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A NEW SPECIES OF *ECHIMYS* CUVIER, 1809 (RODENTIA, ECHIMYIDAE) FROM BRAZIL

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ABSTRACT

Here we describe a new species of Echimyidae Amazonian rodent, Echimys vieirai sp. nou., based on two individuals from the south bank of Amazon river between the lower Madeira river to the right bank of the Tapajós, respectively in the Brazilian states of Amazonas and Pará, Brazil. The main diagnostic characteristic of this new species is the presence of a dorsal median dark maroon stripe on the head, running from the rostrum to the nape. Skull morphology is quite similar to that of Echimys chrysurus (Zimmermann, 1780), but our new species differ from other species in the genus by the development of the alisphenoid canal and dp4 morphology. Additionally, we offer a refinement of the diagnosis of the genera Echimys and Makalata.

KEYWORDS: Echimyidae, Echimys, arboreal spiny rats, taxonomy, distribution.

INTRODUCTION

Arboreal echimyids comprise several species allocated in twelve genera in three subfamilies (Carvalho, 2000). The genus *Echimys* is included in the subfamily Echimyinae, and since Husson (1978), part of its species content has been transferred to other genera, namely *Makalata* Husson, 1978; *Callistomys* Emmons & Vucetich, 1998; and *Phyllomys* Lund, 1839 (Emmons *et al.*, 2002). Currently, *Echimys* is restricted to three species according to Emmons & Feer (1997): *E. chrysurus* (Zimmermann, 1780), *E. saturnus* (Wagner, 1845), and *E. semivillosus* (Geoffroy, 1838). A fourth

species is here described, based on two specimens from the Museu de Zoologia, Universidade de São Paulo, and Museu Nacional, Universidade Federal do Rio de Janeiro. Additional examination of material in European and Brazilian collections allowed us to refine our comparisons. All species are readily distinguished by size, pelage coloration, and some of them by skull characters as well.

Known collecting localities of *Echimys* include the Guyanas, North-Northeastern Brazil (Carvalho & Tocchetton, 1969; Pine, 1973; Husson, 1978; Miles *et al.*, 1981; Eisenberg, 1989; Oliveira & Mesquita, 1998; Eisenberg & Redford, 1999), the eastern Amazon basin

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and the eastern Andean foothills. *Echimys chrysurus* occurs in the Guyana region, from the right bank of Essequibo River eastwards, and in localities around the mouth of the Amazonas River and in the State of Maranhão, in Brazil. *E. saturnus* is known from a few scattered localities in eastern Ecuador and central Peru, in the upper Marañon River. *Echimys semivillosus* occurs in northern Colombia and Venezuela. Our new species, known so far from the type locality, at the right bank of the middle Tapajós River in Pará.

Here we describe *Echimys vieirai* sp. nov., compare it to other species in the genus, and discuss the genus distribution as currently defined.

MATERIALS AND METHODS

We have studied skins and skulls deposited in the following collections: Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); The Natural History Museum, London (BMNH); Museum für Naturkunde, Berlin (MNK); Naturhistorika Riksmuseet, Stockholm (NRM); Zoologische Staatsammlung, München (ZSM); and Musée Nationale d'Histoire Naturelle, Paris (MNHN).

We have recorded measurements from museum specimen tags as follows: head and body length (HB); tail length (T); ear length (E); and hind foot length (HF). When only total length (TL) was originally furnished, we subtracted the recorded tail length (T) from total length to obtain the head and body length, thus making the derived values roughly comparable to our measurement scheme.

We have recorded skull measurements directly from skulls, at the nearest tenth of millimeter. The measurements and their definitions are as follows: skull length (SL): from the tip of the nasals to the posteriormost part of the occipital region; zygomatic breadth (ZB): largest distance across the external sides of the zygomatic arches; frontal constriction (FC): the smaller distance across the orbital border of frontals; nasal length (NL): greatest distance from the tip to the posteriormost part of nasals; squamosal breadth (SB): distance across the external projection of the squamosal crest taken at the level of the external auditory meatus; rostrum breadth (RB): distance across both sides of the rostrum at the premaxilar-maxilar suture; bullar length (BL): greatest distance taken from a lateral aspect of the bulla from its juxtaposition to the paraoccipital process to the bulla's anteriormost portion; postpalatal length (PPL): from the anteriormost border of the foramen magnum to the anteriormost edge of the mesopterygoid fossa; palatal length (PL): from the alveolar edge of incisors to the anteriormost edge of the mesopterygoid fossa; maxillary tooth row length (TRL): largest distance from the anteriormost border of the fourth premolar to the posteriormost border of the third molar; maxillary breadth (MB): greatest distance across the fourth premolars taken from their alveolar borders; first molar breadth (M1B): greatest distance from lingual to buccal borders of crown; median length of parietals (MLP): greatest distance across the parietal's suture; mandible length (MBL): from the lingual border of the incisors' alveoli to the posteriormost border of the postcondyloid process; mandible height (MH): shortest distance taken vertically from the uppermost part of the condyloid process to a plane passing from the lower edge of the symphiseal suture to the lowermost edge of the angular process.

We recognize three morphological age classes, based on maxillary tooth eruption: *adult (III)*: specimens with all maxillary teeth fully erupted; *subadult (II)*: specimens with the third molar fully in the process of eruption; and *young (I)*: all other conditions.

We employed Wahlert (1974, 1983, 1985) and Woods & Howlands (1979) for nomenclature of cranial foramina. Dental nomenclature follows Lavocat (1976) and further considerations by Butler (1985) and Flynn et al. (1985). Our reference to external morphology and coloration for *E. semivillosus* is based on the original description by Geoffroy (1838) and that of Geoffroy (1840), since we only had access to a single skull of this species.

Distributional data on *Echimys* species were obtained either by direct examination of specimens or from the literature. In the latter case, we included only those references that we consider reliable or else the type localities of valid species.

RESULTS

Echimys vieirai sp. nov.

Holotype: MZUSP 26650, skin and skull, young male, collected by P.E. Vanzolini in an E.P.A expedition. (Expedição Permanente à Amazônia) in June 24, 1970, field number E.P.A. 70.1327; *Paratype:* MNRJ 67549, specimen in alcohol, young, collected by A. Parko in Virgem Guajará, Amazonas, field number 16.

Type locality: Barreirinha, right bank of the Tapajós River, near São Luis do Tapajós, Pará State, Brazil; geographic coordinates 04°25'S, 56°13'W (Fig. 1).

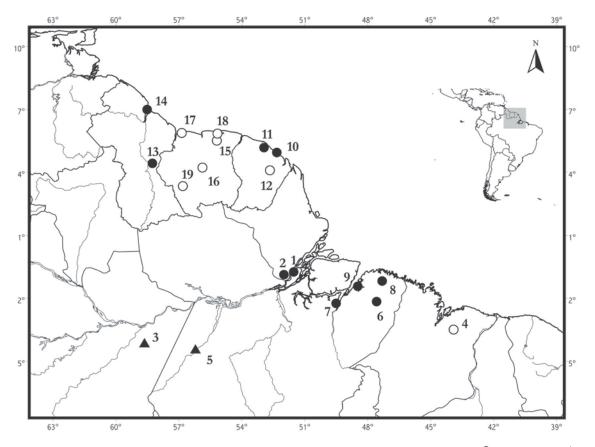


FIGURE 1. Echimys species distribution; open symbols are used to localities taken from literature. Echimys chrysurus (○●); Echimys vieirai (▲).

Distribution: known only from Barreirinha, right bank of the Tapajós River, Pará State, Brazil and Virgem Guajará near to Borba, Madeira river, Amazonas State, Brazil. Probably the distribution of *E. vieirai* ranges from mid to lower Tapajós river to lower Madeira river.

Etymology: This new species is named after Carlos Octaviano da Cunha Vieira, curator in charge of the mammal collection of the Museu de Zoologia, University of São Paulo, from the early 1940's until his death in 1958. Through his efforts, the mammal collection of the MZUSP was greatly improved in both geographic coverage and size.

Diagnosis: A generally brown spiny rat, with a dark head distinct from the dorsum; special chromogenetic fields present in the head, consisting of a black mask extending from the muzzle to above and bellow the eyes, and a dark median maroon (brown tinted with a dark red tone) stripe extending from the rostrum to the nape.

Measurements: See Table 1.

Description

External morphology and pelage (Fig. 2): Head and body length approximately equal to tail length. Color of head distinct from that of body, being darker than adjacent dorsum; the background color of head is dark brown with black extending from around the muzzle to the sides of mouth; from there the black extends to the mystacial region and backwards to the eyes until the anterior half below the eye and to its entire length above. Between the black stripes over the eyes there is a defined dark maroon stripe (brown tinted with red). Mystacial vibrissae short, not extending beyond the pinnae, entirely black. External face of pinnae slightly hirsute covered with short black hairs. Internal face of pinnae only slightly hirsute, with long black hairs in the outer border of pinnae. Body hairs consisting predominantly of spines. Dorsal parts of the body distinct from crown, uniformly colored, with sparse cover hairs dull brown in color and dense bicolored spines, dull brown proximally becoming blackish distally. Dorsal parts of body only slightly distinct from sides, dark brown becoming dull brown to the sides, not sharply distinct from ventral body

TABLE 1. Descriptive statistics of *Echimys* species. $(N)\overline{x} \partial s.d.$ $N = \text{number of specimens}; \overline{x} = \text{average}; s.d. = \text{standard deviation}; Min-4 Max.$

Max. = Minimum and maximum.

			Echimys		
	E. vierai ^a	E. saturnus b	E. semivillosus ^c	E. chrysurus	
Age	class I	class III	class III	class I	class III
НВ	245	_	_	(2) 252 ± 11	(8) 281 ± 26
				245 - 260	250.00 - 310.00
Т	340	_	_	(2) 312 ± 11	(9) 330 ± 47
				305 - 320	270.00 - 415.00
F	50	51	_	$(2) 49.00 \pm 1.41$	(6) 52.89 ± 5.23
				48.00 - 50.00	45.00 - 60.00
Е	15	17	_	-	$(4)\ 20.50 \pm 1.73$
					19.00 - 50.00
SL	55.3	66.92	52.16	$(1) 49.80 \pm 0.0$	(9) 62.20 ± 2.25
				49.80 - 49.80	59.00 - 65.89
ZB	28.1	30.59	24.88	$(2) 25.40 \pm 1.27$	$(10) \ 30.40 \pm 1.91$
				24.50 - 26.30	27.73 - 33.33
FC	14.5	18.28	13.54	$(2) 12.30 \pm 1.13$	(12) 15.28 ± 1.48
				11.50 - 13.10	13.40 - 18.50
NL	16.7	21.63	16.77	$(1) 13.30 \pm 0.00$	$(12) 18.50 \pm 1.84$
				13.30 - 13.30	16.20 - 21.96
MLP	19.9	_	19.88	(2) 18.80 ± 0.28	(9) 21.44 ± 0.76
				18.60 - 19.00	19.69 - 22.38
SB	22.2	24.68	20.59	$(2)\ 20.60 \pm 0.42$	(8) 23.81 ± 1.01
				20.30 - 20.90	21.80 - 24.83
RB	10	11.71	7.63	(2) 8.45 ± 0.78	$(12)\ 10.51 \pm 0.88$
				7.90 - 9.30	9.20 - 11.81
PL	22.3	26.01	20.6	$(2) 19.60 \pm 2.69$	$(11) 24.39 \pm 1.72$
				17.70 - 21.50	21.60 - 27.34
PPL	20.5	25.81	_	(2) 21.35 ± 1.48	(8) 24.63 ± 1.01
				20.30 - 22.40	23.00 - 26.17
TRL	10.9	13.91	11.39	_	$(11)\ 13.51 \pm 0.86$
					12.65 - 14.89
M1B	3	3.54	2.48	$(2) 2.60 \pm 0.00$	$(12) 2.96 \pm 0.25$
				2.60 - 2.60	2.53 - 3.55
MB	8	8.77	6.71	(2) 7.70 ± 0.14	$(11) 8.92 \pm 0.67$
				7.60 - 7.80	7.77 - 9.85
BL	11.9	10.7	12.84	$(2)\ 11.30 \pm 0.56$	$(10)\ 12.47 \pm 0.60$
				10.90 - 11.70	11.71 – 13.46
MBL	31.1	34.26	28.02	(2) 28.15 ± 0.05	(9) 32.80 ± 1.56
				26.70 - 29.60	30.70 - 35.30
MH	15.8	15.7	12.85	(2) 13.00 ± 1.13	(8) 15.30 ± 2.67
				12.20 - 13.80	8.88 – 16.88

^a MZUSP26650 Holotype

color. Fore and hindlegs proximally indistinct from dorsolateral body color, being grayish brown; cover hairs weakly bicolored, grayish proximally and yellowish distally; fore and hindlegt distinct from distal parts of fore and hindlegs, dark brown; cover hairs uniformly dark brown. Ventral surfaces indistinct from sides of body, being hirsute, covered with light-brown hairs. Tail densely covered by long hairs, with tuft present, with tail scales hardly visible. Scales and hairs densely disposed, length of hairs from 10 to 12 rows of scales.

Tail divided in three color sections; proximal one sixth the same color of posterior dorsum; middle section, corresponding to about half of the tail length, black; terminal section, with almost one third of tail length, white.

Skull (Fig. 3): Skull of a medium sized Echimyinae. Nasals with moderate length and broad; rostrum short, broad. Lateral wings of frontal developed forming a roof over the orbital region; post-orbital process of zygoma blunt and weakly developed

^b BMNH34.9.10.182 Holotype

c ZSM1949/788

and formed by the jugal. Lateral jugal fossae sharply defined, with anterior rim sharp pointed, extending until the M1. Incisive foramen formed by premaxillar and maxillar, breadth and length moderate; margins of incisive foramen forming well developed ridges especially in the maxillar portion, which run parallels extending until the DP4; maxillar between the ridges slightly depressed inward at the posterior edge of the incisive foramen. Septum of incisive foramen formed mainly by premaxillar. Palatal region long and slender; palatine extending up to M1. Pterygoyd fossae slitshaped; alisphenoid wide; alisphenoid canal completely developed, with anterior and posterior openings differentiated; buccinator and masticator foramen confluent; medium sized foramen ovale; maxillary vein passing through a foramen; transverse canal welldeveloped. Bulla ovoid, with tiny stilliform process, tegmen timpani short and wide; external auditory meatus separated from squamosal bone by a wall of the petrosal. Upper molariforms tetralophodont, anteroloph and protoloph connected lingually as well as the mesoloph and posteroloph. Lower molars trilophodont; dp4 pentalophodont, with anterolophid and metalophid connected both lingually and labially forming an anterofossetid; mesolophid isolated from the other lophids.

Comparisons

Echimys vieirai can be readily distinguished from E. chrysurus by the presence of a dark maroon head stripe instead of a white median head stripe, and by having a darker dorsum (Fig. 2). E. vieirai is distinguishable from E. saturnus by possessing its head clearly darker than its dorsum, while in E. saturnus the

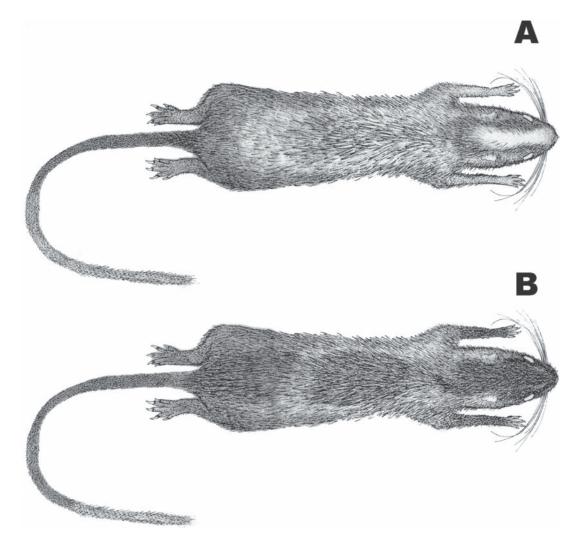


FIGURE 2. Skins of Echimys chrysurus (A) and E. vieirai (B) in dorsal view. Drawing by E.G. Baena.

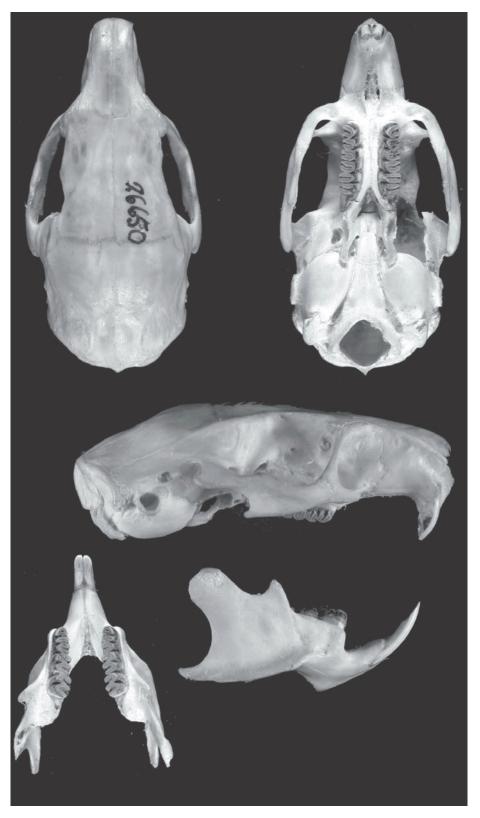


FIGURE 3. Skull of *Echimys vieirai* sp. nov. in dorsal ventral and lateral view, mandible in lateral and ventral view (MZUSP 26650; SL = 55.3).

dorsal parts of head and body are mostly black. *E. vieirai* is further distinguished from *E. saturnus* by the color of the venter, which is uniformly grayish brown in the former and white or spotted with white in the latter (Thomas, 1928). *E. semivillosus* differs from *E. vieirai* by having its body coloration reddish brown speckled with yellow and a scaly tail covered with reddish brown tiny hairs.

The skulls of *E. vieirai* and *E. chrysurus* are indistinguishable, but are different from those of other species in the genus. *E. vieirai* and *E. chrysurus* skulls are distinguished from those of *E. semivillosus* and *E. saturnus* by the possession of a supraorbital process formed by squamosal anterior to frontal-parietal suture, and a pentalophodont dp4 with a large central anterofossetid. Both species have supraorbital process formed by frontal; *E. semivillosus* has a tetralophodont dp4 and *E saturnus* a pentalophodont dp4 with small lingual anterofossetid.

DISCUSSION

The genus *Echimys* was created by Cuvier (1809) to contain all spiny rats then known. After Allen's (1899) exclusion of terrestrial forms from Echimys, the genus was restricted to arboreal spiny rats, and other researchers followed his concept (e.g. Thomas, 1928; Tate, 1935 and Ellerman, 1940; Cabrera, 1961). Moojen (1952) was the first to recognize further groups in Echimys when he allocated eastern Brazilian arboreal spiny rats in Phyllomys Lund, 1839, but this was not adopted by other authors, who mostly followed Tate (1935). Then Husson (1978) created the genus Makalata to contain Nelomys armatus Geoffroy, 1838. Other authors advanced the splitting of Echimys, by creating the genus Callistomys (Emmons & Vucetich, 1998) to include Nelomys pictus Pictet, 1843, and by finally accepting Moojen's (1952) decision regarding Phlyllomys (Emmons et al., 2002; Leite, 2003).

These taxonomic changes make it necessary to redefine *Echimys*, and comparisons with *Makalata* (sensu Husson, 1978) is mandatory, since several species previously included in *Echimys* must be transferred to that genus.

Husson (1978) has created *Makalata* to contain Amazonian echimyids with folds in the cheek teeth opening lingually instead of bucally; externally, the dorsal parts are dark yellowish brown, heavily lined with black and speckled with black specially in the posterior third; the sides of the body are lighter than the dorsum and ventral surface are pale yellowish or grayish brown.

We also included in the diagnosis of *Makalata* the following characters: mistacial region pheomelanic (ferrugineous or rusty, from red to orange), tail with short hair, making scales plainly visible; postorbital process of zygoma formed mostly by jugal, squamosal projects below the postorbital process. The spines are pale gray at the base, becoming darker distally.

The following nominal taxa match Husson's concept of Makalata as modified here: didelphoides group – Echimys didelphoides Desmarest, 1817; Nelomys armatus Geoffroy, 1838; Loncheres obscura Wagner, 1840; Loncheres macrura Wagner, 1842; Echimys guianae Thomas, 1888; Loncheres castaneus Allen & Chapman, 1897, Echimys longirostris Anthony, 1921; Echimys rhipidurus Thomas, 1928; Echimys occasius Thomas, 1921; semivillosus group – Nelomys semivillosus Geoffroy, 1838; Loncheres punctatus Thomas, 1899; Echimys carrikeri Allen, 1911; Loncheres flavidus Hollister, 1914.

The remaining nominal taxa, Myoxus chrysurus Zimmermann, 1780, Echimys cristatus Desmarest, 1817, Loncheres grandis Wagner, 1845; Echimys saturnus Thomas, 1928, and Loncheres paleacea Olfers, 1818, do not belong in Makalata and therefore remain in Echimys. However, the morphology of Loncheres grandis and Echimys saturnus, suggests that Echimys is a composite genus. Loncheres grandis is in the process of being transferred to a new genus (Iack-Ximenes et al., in prep.) and the placement of E. saturnus is under evaluation by one of us (G.E. Iack-Ximenes).

Echimys Cuvier, 1809 originally was described including Myoxus chrysurus ("le rot a queue dorée") and "le rat epineux d'Azara" (Cuvier, 1809, 1812; in Cuvier's view actually a Makalata didelphoides, see also Geoffroy, 1840) and Tate (1935) has designated Myoxus chrysurus Zimmermann, 1780 as type species of Echimys. The placement of E. vieirai in this genus can be justified because the species shares most of its characters with Echimys chrysurus, the type species of Echimys. Examination of Echimys type species led us to consider E. cristatus as a junior synonym of E. chrysurus and E. paleaceus as a valid species.

Our refined diagnosis of *Echimys* is: a medium to large sized echimyine rat with long tricolored tail; white distal portion of tail extending over more than one third of tail length; septum of incisive foramen formed only by premaxillar; dp4 with anterolophid developed and connected to metalophid evenly both lingually and labially; upper molars with protoloph connected to protocone, deep groove formed by continuous hypoflexus and metaflexus present; mesoloph connected with metaloph by hypocone; postorbital process of zygoma formed by jugal.

We believe that the existence of only two specimen of *Echimys vieirai*, the holotype and the paratype, is not problematic to its recognition as a new species because the kind of variation we have described above is consistent with what is known of the taxonomic variation among taxa in this group of rodents. In all specimens (N=28) examined of *E. chrysurus* the stripe of forehead is always present and always white. Only the width of the stripe has varied, still slightly. Amazonian arboreal mammals frequently differ in external characters, mostly hair color, in many groups from rodents to primates.

Coat pattern and coloration can be distinctive, as it occurs in many species of felids, primates and rodents. According to reaction-diffusion model (Turing, 1952), there is a chemical mechanism for generating coat pattern based on differential deposition of eumelanin and pheomelanin, ruled by morphogenes. The mathematics to this model has been created by Turing (1952) and developed by Murray (1981a,b, 1988, 1989). Although genes control the process of coat pattern formation, the actual mechanism is still unknown. The use of coat patterns to distinguish species can be supported, based on Turing's model, which supports the idea that coat patterns are not aleatory.

Additionally, these arboreal taxa have frequently been shown to be associated with different interfluvia in the Amazon basin, and the geographic provenience of our specimen reinforces this pattern.

Echimys, as conceived by Cabrera (1961) and Woods (1993), had a wide distribution ranging from Colombia, Venezuela, and across the entire Amazon Basin to the Atlantic forest in eastern Brazil. As here conceived, the distribution of the remaining species of Echimys is presented in Figure 1.

Specimens examined. Echimys (N=30). Echimys chrysurus (N=28): British Guyana: Potaro Highlands, 1300ft.: BMNH 7.6.10.4 (skin and skull); Supinaam river: BMNH 10.5.4.21 (skin and skull); Upper County [Upper Corentyn according Thomas, 1916]: BMNH 43.8.19.14 (skin and skull); Surinam: Surinam: MNK 1182 (skin and skull); Guyane Française: Cayenne,: MNHN 1995-1398 (skin and skull) Holotype of Echimys cristatus; rive droite du Petit Saut; Programme Faune Sauvage,: MNHN 1999-1082 (skin and skeleton); Brazil: Pará: Cametá, Tocantins River: MZUSP: 4510, 4547, 4548, 4551, 4642 (skin and skull); 4557, 4558 (skin); MNRJ: 21504 (skin and skull); NHRM A58 7194, A58 7195, A58 7196 (skin and skull); Pará: MZUSP: 25809 (skin); Utinga, Belém: MZUSP: 25810 (skin); BR-010 km 87-94: MZUSP: 26200 (skull); Aurá, Belém: MNRJ: 3847 (skin and skull); Peixe-Boi: BMNH: 14.6.10.1 (skin and skull); Amapá: Amapari River: MNRJ: 21505 (skin and skull); Serra do Navio: MNRJ: 20411 (skin and skull). "Pará, Brasilien": MNK: 1181 (skin and skull) Holotype of *Loncheres paleaceus;* No locality: MZUSP: 4011 (skull); MNRJ: 60538 (skeleton). *Echimys vieirai* (N=2): Brazil: Pará: Barreirinhas, Tapajós River: MZUSP: Holotype: 26650 (skin and skull); MNRJ: Paratype: Virgem Guajará, Madeira river, Amazonas: MNRJ: 67549 (alcohol). *Echimys saturnus* (N=2): Ecuador: near rio Napo, Ecuador. 3300 ft.: BMNH: 34.9.10.182 (skin and skull) Holotype; Peru: Pisqui river: AMNH: 98261 (skin and skull, specimen not seen; photographs by G. Carvalho examined). *Echimys semivillosus* (N=1): No locality: ZSM: 1949,788 (skull);

RESUMO

É apresentada a descrição de uma nova espécie de Echimyidae, Echimys vieirai sp. nov., baseado em dois espécimens coletados em Barreirinha, rio Tapajós, Pará e Virgem Guajará, Amazonas. A principal característica diagnóstica desta nova espécie é a presença de uma faixa mediana marrom na cabeça que se extende do dorso até a nuca. A morfologia do crânio é similar a de Echimys chrysurus (Zimmermann, 1780), e difere das demais espécies do gênero em relação ao desenvolvimento do canal do alisfenóide e a morfologia do dp4. É apresentado também uma nova diagnose do gênero Echimys e um refinamento da diagnose dos gênero Makalata.

Palavras-chave: Echimyidae, Echimys, equimídeos arborícolas, taxonomia, distribuição.

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REFERENCES

- Allen, J.A. 1899. The generic names Echimys and Loncheres. Bulletin of the American Museum of Natural History, 12:257-264.
- Butler, P.M. 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent morphology. In: Luckett, W.P. & Hartenberger, J.-L. (Eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. Plenum Press, New York. p.381-401.
- Cabrera, A. 1961. Catálogo de los Mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", 4(part 2):309-732.
- Carvalho, C.T. de & Toccheton, A.J. 1969. Mamíferos do nordeste do Pará. Revista de Biologia Tropical, 15(2):215-226.
- Carvalho, G. 2000. Substitution of the deciduous premolar in Chaetomys subspinosus (Olfers, 1818) (Hystricognathi, Rodentia) and its taxonomic implications. Zeitschrift für Saugertierekunde, 65:187-190.
- Cuvier, G.F. 1809. Extrait des premiers Mémoires de M.F. Cuvier. sur les dents des mammifères considérés comme charactères génerics. Nouveau Bulletin des Sciences, par la Société Philomathique, 1(24):394-395.
- Cuvier, G.F. 1812. Essai sur de nouveaux caractères pour les genres des Mammifères. Annales du Muséum d'Histoire Naturelle,
- Ellerman, J.R. 1940. The families and genera of living rodents: with a list of named forms (1758-1936). Volume I Rodents other than Muridae. British Museum of Natural History, London.
- Emmons, L.H. & Feer, F. 1997. Neotropical Rainforest Mammals: a field Guide. 2. ed. University of Chicago Press, Chicago.
- Emmons, L.H.; Leite, Y.R.; Kock, D. & Costa, L.P. 2002. A review of the named forms of Phyllomys (Rodentia, Echimyidae), with the description of a new species from coastal Brazil. American Museum Novitates, 3380:1-40.
- Emmons, L.H. & Vucetich, M.G. 1998. The identity of Winge's Lasiuromys villosus and the description of a new genus of Echimyid rodent (Rodentia: Echimmyidae). American Museum Novitates, 3223:1-12.
- Eisenberg, J.F. 1989. Mammals of Neotropics. Volume. 1. The Northern Tropics. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago.
- Eisenberg, J.F. & Redford, K.H. 1999. Mammals of Neotropics. Volume 3. The Central Tropics. Ecuador, Peru, Bolivia, Brazil. University of Chicago Press, Chicago.
- Flynn, L.J.; Jacobs, L.L. & Cheema, I.U. 1986. Baluchimyinae, A new Ctenodactyloid Rodent Subfamily from the Miocene of Baluchistan. American Museum Novitates, 2891:1-25.
- Geoffroy, I. 1838. Notices sur les Rongeurs épineux désignés par les auteurs sous les noms d'Echimys, Loncheres, Heteromys et Nelomys. Annales des Sciences Naturelles, Paris, Second Série Zoologie, 10:122-127.
- Geoffroy, I. 1840. Notices sur les Rongeurs épineux désignés par les auteurs sous les noms d'Echimys, Loncheres, Heteromys et Nelomys. Magasin de Zoologie Second Série, 2:1-57.
- Husson, A.M. 1978. The Mammals of Suriname. Zoologische Monographieën van het Rijksmuseum van Natuurlijke Historie, 2:1-569.
- Julio, C.E.A. 2003. Revisão do gênero Anisocerus Lepeletier & Audinet-Serville, 1830 (Coleoptera, Cerambycidae, Lamiinae, Anisocerini). Revista Brasileira de Entomologia, 47(2):149-153.
- Lavocat, R. 1976. Rongeurs caviomorphes de l'Oligocène de Bolivie. II Rongeurs du Bassin Deseadien de Salla-Luribay. Palaeovertebrata, 7(3):15-90.

- Leite, Y.L.R. 2003. Evolution and Systematics of the Atlantic tree rats, genus Phyllomys (Rodentia, Echimyidae) with description of two new species. University of California Publications in Zoology, 132:1-118.
- Mauffrey, J.-F. & Catzeflis, F. 2003. Ecological and isotopic discrimination of syntopic rodents in a neotropical rain forest of French Guiana. Journal of Tropical Ecology, 19:209-214.
- Miles, M.A.; de Souza, A.A. & Póvoa, M.M. 1981. Mammal tracking and nest location in Brazilian forest with an improved spooland-line device. Journal of Zoology, 195:331-347.
- Moojen, J. 1952. Os roedores do Brasil. Biblioteca Científica Brasileira, Sére A-II. Instituto Nacional do Livro, Rio de Janeiro.
- Murray J.D. 1981a. On pattern formation mechanisms for lepidopteran wing patterns and mammalian coat markings. Philosophical Transactions of the Royal Society (B), Biological Sciences, 295:473-496.
- Murray J.D. 1981b. A pre-pattern formation mechanism for animal coat markings. Journal of Theoretical Biology, 88:161-199.
- Murray J.D. 1988. How the leopard gets its spots. Scientific American, 258(3):62-69.
- Murray, J.D. 1989. Mathematical Biology. Springer-Verlag, Heidelberg. Oliveira, T.G. & Mesquita, E.R.L. 1998. Notes on the distribution of the white faced tree rat, Echimys chrysurus (Rodentia, Echimyidae) in northeastern Brazil. Mammalia, 62(2):305-306.
- Pine, R.H. 1973. Mammals (exclusive of bats) of Belém, Pará, Brazil. Acta Amazônica, 3(2):1-79.
- Tate, G.H.H. 1935. The taxonomy of the genera of Neotropical hystricoid rodents. Bulletin of the American Museum of Natural History, 68:295-447.
- Thomas, O. 1910 Mammals from the River Supinaam, Demerara, presented by Mr. F.V. McConnell to the British Museum. Annals and Magazine of Natural History, Series 8(6):111-14.
- Thomas, O. 1928. A new Echimys from Eastern Ecuador. Annals and Magazine of Natural History, Series 10(2):409-410.
- Turing, A.M. 1952. The chemical basis of morphogenesis. Philosophical Transactions of the Royal Society of London, 237:37-72.
- Wahlert, J.H. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bulletin of the Museum of Comparative Zoology, Harvard, 113:113-214.
- Wahlert, J.H. 1983. Relationships of Florentiamyidae (Rodentia, Geomyidae) based on cranial and dental morphology. American Museum Novitates, 2769:1-23.
- Wahlert, J.H. 1985. Cranial foramina of rodents. In: Luckett, W.P. & Hartenberger, J.-L. (Eds.). Evolutionary relationships among rodents: a multidisciplinary analysis. Plenum Press, New York. p.311-333.
- Wolfheim, J.H. 1983. Alouatta seniculus In: Primates of the World -Distribution, Abundance, and Conservation. University of Washington Press, Seattle. p.228-236.
- Woods, C.A. 1993. Hystricognathi. In: Wilson, D.E. & Reeder, D.A. (Eds.). Mammals species of the world. A taxonomic and geographic reference. 2. ed. Smithsonian Institution Press/American Society of Mammalogists, Washington. p.771-806.
- Woods, C.A. & Howland, E.B. 1979. Adaptive radiation in capromyid rodents. Journal of Mammalogy, 60:95-115.

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APPENDIX

Gazetteer

Brazil: Amapá: 1 – rio Amapari. 00°45'N 51°32'W; 2 – Serra do Navio. 00°53'44"N 52°00'08"W; Amazonas: 3 – Virgem Guajará, Amazonas Not located. Here considered as Guajará. 04°19'44"S 59°42'26"W*1; Maranhão: 4 – Vargem Grande. 03°30'S 43°55'W*2; Pará: 5 – Barreirinhas, rio Tapajós. 04°25'S 56°13'W; 6 – BR-010 km 87-94. circa. 02°10'S 47°35'W.; 7 – Cametá, rio Tocantins. 02°15'S 49°31'W.; 8 – Peixe-Boi. 1°11'32"S 47°18'50"W; 9 – Utinga, Belém (as Belém). 01°26'S 48°29'W; French Guyana: 10 – Cayenne, Guyana Française. 4°56'00"N 52°00'00"W; 11 – rive droite du Petit Saut; Programme Faune Sauvage, Guyane Française. 05°04'N 53°03'W; 12 – Nouragues. 4°05'N 52°40'W*3; Guyana: 13 – Potaro Highlands, 1300ft. 4°25'00"N 58°16'00"N/5°22'00"N 58°54'00"W; 14 – Supinaam river, 1300ft*4. 6°59'00"N 58°31'00"W; Upper County [Sir R. Schomburgh]. Not located; Surinam. [Eimbeck]. Not located; 15 – Agricultural Experimental Station (Cultuurtuin), Paramaribo 5°50'00"N 55°10'00"W*5; 16 – Bedoti, south of Gansee on West Bank of Suriname River, locality now submerged by the Brokopondo, Lake, Brokopondo District. 4°13'00"N 55°53'00"W*5; 17 – Groot Henarpolder South east of Nieuw Nickerie, northwestern Nickerie district. 5°52'00"N 56°52'00"W*5; 18 – Republiek, about 35km South of Paramaribo, Para District. 5°30'00"N 55°12"00"W*5; 19 – Zuid River, near Kayserberg Airstrip, southern Nickerie District 3°20'00"N 56°49'00"W*5.

^{*}¹ The specimen MNRJ 67549 was collected in Virgem Guajará, Amazonas by A. Parko, collector number 16, with no further information in the label. A Parko was a professional collector of Museu Nacional, who lived in Borba and Benjamin Constant in Amazonas State, Brazil. A considerable collection of reptiles, amphibians, mammals and insects, and was made in both localities and Manaus. The locality Virgem Guajará was not located. However, Julio (2003) records Jaraguá near to Borba, where A. Parko has collected 2 males of *Anisocerus stellatus* (Coeloptera; Cerambycidae) in VII.1943, and a large collection of Cerambycidae was collected in Guajará-Mirim. Five localities named Guajará are near to Borba: Guajará 02°58′00″S 57°40′00″W (BR 04; SA21-10); Guajará 04°07′29″S 58°38′36″W (BR 04; SB21-01); Igarape do Guajará 04°19′10″S 59°44′19″W (BR 04; SB21-01); Ilha Guajará 04°19′44″S 59°42′26″W (BR 04; SB21-01); Guajará 05°32′00″S 59°33′00″W (BR 04; SB21-05). Since no other information is available, we arbitrarily choose Guajará (04°07′29″S 58°38′36″W).

 $^{^{\}ast 2}$ Locality taken of Oliveira & Mesquita (1998). Four specimens were collected.

^{*3} Locality taken of Mauffrey & Catzeflis (2003).

^{*4} Given in CIA Gazetteer as Supenaam river. See also Thomas (1910) and Wolfheim (1983).

^{*5} Localities taken of Husson (1978), who examined 13 specimens but only eight with skins.