

Thrichomys apereoides. By Sérgio Furtado dos Reis and Leila Maria Pessôa

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Thrichomys Trouessart, 1880

- Cercomys* É. Geoffroy St. Hilaire and Cuvier, 1829:Vol. 6 (livr. 60). Type species *Cercomys cunicularius* F. Cuvier 1829. The type specimen of *Cercomys cunicularius* is a composite consisting of a skin referable to *Nectomys squamipes* Brants, 1827, a skull referable to *Proechimys* Allen, 1899, and a mandible referable to *Echimys* G. Cuvier, 1809 (Petter 1973).
- Echimys* Lund, 1839:98. Part, not *Echimys* G. Cuvier, 1809.
- Nelomys* Lund, 1841b:242. Part, not *Nelomys* Jourdan, 1837.
- Isotrix* Wagner, 1845:146. Part.
- Thrichomys* Trouessart, 1881[1880]:179. Type species *Nelomys apereoides* by subsequent designation (Woods 1993:798).
- Thrichomys* Trouessart, 1897:606. Incorrect subsequent spelling of *Thrichomys* Trouessart.
- Tricomys* Trouessart, 1904:504. Unjustified emendation of *Thrichomys* Trouessart.
- Thrichomys* Cabrera 1961:534. Incorrect subsequent spelling of *Thrichomys* Trouessart (in synonymy).
- Thrichomys* Petter, 1973:422. Incorrect subsequent spelling of *Thrichomys* Trouessart.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognathi, family Echimyidae, subfamily Eumysopinae. Goldman (1912), Petter (1973), Tate (1935), and Thomas (1912) discuss the confusion regarding the type for *Cercomys*. *Thrichomys* is monotypic.

Thrichomys apereoides (Lund, 1839)

Punaré

- Cercomys cunicularius* F. Cuvier in É. Geoffroy St. Hilaire and Cuvier, 1829:Vol. 6 (livr. 60). Type locality “Capitainerie des Mines,” Minas Gerais, Brazil; based on a composite of which no element represents *Thrichomys apereoides*; see above.
- E[chimys]*. *apereoides* Lund, 1839:41 [1840:26]. Type locality “Lagoa Santa,” Minas Gerais, Brazil.
- E[chimys]*. *antricola* Lund, 1840:26 [1841b:242]. Name substituted for *Echimys apereoides* Lund, 1839 (see Lund 1840:26, footnote [preprint]; or Lund 1841b:242, footnote).
- Nelomys antricola* Lund, 1841b:242. Name combination.
- Echimys inermis* Pictet, 1843:33. Type locality “Jacobina,” Bahia, Brazil.
- Isotrix pachyura* Wagner, 1845:146. Type locality not specified; subsequently identified as “Cuyabá” = Cuiabá, Mato Grosso, Brazil by Wagner (1847:292).
- Isotrix pachyurus*: Wagner, 1850:291. Gender agreement.
- [*Thrichomys*] *antricola*: Trouessart, 1881:179. Name combination.
- [*Thrichomys*] *inermis*: Trouessart, 1881:179. Name combination.
- [*Thrichomys*] *antricola*: Trouessart, 1897:606. Name combination.
- [*Thrichomys*] *pachyurus*: Trouessart, 1897:607. Name combination.
- [*Thrichomys*] *inermis*: Trouessart, 1897:607. Name combination.
- Thrichomys fosteri* Thomas, 1903:227. Type locality “Sapucay, Paraguay.”
- [*Thrichomys*] *apereoides*: Thomas, 1903:227. First use of current name combination.
- Thrichomys laurentius* Thomas, 1904:254. Type locality “São Lourenço, near Pernambuco,” Brazil.
- [*Tricomys*] *apereoides*: Trouessart, 1904:504. Name combination.
- [*Tricomys*] *fosteri* Trouessart, 1904:504. Incorrect subsequent spelling of *Thrichomys fosteri* Thomas.
- [*Tricomys*] *pachyurus*: Trouessart, 1904:504. Name combination.
- [*Tricomys*] *inermis*: Trouessart, 1904:504. Name combination.
- [*Cercomys*] *fosteri*: Thomas, 1912:116. Name combination.
- [*Cercomys*] *laurentius*: Thomas, 1912:116. Name combination.

- Cercomys cunicularius laurentius*: Ellermann, 1940:124. Name combination.
- Cercomys cunicularius fosteri*: Ellermann, 1940:124. Name combination.
- Cercomys inermis*: Tate, 1935:409. Name combination.
- Nelomys apereoides*: Petter, 1973:422. Name combination.
- Thrichomys apereoides*: Petter, 1973:422. Name combination.
- [*Thrichomys*] *fosteri* Petter, 1973:425. Incorrect subsequent spelling of *Thrichomys fosteri* Thomas.
- Nelomys apereoides* Woods, 1993:798. Incorrect subsequent spelling of *Nelomys apereoides* Lund.

CONTEXT AND CONTENT. As for genus. *Thrichomys apereoides* has 5 subspecies (Anderson 1997; Cabrera 1961; Moojen 1952).

- T. a. apereoides* (Lund, 1839), as above; *antricola* (Lund) is a synonym.
- T. a. fosteri* Thomas, 1903, as above.
- T. a. inermis* (Pictet, 1843), as above.
- T. a. laurentius* Thomas, 1904, as above.
- T. a. pachyurus* (Wagner, 1845), as above.

DIAGNOSIS. *Thrichomys apereoides* (Fig. 1) can be distinguished from other genera within the Echimyidae by its soft fur and densely-haired tail. All other genera have spiny hair and thinly-haired tail. Skull is less heavily ridged and braincase is broader than in *Hoplomys* and *Proechimys* (Ellerman 1941).

GENERAL CHARACTERS. Fur of the punaré is dense and soft. Dorsum is gray-brown in color, and ventrum is whitish. In orbital region on head are 2 white spots, 1 superior and 1 inferior. A little spot of white hairs is present at base of ear. Ear is covered by white thin hairs (Moojen 1952). Vibrissae are elongated, thin, and extend forward as far as omoplate (Moojen 1952).

Length of head and body is 225–256 mm and length of tail is 182–226 mm. Average weight is 339 g (Redford and Eisenberg 1992). *Thrichomys apereoides* shows slight sexual dimorphism, with females smaller in size in some cranial characters (Moojen et al. 1988). Females have 4 mammae; 1 pair on the flank behind axillae and a second pair more posterior (4–5cm) in front of hips (Thomas 1904).

Average and ranges (in parentheses) of cranial measurements (in mm) of *T. apereoides* (Moojen et al. 1988) for 44 males and 44 females, respectively, are as follows: greatest length of skull, 51.92



FIG. 1. *Thrichomys apereoides*. Photograph by F. Olmos.

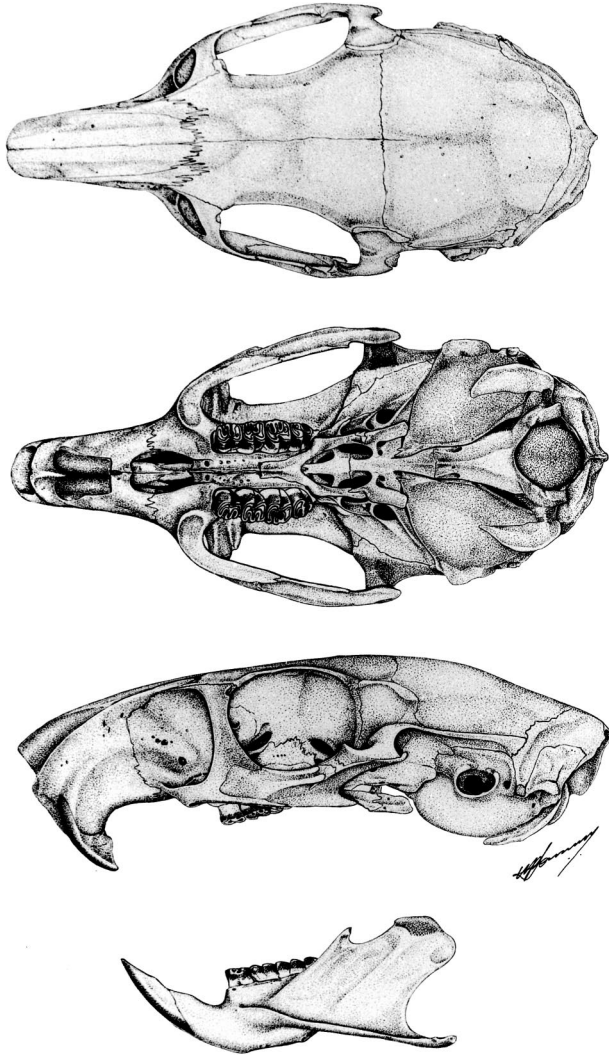


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Thrichomys apereoides*. Greatest length of cranium is 54.7 mm.

(48.30–55.54), 51.07 (47.34–55.38); condylobasal length, 47.20 (43.52–51.10), 46.52 (43.56–50.82); zygomatic width, 25.59 (23.02–28.10), 25.30 (23.94–27.72); rostral length, 20.44 (17.80–23.68), 20.21 (18.06–22.90); length of diastema, 10.21 (8.82–11.24), 9.94 (9.14–11.44); length of nasal, 17.84 (16.20–20.02), 17.59 (15.56–19.80); bullar length, 11.72 (10.36–12.92), 11.62 (11.06–12.60).

Skull (Fig. 2) is short and broad with wide incisive foramen varying in length. Mesopterygoid fossa has a “V” shape extending forward as far as middle part of third molar. Pterygoid is broad with parallel sides. Bulla is large and well inflated. Rostrum is short, wide, and strong. Nasals bones do not extend to posterior limits of premaxillary. Premaxillary portion of septum is elongated and maxillary part is reduced to a small process. Infraorbital foramen is very broad and has separate canal for nerves. Jugal is not thickened anteriorly. Zygoma is narrow, usually with weak process on lower posterior border. Upper molar tooth row contains teeth of same size, only M3 and P4 can be sometimes smaller (Winge 1888). Upper molariform teeth have 1 internal and 2 external counterfolds. Lower cheek teeth reverse pattern of upper series. P4 often has a small, extra, inner fold. Palatal foramina usually abnormally broadened (Ellerman 1941).

DISTRIBUTION. *Thrichomys apereoides* ranges from northeastern, central, and southeastern Brazil into Paraguay and Bolivia (Fig. 3; Anderson 1997; Cabrera 1961; Moojen 1952). In Brazil, *T. apereoides* is closely associated with a diagonal belt of open vegetation that stretches in a northeast to southwest direction

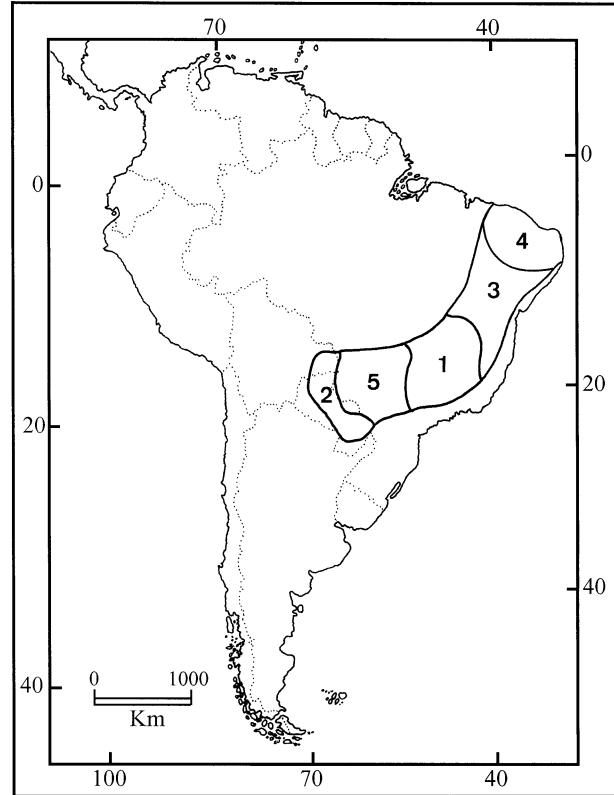


FIG. 3. Distribution of *Thrichomys apereoides* in northeastern, central, southeastern Brazil, Bolivia, and Paraguay: 1, *T. a. apereoides*; 2, *T. a. fosteri*; 3, *T. a. inermis*; 4, *T. a. laurentius*; 5, *T. a. pachyurus*.

between the Amazonian and Atlantic forests (Alho 1982; Mares and Ojeda 1982). In Bolivia, *T. apereoides* inhabits the northern edge of the Chaco (Anderson 1997).

FOSSIL RECORD. *Thrichomys apereoides* is known from the Pleistocene of Lagoa Santa, Minas Gerais, Brazil (Paula Couto 1950).

FORM AND FUNCTION. Dental formula is $i\ 1/1, c\ 0/0, p\ 1/1, m\ 3/3$, total 20. Upper and lower incisors are orange on anterior side and white on posterior side.

Seven age classes, based on tooth eruption and wear, are as follows (Moojen et al. 1988): 1, M2 not fully erupted, without formation of occlusal surface, M3 not erupted; 2, M2 fully erupted, with occlusal surface formed, M3 not erupted; 3, M3 beginning to appear at the alveolus; 4, M3 almost fully erupted but with occlusal surface not formed; 5, P4 with external folds tending to isolate, M3 with occlusal surface already formed; 6, P4 with external folds isolated forming islands, M1 with external folds tending to isolate; 7, P4 worn-down with only vestiges of the external folds, which appear as tiny enamel islands, M1 with external folds isolated. Age class 1 is subdivided into 2 categories, as follows: A, P4 completely developed, M1 developed or starting to appear on alveolus; B, M2 not completely developed, without occlusal surface, M3 not completely developed (Monteiro et al. 1999).

Major differences in mandible shape among groups of populations are due to localized changes at smaller (geometric) scales and involve anatomical landmarks that approximate coronoid and angular processes and anterior alveolar region of mandible. Latitude and longitude were associated with variation in mandible shape, although the differentiation does not follow a simple pattern of isolation-by-distance (Duarte et al. 2000). Geometric analyses of cranial shape applied to 20 populations from northeastern, central, and southeastern Brazil detected 2 morphometrically differentiated geographic units; the first including population samples from Ceará, Paraíba, Pernambuco, and Alagoas, and the second represented by populations from Bahia, Minas Gerais, and Goiás (Reis et al. 2002a, 2002b).

Thrichomys apereoides from caatinga habitats near Exu (7°31'S, 39°43'W), Pernambuco, Brazil (Streilein 1982b) can withstand total water deprivation for 18 days. Twenty individuals (10 females and 10 males) were kept solely on sun-dried field corn. The 19 survivors lost on average only 12.0% of their original mass. Females and males did not differ significantly in percent body weight change. After water deprivation, a 12 h exposure to free water decreased average percent loss of body mass from 12.0% to 2.8%. When cactus pads of *Opuntia palmadora* were offered as an alternate water source to 7 males and 7 females, loss of mean mass was 2.5%. Thus, *T. apereoides* can use *Opuntia* as a source of water.

Milk production in *T. apereoides* increases from <0.2 ml after 2 days of delivery to an average maximum of 2.0 ± 0.2 ml (\pm SD) per female (range, 1.5–3.0 ml; $n = 16$). Milk yield decreased to 1.25 ± 0.2 ml by day 21 postpartum and ceased by day 28. Fat content had a mean (\pm SD) at day 2 after delivery of $30.2 \pm 0.8\%$ and decreased to $20.8 \pm 2.0\%$. Percent protein decreased from $13.9 \pm 0.6\%$ (\pm SD) at day 7 postpartum to $11.9 \pm 0.6\%$ on day 14. Lactose decreased from $4.62 \pm 0.09\%$ (\pm SD) on day 7 after delivery to $4.31 \pm 0.06\%$ at day 14 (Meyerson-McCormick et al. 1990).

ONTOGENY AND REPRODUCTION. Skull changes after birth in *T. apereoides* include both global changes, manifested as an overall lateral compression of skull, and large scale, localized changes involving an elongation of rostrum, widening of posterior region of premaxilla, and an elongation of palate associated with a strong negative allometry resulting from absence of molar growth. Skull shape varies as a function of size and age as estimated by the pattern of dental eruption and wearing of crown, but size estimated by the metric of the centroid size predicts changes in cranial shape through ontogeny better than age (Monteiro et al. 1999).

Female *T. apereoides* were either pregnant or lactating ($n = 124$) from January 1977 to February 1978 in the semiarid caatinga environment of Exu in the state of Pernambuco in northeastern Brazil (Streilein 1982c). Reproductive activity occurred throughout the year but was reduced in December and January (Streilein 1982c). Mean litter size in the field is 3.1 (range, 1–6; $n = 27$ —Streilein 1982c).

In captivity, reproduction occurred throughout the year (Roberts et al. 1988). Gestation, estimated as the interval between pairing and birth, has a mean of 97.0 days ($SD, 1.2$; range, 95–98; $n = 7$ —Roberts et al. 1988). Mean litter size in captivity is 3.2 ($SD, 1.43$; range, 1–7; $n = 174$ —Roberts et al. 1988).

Neonate *T. apereoides* are precocial. Eyes and ears are open, body is fully furred, and upper and lower incisors are erupted. Neonates have a mean mass at birth of 21.1 g ($SD, 4.7$ g—Roberts et al. 1988). Coordinated movement and nibbling of solid food occurs within few hours of birth. Behavior patterns typical of adults such as grooming, coprophagy, and predator avoidance are displayed by young soon after birth (Roberts et al. 1988). Agonistic interactions occur in juveniles at 7 days of age. The most frequent social interactions among siblings and between parents and offspring include huddling, nosing, and play. Suckling ceased at a mean of 21.7 ($SD, 6.1$ days; range, 10–35—Roberts et al. 1988).

ECOLOGY. *Thrichomys apereoides* inhabits xeric and rocky environments in caatinga and cerrado domains in Brazil and chaco in Paraguay (Mares and Ojeda 1982; Mares et al. 1985; Moojen 1952; Streilein 1982a). In Exu, Brazil, *T. apereoides* is associated primarily with granitic outcroppings (Streilein 1982d). In Bolivia, *T. apereoides* inhabits flat and arid shrub-dominated habitat devoid of large rocks (Anderson 1997).

In Exu, Pernambuco in northeastern Brazil, mean size of home ranges (with parentetical SD) for male ($n = 17$), female ($n = 21$), adult ($n = 22$), and subadult ($n = 17$) *T. apereoides* were 1987.8 (1554.1), 1840.2 (228.8), 2022.4 (1517.3), and 1746.5 (2437.4) m², respectively. Individual residency on the trapping grid varied extensively, with a mean length of residency of 110.3 days ($SD, 103.0$) for males ($n = 58$) and 63.3 ($SD, 52.6$) for females ($n = 29$ —Streilein 1982a, 1982c, 1982d).

BEHAVIOR. *Thrichomys apereoides* is agile and maneuvers well in boulder habitats characteristic of granite outcroppings in the caatinga (Streilein 1982a). Boulder areas are usually used for nesting places, and cracks and crevices in the granite rocks are used as temporary refuges (Streilein 1982a). Most activity is con-

centrated at dawn, although punarés can also be active for short periods during the day or night. Punarés are semi-arboreal as determined by their ability of traversing branches less than one-half cm in diameter (Streilein 1982a).

The basic agonistic behavioral repertoire of *T. apereoides* is a series of displays and postures, identified as semi-erect, full erect, locked upright, strike with forepaws, chest kick, wrestle, and chase (Streilein 1982e). In intraspecific pairings, agonistic behavior occurred in 21 of 59 trials (Streilein 1982e). Interspecific interactions were more frequent between *T. apereoides* and *Galea spixii* and *Kerodon rupestris* than between *T. apereoides* and the smaller species *Bolomys lasiurus* (Streilein 1982e).

GENETICS. *Thrichomys apereoides* has multiple chromosomal forms (Leal-Mesquita et al. 1993; Souza and Yonenaga-Yassuda 1982). One, with a diploid ($2n$) of 30 and fundamental number (FN) of 54, occurs in the states of Pernambuco (Floresta do Navio, Bom Conselho, São Caetano, Exu, and Buique) and Bahia (Ibiraba and Queimadas). Chromosomal pairs were identified based on G-banding patterns. The $2n = 30$ karyotype has 13 metacentric or submetacentric pairs and 1 acrocentric pair; the X chromosome is a large acrocentric and the Y chromosome is a small submetacentric. A second chromosomal form, with $2n = 48$ and $FN = 48$, occurs in the state of Bahia (Santo Inácio, Mucujê, and Vacaria). It has 13 metacentric or submetacentric pairs, with 1 of the pairs very much larger than the others. In this karyomorph the X chromosome is a large subtelocentric and the Y chromosome is a small metacentric. Homologies between the two karyotypes were established on the basis of G-banding patterns for 8 pairs of autosomes. Chromosomal differences between the 2 karyotypes are due to complex rearrangements, including centric fusions or centric fission and pericentric inversions (Leal-Mesquita et al. 1993). The nucleolus organizer region (NOR) is an interstitial secondary constriction in chromosomal pair 1 for the $2n = 30$ karyotype (Souza and Yonenaga-Yassuda 1982), whereas for karyotype $2n = 26$ the NOR is in chromosomal pair 2 (Leal-Mesquita et al. 1993). Polymorphism for staining and size in the NOR occurs for both karyomorphs.

An additional 4 chromosomal forms (Bonvicino et al. 2002) include 1 with $2n = 34$ ($FN = 64$) from Corumbá in the state of Mato Grosso do Sul that has 16 metacentrics of varying size; a large submetacentric X chromosome and a small submetacentric Y chromosome. A second karyotype, with $2n = 30$ ($FN = 56$) from Teresina de Goiás in the state of Goiás, has 14 pairs of metacentrics of varying size, a medium acrocentric X chromosome, and a medium submetacentric Y chromosome. A third karyotype, with $2n = 28$ ($FN = 52$) from Jaborundi in the state of Bahia, has 13 pairs of metacentrics, a medium acrocentric X chromosome, and a small submetacentric Y chromosome. A fourth karyotype, with $2n = 28$ ($FN = 50$) from Matosinho and Juramento in the state of Minas Gerais, has 12 pairs of metacentrics and 1 large pair of acrocentric autosomes, a medium acrocentric X chromosome, and a small submetacentric Y chromosome.

Autosomal and sexual bivalent pairing was characterized for the $2n = 26$ ($FN = 54$) karyotype by both light and electron microscopy (Fagundes and Yonenaga-Yassuda 1996). Pairing of synaptonemal complex axes initiates at early zygonema and is complete at the beginning of pachynema. The axes of sex chromosomes can only be distinguished from autosomal axes at late stages of zygonema, and by early pachynema the XY axes are completely heteropycnotic (Fagundes and Yonenaga-Yassuda 1996). Synapsis of X and Y axes begins at the telomers and progresses through pachynema.

Cranimetric differences among populations of in *T. apereoides* in northeastern Brazil may be due to selection and not to random genetic drift (Bandouk et al. 1996). Assuming truncation selection, minimum intensities of selection necessary to account for observed cranial differences were low, with selective mortality per generation of ca. 10^{-3} (Bandouk et al. 1996).

REMARKS. Woods (1993) designated *Nelomys apereoides* Lund as the type species of the genus *Thrichomys*. This subsequent designation must be understood as *Echimys apereoides* Lund, 1839:41 [1840:26]. *Thrichomys apereoides* is currently regarded as monotypic (Moojen 1952; Woods 1993). Based on chromosomal evidence Leal-Mesquita et al. (1993; Fagundes and Yonenaga-Yassuda 1996) suggested the existence of two separate species. Four available names have been mapped to chromosomal complements

as follows: *T. a. apereoides* (2n = 28, FN = 50), *T. a. laurentius* (2n = 30, FN = 54), *T. a. pachyurus* (2n = 34, FN = 64), and *T. inermis* (2n = 26, FN = 48—Bonvicino et al. 2002). Substantial levels of sequence divergence in the cytochrome-*b* gene in individuals sampled across a 2000 km range (latitude 9°23'S–20°27'S) over an area including the states of Alagoas, Bahia, and Mato Grosso do Sul were documented by Lara et al. (1996), leading these authors to suggest that *T. apereoides* is a composite.

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