

A Revised Subgeneric Classification of Short-tailed Opossums (Didelphidae: *Monodelphis*)

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ABSTRACT

Members of the didelphid marsupial genus *Monodelphis* have previously been classified into species groups, but such informal subdivisions are inconsistent among authors and have contributed little but confusion to the taxonomic history of the genus. Recent molecular phylogenetic studies, however, have consistently recovered several strongly supported multispecies clades that merit formal recognition. Here we define and illustrate morphological characters that are useful for diagnosing these monophyletic groups, which we name and rank as subgenera to conserve binomial usage: *Monodelphis* Burnett, 1830 (for *M. arlindoi*, *M. brevicaudata*, *M. domestica*, *M. glirina*, *M. palliolata*, *M. sanctaerosae*, and *M. touan*), *Microdelphys* Burmeister, 1856 (for *M. americana*, *M. gardneri*, *M. iheringi*, and *M. scalops*), *Monodelphiops* Matschie, 1916 (for *M. dimidiata* and *M. unistriata*); *Mygalodelphys*, new subgenus (for *M. adusta*, *M. handleyi*, *M. kunsii*, *M. osgoodi*, *M. peruviana*, *M. pinocchio*, *M. reigi*, and *M. ronaldi*); and *Pyrodelphys*, new subgenus (for *M. emiliae*). We provide morphological diagnoses and describe pairwise comparisons to facilitate subgeneric identification, and we summarize subgeneric patterns of geographical distribution and sympatry to supplement recently published biogeographic analyses of the genus.

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INTRODUCTION

Monodelphis Burnett, 1830, is the most speciose genus of didelphid marsupials, with 22 currently recognized species (Pavan et al., 2014; Pavan, 2015). Insofar as known, species of *Monodelphis* are terrestrial or semifossorial, predominantly insectivorous opossums that exhibit conspicuous variation in pelage coloration, behavior, and reproductive strategies (Streilein, 1982a, 1982b; Emmons and Feer, 1997; Pine et al., 1985; Pine and Handley, 2008). Unlike most other didelphid genera, which are restricted to either humid forest or savanna-like habitats, *Monodelphis* inhabits a wide range of environments, including lowland rain forest, dry forest, montane forest, and savannas (Pine and Handley, 2008; Voss and Jansa, 2009).

To date there has been no comprehensive revision of the genus, and most relevant taxonomic publications have treated single species or species complexes (Pine, 1975, 1976, 1977, 1980; Pine and Handley, 1984; Pine et al., 1985; Ventura et al., 1998; Lemos et al., 2000; Voss et al., 2001; Lew and Pérez-Hernández, 2004; Solari, 2004; Lew et al., 2005; Solari, 2007; Vilela et al., 2010; Pavan et al., 2012; Solari et al., 2012; Voss et al., 2012; Pavan, 2015). The most inclusive morphology-based revisionary study (Gomes, 1991) was exclusively based on Brazilian specimens and remains unpublished.

Historically, a number of species groups of *Monodelphis* have been recognized informally, primarily based on pelage markings (Matschie, 1916; Gilmore, 1941; Pine, 1976). However, such morphology-based subdivisions have contributed little but taxonomic confusion (Pine et al., 2013), and none is convincingly supported by character data. By contrast, recent molecular phylogenetic studies based on dense taxonomic sampling and multiple unlinked genes (Pavan et al., 2014; Vilela et al., 2015; Pavan et al., 2016) have consistently recovered several robustly supported multispecies clades (table 1), and some morphological studies (e.g., Voss et al., 2012; Pavan, 2015) suggest that at least some of the groups recovered by molecular phylogenetic research are morphologically diagnosable.

Unfortunately, informal nomenclature for these clades is not sufficient for the purposes of biological communication. For example, the monophyletic group that Pavan et al. (2014) called “Clade E” corresponds to the “*Adusta* Group” of Pavan et al. (2016) and to the combined *adusta* and *kunsi* “complexes” of Vilela et al. (2015). Formally diagnosing and naming such groups has the advantage that usage is constrained by typification and priority according to widely accepted rules (ICZN, 1999), and ranking these clades as subgenera promotes stability by preserving long-established binomial combinations.

In this report, we define and illustrate morphological characters that are useful for recognizing and diagnosing the monophyletic groups previously established by molecular research. These results provide the materials for a formal subgeneric classification, which we intend to serve as the basis for future revisionary research at the species level. Additionally, we summarize subgeneric patterns of distribution and sympatry consistent with our previously published biogeographic analyses (Pavan et al., 2016).

TABLE 1. Species-group Classification of *Monodelphis* (after Pavan et al., 2016).

Adusta Group ^{a, b}	Americana Group ^{d, e}	Brevicaudata Group ^f	Monotypic “groups”	Unsequenced species
<i>M. adusta</i>	<i>M. americana</i>	<i>M. arlindoi</i>	<i>M. dimidiata</i> ^{g, h}	<i>M. ronaldi</i> ^b
<i>M. handleyi</i>	<i>M. gardneri</i>	<i>M. brevicaudata</i>	<i>M. emiliae</i> ⁱ	<i>M. unistriata</i> ^h
<i>M. kunsii</i>	<i>M. iheringi</i>	<i>M. domestica</i>	<i>M. scalops</i> ^{e, j}	
<i>M. osgoodi</i>		<i>M. glirina</i>		
<i>M. peruviana</i>		<i>M. palliolata</i>		
<i>M. pinocchio</i> ^c		<i>M. sanctaerosae</i>		
<i>M. reigi</i>		<i>M. touan</i>		
<i>M. “species 2”</i>		<i>M. “species 3”</i>		
		<i>M. “species 4”</i>		

^a Equivalent to “Clade E” of Pavan et al. (2014) and the combined “*adusta*” and “*kunsii*” complexes of Vilela et al. (2015).

^b Referred to subgenus *Mygalodelphys* in this report.

^c Referred to as *M. “species 1”* by Pavan et al. (2014) and Vilela et al. (2015), subsequently named as *M. pinocchio* by Pavan (2015).

^d Equivalent to “Clade D” of Pavan et al. (2014) and the “*americana* complex” of Vilela et al. (2015).

^e Referred to subgenus *Microdelphys* in this report.

^f Equivalent to “Clade F” of Pavan et al. (2014) and the “*brevicaudata* complex” of Vilela et al. (2015). Referred to subgenus *Monodelphis* in this report.

^g “Clade B” of Pavan et al. (2014).

^h Referred to subgenus *Monodelphiops* in this report.

ⁱ “Clade A” of Pavan et al. (2014). Referred to subgenus *Pyrodelphys* in this report.

^j “Clade C” of Pavan et al. (2014).

Materials and Methods

SOURCE OF MATERIAL: Specimens listed in this report are deposited in the following collections: AMNH (American Museum of Natural History, New York); ANSP (Academy of Natural Sciences of Drexel University, Philadelphia); BMNH (Natural History Museum, London, UK); CM (Carnegie Museum of Natural History, Pittsburgh); EBRG (Museo de la Estación Biológica de Rancho Grande, Maracay, Venezuela); FMNH (Field Museum, Chicago); IEPA (Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá, Brazil); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil); ISEM (Institut des Sciences de l'Évolution, Montpellier, France); KU (Biodiversity Research Center, University of Kansas, Lawrence); LZUFPI (Laboratório de Zoologia Prof. Antônio J. Dumbra, Universidade Federal do Piauí, Teresina, Brazil); MACN-Ma (Colección de Mamíferos del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina); MCN-M (Coleção de Mamíferos, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge); MHNCI (Museu de História Natural Capão da Imbuia, Curitiba, Brazil); MN (Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil); MNHN (Muséum National d'Histoire Naturelle, Paris, France); MPEG (Museu Paraense Emílio Goeldi, Belém, Brazil); MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque); MSU

(Michigan State University, Michigan); MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru); MVZ (Museum of Vertebrate Zoology, University of California, Berkeley); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil); NMW (Naturhistorisches Museum Wien, Vienna, Austria); OMNH (Sam Noble Oklahoma Museum of Natural History, Oklahoma); ROM (Royal Ontario Museum, Toronto, Canada); TTU (Museum of Texas Tech University, Lubbock); UFMG (Universidade Federal de Minas Gerais, Belo Horizonte, Brazil); UFPA (Universidade Federal do Pará, Belém, Brazil); UFSC (Universidade Federal de Santa Catarina, Florianópolis, Brazil); USNM (National Museum of Natural History, Smithsonian Institution, Washington D.C.); ZMB (Zoologisches Museum Berlin, Berlin, Germany).

Uncataloged material is identified by the abbreviation of the museum where it is currently housed followed by field numbers with the following prefixes: AN = A. Nunes; APC = A.P. Carmignoto (Universidade Federal de São Carlos, Brazil); BDP = B.D. Patterson (FMNH); CGB = C.G. Bantel (INPA); JFV = J.F. Vilela (FMNH); LHE = L.H. Emmons (USNM); MTR = M.T. Rodrigues (Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Brazil).

The prefixes ARP, CB, EDH, MN6, PEU, PNSC, RL, SAPO, and UNIBAN correspond to field series of the MZUSP; CZ, IAVRD, JUR, LPP, MBA, MS, STA, TF, TGP correspond to field series at the MPEG; the prefix A corresponds to a field series at the MN; “masto” corresponds to a field series at the MACN-Ma; the prefixes CC, LFS, and RM correspond to field series of the UFMG. The unprefixed numeral “144” corresponds to a field series at the UFSC.

TAXON SAMPLING: We examined 1931 specimens of *Monodelphis* for this study, including representative material of all of the 22 species currently recognized as valid. Among the specimens we examined are 280 specimens that were sequenced in previous DNA-based phylogenetic studies. We provide a list of the material examined in appendix 1.

AGE CRITERIA: Specimens were classified into dental age classes following Pavan et al. (2012), who refined the system originally proposed by Van Nievelt and Smith (2005). Specimens were considered juvenile if M4 was not present, subadult if M4 was present but still incompletely erupted,² and adult if M4 was completely erupted. Adult specimens with only incipient wear on M3 and M4 (cristae unworn or with very narrow and discontinuous strips of exposed dentine) were considered young adults. Those with light wear on M3 and M4 (dentine narrowly exposed on M3 cristae and very narrowly exposed on M4 cristae) were considered full adults, and those with conspicuous wear on M3/M4 (dentine broadly exposed on M3 cristae and narrowly to broadly exposed on M4 cristae) were considered old adults.

QUALITATIVE CHARACTERS: We examined skulls, skins, and fluid-preserved material for taxonomic variation in qualitative morphological characters. Surveyed characters include those previously described in the literature (e.g., Thomas, 1888a; Pine, 1975; Pine and Handley, 1984; Voss et al., 2001; Voss and Jansa, 2003; Lew and Pérez-Hernández, 2004; Solari, 2004, 2007; Pine and Handley, 2008; Voss and Jansa, 2009; Pavan et al., 2012; Voss et al., 2012; Pine et al.,

² Eruption of M4 and P3 are usually simultaneous in *Monodelphis*, so subadults by this definition (with incompletely erupted M4) usually also have incompletely erupted P3.

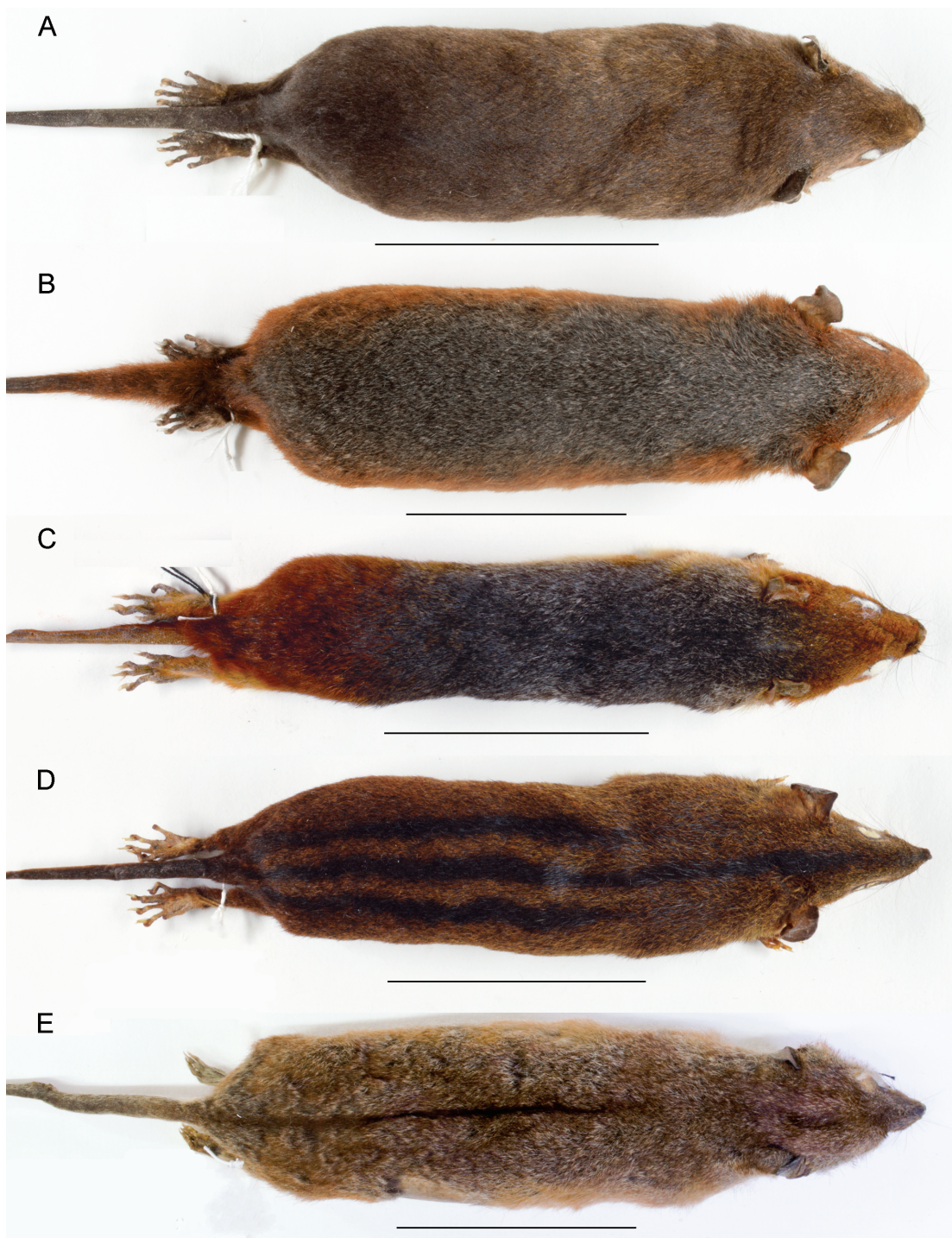


FIG. 1. Dorsal views of skins with alternative color patterns (see text for pelage descriptors): **A**, *Monodelphis adusta* (KU 157978); **B**, *M. arlindoi* (CM 68359); **C**, *M. emiliae* (AMNH 268221); **D**, *M. americana* (AMNH 133241); **E**, *M. unistriata* (MACN-Ma 250). Scale bars = 50 mm.

2013; Duda and Costa, 2015; Pavan, 2015) as well as other characters newly described herein. Descriptive terminology that we use to describe external and craniodental morphology in this report follows Cope (1880), Gregory (1910), Archer (1976), Wible (2003), and Voss and Jansa (2003, 2009). We recorded the sex and age of each specimen to evaluate qualitative characters for sexual dimorphism and ontogenetic variation, respectively, although no formal tests for the effects of age and sex on character variation among conspecific individuals is reported here.

COMPARATIVE MORPHOLOGY

Species of *Monodelphis* differ from one another in numerous morphological characters, of which those of the integument, skull, and dentition are maximally useful for taxonomic diagnoses. In particular, we emphasize characters with alternative states that distinguish the monophyletic groups of species recognized as subgenera in this report. Therefore, we omit descriptions of characters that are primarily useful for distinguishing closely related species within subgenera, which will be treated in subsequent publications.

In the following descriptive accounts of taxonomic character variation, we follow the species-group classification of Pavan et al. (2016), which is summarized in table 1.

External Characters

DORSAL COLOR PATTERN: The dorsal body pelage of *Monodelphis* can be either uniformly colored (unpatterned) or distinctively marked. Unpatterned dorsal pelage, lacking any abrupt color transition (fig. 1A), is observed in *M. domestica*, *M. sanctaerosae*, some specimens of *M. brevicaudata* (those from NW Guyana and NE Venezuela), some old adult male specimens of *M. americana*, and all species of the Adusta Group. By contrast, a grizzled-grayish or -brownish middorsum contrasting with clear (ungrizzled) yellowish, orange, or reddish flanks (fig. 1B) is exhibited by *M. dimidiata* and by most species of the Brevicaudata Group, whereas a grayish midbody contrasting with reddish head and rump (fig. 1C) is seen in *M. emiliae* and in adult male specimens of *M. scalops*. A fourth dorsal pelage phenotype, consisting of three dark longitudinal stripes (fig. 1D), characterizes juveniles and females of *M. scalops* and most age-sex classes of species in the Americana Group (old adult males of *M. americana* are the exception; see above). Clear yellowish or orange flanks with a grizzled-brownish or -grayish middorsum that contrasts with a single dark median longitudinal stripe (fig. 1E) is apparently unique to *M. unistriata*.

VENTRAL PELAGE MARKINGS: Most species of *Monodelphis* have uniformly colored underparts that usually consist of hairs that are grayish basally and variously colored distally (e.g., with brownish, reddish, or whitish tips; fig. 2B, C). Some species, however, have self-whitish midventral markings (comprising hairs that are whitish from root to tip) that contrast with the darker (usually brownish or grayish) coloration of the surrounding ventral pelage (fig. 2A). Such markings were observed uniquely on species of the Adusta Group.

MAMMAE: Mammary exhibit greater taxonomic variation in *Monodelphis* than in any other didelphid genus, encompassing the entire range of morphologies previously reported for the



FIG. 2. Ventral views of skins with alternative pelage markings (see text): A, *Monodelphis handleyi* (MUSM 23810); B, *M. glirina* (MVZ 197456); C, *M. touan* (USNM 549280). Scale bar = 50 mm.

family as a whole. Observed mammary formulae (defined by Voss and Jansa, 2009: 23) range from 2–0–2 = 4 (in *M. peruviana*) to 13–1–13 = 27 (in *M. dimidiata*). Lower mammary counts (of nine or fewer mammae) include only abdominal-inguinal teats, but higher counts (≥ 13 mammae in this study) include both abdominal-inguinal and pectoral teats. Mammary morphology could not be determined for several species that are currently known only from adult males, or for which we did not examine any females with visible teats.

PEDAL THENAR PAD: The plantar (ventral) surface of the hind foot of most plantigrade mammals includes two tarsal and four interdigital pads (Brown and Yalden, 1973). Of these, the thenar (medial tarsal) and the first interdigital pad are clearly separated from one other in most species of *Monodelphis* (e.g., *M. americana*; fig. 3B), but in *M. emiliae* the thenar and first interdigital pad are either fused or in contact (fig. 3A).

PEDAL HYPOTHENAR PAD: The hypothernar (lateral tarsal) pad of the hind foot is usually absent or vestigial in several species of *Monodelphis*, including *M. americana*, *M. scalops* (fig. 3C), *M. dimidiata*, and species of the Brevicaudata Group. By contrast, a small but distinct hypothernar pad is consistently present in members of the Adusta Group, *M. iheringi* (fig. 3D) and in *M. emiliae*.

EXTENSION OF BODY PELAGE ONTO TAIL: In most species of *Monodelphis* the body pelage (comprising soft underfur and long guard hairs) extends farther onto the tail dorsally than ventrally (e.g., in *M. brevicaudata*; Voss et al., 2001: fig. 29A), or it extends to about the same extent dorsally and ventrally (e.g., in *M. palliolata*; Voss et al., 2001: fig. 29B). By contrast, although the tail base seems almost completely unfurred in species of the Adusta Group, close inspection reveals that body pelage uniquely extends farther onto the tail ventrally than dorsally (e.g., in *M. handleyi*).

CAUDAL SCALE PATTERN: In most species of *Monodelphis* the scales that encircle the tail are arranged in predominantly annular series, but some species have caudal scales arranged in spiral series. The annular pattern was observed in *M. emiliae*, *M. scalops*, and in species of the Americana and Brevicaudata groups (e.g., *M. glirina*; fig. 4A), whereas examined specimens of *M. dimidiata* (fig. 4B) and *M. unistriata* have caudal scales that are arranged in unambiguously spiral series. Tail scales are small and often inapparent in species of the Adusta Group, in which some species seem to have scales arranged in both annular and spiral series (e.g., *M. adusta*), whereas others have scales that are mostly in spiral series (e.g., *M. pinocchio*) or annular series (e.g., *M. kunsii*).

Craniodental Characters

INFRAORBITAL FORAMEN: The infraorbital foramen varies taxonomically in its position with respect to the maxillary dentition. In some species this foramen is dorsal to P3 (e.g., in *Monodelphis domestica*; fig. 5A), while in others it is dorsal to M1 (e.g., in *M. adusta*; fig. 5B) or to the P3/M1 commissure. Quite variable in a few species (e.g., in *M. dimidiata*), this character is conservative in many others, and in combination with additional characters it is useful for diagnosing groups of species. For example, the infraorbital foramen is usually dorsal to M1

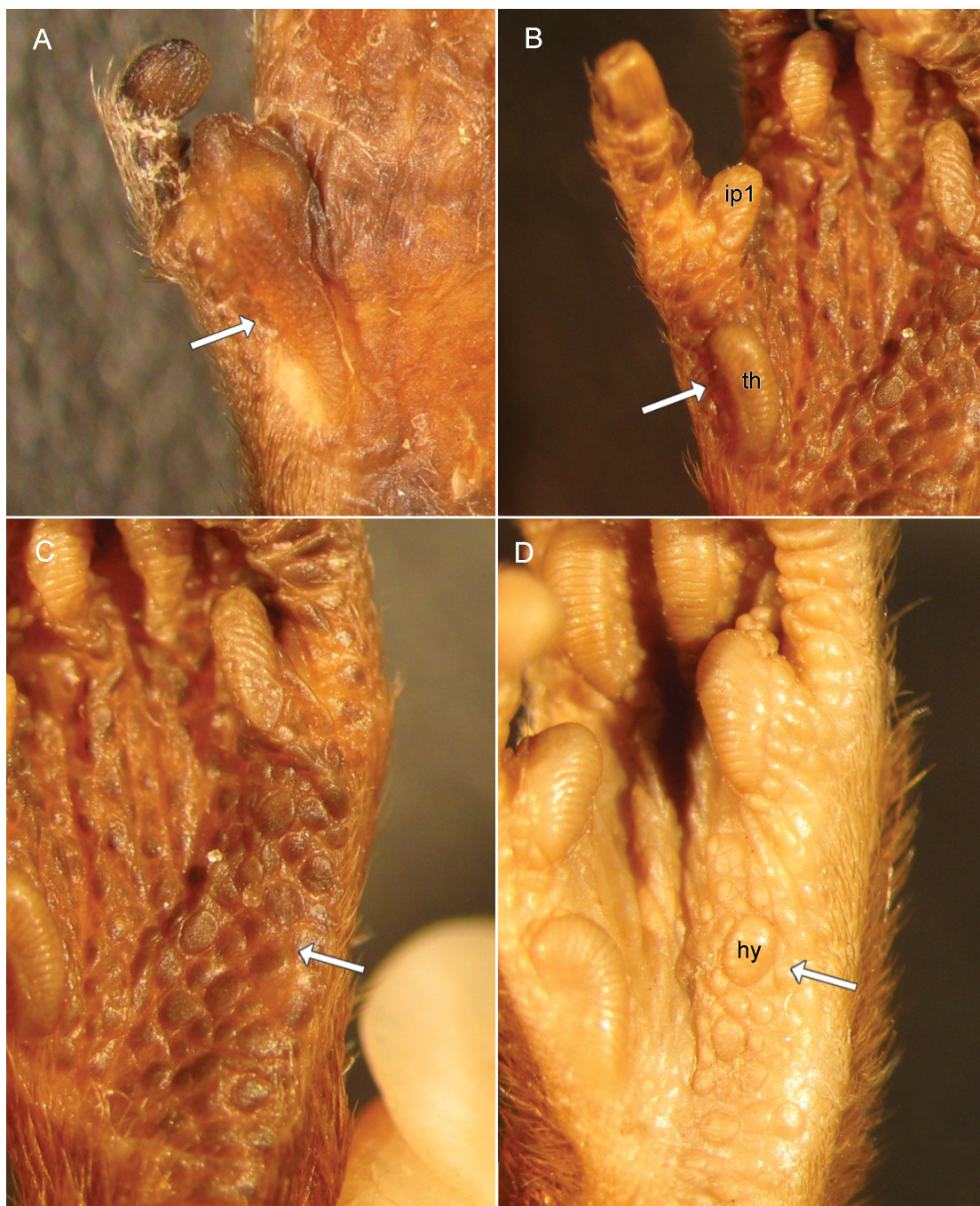


FIG. 3. Plantar views of left hind feet, illustrating taxonomic differences in plantar pad morphology. The thenar (**th**) and first interdigital pad (**ip1**) are fused in *M. emiliae* (A, MZUSP 35062), and separate in *M. americana* (B, MZUSP 29469). The hypothenar pad (**hy**) is absent in *M. scalops* (C, MZUSP 29203), and present in *M. iheringi* (D, MZUSP 3421). Not to the same scale.

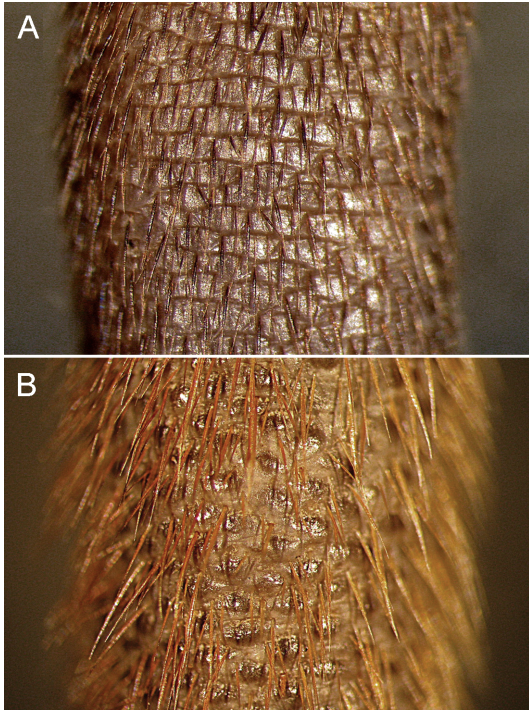


FIG. 4. Close-up views of tail illustrating caudal scales arranged in annular series (A, *Monodelphis glirina*, MZUSP MTR 10164) and spiral series (B, *M. dimidiata*, MZUSP 34257). Not to the same scale.

in the Adusta and Americana groups, but it is often dorsal to P3 among members of the Brevicaudata Group.

FRONTAL PROCESS OF JUGAL: In most species of opossums, the frontal process of the jugal is a prominent landmark that defines the posteroventral limit of the orbital fossa. By contrast, this structure exhibits noteworthy taxonomic variation in *Monodelphis*. The frontal process is usually absent or indistinct in species of the Adusta Group, in which the jugal never projects dorsally above the zygomatic process of the squamosal (e.g., in *M. peruviana*; fig. 6A), whereas the frontal process forms a smoothly rounded dorsal projection in *M. emiliae* (fig. 6B), *M. dimidiata*, and members of the Brevicaudata Group. By contrast, in *M. scalops* and members of the Americana Group (e.g., *M. americana*; fig. 6C) the frontal process is well defined and distinctly angular.

PARIETAL/MASTOID CONTACT: The parietal is usually in contact with the mastoid (the occipital exposure of the petrosal bone) in *Monodelphis*, because the interparietal

does not extend laterally to contact the squamosal (e.g., in most specimens of *Monodelphis glirina*; fig. 7A). In most species of the Adusta Group, however, the interparietal consistently extends laterally to reach the squamosal and, as a result, the parietal is not in contact with the mastoid (e.g., in *M. handleyi*; fig. 7B). In *M. pinocchio* the interparietal is absent in all specimens examined, but the parietal does not contact the mastoid because the supraoccipital is in contact with the squamosal.

INCISIVE FORAMINA: The length of the incisive foramina exhibits modest taxonomic variation in *Monodelphis*. We distinguish “long” and “short” incisive foramina based on their posterior endpoints in relation to the upper canines. In *M. dimidiata* and *M. unistriata*, for example, the incisive foramina are notably short, extending from the level of I3 or I4 to a point between the left and right paracanine fossae or just to—but not appreciably between—the canines. In most other species the incisive foramina are long, extending posteriorly well between the canines.

MAXILLOPALATINE FENESTRAE: For diagnostic purposes, we distinguish “long” and “short” maxillopalatine fenestrae based on their anterior and posterior endpoints in relation to adjacent maxillary teeth. Whereas most species have long maxillopalatine fenestrae that extend

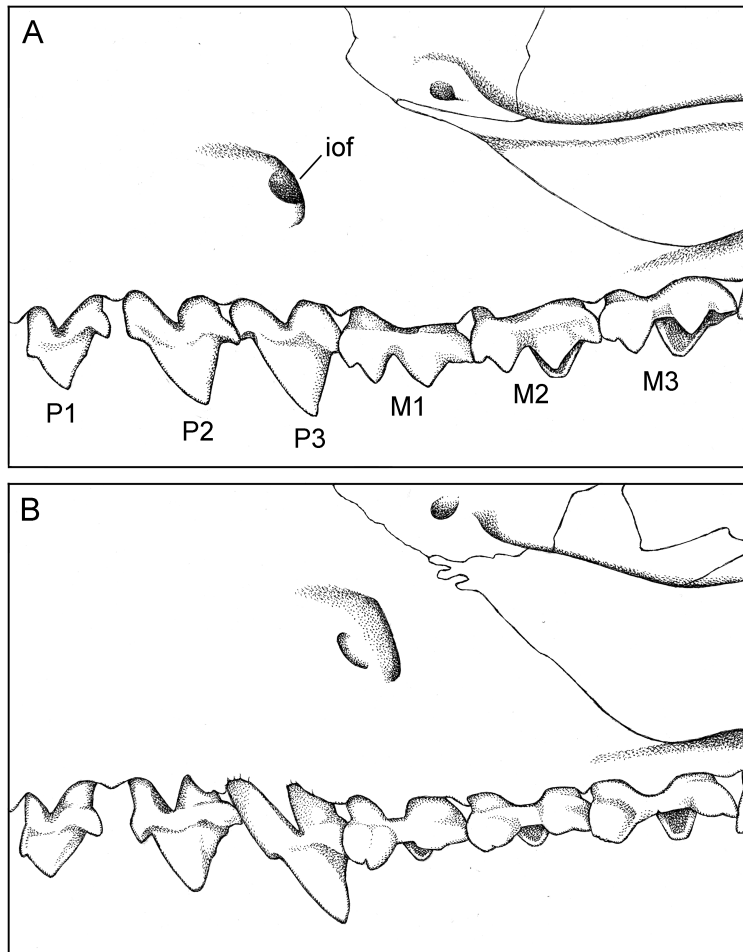


FIG. 5. Left lateral cranial views of *Monodelphis domestica* (A, FMNH 20256) and *M. adusta* (B, KU 157978) illustrating taxonomic differences in the position of the infraorbital foramen (iof) with respect to the maxillary dentition. Not to the same scale.

from P3 or from the P3/M1 commissure to M3, others have conspicuously shorter maxillopalatine fenestrae that extend only from P3 to M2 (e.g., *Monodelphis emiliae*) or from M1 to M3 (e.g., *M. dimidiata*, *M. unistriata*).

SIZE OF SPHENORBITAL FISSURE/BASISPHENOID EXPOSURE: The sphenorbital fissure is a lateral opening in the braincase onto the orbital floor that is bordered medially by the orbitosphenoid, laterally by the alisphenoid, and ventrally by the presphenoid and basisphenoid. In most species of *Monodelphis* the sphenorbital fissure is large, broadly exposing the basisphenoid to lateral view (e.g., in *M. arlindoi*; fig. 8B). In other species, however, the sphenorbital fissure is consistently small because its lateral (alisphenoid) margin is produced anteriorly, effectively concealing the basisphenoid in lateral view (e.g., in *M. handleyi*; fig. 8A). Although the marsupial sphenorbital fissure transmits several nerves and blood vessels (Wible, 2003:

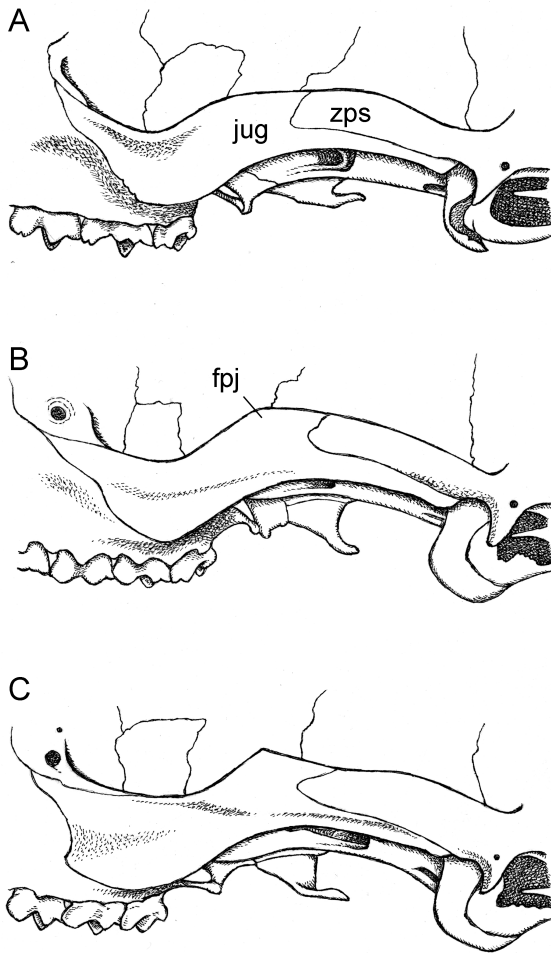


FIG. 6. Left lateral cranial view of *Monodelphis peruviana* (A, FMNH 172032), *M. emiliae* (B, MUSM 13298), and *M. americana* (C, OK 17381) illustrating taxonomic differences in zygomatic morphology. In *M. peruviana* the jugal (**jug**) is not produced dorsal to the zygomatic process of the squamosal (**zps**) and the frontal process is absent or indistinct. By contrast, in *M. emiliae* a rounded frontal process of the jugal (**fpj**) extends dorsal to the zygomatic process of the squamosal, whereas in *M. americana* the frontal process of the jugal is well developed and distinctly angular. Not to the same scale.

182), we conjecture that the small size of this opening (in *Monodelphis* species with laterally concealed basisphenoids) is correlated with a smaller optic nerve and ophthalmic blood supply in small-eyed taxa.

A small sphenorbital fissure and laterally concealed basisphenoid are consistently exhibited only by members of the Adusta Group, whereas members of the Americana Group, *Monodelphis scalops*, and *M. emiliae* consistently have a large sphenorbital fissure and a basisphenoid that is widely exposed to lateral view. Most members of the Brevicaudata Group also have a relatively large sphenorbital fissure that exposes a broad part of the basisphenoid in lateral view, as do most specimens of *M. dimidiata*.

INFRATEMPORAL CREST OF ALISPHE-NOID: An infratemporal crest demarcating the lateral and the ventrolateral faces of the alisphenoid is observed in several species of *Monodelphis*, mainly in old adult specimens (e.g., in *M. touan*; fig. 9A). A distinct infratemporal crest is commonly present in species of the Brevicaudata Group (even young adults in this group may exhibit it), and it is also observed in old adult specimens of *M. emiliae* and *M. dimidiata*. No distinct infratemporal crest was observed in members of the Americana Group (e.g., *M. americana*; fig. 9B) or in *M. scalops*. Among members of the Adusta Group, the infratemporal crest is present in some species (e.g., *M. handleyi*) and absent in others (e.g., *M. pinocchio*).

SECONDARY FORAMEN OVALE: In most species of *Monodelphis*, the extracranial course of the mandibular nerve is not enclosed by bone, and a secondary foramen ovale (sensu Voss and Jansa, 2003) is absent; *M. brevicaudata* exemplifies this morphology (fig. 10A). By contrast, in *M. americana*, *M. gardneri*, and *M. scalops* the extracranial course of mandibular nerve is consistently enclosed by an anteromedial

bullar lamina that forms a secondary foramen ovale (fig. 10B). *Monodelphis emiliae* is polymorphic for this character.

TYMPANIC WING OF ALISPHEOID: The morphology of the auditory bulla is quite variable and taxonomically informative within *Monodelphis*. As in other didelphids, the middle ear cavity of *Monodelphis* is partially enclosed anteriorly by a cup-shaped tympanic process (or “wing”) of the alisphenoid and, posteriorly, by the rostral tympanic process of the petrosal. Species in the *Adusta* and *Brevicaudata* groups have a small alisphenoid tympanic wing that is separated by a wide gap from the rostral tympanic process. In these species, the gap between the alisphenoid tympanic wing and the rostral tympanic process is approximately equal to or greater than the length (anteroposterior dimension) of the alisphenoid tympanic wing (fig. 10A). By contrast, *M. scalops*, *M. emiliae*, and members of the *Americana* Group have a larger alisphenoid tympanic process that is more narrowly separated from the rostral tympanic process (fig. 10B).

Monodelphis dimidiata is polymorphic for this character. Most examined specimens exhibit an alisphenoid tympanic wing that is intermediate in size between the two phenotypes described above (i.e., the gap between the alisphenoid tympanic wing and the rostral tympanic process is about as wide as the alisphenoid tympanic wing or even slightly narrower), but some specimens exhibit a smaller alisphenoid tympanic wing and a correspondingly wider gap.

ANTERIOR PROCESS OF MALLEUS: Certain other aspects of the auditory morphology of *Monodelphis* appear to be correlated with size of the alisphenoid tympanic wing, but are usefully described as distinct characters. Among other correlated traits, in species with a small alisphenoid tympanic wing, the tip of the anterior process of the malleus is exposed on the outer surface of the bulla between the ectotympanic and the alisphenoid (adjacent to the Glaserian fissure; fig. 10A), whereas in species with a large alisphenoid tympanic wing the anterior process of the malleus is not exposed on the outside of the bulla (e.g., in *M. scalops*; fig. 10B). *Monodelphis dimidiata* is polymorphic for this character.

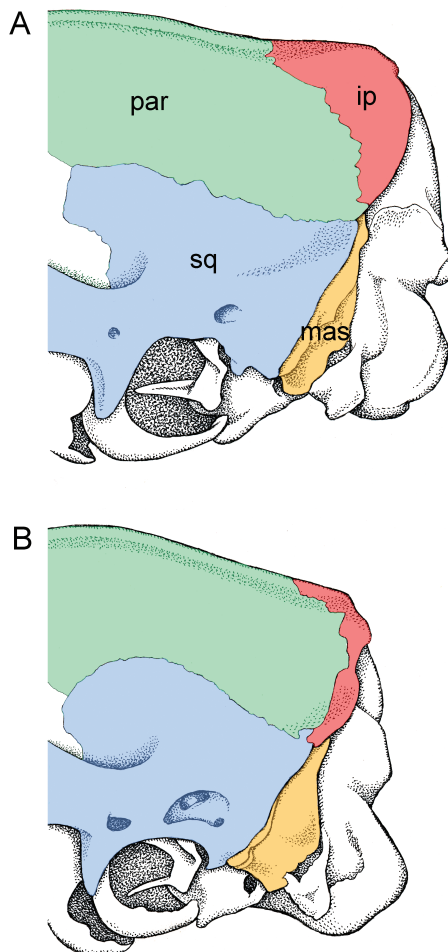


FIG. 7. Left lateral view of posterior braincase of *Monodelphis glirina* (A, MVZ 197456) and *M. handleyi* (B, AMNH 276709) illustrating taxonomic differences in parietal-mastoid versus interparietal-squamosal contact. Abbreviations: **ip**, interparietal; **mas**, mastoid (occipital exposure of petrosal); **par**, parietal; **sq**, squamosal. Not to the same scale.

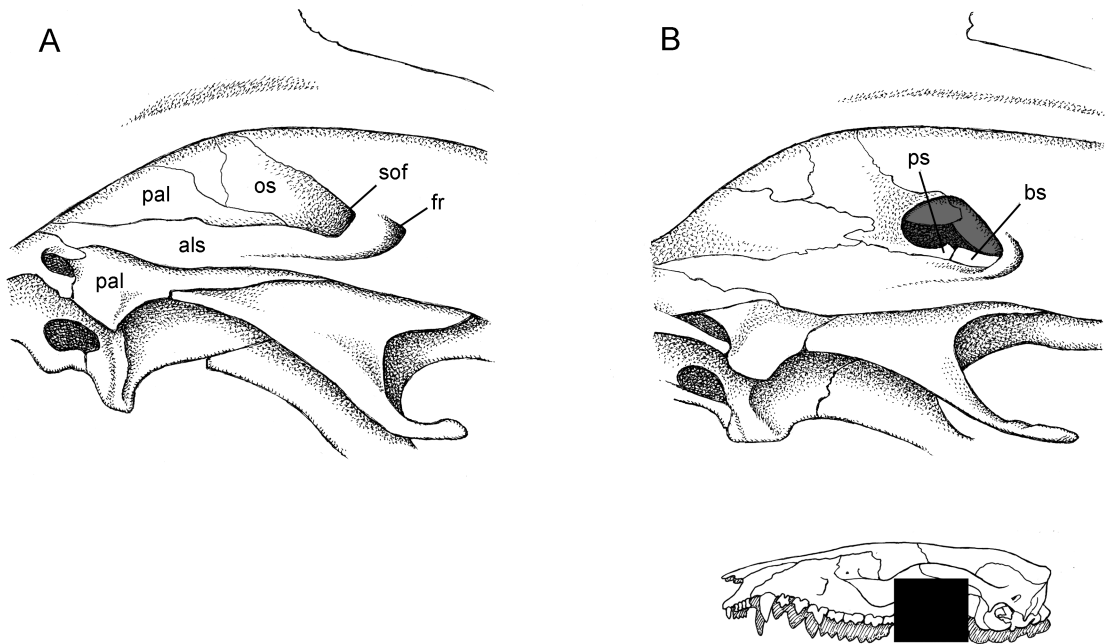


FIG. 8. Left ventrolateral cranial view of *Monodelphis handleyi* (A, MUSM 23809) and *M. arlindoi* (B, ROM 108477) illustrating taxonomic differences in size of the sphenorbital fissure (sof). In *M. handleyi* the sphenorbital fissure is small and does not expose the basisphenoid, but this opening is much larger in *M. arlindoi*, in which the basisphenoid is laterally exposed. Other abbreviations: als, alisphenoid; bs, basisphenoid; fr, foramen rotundum; os, orbitosphenoid; pal, palatine; ps, presphenoid (fused with orbitosphenoid). Not drawn to same scale.

ROSTRAL TYMPANIC PROCESS OF PETROSAL: Another auditory feature correlated with bullar size is the shape of the rostral tympanic process of the petrosal. In species of *Monodelphis* with a small alisphenoid tympanic wing, the rostral tympanic process is narrow and more or less triangular, and it does not conceal the fenestra cochleae in ventral view (fig. 10A). By contrast, in species with a large alisphenoid tympanic wing, the rostral tympanic process is rounded and broad, usually concealing the fenestra cochleae in ventral view (fig. 10B). As in the preceding characters, *M. dimidiata* exhibits an intermediate condition in which the rostral tympanic process tends to be roughly triangular but broad, partially concealing the fenestra cochleae.

STAPES: The stapes, the innermost bone of the ossicular chain, is usually columelliform (more or less rodlike) and imperforate or microperforate in most species of *Monodelphis*. Members of the Brevicaudata Group, however, have a triangular or subtriangular stapes with a large obturator foramen for the stapedia artery (Wible, 2003: fig. 6).

SIZE OF SUBSQUAMOSAL FORAMEN: The subsquamosal foramen³ is usually large in *Monodelphis*, a condition that we define as substantially wider than the squamosal strut that separates this opening from the postglenoid foramen. In *M. emiliae*, however, the subsquamosal foramen is smaller,

³ Our use of the term “subsquamosal foramen” is consistent with its original definition (Cope, 1880) and with well-established anatomical usage in the marsupial literature (e.g., Gregory, 1910; Archer, 1976), but Wible (2003: 183) referred to this opening as the “suprameatal foramen.”

either narrower or similar in width to the bone that separates it from the postglenoid foramen.

ANTERIOR CINGULID: The anterior cingulids of the lower molars are broad, well-developed shelves in most species of *Monodelphis*. In such species, the anterior cingulids of m2 and m3 extend labial to or level with the hypoconids of the preceding teeth (m1 and m2, respectively; fig. 11A–D). By contrast, in species of the *Adusta* Group, the anterior cingulids are substantially narrower; on m2 and m3 they are unambiguously lingual to the hypoconids of m1 and m2, respectively (fig. 11E–F).

MORPHOLOGY OF dp3: In most species of *Monodelphis* (e.g., *M. dimidiata*, *M. emiliae*, *M. scalops*, members of the *Americana* Group, and most members of the *Adusta* Group), the lower milk premolar (dp3) is a narrow, only partially molariform tooth, usually with an incomplete (bicuspid) trigonid and an indistinct or minimally differentiated anterior cingulid (fig. 11A, C–E). By contrast, in *M. handleyi* and species of the *Brevicaudata* Group, dp3 is robust and fully molariform, usually with a complete (tricuspid) trigonid and a well-developed anterior cingulid (fig. 11B, F).

ENTOCONID OF m1–m3: The entoconid is consistently smaller in *Monodelphis* than it is in most other didelphids, in which this lingual talonid cusp is approximately as tall as the hypoconid (on the labial side of the talonid basin) and much exceeds the adjacent hypoconulid in height (Voss and Jansa, 2003: fig. 14). Nevertheless, we observed noteworthy taxonomic variation in entoconid size among species of *Monodelphis* by carefully comparing unworn lower dentitions. In most species of *Monodelphis* the entoconid of m1–m3 is a distinct cusp that is about as tall or taller than the hypoconulid (e.g., in *M. scalops*; fig. 12A), but in species of the *Adusta* Group the entoconid is indistinct or very small (shorter than the adjacent hypoconulid; e.g., in *M. handleyi*, fig. 12B).

TAXONOMIC ACCOUNTS

Genus *Monodelphis* Burnett, 1830

TYPE SPECIES: *Monodelphis brevicaudata* (Erxleben, 1777).

CONTENTS: Twenty-two currently recognized species in five subgenera, as diagnosed below.

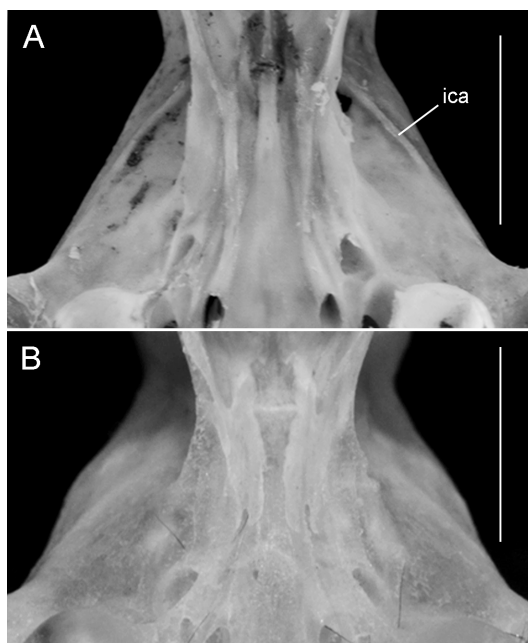


FIG. 9. Ventral cranial view of old adult males of *Monodelphis touan* (A, USNM 393441) and *M. americana* (B, UFMG 2004), illustrating the presence of an infratemporal crest of alisphenoid (ica) in *M. touan*. The crest is absent or indistinct in *M. americana*. Scale bars = 5 mm.

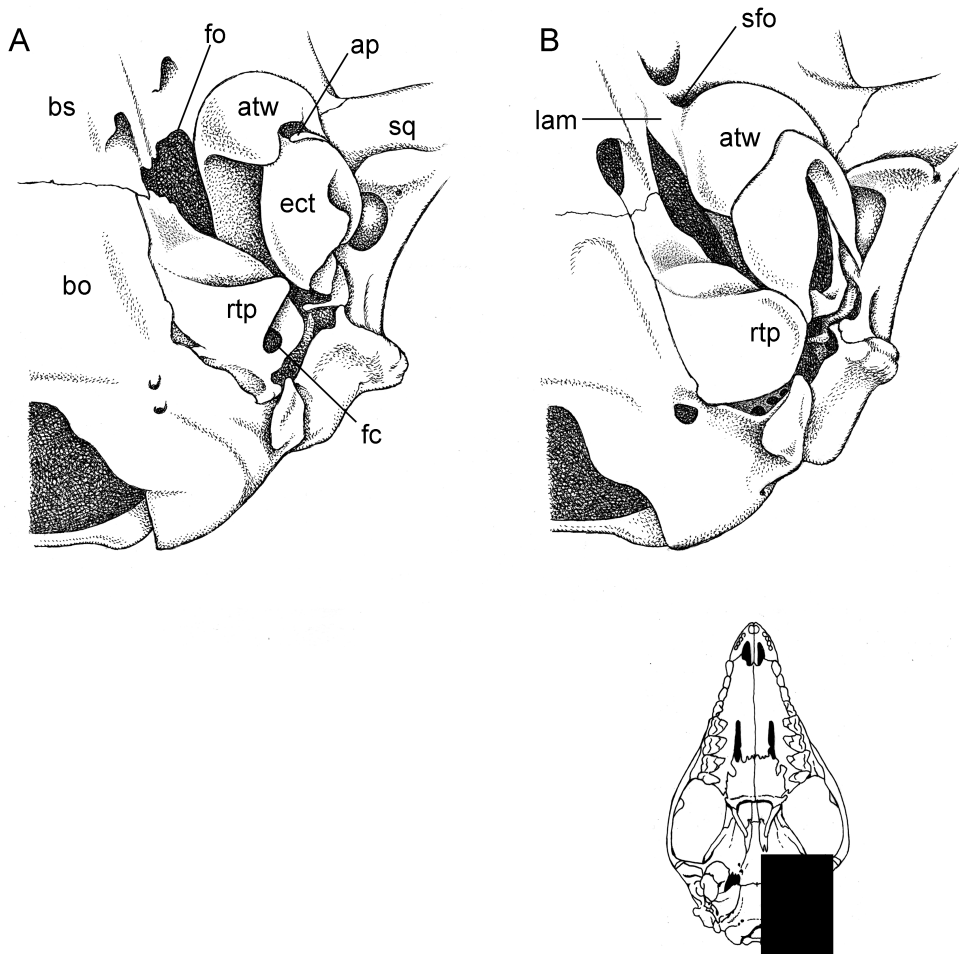


FIG. 10. Ventral cranial views of *Monodelphis brevicaudata* (A, AMNH 257203) and *M. scalops* (B, MVZ 182776) illustrating taxonomic differences in the ear region. In *M. brevicaudata* (and most other species of *Monodelphis*) the mandibular nerve emerges from the foramen ovale (fo), and its extracranial course is not enclosed by bone; there is no secondary foramen ovale. In *M. scalops*, however, a secondary foramen ovale (sfo) is formed by an anteromedial bullar lamina (lam). Additionally, *M. brevicaudata* has a small alisphenoid tympanic wing (atw) separated by a wide gap from the rostral tympanic process of petrosal (rtp), which is narrow, triangular, and does not conceal the fenestra cochleae (fc) in ventral view. By contrast, *M. scalops* has a larger alisphenoid tympanic wing that is separated from the rostral tympanic process by a much narrower gap; additionally, the rostral tympanic process of this species is much broader and conceals the fenestra cochleae in ventral view. Lastly, the anterior process of the malleus (apm) is exposed distally between the ectotympanic (ect) and the alisphenoid tympanic wing in *M. brevicaudata*, but the anterior process of the malleus is not exposed in *M. scalops*. Other abbreviations: bo, basioccipital; bs, basisphenoid; sq, squamosal. Not drawn to the same scale.

DESCRIPTION⁴: Combined length of adult head and body ca. 60–200 mm; adult weight ca. 10–150 g. Rhinarium with one ventrolateral groove on each side of median sulcus; dark circumocular mask absent; pale supraocular spot absent; throat gland present in adult males of most species but apparently polymorphic in some (e.g., *M. americana*) and absent in *M. gardneri*. Dorsal pelage coloration highly variable, but dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-colored or gray based, highly variable in surface pigmentation. Manus mesaxonic (dIII > dIV); manual claws very long, extending well beyond fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present, but pads small and dermatoglyphs sometimes indistinct; central palmar epithelium smooth or tuberculate; carpal tubercles absent in both sexes. Pedal digits unwebbed; pedal digit III longer than digit IV; plantar surface of heel naked. Pouch absent; mammae 2–0–2 = 4 (all abdominal-inguinal; e.g., in *M. peruviana*) to 13–1–13 = 27 (including pectoral teats; e.g., in *M. dimidiata*); cloaca present. Tail much shorter than combined length of head and body; thick but muscular, not incrassate; extension of body fur on tail varies among included species; unfurred caudal surfaces covered with macroscopic bristlelike hairs, not naked appearing; caudal scales often inapparent, either in annular series (e.g., in *M. emiliae*), or in spiral series (e.g., in *M. dimidiata*); relationship between caudal scales and hairs usually obscure, but subequal hairs usually arranged in triplets; ventral caudal surface not modified for prehension.

Premaxillary rostral process absent. Nasals long, extending anteriorly above or beyond I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals (viewed through the nasal orifice) simple or sparsely ornamented scrolls, not elaborately branched. Lacrimal foramina (from one to three on each side, usually two) prominently exposed on orbital margin (e.g., in *M. scalops*) or concealed from lateral view inside the anterior orbital margin (e.g., in *M. handleyi*). Orbits small, orbito-temporal region usually without conspicuous constrictions (except in some old adult males); supraorbital margins smoothly rounded, without beads or distinct postorbital processes (e.g., in *M. peruviana*), or with small but distinct postorbital processes in old adult males (e.g., in *M. americana*). Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent (e.g., in *M. adusta*), or variously developed (e.g., extending to frontals in old male specimens of *M. dimidiata*). Petrosal not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal, e.g., in *M. americana*) or absent (interparietal contacts squamosal, e.g., in *M. handleyi*). Maxillopalatine fenestrae present; palatine fenestrae present or absent; maxillary fenestrae absent; posterolateral palatal foramina usually small (but large and extending anteriorly between M4 protocones in *M. sanctaerosae*); posterior palatal morphology conforms to *Didelphis* morphotype (with moderately well-developed lateral corners, the choanae somewhat constricted behind). Maxillary and alisphenoid in contact on floor of orbit (not separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular; anteromedial lamina forming secondary foramen ovale present in some

⁴ After Voss and Jansa (2009: 105–107), but modified to accommodate additional character variation observed in several species not analyzed in that study.

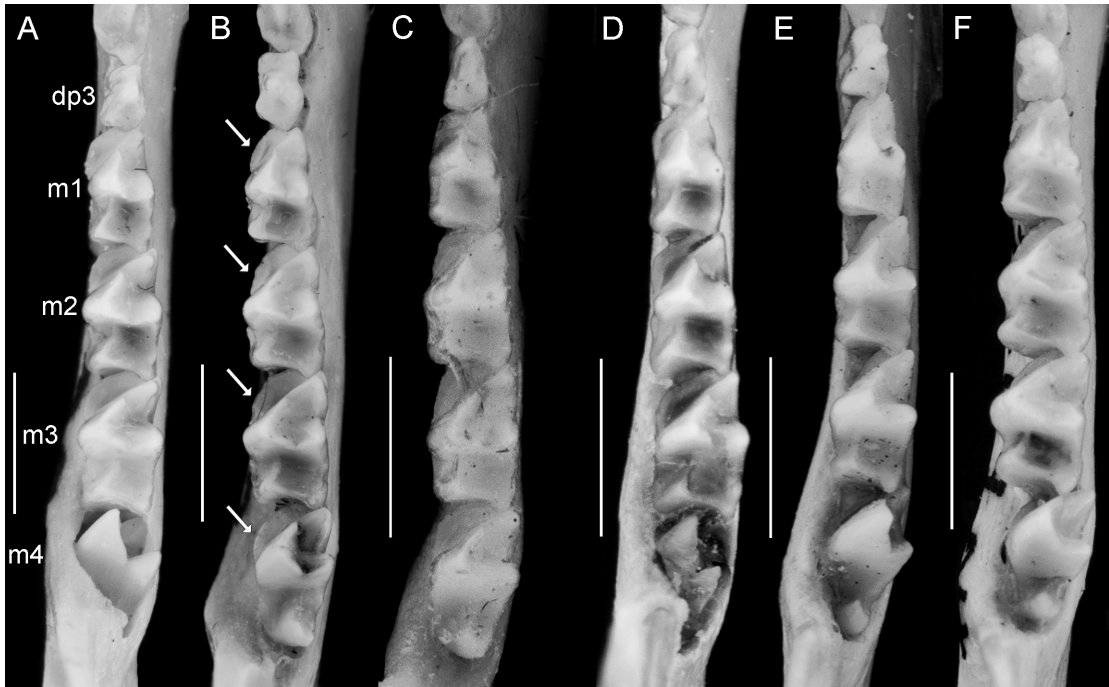


FIG. 11. Oclusal view of the left mandibular dentition of juvenile specimens of *Monodelphis emiliae* (A, AMNH 94293), *M. glirina* (B, AMNH 262397), *M. dimidiata* (C, MSU 17469), *M. scalops* (D, FMNH BDP3282), *M. reigi* (E, ROM 114699), and *M. handleyi* (F, AMNH 276704), illustrating taxonomic variation in the lower molars (m1–m4) and deciduous premolar (dp3) as described in the text. Scale bars = 2 mm.

species (e.g., *M. scalops*) or lamina and secondary foramen ovale absent (e.g., in *M. iheringi*). Anterior limb of ectotympanic suspended directly from basicranium. Stapes triangular with large obturator foramen (e.g., in *M. touan*), or columellar and microperforate or imperforate (e.g., in *M. osgoodi*). Fenestra cochleae exposed (e.g., in *M. pinocchio*) or concealed in sinus formed by rostral and caudal tympanic processes of petrosal (e.g., in *M. emiliae*). Paroccipital process small and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (“premolariform”), with subequal anterior and posterior cutting edges; I5 wider (mesiodistal dimension) than I2 (e.g., in *M. scalops*) or I5 and I2 of similar width (e.g., in *M. kunsii*). Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple (without accessory cusps; e.g., in *M. dimidiata*) or C1 with small posterior accessory cusp sometimes present (e.g., in *M. peruviana*).

First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dp3) large and molariform. Molars highly carnassialized (postmetacristae much longer

than postprotocristae); relative widths consistently $M1 < M2 < M3 < M4$; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow on M1, deeper on M2, and consistently deep on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3. Last upper tooth to erupt is P3 in some species (e.g., *M. peruviana*), or P3 and M4 erupt simultaneously (e.g., in *M. arlindoi*).

Lower incisors (i1–i4) with distinct lingual cusps. Second lower premolar (p2) subequal in height to p3 (e.g., in *M. glirina*), p3 taller than p2 (e.g., in *M. emiliae*), or p2 taller than p3 (e.g., in *M. pinocchio*); lower milk premolar (dp3) trigonid complete (tricuspid, e.g., in *M. brevicaudata*) or incomplete (bicuspid, e.g., in *M. reigi*). Hypoconid lingual to protoconid (not labially salient) on m3; hypoconulid twinned with entoconid on m1–m3; entoconid smaller than hypoconulid on m1–m3 (e.g., in *M. kunsii*) or entoconid higher or subequal to hypoconulid on m1–m3 (e.g., in *M. scalops*).

REMARKS: The monophyly of *Monodelphis* was robustly supported by Voss and Jansa's (2009) phylogenetic analyses of four exemplar species using sequence data from five nuclear genes, and by a unique deletion at the BRCA1 locus. More recently, generic monophyly was strongly corroborated by phylogenetic analyses based on much denser taxonomic sampling and multiple genes (Pavan et al., 2014). The 10 unambiguous nonmolecular synapomorphies identified by Voss and Jansa (2009), however, remain to be evaluated with phylogenetic analyses of more taxonomically comprehensive datasets.

The subgeneric classification that follows is based on the results of two recent phylogenetic analyses of molecular datasets that consistently recovered these clades (fig. 13), which are here diagnosed morphologically using characters defined above.

Mygalodelphys, new subgenus

TYPE SPECIES: *Monodelphis adusta* (Thomas, 1897).

CONTENTS: *adusta* Thomas, 1897 (including *melanops* Goldman, 1912); *peruviana* Osgood, 1913; *osgoodi* Doult, 1938; *kunsii* Pine, 1975; *reigi* Lew and Pérez-Hernández, 2004; *ronaldi* Solari, 2004; *handleyi* Solari, 2007; and *pinocchio* Pavan, 2015.

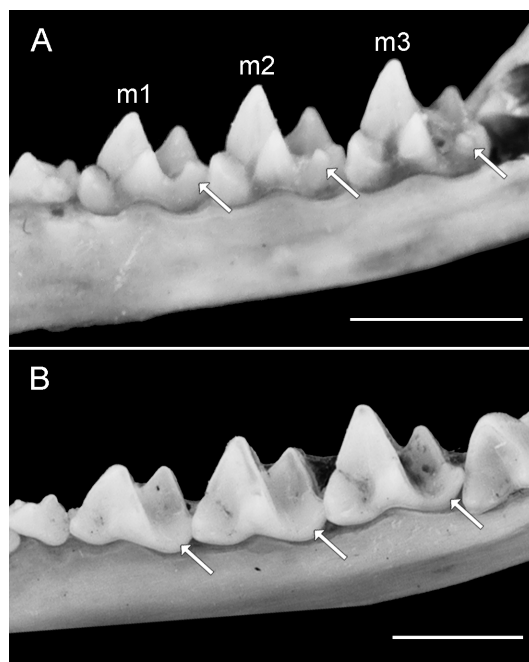


FIG. 12. Lingual view of the unworn right mandibular dentition of *Monodelphis scalops* (A, FMNH BDP3282) and *M. handleyi* (B, AMNH 276704), illustrating taxonomic differences in size of the entoconid (arrows) on m1–m3 (see text). Scale bars = 2 mm.

DIAGNOSIS: Dorsal body pelage unpatterned; ventral pelage uniformly colored or with self-whitish median markings.⁵ Mammae 2–0–2 = 4 (e.g., in *M. peruviana*; AMNH 264562), 3–0–3 = 6 (e.g., in *M. adusta*; AMNH 202650), or 3–1–3 = 7 (e.g., in *M. pinocchio*; MZUSP MTR15815), all abdominal-inguinal. Thenar and first interdigital pad of pes separate, not fused; hypothenar pad of pes present (but unknown for *M. reigi*, *M. peruviana*, and *M. ronaldi*). Body pelage extends onto tail farther ventrally than dorsally; tail scales arranged in annular or spiral series. Infraorbital foramen dorsal to M1; frontal process of jugal absent or indistinct; parietal usually (> 90% of examined specimens) not in contact with mastoid; length of incisive foramina variable; length of maxillopalatine fenestra variable; sphenorbital fissure small (basisphenoid laterally concealed); infratemporal crest of alisphenoid distinct or indistinct; secondary foramen ovale usually absent⁶; tympanic wing of alisphenoid small; tip of anterior process of malleus exposed on external bullar surface between ectotympanic and alisphenoid; rostral tympanic process of petrosal narrow and triangular, not concealing fenestra cochleae in ventral view; stapes columelliform, imperforate or microperforate; subsquamosal foramen large. Anterior cingulids of m2 and m3 narrow; entoconids of m1–m3 very small, indistinct; dp3 small, with incomplete trigonid and indistinct anterior cingulid in some species (e.g., *M. adusta*, *M. reigi*), but dp3 large, with complete trigonid and distinct anterior cingulid in other species (e.g., *M. handleyi*; the morphology of dp3 is unknown for *M. peruviana*, *M. osgoodi*, *M. ronaldi*, *M. pinocchio*, and *M. kunsii*).

COMPARISONS: Members of the subgenus *Mygalodelphys* differ from currently recognized species in other subgenera of *Monodelphis* by several unique external and craniodental traits, including: (1) soft body pelage that extends onto the tail farther ventrally than dorsally; (2) frontal process of jugal absent or indistinct; (3) parietal-mastoid contact absent; (4) a small sphenorbital fissure that does not expose the basisphenoid to lateral view; (5) narrow lower molar anterior cingulids; and (6) indistinct entoconids on m1–m3. Self-whitish midventral pelage markings are also unique to *Mygalodelphys*, although they are often polymorphic and are not present in all member species.

Among other diagnostic comparisons (table 2), *Mygalodelphys* additionally differs from *Pyrodelphys* by its unpatterned dorsal pelage, separate thenar and first interdigital pads on the hind foot, small alisphenoid tympanic wing, exposure of the anterior process of the malleus on the external surface of the bulla, narrow-triangular rostral tympanic process of the petrosal, and a large subsquamosal foramen. *Mygalodelphys* additionally differs from the usual morphology seen in the nominotypical subgenus by possessing a distinct hypothenar pad on the hind-foot, an infraorbital foramen that is dorsal to M1, and a columelliform stapes. *Mygalodelphys* additionally differs from *Microdelphys* by its consistently unpatterned dorsal pelage, small alisphenoid tympanic wing, exposure of the anterior process of the malleus on the external surface of the bulla, and narrow-triangular rostral tympanic process of the petrosal. *Mygalodelphys*

⁵ Self-whitish ventral markings were observed on all examined specimens of *M. handleyi*, most examined specimens of *M. adusta* and *M. peruviana*, and a few specimens of *M. kunsii*. They were not observed in *M. osgoodi*, *M. pinocchio*, *M. reigi*, or *M. ronaldi*.

⁶ A few specimens of *M. kunsii* (< 10% of those examined) have a complete bullar lamina forming a secondary foramen ovale on one side of the skull.

additionally differs from *Monodelphiops* by its unpatterned dorsal pelage, lack of pectoral mammae, and possession of a hypothenar pad of the hind foot.

ETYMOLOGY: From *mygale*, ancient Greek for “shrew,” which members of this clade strikingly resemble in general aspect.

REMARKS: *Mygalodelphys* corresponds to “clade E” or the “Adusta Group” (Pavan et al., 2014; Pavan et al., 2016), which was recovered with consistently robust support in our previous phylogenetic analyses. Although taxon-dense phylogenetic analyses incorporating morphological characters have yet to be done, it seems likely that several features unique to this subgenus (e.g., body pelage extending onto the tail farther ventrally than dorsally; frontal process of the jugal absent or indistinct; no parietal-mastoid contact; narrow lower molar anterior cingulids) will eventually be found to optimize as subgeneric synapomorphies.

Phylogenetic analyses based on mitochondrial and nuclear gene sequences (Pavan et al., 2014; Vilela et al., 2015; Pavan et al., 2016) have consistently recovered a basal dichotomy among the species that we refer to *Mygalodelphys*: one clade including *Monodelphis kunsii* and *M. pinocchio* (*M.* “species 1” of Pavan et al., 2014; Vilela et al., 2015), and another including *M. adusta*, *M. reigi*, *M. peruviana*, *M. osgoodi*, *M. handleyi*, and a still-undescribed form (*M.* “species 2”). Although these clades are robustly supported by sequence data, morphological data does not support their formal taxonomic recognition. Despite being sister taxa, *M. pinocchio* and *M. kunsii* are externally and cranially dissimilar (Pavan, 2015), and we are not aware of any phenotypic trait shared by these two species that consistently distinguish them from the remaining species of *Mygalodelphys*.

Although *Monodelphis ronaldi* has not been included in any phylogenetic analysis to date, we allocate this species to the subgenus *Mygalodelphys* based on its close phenetic similarity to *M. handleyi* (previously noted by Solari, 2007) and to its shared possession of morphological traits that seem likely to optimize as subgeneric synapomorphies, including (1) lack of a distinct frontal process of the jugal, (2) a small sphenorbital fissure within which the basisphenoid is not laterally exposed, (3) lack of parietal-mastoid contact, and (4) narrow anterior cingulids on m2 and m3. Including *M. ronaldi* in future phylogenetic analyses will effectively test the hypothesis that it is a member of *Mygalodelphys*.

NOTES ON DISTRIBUTION AND SYMPATRY: Species of the subgenus *Mygalodelphys* are known from eastern Panama; the humid tropical and subtropical Andes (to ca. 3000 m) of Colombia, Ecuador, Peru, and Bolivia; the Guiana Highlands of southern Venezuela and western Guyana; western and southeastern Amazonia⁷; the Atlantic Forest of southeastern Brazil; the Cerrado landscapes of central Brazil; and the Cerrado, Chaco, and adjacent dry-forested biomes of Bolivia, Paraguay, and northeastern Argentina (table 3). Species of *Mygalodelphys* are sympatric with *Pyrodelphys* in southwestern and southeastern Amazonia (e.g., in the lower Urubamba region of eastern Peru; Solari et al., 2001), with species of the subgenus *Monodelphis* in Amazonia and the Cerrado (e.g., at Bosque Mbaracayú in eastern Paraguay; de la Sancha et al., 2007), with species of the subgenus *Microdelphys* in the Andes and the Atlantic Forest (e.g., at

⁷ The southeastern Amazonian representative of *Mygalodelphys* is the still-undescribed “species 2” of Pavan et al. (2014).

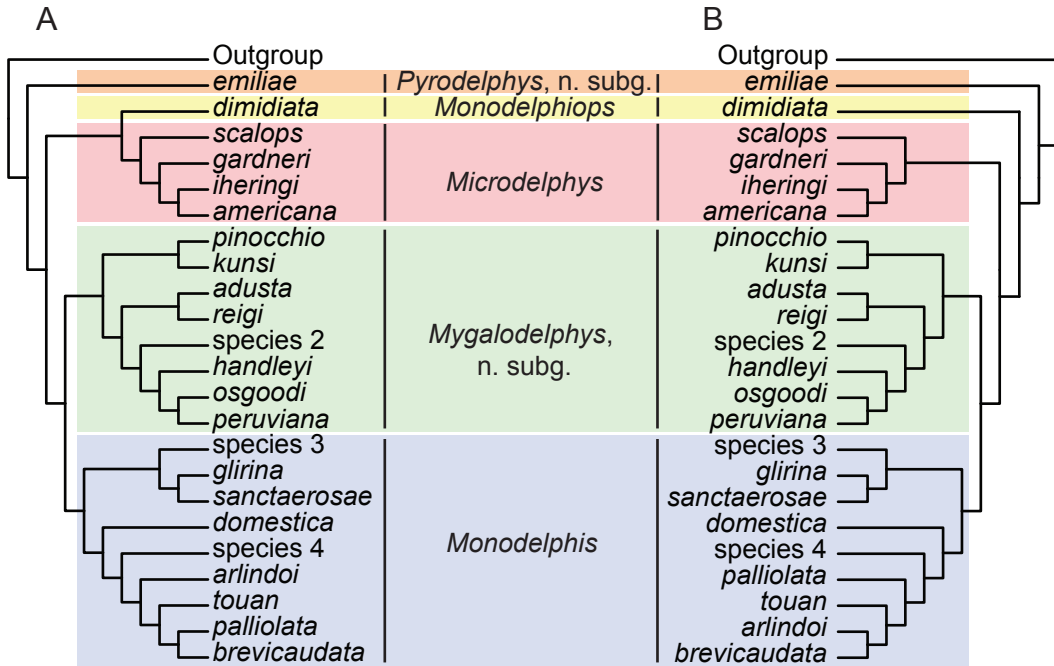


FIG. 13. Phylogenetic hypotheses for species of *Monodelphis* based on maximum-likelihood, maximum-parsimony, and Bayesian analyses (A, after Pavan et al., 2014) and coalescent analyses (B, after Pavan et al., 2016) of DNA sequence data from one mitochondrial and four nuclear genes.

Riacho Grande, São Paulo, southeastern Brazil; Pavan, 2015), and with species of *Monodelphiops* in the Atlantic Forest (e.g., at Parque Nacional do Itatiaia, southeastern Brazil; Pavan, 2015).

Given this wide distribution and extensive sympatry, the absence of *Mygalodelphys* throughout most of northeastern Amazonia (north of the Amazon and east of the Rio Negro), where only species of the nominotypical subgenus are known to occur in lowland habitats, is noteworthy. It is also worth noting that *Mygalodelphys* is the only subgenus known to occur in the northern Andes (north of the Huancabamba Deflection), and in northwestern Amazonia (north of the upper Amazon and west of the Rio Negro). Whether historical or ecological factors account for such distributional phenomena is unknown.

Pyrodelphys, new subgenus

TYPE SPECIES: *Monodelphis emiliae* (Thomas, 1912).

CONTENTS: *emiliae* Thomas, 1912.

DIAGNOSIS: Dorsal body pelage with grayish midbody contrasting with reddish head and rump (fig. 14A); ventral pelage uniformly colored (without self-whitish median markings), yellowish or orangish on museum skins, but much brighter in life (fig. 14B). Mammae 2-1-2 = 5 (MZUSP 35064), 3-1-3 = 7 (MPEG JUR 79), or 4-1-4 = 9 (MPEG 39106, 39182, 42955), all abdominal-inguinal. Thenar and first interdigital pad of pes usually

TABLE 2. Diagnostic Characters of Subgenera of *Monodelphis* Recognized in this Study.

	<i>Mygalodelphys</i>	<i>Pyrodelphys</i>	<i>Monodelphis</i>	<i>Microdelphys</i>	<i>Monodelphiops</i>
Dorsal body pelage	unpatterned	reddish head & rump	reddish sides or unpatterned	stripes, reddish head & rump, or unpatterned	reddish sides with or without mid-dorsal stripe
Self-whitish ventral marking	variable ^{a,b}	absent	absent	absent	absent
Pectoral mammae	absent	absent	absent	present or absent ^{a, b}	present
Thenar & 1st interdigital pads of hind foot	separate	fused or in contact	separate	separate	separate
Hypothenar pad of hind foot	present	usually present	usually absent	variable ^a	absent
Extension of body pelage onto tail	farther ventrally than dorsally	farther dorsally or to about the same extent	farther dorsally or to about the same extent	to about the same extent dorsally and ventrally	to about the same extent dorsally and ventrally
Tail scale arrangement	variable ^{a,b}	annular	annular	annular	spiral
Infraorbital foramen	dorsal to M1	dorsal to M1	dorsal to P3 or P3/M1	usually dorsal to M1	dorsal to P3 or M1
Frontal process of the jugal	absent/indistinct	rounded	rounded	distinctly angular	rounded
Parietal/mastoid contact	absent	present	present	present	present
Incisive foramina	variable ^a	usually short	long	long	short
Maxillopalatine fenestra	variable ^a	short	usually long	long	short
Sphenorbital fissure	narrow	broad	broad	broad	broad
Infratemporal crest of alisphenoid	variable ^a	distinct	distinct	indistinct	distinct
Secondary foramen ovale	absent	variable ^b	absent	variable ^a	absent
Alisphenoid tympanic wing	small	large	small	large	variable ^b
Anterior process of malleus	exposed	concealed	exposed	concealed	variable ^b
Rostral tympanic process of petrosal	triangular	broad and rounded	triangular	broad and rounded	roughly triangular
Stapes	columelliform	columelliform	triangular	columelliform	columelliform
Subsquamosal foramen	large	small	large	large	large
Anterior cingulids	narrow	broad	broad	broad	broad
Entoconids of m1-m3	indistinct	distinct	usually distinct	distinct	distinct
Dp3	variable ^a	small & incompletely molariform	large & molariform	small & incompletely molariform	small & incompletely molariform

^a Differs among member species.^b Intraspecific variation.

fused or in contact; hypothenar pad of pes usually present.⁸ Body pelage extends onto tail farther dorsally than ventrally, or to about the same extent dorsally and ventrally; tail scales arranged in annular series. Infraorbital foramen dorsal to M1; frontal process of jugal present but rounded, not distinctly angular; parietal usually (ca. 80% of examined specimens) in contact with mastoid; incisive foramina usually short; maxillopalatine fenestrae short; sphenorbital fissure large, exposing basisphenoid in lateral view; infratemporal crest of alisphenoid distinct; secondary foramen ovale present or absent; tympanic wing of alisphenoid large; tip of anterior process of malleus not exposed on external bullar surface; rostral tympanic process of petrosal broad and rounded, concealing fenestra cochleae in ventral view; stapes columelliform, imperforate or microperforate; subsquamosal foramen small. Anterior cingulids of m2 and m3 broad; entoconids of m1–m3 distinct; dp3 small, with incomplete trigonid and indistinct anterior cingulid.

COMPARISONS: *Pyrodelphys* is uniquely distinguished from other subgenera of *Monodelphis* by fusion or contact between the thenar and first interdigital pads of the hind foot (the thenar and first interdigital are separate in members of other subgenera) and by having a small subsquamosal foramen (the subsquamosal foramen is distinctly larger in members of other subgenera).

Among other diagnostic comparisons (table 2), *Pyrodelphys* is additionally distinguished from the subgenus *Monodelphis* by having a reddish head and rump separated by a grayish midbody, an infraorbital foramen dorsal to M1, large alisphenoid tympanic wing, unexposed tip of the anterior process of the malleus, broadly rounded rostral tympanic process of the petrosal, columelliform stapes, and smaller dp3. *Pyrodelphys* is additionally distinguished from *Microdelphys* by lacking dorsal stripes in all age-sex classes, by lacking a distinctly angular frontal process of the jugal, and by having a distinct infratemporal crest of the alisphenoid. *Pyrodelphys* is also distinguished from *Monodelphiops* by its dorsal pelage pattern, by lacking pectoral mammae, and by having tail scales in annular series, a large alisphenoid tympanic wing, and a broadly rounded rostral tympanic process of the petrosal. Diagnostic comparisons between *Pyrodelphys* and *Mygalodelphys* have already been provided (see above).

ETYMOLOGY: From *pyr*, ancient Greek for “fire,” in reference to the flame-colored underparts of living and freshly dead specimens of this clade (fig. 14B).

REMARKS: This taxon is widely divergent from other clades in the genus *Monodelphis* and appears to represent an ancient lineage with no close extant relatives (Pavan et al., 2014; Pavan et al., 2016).

NOTES ON DISTRIBUTION AND SYMPATRY: *Monodelphis (Pyrodelphys) emiliae* is known from southwestern and southeastern Amazonia (table 3), where it ranges from near the base of the Andes in Peru and Bolivia to eastern Pará, Brazil. Based on geographic range overlap and published reports of cooccurring species (e.g., in the lower Urubamba region of eastern Peru;

⁸ The thenar and first interdigital pads are separate in two specimens (MPEG 39138, 42955) out of 14 examined for this trait. The hypothenar pad is absent in two, and vestigial in four out of 14 specimens examined.

Solari et al., 2001), *Pyrodelphys* may occur sympatrically with species of the subgenera *Mygalodelphys* and/or *Monodelphis* throughout its geographic range.

Subgenus *Monodelphis* Burnett, 1830

TYPE SPECIES: *Monodelphis brachyuros* (Schreber, 1777), an objective junior synonym of *M. brevicaudata* (Erxleben, 1777), by subsequent designation (Matschie, 1916).

SYNONYMS: *Peramys* Lesson, 1842 (see Remarks, below).

CONTENTS: *arlindoi* Pavan et al., 2012; *brevicaudata* Erxleben, 1777 (including *brachyuros* Schreber, 1777; *dorsalis* Allen, 1904; *hunteri* Waterhouse, 1841; *orinoci* Thomas, 1899; and *sebae* Gray, 1827); *domestica* Wagner, 1842; *glirina* Wagner, 1842 (including *maraxina* Thomas, 1923); *palliolata* Osgood, 1914; *sanctaerosae* Voss et al., 2012; and *touan* Shaw, 1800 (including *touan* Bechstein, 1800; *touan* Daudin in Lacépède, 1802; and *tricolor* Geoffroy St.-Hilaire, 1803).

DIAGNOSIS: Dorsal body pelage unpatterned, or with a grayish middorsum contrasting with clear yellowish, orange, or reddish flanks; ventral pelage uniformly colored, without self-whitish median markings. Mammæ 3–1–3 = 7 (e.g., in *M. domestica*; MZUSP 20597), 4–1–4 = 9 (e.g., in *M. brevicaudata*; AMNH 130574), or 6–1–6 = 13 (e.g., in *M. domestica*; MZUSP 17500), all abdominal-inguinal. Thenar and first interdigital pads of hind foot separate; hypothenar pad of hind foot usually absent. Body pelage extends onto tail farther dorsally than ventrally, or to about the same extent dorsally and ventrally; tail scales arranged in predominantly annular series. Infraorbital foramen usually dorsal to P3 or P3/M1 commissure; frontal process of jugal present but rounded, not distinctly angular; parietal usually (ca. 80% of examined specimens) in contact with mastoid; incisive foramina long; maxillopalatine fenestra usually long; sphenorbital fissure large, basisphenoid laterally exposed; infratemporal crest of alisphenoid distinct; secondary foramen ovale absent; tympanic wing of alisphenoid small; tip of anterior process of malleus exposed on external surface of bulla; rostral tympanic process of petrosal narrow and triangular, not concealing the fenestra cochleae in ventral view; stapes triangular or subtriangular, with a large obturator foramen; subsquamosal foramen large. Anterior cingulids of m2 and m3 broad; entoconids of m1–m3 distinct; dp3 large, with complete trigonid and distinct anterior cingulid.

COMPARISONS: Members of the subgenus *Monodelphis* uniquely differ from other congeners by their triangular or subtriangular stapes (with a large obturator foramen; Wible, 2003: fig. 6). Additionally, species of the subgenus *Monodelphis* differ from species of *Microdelphys* by lacking striped dorsal pelage at any age in either sex; by the position of the infraorbital foramen over P3 or over the P3/M1 commissure; by lacking a distinctly angular frontal process of the jugal; and by having a distinct infratemporal crest, small alisphenoid tympanic wing, an exposed tip of the anterior process of the malleus, a narrow-triangular rostral process of the squamosal, and a large and fully molariform dp3. Species of the subgenus *Monodelphis* additionally differ from species of *Monodelphiops* by lacking pectoral mammae, and by having tail

TABLE 3. Geographic Distribution of the Subgenera of *Monodelphis*.^a

	Andes	Northern Venezuela	Guiana Highlands	Amazonia	Arid Diagonal	Atlantic Forest	Pampas
<i>Mygalodelphys</i>	X		(X) ^b	(X) ^c	(X) ^d	(X) ^e	
<i>Pyrodelphys</i>				(X) ^f			
<i>Monodelphis</i>		X		(X) ^g	X		
<i>Microdelphys</i>	(X) ^h			(X) ⁱ	(X) ^j	X	
<i>Monodelphiops</i>						(X) ^e	X

^a Key: X = present; (X) = present but not throughout region.

^b Possibly widespread but currently known from only two localities.

^c Not known to occur in NE Amazonian lowlands.

^d Not known to occur in the Caatinga.

^e Not known to occur in northern part of Atlantic Forest.

^f Only in SE and SW Amazonia.

^g Not known to occur in NW Amazonia.

^h Only known from a few localities in central Peru.

ⁱ Restricted to the lower Tocantins.

^j Only in gallery forests.

scales in predominantly annular series, longer incisive foramina and maxillopalatine fenestrae, and a large and fully molariform dp3.

Comparisons of the nominotypical subgenus with *Mygalodelphys* and *Pyrodelphys* have already been described (see above).

REMARKS: The nominotypical subgenus corresponds to “clade F” or the “Brevicaudata Group” as reported in our previous phylogenetic analyses, which recovered it with consistently robust support (Pavan et al., 2014; Pavan et al., 2016).

The status of *Peramys* Lesson, 1842, as an objective junior synonym of *Monodelphis* merits comment. Lesson (1842) included only four nominal species in *Peramys*, listing “Plata; Maldonado” as the geographic distribution of *P. brachyurus* and *P. crassicaudata*, “Brésil” as the geographic origin of *P. tristriata*, and “Paraguay” as the geographic origin of *P. pusilla*. He did not mention the authors of these epithets, although he did mention the authors of other binomina (e.g., of *Didelphis*) in the same work, so it might be assumed that Lesson wished the species of *Peramys* to be understood in a geographically restricted sense, or at least in a sense not necessarily the same as that of the original authors of these names. However, this intention was not made explicit, and his formatting of other generic accounts suggests that Lesson was simply inconsistent as to whether authors, geography, or both were provided for listed species. Lesson did not indicate which of the nominal species of *Peramys* should be considered the type species, because the type concept was not current at the time he wrote.

The type species of *Peramys* was first designated by Thomas (1888b: 354) as “*D[idelphys]. brevicaudata*,” but *brevicaudata* is not eligible for type designation because it was not listed among the nominal species originally included in *Peramys* (ICZN, 1999: Article 67.2). However, Thomas often indicated type species indirectly, by using their senior synonyms, and this intention is sup-

ported by his listing *brachyura* Schreber, 1777 ("1778"),⁹ among the junior synonyms of *D. brevicaudata* Erxleben, 1777. Therefore, there can be no doubt that Thomas intended to designate the nominal species that Lesson called *P. brachyurus* as the type species of *Peramys*.

Although *Didelphis brachyura* Schreber is an objective synonym of the Guianan species *D. brevicaudata* Erxleben, Lesson's (1842) geographic indication suggests that he might have used *brachyurus* in the sense of Waterhouse (1839), who mistakenly applied Schreber's name to a specimen that Darwin collected at Maldonado (Uruguay), the holotype of *D. dimidiata* Wagner, 1847. According to the Code (ICZN, 1999: Article 11.10), "if an author employs a specific or subspecific name for the type species of a new nominal genus-group taxon, but deliberately in the sense of a previous misidentification of it, then the author's employment of the name is deemed to denote a new nominal species, and the specific name is available with its own author and date as though it were newly proposed in combination with the new genus-group name." Gardner (2005) and Pine and Handley (2008) have interpreted this to mean that the type species of *Peramys* is *P. brachyurus* Lesson, an objective senior synonym of *D. dimidiata* Wagner. However, it is quite clear that Thomas (1888b) did *not* deliberately indicate *brachyurus* in the sense of Waterhouse (1839), because he (Thomas, 1888b: 355) listed Waterhouse's misidentification in the synonymy of *D. dimidiata*.

Therefore, we follow Palmer (1904) and Cabrera (1919, 1957) in interpreting Thomas's (1888b) designation of a type species for *Peramys* as so indicating *P. brachyurus* (Schreber). Because *Didelphis brachyura* Schreber is also the type species of *Monodelphis* Burnett, 1830, it follows that *Peramys* is an objective junior synonym of the nominotypical subgenus.

NOTES ON DISTRIBUTION AND SYMPATRY: Species of the subgenus *Monodelphis* occur throughout northeastern Amazonia (north of the Amazon and east of the Rio Negro), southeastern Amazonia (south of the Amazon and east of the Rio Madeira), and throughout the



FIG. 14. Dorsal (A) and ventral (B) views of a freshly killed specimen of *Monodelphis* (*Pyrodelphys*) *emiliae*, illustrating the diagnostically flame-colored ventral pelage (photo courtesy of M. Hoogmoed). Whereas the dorsal coloration of this species is faithfully preserved even in decades-old museum skins, the ventral coloration quickly fades after death.

⁹ Schreber's epithet is available from plates that were published in 1777, the year before his text (Sherborn, 1891).

so-called Arid Diagonal (Caatinga, Cerrado, and Chaco); additionally, one species (*M. glirina*) is marginally distributed in southwestern Amazonia (Pine and Handley, 2008; Pavan et al., 2012; Voss et al., 2012; Pavan et al., 2014) (table 3). The nominotypical subgenus is not known to occur in northwestern Amazonia (north of the upper Amazon and west of the Rio Negro), nor does it occur in the Andes or in the Atlantic Forest, where it is replaced by species of *Mygalodelphys* and/or *Microdelphys*. Species of the subgenus *Monodelphis* are known to occur sympatrically with *Pyrodelphys* on Amazonia, with species of *Mygalodelphys* in Amazonia and the Cerrado (see previous accounts), and one species (*M. domestica*) occurs sympatrically with *Microdelphys* in the Arid Diagonal (e.g., near Brasília; Alho et al., 1987).

Subgenus *Microdelphys* Burmeister, 1856

TYPE SPECIES: *Monodelphis tristriata* (Illiger, 1815), an objective junior synonym of *M. americana* (Müller, 1776), by subsequent designation (Thomas, 1888b).

CONTENTS: *americana* Müller, 1776 (including *brasiliensis* Erxleben, 1777; *brasiliensis* Daudin in Lacépède, 1802; *rubida* Thomas, 1899; *trilineata* Lund, 1840; *tristriata* Illiger, 1815; and *umbristriata* Miranda-Ribeiro, 1936); *iheringi* Thomas, 1888a; *scalops* Thomas, 1888a (including *theresa* Thomas, 1921); and *gardneri* Solari et al., 2012.

DIAGNOSIS: Dorsal body pelage usually marked with dark longitudinal stripes (but uniformly reddish in mature males of *M. americana*, and with grayish midbody contrasting with reddish head and rump in mature males of *M. scalops*); ventral pelage uniformly colored, without self-whitish median markings. Mammae 4-1-4 = 9 to 8-1-8 = 17, all abdominal-inguinal or abdominal-inguinal and pectoral. Thenar and first interdigital pads of hind foot separate; hypothenar pad of hind foot present or absent. Body pelage extends onto tail to about the same extent dorsally and ventrally; tail scales arranged in annular series. Infraorbital foramen usually dorsal to M1; frontal process of jugal well-developed and distinctly angular; parietal in contact with mastoid; incisive foramina long; maxillopalatine fenestra long; sphenorbital fissure large, basisphenoid laterally exposed; infratemporal crest of alisphenoid indistinct; secondary foramen ovale present or absent; tympanic wing of alisphenoid large; tip of anterior process of malleus not exposed on external surface of bulla; rostral tympanic process of petrosal broad and rounded, concealing fenestra cochleae in ventral view; stapes columelliform, imperforate or microperforate; subsquamosal foramen large. Anterior cingulids of m2 and m3 broad; entoconids of m1-m3 distinct; dp3 small and incompletely molariform (with bicuspid trigonid and indistinct anterior cingulid).

COMPARISONS: A dorsal pelage that includes three dark longitudinal stripes is unique to *Microdelphys* and is present in all member species, although it is lost ontogenetically in adult males of *M. americana* and *M. scalops*. Another feature that distinguishes *Microdelphys* from all other congeners is a well-developed and distinctly angular frontal process of the jugal.

Microdelphys additionally differs from *Monodelphiops* by having caudal scales in annular series, longer incisive foramina and maxillopalatine fenestrae, an indistinct infratemporal crest of the alisphenoid, a large alisphenoid tympanic wing, and a broadly rounded rostral tympanic process that conceals the fenestra cochleae in ventral view.

Comparisons of *Microdelphys* with other subgenera of *Monodelphis* have already been provided (see above).

REMARKS: As recognized in this report, *Microdelphys* includes “Clade C” and “Clade D” as recovered by the molecular analyses of Pavan et al. (2014). Although the sister-group relationship between clades C and D was not recovered by phylogenetic analyses based on mitochondrial sequence data (e.g., by Solari, 2010; Pavan et al., 2014; Vilela et al., 2015), compelling support for this relationship is provided by Bayesian analyses of multigene datasets (e.g., Pavan et al., 2016), and by the three-striped dorsal pelage pattern uniquely shared by juvenile and female specimens of all included species. An alternative nomenclatural solution would be to restrict *Microdelphys* to “Clade D” and to name a new subgenus for *Monodelphis scalops* (“Clade C”), but this seems unnecessary and would effectively discard important information about shared ancestry.

NOTES ON DISTRIBUTION AND SYMPATRY: Species of *Microdelphys* occur in forested areas of easternmost Para, in the Brazilian Atlantic Forest, in northeastern Argentina (Misiones), in some gallery forests of central and northeastern Brazil, and in the central Andes of Peru (Solari et al., 2012; Pavan et al., 2014) (table 3). *Microdelphys* is broadly sympatric with *Monodelphiops* in the southern Atlantic Forest, where these taxa have been collected together at several localities (Pavan, 2015), and it also occurs sympatrically with species of *Mygalodelphys* and *Monodelphis* (see previous accounts).

Subgenus *Monodelphiops* Matschie, 1916

TYPE SPECIES: *Monodelphis sorex* (Hensel, 1872), a subjective junior synonym of *Monodelphis dimidiata* (Wagner, 1847), by original designation.

SYNONYMS: *Minuania* Cabrera, 1919.

CONTENTS: *dimidiata* Wagner, 1847 (including *fosteri* Thomas, 1924; *henseli* Thomas, 1888a; *itatiayae* Miranda-Ribeiro, 1936; *lundi* Matschie, 1916; *paulensis* Vieira, 1950; and *sorex* Hensel, 1872); and *unistriata* Wagner, 1842.

DIAGNOSIS: (Asterisks in this section indicate traits exhibited by *Monodelphis dimidiata* that have yet to be confirmed for *M. unistriata*.) Dorsal body pelage grayish middorsally, with (*M. unistriata*) or without (*M. dimidiata*) a single dark longitudinal stripe, contrasting with clear yellowish, orange, or reddish flanks; ventral pelage uniformly colored (yellowish, orangish, or reddish), without self-whitish markings. Mammae 6–5–6 = 17 to 11–5–11 = 27 (Thomas, 1888b: 361), including abdominal-inguinal and pectoral teats.* Thenar and first interdigital pads of hind foot separate*; hypothenar pad of hind foot absent.* Body pelage extends onto the tail to about the same extent dorsally and ventrally; tail scales arranged in spiral series. Infraorbital foramen dorsal to P3 or M1; frontal process of jugal present but rounded, not distinctly angular*; parietal usually (> 90% of examined specimens) in contact with mastoid*; incisive foramina short; maxillopalatine fenestrae short; sphenorbital fissure usually large, exposing basisphenoid laterally*; infratemporal crest of alisphenoid distinct*; secondary foramen ovale usually absent (rarely present bilaterally)*; tympanic wing of alisphenoid usually small*; tip of anterior process of the malleus exposed or not on external surface of bulla*; rostral tympanic process of petrosal triangular (not broadly rounded), but

sometimes concealing fenestra cochleae ventrally*; stapes columelliform, imperforate or microperforate*; subsquamosal foramen large*. Anterior cingulids of m2 and m3 broad; entoconids of m1–m3 distinct; dp3 small and incompletely molariform, with bicuspid trigonid and indistinct anterior cingulid*.

COMPARISONS: Comparisons of *Monodelphiops* with other subgenera of *Monodelphis* have already been provided (see above).

REMARKS: Molecular sequence data are currently unavailable from *Monodelphis unistriata*, so inferences about its relationships are necessarily based on morphology. Although Pine et al. (2013) recovered *M. unistriata* as the sister taxon of *M. iheringi* based on a combined analysis of morphological characters and cytochrome-*b* sequences (the latter coded as missing for *M. unistriata*), the authors themselves stated that the characters sampled for their study were not “sufficiently informative as to allow refined elucidation of the relationships in this genus” (Pine et al., 2013: 433), and that additional characters as well as inclusion of other species would be necessary to “ever more firmly ascertain the relationships of this enigmatic taxon” (Pine et al., 2013: 435). They also noted multiple morphological similarities between *M. unistriata* and *M. dimidiata*, suggesting that *M. unistriata* could be more closely related to *M. dimidiata* than to any other species (Pine et al., 2013: 432).

Among several possible explanations for such anomalous results, *M. unistriata* is known from just two specimens, one consisting only of a skin and the other of a skin and part of the skull (Pine et al., 2013: fig. 2), so information is missing for many morphological characters, including those of the posterior braincase, zygomatic arches, and ear region. We hypothesize that *M. unistriata* and *M. dimidiata* are sister taxa based on shared attributes that seem likely to optimize as synapomorphies in future phylogenetic analyses. Such attributes include: a dorsal body pelage with a grizzled middorsum contrasting with clear yellowish, orange, or reddish flanks; large tail scales arranged in spiral series; very short incisive foramina (a striking similarity previously noted by Pine et al., 2013); and short maxillopalatine fenestrae. Of course, this hypothesis needs to be tested using taxon-dense phylogenetic analyses of morphological and molecular data when fresh material of this apparently elusive species become available.

NOTES ON DISTRIBUTION AND SYMPATRY: *Monodelphiops* occurs in southeastern Brazil, eastern Paraguay, Uruguay, and northeastern Argentina (Vilela et al., 2010; Pine et al., 2013) (table 3), where it is sometimes sympatric with *Mygalodelphys* and *Microdelphys* (see previous accounts).

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APPENDIX 1

SPECIMENS EXAMINED

Subgenus *Mygalodelphys*

Monodelphis adusta ($N = 24$)—COLOMBIA, *Boyacá*, Guaicaramo (AMNH 75232); *Cundinamarca*, Paime (MNHN 1929-672), Susumuco (BMNH 21.5.2.6), “W. Cundinamarca” (BMNH 97.7.2.1 [holotype of *adusta*]); *Magdalena*, Colonia Agrícola de Caracolicito (USNM 280894); *Meta*, Villavicencio (AMNH 136158, 139227, 202650), 7 km NE Villavicencio (AMNH 207765); *Tolima*, Mariquita (BMNH 12.4.2.10, 12.9.8.3). ECUADOR, *Napo*, Lumbaqui (USNM 534286), San Jose Abajo (AMNH 68136); *Pastaza*, Mera (AMNH 67274), Safari Hostería Park (TTU 84865, 84899); *Tunguragua*, Palmera (AMNH 67275); *Zamora-Chinchipe*, Zamora (AMNH 47189). PANAMA, *Darien*, Cana (USNM 179609 [holotype of *melanops*]), Guayabo (ANSP 19676), Tacarcuna Village Camp (USNM 309263). PERU, *Loreto*, 1.5 km N Teniente Lopez (KU 157978), Estación Biológica Allpahuayo (TTU 98923, 101164).

Monodelphis handleyi ($N = 6$)—PERU, *Loreto*, Jenaro Herrera (AMNH 276698, 276704, 276709, MUSM 23808–23810).

Monodelphis kunsii ($N = 36$)—ARGENTINA, *Salta*, Finca Falcón (MACN-Ma 23783, 23784). BOLIVIA, *El Beni*, La Granja (USNM 461348 [holotype of *kunsii*]); *Santa Cruz*, El Refugio (USNM LHE 1692); *Tarija*, Río Lipeo (ANSP 18191), Tapequa (AMNH 263968). BRAZIL, *Distrito Federal*, Fazenda Agua Limpa (OMNH 22265–22266); *Goiás*, Silvânia (MN A 191); *Mato Grosso*, Fazenda Tanguro (MPEG 43016–43017), Reserva do Patrimônio Particular Natural SESC Pantanal (MN 64323, 64411, 64424); *Mato Grosso do Sul*, margem direita Córrego Urucum (UFMG LFS 202), Mineração Rio Tinto (UFMG RM 318–319, 324, 340); *Minas Gerais*, Aiuruoca (MCN-M 1570, 1607), Betim (MCN-M 1470, 1531), Divinópolis (MCN-M 1256), Palmital (MCN-M 2964), Parque Nacional da Serra do Cipó (MZUSP MTR 20361, MCN-M 1465), Pompéu (MCN-M 1420, 1421), Rio Manso (MCN-M 2273), Serra do Salitre (MCN-M 2304), Unidade Ambiental Jacob (UFMG 1965); *São Paulo*, Nadiu Figueredo (MN 46571); *Tocantins*, Peixe (MZUSP 35059). PARAGUAY, *Canendeyú*, Reserva de Biosfera del Bosque Mbaracayú (TTU 116526); *Presidente Hayes*, Trans-Chaco Highway, Km 412 (FMNH 164094). Locality unknown (MN 73381).

Monodelphis osgoodi ($N = 3$)—BOLIVIA, *Cochabamba*, 4.4 km N Tablas Monte (AMNH 264922), Incachaca (CM 5242 [holotype of *osgoodi*]). PERU, *Cusco*, Ocobamba Valley (USNM 194379).

Monodelphis peruviana ($N = 13$)—BOLIVIA, *La Paz*, Serranía Bella Vista (AMNH 264562). PERU, *Cusco*, 2 km SW Tangoshiari (USNM 588019), 3 km E Amaybamba (MVZ 173928), Cashiriari (USNM 582782), Pillahuata (FMNH 172032), Suecia (FMNH 189811); *Huánuco*, Hacienda San Antonio (USNM 259433); *Junín*, Cordillera Vilcabamba (USNM 582110); *Loreto*, Nuevo San Juan (AMNH 272695, 272781, MUSM 13297, 15318); *Madre de Dios*, Reserva Cusco Amazónico (MUSM 7157).

Monodelphis pinocchio ($N = 7$)—BRAZIL, *Espírito Santo*, Serra do Caparaó (MZUSP MTR 15815); *Rio de Janeiro*, Alto do Itatiaia (AMNH 61547), Serra de Macaé (MZUSP 2793);

São Paulo, Reserva Florestal do Morro Grande (MN 78651, 78680 [holotype of *pinocchio*]), Riacho Grande (MZUSP 30740). Locality unknown (MZUSP 33878).

Monodelphis reigi ($N = 2$)—GUYANA, *Potaro-Siparuni*, Mount Ayanganna (ROM 114699, 114864).

Monodelphis ronaldi ($N = 1$)—PERU, *Madre de Dios*, Pakitza (MUSM 17027).

Subgenus *Pyrodelphys*

Monodelphis emiliae ($N = 80$)—BOLIVIA, *Abuna*, 18 km N San Juan de Nuevo Mundo (USNM 579574). BRAZIL, *Acre*, Igarapé Porongaba (MPEG 28113, MVZ 190335), Sobral (MPEG 28114 [= MVZ 193609]); *Amazonas*, Rio Abacaxis, (MZUSP 35062–35066), Seringal Condor (MVZ 190334); *Mato Grosso*, Aripuanã (MZUSP 35057–35058, MZUSP APC 254, MZUSP PEU 960014), Juruena (MZUSP APC 157); *Pará*, Baião (AMNH 96810), Belterra (MPEG 12585), Boim (AMNH 37491, BMNH 11.12.22.16 [holotype of *emiliae*], MPEG 539), Cametá (MCZ 30418), Estrada Santarem–Cuiaba, Km 217 (USNM 461883), Fordlândia (FMNH 94293), Igarapé Amorim (AMNH 95816), Mina do Palito (MPEG 42955), Jatobá (UFPA 1206, 1376–1377), Juruti (MPEG 38366, 38398, 38427, 38525–38526, 38533, 38691, 38693, 38697, 38701, 40660, 40664, 40675–40677, MPEG JUR 20, 41, 47, 55, 57, 71, 79), Transamazônica Itaituba–Jacareacanga, Km 200 (USNM 461884), Vila Braga (MN 1299, 1300); *Rondônia*, Porto Velho (MCN-M 2078), UHE Samuel (MPEG 22546–22547). PERU, *Loreto*, Jenaro Herrera (AMNH 276721, MUSM 23807), Nuevo San Juan (AMNH 268221, MUSM 13298), Quebrada Aucayo (FMNH 58955). Locality unknown (MPEG 11839, 35272–35274, 39106, 39138–39139, 39182, 39191, 39244, 41814, 41821–41822, 41826, 41833, 41836, 41841, MPEG STA07).

Subgenus *Monodelphis*

Monodelphis arlindoi ($N = 89$)—BRAZIL, *Pará*, Cachoeira Porteira (MPEG 10035, 10037–10048, 10260–10265, 12739–12741, 12744, 12927, 12930–12931, 12936, 12942, 12951, USNM 546209–546219), ESEC Grão Pará Sul (MPEG 40048), FLOTA de Faro (MPEG 39988, MPEG MBA 62), Porto Trombetas (MPEG 38052 [holotype of *arlindoi*], 38054, 38056, 38063, 38074, 38093, 38095, 39810–39812, 39815, 42371, 42399, 42428, 42438, 42440, UFMG 2283, 3184–3190), Rio Jamundá (AMNH 93971–93974, 94161, 94221); *Roraima*, Usina Hidrelétrica de Alto Jatapu (MN 51660). GUYANA, *Potaro-Siparuni*, Anundebaru (AMNH 75830–75831), Minehaha Creek (AMNH 36317), Mount Wokomung (ROM 115765), Iwokrama Reserve (ROM 108692, ROM 108477); *Upper Takutu-Upper Essequibo*, Upper Essequibo Conservation Concession (ROM 118998). SURINAME, *Brokopondo*, Brownsberg Nature Park (CM 52729); *Sipaliwini*, Avanavero (CM 68358), Kayserberg airstrip (CM 68359), Raleigh Falls (CM 63509–63511, 68361), Werehpai Camp (ROM 120710).

Monodelphis brevicaudata ($N = 100$)—BRAZIL, *Amazonas*, Barcelos (MN 56824, 69058, 69367, 69371), Barreira (INPA CGB 82, 90); *Roraima*, Barreira (INPA CGB 80, 81), Estação Ecológica Maracá (MPEG 34057, MPEG AN 305). GUYANA, *Barima-Waini*, Baramita (USNM 568009), Waikerebi (ROM 98909); *Cuyuni-Mazaruni*, Kartabo (AMNH 48133, 60639). VEN-

EZUELA, *Amazonas*, Boca Río Ocamo (AMNH 78093–78095), Capibara (USNM 406907, 406908, 415277), Esmeralda (USNM 385010), Mt. Duida (AMNH 7281–7285, 77287–77296, 77565–77566), Raya (USNM 406910–406913), Buena Vista (AMNH 77286), El Merey (AMNH 78096–78099), Frente el Merey (AMNH 78100), “Río Casaquiare” (AMNH 77286), Río Orinoco (AMNH 78092), Serra de Neblina (AMNH 244469), Tamatama (USNM 388355, 388357, 406906, 490231–490233, 490235); *Bolívar*, Arabupu (AMNH 75681–75687, 75838, 75842), Auyán-tepuí (AMNH 130516, 130560–130565, 130573–130576, 130727), Caicara (BMNH 98.12.1.22 [holotype of *orinoci*], Ciudad Bolívar (AMNH 16124–16126 [syntypes of *dorsalis*], Rio Caroni (EBRG L-1917, L-1918, L-1920), San Ignacio de Yuruaní (USNM 448511, 448512, 448750), Suapure (AMNH 16953, 16954), 45 km NE Icabarú (USNM 443781, 443782, 490247), 5.2 km NE San Ignacio de Yuruaní (AMNH 257201, 257203), 50 km SE El Manteco (USNM 385004), 65 km SSE El Dorado (USNM 385005). Locality unknown (BMNH 67.4.12.540 [holotype of *brevicaudata*], BMNH 88.1.31.1 [holotype of *hunteri*]).

Monodelphis domestica ($N = 319$)—BOLIVIA, *Chuquisaca*, Porvenir (AMNH 261231), Tihumayu (USNM 290898); *El Beni*, La Granja (USNM 461347), San Joaquin (USNM 364714–374715, 460728–460731); *Santa Cruz*, Basilio (USNM 390568), San Ignacio de Velasco (USNM 390015, 391454–391463, 391470), Tita (AMNH 260024), 3.4 km S Basilio (USNM 390566–390567). BRAZIL, *Alagoas*, Estaleiro EISA (UFSC 4775–4784); *Bahia* (MACN-Ma 24577), Curaçá (UFSC 2818), Feira de Santana (MZUSP 9934), Jequié (MZUSP 10461), Machado Portela (MZUSP 1515), Morro do Chapéu (MZUSP MTR 22551, 22558–22560), Mucugê (MZUSP 28939), Rio do Peixe (FMNH 20418), Santo Inácio (MZUSP 35061, MZUSP MTR 11314, 11223); *Ceará* (MCN-M 1285, 1312–1315), Baturité (MZUSP 8710, 17500), Jua (FMNH 20256–20267), Quixadá (FMNH 20255, USNM 259431), Santana do Cariri (USNM 304585), São Gonçalo do Amarante (MCN-M 2591), Serra de Batutité (MZUSP 29470–29471; *Goiás*, Cana Brava (MZUSP 4103–4104, 4106, 4108–4109, 4111, 4114–4116, 4118, 4121–4122, 4124–4125, 4127–4128, 12884), Minaçu (MPEG 26392–26396); *Maranhão*, Bacabal (MPEG 35317, 35330, MPEG CZ 1417); *Mato Grosso*, Chapada dos Guimarães (MZUSP 35054, 35197), Cocalinho (MZUSP 35199), Cuiabá (BMNH 87.10.25.1, NMW B-2604–B-2608, B-2611–B-2612, B-2617, B-2625, ZMB 3195 [syntypes of *domestica*]), Estação Ecológica Serra das Araras (MZUSP 35198), 3–15 km SE Carceres (USNM 390017), 4–10 km NW Cuiabá (USNM 391453), 48 km W Carceres (USNM 391464–391469); *Mato Grosso do Sul*, Corumbá (USNM 390016), Fazenda Acurizal (MZUSP 17424), Fazenda Toboco (MVZ 197457), Porto Faia (MZUSP 1705–1707, 1709–1711, 3781), Reserva Particular do Patrimônio Natural Fazenda Acurizal e Fazenda Penha (MZUSP 35211–35218, 35220. 35222–35226); *Minas Gerais* (MCN-M 17, 24, 41, 43, 312–314, 467, 578, 600, 654, 765, 844, 853, 988, 1042, 1243, 1245, 1298–1299, 1357, 1434, 1457, 1475, 1478, 1596, 1681, 1936, 1938, 1942, 2000, 2014, 2042, 2177, 2278, 2291, 2300, 2352, 2462, 2499, 2596, 2772, 2878, 2909, 2972), Araguari (MZUSP 30554), Barro Alto (MZUSP 4100–4102, 4105, 4107, 4110, 4117, 4119, 4123, 4126), Belo Horizonte (UFMG 906), Bocaiúva (UFMG 2439), Brasilândia de Minas (UFMG 2387), Itinga (UFMG 1463), Mateus Leme (UFMG 1495), Perdizes (UFMG 1760–1761); *Pernambuco* (MACN-Ma 24576, USNM 268744), Exu (MZUSP 16611, 16612, 16615–16623, 16625, 18908, 20589–20600, USNM 528401–

528406), Serra Talhada (MZUSP 16613–16614), Sítio Seriema (MACN-Ma 24580); *Piauí*, Bom Conselho (MZUSP 11699–11700), Castelo do Piauí (LZUFPI 201), Estação Ecológica Uruçuí-Una (MZUSP 30552–30553, 30545–30551, 30555–30556), José de Freitas (LZUFPI 158), Parque Nacional de Sete Cidades (LZUFPI 1098), Parque Nacional Serra das Confusões (MZUSP 34940, 34946, MZUSP PNSC 20, 49), União (LZUFPI 146), Valença do Piauí (MZUSP 16624); *Tocantins* (MPEG 34994), Aliança do Tocantins (MPEG 31574, 35231), Figueirópolis (MZUSP 35024–35025), Palmeirante (MPEG 34983), Paranã (MZUSP 35055–35056), Peixe (MZUSP 35057–35058). PARAGUAY, *Alto Paraguay*, Fortín Pikyrenda (TTU 116524); *Ambay*, Estancia Ocaris (MSB 82535), Parque Nacional Cerro Corá (USNM 554540); *Boquerón*, Parque Nacional Teniente Agripino Enciso (TTU 116523, USNM 555659); *Canindeyu*, Reserva Mbaracayú (TTU 116525); *Concepción*, Escuela Agropecuaria (MSB 82534); *San Pedro*, Tacuati (USNM 293130–293131). Locality unknown (LZUFPI 32, 56, 73, 147, 167, 168, 190, 208, 231, 232, MACN-Ma 20942, 24575, MZUSP 1708, 19698, 35200, 35228, 35210, MZUSP MN6 10, 12, 13, 24, 33, 36, 39, USNM 464976–464979, 464981, 540044–540045, 540050, 541403–541405, 541409).

Monodelphis glirina ($N = 358$)—BOLIVIA, *La Paz*, Guanay (AMNH 72570), *Pando*, Santa Rosa (AMNH 262398, 262399), Independencia (AMNH 262397). BRAZIL, *Acre*, Sena Madureira (MPEG 10553, 10694–10697, 12738), Plácido de Castro (UFMG 1613); *Amazonas*, Humaitá (MPEG 12745, 22690, 34395, MPEG AN 213, 224, 227–229, 235, 248, 252, 258, 268, USNM 545552–545554), São José das Pombas (MZUSP 35060); *Mato Grosso*, Alta Floresta (UFMG 2653, MVZ 197456), Apiacás (MZUSP 35077–35080), Aripuanã (MN 59608, MPEG 12718–12735, 12749, 12934–12935, 12937–12940, 12952, MZUSP 35073–35076, MZUSP APC 222, MZUSP PEU 960062, USNM 545555–545582), Jauru (MN 69849, 71606), Juruena (MN 59606–59607, MZUSP 35069–35072); *Pará*, Agrovila da União (MPEG 8934, 8936, 11528–11532, 15284, 15310, 15347, USNM 521431, 521508–521510), Aramanai (AMNH 94901), Belterra (MPEG 11840), Canaã dos Carajás (MCN-M 1468, 1499), Curuá-Una (MPEG 11841–11842, 15415–15421), Floresta Nacional de Carajás (MCN-M 1395–1396, 1486, 2272), Floresta Nacional do Crepori (MPEG 40574, MHNCI 6218), Fordlândia (AMNH 133248), Ilha do Marajó (BMNH 23.8.9.9 [holotype of *maraxina*], 1924.2.4.40, 1924.2.4.43), Itaituba (MPEG 15234–15235), Itaituba–Altamira, Km 25 (USNM 543299–543301), Itaituba–Jacareacanga, Km 19 (USNM 461664–461665), Marabá (UFSC 5209), Miritituba (CM 5061, MPEG TF 04, 07), Mojuí dos Campos (MPEG 12586, 12742–12743, USNM 545583), Piquiatuba (AMNH 94903), Santarém (CM 4681), Santarém–Cuiabá (MPEG 8091), Santarém–Cuiabá, Km 82 (MPEG 15230), Santarém–Cuiabá, Km 84 (MPEG 8089, 15231–15233, USNM 461666–461670), Santarém–Cuiabá, Km 212 (MPEG 8678, USNM 544480), Santarém–Cuiabá, Km 216 (MPEG 8092, 12717, 15236–15238, USNM 544486), Santarém–Cuiabá, Km 217 (MPEG 8082–8088, 8679, 8681, 15225, USNM 544478–544479, 544481–544485, 544487–544495), Santarém–Cuiabá, Km 446 (MPEG 12736, 12746–12748, 12932–12933, 12941, 12943, 12946–12950, USNM 546192–546208), Santarém–Cuiabá, Km 448 (MPEG 12737, 12928, 12944–12945), São Félix do Xingu (MPEG 1318, MZUSP 9931), São Geraldo do Araguaia (MN 75068), São João do Araguaia (MPEG 10134), Serra do Cristalino (MPEG 39951), Serra dos Carajás (MPEG

11824, 38928, 38948, 38953, 38955–38956, 38974, 38985, 38988, MPEG IAVRD 114, 1260, MPEG LPP 15, MPEG MS 41), Taperinha (MPEG 313, 3381–3385, 5012, 5023–5025, MZUSP 3693), Tauari (AMNH 94902), Vitória do Xingu (MPEG 39750, 39757, 39771, 39780, 39784, 39786, 39813, 41525), 54 km S and 150 km W Altamira (MPEG 8928–8933, 8935, 8937, 8938, 11390, 15400–15404, 15465, 24014, USNM 519727, 519728, 521429, 521430, 521501–521507); Rondônia, “Cachoeira da Pau grande” (NMW B-2626 [holotype of *glirina*]), Pacaás Novos (MPEG 39067, 39083, 39097, 39107–39110, 39112, 39115, 39120–39123, 39133, 39140, 39150–39152, 39181, 39192, 39202, 39206, 39216–39217), Ouro Preto D’Oeste (MPEG 16116), Santa Bárbara (MZUSP 20082, 20085, 20089, 20093, 20137), Vilhena (MPEG 34932, 34934). Locality unknown (MPEG 41818, MZUSP 35229–35233, 35239–35243, 35245–35256).

Monodelphis palliolata ($N = 103$)—VENEZUELA, Aragua, Guamita (USNM 517247), Rancho Grande (AMNH 144831, 144833–144834, 144836, 150145, USNM 517244–517246, 517248–517251), 3 km S Ocumare de La Costa (USNM 517242–517243); Barinas, Altamira (USNM 418492–418494, 418496–418497); Carabobo, Las Quiguas (USNM 296801), Montalbán (USNM 418484–418491, USNM 490242–490244), Urama (USNM 372920, 372921); Distrito Federal, Hda. Carapiche (USNM 385003), Los Canales (AMNH 135157–135158), San Julian (USNM 143800); Falcon, Boca De Yaracuy (USNM 371282), near Mirimire (USNM 406905), Serranía de San Luis (AMNH 276508), 14 km ENE Mirimire (USNM 418469, 418470, 418474–418476, 418478), 19 km NW Urama (USNM 372917); Guárico, Estación Biológica De Los Llanos (KU 123941, USNM 443774–443777, 443780, 490240), Parque Nac. Guatopo (USNM 385006); Merida, La Azulita (FMNH 22180–22182); Miranda, Birongo (USNM 416935), Curupao (USNM 385007, 385100), 6 km SSE Río Chico (USNM 385008–385009, 385012–385013); Monagas, Caripito (AMNH 142610), Río Cocollar (AMNH 69942); Sucre, Cuchivano (AMNH 69941), Cumanacoa (AMNH 69943), Finca Vuelta Larga (AMNH 257202), Manacal (USNM 406903–406904), San Rafael (CM 6392); Táchira, San Juan de Colón (FMNH 20524 [holotype of *palliolata*]); Trujillo, La Ceiba (USNM 371293–371294), 12 km WNW Valera (USNM 370015–370016), 19 km N Valera (USNM 371285), 23 km NNW Valera (USNM 371283), 25 km NW Valera (USNM 370013), 30 km NW Valera (USNM 371289, 371291); Yaracuy, Finca El Jaguar (AMNH 257204–257205), Minas De Aroa (USNM 418479–418482, 490237); Zulia, Kasmera (USNM 418483, 490238), Mision Tukuko (USNM 448513–448518, 448751), Sierra de Perija (FMNH 22178–22179).

Monodelphis sanctaerosae ($N = 1$)—BOLIVIA, Santa Cruz, Santa Rosa de la Roca (AMNH 263548).

Monodelphis touan ($N = 191$)—BRAZIL, Amapá (MPEG AN 503, 511, 565, 567, 603, 623, 678), Cachoeira Santo Antônio (IEPA 1166), Colônia Matapi (MPEG 33907), Floresta Nacional do Amapá (IEPA 165, 173), Macapá (MPEG AN 191, MZUSP 9932), Mazagão (MPEG 2500, 2515), Parque Nacional Montanhas do Tumucumaque (IEPA 305, 909, 913), Parque Zoobotânico de Macapá (IEPA 19, 1158), Porto Platon (MN 20217, 20221, 20225), Reserva de Desenvolvimento Sustentável do Rio Iratapuru (IEPA 307, 1154, 1155), Reserva Extrativista Cajari (IEPA 1143, 1156, 1157), Rio Amapari (MN 20218, MZUSP 11693, 24151), Rio Araguari (MZUSP 9933), Serra do Navio (MN 20214–20216, 20219, 20220, 20222–20225, 20226–20227, 24547–

24548, MPEG 8682, 8683, 8772, 12929, 15218–15224, 15226–15229, 20146, 20147, MZUSP 11692, USNM 392050–392051, 393423–393436, 393438–393442, 461433–461435), Tartarugalzinho (MPEG AN 322, 337), Vicinity Amapá and Calçoene (USNM 543303); *Pará*, Anapu (MPEG 39814, 39762, 39779, 39788, 39789), Cachoeira do Espelho (MZUSP 21284–21285, USNM 549279–549280), Cametá (FMNH 140784), Floresta Nacional de Carajás (MCN-M 1397–1400, 1454, 1485, 2271), Floresta Nacional de Caxiuanã (MPEG 41512–41524, 41526–41548), Floresta Nacional do Tapirape-aquiri (MPEG 38201, 41549–41561), Ilha do Marajó (MPEG 40442, 40444–40445), Marabá (UFSC 5211), Porto de Moz (AMNH 95976), Serra das Andorinhas (MPEG 25402), 26 km N e 30 km W Marabá (MPEG 10248–10249, 11698–11699), 73 km N e 45 km W Marabá (MPEG 10247, 11289–11293, USNM 519725–519726, 521432). FRENCH GUIANA, *Arataye*, River Arataye (USNM 578009); *Cayenne* (FMNH 21720 [neotype of *touan*]), Montagne du Tigre (ISEM V-1084), Camp du Tigre (ISEM V-1563, V-1568); *Macouria*, Savane (ISEM V-937); *Paracou*, near Sinnamary (AMNH 267000); *Saul* (ISEM V-1125); *Tamanoir*, Mana River (FMNH 21793). SURINAME, *Sipaliwini*, Oelemarie (CM 76731–76734). Locality unknown (MPEG 15217).

Subgenus *Microdelphys*

Monodelphis americana ($N = 213$)—BRAZIL, *Bahia* (MACN-Ma 24442, BMNH 55.11.26.9 [holotype of *rubida*]), Canavieiras (UFMG CC 34), Chapada Diamantina (MN 67812, 67820–67821, 67823–67825, 67836), Estação Ecológica Estadual Wenceslau Guimarães (MZUSP MTR 22034, 22215), Ilhéus (MACN-Ma 17284, MN 11075, 11179, 11483, 11485, 11492, 11498, 11505, 11524, 70051, 70054), Itacaré (UFMG RM 245–247), Itamari (UFMG 2081), Jaguaquara (MN 24550–24551), Parque Nacional do Descobrimento (UFMG RM 331, 364), Reserva Particular do Patrimônio Natural Salto Apepiquei (UFMG CC 20), Reserva Particular do Patrimônio Natural Serra do Teimoso (MN 29783, 29786–29787), Salvador (MCN-M 2149–2152, 2234, 2236) Trancoso (MZUSP MTR 13506, 13509, 13557), Una (UFMG 2003–2006, 2082), Urucutuca (FMNH 63767–63768, MN 20976); *Ceará*, Serra de Batutité (MZUSP 29461–29462, 29465–29469); *Distrito Federal*, 20 km S Brasília (OK 17376–17381); *Espírito Santo*, Mineroduto P. Neves (MCN-M 2559); *Goiás*, Annapolis (AMNH 133241), Parque Nacional da Chapada dos Veadeiros (MN 46570), Veadeiros (MN 1313 [lectotype of *umbristriata*], MN 1314); *Minas Gerais*, Aiuruoca (MCN-M 1567, 1606), Além Paraíba MN 7568–7569, 7571, 69778), Almenara (MCN-M 1752), Barão de Cocais (MCN-M 1616), Belo Horizonte (MCN-M 705, 716), Betim (MCN-M 1470), Brumadinho (MCN-M 1150, 2025, 2204), Caeté (MCN-M 2166, 2518), Caratinga (UFMG 1217), Catas Altas (MCN-M 1102, 1591, 2974–2975, Conceição do Mato Dentro (MCN-M 1651, 2164, 2169, 2409, 2413–2414, 2422, 2524, 2853), Estação de Pesquisa e Desenvolvimento Ambiental de Peti (UFMG 1435), Igarapé (MCN-M 2477), Itabira (MCN-M 1964, 2437), Mariana (MCN-M 2016, MZUSP 2139, 3418, 21939), Mata da Prefeitura (USNM 552400–552404), Nova Lima (MCN-M 591, 749, 2736), Pains (MCN-M 1688), Parque Natural do Caraça (UFMG 1930), Passos (MN 11728, 20971–20974, USNM 304593, 304595), Porto Novo (MN 7312), Santa Maria de Itabira (MCN-M 2825), São Gonçalo do Rio Abaixo (MCN-M

2168), São Joaquim de Bicas (MCN-M 2476), Serra do Cipó (MZUSP MTR 23767); *Pará* (MN 1304–1305, MPEG 315–316, 318, 327, 1975, 2573–2574, 3543, 15239, 24067, 37492), Baião (AMNH 96810), Benevides (AMNH 37490), BR 14, Km 94 (AMNH 203354), Dom Eliseu (MPEG TGP 07), Maracangalha (AMNH 203353), Patagonia, Km 72 (AMNH 75170), Vorsladt (AMNH 37491, MN 1303); *Pernambuco*, Caruaru (MN 24544); *Rio de Janeiro*, Cambuci (MN 71941), Campo dos Goytacazes (MCN-M 1650, 1779, 2128, 2131, 2167), Comendador Levy Gasparian (MN 43899–43900), Itatiaia [“possibly”] (MN 42026), Mangaratiba (MN 73745–73750), Parque Nacional do Itatiaia (MN 42027, 78911, MZUSP 11695), Reserva Biológica de Poço das Antas (UFMG 1588), Santo Antônio de Pádua (MN 72722–71724, 71727, 72731), Sumidouro (MN 66070, 66072), Teresópolis (FMNH 25739, MN 7250); *São Paulo* (MZUSP RL 58), Biritiba Mirim (MZUSP UNIBAN 2072, 2133, 2311), Caucaia do Alto (MZUSP 29202), Ipiranga (MZUSP 1185), Jambeiro (MZUSP 34229), Juquitiba (MZUSP 33097), Paraibuna (MN 10988), Parelheiros (USNM 484014), Parque do Estado (UFSC 2584), Piquete (MZUSP 118, 1520), Piracicaba (MZUSP 1516, 1518–1519, 1523), Reserva Morro Grande (MZUSP 10206), São Luiz do Paraitinga (MZUSP 35046–35047), Serra da Cantareira (USNM 236676), Ubatuba (MZUSP 1855), Victoria (BMNH 37.2.5.12, 37.2.5.13); *Sergipe*, Estação Ecológica Serra de Itabaiana (MPEG 26349), Fazenda Cruzeiro (MN 30553–30555). Locality unknown (MPEG 43018, MZUSP 35197, ZMB 2333 [holotype of *tristriata*]).

Monodelphis gardneri ($N = 1$)—PERU, *Junín*, Cordillera Vilcabamba (USNM 582109).

Monodelphis iheringi ($N = 87$)—BRAZIL, *Espírito Santo*, Lagoa Juparanã (MN 1307), Santa Leopoldina (MZUSP 6674); *Rio de Janeiro*, Angra dos Reis (MN 24400, 46851), Cachoeiras de Macacu (MN 71793, 71795, 71814, 71816, 71830, 71947), Casimiro de Abreu (MN 71804), Guapimirim (MN 71794, 73751), Ilha Grande (MZUSP 1979), Jacarepaguá (MN 24545), Pacamiri (MCN-M 2026), Parque Nacional do Desengano (MN 71935) Serra do Mendanha (MN JFV 371, 372), Parque Nacional Serra da Bocaina (MN 77794), Pedra Branca (MN 6221, 8203, 66077), Restinga de Marambaia (MN 1308), Teresópolis (MN 1309), Tijuca (MN 10305); *Rio Grande do Sul*, Taquara (BMNH 82.9.30.43 [holotype of *iheringi*]); *Santa Catarina*, Caldas da Imperatriz (UFSC [144], 857–858, 3797, 4586–4587, 4678–4680, 4858), Campus da Universidade Federal de Santa Catarina (UFSC 4585), Colônia Hansa (MZUSP 847, 873, 1095), Guaramirim (UFSC 5589–5591, 5704), Hammonia (MZUSP 3417), Joinville (MZUSP 3421, 17423, MN A 180), Parque Estadual da Serra do Tabuleiro (UFSC 4055, 4600, 5192, 5235, 5435–5438), Praia Grande (UFSC 5756), Reserva Biológica Estadual do Aguai (UFSC 5587–5588, 5594–5595), Reserva Particular do Patrimônio Natural Chácara Edith (UFSC 4604–4605, 4681–4682), São Francisco do Sul (UFSC 5592–5593), Siderópolis (UFSC 4607, 4863); *São Paulo*, Iguape (MZUSP 1517, 1521), Iporanga (FMNH 94736), Parque Estadual Carlos Botelho (MZUSP CB 14, 17, 35), Parque Estadual da Serra do Mar (MN 78957–78960), Perus (MZUSP 11), Riacho Grande (MZUSP 30638), Ribeirão da Lagoa (USNM 484015), Parque Estadual da Serra do Mar (MN 69875). Locality unknown (MZUSP ARP 22, MZUSP 32839, 32848, USNM 114846).

Monodelphis scalops ($N = 87$)—ARGENTINA, *Misiones*, Parque Nacional Iguazu (MACN-Ma 23638, MACN-Ma masto 213), Puerto Península (MACN-Ma 22473). BRAZIL, *Espírito Santo*, Santa Tereza (MN 59108); *Minas Gerais*, Reserva Particular do Patrimônio Natural Mata

do Sossego (UFMG 2251); *Paraná*, Ortigueira (MZUSP 31624, 31628, 31634, 31648), Telêmaco Borba (MN 68215, 68228, 68268); *Rio de Janeiro* (MN 81040–81041), Corcovado (MN 24546), Itatiaia [“possibly”] (MN 42032), Nova Friburgo (MN 68121, 80392), Parque Nacional da Serra da Bocaina (MN 81481), Parque Nacional do Itatiaia (MN 42023, 42025), Pedra Branca (MN 6102, 6419), Petrópolis (MN 10209), Teresópolis (BMNH 21.8.6.2 [holotype of *theresa*], 51.7.21.23 [holotype of *scalops*], MN 1301, 1302, 1310, 7233, 7245–7249); *Santa Catarina* (MN JFV 379), Chapecó (UFSC 3379–3380, 3858–3859, 4056, 5193), Guatambu (UFSC 3860, 4836), Itapema (UFSC 4369), Praia Grande (UFSC 4859), Reserva Biológica Estadual do Aguai (UFSC 5594–5595), Santo Amaro da Imeratriz (UFSC 3344, 3533, 3798, 4676–4677), Xaxim (UFSC 3915–3916, 4965); *São Paulo*, Buri (MZUSP 31681), Capão Bonito (MZUSP 29201), Estação Ecológica de Boracéia (FMNH BDP 3282, MZUSP 32033), Ilha do Cardoso (FMNH 141587), Parque Estadual Carlos Botelho (MZUSP CB 15), Parque Estadual da Serra do Mar (MN 78961), Parque Estadual de Ilhabela (MVZ 182775–182776, MZUSP 29200, 29203), Piedade (MZUSP 31095, 31098, 31128, 31130–31131, 31135, 31170, 33087–33089), Reserva Morro Grande (MN 78679), Riacho Grande (MZUSP 30629, 30652, 30702, 30712, 30748, 30757, 30759), São Luiz do Paraitinga (MZUSP 35051), São Sebastião (MZUSP 1528). Locality unknown (MZUSP EDH 404).

Subgenus *Monodelphiops*

Monodelphis dimidiata ($N = 208$)—ARGENTINA (MACN-Ma 25945, MN 32853), *Buenos Aires* (MACN-Ma 19192), Abra de la Ventana (MACN-Ma 14954, 14961, 15718–15719), Arroyo Brusquitas (MACN-Ma 17281–17283), Partido Balcarce (CM 86609–86611, MSU 17469–17470, 17586, 17599, 17887, 18262, 18339, 18524–18525, 18579, 18652, 18691, 18781, 18789, 19182, 19228, 19230–19231, 20247–20250), Partido de General Pueyrredón (CM 86608), Pergamino (MACN-Ma 17285–17286, 18734, 18998), Sierra de la Ventana (MACN-Ma 18558–18659, MACN-Ma w/o n°), Tambo Nuevo (MN 24605); *Córdoba*, Yacanto (MACN-Ma 14751–14756, 14798, 14775–14777, 14788–14794, 14802–14807); *Misiones*, Arroyo Uruguayá, Km 10 (MACN-Ma 13368–13370), Caragatatay (FMNH 44774), Estancia Alicia (MACN-Ma 22472, 22474, 22476); *Santa Fé*, Uranga (MSB 140303, 140307). BRAZIL, *Minas Gerais*, Passos (MN 20975, USNM 304594); *Paraná*, São Mateus do Sul (UFSC 4608, 5194–5196, 5931); *Rio de Janeiro*, Alto do Itatiaia (AMNH 61546), Cachoeiras de Macacu (MN 80409), Itatiaia (USNM 461068 [holotype of *itaiayae*], Parque Nacional do Itatiaia (MN 24552–24553, 42021, 42024, 42028, 69747, 69684, 69678, 69694, 71746–71747), Resende (MN 29814), Visconde de Mauá (MN 71865); *Rio Grande do Sul* (MN 1312, USNM 114845), Bento Gonçalves (MZUSP 3286), Parque Nacional da Serra Geral (MN 78493, 78518, 78520, 78536, 78547–78549, 78558), São Francisco de Paula (MN 68937), São Lourenço (MZUSP 1427, 1435, 1440), Taquara (BMNH 82.9.3.37 [holotype of *henseli*], ZMB 4307 [holotype of *sorex*]; *Santa Catarina*, Anitápolis (UFSC 3467), Chapecó (UFSC 4835), Concórdia (UFSC 3428), Ipuacu (UFSC 5055), Parque Nacional de São Joaquim (MN 78569, 78574–78577, 78580, 78586, 78603, 78618, UFSC 5579–5586), Passos Maia (UFSC 4609, 4822–4823, 4833–4834), Praia Grande (UFSC 4860–4862, 5755), Rancho Queimado (UFSC 3696, 3799), São Joaquim (UFSC 5740), São José do Cerrito

(UFSC 3700), Urubici (UFSC 5712, MN 78578, 78587–78589, 78595, 78605, 78622), Vargem (UFSC 5056), Xavantina (UFSC 3777–3778, 3824–3828, 3880, 4057, 4058); São Paulo, Biritiba Mirim (MZUSP UNIBAN 2575–2576), Casa Grande (MN 24549), Caucaia do Alto (MZUSP 34189, 34214), Estação Ecológica de Boracéia (FMNH 145326, USNM 460504), Ex Prefeitura Municipal (MZUSP 13666), Freguesia do Ó (MZUSP 7671), Ibiti (MZUSP 6611–6612 [syntypes of *paulensis*]), Ipiranga (MZUSP 2563), Jundiaí (MZUSP 17501), Mogi das Cruzes (MZUSP 4146 [syntypes of *paulensis*]), Parque Continental (MZUSP 31865), Parque Estadual de Campos do Jordão (MZUSP 32576, 32579, 34257), Pinhal (MZUSP 7434), Piquete (MN 23869, MZUSP 25 [syntypes of *paulensis*], MZUSP 1526), Riacho Grande (MZUSP 30698, 30726), Ribeirão da Lagoa (USNM 484016), São Luiz do Paraitinga (MZUSP 35053). PARAGUAY, Alto Paraná, Puerto Yaguarazapá (MZUSP 2823); *Canindeyú*, Reserva de Biosfera del Bosque Mbaracayú (TTU 116522); *Itapúa*, 3.2 km N and 0.4 km E Ape Aimé (TTU 116520), Estancia Parabel (TTU 116520). URUGUAY (MACN-Ma 33174), *Canelones*, Soca (AMNH 208970); *La Pampa*, Calefú (BMNH 24.4.5.1 [holotype of *fosteri*]; *Maldonado* (BMNH 55.12.24.72 [holotype of *dimidiata*]). Locality unknown (MN 8270, 43943, MZUSP 2820, MZUSP SAPO 083, 111).

Monodelphis unistriata ($N = 2$)—ARGENTINA, *Misiones*, “Misiones, alrededores” (MACN-Ma 250). BRAZIL, São Paulo, Itararé (NMW B-1063 [holotype of *unistriata*]).

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