered *Thylamys tatei* as a member of the robustly supported Elegans Group, within which it appears to be most closely related to one or more undescribed taxa from coastal Peru.

*Thylamys (Thylamys) venustus* (Thomas, 1902)

**TYPE MATERIAL AND TYPE LOCALITY:** BMNH 2.1.1.120, the holotype by original designation, consists of the skin and skull of a very old adult female collected at "Paratani" (= Parotani: 17.57° S, 66.35° W; 2800 m), Cochabamba department, Bolivia.

**SYNONYMS:** *cinderella* Thomas, 1902.

**DISTRIBUTION:** *Thylamys venustus* occurs from about 350 to 4000 m above sea level along the foothills and eastern slopes of the Andes from northern Bolivia (La Paz) to northern Argentina (Jujuy and Tucumán) (Giarla et al., 2010: fig. 10).

**REMARKS:** Giarla et al. (2010) redescribed this species, summarized morphometric data, and provided comparisons with congeneric taxa. *Thylamys venustus* includes three robustly supported haplogroups, but none is morphologically diagnosable from the others. Phylogenetic analyses of multilocus sequence datasets (Giarla et al., 2010; Díaz-Nieto et al., 2016a; Amador and Giannini, 2016) consistently recover *T. venustus* and *T. sponsorius* as sister species.

Subgenus *Xerodelphys* Giarla et al., 2010

**TYPE SPECIES:** *Thylamys karimii* (Petter, 1968), by original designation.

**SYNONYMS:** None.

**REMARKS:** Although the monophyly of *Xerodelphys* has been consistently supported by phylogenetic analyses of multilocus sequence datasets (e.g., Giarla et al., 2010; Díaz et al., 2016a; Amador and Giannini, 2016), nodal support for this clade is seldom strong. However, compelling evidence for subgeneric monophyly is provided by the unusual caudal and manual morphologies illustrated by Carmignotto and Monfort (2006). Two species are currently recognized as valid.

*Thylamys (Xerodelphys) karimii* (Petter, 1968)

**TYPE MATERIAL AND TYPE LOCALITY:** MNHN 1968-148, the holotype by original designation, consists of a skin and skull of an adult male collected at Exu (7.52° S, 39.72° W; ca. 500 m), Pernambuco state, Brazil.

**SYNONYMS:** None.

**DISTRIBUTION:** *Thylamys karimii* is known from the Cerrado and Caatinga biomes of central and northeastern Brazil (Carmignotto and Monfort, 2006: fig. 7).

**REMARKS:** An emended description of *Thylamys karimii* accompanied by illustrations, morphometric data, and taxonomic comparisons were provided by Carmignotto and Monfort (2006). Giarla et al. (2010) also described this species, analyzed its phylogenetic relationships, and commented on misidentifications in the ecological literature.

*Thylamys (Xerodelphys) velutinus*  
(Wagner, 1842)

**TYPE MATERIAL AND TYPE LOCALITY:** NMW B-2621, the holotype by monotypy, consists of the skin and skull of an adult male collected at "Ypanema" (= Ipanema: 23.43° S, 47.60° W; 950 m), São Paulo state, Brazil.

**SYNONYMS:** *pimelurus* Reinhardt, 1851.

**DISTRIBUTION:** *Thylamys velutinus* is only known from a few localities in the Cerrado

biome of central and southeastern Brazil (Carmignotto and Monfort, 2006: fig. 7).

REMARKS: An emended description of this species accompanied by illustrations, morphometric data, and taxonomic comparisons was provided by Carmignotto and Monfort (2006). Giarla et al. (2010) also described this species and analyzed its phylogenetic relationships.

## DISCUSSION

Didelphid classification has undergone numerous changes over the last several decades, as evidenced by the numbers of taxa recognized at different taxonomic ranks from 1993 to the present (table 4). The proliferation of higher taxa—genera, tribes, and subfamilies—prompted by phylogenetic research has been reviewed and discussed elsewhere (Voss and Jansa, 2009), but the growth in numbers of species is a striking trend that merits explanation. As a matter of taxonomic process, this increase is the result of (1) the revalidation of species previously regarded as synonyms or subspecies, and (2) the discovery of new species. Although both categories of revisionary research have been productive, the first has had the greater impact on species numbers to date. A total of 47 taxa treated as synonyms or subspecies by Gardner (1993) are now recognized as valid species (appendix 2), whereas only 23 new species have been described over the same interval (appendix 3). As opposed to such increments, eight species recognized as valid by Gardner (1993) are herein treated as junior synonyms, nomina dubia, or candidates for nomenclatural suppression (appendix 4).

The net result of this taxonomic activity, an almost twofold increase in opossum species since Gardner's (1993) synopsis, might seem surprising—even a matter of concern—so it is worth considering whether this is just “taxonomic inflation” (sensu Isaac et al., 2004): an artifact of adopting some radically new species concept. In fact, species concepts are seldom discussed by opossum taxonomists, but there is a broad consensus that evidence for species delimitation

includes reciprocal monophyly, substantial DNA sequence divergence, morphological diagnosability, ecological differences, and sympatry. In the aggregate, these criteria are consistent with the notion that species are independently evolving lineages, hardly a radical concept (de Queiroz, 1998, 2007). There is, however, an equally widespread consensus that the polytypic “species” of mid- to late-20th century taxonomy are hypotheses that ought to be tested, and revisionary experience has repeatedly shown that they often include multiple lineages that would be recognized as valid species by almost any evidence-based criterion.

A relevant example concerns several species of *Marmosa* widely regarded as valid by early-20th century authors (e.g., Tate, 1933), but which were treated as synonyms or subspecies of *Marmosa mitis* by Hershkovitz (1951). Although Hershkovitz provided no supporting analysis of character data, his concept of *M. mitis*—doubtless motivated by contemporaneous enthusiasm for polytypic species—was accepted by Cabrera (1958), Hall and Kelson (1959), and most subsequent mammalogists, and it persisted in the taxonomic literature until Rossi et al. (2010) and Gutiérrez et al. (2010) showed that *M. isthmica*, *M. robinsoni*, and *M. simonsi* are morphologically distinct, genetically divergent, and maintain their diagnostic differences in sympatry. Erstwhile polytypic concepts of *Gracilinanus agilis*, *Philander opossum*, *Marmosops parvidens*, *Thylamys elegans*, and many others inherited from late-20th century taxonomists have similarly been shown to be composite.

Of greater importance than the influence of new species concepts for opossum taxonomy has been the widespread availability of new kinds of data and new analytical methods. Mitochondrial DNA sequences and model-based phylogenetic analyses, in particular, have played a key role in recent revisionary research. However, although mtDNA is often a leading indicator of population divergence (Zink and Barrowclough, 2008), taxonomic inference based on a single maternally inherited locus can be misleading. Among other

TABLE 4  
Taxa of Recent Opossums in Four Synoptic Publications

|                | Subfamilies | Tribes | Genera | Species |
|----------------|-------------|--------|--------|---------|
| Gardner (1993) | 2           | 0      | 15     | 63      |
| Gardner (2005) | 2           | 0      | 17     | 87      |
| Astúa (2015)   | 4           | 4      | 18     | 103     |
| This report    | 4           | 4      | 18     | 125     |

relevant problems, mtDNA sequences can exhibit abrupt phylogeographic breaks in the presence of uninterrupted nuclear gene flow (Irwin, 2002), and adaptive introgression of mtDNA from one species to another is a well-documented phenomenon (Ballard and Whitlock, 2004; Toews and Brelsford, 2012). Additionally, simulation studies suggest that species delimitation based on mtDNA distances and reciprocal monophyly can result in unacceptably high rates of false positives and false negatives when dispersal is sex biased, as it is believed to be in most mammals (Dávalos and Russell, 2014).

These potential problems with mtDNA-based species delimitation are not necessarily mitigated by coalescent modelling which, among other limitations, cannot distinguish gene trees from species trees in single-locus applications (Pons et al., 2006). Although multilocus data offer substantial advantages for sequence-based species delimitation (Fujita et al., 2012), multilocus data can be difficult to obtain from the biochemically degraded materials (old museum specimens) commonly available to taxonomic researchers. Additionally, collecting multilocus data is prohibitively expensive for many research projects, so it seems likely that mtDNA will continue to be important for opossum revisionary taxonomy for years to come. Nevertheless, the putative species resulting from coalescent analysis of mitochondrial sequence data must always be interpreted with caution for the reasons explained above, and because coalescent-based species delimitation—whether based on single-locus or multilocus datasets—is sensitive to

inadequate geographic sampling and isolation by distance (Mason et al., 2020). Therefore, the results of genetic analyses are best interpreted in combination with other kinds of data (Pons et al., 2006; Carstens et al., 2013; Dávalos and Russell, 2014; Sukumaran and Knowles, 2017). Of the many kinds of data that might be relevant for this purpose, however, only morphology and geography are commonly available for opossum revisionary studies.

In the happy circumstance that putative species identified by analyses of genetic data are morphologically diagnosable and occur sympatrically, species recognition is straightforward. Often, however, putative species are allopatric, and many allopatric putative species seem to be morphologically indistinguishable. In the absence of other evidence, such cryptic entities might be nothing more than spatially segregated populations of a single species (Sukumaran and Knowles, 2017), but whatever they are, they can be numerous (e.g., in *Cryptonanus*; Fegies et al., 2021). Although such discoveries reveal previously unsuspected dimensions of opossum diversity, they raise vexing questions about which entities should be formally recognized (with Latin binomina) and which should be indicated informally (e.g., with alphabetical suffixes). As suggested by Cartstens et al. (2013), nomenclatural conservatism seems the more defensible option when taxonomic distinctions are ambiguous.

Most didelphid genera have now received at least some scrutiny with genetic methods, so it is likely that we are approaching an inflection point beyond which the discovery of new species will

outpace the revalidation of improperly synonymized taxa, and the rate of species increase will begin to decline. There can be, after all, only a finite number of opossum species and a dwindling number of places to look for new ones. Most of the new species described in the last few decades have been found in remote parts of tropical South America (appendix 3), where it would be reasonable to expect even more discoveries in the years to come. Although biomes that remain poorly known mammalogically—such as cloud forests at middle elevations on the eastern slopes of the Andes—seem the likeliest places to expect new species, novelties doubtless remain to be discovered even in relatively well-inventoried regions (Voss et al., 2021).

The proper goal of taxonomy is not, however, simply to describe new taxa, nor to revise existing ones, but to achieve increasingly accurate and stable classifications that can serve as frameworks for future research on a wide variety of topics. To the extent that classifications fulfill this objective, the work of taxonomists will be appreciated and respected, but unnecessary nomenclatural innovations—replacing familiar names with long-forgotten synonyms, changes in rank without adequate justification, or naming every novel mtDNA haplogroup—will erode user confidence. Opossum taxonomists should be mindful of their responsibility to the wider community of biodiversity researchers as they expand and refine the current classification.

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## APPENDIX 1

### ON THE PHYLOGENETIC CLASSIFICATION OF SPARASSOCYNIDS

As traditionally recognized in the paleontological literature, the family Sparassocynidae includes several small fossil marsupials that are believed to have been highly carnivorous and adapted to open habitats at temperate latitudes in South American (Reig and Simpson, 1972; Forasiepi et al., 2009). Recently published phylogenetic analyses of two sparassocynid species—*Hesperocynus dolgopolae* and *Sparassocynus derivatus*—have challenged traditional notions of marsupial relationships by suggesting that these taxa are, in fact, didelphids, and that the lineage represented by *H. dolgopolae* and *S. derivatus* (hereafter *Hesperocynus*+*Sparassocynus*) may be the sister taxon to *Monodelphis*. The authors (Beck and Taglioretti, 2020) propose to rank “sparassocynids” as a didelphid tribe (Sparassocynini), to recognize its putative sister taxon as another tribe (Monodelphini), and to restrict the contents of Marmosini to *Marmosa* (with or without *Tlacuatzin*; see Remarks for Marmosini, above).

Although it is certainly plausible that sparassocynids are closely related to didelphids (as most previous researchers have assumed), it is noteworthy that *Hesperocynus dolgopolae* lacks a key didelphid synapomorphy: precocious fusion of the interparietal with the supraoccipital (Voss and Jansa, 2009: 88). As noted by Beck and Taglioretti (2020), interparietal-supraoccipital fusion is exhibited by all Recent didelphids and by the Pliocene species *Sparassocynus derivatus*. The authors coded the Miocene species *H. dolgopolae* as missing (“?”) for their interparietal-supraoccipital fusion character, but the interparietal and supraoccipital are unfused—suturally distinct—in a well-preserved partial cranium (FMNH P-15225) that they did not examine. Because the geologically older taxon exhibits the plesiomorphic condition, it seems likely that the apomorphic state evolved convergently in *S. derivatus* and didelphids.

Another cause for concern is the list of “unambiguous” synapomorphies said to support the sister-group relationship of *Hesperocynus*+*Sparassocynus* with *Monodelphis*. (Unambiguous synapomorphies in phylogenetic jargon are those that are optimized as synapomorphies by both algorithms—Accelerated Transformation and Delayed Transformation—commonly used for this purpose in parsimony analysis.) Six traits optimize unambiguously as synapomorphies of *Hesperocynus*+*Sparassocynus*+*Monodelphis* in Beck and Taglioretti’s tip-and-node-dated Bayesian analysis (see table, below), but all are homoplastic, and most of them are dental features exhibited by other animalivorous marsupials (e.g., as correlates of posterior premolar dominance or molar carnassialization). Interestingly, the single nondental synapomorphy in this list (contact between the maxillary and alisphenoid bones on the orbital floor) is also seen in other short-faced marsupial predators (e.g., *Lutreolina*). Therefore, an alternative hypothesis to recency of common ancestry is that sparassocynids and *Monodelphis* (species of which prey on small vertebrates as well as insects; Voss and Jansa, 2021) have convergently evolved many of the same craniodental dietary adaptations.

In summary, although Beck and Taglioretti’s (2020) study is a welcome contribution to knowledge of sparassocynid morphology and an impressive attempt to place these taxa in an explicitly phylogenetic classification, the evidence that sparassocynids are didelphids (members of the didelphimorph crown clade) is less than compelling, and support for the hypothesis that they are closely related to *Monodelphis*, in particular, does not seem sufficient to justify changes to the current tribal classification of Recent opossums.

Unambiguous Synapomorphies Supporting a Sister-Group Relationship between Sparassocynids and *Monodelphis*<sup>a</sup>

| Character | Change | CI <sup>b</sup> | Apomorphic state                                     |
|-----------|--------|-----------------|--|
| 51        | 0 → 1  | 0.50            | maxillary contacts alisphenoid on orbital floor      |
| 96        | 1 → 2  | 0.25            | P3 distinctly taller than P2                         |
| 105       | 0 → 1  | 0.17            | M3 anterolabial cingulum and preprotocrista separate |
| 114       | 0 → 1  | 0.22            | p2 and p3 subequal in height                         |
| 120       | 0 → 1  | 0.20            | m3 hypoconid lingual to salient protoconid           |
| 121       | 0 → 1  | 0.50            | entoconids on m1–m3 very small or indistinct         |

<sup>a</sup> From Beck and Taglioretti (2020: Electronic Supplementary Material).

<sup>b</sup> Consistency index (values <1.00 indicate homoplasy).



## APPENDIX 2

## OPOSSUM SPECIES REVALIDATED FROM SYNONYMIES (1993–PRESENT)

| Current name (as valid species) | Senior synonym in Gardner (1993) <sup>a</sup> |
|---------------------------------|---|
| <i>Marmosa isthmica</i>         | <i>Marmosa robinsoni</i>                      |
| <i>Marmosa simonsi</i>          | <i>Marmosa robinsoni</i>                      |
| <i>Marmosa zeledoni</i>         | <i>Marmosa mexicana</i>                       |
| <i>Marmosa macrotarsus</i>      | <i>Marmosa murina</i>                         |
| <i>Marmosa waterhousei</i>      | <i>Marmosa murina</i>                         |
| <i>Marmosa germana</i>          | <i>Micoureus regina</i>                       |
| <i>Marmosa nicaraguae</i>       | Not listed                                    |
| <i>Marmosa paraguayana</i>      | <i>Micoureus demerarae</i>                    |
| <i>Marmosa parda</i>            | <i>Micoureus regina</i>                       |
| <i>Marmosa perplexa</i>         | <i>Micoureus regina</i>                       |
| <i>Marmosa phaea</i>            | <i>Micoureus regina</i>                       |
| <i>Marmosa rapposa</i>          | <i>Micoureus regina</i>                       |
| <i>Marmosa rutteri</i>          | <i>Micoureus regina</i>                       |
| <i>Monodelphis glirina</i>      | <i>Monodelphis brevicaudata</i>               |
| <i>Monodelphis palliolata</i>   | <i>Monodelphis brevicaudata</i>               |
| <i>Monodelphis touan</i>        | <i>Monodelphis brevicaudata</i>               |
| <i>Monodelphis peruviana</i>    | <i>Monodelphis adusta</i>                     |
| <i>Tlacuatzin gaumeri</i>       | <i>Marmosa canescens</i>                      |
| <i>Tlacuatzin insularis</i>     | <i>Marmosa canescens</i>                      |
| <i>Tlacuatzin sinaloae</i>      | <i>Marmosa canescens</i>                      |
| <i>Metachirus myosuros</i>      | <i>Metachirus nudicaudatus</i>                |
| <i>Didelphis imperfecta</i>     | <i>Didelphis albiventris</i>                  |
| <i>Didelphis pernigra</i>       | <i>Didelphis albiventris</i>                  |
| <i>Philander canus</i>          | <i>Philander opossum</i>                      |
| <i>Philander mcilhennyi</i>     | <i>Philander andersoni</i>                    |
| <i>Philander melanurus</i>      | <i>Philander opossum</i>                      |
| <i>Philander nigratus</i>       | <i>Philander andersoni</i>                    |
| <i>Philander quica</i>          | <i>Philander opossum</i>                      |
| <i>Philander vossi</i>          | <i>Philander opossum</i>                      |
| <i>Chacodelphys formosa</i>     | <i>Gracilinanus agilis</i>                    |
| <i>Cryptonanus agricolai</i>    | <i>Gracilinanus emiliae</i>                   |
| <i>Cryptonanus chacoensis</i>   | <i>Gracilinanus agilis</i>                    |
| <i>Cryptonanus guahybae</i>     | <i>Gracilinanus microtarsus</i>               |
| <i>Cryptonanus unduaviensis</i> | <i>Gracilinanus agilis</i>                    |
| <i>Gracilinanus peruanus</i>    | <i>Gracilinanus agilis</i>                    |
| <i>Marmosops cauae</i>          | <i>Marmosops impavidus</i>                    |
| <i>Marmosops ocellatus</i>      | <i>Marmosops dorothea</i>                     |

APPENDIX 2 *continued*

| Current name (as valid species) | Senior synonym in Gardner (1993) <sup>a</sup> |
|---------------------------------|---|
| <i>Marmosops paulensis</i>      | <i>Marmosops incanus</i>                      |
| <i>Marmosops bishopi</i>        | <i>Marmosops parvidens</i>                    |
| <i>Marmosops carri</i>          | <i>Marmosops fuscatus</i>                     |
| <i>Marmosops juninensis</i>     | <i>Marmosops parvidens</i>                    |
| <i>Marmosops pinheiroi</i>      | <i>Marmosops parvidens</i>                    |
| <i>Marmosops woodalli</i>       | <i>Marmosops parvidens</i>                    |
| <i>Thylamys sponsorius</i>      | <i>Thylamys elegans</i>                       |
| <i>Thylamys tatei</i>           | <i>Thylamys elegans</i>                       |
| <i>Thylamys venustus</i>        | <i>Thylamys elegans</i>                       |
| <i>Thylamys karimii</i>         | <i>Thylamys pusillus</i>                      |

<sup>a</sup> Note that subspecies were not distinguished from synonyms in Gardner (1993), although this distinction was made in subsequent synopses (e.g., by Gardner, 2005, 2008).

## APPENDIX 3

## OPOSSUM SPECIES DESCRIBED AS NEW SINCE GARDNER (1993)

| Species                         | Geographic origin of type material |
|---------------------------------|------------------------------------|
| <i>Hyladelphys kalinowskii</i>  | Southwestern Amazonia              |
| <i>Marmosa adleri</i>           | Eastern Central America            |
| <i>Marmosa jansae</i>           | Northwestern Amazonia              |
| <i>Monodelphis gardneri</i>     | Peruvian Andes                     |
| <i>Monodelphis arlindoi</i>     | Northeastern Amazonia              |
| <i>Monodelphis sanctaerosae</i> | Cerrado                            |
| <i>Monodelphis vossi</i>        | Northeastern Amazonia              |
| <i>Monodelphis handleyi</i>     | Southwestern Amazonia              |
| <i>Monodelphis pinocchio</i>    | Atlantic Forest                    |
| <i>Monodelphis reigi</i>        | Pantepui                           |
| <i>Monodelphis ronaldi</i>      | Southwestern Amazonia              |
| <i>Monodelphis saci</i>         | Southern Amazonia                  |
| <i>Tlacuatzin balsasensis</i>   | Mexico                             |
| <i>Lutreolina massaia</i>       | Bolivian and Argentinian Andes     |
| <i>Philander deltae</i>         | Orinoco delta                      |
| <i>Philander pebas</i>          | Southwestern Amazonia              |
| <i>Marmosops creightoni</i>     | Bolivian Andes                     |
| <i>Marmosops soinii</i>         | Southwestern Amazonia              |
| <i>Marmosops chucha</i>         | Colombian Andes                    |
| <i>Marmosops magdalenae</i>     | Colombian Andes                    |
| <i>Marmosops marina</i>         | Southeastern Amazonia              |
| <i>Marmosops ojastii</i>        | Northern Venezuela                 |
| <i>Marmosops pakaraimae</i>     | Pantepui                           |

## APPENDIX 4

## OPOSSUM SPECIES NAMES SYNONYMIZED OR DISUSED SINCE 1993

| Name in Gardner (1993)      | Current status <sup>a</sup>             |
|-----------------------------|---|
| <i>Marmosa regina</i>       | Candidate for suppression               |
| <i>Monodelphis maraxina</i> | Synonym of <i>Monodelphis glirina</i>   |
| <i>Monodelphis rubida</i>   | Synonym of <i>Monodelphis americana</i> |
| <i>Monodelphis sorex</i>    | Synonym of <i>Monodelphis dimidiata</i> |
| <i>Monodelphis theresa</i>  | Synonym of <i>Monodelphis scalops</i>   |
| <i>Marmosops cracens</i>    | Synonym of <i>Marmosops fuscatus</i>    |
| <i>Marmosops dorothea</i>   | Synonym of <i>Marmosops noctivagus</i>  |
| <i>Marmosops impavidus</i>  | Nomen dubium                            |

<sup>a</sup> See text for explanations.





