

Kunsia tomentosus (Rodentia: Cricetidae)

ALEXANDRA M. R. BEZERRA AND ULYSES F. J. PARDIÑAS

Departamento de Zoologia, Universidade de Brasília, Campus Darcy Ribeiro, 70910-900 Brasília, Distrito Federal, Brazil; amrbezerra@hotmail.com (AMRB)

Instituto de Diversidad y Evolución Austral (IDEAus-CONICET), Casilla de Correo 128, 9120 Puerto Madryn, Chubut, Argentina; ulyses@cenpat-conicet.gob.ar (UJFP)

Present address of AMRB: Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, FIOCRUZ-IOC, Rio de Janeiro, RJ, Brazil

Abstract: *Kunsia tomentosus* (Lichtenstein, 1830), the woolly giant rat, is a semifossorial cricetid typically associated with the Cerrado and Beni domains in central South America. *Kunsia* was recently revised and includes only 1 species. It is the largest extant sigmodontine and is readily distinguishable by its size, a body covered with dark-gray fur that is coarse and dense, moderately short tail, short limbs, bicolored manus and pes, and long, powerful claws. It inhabits primarily open grasslands and savannas from central and southwestern Brazil and northern Bolivia. *K. tomentosus* presently is not considered threatened; however, westernmost populations have presumably been extirpated in the past 2 centuries.

Key words: Akodontini, Bolivia, Brazil, Cerrado, Neotropical savanna, semifossorial, Sigmodontinae, woolly kunsia

© 2016 by American Society of Mammalogists

Synonymy completed 1 January 2015

DOI:10.1093/mspecies/sev013

Nomenclatural statement.—A life science identifier (LSID)

number was obtained for this publication: [urn:lsid:zoobank.org:](http://urn:lsid:zoobank.org:pub:CC9A1160-F940-48C1-9ABD-83D230901979)

pub:CC9A1160-F940-48C1-9ABD-83D230901979

www.mammalogy.org



Kunsia tomentosus (Lichtenstein, 1830) Woolly Giant Rat

Mus tomentosus Lichtenstein, 1830:plate 33, figure 1, and unnumbered text page. Type locality “waldigen Gegenden am Uruguay entdeckt,” country unknown; restricted to “Rio Uruguay in southeastern Brazil” by Hershkovitz (1966:120).

Mus principalis Lund, 1839:208. Nomen nudum.

Mus principalis Lund, 1840 (1841:276). Type locality “Rio das Velhas’s Floddal” (Lund 1841:292) but listed as “Lapa da Escrivania Nr. 5” (according to Winge 1887:42), a cave excavated by P. W. Lund near Lagoa Santa, Minas Gerais State, Brazil.

[*Hesperomys* (*Scapteromys*)] *tomentosus*: Peters, 1861:135. Name combination.

Habrothrix tomentosus: Fitzinger, 1867:80. Name combination.

Scapteromys principalis: Winge, 1887:42. Name combination.

Scapteromys tomentosus: Trouessart, 1897:534. Name combination

Scapteromys gnambiquaræ Miranda Ribeiro, 1914:37. Type locality unknown, stated as “Campos Novos,” Mato Grosso State, Brazil, by Massoia and Fornes (1965:6; see also Moojen 1952:80).



Fig. 1.—An adult *Kunsia tomentosus* (sex unknown) obtained in a mark-release study carried out about 6 km S Los Fierros, Parque Nacional Noel Kempff Mercado, Santa Cruz Department, Bolivia. Used with permission of the collector and photographer, Louise H. Emmons.

Scapteromys principalis principalis: Massoia and Fornes, 1965:4. Name combination.

Scapteromys principalis gnambiquaræ: Massoia and Fornes, 1965:6. Name combination.

Kunsia tomentosus: Hershkovitz, 1966:117. First use of current name combination.

Kunsia tomentosus tomentosus: [Hershkovitz, 1966](#):119. Name combination.

Scapteromys gnambiquarae: [Hershkovitz, 1966](#):119. Correction of ligature.

Kunsia tomentosus principalis: [Hershkovitz, 1966](#):121, plate 8. Name combination.

Scapteromys tomentosus principalis: [Hershkovitz, 1966](#):122. *Lapsus calami*.

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Sigmodontinae, tribe Akodontini. Two subspecies have been traditionally recognized ([Hershkovitz 1966](#)): *Kunsia tomentosus tomentosus*, occurs throughout most of the distribution of the species, and *K. tomentosus principalis*, restricted to Lagoa Santa, Minas Gerais State, Brazil. In a direct examination of the type materials and additional specimens, [Pardiñas et al. \(2009\)](#) suggested that this subspecific arrangement is weakly supported and differences between *tomentosus* and *principalis* could be individual or age variability. More work is needed on these taxa to solidify the taxonomy.

NOMENCLATURE NOTES. *Kunsia* traditionally has included 2 species, *K. fronto* ([Winge, 1887](#)) and *K. tomentosus* ([Musser and Carleton 2005](#)); however, the genus was recently reviewed and *fronto* was assigned to a new genus, *Gyldenstolpia* [Pardiñas, D'Elía, and Teta, 2009](#) (see [Pardiñas et al. 2009](#); [Pardiñas and Bezerra 2015](#)). The genus *Kunsia* was previously placed in the tribe Scapteromyini, a group derived from the informal Scapteromyine of [Hershkovitz \(1966\)](#), together with the genera *Bibimys* and *Scapteromys* ([Hershkovitz 1966](#); [Reig 1972](#); [Massoia 1979](#); [Pardiñas 1996](#); [D'Elía et al. 2005](#); [Pardiñas et al. 2009](#); [Bezerra 2015](#)). Molecular phylogenetic analyses ([Smith and Patton 1999](#); [D'Elía 2003](#); [D'Elía and Pardiñas 2015](#)) support the placement of these 3 genera in the tribe Akodontini, the 2nd most speciose group of the sigmodontine radiation ([Musser and Carleton 2005](#); [Patton et al. 2015](#)).

The genus name *Kunsia* is a tribute to Merle L. Kuns (1923–2008), of the Middle American Research Unit, National Institutes of Health, who investigated hemorrhagic fever in Bolivia, studying rodent reservoirs of the disease. Kuns assembled a collection of mammals in that country, among them *K. tomentosus* ([Hershkovitz 1966](#)). The specific epithet, *tomentosus*, is a reference to its woolly fur ([Lichtenstein 1830](#)). The woolly giant rat is also known as woolly kunsia, rata gigante (Spanish), colori (Pareci Indian Language; recorded by [Miranda Ribeiro 1914](#)), and arantacú (Nhambiquara Indian Language; recorded by [Miranda Ribeiro 1914](#)).

DIAGNOSIS

Kunsia tomentosus can be easily distinguished from the other sigmodontines by its very large body size, its uniformly dark-gray or dark-brown pelage with almost no dorsal-ventral contrast perceptible, and its bicolored dorsal surface of both the manus and pes, on which the distal portion is white.

Weights of adult individuals of *K. tomentosus* can be as much as 600 g, in comparison the next larger sigmodontines, the rats of the genera *Lundomys*, *Mindomys*, and *Nectomys* (Oryzomyini) have maximum weights of about 300–400 g. *K. tomentosus* is also distinguished by a suite of characters that include: poorly developed mystacial vibrissae, rounded ears covered by tufts of hairs, a moderately short tail covered by sets of 5–7 rigid dark hairs per scale, and powerful claws on both manus and pes ([Miranda Ribeiro 1914](#); [Gyldenstolpe 1932](#); [Hershkovitz 1966](#); [Bezerra et al. 2007](#); [Pardiñas et al. 2009](#); [Bezerra 2015](#)).

GENERAL CHARACTERS

Kunsia tomentosus ([Fig. 1](#)) is a large-sized semifossorial rodent with dense and coarse fur, proportionally short limbs with large and powerful feet and claws, and a moderately short tail (about 65% of the head-body length). The rhinarium is large and naked and highlighted by a ring of whitish hair. The ears are small and round (about 13% of the head-body length); pinnae are covered with short hairs that match the color the dorsal pelage. The moderately short tail is unicolored, scarcely covered with short rigid hairs, and has large subrectangular scales ([Pardiñas et al. 2009](#):figure 3). General pelage color is dark-gray or dark-brown on the dorsal surface and grayish on gular and ventral surfaces. Eight mammae are present arranged in pectoral, postaxial, abdominal, and inguinal pairs ([Miranda Ribeiro 1914](#); [Hershkovitz 1966](#); [Gonçalves et al. 2005](#); [Bezerra et al. 2007](#); [Pardiñas et al. 2009](#)).

Kunsia tomentosus is the largest extant Sigmodontinae with head and body length in adults from 4 geographically distant populations ranging from 185 to 287 mm; length of tail ranges from 147 to 196 mm, and body mass from 241 to 630 g (data from [Bezerra et al. 2007](#) and data from specimens deposited in the Natural History Museum of London by AMRB). There is a great amount of size variation even within a single population ([Bezerra et al. 2007](#):figure 4).

The skull of *K. tomentosus* is robust with thick bones and a short, sturdy rostrum ([Fig. 2](#)). Mean cranial measurements (mm; ranges in parentheses) of 6 adult specimens (mixed sexes) from Parque Nacional das Emas, Goiás State, Brazil (the largest pooled sample known for this species—[Bezerra et al. 2007](#)) were: greatest length of tympanic bulla, 8.16 (7.82–8.78); greatest breadth of tympanic bulla, 10.68 (10.20–11.38); greatest breadth of M1, 3.72 (3.39–4.01); cranial breadth immediately posterior to zygomatic arches, 20.03 (19.28–21.32); cranial depth at tympanic bulla, 16.9 (15.95–18.00); condyloincisive length, 48.79 (45.84–49.55); cranial breadth at external auditory meatus, 20.64 (19.98–22.59); diastema length, 12.87 (12.06–14.66); greatest length of skull, 49.68 (47.50–55.07); incisive foramina breadth, 2.73 (2.53–2.88); incisive foramina length, 10.65 (9.90–11.99); interorbital constriction, 8.11 (7.91–8.23); length of lower molar row, 10.08 (10.31–11.34); mandible length, 29.97 (29.38–32.29); mesopterygoid fossa breadth, 3.49



Fig. 2.—Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult male of *Kunsia tomentosus* (BMNH 79.325, deposited in the Natural History Museum, London, United Kingdom) from 260 km N of Xavantina, Serra do Roncador, Mato Grosso State, Brazil. Condylbasal length is 49.95 mm. Photographed by Alexandra M. R. Bezerra.

(3.05–3.69); mandibular ramus length, 15.78 (15.04–17.42); palatal breadth measured at M1-M2, 12.91 (12.06–13.88); nasal length, 18.57 (17.27–21.11); palatal length, 26.09 (24.08–29.98); palatilar length, 22.61 (21.64–25.47); postpalatal length, 21.97 (20.93–23.42); rostral breadth, 8.61 (8.04–9.33); rostral depth, 9.87 (9.38–11.16); rostral length, 19.88 (18.04–22.37); length of upper molar row, 10.32 (9.93–10.73); and greatest zygomatic breadth, 28.39 (26.95–30.80). Measurements (mm) of the type specimens of the nominal forms, reported by [Miranda Ribeiro \(1914\)](#), and [Hershkovitz \(1966\)](#), were: length of head

and body, 287 (*tomentosus*), 267 (*gnambiquarae*); length of tail, 157 (*tomentosus*), 160 (*gnambiquarae*); width of braincase, 19.3 (*tomentosus*); greatest length of skull, 55 (*gnambiquarae*); width of interorbital constriction, 8.0 (*principalis*); length of nasals, 20.5 (*gnambiquarae*); incisive foramina length, 12.3 (*principalis*); length of diastema, 14.0 (*principalis*); least interorbital breadth, 10 (*gnambiquarae*); length of upper molar series, 11.5 (*gnambiquarae*); and alveolar length of molar row, 10.5 (*tomentosus*), 11.3 (*principalis*).

Exploratory principal component analysis performed on the covariance matrix of log-transformed of 26 craniodental measurements of 17 specimens (representing almost all available *K. tomentosus* from Brazilian and Bolivian) did not reveal any grouping and indicated a strong influence of the “size” factor ([Bezerra et al. 2007](#)). Among the samples with the larger means of craniodental measurements, the population from Campos Novos, Mato Grosso State, was larger for 11 characters, Santa Cruz Department for 9 characters, and Humaitá, Amazonas State, was larger for 5 and smaller in 1 character. The population sampled from Parque Nacional das Emas, Goiás State, was smaller for 16 characters, and those from Vilhena, Rondônia State, were smaller for 9, but larger in 1 character ([Bezerra et al. 2007](#)).

DISTRIBUTION

Kunsia tomentosus is known from open areas and savannas of the Cerrado and Beni domains of central Brazil and northern Bolivia from 60 to 750 m elevation, respectively ([Hershkovitz 1966](#); [Musser and Carleton 2005](#); [Bezerra et al. 2007](#); [Terán et al. 2008](#); [Pardiñas et al. 2009](#); [Fig. 3](#)). Its geographic range in Brazil extends from southwestern Goiás State ([Rodrigues et al. 2002](#)) to the north through Mato Grosso State ([Miranda Ribeiro 1914](#); [Santos-Filho et al. 2001](#); [Bezerra et al. 2007](#)), Rondônia State ([Andrades-Miranda et al. 1999](#); [Bezerra et al. 2007](#)), and Amazonas State ([Bezerra et al. 2007](#)). In Bolivia, *K. tomentosus* has been recorded in the departments of Santa Cruz ([Ibáñez et al. 1994](#); [Anderson 1997](#); [Emmons 1998](#); [D’Elía and Pardiñas 2004](#); [Bezerra et al. 2007](#)), Beni ([Hershkovitz 1966](#); [Anderson 1997](#)), and La Paz ([Terán et al. 2008](#)).

Although the type locality of *K. tomentosus* was restricted to the Uruguay River, in south Brazil ([Hershkovitz 1966](#)), the nearest confirmed record to this species is about 1,040 km north, from Parque Nacional das Emas, Goiás State ([Bezerra et al. 2007](#)). The Uruguay River dissects the Atlantic Forest interior, but not the Cerrado nor transitional open areas, casting doubts about the correctness of [Hershkovitz’s \(1966\)](#) restriction. The type specimen of *K. tomentosus* was obtained in 1827 by Friedrich Sellow (or Sello) and sent to Berlin, Germany, where it was preserved as a mounted animal and subsequently housed (under the number ZMB-MAM 1699, Museum für Naturkunde) as a skin with a damaged skull removed. Sellow also secured materials from other collectors and local dealers that worked across the Brazilian territory, and there is no solid

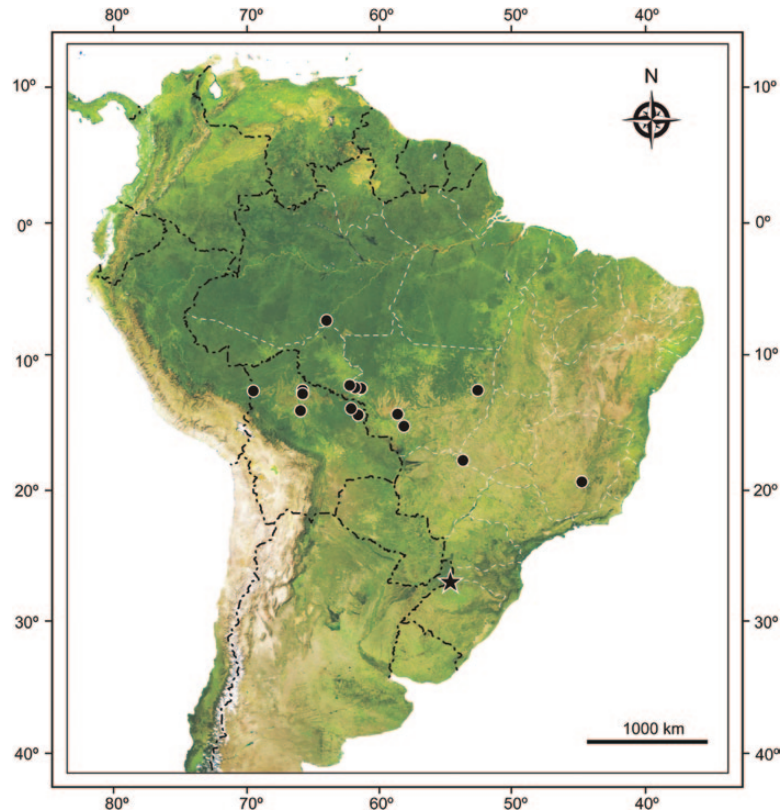


Fig. 3.—Geographic distribution of *Kunsia tomentosus* as indicated by documented collection localities (dots) and the restricted type locality (star) reported by [Herskovitz \(1966\)](#); modified from [Bezerra et al. \(2007\)](#), [Pardiñas et al. \(2009\)](#), and [Téran et al. \(2008\)](#).

evidence to fix the type locality of *K. tomentosus* to anywhere along the Uruguay River ([Cerqueira 1975](#); [Bezerra et al. 2007](#); [Pardiñas et al. 2009](#)).

The easternmost known locality for *K. tomentosus* is Lagoa Santa, Minas Gerais State, Brazil, from where both Pleistocene and Holocene specimens have been recorded ([Winge 1887](#)). The recent material corresponds to a few cranial remains of juvenile individuals and the attached label indicated that they were derived from owl pellets collected by Peter Lund around 1840; no additional animals have been obtained in the last 175 years. The record of *K. tomentosus* in Pampas del Heath, La Paz Department, Bolivia ([Terán et al. 2008](#)), suggests the plausible occurrence of the species in southern Peru, taking into account the continuity of habitat between both countries ([Montambault 2002](#)).

FOSSIL RECORD

Kunsia tomentosus has been recorded from Pleistocene cave sediments excavated by Peter Lund in Lagoa Santa area, Minas Gerais State, Brazil ([Lund 1840](#); [Winge 1887](#)). The lectotype of *Scapteromys principalis* is a fossil anterior skull fragment collected in “Lapa da Escrivania Nr. 5” (= Lapa da Escrivânia) a cave chamber filled by Quaternary sediments ([Voss and Myers 1991](#); [Pardiñas et al. 2009](#)) located about

12.5 km N Matozinhos (Minas Gerais State, Brazil). From the same cave chamber, numerous additional fossil remains of this rodent, representing about 65 individuals, were obtained ([Pardiñas et al. 2009](#)). *K. tomentosus* is listed within the fossil fauna recovered by lift aspiration technique from the flooded Japonês Cave, a submerged channel of crystalline waters in the Municipality of Bela Vista, Mato Grosso do Sul State, Brazil ([Salles et al. 2006](#)). In a current study of faunal remains from archaeological sites located near Porto Alegre, Rio Grande do Sul State, Brazil, Holocene remains of *K. tomentosus* have been identified (P. Hadler, in litt.). Both Mato Grosso do Sul and Rio Grande do Sul findings are notable because they indicate the species had in the recent past a widespread distribution in southern Brazil.

Based on phylogenetic reconstructions it has been hypothesized that *Kunsia* is sister to *Scapteromys*, a palustrine sigmodontine widely distributed in Río de La Plata basin ([D’Elía 2003](#); [D’Elía and Pardiñas 2004](#); [Pardiñas et al. 2009](#)). *Scapteromys* is known from Early to Middle Pleistocene deposits of northeastern Buenos Aires Province, Argentina ([Voglino and Pardiñas 2005](#)). *Scapteromys herskovitzi* [Reig, 1994](#), a putative fossil species of the Pliocene ([Reig 1972, 1994](#)), is more likely an extinct unnamed genus related to *Kunsia* and *Gyldenstolpia* (see [Pardiñas et al. 2009](#)), an issue that deserves further scrutiny.

FORM AND FUNCTION

Kunsia tomentosus is a semifossorial rodent (Miranda Ribeiro 1914; Bezerra et al. 2007). Its short extremities (tail and limbs), large and powerful fore and hind feet with long and powerful claws, coarse pelage, short ears, and tail covered with large scales and stiff hairs have been considered adaptations for fossorial life. In fact, *K. tomentosus* is highlighted as the extreme example of a “gopher-like” sigmodontine (Hershkovitz 1966:95).

Manus with 5 digits; digits II–V have long claws (almost the same length as the digit), and the pollux is reduced with a pointed nail. Plantar surface of the manus has 5 pads: 3 small interdigital pads (II, III, IV) and 2 proximal (carpal) pads, the thenar (at base of pollux) and the hypothenar. Interdigital pads are small, rounded, and equidistant. Carpal pads are larger, elongate, wide, and separated. Skin between pads is corrugated. Digits I and V are the smallest of the 5 digits of the hind foot. Plantar surface of hind feet has 4 small and rounded interdigital pads and 2 tarsal pads (a reduced hypothenar and an elongate thenar). Thenar pad elongated in dry skin preparations but appears reduced to a small oval pad in fresh specimens. Skin between the pads is corrugate from distal pads up to the thenar and hypothenar pads limit; remainder of plantar surface is smooth. There is no webbing between digits in either manus or pes (Hershkovitz 1966; Bezerra et al. 2007; Pardiñas et al. 2009).

Occipital and lambdoid crests of the skull are well developed, the interorbital region is narrow, and the coronal suture typically U-shaped. The zygomatic plate is high and very broad in lateral view, with the anterior border nearly perpendicular and close to the nasolacrimal capsules. The zygomatic arches have a medial dorsoventral enlargement, involving jugal and maxillary bones. Upper corner of zygomatic plate has a moderately well-developed spinous blunt process. The nasal bones are scalloped distally; nasofrontal suture typically straight. Zygomatic notch almost closed (in dorsal view) and very well developed. Incisive foramina reach the anterior root of M1. The mesopterygoid fossa is wide open and the mesopterygoid roof is deeply excised by paired sphenopalatine vacuities. Auditory bullae are inflated. Carotid circulation pattern 1 (sensu Voss 1988), which is osteologically typified by a conspicuous anteroposterior groove on the inner surface of the squamosal and alisphenoid bones (“squamosal-alisphenoid groove”), together with the presence of a small sphenofrontal foramen, a small posterior opening of the alisphenoid canal and a large stapedial foramen is present. Some specimens exhibit the presence of a small foramen in the alisphenoid bone anterior to the squamosal-alisphenoid groove, in the intersection with the trough for the masticatory-buccinator nerve. The occurrence and localization of this latter foramen varied among specimens and is independent from the geographic provenance of the specimen. A massive alisphenoid strut partially covering the anterior opening of the alisphenoid canal is present (Bezerra et al. 2007; Pardiñas et al. 2009).

Mandible is robust, with a short transverse ramus and high ascendant portion. The coronoid process is well developed and the condyloid process is wide and rounded. Angular process slightly projected forward determining a reduced lunar notch. Capsular projection is well developed and medially located between coronoid and condyloid processes (Hershkovitz 1966; Bezerra et al. 2007; Pardiñas et al. 2009).

Dental formula is: 1/1 i, 0/0 c, 0/0 p, 3/3 m, total 16. Molar topography allowed the recognition of 3 ontogenetic classes based on upper molar eruption and enamel wear (Bezerra et al. 2007): “juvenile” (M3 unerupted or unworn), “adult” (all upper molars erupted and functional), and “old adult” (all upper molars worn; without folds and with the widest part of crowns concave). Number of vertebrae for 1 specimen of *K. tomentosus* from Mato Grosso State was recorded as 12 T, 6 L, 3 S, and 23 CA (Miranda Ribeiro 1914).

Kunsia tomentosus has strong, smooth, orthodont, saturated orange upper incisors, and conspicuous unilateral hypsodont molars. The upper molar rows are parallel. Unworn molar teeth are plane and trilofodont; wear occurs quickly closing the major folds. M1 is transversally expanded; the procingulum narrows anteroposteriorly and projects labially. Anteromedian flexus-flexid persistent at M1-m1. Vestigial or absent mesoloph; reduced mesolophids fused to complex entolophulids in adult individuals. M3 cylindrical in outline, retaining a major mesoposetus, but lacking evidence of hypoflexus in adult individuals. The m1 has a well-developed anterolabial cingulum and the m3 is subtriangular in outline and reduced with respect to the m2. The m1 is 4-rooted (Hershkovitz 1966; Bezerra et al. 2007; Pardiñas et al. 2009).

Subtle variation in the shape of the posterior margin of the palate was observed among populations. This margin in specimens from Parque Nacional das Emas, Goiás State, is concave like an inverse “U,” whereas in specimens from the Rondônia and Amazonas states, Brazil, and Beni and Santa Cruz departments, Bolivia, this margin is like an inverse “W” with rounded edges and a median palatine process, which is a caudal extension of the palatine bones. In adults of the type series of *Scapteromys gnambiquarae* (= *K. t. tomentosus*) from Campos Novos, Mato Grosso State, posterior border of the palate shows a median projection smoother than the one found in the specimens of Vilhena, Rondônia State, and Humaitá, Amazonas State. In the Bolivian specimens, this structure tends to be more conspicuous than in Brazilian animals. Considerable age-related variation with respect to this character was detected in a single population sample in Parque Nacional das Emas, Goiás State (Bezerra et al. 2007).

Kunsia tomentosus has a unilocular-discoglandular stomach (sensu Carleton 1973:28), with incisura angularis that does not extend beyond the level of the opening of the esophagus. Both antrum and corpus are covered by cornified epithelium, and glandular epithelium is confined to a diverticulum located on the greater curvature of the stomach. A minute aperture connects this glandular pouch with the main lumen of the stomach (Bezerra et al. 2007). A large sacular gall bladder is present

(Voss 1991; Bezerra et al. 2007). A pouched stomach like that of *K. tomentosus* is also found in other muroids with a predominance of insects in the diet (Carleton 1973). Within the akodontines, *Kunsia* shared this general morphology with *Blarinomys* (contra Geise et al. 2008:7; see Teta and Pardiñas 2015:209), *Brucepattersonius*, *Juscelinomys*, *Lenoxus*, *Oxymycterus*, and *Scapteromys* (Hershkovitz 1966; Carleton 1973; Hershkovitz 1994, 1998; Emmons and Patton 2012; Patton 2015).

The phallus of *K. tomentosus*, based on 1 individual, is straight, elongate, and subcylindrical, with simple spinous epidermis throughout the body wall and edge of crater. Bacular mound is spineless and slightly trifurcate, supported by a reduced tridigitate bacular cartilage. The phallus has bilobed urethral flaps and a simple dorsoventrally flattened and spineless dorsal papilla. Proximal portion of osseous baculum is an inverted heart-like shape (Bezerra 2005).

ONTOGENY AND REPRODUCTION

Lack of information on breeding makes it difficult to determine the exact number of annual estrous cycles; however, available data indicate that breeding may be twice a year (Bezerra et al. 2007). A pregnant female was captured at Estação Ecológica Serra das Araras, Mato Grosso State, Brazil, in July (dry season) with 3 embryos (Santos-Filho et al. 2001). Another pregnant female was captured at Parque Nacional das Emas, Goiás State, Brazil, in October (early wet season) with 1 embryo (Bezerra et al. 2007). Juveniles were taken in June (1 male—Terán et al. 2008), July (1 female—Santos-Filho et al. 2001), and November (1 male—Bezerra et al. 2007).

ECOLOGY

Kunsia tomentosus occurs in tropical savanna and grassland habitats from the Cerrado and Beni domains within Brazil and Bolivia, respectively. Two records are also known for 2 Amazon savannas, Vilhena, Rondônia State (Andrades-Miranda et al. 1999), and Humaitá, Amazonas State (Bezerra et al. 2007), Brazil, which are an enclave of savannas in the south of the Amazon domain. It has been reported to occur almost exclusively in unflooded grasslands termed “campo sujo” (an open grassland with some trees and shrubs) and “campo cerrado” (a shrubby vegetation with a ground cover of grasses—Miranda Ribeiro 1914; Hershkovitz 1966; Andrades-Miranda et al. 1999; Santos-Filho et al. 2001; Rodrigues et al. 2002; Bezerra et al. 2007), the arboreal dense savannas known as “cerrado sensu stricto” (woodland with an open canopy and some grass covering the ground—Bezerra et al. 2007), the arboreal savanna semi-evergreen “pampas-termitero” (a vegetation type of Bolivian savannas—Terán et al. 2008), and a flooded bamboo forest close to open grassland known as “la pampa” (Bezerra et al. 2007). These records, and the lack of occurrences in forested areas, suggest that *K. tomentosus* is apparently restricted to open savanna

and grassland habitats and it displays considerable patchiness in its distribution through Brazil and Bolivia, despite the availability of potential optimal habitats (Bezerra et al. 2007).

There are only a few reports based on direct observations documenting that *K. tomentosus* has fossorial habits, roosting in burrows, and feeding on roots of grasses and arthropods (Miranda Ribeiro 1914; Hershkovitz 1966; Bezerra et al. 2007). In Parque Nacional das Emas, Goiás State, individuals were observed hunting and ingesting insects (Orthoptera and Isoptera) that were moving in the leaf litter inside the vivary where they were captive; insects were located by smell, captured with the forefeet and transferred to the mouth (Bezerra et al. 2007).

Miranda Ribeiro (1914) reported observing *K. tomentosus* building small galleries with grasses that were pulled from the surrounding area. Both adults and juveniles were captured in several localities in both rainy and dry seasons (Bezerra et al. 2007), rejecting the hypothesis advanced by Hershkovitz (1996) that *K. tomentosus* is seasonally fossorial, living in burrows during the rainy seasons.

Adult individuals have been captured only with the use of Tomahawk® live traps (145 by 145 by 410 mm; Tomahawk Live Trap, LLC, Hazelhurst, Wisconsin), including 1 individual from Estação Ecológica Serra das Araras, Mato Grosso State (Bezerra et al. 2007), and 7 individuals from Parque Nacional das Emas, Goiás State (Rodrigues et al. 2002; Bezerra et al. 2007). One juvenile was captured in a pitfall trap of 30 liters from Estação Ecológica Serra das Araras, Mato Grosso State (Bezerra et al. 2007), and another juvenile was captured with a Sherman® live trap (76 by 89 by 229 mm; H. B. Sherman Traps, Inc., Tallahassee, Florida) in Pampas del Heath, La Paz Department (Terán et al. 2008). The use of traditional live traps for capturing nonvolant small mammals is not an efficient means to capture *K. tomentosus* because of its semifossorial habits and large body size (Hershkovitz 1966). The use of larger live traps and pitfall traps with buckets up to 60 liters is likely a better capture method to survey this species (Bezerra et al. 2007). Baits utilized to capture *K. tomentosus* have been described as a mixture of barley with canned tuna, oats, and vanilla essence (Terán et al. 2008), or one of us (AMRB) has had success using a mixture of banana, corn flour, and canned sardines.

Eight records of *K. tomentosus* (6 captures and 2 sightings) obtained at Parque Nacional das Emas, Goiás State, suggest that this species is nocturnal or crepuscular because the traps were reset twice per day (morning after 0800 h and afternoon after 1400 h—Bezerra et al. 2007). One individual was hand-captured during the night at Parque Nacional Noel Kempff Mercado, Santa Cruz Department (Cabot-Nieves 1996). Additional individuals have been secured by dogs (Miranda Ribeiro 1914; Hershkovitz 1966).

Kunsia tomentosus hosts the ectoparasite *Gyropus riberoi* (Insecta: Phthiraptera: Amblycera), described from the type series of *Scapteromys gnambiquarae* (Werneck 1935, 1936). This louse is widespread in caviomorph rodents (Castro and Cicchino 1978), suggesting its presence in *Kunsia* as a case of accidental infection (Pardiñas et al. 2009).

There are no data about predation on *Kunsia*. However, the fossil and recent material recovered from the Lagoa Santa area have been attributed to owl trophic activities (Lund 1840; Winge 1887). The age of the fossils from “Lapa da Escrivania Nr. 5,” mostly juvenile individuals, is in accordance with the expected age profile for a preyed sample of this large rodent (Pardiñas et al. 2009). The human consumption of *K. tomentosus* was recorded for the ethnographical group Nhambiquara (= Nambikwara) that inhabit the northwestern Mato Grosso State, Brazil (Miranda Ribeiro 1914).

GENETICS

The karyotype of *Kunsia tomentosus*, based on 1 male of Vilhena, Rondônia State, is formed by 21 pairs of acrocentric autosomes (diploid number $[2n] = 44$, fundamental autosome number $[FN] = 42$ —Andrades-Miranda et al. 1999). Sex-determining chromosomes are a median acrocentric X and a small acrocentric Y. C-banding revealed blocks of constitutive heterochromatin associated with the centromeres of all autosomes and of the X chromosome. Chromosome comparisons between *Kunsia* and *Scapteromys* suggest that they are sister taxa and show differences in diploid numbers with a $2n$ of 36, 34, 32, and 24 reported in *Scapteromys* (Andrades-Miranda et al. 1999). Further differences include the lack of any shared G-banded autosomes, very different C-band patterns, a different number of chromosomal arms associated with the nuclear organizing region between the 2 genera, and differences in the sequence composition of the telomeric DNA (Andrades-Miranda et al. 1999).

Within the tribe Akodontini, molecular markers, both nuclear and mitochondrial gene sequences (IRBP and Cyt *b*, respectively), consistently recovered *Kunsia* as a sister group to *Scapteromys* (Smith and Patton 1999; D’Elía 2003; D’Elía et al. 2005; Pardiñas et al. 2009; Schenk et al. 2013). In a combined analysis, both genera were grouped into the informal *Scapteromys* Division (D’Elía 2003; Parada et al. 2013). It is important to remark that there are no molecular data for *Gyldenstolpia*, an akodontine genus that is phenotypically close to both *Kunsia* and *Scapteromys* (Pardiñas et al. 2009). Divergence in the mtDNA cytochrome-*b* gene for 4 specimens of *K. tomentosus*, 3 Bolivian and 1 Brazilian, ranged from 0.2% to 2.1%; for the same marker, the divergence observed between *Kunsia* and *Scapteromys* is about 15% (Pardiñas et al. 2009:548).

CONSERVATION

Currently, *Kunsia tomentosus* is not included as a threatened species in any threatened red list. It is classified as “Least Concern” by the *International Union for Conservation of Nature and Natural Resources Red List of Threatened Species* because although it is rarely recorded, not abundant and patchy within its wide distribution, it is unlikely to be declining at nearly the rate

required to qualify for listing in a threatened category (Marinho-Filho and Vieira 2008). However, the lack of new records for Lagoa Santa area, Minas Gerais State, Brazil, from where it was recorded around 1840 (Winge 1887) strongly suggests the possibility of recent local or regional extirpation.

ACKNOWLEDGMENTS

We thank A. P. Carmignotto, Universidade de São Carlos, Campus Sorocaba, for shared field data (bait composition) and provided literature; L. H. Emmons for kindly provided photos of a live specimen of *Kunsia tomentosus*; P. Jenkis and L. Tomsett, Natural History Museum of London, for hospitality and granted access to the collection; F. H. G. Rodrigues, Universidade Federal de Minas Gerais, for shared field data (bait composition); D. Voglino generously constructed the map in Fig. 3. We thank 2 anonymous referees for their comments. AMRB received a researcher fellowship from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, proc. 372459/2013-7). UFJP is supported by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and Agencia (PICT 2008-547 and PICT 2014-1039).

LITERATURE CITED

- ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History* 231:1–652.
- ANDRADES-MIRANDA, J., A. P. NUNES, L. F. B. OLIVEIRA, AND M. S. MATTEVI. 1999. The karyotype of the South American rodent *Kunsia tomentosus* (Lichtenstein, 1830). *Cytobios* 98:137–147.
- BEZERRA, A. M. R. 2005. Phallic morphology of *Kunsia tomentosus* (Rodentia: Sigmodontinae). *Mastozoología Neotropical* 12:227–232.
- BEZERRA, A. M. R. 2015. Genus *Kunsia* Hershkovitz, 1966. Pp. 228–231 in *Mammals of South America, volume 2 - rodents* (J. L. Patton, U. F. J. Pardiñas, and G. D’Elía, eds.). University of Chicago Press, Chicago, Illinois.
- BEZERRA, A. M. R., A. P. CARMIGNOTTO, A. P. NUNES, AND F. H. G. RODRIGUES. 2007. New data on the distribution, natural history and morphology of *Kunsia tomentosus* (Lichtenstein, 1830) (Rodentia: Cricetidae: Sigmodontinae). *Zootaxa* 1505:1–18.
- CABOT-NIEVES, J. 1996. La Expedición Zoológica Hispano-Boliviana al Parque Nacional de Huanchaca. Landívar SRL, Santa Cruz de la Sierra, Bolivia.
- CARLETON, M. D. 1973. Survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. *Miscellaneous Publications Museum of Zoology, University of Michigan* 146:1–43.
- CASTRO, D. DEL, AND A. C. CICCHINO. 1978. Contribución al conocimiento de los malófagos argentinos III. *Revista de la Sociedad Entomológica Argentina* 37:77–83.
- CERQUEIRA, R. 1975. Sobre a localidade tipo de *Holochilus brasiliensis* (Brants, 1827) (Rodentia, Cricetidae). *Revista Brasileira de Biologia* 35:31–34.
- D’ELÍA, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. *Cladistics* 19:307–323.
- D’ELÍA, G., AND U. F. J. PARDIÑAS. 2004. Systematics of Argentinean, Paraguayan, and Uruguayan swamp rats of the genus *Scapteromys* (Rodentia, Cricetidae, Sigmodontinae). *Journal of Mammalogy* 85:897–910.

- D'ELÍA, G., AND U. F. J. PARDIÑAS. 2015. Tribe Akodontini Vorontsov 1959. Pp. 140–144 in *Mammals of South America, volume 2 - rodents* (J. L. Patton, U. F. J. Pardiñas, and G. D'Elía, eds.). University of Chicago Press, Chicago, Illinois.
- D'ELÍA, G., U. F. J. PARDIÑAS, AND P. MYERS. 2005. An introduction to the genus *Bibimys* (Rodentia: Sigmodontinae): phylogenetic position and alpha taxonomy. Pp. 211–246 in *Mammalian diversification: from chromosomes to phylogeography. A celebration of the career of James L. Patton* (E. A. Lacey and P. Myers, eds.). University of California Publications in Zoology 133.
- EMMONS, L. H. 1998. Mammal Fauna of Parque Nacional Noel Kempff Mercado. Fauna de Mamíferos del Parque Nacional Noel Kempff Mercado. Pp. 129–143 + Appendix 3 (pp. 341–347) in *A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia* (T. J. Killeen and T. S. Schulenberg, eds.). RAP Working Papers 10. Conservation International, Washington, D.C.
- EMMONS, L. H., AND J. L. PATTON. 1998. Taxonomic revision of Bolivian *Juscelinomys* (Rodentia, Cricetidae) with notes on morphology and ecology. *Mammalia* 76:285–294.
- FITZINGER, L. J. 1867. Versuch einer natürlichen Anordnung der Nagethiere (Rodentia). *Sitzungsberichte der Akademie der Wissenschaften in Wien* 16:57–168.
- GEISE, L. U., H. G. BERGALLO, C. E. L. ESBERARD, C. F. D. ROCHA, AND M. VAN SLUYS. 2008. The karyotype of *Blarinomys breviceps* (Mammalia: Rodentia: Cricetidae) with comments on its morphology and some ecological notes. *Zootaxa* 1907:47–60.
- GONÇALVES, P. R., J. A. OLIVEIRA, M. OLIVEIRA CORRÊA, AND L. M. PESSÔA. 2005. Morphological and cytogenetic analyses of *Bibimys labiosus* (Winge, 1887) (Rodentia, Sigmodontinae): implications for its affinities with the scapteromyine group. Pp. 175–210 in *Mammalian diversification: from chromosomes to phylogeography. A celebration of the career of James L. Patton* (E. A. Lacey and P. Myers, eds.). University of California Publications in Zoology 133.
- GYLDENSTOLPE, N. 1932. A manual of Neotropical sigmodont rodents. *Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien* 11:1–164.
- HERSHKOVITZ, P. 1966. South American swamp and fossorial rats of the scapteromyine group (Cricetinae, Muridae) with comments on the glans penis in murid taxonomy. *Zeitschrift für Säugetierkunde* 31:81–149.
- HERSHKOVITZ, P. 1994. The description of a new species of South American Hociucido, or long-nose mouse genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. *Fieldiana Zoology, New Series* 79:1–43.
- HERSHKOVITZ, P. 1998. Report on some sigmodontine rodents collected in southeastern Brazil with descriptions of a new genus and six new species. *Bonner Zoologische Beiträge* 47:193–256.
- IBÁÑEZ, C., J. CABOT, AND S. ANDERSON. 1994. New records of Bolivian mammals in the collection of the Estación Biológica de Doñana. *Doñana, Acta Vertebrata* 21:79–83.
- LICHTENSTEIN, H. 1830. Darstellungen neuer oder wenig bekannte Säugethiere Abbildungen und Beschreibungen von fünf und sechzig Arten und fünfzig colorirten Steindrucktafeln nach den Originalen des Zoologischen Museum der Universität zu Berlin. C. G. Luderitz, Berlin, unpaginated text belonging to 50 plates.
- LUND, P. W. 1840. Tillaeg til de to sidste Afhandlinger over Brasiliens Dyreverden for sidste Jordomvaeltning. *Lagoa Santa, den 4^{de} April 1839*. Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandling 3:1–24, 3 pls. [Preprint of Lund, P. W. 1841.]
- LUND, P. W. 1841. Blik paa Brasiliens Dyreverden for sidste Jordomvaeltning. Tillaeg til de to sidste Afhandlinger over Brasiliens Dyreverden for sidste Jordomvaeltning. *Lagoa Santa, den 4^{de} April 1839*. Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandling 8:273–296, pls. 25–27.
- MARINHO-FILHO, J., AND E. VIEIRA. 2008. *Kunsia tomentosus* in *International Union for Conservation of Nature and Natural Resources 2015*. International Union for Conservation of Nature and Natural Resources Red List of Threatened Species. Version 2015.2. www.iucnredlist.org. Accessed 6 July 2015.
- MASSOIA, E. 1979. Descripción de un género y especie nuevos: *Bibimys torresi* (Mammalia – Rodentia – Cricetidae – Sigmodontinae – Scapteromyini). *Physis* 38:1–7.
- MASSOIA, E., AND A. FERNES. 1965. Notas sobre el género *Scapteromys* (Rodentia – Cricetidae). II. Fundamentos de la identidad específica de *S. principalis* (Lund) y *S. gnambiquarae* (M. Ribeiro). *Neotrópica* 11:1–7.
- MIRANDA RIBEIRO, A. 1914. *Historia Natural. Zoologia. Cebidae, Hapalidae; Vespertilionidae, Emballonuridae, Phyllostomatidae; Felidae, Mustelidae, Canidae, Procyonidae; Tapyridae; Suidae, Cervidae; Sciuridae, Muridae, Octodontidae, Coenduidae, Dasyproctidae, Caviidae e Leporidae; Platanistidae; Bradynodidae, Myrmecophagidae, Dasypodidae; Didelphyidae. Comissão de linhas telegráficas estratégicas de Mato Grosso ao Amazonas 13, Anexo* 5:37–39.
- MONTAMBAULT, J. R. (ED.). 2002. *Informes de las evaluaciones biológicas de Pampas del Heath, Perú, Alto Madidi, Bolivia, y Pando, Bolivia*. Conservation International, Washington, D.C.
- MOOJEN, J. 1952. *Roedores do Brasil*. Ministério da Educação e Saúde, Instituto Nacional do Livro. Biblioteca Científica Brasileira, Serie A-II.
- MUSSER, G. G., AND M. D. CARLETON. 2005. Superfamily Muroidea. Pp. 894–1531 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- PARADA, A., U. F. J. PARDIÑAS, J. SALAZAR-BRAVO, G. D'ELÍA, AND E. PALMA. 2013. Dating an impressive Neotropical radiation: molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. *Molecular Phylogenetics and Evolution* 66:960–968.
- PARDIÑAS, U. F. J. 1996. El registro fósil de *Bibimys* Massoia, 1979 (Rodentia). Consideraciones sobre los Scapteromyini (Cricetidae, Sigmodontinae) y su distribución durante el Plioceno-Holoceno en la región pampeana. *Mastozoología Neotropical* 3:15–38.
- PARDIÑAS, U. F. J., AND A. M. R. BEZERRA. 2015. Genus *Gyldenstolpia* Pardiñas, D'Elía, and Teta, 2009. Pp. 222–225 in *Mammals of South America, volume 2 - rodents* (J. L. Patton, U. F. J. Pardiñas and G. D'Elía, eds.). The University of Chicago Press, Chicago, Illinois.
- PARDIÑAS, U. F. J., G. D'ELÍA, AND P. TETA. 2009. Una introducción a los mayores sigmodontinos vivientes: revisión de *Kunsia* Hershkovitz, 1966 y descripción de un nuevo género (Rodentia: Cricetidae). *Arquivos do Museu Nacional, Rio de Janeiro* 66:509–594 [Number 3–4 of the Arquivos in which this paper appeared is dated “jul./dez.2008” but did not appear until 2009.]
- PATTON, J. L. 2015. Genus *Lenoxus* Thomas, 1909. Pp. 231–232 in *Mammals of South America, volume 2 - rodents* (J. L. Patton, U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press, Chicago, Illinois.
- PATTON, J. L., U. F. J. PARDIÑAS, AND G. D'ELÍA (EDS.). 2015. *Mammals of South America, volume 2 – rodents*. The University of Chicago Press, Chicago, Illinois.
- PETERS, W. 1861. Über einige merkwürdige Nagethiere (*Spalacomys indicus*, *Mus tomentosus* und *Mus squamipes*) des Königl. zoologischen Museums. *Physikalische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* 1860:139–156 + 2 pls.
- REIG, O. A. 1972. The evolutionary history of the South American cricetid rodents. Ph.D. dissertation, College University, London, United Kingdom.
- REIG, O. A. 1994. New species of akodontine and scapteromyine rodents (Cricetidae) and new records of *Bolomys* (Akodontini) from the Upper Pliocene and Middle Pleistocene of Buenos Aires Province, Argentina. *Ameghiniana* 31:99–113.
- RODRIGUES, F. H. G., ET AL. 2002. Composição e caracterização da fauna de mamíferos do Parque Nacional das Emas, Goiás. *Revista Brasileira de Zoologia* 19:589–600.
- SALLES, L. O., C. CARTELLE, P. G. GUEDES, P. C. BOGGIANI, A. JANOO, AND C. A. M. RUSSO. 2006. Quaternary mammals from Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Boletim do Museu Nacional, Nova Série, Rio de Janeiro* 521:1–12.

- SANTOS-FILHO, M., M. N. F. SILVA, AND D. J. SILVA. 2001. Ocorrência da espécie *Kunsia tomentosus* (Lichtenstein, 1830), (Mammalia, Rodentia) em Unidade de Conservação. In III Simpósio Sobre Recursos Sócios Econômicos do Pantanal - Um Desafio do Novo Milênio. EMBRAPA, Corumbá, Mato Grosso do Sul. <http://www.cpap.embrapa.br/agencia/congresso/Bioticos/SANTOSFILHO-047.pdf>. Accessed 1 October 2011.
- SCHENK, J. J., K. C. ROWE, AND S. J. STEPPAN. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Systematic Biology* 62:837–864.
- SMITH, M. F., AND J. L. PATTON. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. *Journal Mammalian Evolution* 6:89–128.
- TERÁN, M. F., J. AYALA, AND J. C. HURTADO. 2008. Primer registro de *Kunsia tomentosus* (Rodentia: Cricetidae: Sigmodontinae) en el norte del Departamento de La Paz, Bolivia. *Mastozoología Neotropical* 15:129–133.
- TETA, P., AND U. F. J. PARDIÑAS. 2015. Genus *Blarinomys* Thomas, 1896. Pp. 208–211 in *Mammals of South America, volume 2 - rodents* (J. L. Patton, U. F. J. Pardiñas, and G. D'Elía, eds.). The University of Chicago Press, Chicago, Illinois.
- TROUESSART, E.-L. 1897. *Catalogus Mammalium tam viventium quam fossilium. Fasciculus I. Rodentia*. R. Friedländer & Sohn, Berlin, Germany.
- VOGLINO, D., AND U. F. J. PARDIÑAS. 2005. Roedores sigmodontinos (Mammalia: Rodentia: Cricetidae) y otros micromamíferos pleistocénicos del norte de la provincia de Buenos Aires (Argentina): reconstrucción paleoambiental para el Ensenadense cuspidal. *Ameghiniana* 42:143–158.
- VOSS, R. S. 1988. Systematics and ecology of Ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188:259–493.
- VOSS, R. S. 1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. *Bulletin of the American Museum of Natural History* 210:1–113.
- VOSS, R. S., AND P. MYERS. 1991. *Pseudoryzomys simplex* (Rodentia: Muridae) and the significance of Lund's collections from the caves of Lagoa Santa, Brazil. *Bulletin of the American Museum of Natural History* 206:414–432.
- WERNECK, F. L. 1935. Oito especies novas de Mallophaga encontradas em mamíferos (Nota prévia). *Brasil-Medico* 49:597–599.
- WERNECK, F. L. 1936. Contribuição ao conhecimento dos Mallophagos encontrados nos mamíferos sul-americanos. *Memórias do Instituto Oswaldo Cruz* 31:391–589.
- WINGE, H. 1887. Jordfundne og nulevende Gnave (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. *E Museo Lundii* 1:1–178 + 18 pls.

Associate Editor of this account was C. WILLIAM KILPATRICK. SERGIO SOLARI reviewed the synonymy and PAMELA OWEN reviewed the fossil record. Editor was MEREDITH J. HAMILTON.