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Caluromys lanatus. By N. C. Cáceres and A. P. Carmignotto

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Caluromys J. A. Allen, 1900

Didelphis Linnaeus, 1758:54. Part.

Didelphys Schreber, 1778:532. Part, unjustified emendation of *Didelphis* Linnaeus, 1758.

Sarigua Muirhead, 1819:429. Part, vide Allen (1900:186).

Micoureus Lesson, 1842:186. Part.

Philander Burmeister, 1856:74. Type species *Philander cayopolin* Burmeister, 1856 (= *Didelphis philander* Linnaeus, 1758), by subsequent designation (Hershkovitz 1949:12). Preoccupied by *Philander* Brisson, 1762 and *Philander* Tiedemann, 1808.

Gamba Liais, 1872:330. Part.

Cuica Liais, 1872:330. Part.

Micoureas: Ihering, 1894:11. Part.

Caluromys J. A. Allen, 1900:189. Type species *Didelphis philander* Linnaeus, 1758 by original designation. Replacement name for *Philander* Burmeister, 1856.

Micoureas: Matschie, 1916:269. Part, not *Micoureas* Lesson, 1842.

Mallodelphys Thomas, 1920:195, footnote. Type species *Didelphis lanigera* Desmarest, 1820 by original designation. Described as a subgenus of *Philander* sensu Burmeister (1856).

Calaromys Miranda-Ribeiro, 1936:324. Incorrect subsequent spelling of *Caluromys* J. A. Allen, 1900.

Mallodelphys Miranda-Ribeiro, 1936:328. Incorrect subsequent spelling of *Mallodelphys* Thomas, 1920; considered a valid genus.

Caluromys Ávila-Pires, 1964:11. Incorrect subsequent spelling of *Caluromys* J. A. Allen, 1900.

CONTEXT AND CONTENT. Order Didelphimorphia, family Didelphidae, subfamily Caluromyinae. A key to the 3 species of *Caluromys*, *C. derbianus* (Waterhouse, 1841), *C. lanatus* (Olfers, 1818), and *C. philander* (Linnaeus, 1758), follows:

1. Total length 587–760 mm, ears whitish to pink; forelimbs and feet creamy white; gray patch between shoulders usually present; undersides buffy white to golden tawny; proximal 30–50% of tail with dorsal hair *C. derbianus*
Total length 410–730 mm; ears pinkish tan to brownish; forelimbs and feet red-brown to grayish; gray patch between shoulders rarely present; undersides orange or yellowish white to grayish; proximal 10–70% of tail with dorsal hair 2
2. Total length 510–730 mm; proximal 50% of tail haired dorsally, up to 20% of tail haired ventrally; naked ventral surface of tail base covered with hard raised tubercles; pouch has lateral skin folds joined posteriorly and opens anteriorly *C. lanatus*
Total length 410–690 mm; pelage extending onto tail to same length dorsally and ventrally, at maximum to 33% of total length of tail; naked ventral surface of tail base covered with smooth flat scales; pouch has separate and deep lateral skin folds and opens along midline *C. philander*

Caluromys lanatus (Olfers, 1818) Western Woolly Opossum

[*Didelphys*] *lanata* Illiger, 1815:107. Nomen nudum.

D[idelphys]. lanata Olfers, 1818:206. Type locality “Paraguay;” restricted to Caazapá, Paraguay, by Cabrera (1916:516); based on Azara’s (1801) “*Micouré laineux*.”

Didelphis lanigera Desmarest, 1820:258. Type localities “dans le Caapeza, à cinquante lieues de la cité de l’Assomption, Paraguay” and “dans les champs du village de Sainte-Marie de

la Foi, Paraguay;” restricted to “Caazapá, Paraguay” by Cabrera (1916:516); based on Azara’s (1801) “*Micouré second*” or *micouré laineux*.”

Didelphys lanigera: Waterhouse, 1841:98. Name combination.

Micoureas lanigera: Lesson, 1842:186. Name combination.

Didelphys ochropus Wagner, 1842:359. Type locality “Barra;” (Cabrera 1958:3) Barra do Rio Negro, Amazonas, Brazil.

D[idelphys]. ornata Tschudi, 1845:146. Type locality “der mittleren und tiefen Waldregion,” Peru.

Didelphys [Philander] lanigera: Thomas, 1888:339. Part; name combination.

Philander cicur Bangs, 1898:161. Type locality “Pueblo Viejo, Colombia, altitude 8000 ft.”

P[hilander]. ornatus: Bangs, 1898:162. Name combination.

[*Didelphys* (*Philander*)] *cicur*: Trouessart, 1898:1238. Name combination.

[*Didelphys* (*Philander*) *laniger*] *ochropus*: Trouessart, 1898:1238. Name combination; in synonymy of *Didelphys* (*Philander*) *laniger derbiana*.

[*Didelphys* (*Philander*) *laniger*] *ornata*: Trouessart, 1898:1238. Name combination.

Caluromys cicur: Allen, 1900:189. Name combination.

Caluromys laniger: Allen, 1900:189. Name combination for *Didelphis lanigera* Desmarest, 1820.

Caluromys derbianus ornatus: Allen, 1900:189. Name combination.

[*Caluromys*] *ochropus*: Thomas, 1901:196. Name combination.

[*Caluromys*]. [*Ianiger*]. *cicur*: Thomas, 1901:196. Name combination.

[*Caluromys*] *ornatus*: Thomas, 1901:196. Name combination.

[*Didelphys* (*Philander*) *laniger*] *ornatus*: Trouessart, 1905:855. Name combination and incorrect gender concordance.

P[hilander]. Ianiger. cicur: Thomas, 1913:358. Name combination.

P[hilander]. Ianiger. ornatus: Thomas, 1913:358. Name combination.

Philander laniger jivaro Thomas, 1913:360. Type locality “Sarayacu on the Pastaza River,” Pastaza, Ecuador.

Philander laniger: Cabrera, 1916:514. Name combination.

Micoureas ochropus: Matschie, 1916:269. Name combination.

Micoureas ornatus: Matschie, 1916:269. Name combination.

Micoureas juninensis Matschie, 1917:283. Type locality “Chan-



FIG. 1. An adult *Caluromys lanatus* from Salto Caxias Dam, Paraná State, Brazil.

- chamayo in der Nähe von La Merced, Provinz Junin, Peru, in her Höhe von 1000 m."
- Micoureus meridensis* Matschie, 1917:285. Type locality "von Briceno in der Montana de la Sierra bei Merida in Venezuela in der Höhe von 2500 m."
- Micoureus cahyensis* Matschie, 1917:288. Type locality "Am Rio Cahy in Rio Grande do Sul," Brazil.
- Micoureus bartletti* Matschie, 1917:288. Type locality "Chamicaros-Fluß, südlicher Nebenfluß des Marañon zwischen Hualaga and Ucayali," Loreto, Peru.
- Micoureus nattereri* Matschie, 1917:291. Type locality "von Caisara, Matto Grosso," Brazil.
- [*Philander laniger*] *ochropus*: Cabrera, 1919:33. Name combination.
- Mallo delphis lanigera ochropus*: Miranda-Ribeiro, 1936:355. Name combination.
- Mallo delphis lanigera hemiura* Miranda-Ribeiro, 1936:355. Type locality unknown.
- Mallo delphis lanigera vitalina* Miranda-Ribeiro, 1936:355. Type locality "Barra do Paraopéba, Minas Geraes," Brazil.
- Mallo delphis lanigera nattereri*: Miranda-Ribeiro, 1936:356. Name combination.
- Mallo delphis lanigera modesta* Miranda-Ribeiro, 1936:356. Type locality "Mato Grosso, provavelmente Pantanal," Brazil.
- Caluromys laniger ochropus*: Tate, 1939:163. Name combination.
- [*Caluromys laniger*] *meridensis*: Tate, 1939:163. Name combination.
- [*Caluromys laniger*] *jivaro*: Tate, 1939:163. Name combination.
- Caluromys laniger ornatus*: Sanborn, 1949:277. Name combination.
- P[hilander]. *lanata*: Hershkovitz, 1951:552. Name combination.
- Philander calmensis* Vieira, 1955:347. Incorrect subsequent spelling of *Micoureus cahyensis* Matschie, 1917.
- Caluromys lanatus cicur*: Cabrera, 1958:2. Name combination.
- Caluromys lanatus lanatus*: Cabrera, 1958:2. Name combination.
- Caluromys lanatus ochropus*: Cabrera, 1958:3. Name combination.
- Caluromys lanatus ornatus*: Cabrera, 1958:3. Name combination.

CONTEXT AND CONTENT. Content as above. *Caluromys lanatus* has 4 subspecies (Cabrera 1958):

- C. l. cicur* (Bangs, 1898:161); see above; *meridensis* (Matschie) is a synonym.
- C. l. lanatus* (Olfers, 1818:206); see above; *cahyensis* (Matschie), *hemiura* (Miranda-Ribeiro), *lanigera* (Desmarest), *modesta* (Miranda-Ribeiro), and *nattereri* (Miranda-Ribeiro) are synonyms.
- C. l. ochropus* (Wagner, 1842:359); see above; *vitalina* (Miranda-Ribeiro) is a synonym.
- C. l. ornatus* (Tschudi, 1845:146); see above; *bartletti* (Matschie), *jivaro* (Thomas), and *juninensis* (Matschie) are synonyms.

DIAGNOSIS. Fur of *C. lanatus* is long, dense, and woolly; with a reddish brown dorsum that is brightest red over shoulders, forearms, and hind legs; with an underside orange to yellowish; and with reddish brown feet. In contrast, *C. derbianus* has a pale gray patch between shoulders, creamy white forelimbs and feet, and buffy white to golden tawny venter. *C. philander* has uniform reddish brown to grayish upperparts and forelimbs, and *C. philander* also differs from *C. lanatus* in having a tail furred to the 1st one-third of its length dorsally and ventrally, whereas *C. lanatus* has up to 50% of its tail length furred dorsally and 20% of it furred ventrally.

GENERAL CHARACTERS. *Caluromys lanatus* is a medium-sized opossum with long, dense, and soft guard hairs and a tail ca. 140% of length of head and body (Fig. 1). Dorsal color is reddish brown to pale brown mixed with gray and grades to orange on shoulders, forelimbs, hind limbs, and top of head; rarely, individuals have a gray patch between shoulders. Head is grayish, and face has a prominent median dark stripe from between ears to nose, brown to orange eye rings, naked ears that are pinkish tan, and whitish cheeks. Ventral surface of body is yellowish white laterally and grayish at midline. Feet are reddish brown to dark gray. All digits have well developed pads and claws, except for thumb of hind feet. Tail is furred dorsally for one-half of its length and ventrally for one-fifth of its length. Terminal portion of tail is naked (usually whitish yellow mottled with brown spots) and fully prehensile. Pouch of females is developed only when carrying young;



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Caluromys lanatus* (MZUSP [Museu de Zoologia da Universidade de São Paulo mammal collection] 4532) from Igarapé Grande, Rio Juruá, Amazonas, Brazil, collected by A. M. Ollala (field number 1981) on 15 January 1937. Greatest length of skull is 61.64 mm.

young are more grayish than adults (Eisenberg and Redford 1999; Emmons and Feer 1997; Patton et al. 2000; Vieira 1949). External measurements (range, in mm or g) of 26 adults of both sexes: length of head and body, 201–319; length of tail, 330–446; length of hind foot, 30–51; length of ear, 30–41; and body mass, 310–520 (Emmons and Feer 1997; Patton et al. 2000; Redford and Eisenberg 1992).

Caluromys l. cicur from Magdalena Valley, Colombia, is grayish brown dorsally, with gray sides, and sometimes completely gray ventrally, whereas *C. l. lanatus* from Paraguay is pale brown, with tail lacking brown spots (Emmons and Feer 1997). *C. l. ochropus* from Amazonia has a markedly red-brown dorsal color (Patton et al. 2000), and is larger than *C. l. lanatus* from central and southern ranges (Costa and Patton 2005; Patton et al. 2000; Vieira 1949).

Skull (Fig. 2) has a short and robust rostrum, small paraoccipital process that never surpasses occipital condyle, reduced lambdoidal and sagittal crests, well developed postorbital process-

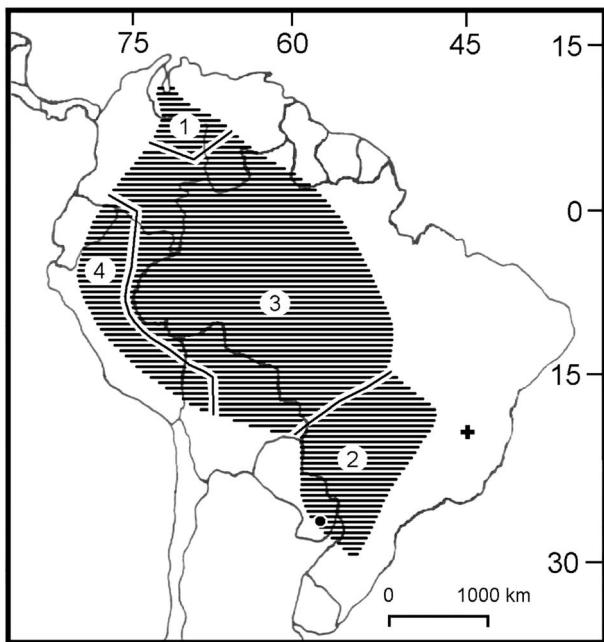


FIG. 3. Geographic distribution of *Caluromys lanatus* in South America, 1, *C. l. cicur*; 2, *C. l. lanatus*; 3, *C. l. ochropus*; 4, *C. l. ornatus*. Square is type locality in Caazapá, Paraguay. Cross is Lagoa Santa, Brazil, with Pleistocene–Holocene remains of *C. lanatus* (Cartelle 1999; Winge 1893). Map redrawn with modifications from Costa (2003), Eisenberg (1989), Eisenberg and Redford (1999), Emmons and Feer (1997), and Lambert et al. (2005).

es, small palatine foramina, dorsal projection of superior portion of zygomatic that reduces size of orbit, no foramen ethmoidale, and a small foramen rotundum (Pérez-Hernández 1985). *C. lanatus* also has a rostral process of the premaxillae, but lacks a palatal process, resulting in insertion of upper canine in maxillary bone. Nasal bones are wider posteriorly than anteriorly with tips extending anteriorly above or beyond II, thereby obscuring nasal orifice in dorsal view. *C. lanatus* lacks maxillopalatine, palatine, and maxillary fenestrae, and a transverse canal foramen. Mandible has 2 mental foramina and an angular process that is obtuse and weakly inflected (Voss and Jansa 2003).

Means and parenthetical ranges of cranial measurements (in mm) of 8 adults of both sexes are: length of condyloincisive, 59.5 (56.5–62.8); breadth of zygomatic, 34.8 (32.7–37.1); width of braincase, 20.6 (19.4–22.3); breadth of interorbital constriction (taken posterior to postorbital processes), 8.4 (7.6–9.2); length of rostrum, 22.8 (21.7–24.0); length of nasal bones, 25.8 (22.2–27.1); width of rostrum, 13.0 (12.3–13.8); length of palate, 31.9 (30.5–33.4); width of palate, 17.7 (17.1–18.2); breadth of mastoid, 23.3 (21.4–25.6); length of basioccipital, 8.7 (8.2–9.2); depth of cranium, 18.9 (16.6–21.1); length of molar row, 9.8 (9.2–10.1); and length from C to M4, 20.6 (18.2–22.2)—Patton et al. 2000.

DISTRIBUTION. *Caluromys lanatus* ranges from east of the Andes in central Colombia, western and southern Venezuela, eastern Ecuador, Peru, and Bolivia to western, central, and southern Brazil, northeastern Argentina (Misiones), and eastern and southern Paraguay (Fig. 3; Costa 2003; Costa and Patton 2005; Eisenberg 1989; Eisenberg and Redford 1999; Emmons and Feer 1997; Gardner 2005; Patton et al. 2000). Elevational range is 0–2,600 m (Alberico et al. 2000). Distributions of 4 subspecies are: *C. l. cicur*, eastern Colombia and western Venezuela; *C. l. lanatus*, Paraguay and Brazil, from Mato Grosso to São Paulo states; *C. l. ochropus*, Orinoco and Amazon basins to eastern Brazil; and *C. l. ornatus*, Peru and Ecuador, east of the Andes (Cabrera 1958; Pérez-Hernández 1989).

FOSSIL RECORD. Remains of *C. lanatus* occur in Pleistocene–Holocene cave deposits of Lagoa Santa, Minas Gerais, Brazil (Cartelle 1999; Winge 1893).

FORM AND FUNCTION. Female *C. lanatus* have abdominal and inguinal mammae confined to the pouch region (Voss and Jansa 2003). Dental formula is i 5/4, c 1/1, p 3/3, m 4/4, total 50. Crowns of I2–I5 are asymmetrical with longer anterior than posterior cutting edges. Upper canine is simple and without accessory cusps. P1 is very small, without prominent occlusal features, and situated directly behind upper canine. A gap occurs between P1 and the much larger P2. P2 is taller than P3, which has well-developed anterior and posterior cutting edges. M1 is wider than M4. Molar dentition is weakly carnassialized and weakly dilambodont. Upper molars lack ectoflexus. A continuous shelf occurs along anterior margin of crowns of M1–M3. Mandibular teeth have distinct lingual cusps in i1–i4, a p2 taller than p3, a deciduous p3 with a complete tricuspid trigonid, a labially salient hypoconid in m3, and a large and well-developed entoconid in m1–m3 (Redford and Eisenberg 1992; Voss and Jansa 2003). Occlusal area of molars is reduced (Cáceres 2000).

Caluromys lanatus has a relatively large braincase and long tail, which are associated with its high degree of arboreal activity (Cáceres 2000; Eisenberg and Wilson 1981). The protein transthyretin occurs in plasma (Richardson et al. 1996). *C. lanatus* has a large hind gut and caecum, a small stomach, and a short small intestine (Cáceres 2005). The large hind gut and caecum are associated with a diet mainly of plant material (Chivers and Hladik 1980; Crowe and Hume 1997; Schieck and Millar 1985), and the small stomach chamber is associated with a frugivorous diet (Hildebrand 1995). Digestive tract anatomy is specialized for consumption of fruits, gums, and twigs.

Penis of *C. lanatus* is postsrotal, forming an evident sigmoid flexure, and partially located in preputial sac when in nonerected state. Two muscles, ischiocavernous and bulbospongiosus, situated outside pelvic cavity, comprise bulk of penis musculature. These muscles join in radix penis, where paired levator muscles are encased and insert by a single tendon. Paired penis retractor muscles arise in sublumbar region and insert on both sides of dorsal curvature of sigmoid flexure. Glans is same length as penis, bifid, deeply cleft, and with elliptical tips lacking a diverticulum. Urethra ends in body–glans transition, with 2 urethral grooves extending for different lengths along medial surfaces of each glans tip. When erected, penis projects through cloaca, with preputial opening ventral to anus (Nogueira et al. 1999). Urogenital and rectal openings are closely juxtaposed and share a common mucosa (Voss and Jansa 2003).

A median cylindrical structure is located between uterine cervixes and the origin of lateral vaginal canals. An incomplete, thin, and perforated vaginal septum forms a short common vagina with lining markedly folded. A rudimentary pseudovaginal canal has lateral vaginal canals that form closed loops (Reig et al. 1987).

ONTOGENY AND REPRODUCTION. In Brazil, 2 females with pouch young were trapped at Rio Juruá, Amazon Basin, during June and November. Postlactating females were trapped in February, March, and October in the same region (Patton et al. 2000). In Brazil, modal estrous cycle length was 27–29 days, and females cycle throughout the year (Bucher and Fritz 1977). Litter size is 1 or 2 young in the Amazon Basin (Patton et al. 2000) and 3 or 4 in southern range of distribution (Monteiro-Filho and Cáceres 2005). Females develop a pouch only when carrying young (Emmons and Feer 1997). Body mass of young averaged 3.5 g in October 1998 at a seasonal forest in southern Brazil, and sex ratio was male-biased (1.00:0.22; n = 3 litters—N. C. Cáceres, in litt.).

ECOLOGY AND BEHAVIOR. *Caluromys lanatus* occurs in small, secondary forest fragments in Amazonian rain forest (Malcolm 1995) and in disturbed, fragmented forests in southern Brazil (Quadros et al. 2000). *C. lanatus* was trapped mostly in canopy and subcanopy, from 5 to 15 m high (Eisenberg and Redford 1999; Malcolm 1991b; Patton et al. 2000). *C. lanatus* occurs in dense multistratal rain forest (terra firme and várzea); in gallery, mangrove, semideciduous, transitional, and xerophytic forests; and in dense savanna (Carmignotto 2004; Gargagliani et al. 1998; Gribel 1988; Moreno-Bejarano and Álvarez-León 2003; Patton et al. 2000; Talamoni and Dias 1999). In its southern range, *C. lanatus* occurs in more seasonal forests when compared to its northern range.

Continuous distribution of *C. lanatus* from southern Brazil to the Amazonian rain forest occurs along the southern Cerrado and Pantanal biomes (Carmignotto 2004). Phylogeny of Atlantic

and Amazon rain-forest populations shows a closer relationship between the seasonal Atlantic forest and the southwestern Amazon populations (Costa 2003). *C. lanatus* is parapatric with *C. philander* and *C. derbianus*, and is replaced by *C. philander* in eastern Brazil (Eisenberg and Redford 1999; Emmons and Feer 1997). Sympatry with *C. philander* occurs in northern and central Brazil (central Amazonia, north of Mato Grosso, Goiás and Minas Gerais states), Guyana, and eastern Bolivia (Carmignotto 2004; Eisenberg 1989; Malcolm 1991a; Patton and Costa 2003; Patton et al. 2000). No contact occurs with *C. derbianus* in northwestern South America (Eisenberg 1989; Eisenberg and Redford 1999).

In central Brazil, Peru, and Ecuador, *C. lanatus* is a nectar consumer and probable pollinator of *Pseudobombax tomentosum* and *Quararibea cordata* (Gribel 1988; Janson et al. 1981). The caecum of 1 individual contained hundreds of small seeds of *Ficus luschnatiana* in southern Brazil (Cáceres 2000, 2005). *C. lanatus* consumed fruits of *Cecropia pachystachya*, *Piper*, and Solanaceae in southern Brazil (Casella and Cáceres 2006). *C. lanatus* ingests vertebrates and invertebrates (Fonseca et al. 1996; Peres 1999). Captive *C. lanatus* subsisted on a meat–egg–fruit diet and preferred bananas (Bucher and Fritz 1977).

Population density was 13.3 individuals/km² and biomass was 4.6 kg/km² in central Amazonas State, Brazil (Peres 1999). Abundance varies seasonally (Fleck and Harder 1995), but *C. lanatus* was never trapped in high numbers (Nowak 1999). *C. lanatus* is solitary, but can be seen foraging in pairs, usually at night (Hunsaker 1977). No vocalizations are usual in the field (Emmons and Feer 1997). *Trypanosoma cruzi* occurred in *C. lanatus* from Colombia and Brazil (Montilla et al. 2002; Ribeiro and Barreto 1977) and nymphs of *Amblyomma* were found on a specimen from Peru (Walter 1990).

Captive western woolly opossums are nocturnal. Behavior is associated with individual temperament and cage size, with animals being more excited in small cages. Sexual behavior included pre-mont and pelvic-thrust displays by males, with complete repulsion by females; no breeding occurred during 3 years in captivity (Bucher and Fritz 1977).

GENETICS. *Caluromys lanatus* has a diploid number of 14 with a fundamental number of 24. Karyotype consists of 4 pairs of large biarmed autosomes, 2 pairs of medium-sized subtelocentric autosomes, a small and biarmed X chromosome, and a very small and distinctly biarmed Y chromosome (Palma and Yates 1996; Patton et al. 2000; Reig et al. 1977; Yunis et al. 1972). A fundamental number of 20 was found in 3 individuals from northern Brazil, with the 2 pairs of medium-sized autosomes being acrocentrics, and a punctiform Y chromosome (Souza et al. 1990). An examination of location of the nucleolar organizer regions found that karyotype of *C. lanatus* had only 1 bearing pair, representing the most primitive form of nucleolar organizer region distribution.

Analysis of different cytochrome-*b* sequence haplotypes showed uniformity among Amazonian populations, with specimens differing by only 1.5% (Patton et al. 1996, 2000). When populations from southern Brazil were included, divergence between samples was 2.3% (Patton and Costa 2003).

CONSERVATION STATUS. Habitat destruction has led to a decline in natural populations. *C. lanatus* is classified as near threatened (International Union for the Conservation of Nature and Natural Resources 2004).

REMARKS. Phylogenetic analyses of didelphid marsupials using molecular and nonmolecular data indicate *C. derbianus*, *C. lanatus*, and *C. philander* are distinct species, but closely related (Cardillo et al. 2004; Costa and Patton 2005; Jansa and Voss 2000; Patton and Costa 2003; Voss and Jansa 2003).

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LITERATURE CITED

- ALBERICO, M., A. CADENA, J. HERNÁNDEZ-CAMACHO, AND Y. MUÑOZ-SABA. 2000. Mamíferos (Synapsida: Theria) de Colombia. Biota Colombiana 1:43–75.
- ALLEN, J. A. 1900. Note on the generic names *Didelphis* and *Philander*. Bulletin of the American Museum of Natural History 13:185–190.
- ÁVILA-PIRES, F. D. DE. 1964. Mamíferos colecionados na região do Rio Negro (Amazonas, Brasil). Boletim do Museu Paraense Emílio Goeldi (Nova Série), Zoologia 42:1–23.
- AZARA, F. DE. 1801. Essais sur l'histoire naturelle des quadrupèdes de la Province du Paraguay. Charles Poujens, Paris, France.
- BANGS, O. 1898. Descriptions of some new mammals from the Sierra Nevada de Santa Marta, Colombia. Proceedings of the Biological Society of Washington 12:161–165.
- BRISSON, M. J. 1762. Regnum animale in classes IX. Theodorus Haak, Leiden, The Netherlands.
- BUCHER, J. E., AND H. I. FRITZ. 1977. Behavior and maintenance of the woolly opossum (*Caluromys*) in captivity. Laboratory Animal Science 27:1007–1012.
- BURMEISTER, H. 1856. Erläuterungen zur Fauna Brasiliens, enthaltend Abbildungen und ausführliche Beschreibungen neuer oder ungenügend bekannter Thier-Arten. Georg Reimer, Berlin, Germany.
- CABRERA, A. 1916. El tipo de *Philander laniger* Desm. en el Museo de Ciencias Naturales de Madrid. Boletín de la Real Sociedad Española de Historia Natural 16:514–516.
- CABRERA, A. 1919. Genera Mammalia: Marsupialia, Monotremata. Museo Natural de Ciencias Naturales, Madrid, Spain.
- CABRERA, A. 1958. Catalogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Ciencias Zoológicas 4:1–308.
- CÁCERES, N. C. 2000. Dieta, adaptação à alimentação e dispersão de sementes por marsupiais do sul do Brasil. Ph.D. dissertation, Federal University of Paraná, Curitiba, Brazil, 132 pp.
- CÁCERES, N. C. 2005. Comparative lengths of digestive tracts of seven didelphid marsupials (Mammalia) in relation to diet. Revista Brasileira de Zoologia 22:181–185.
- CARDILLO, M., O. R. P. BININDA-EMONDS, E. BOAKES, AND A. PURVIS. 2004. A species-level phylogenetic supertree of marsupials. Journal of Zoology 264:11–31.
- CARMIGNOTTO, A. P. 2004. Pequenos mamíferos terrestres do bioma Cerrado: padrões faunísticos locais e regionais. Ph.D. dissertation, University of São Paulo, São Paulo, Brazil, 404 pp.
- CARTELLE, C. 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. Pp. 27–46 in Mammals of the Neotropics, the central Neotropics: Ecuador, Peru, Bolivia, Brazil (J. F. Eisenberg and K. H. Redford, eds.). University of Chicago Press, Illinois.
- CASELLA, J., AND N. C. CÁCERES. 2006. Diet of four small mammal species from Atlantic forest patches in south Brazil. Neotropical Biology and Conservation 1:5–11.
- CHIVERS, D. J., AND C. M. HLADIK. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. Journal of Morphology 166:337–386.
- COSTA, L. P. 2003. The historical bridge between the Amazon and the Atlantic forests of Brazil: a study of molecular phyogeography with small mammals. Journal of Biogeography 30:71–86.
- COSTA, L. P., AND J. L. PATTON. 2005. Diversidade e limites geográficos e sistemáticos de marsupiais brasileiros. Pp. 321–341 in Os marsupiais do Brasil: biologia, ecologia e evolução (N. C. Cáceres and E. L. A. Monteiro-Filho, eds.). Editora da Universidade Federal de Mato Grosso do Sul, Campo Grande, Brasil.
- CROWE, O., AND I. D. HUME. 1997. Morphology and function of the gastrointestinal tract of Australian folivorous possums. Australian Journal of Zoology 45:357–368.
- DESMARET, M. A. G. 1820. Mammalogie ou description des espèces de mammifères. Première partie, contenant les ordres des binames, des quadrupènes et des carnassiers. V. Agasse, Paris, France.
- EISENBERG, J. F. 1989. Mammals of the Neotropics, the northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Illinois.
- EISENBERG, J. F., AND K. H. REDFORD. 1999. Mammals of the Neotropics, the central Neotropics: Ecuador, Peru, Bolivia and Brazil. University of Chicago Press, Illinois.
- EISENBERG, J. F., AND D. E. WILSON. 1981. Relative brain size

- and demographic strategies in didelphid marsupials. American Naturalist 118:1–15.
- EMMONS, L. H., AND F. FEER. 1997. Neotropical rainforest mammals: a field guide. Second edition. University of Chicago Press, Illinois.
- FLECK, D. W., AND J. D. HARDER. 1995. Ecology of marsupials in two Amazonian rain forests in northeastern Peru. Journal of Mammalogy 76:809–818.
- FONSECA, G. A. B., G. HERRMANN, Y. R. L. LEITE, R. A. MITTERMEIER, A. B. RYLANDS, AND J. L. PATTON. 1996. Lista anotada dos mamíferos do Brasil. Occasional Papers on Conservation Biology 4:1–38.
- GARDNER, A. L. 2005. Order Didelphimorphia. Pp. 3–18 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Third edition. Johns Hopkins University Press, Baltimore, Maryland.
- GARGAGLIONI, L. H., M. E. BATALHÃO, M. J. LAPENTA, M. F. CARVALHO, R. V. ROSSI, AND V. P. VERULLI. 1998. Mamíferos da Estação Ecológica de Jataí, Luiz Antônio, São Paulo. Papéis Avulsos de Zoologia, São Paulo 40:267–287.
- GRIBEL, R. 1988. Visits of *Caluromys lanatus* (Didelphidae) to flowers of *Psedobombax tomentosum* (Bombacaceae): a probable case of pollination by marsupials in central Brazil. Biotropica 20:344–347.
- HERSHKOVITZ, P. 1949. Generic names for the four-eyed pouch opossum and the woolly opossum (Didelphidae). Proceedings of the Biological Society of Washington 62:11–12.
- HERSHKOVITZ, P. 1951. Mammals from British Honduras, México, Jamaica and Haiti. Fieldiana: Zoology 31:547–569.
- HILDEBRAND, M. 1995. Análise da estrutura dos vertebrados. Atenau, São Paulo, Brasil.
- HUNSAKER, D. 1977. Ecology of New World marsupials. Pp. 95–156 in The biology of marsupials (D. Hunsaker II, ed.). Academic Press, New York.
- IHERING, H. VON. 1894. Os mammíferos de S. Paulo. Catálogo. Typographia do Diário Official, São Paulo, Brasil.
- ILLIGER, J. K. W. 1815. Ueberblick der Säugthiere nach ihrer Vertheilung über die Welttheile. Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin 1804–1811:39–159.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE AND NATURAL RESOURCES. 2004. IUCN red list of threatened species. Available at www.redlist.org. Accessed on 21 September 2005.
- JANSA, S. A., AND R. S. VOSS. 2000. Phylogenetic studies on didelphid marsupials I. Introduction and preliminary results from nuclear IRBP gene sequences. Journal of Mammalian Evolution 7:43–77.
- JANSON, C. H., J. TERBORGH, AND L. H. EMMONS. 1981. Non-flying mammals as pollinating agents in the Amazon forest. Biotropica 13:1–6.
- LAMBERT, T. D., J. R. MALCOLM, AND B. L. ZIMMERMAN. 2005. Variation in small mammal richness by trap height and trap type at a southeastern Amazonian site, with notes on a new method of canopy trapping. Journal of Mammalogy 86:982–990.
- LESSON, R. P. 1842. Nouveau tableau de règne animal. Mammifères. Arthus-Bertrand, Paris, France.
- LIAIS, E. 1872. Climats, géologie, faune et géographie botanique du Brésil. Garnier Frères, Paris, France.
- LINNAEUS, C. 1758. *Sistema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.* Laurentii Salvii, Stockholm, Sweden.
- MALCOLM, J. R. 1991a. The small mammals of Amazon forest fragments: pattern and process. Ph.D. dissertation, University of Florida, Gainesville, Florida, 217 pp.
- MALCOLM, J. R. 1991b. Comparative abundances of Neotropical small mammals by trap height. Journal of Mammalogy 72:188–192.
- MALCOLM, J. R. 1995. Forest structure and the abundance and diversity of Neotropical small mammals. Pp. 179–197 in Forest canopies (A. D. Lowman and N. M. Nadkarni, eds.). Academic Press, San Diego, California.
- MATSCHE, P. 1916. Bemerkungen über die Gattung *Didelphis* L. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 8:259–272.
- MATSCHE, P. 1917. Einige neue Formen der *Didelphis lanigera*-Gruppe. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 4:280–294.
- MIRANDA-RIBEIRO, A. DE. 1936. Didelphia ou Mammalia-Ovovipara. Revista do Museu Paulista 20:245–424.
- MONTEIRO-FILHO, E. L. A., AND N. C. CÁCERES. 2005. Biologia reprodutiva de marsupiais didelfídeos. Pp. 99–110 in Os marsupiais do Brasil: biologia, ecologia e evolução (N. C. Cáceres and E. L. A. Monteiro-Filho, eds.). Editora da Universidade Federal de Mato Grosso do Sul, Campo Grande, Brasil.
- MONTILLA, M. M., ET AL. 2002. Isoenzyme clustering of Trypanosomatidae Colombian populations. American Journal of Tropical Medicine and Hygiene 66:394–400.
- MORENO-BEJARANO, L. M., AND R. ÁLVAREZ-LEÓN. 2003. Fauna asociada a los manglares y otros humedales en el delta-estuario del Río Magdalena, Colombia. Revista da Academia Colombiana de Ciencias 27:517–534.
- MUIRHEAD, L. 1819. Mazology. Pp. 393–486, pls. 353–358 in The Edinburgh encyclopaedia (D. Brewster, ed.). Fourth edition. Volume 13. William Blackwood, Edinburgh, Scotland (not seen, cited in Allen 1900:186).
- NOGUEIRA, J. C., P. M. MARTINELLI, S. F. COSTA, G. A. CARVALHO, AND B. G. O. CAMARA. 1999. The penis morphology of *Didelphis*, *Lutreolina*, *Metachirus* and *Caluromys* (Marsupialia, Didelphidae). Mammalia 63:79–92.
- NOWAK, R. M. 1999. Order Didelphimorphia. Pp. 17–35 in Walker's mammals of the world. Sixth edition. Volume I. Johns Hopkins University Press, Baltimore, Maryland.
- OLFERS, I. [F. J. M.] VON. 1818. Bemerkungen zu Illiger's Ueberblick der Säugthiere nach ihrer Vertheilung über die Welttheile, rücksichtlich der Südamerikanischen Arten (Species). Pp. 192–237 in Journal von Brasilien, oder vermischt Nachrichten aus Brasilien, auf wissenschaftlichen Reisen gesammelt (W. L. von Eschwege, ed.). Verlage des Gr. H. S. Landes-Industries-Comptoirs, Weimar, Germany.
- PALMA, R. E., AND T. L. YATES. 1996. The chromosomes of Bolivian didelphid marsupials. Occasional Papers, The Museum, Texas Tech University 162:1–20.
- PATTON, J. L., AND L. P. COSTA. 2003. Molecular phylogeography and species limits in rainforest didelphid marsupials of South America. Pp. 63–81 in Predators with pouches: the biology of carnivorous marsupials (M. Jones and C. R. Dickman, eds.). CSIRO Publishing, Collingwood, Australia.
- PATTON, J. L., S. F. DOS REIS, AND M. N. F. DA SILVA. 1996. Relationships among didelphid marsupials based on sequence variation in the mitochondrial cytochrome *b* gene. Journal of Mammalian Evolution 3:3–29.
- PATTON, J. L., M. N. F. DA SILVA, AND J. R. MALCOLM. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bulletin of the American Museum of Natural History 244:1–306.
- PERES, C. A. 1999. The structure of nonvolant mammal communities in different Amazonian forest types. Pp. 564–581 in Mammals of the Neotropics, the central Neotropics: Ecuador, Peru, Bolivia and Brazil (J. F. Eisenberg and K. H. Redford, eds.). University of Chicago Press, Illinois.
- PÉREZ-HERNÁNDEZ, R. 1985. Notas preliminares acerca de la taxonomía de la familia Didelphidae (Mammalia—Marsupialia) en Venezuela. Memorias de la Sociedad de Ciencias Naturales de La Salle 45:47–76.
- PÉREZ-HERNÁNDEZ, R. 1989. Distribution of the family Didelphidae (Mammalia—Marsupialia) in Venezuela. Pp. 363–410 in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Inc., Gainesville, Florida.
- QUADROS, J., N. C. CÁCERES, L. TIEPOLO, AND M. S. WÄNGLER. 2000. Mastofauna do Parque Estadual do Rio Guarani e área de influência da Usina Hidrelétrica de Salto Caxias, Baixo Rio Iguaçu, Estado do Paraná, Brasil. II Congresso Brasileiro de Unidades de Conservação, Anais, Campo Grande 1:822–829.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics, the southern cone. Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Illinois.
- REIG, O. A., A. L. GARDNER, N. O. BIANCHI, AND J. L. PATTON. 1977. The chromosomes of the Didelphidae (Marsupialia) and their evolutionary significance. Biological Journal of the Linnean Society 9:191–216.

- REIG, O. A., J. A. KIRSCH, AND L. G. MARSHALL. 1987. Systematic relationships of the living and Neocenozoic American opossum-like marsupials (suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. Pp. 1–90 in *Possums and opossums, studies in evolution* (M. Archer, ed.) . Surrey Beatty and Sons Pty. Ltd. and Royal Zoological Society of New South Wales, Sydney, Australia.
- RIBEIRO, R. D., AND M. P. BARRETTO. 1977. Estudos sobre reservatórios e vectores silvestres do *Trypanosoma cruzi*. LXIII: infecção natural da cuíca, *Caluromys lanatus ochropus* (Wagner, 1842) pelo *T. cruzi*. Revista Brasileira de Biologia 37: 195–200.
- RICHARDSON, S. J., R. E. WETTENHALL, AND G. SCHREIBER. 1996. Evolution of transthyretin gene expression in the liver of *Didelphis virginiana* and other American marsupials. Endocrinology 137:3507–3512.
- SANBORN, C. C. 1949. Mammals from the Rio Ucayali, Peru. Journal of Mammalogy 30:277–288.
- SCHIECK, J. O., AND J. S. MILLAR. 1985. Alimentary tract measurements as indicators of diets of small mammals. Mammalia 49:93–104.
- SCHREBER, J. C. D. 1778. Die Saugthiere in Abbildungen nach der Natur, mit Beschreibungen von D. Johan Cristian Daniel von Schreber; fort gesetzt von D. August Goldfuss [and afterwards] Johann Andreas Wagner. Volume 1, part 3. W. Walter, Erlangen, Germany.
- SOUZA, M. J. DE, V. MAIA, AND J. F. DOS SANTOS. 1990. Nucleolar organizer regions, G and C-bands in some Brazilian species of Didelphidae. Revista Brasileira de Genética 13:767–775.
- TALAMONI, S. A., AND M. M. DIAS. 1999. Population and community ecology of small mammals in southeastern Brazil. Mammalia 63:167–181.
- TATE, G. H. H. 1939. The mammals of the Guiana region—general environment and faunistic treatment. Bulletin of the American Museum of Natural History 76:151–229.
- THOMAS, O. 1888. Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History). Trustees of the British Museum (Natural History), London, England.
- THOMAS, O. 1901. New South American Sciuri, *Heteromys*, *Cavia* and *Caluromys*. Annals and Magazine of Natural History, Series 7, 7:192–196.
- THOMAS, O. 1913. The geographical races of the woolly opossum (*Philander laniger*). Annals and Magazine of Natural History, Series 8, 12:358–361.
- THOMAS, O. 1920. A further collection of mammals from Jujuy. Annals and Magazine of Natural History, Series 9, 5:188–196.
- TIEDEMANN, F. 1808. Zoologie. Zu seinen Vorlesungen entworfen. Ester Band. Allgemeine Zoologie mensch und Säugethiere. Webersche Buchhandlung, Landshut & Heidelberg, Germany.
- TROUESSART, E.-L. 1898. Catalogus mammalium tam viventium quam fossilium. Fasciculus V. Sirenia, Cetacea, Edentata, Marsupialia, Allotheria, Monotremata. Volume 2. R. Friedländer and Sohn, Berlin, Germany.
- TROUESSART, E.-L. 1905. Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementum (1899–1904). Cetacea, Edentata, Marsupialia, Allotheria, Monotremata.—Index alphabeticus. Fascicle 4. R. Friedländer and Sohn, Berlin, Germany.
- TSCHUDI, J. J. VON. 1844–1846. Untersuchungen über die Fauna Peruana auf einer Reise in Peru während der Jahre 1838, 39, 40, 41 und 42. Scheitlin und Zollikofer, Saint Gallen, Switzerland.
- VIEIRA, C. V. 1949. Xenartros e marsupiais do Estado de São Paulo. Arquivos de Zoologia do Estado de São Paulo 7:325–362.
- VIEIRA, C. V. 1955. Lista remissiva dos mamíferos do Brasil. Arquivos de Zoologia 8:341–353.
- VOSS, R. S., AND S. A. JANSA. 2003. Phylogenetic studies on didelphid marsupials 2. Nomenclatural data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bulletin of the American Museum of Natural History 276:1–82.
- WAGNER, A. 1842. Diagnosen neuer Arten brasilischer Säugetiere. Archiv für Naturgeschichte 8:356–362.
- WALTER, G. 1990. Records of ticks (Ixodoidea, Ixodidae) from Paraguay and Peru. Andrias 7:169–170.
- WATERHOUSE, G. R. 1841. Marsupialia or pouched animals [Volume 24 of The Naturalist's Library, edited by W. Jardine]. W. H. Lizars, Edinburgh, Scotland.
- WINGE, H. 1893. E Museo Lundii. Jordfundne og Nulevende Pungdyr (Marsupialia) fra Lagon Santa, Minas Geraes, Brasilien. Volume 2, part 2. H. Hagerups Boghandel, Copenhagen, Denmark.
- YUNIS, E., E. RAMIREZ, J. CAYON, AND J. HERNANDEZ. 1972. The chromosomes of the didelphids *Caluromys lanatus* Illiger and *Chironectes minimus* Zimmermann (Marsupialia: Didelphidae). Australian Journal of Zoology 20:265–269.

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