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A Review of the Named Forms of *Phyllomys* (Rodentia: Echimyidae) with the Description of a New Species from Coastal Brazil

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ABSTRACT

To clarify the taxonomy and serve as a foundation for future systematic studies, we searched for the type material associated with all named forms of Brazilian Atlantic tree rats of the genus *Phyllomys*. For the following ten taxa we found either the originally designated holotypes, syntype series, or contemporary specimens likely to have been seen by the authors: *P. blainvillii*, *P. brasiliensis*, *P. fossilis*, *P. nigrispinus*, *P. unicolor*, *P. dasythrix*, *P. lamarum*, *P. medius*, *P. thomasi*, and *P. kerri*. For five species the holotype was unambiguously identified. For five other named forms no holotype was originally designated but we found several candidate specimens and for all of these we designate lectotypes. We identify the type localities for all named *Phyllomys* species and amend those which are ambiguous. We review the taxonomy, diagnosing and redescribing all the named forms of the genus. After examining the type material, we concluded that the rusty-sided tree rat from coastal Brazil, usually identified in the literature as *P. brasiliensis*, belongs to an unnamed species. We describe and name it here.

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RESUMEN

Com o objetivo de esclarecer a taxonomia e servir de base para futuros estudos sistemáticos, nós procuramos identificar os tipos associados a todas as formas descritas dos ratos arbóreos do gênero *Phyllomys*. Encontramos, para as seguintes 10 espécies, o holótipo designado originalmente, ou séries de sítipos, ou ainda espécimes contemporâneos provavelmente vistos pelos autores: *P. blainvillii*, *P. brasiliensis*, *P. fossilis*, *P. nigrispinus*, *P. unicolor*, *P. dasythrix*, *P. lamarum*, *P. medius*, *P. thomasi* e *P. kerri*. Para cinco delas o holótipo foi identificado sem nenhuma dúvida, enquanto que vários espécimes candidatos foram encontrados para cinco outras onde nenhum holótipo foi designado originalmente. Para todos esses nós designamos lectótipos. Nós identificamos as localidades tipo de todas as espécies descritas, corrigindo e restringindo as que eram ambíguas. Também revimos a taxonomia, diagnosticando e descrevendo todas as espécies nomeadas do gênero. Após examinarmos os tipos, concluímos que o rato de espinho ferrugíneo da costa do Brasil, geralmente identificado na literatura como *Phyllomys brasiliensis*, pertence à uma espécie distinta que ainda não tem nome. Nesse artigo, nós descrevemos e nomeamos essa espécie.

INTRODUCTION

The genus *Phyllomys* comprises a radiation of arboreal rats geographically restricted to the forested habitats of eastern Brazil, from Ceará to Rio Grande do Sul. It is the most speciose genus of the arboreal echimyid rodents (Echimyidae: Echimyinae; Emmons, submitted), and apart from one rare monospecific taxon, *Callistomys pictus*, it is the only echimyine genus within its current geographic range. The species within the genus have been subject to frequent confusion (see synonymies below) and apart from some external descriptions in field guide format (Emmons and Feer, 1990, 1997) they have not received modern diagnoses based on type specimens. With the type material dispersed throughout many European and Brazilian museums, it has proven difficult to assign specimens to species with any confidence.

As a first step in understanding the content and scope of the genus *Phyllomys*, we tried to find and examine all of the specimens upon which published names were, or may have been, based. Most members of the genus were described before taxonomists generally designated holotypes. Seven of the ten forms were named prior to 1900, and only one after 1916. We review the taxonomy and diagnose the nine living taxa that we determined to be represented by the published names. We have examined all important and many smaller museum holdings of *Phyllomys* species and we list below all encountered specimens of the named forms. The phylo-

genetic relationships within the genus are reviewed elsewhere (Leite, 2001).

REVIEW OF THE NAMED TAXA OF
PHYLLOMYS

SPECIMENS EXAMINED

We examined specimens of *Phyllomys* preserved in the following museums: National Museum of Natural History, Washington (USNM); American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Muséum d'Histoire Naturelle, Geneva (MHNG); Zoologische Museum und Institut für Spezielle Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB); Senckenburg Museum, Frankfurt (SMF); Naturhistorisches Museum, Vienna (NMW); Universitets Zoologisk Museum, Copenhagen (UZMC); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional, Rio de Janeiro (MNRJ); Muséum d'Histoire Naturelle de Lyon (MHNL, only photos examined); Museu de Biologia Mello Leitão, Santa Teresa (MBML); Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCNFZB); Museu de História Natural Capão da Imbuia, Curitiba (MHNCI); Museu de Zoologia da Pontifícia Universidade Católica do Paraná, Curitiba

(MZPUCPR); Coleção de Mamíferos do Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte (UFMG); Coleção do Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa (UFPB); Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa, Viçosa (UFV).

Phyllomys blainvillii (n = 196).

CANDIDATES FOR TYPE SPECIMENS: MNHN 310, 402, A7788, A7789; MHNG 321.1, 250/19; BMNH 55.12.4.116; MHNL 40001298, 50000747 (photos).

OTHER SPECIMENS: MNHN 14868; MNRJ 1345, 1350, 1512, 1516, 1517, 1521, 1523, 1528, 1548, 1762, 2238, 4125, 4126, 4127, 4128, 4129, 4130, 4131, 4132, 4133, 4134, 4135, 4136, 4137, 4138, 4139, 4140, 4258, 7819, 21512, 21513, 21514, 21515, 21516, 21518, 21519, 21520, 21521, 21522, 21523, 21524, 21525, 21526, 21527, 21528, 21529, 21530, 21531, 21532, 21533, 21534, 21535, 21536, 21537, 21538, 21539, 21540, 21541, 21542, 21543, 21544, 21545, 21546, 21547, 21548, 21549, 21550, 21551, 21552, 21554, 21555, 21556, 21557, 21558, 21559, 21560, 21561, 21562, 21563, 21564, 21565, 21566, 21567, 21568, 21569, 21570, 21571, 21572, 21573, 21574, 21575, 21576, 21577, 21578, 21579, 21580, 21581, 21582, 21583, 21584, 21585, 21586, 21587, 21588, 21589, 21590, 21591, 21592, 21593, 21594, 21595, 21596, 21597, 21598, 21599, 21600, 21601, 21602, 21603, 21604, 21605, 21606, 21607, 21608, 21609, 21610, 21611, 21612, 21613, 21614, 21615, 21616, 21617, 21618, 21619, 21620, 21621, 21622, 21623, 21624, 21625, 21626, 21627, 21628, 21629, 21630, 21631, 21632, 21633, 21634, 21635, 21636, 21637, 21638, 21639, 21640, 21641, 21642, 21643, 21644, 21645, 21646, 21647, 21648, 21649, 21651, 31533, 31534, 31535, 31536, 31537, 31538, 31539, 31540, 31542, 31543, 31544, 31554, 43810, 52090, 2P.1641, 2P.1647, 2P.1664; MZUSP 6146, 6147; NMW B1101; UFPB APO62; USNM 304580.

Phyllomys brasiliensis (n = 5):

TYPE MATERIAL: Type material from Lagoa Santa, UZMC not numbered.

OTHER SPECIMENS: UFMG AP48; UZMC 81, 82, 83, 601.

Phyllomys fossilis (n = 1):

Type material from Lagoa Santa, UZMC not numbered.

Phyllomys dasythrix (n = 13).

TYPE MATERIAL: ZMB 38794, 38799, 38800, 4278, 8237, syntypes; BMNH 12.3.1, paratype.

OTHER SPECIMENS: BMNH 0.6.29.20; MCNFZB 44, 46, 47, 48; MNRJ 6238, 21503.

Phyllomys kerri (n = 3):

TYPE MATERIAL: MNRJ 6241, holotype.

OTHER SPECIMENS: MNRJ 5463, 5464.

Phyllomys lamarum (n = 46):

TYPE MATERIAL: BMNH 3.9.5.96, holotype; BMNH 3.9.5.101, 3.9.5.102, 3.9.5.103, 3.9.5.104, 3.9.5.92, 3.9.5.93, 3.9.5.94, 3.9.5.95, 3.9.5.97, 3.9.5.98, 3.9.5.99; FMNH 35356, paratypes.

OTHER SPECIMENS: BMNH 3.9.5.1; MNHN 754, 1821A; MNRJ 11259, 11260, 21553, 21650, 21652, 21653, 21654, 21655, 21656, 21657, 21658, 21659, 21660, 21661, 21662, 21663, 21664, 21665, 21666, 21667, 21668, 21669, 2F.691; MZUSP 8413, 8414, 8415, 8416, 8417, 8418; UZMC 1281, 1282.

Phyllomys medius (n = 27).

TYPE MATERIAL: BMNH 3.4.1.84, holotype.

OTHER SPECIMENS: BMNH 3.7.1.84, 9.11.19.27; MCNFZB 391; MHNCI 3033; MNRJ 6237, 6240, 6742, 31561, 31568, 31569, 31570, 31571, 31572, 48864; MZPUCPR 129, EDR11, EDR8, FK21, FK22, FK23, FK24, FK25; MZUSP 528, 7716, 7717, 10629; UFPB AX30.

Phyllomys nigrispinus (n = 53).

TYPE MATERIAL: NMW B 918, holotype.

OTHER SPECIMENS: BMNH 33.10.9.18, 33.10.9.19; FMNH 93045, 94358, 94359; MNRJ 6440, 6441, 6442, 6443, 6444, 6445, 31522; MZUSP 175, 664, 665, 666, 1949, 1950, 1951, 1952, 1953, 1954, 3738, 6431, 10311, 10312, 10316, 10317, 10318, 10319, 10320, 24939, 24941, 25853, 25854, 25855, 25856, 25857, 25858, 25859, 25860, 25861, 25862, 25863, 26652, 26712, 26713, 26715, 26716, 26721, 27755; UFMG 948.

Phyllomys thomasi (n = 22).

TYPE MATERIAL: MZUSP 45, 47, 51, 223, 526, 527, 532; FMNH 41360 (ex-MZUSP 1408); BMNH 2.8.25.2 (ex-MZUSP 224), syntypes.

OTHER SPECIMENS: BMNH 99.8.12.1;

MNRJ 6448; MZUSP 535, 2148, 2149, 2151, 3197, 3198, 3199, 6433, 25816, 29017; USNM 296336.

Phyllomys unicolor (n = 1):

TYPE SPECIMEN: SMF 4319 (VII.T.4.a), holotype.

Genus *Phyllomys* Lund

Phyllomys Lund, 1839a: 226.

Species of the Brazilian laminate-toothed echimyid rodents have historically been grouped with nonlamine-toothed arboreal echimyids under the generic names *Echimyus* Cuvier 1809, *Loncheres* Illiger 1811, or *Nelomys* Jourdan 1837. Oldfield Thomas (1916a, 1916b) segregated them under *Nelomys* Jourdan, but Tate (1935) again grouped them under *Echimyus* along with Amazonian taxa with nonlamine teeth. João Moojen once more partitioned the genus *Phyllomys* from other echimyids (Moojen, 1952), but he was not followed by other authors (Cabrera, 1961; Woods, 1993). Emmons (submitted) recently revised the genera of Echimyidae, once again separating the genus *Phyllomys* from *Echimyus*, as have some other recent authors (Emmons and Feer, 1990, 1997, as *Nelomys*; Leite, 2001). She diagnosed the genus and commented briefly on the taxonomy (Emmons, submitted), but we here expand the taxonomic notes and designate a lectotype for the type species.

The first described species that we now recognize as a *Phyllomys* was *Nelomys blainvillii* Jourdan, published in the Comptes Rendus of the Académie des Sciences for July–December 1837. Jourdan stated of *Nelomys*: “Ce genre formé aux dépens du genre Échymys [sic] des auteurs, a pour type l’Échymys *crsitatus* [sic].” Thus *Nelomys* is a junior synonym of *Echimyus* by designation of the author. Jourdan’s memoir was presented again by Cuvier (1838) at the Académie des Sciences on 2 January 1838. Confusingly, Cuvier (1838) stated that the type of *Nelomys* was *blainvillii*. Jourdan’s earlier paper was overlooked by Thomas (1916a, 1916b), Tate (1935), and many subsequent authors, all of whom considered Cuvier’s report to be the original description and consequently, that *blainvillii* was the type of *Nelomys*. With *Ne-*

lomys unavailable, the next available generic name is *Phyllomys* Lund, 1839.

Lund (1839a) first used the name in a preprint in French of his Danish work, and he gave a short diagnosis: “Les *Phyllomys* ont les mâcheliers supérieurs composés de quatre lames transversales simples” (“*Phyllomys* have upper molars composed of four simple transverse laminae”: Lund, 1839a: 226). He contrasted this laminar structure with molars of “*Loncheres*” (*Clyomys*), “*Echimyus*” (*Proechimyus*), and “*Nelomys*” (*Thrichomys*). The upper molars are diagnostic for the genus in Brazil. The only other echimyid taxa with similar teeth are *Diplomys* spp., which are not found within the geographic range of *Phyllomys* spp., and were not described until 1877 (Günther, 1877). We therefore accept *Phyllomys* Lund, 1839, as a valid generic name, adequately diagnosed.

SPECIES ACCOUNTS

Phyllomys brasiliensis Lund, 1840

Phyllomys brasiliensis Lund, 1840c: 294.

[*Loncheres*] *brasiliensis*: Waterhouse, 1848: 330 (name combination and subsequent incorrect spelling).

[*Loncheres* (*Loncheres*) *armatus*] *brasiliensis*: Trouessart, 1881: 177 (as subspecies, name combination).

Loncheres armatus: Winge, 1887: 71 (name combination, not *Nelomys armatus* I. Geoffroy, 1838).

Echimyus (*Echimyus*) *armatus*: Trouessart, 1904: 503 (part, name combination, not *Nelomys armatus* I. Geoffroy, 1838a)⁴.

Phyllomys armatus: Goldman, 1916: 126 (part,

⁴ Based on a verbal paper read at the Paris Academy 25 June 1838, Isidore Geoffroy St. Hilaire published the same material, close to verbatim, four times in 1838 (Geoffroy, 1838a, 1838b, 1838c, 1838d). These articles include the first descriptions of *Echimyus semivillosus* and *Trinomys albispinis*, and the first use of *Dactylomys* as a genus. It is thus important to establish the publication order of the four papers. The Comptes Rendues Hebdomadaires published a list of all publications received during each weekly séance. Geoffroy 1838a and 1838b were both received during the week 2 July 1838; Geoffroy 1838c was received 21 January 1839 (although it has printed on the cover that it was the August 1838 issue); and 1838d was a newspaper published 7 July 1838. Geoffroy 1838a and 1838b clearly preceded the others, but apparently appeared the same week. We here fix Geoffroy 1838a as the first publication (ICZN article 24.2.1).

name combination, not *Nelomys armatus* I. Geoffroy, 1838a).

[*Nelomys*] *brasiliensis*: Thomas, 1916a: 240 (name combination).

[*Echimyus*] *braziliensis*: Tate, 1935: 431 (name combination and subsequent incorrect spelling).

Echimyus (Nelomys) brasiliensis: Eisenberg and Redford, 1999: 487 (name combination).

TYPE MATERIAL: Lund included only one species epithet under his *Phyllomys*, *P. brasiliensis*. His first use of the name was a nomen nudum in a table (Lund, 1839b). The binomial *Phyllomys brasiliensis* again appeared in a table in Lund (1840a: 312), where he listed *P. brasiliensis* among living rodents, and "*Phyllomys aff. brasiliensi*." among fossil forms. In 1840 he republished the generic name, this time accompanied by two figures (Lund, 1840b: pl. XXI, fig. 12, 13) cited in the text under *Phyllomys*, but erroneously in the figure legend as *Phyllostomus*. *Phyllomys brasiliensis* is thus the type species of the genus by subsequent monotypy (ICZN, 4th ed. Article 69.3), although Lund never diagnosed or figured the species. A figure in Lund (1840c: pl. XXV, fig. 10) has the legend "*Phyllomys aff. Brasiliensi*". The figures in Lund, 1840b, were colored, and figure 13 is pale bluish, while figure 12 is red.

The material examined by Lund and selection of a lectotype: The specimens collected and described by Lund, and later treated in more detail by Winge (1887), are stored in boxes at UZMC as Winge left them, including his handwritten labels, but they are not individually numbered. The *Phyllomys* fragments all appear to be from owl pellets, with the rostrum and braincase clipped from the crania and the larger bones fragmentary. Older fossils or subfossils are stained red, while more recent material is unstained, of bone or bluish color. The *Phyllomys* material is grouped in a large box, under the name *Loncheres armatus* (Winge's 1887 synonym of *P. brasiliensis*), subdivided into many smaller boxes that each contain a number of specimens. Two boxes include labels with "*Phyllomys Original*" written on them, and in another box the label includes "*Lonchophorus fossilis Original*" (fig. 1A, C, G). Each of these three boxes contains several items, one of which corresponds well with

one of the four original figures published by Lund (fig. 1B, E). A box: "*Loncheres armatus 'Phyllomys' Orig.? etc.*" is the only one with Lund's own label, and it has numbers assigned to the fragments (but not written on them). A left maxillary fragment with two teeth and a fraction of zygoma, no. 744, best matches Lund's plate XXI, fig. 12 (fig. 1B, C), which could be interpreted as illustrating either one or two teeth. A box, "*Loncheres armatus Phyllomys Original*" Lapa das Quatro Bocas, contains two complete maxillaries, one a reddish subfossil with four cheekteeth; one a bluish, recent-looking fragment, from a younger animal, with three teeth; as well as one maxillary encased in limestone; a subadult maxillary with M2 missing, and several mandibles. The recent-looking maxillary is the only likely candidate for the original of Lund's *Phyllomys* plate XXI, fig. 13 (fig. 1 A, D). Lund's figure 13 shows four cheekteeth, but the fragment, from a young individual, has only three teeth and is broken off behind M2. We consider this maxillary nonetheless to be the model for figure 13 as it is the only bluish maxillary among all material marked "Original" and consequently most likely to have been viewed by Lund. Artists of the day often used some license and M3 was probably added by the artist: the M3 shown differs in posterior loph size from actual *Phyllomys brasiliensis* posterolophs, which are much narrower than the more anterior lophs or become obsolescent (fig. 2). We designate the figured maxillary fragment (fig. 1D) as the lectotype of *Phyllomys brasiliensis*.

Two contemporary specimens (UZMC 81; UZMC 83), one with an embryo, collected by Reinhardt at Sumidouro, ca. 12 km NW Lagoa Santa, (19°32'28"S 43°56'28"W) in 1849 and 1852, were considered by both Reinhardt (1849, 1887) and Winge (1887: 71) to be conspecific with Lund's *P. brasiliensis* (although Winge synonymized *P. brasiliensis* with *Loncheres armatus* Geoffroy). We likewise identify them as *P. brasiliensis*, along with a single recent specimen collected by M.A. Sabato and prepared by one of us (YL). We cannot unambiguously equate these with the lectotype, but they are consistent with it (for example, in size and in the unique, subtly recurved ogee arch-

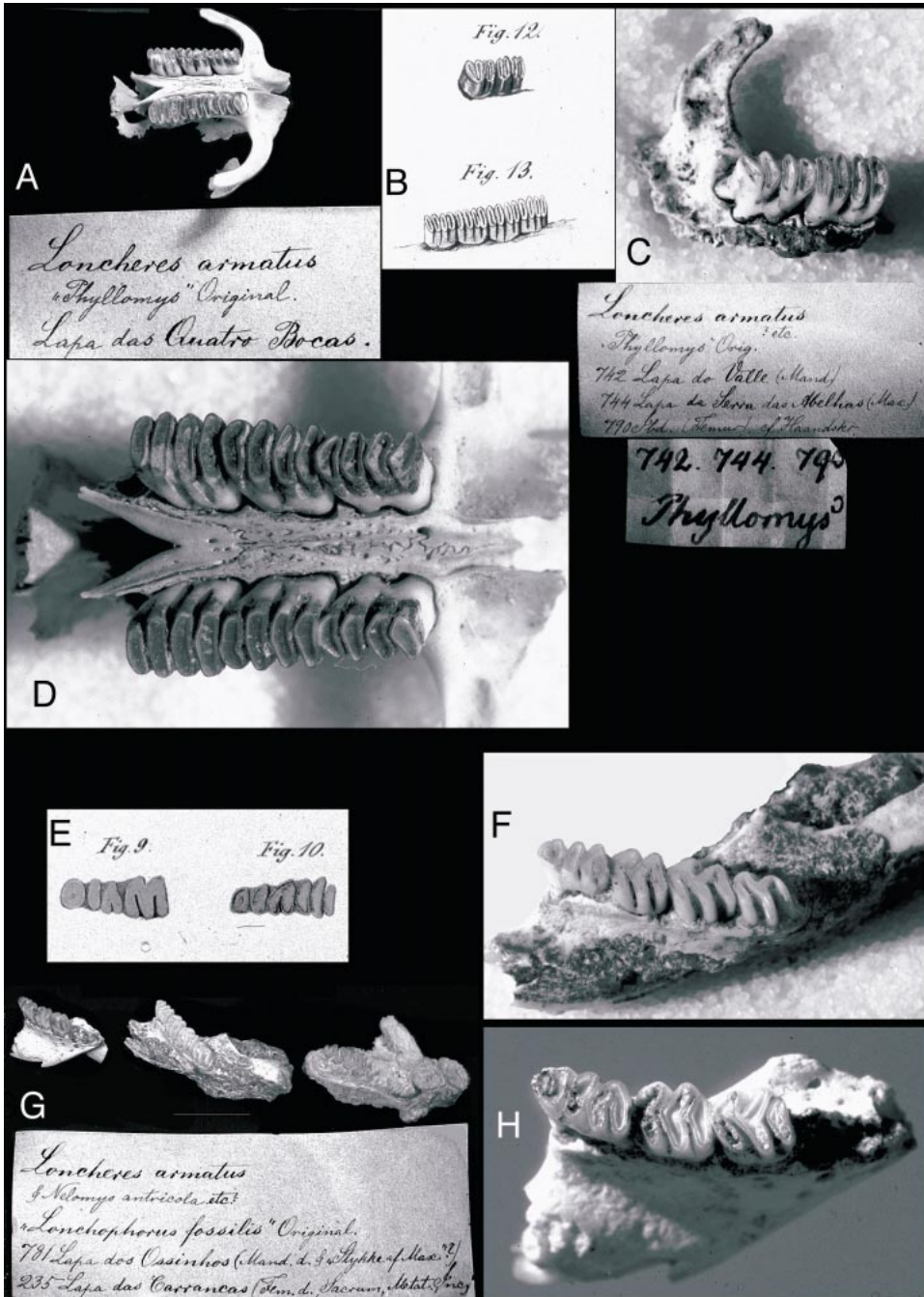


Fig. 1. Original illustrations and Lagoa Santa material examined by Lund, as matched by the authors. **A**, The maxillary fragment matching Lund's fig. 13, chosen as lectotype of *Phyllomys brasiliensis* (above), and a label from its box (below); **B**, Lund's (1840b) figs. 12, 13; **C**, the maxillary fragment matching fig. 12 (above) and the labels included in the box (below); **D**, the lectotype of *P. brasiliensis*, enlarged view; **E**, Lund's (1840c) figs. 9, 10; **F**, the mandibular fragment whose first two teeth match fig. 9, and therefore the holotype of *Lonchophorus fossilis*; **G**, the three mandibular fragments and associated label of the *Lonchophorus fossilis* box; **H**, the mandibular fragment that matches Lund's (1840c) fig. 10, *Phyllomys aff. brasiliensis*.

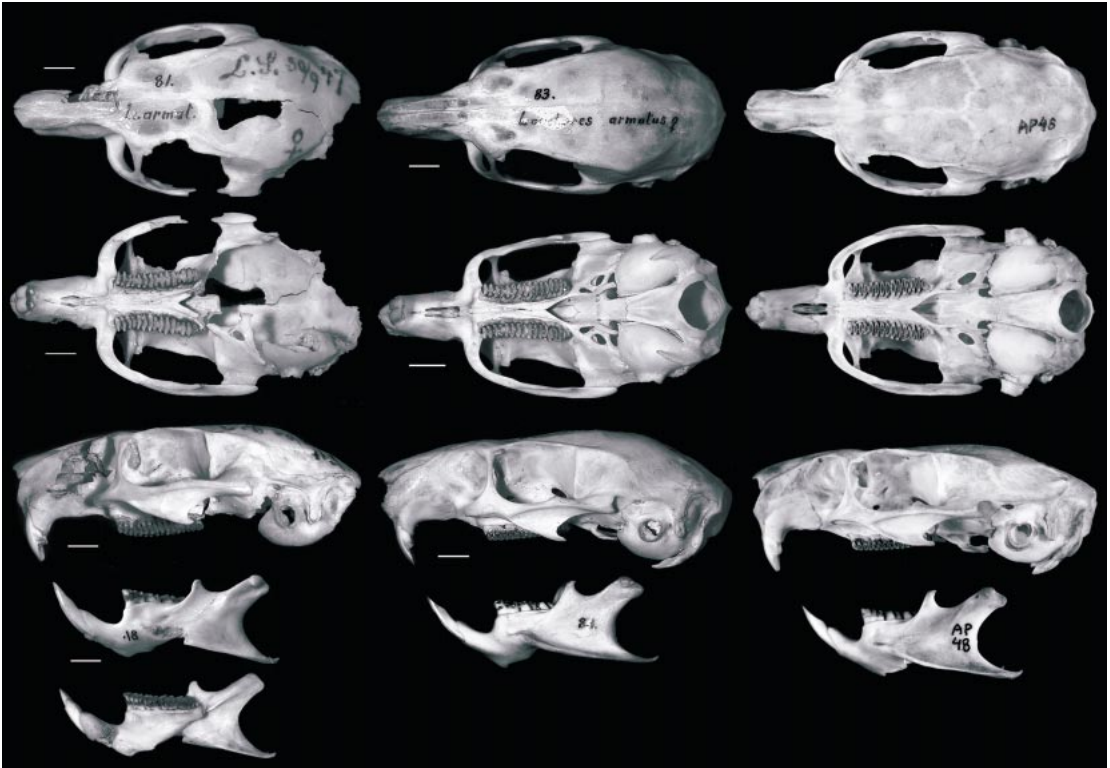


Fig. 2. All known adult specimens of *Phyllomys brasiliensis*. **Left**, Reinhardt's first specimen UZMC 81 (Reinhardt, 1849); **middle**, Reinhardt's second specimen UZMC 83; **right**, the recent specimen collected by M.A. Sábato (UFMG AP48). Scale bars = 10 mm.

shaped postpalatal notch; fig. 2). Furthermore, they were collected near the type locality, two of them in the decade when Lund collected his *Phyllomys* from currently forming piles of owl pellets. These three are the only known complete specimens, and we use them to diagnose the species.

TYPE LOCALITY: Lund stated: "I used, to create this first genus [*Phyllomys*] a few maxillaries found on piles of bones still in formation in a cave in the valley of rio das Velhas, at 18° south latitude." He further noted that as he had found no remains of this taxon in more southerly caves, he fixed its southern limit in the region at 18°S (Lund, 1839a). The cave near Lagoa Santa, Minas Gerais (fig. 3, locality 4), where the lectotype was found is Lapa das Quatro Bocas. We have not located its exact coordinates.

REMARKS: After examining the type material, we concluded that the species frequently referred to as *P. brasiliensis* in mu-

seums and in the literature (e.g., Thomas, 1916b; Moojen, 1952), is in fact a distinct and unnamed species, which we are describing below.

DIAGNOSIS: A medium-sized species (table 1). Dorsal pelage orange-brown sprinkled with black bands on hairs. Aristiforms relatively long (27 mm) and very wide (1.3 mm) on the rump (fig. 4B). Venter cream-yellow; inguinal and axillary regions with cream-white, white-based hair along the midline. Tail about equal to head and body length; covered with short brown hair; scales visible except near the tip, where longer hairs form a 20 mm tuft. Cheekteeth narrow, palatine width equal to tooth width at M1; tooththrows nearly straight, diverging posteriorly in older individuals (fig. 2). Supraorbital ridges well developed, beaded. Interorbital region slightly divergent posteriorly, postorbital process moderate. Zygomatic arch slender to moderately robust, maximum height less than or

TABLE 1
Selected External and Skull Measurements (in millimeters) of Type Specimens of *Phyllomys*

For species where the holotype or lectotype lack measurable material, a paratype or another specimen has been substituted. Measurements as in Patton and Rogers (1983).*

	<i>P. dasythrix</i> ZMB 38800 ? sex	<i>P. kerri</i> MNRJ 6241 ♀	<i>P. tamarum</i> BMNH 3.9.5.96 ♀	<i>P. medius</i> BMNH 3.7.1.84 ♀	<i>P. thomasi</i> MZUSP 47 ♂	<i>P. brasiliensis</i> UZMC 83 ^a ♀	<i>P. blainvilli</i> MHNG250 skin ^b 250/19 skull ♀	<i>P. unicolor</i> SMF4319 ? sex	<i>P. nigrispinus</i> NMW B918 skin only ♂	<i>P. nigrispinus</i> MZUSP 175 skull ^c ♂
HB	—	212	225	230	285 ^d	—	≈260	280 ^e	241 ^e	—
TAIL	—	223	216	240	[0] ^d	—	≈200	202 ^e	157 ^e	—
HF	—	38	35	40	47 ^d	37	43, 45 ^f	40.4, 37 ^f	37	—
EAR	—	17	13	17	14 ^d	17	15, 17 ^f	16.4	—	—
GSL	46.36	51.69	50.31	53.13	56.18	48.55	—	—	—	51.48
NL	13.9	16.42	15.51	16.31	17.31	13.79	15.69	—	—	16.59
RL	16.47	19.61	17.46	19.53	19.85	17.48	18.45	—	—	18.58
OL	13.33	13.92	14.09	14.64	15.84	13.33	14.52	—	—	14.72
RB	7.33	8.41	6.78	7.47	9.19	7.01	7.77	9.56	—	8.03
IOC	9.88	12.05	10.53	10.96	12.71	11.14	12.10	—	—	10.04
MB	19.23	19.1	18.84	21.35	21.88	18.48	20.01	22.73	—	21.15
ZB	22.8	23.28	23.54	24.92	28.01	22.55	25.61	27.73	—	25.14
CIL	42.24	46.14	44.29	48.35	50.56	41.99	—	—	—	46.11
BaL	35.92	39.81	—	—	43.7	36.04	—	44.91	—	39.17
D	9.6	12.08	10.32	11.14	12.57	10.07	10.74	11.22	—	11.21
MTRL	12.28	11.25	11.13	12.66	13.35	11.79	12.53	13.85	—	12.02
PLb	9.51	8.28	—	—	9.7	9.46	10.14	12.22	—	9.17
IFL	3.11	4.7	4.19	3.57	5.14	4.83	—	4.56	—	3.13
BuL	9.47	9.87	10.76	10.65	10.92	10.07	10.65	12.79	—	10.64
Pla	18.73	20.44	18.57	21.01	22.22	18.93	20.39	23.07	—	20.45
PPL	18.43	20.74	—	—	23.62	22.82	—	—	—	20.51
MPF	3.57	3.52	3.76	3.92	4.13	3.52	3.61	3.46	—	3.96
MaxB	7.66	8.12	7.19	7.95	9.23	8.24	8.21	8.83	—	8.88
OccW	7.83	8.56	—	—	9.76	8.45	—	—	—	9.36
RD	10.32	11.33	9.68	10.07	12.66	10.07	11.04	12.36	—	11.40
CDM1	13.77	14.37	—	—	16.51	13.69	14.75	—	—	14.32
CD	—	19.4	17.87	18.12	—	14.96	16.92	—	—	19.86

See opposite page for footnotes.

equal to $\frac{1}{3}$ of jugal length. Squamosal does not contribute to the spinose postorbital process of zygoma. Mastoid process long, extending below the horizontal midline of the external auditory meatus (EAM). Mesopterygoid fossa sharply pointed, wide posteriorly, forming an angle of more than 60° , but narrower at anterior point, which reaches posterior lamina of M2. Incisive foramen ovate. Ventral root of the angular process of the mandible deflected laterally (fig. 5, bottom). Ventral spine present posterior to the junction of the mandibular rami (fig. 5, top). Upper incisors orthodont.

SIMILAR SPECIES: *P. brasiliensis* is similar to *P. lamarum* in cranial features, but is larger (table 1). Externally, *P. brasiliensis* is orange-brown sprinkled with black, whereas *P. lamarum* is a paler, yellowish animal speckled with more conspicuous orange-tipped spines.

Phyllomys fossilis (Lund, 1840)

Lonchophorus fossilis Lund, 1840c: pl. XXV, fig. 9.

TYPE MATERIAL: Lund's first use of this name (1840c: 294) was in the same table in which the name *Phyllomys brasiliensis* also appears, and the only description of the taxon is an illustration in an accompanying colored plate (pl. XXV, fig. 9; our fig. 1E). The UZMC box with label "'*Lonchophorus fossilis*' Original" includes three mandible fragments, each a single toothrow (collection no. 781 from Lapa dos Ossinhos). The teeth on each of the three mandibles are so different in size that they certainly represent three species, all of the genus *Phyllomys* (our fig. 1F,

G, H). Two of these are the models for Lund's plate XXV, figs. 9 and 10, with the mid-sized toothrow (the holotype, our fig. 1F) depicted in Lund's fig. 9, as *Lonchophorus fossilis*, and that from a very tiny animal in fig. 10, as *Phyllomys aff. brasiliensis* (our fig. 1H). However, the mandible corresponding to the figured *L. fossilis*, of the three in the box, is the closest in size (toothrow = 10.59 mm) to both the *P. brasiliensis* from Lapa das Quatro Bocas, and those collected by Reinhardt. Either the figure legends were mixed up (the figures are not to scale) or perhaps Lund classified them in this way because he thought that all cheekteeth of *Phyllomys* spp., including mandibular, had separate laminae, as do those of the smallest specimen.

TYPE LOCALITY: Based on Lund's itinerary, described by Reinhardt (1887) we restrict the type locality to: Lapa dos Ossinhos, near Serra das Abelhas and Poções, Lagoa Santa, Minas Gerais, Brazil, ca. $19^\circ 32'S$ $44^\circ 01'W$ (fig. 3, locality 4).

REMARKS: We cannot with certainty identify the holotype of *P. fossilis* with a particular living species, although *Lonchophorus* is clearly a junior synonym of *Phyllomys*. We consider *P. fossilis* a nomen dubium, perhaps a synonym of *P. brasiliensis*, but at present referable only to the type specimen.

Phyllomys blainvillii (Jourdan, 1837)

Nelomys blainvillii Jourdan, 1837: 522.

Loncheres (Nelomys) blainvillei: Wagner, 1840: 203 (part, name combination and subsequent incorrect spelling).

Notes to table 1

* Measurements: External body measurements: HB = head and body length, TAIL = tail length, HF = hindfoot length (claw included), EAR = ear height (from notch to top). Skull measurements: GSL = greatest skull length, NL = nasal length, RL = rostral length, OL = orbital length, RB = rostral breadth, IOC = interorbital constriction, MB = mastoid breadth, ZB = zygomatic breadth, CIL = condyloincisive length, BaL = basilar length, D = diastema length, MTRL = maxillary toothrow length, PLb = palatal length *b* (anterior edge of PM4 to anterior edge of mesopterygoid fossa), IFL = incisive foramina length, BuL = bullar length, Pla = palatal length *a* (midline distance between posterior margins of upper incisors to anterior margin of mesopterygoid fossa), PPL = postpalatal length, MPF = mesopterygoid fossa width, MaxB = maxillary breadth, OccW = occipital condyle width, RD = rostral depth, CDM1 = cranial depth at M1, CD = cranial depth.

^a Reinhardt's second and most complete specimen.

^b Mounted skin measured with string by LHE.

^c Specimen from Itapeninga, less than 50 km from Ipanema, the type locality of *P. nigrispinus*.

^d Taken from the study skin.

^e Wagner's original measurements converted as "pied du ro".

^f Measurements taken from the left and right ear/hindfoot are different.



Fig. 3. Type localities of *Phyllomys* species, see text for coordinates: **1**, *P. lamarum*; **2**, *P. blainvillii*; **3**, *P. unicolor*; **4**, *P. brasiliensis*, *P. fossilis*; **5**, *P. kerri*; **6**, *P. thomasi*; **7**, *P. nigrispinus*; **8**, *P. medius*; **9**, *P. dasythrix*. The known geographic range of the genus *Phyllomys* is shaded.

[*Loncheres* (*Loncheres*)] *blainvillii*: Trouessart, 1881: 177 (part, name combination).

[*Echimyus* (*Echimyus*)] *blainvillei*: Trouessart, 1904: 503 (name combination and subsequent incorrect spelling).

Nelomys blainvillei: Thomas, 1916a: 240 (name combination and subsequent incorrect spelling).

Phyllomys lamarum: Moojen, 1952: 140, pl. 20 (not *Nelomys lamarum* Thomas, 1916).

Echimyus blainvillei blainvillei: Cabrera, 1961: 539

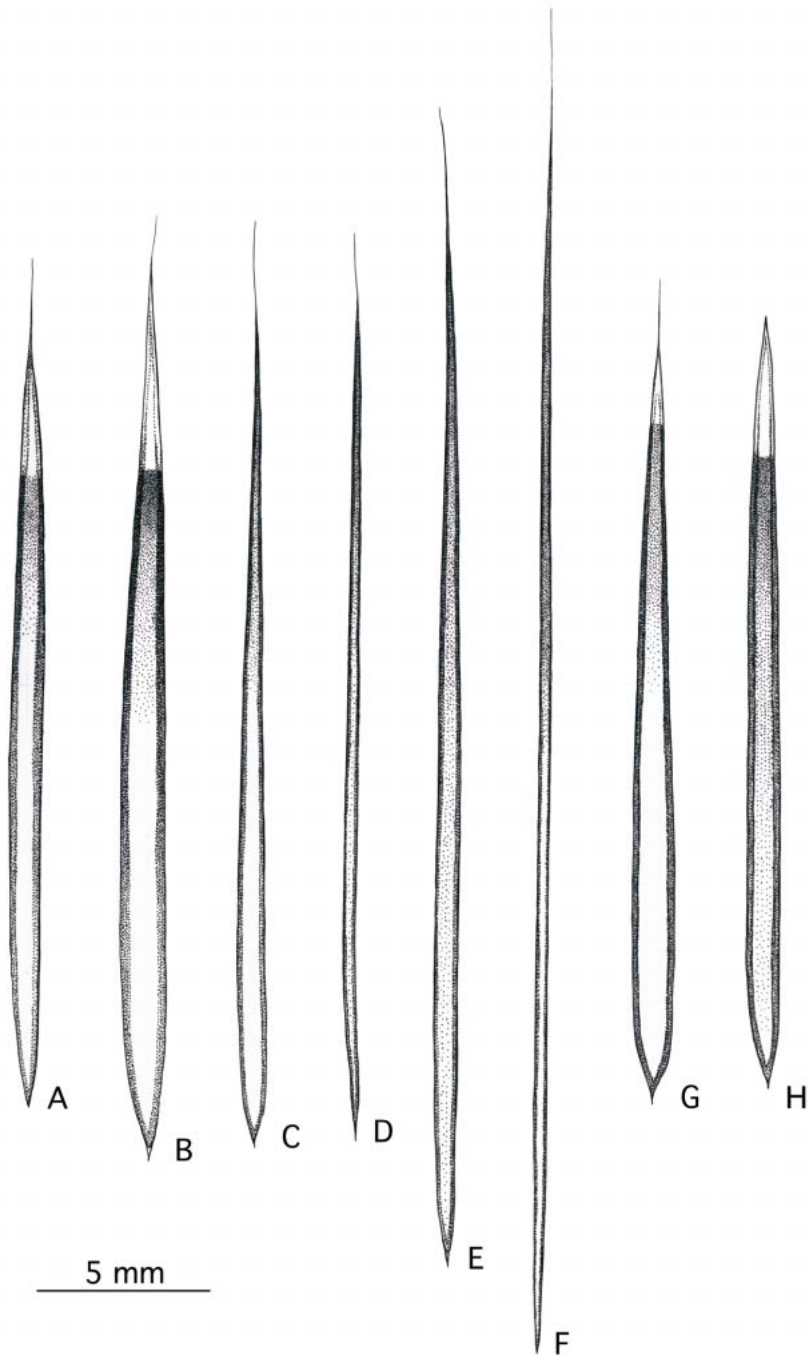


Fig. 4. Middorsal aristiform hairs of eight species of *Phyllomys*: **A**, *P. blainvillii* (LPC 290); **B**, *P. brasiliensis* (UFMG AP48); **C**, *P. nigrispinus* (MZUSP 1031); **D**, *P. dasythrix* (MCNFZB 46); **E**, *P. thomasi* (MZUSP 3198); **F**, *P. medius* (MNRJ 48864); **G**, *P. lamarum* (LC 73); **H**, the rusty-sided tree rat (MNRJ 62391).

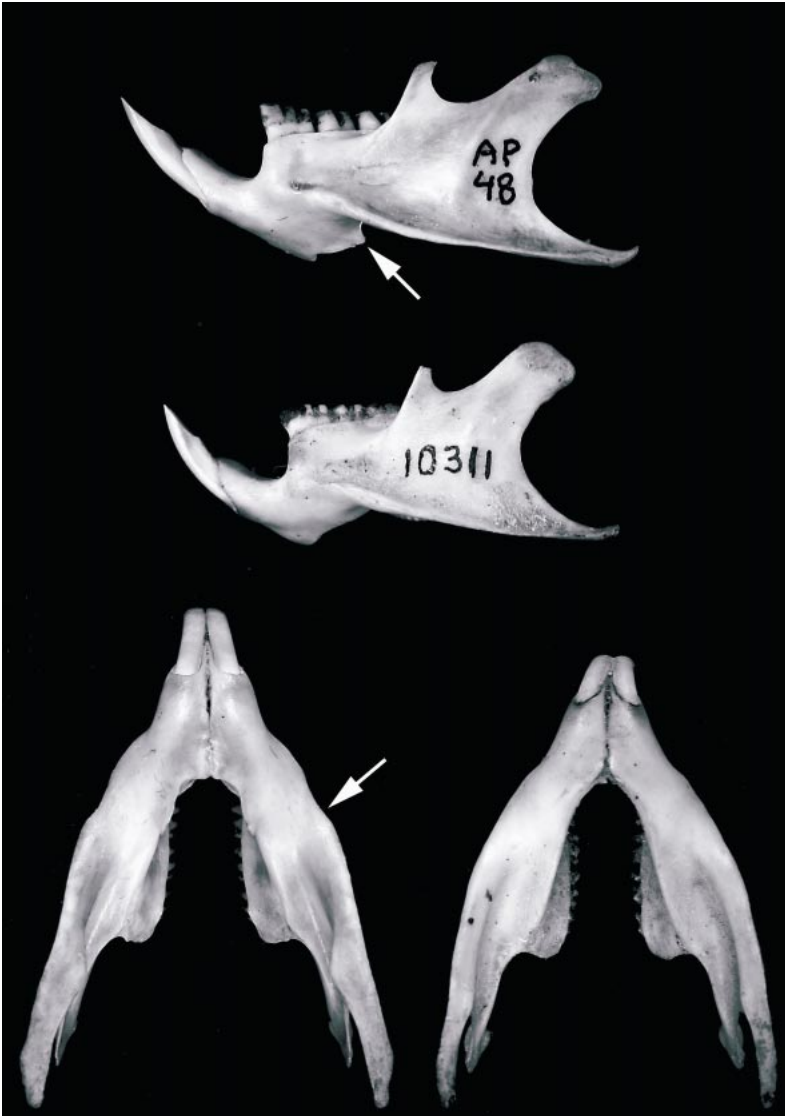


Fig. 5. Mandibular characters of *Phyllomys* species. **Top**, above, ventral mandibular spine present, *P. brasiliensis* UFMG AP48; below, spine absent, *P. nigrispinus* MZUSP 10311. **Bottom**, left, ventral root of angular process deflected laterally, *P. brasiliensis* UFMG AP48; right, ventral root of angular process not deflected laterally, *P. nigrispinus* MZUSP 10311.

(as subspecies and subsequent incorrect spelling).

Echimys (Nelomys) blainvillei: Eisenberg and Redford, 1999: 487 (name combination and subsequent incorrect spelling).

TYPE MATERIAL: Jourdan (1837) designated no holotype in his original description of *Nelomys blainvillii*, nor did he or Cuvier (1838) state in which collection Jourdan,

then a professor at Lyon, examined specimens. The brief original description, from a paper read on 9 October 1837, did not state the collector, but only that "Blainville's nelomys was killed in a small island off the coast of Brazil, near Bahia." (Jourdan, 1837, our translation). In 1840, F.-J. Pictet read a paper which stated: "The Musée academique of Geneva has received, in recent years, from



Fig. 6. *Phyllomys blainvillii* from I. Geoffroy, 1840 (pl. 22).

Mr. Blanchet by intermediary of Mr. Moricand, many specimens of spiny rodents which authors have given the names of *Echymys* and *Nelomys*. Two new species for science were acquired by this means: the *Nelomys blainvillii* which was described by Mr. Jourdan. . . .” (Pictet, 1841:1, our translation). Pictet further noted that he sent some of this material to Isidore Geoffroy St. Hilaire in Paris, who verbally reported on it on 25 June 1838 (I. Geoffroy, 1838a, 1840). He follows this statement with: “We received from Bahia some spiny rats which belong to four very distinctive species, of which *Nelomys blainvillii* Jourdan. . . . The two first [including *Nelomys*] were sufficiently described by Jourdan and Geoffroy, and the figure in the *Magasin de Zoologie* is good, especially for the *Nelomys*.” (Pictet, 1841: 2; our fig. 6). Geoffroy (1840), in Paris, likewise stated that he was reviewing the spiny rodents consequent to having been requested to examine and publish on a collection of rodents sent to Paris by F.-J. Pictet of the museum of Geneva.

Therefore, the material on which Jourdan based his description of *Nelomys blainvillii* was originally part of the collections Blanchet sent to the Museum in Geneva. It now remains to determine whether any extant

specimen can be identified as that seen by Jourdan, who gave the following measurements for his new species: TL = 45 cm; HB = 25 cm; T = 20 cm. We have discovered specimens in four museums that are all candidates for the holotype of *P. blainvillii*.

A. THE GENEVA SPECIMENS: The Muséum d’Histoire Naturelle de la Ville de Genève houses two well-documented specimens cataloged on 2 November 1837, in a lot under the same number, 250/19. The original 1837 catalog entry states: “250. 19 Novembre 2 *Echymys* [blainvillei Jour] 2 Ihs Eos pa? Bahia Ach. Dr. Blanchet [voir 321/1 cr.] 1 réformé 1901” (fig. 7). One specimen is a partly mounted skin with skull still inside. The other is a skull with the catalog reference 324/1. This catalog note states: “1. Fevrier 1 1843 Tete du *Nélomys* de Blainville 1 squelette Bahia” and in later handwriting and other ink: “[*Echymys blainvillei* Jourd.=] *Nelomys blainvillii*. Jourd. id. que 250/19 [de la peau reformé en 1901]”. This indicates that the skull came from a skin lost or destroyed in 1901 (Manuel Ruedi, personal commun.), and it is not now present in the museum.

The skin corresponds closely in color with Jourdan’s original description. Our measurements (in cm) are nearly the same as his: TL = about 45; HB about 26; T = 20; HF =

"Muséum National d'Histoire Naturelle"		"H. de la pte Bahia Ach. Dr? Blanchet"			(voir 324)	
<i>Echimus blainvillei</i> Jour?		enq. nill	ad	ad		
<i>Echimus</i>	/	ad	ad	ad		
<i>Nectomys</i>	/	ad. blanc	ad	ad	<i>Nectomys squamipes</i> Pictet. (Muséum National)	
<i>ad</i>	/	ad	ad	ad	<i>Oryzomys hispidus</i> Pictet. type?	

Fig. 7. Entry for lectotype of *P. blainvillii* in Geneva museum catalog: "*Echimus blainvillei* Jour. 2 empailé Ilh Eos [?] Ach. Dr? Blanchet". Note entries below for *Oxymycterus hispidus* Pictet, and *Nectomys squamipes* from the same shipment.

43–45; E = 15–17, but they are imprecise, as the mounted skin was difficult to measure (HB was measured with string along the lateral aspect). These two specimens are consistent with the same species and are also the same species as the paratype in the British Museum (see below). We were unable to find more archival material about the specimens in Geneva, as many records from that period were destroyed in a fire.

B. THE PARIS SPECIMENS: The Muséum National d'Histoire Naturelle, Paris, has three skins and two skulls that are also candidates for the material of *N. blainvillii* seen by Jourdan, F. Cuvier, and I. Geoffroy, but none have any original data or provenance:

1) An unmounted skin no. 402 marked Type CG 1849 no. 310 on a recent tag. An older tag reads: "Reçu de Mr. F. Cuvier juin jul 1849". This has recently been considered the holotype of *Nelomys blainvillii* (Rode, 1945; and current catalog). We measured it with string in 2000: TL = 40.7 (in cm, laterally); 45.0 (over back); T = 19.7; HB = 21.0 (laterally), 25.3 (over back); HF = 31; E = 9. This specimen closely fits Jourdan's measurements and description, including "moustaches noires, nombreuses, et longues" and correct back, venter and foot color—gray-red [roux]. The specimen is blackened with age but appears to have robust banded spines with subterminal dusky bands and orange tips, and a white venter: it may not be the same species as the Geneva specimens.

2) A mounted skin: mount no. 1803. On the bottom of the wooden base is written: "no. 310, N. Blainvillii Jourdan. Cuvier 1849". No. 1803 was also painted on the side of the wooden base, which has been overpainted in white, but the number is still legible. The Laboratoire de Zoologie likely re-

ceived the skin from Cuvier in 1849, in the same lot (310) as the previous skin. Our measurements (cm) do not correspond with Jourdan's: TL 40.8 (laterally), 40.0 (over back) T = 18.7; HF = 38?, E = 13? HB = 22.1 (laterally); 21.3 (over back). Moreover the color does not match well (tail and feet paler, moustaches not so black and prominent and dusky/rusty venter). However, it is the same species as the Geneva specimens and the BMNH paratype.

3) A mounted skin on the wooden base of which is written "# 1804, de la? de Deos? Bahia, acqui de Musée de Gand par échange 6". We measured it (in cm) as: TL = 44.2 (laterally), 50.2 (over back); T = 22.7; HF = 38; E = 15; HB = 21.5 (laterally), 27.5 (over back). These measurements do not closely correspond to Jourdan's. This is the same species as # 310 mounted, but it is not a good candidate for the holotype because of its provenance from Gand, although it is likely a paratype sent to Gand by Pictet.

4) A skull without mandible, no. A7788 (1850 catalog number), Si—R.C. +107 2809, previously deposited in the Laboratoire Anatomie Comparée. Formerly labeled as "*Loncheres cristatus*", in 1988 LHE determined it to be an "*N. blainvillii*". Written on it is "[*Nelomys*] de l'Amérique méridionale no 2809". The old catalog from the Galerie d'Anatomie reads "*Nelomys* de l'Amérique méridionale crâne sans mâchoire".

5) A skull A7789, written on it is "[*Nelomys* de Blainville (*Nelomys blainvillei*)]. 2804". The old catalog entry reads "*Nelomys* de Blainville, *Nelomys Blainvillei* de Carthagène? Tête adulte". Carthagène (Cartagena) is in Colombia, so the locality is erroneous.

The above material belongs to two species: skins 1803, 1804 and skull A7788 are

consistent with one, while skull A7789 is a second. Skin no. 402 is of uncertain identification, but it could be the same species as 1803. The first general catalog at MNHN, in Anatomie, was begun in 1850, 12 years after Jourdan's description. Cuvier, in the *Laboratoire d'Anatomie Comparée*, was interested only in osteological material and customarily removed the skulls, then sent skins in lots, with no reference with which to match them to individual skulls, to the *Laboratoire de Zoologie (Mamifères et Oiseaux; M. Tranier, personal commun.)*. Several number series have been applied to each specimen (serial general catalogs, catalog of mounted specimens in the Grande Galerie, type catalogs, etc.), but there is no continuous record that permits indisputable identification of type material from this period (J. Cuisin, personal commun.). Skin no. 402 and skull no. A7789 have been recently labeled as the holotype material of *N. blainvillii*.

Isidore Geoffroy remarked that he had examined three similar specimens he ascribed to *N. blainvillii* (1840: 41): these may be the three skins listed above. His measurements, which he stated merely to be of one of the three, and not necessarily the holotype (HB = 24.0; T = 24.0) differ from Jourdan's (HB = 25.0, T = 20.0).

C. THE LYON SPECIMENS: Two specimens, a mounted skin with skull inside (MHNL40001298) and a skull with a mismatched mandible (MHNL50000747), are housed in the museum in Lyon, where Jourdan was a professor. We have not examined them, but photographs show them to be the same species as those in Geneva and London. Their location makes the specimens those most likely to have been seen by Jourdan himself; however, they have no documentation, and the handwritten catalog, with the entry "*Nelomys blainvillei*, Bahia" dates from the 20th century (Dr. Joël Clary, personal commun.).

D. THE LONDON SPECIMEN: The British Museum preserves a skin and mandible, BMNH 55.12.24.116, labeled as a cotype of *Nelomys blainvillei* [sic] ("coll. M. Blanchet, Bahia, I. de Dios"), which it acquired on May 22 1838 in exchange from F.-J. Pictet.

Designation of a lectotype: We designate as the lectotype of *P. blainvillii* Jourdan the

Geneva specimen, MHNG 250/19, a partially mounted skin with skull inside, because of its excellent documentation, unequivocally associated skin and skull, accessibility, and because contemporary documents unambiguously indicate that the material described by Jourdan was originally in Geneva. Paralectotypes include MNHG 324/1 (skull) and BMNH 55.12.24.116 (skin and mandible). The Paris specimens 1803, and skull A7788, and Lyon MHNL 40001298, and MHNL 50000747 lack documentary proof that they are paralectotypes although it is probable that they are.

TYPE LOCALITY: Jourdan stated that *P. blainvillii* "... a été tué dans une petite île sur les côtes du Brésil, près de Bahia." (Jourdan, 1837: 523), and Isidore Geoffroy (1840) further defined the type locality as "Brazil, near Bahia; the small island Deos, off the coast of Brazil, likewise near Bahia" (our translation). Later authors gave the locality as "Ilha de Deos". The source of this locality is apparently the catalog in Geneva, where the locality is poorly written and looks like Ilh Eos, which was later misinterpreted as "Ilha de Deos", but it probably was Ilhéus (fig. 7) and referred to the port town. Our recent review of nearly all extant specimens of *Phyllomys* spp. and major new collecting efforts by Y. Leite and L. Costa, show that: 1) there are no museum specimens of *P. blainvillii* from the coast of Bahia; 2) *P. blainvillii* is typically found in interior forests; and 3) all recent museum specimens of *Phyllomys* collected near Ilhéus belong to a different species. Blanchet obtained a number of specimens through a collector ("Gaucho Manoel") who made an inland journey with a documented route (Urban, 1895); we believe it is best to restrict the type locality to the place closest to Manoel's itinerary where specimens of *P. blainvillii* are known to occur. We therefore restrict the type locality to: Seabra, Bahia, Brazil, ca. 12°25'S 41°46'W (fig. 3, locality 2), where a series of specimens housed at the MNRJ were collected in the 1950s. Other taxa sent by Blanchet to Geneva, with the same locality, are also known only from inland Bahia, including *Trinomys albispinus* I. Geoffroy and *Thrichomys apereoides* Lund. This problem



Fig. 8. *Phyllomys blainvillii* (MZUSP 6147; ex-MNRJ 1518) from Crato, Ceará.

was recently discussed by Oliveira (1998), who reached the same conclusion in the context of a specimen of *Oxymycterus*.

DIAGNOSIS: A small- to medium-sized spe-

cies (table 1). Dorsal surface ochraceous-brown streaked with black, paler on sides. Aristiforms average 24 mm long and 1 mm wide, pale at the base, darker in the middle,

and orange near the thin, whiplike tip (fig. 4). Venter pale cream with a hint of yellowish overwash. Tail robust, usually slightly longer than head and body, thickly covered with long blackish-brown or gold hair forming a 15 mm, slightly wavy tuft at the tip (fig. 6). Tail darkens from base to tip, usually strongly contrasting with pale color of body. Cheekteeth narrow, palatine width larger than tooth width at M1, tooththrows slightly divergent at either end (fig. 8). Supraorbital ridges well developed. Interorbital region nearly straight, diverging posteriorly. Zygomatic arch slender, maximum height less than or equal to $\frac{1}{3}$ of jugal length. Postorbital process of zygoma usually spinose and formed by the jugal. Mastoid process short, extending to the horizontal midline of the external auditory meatus. Mesopterygoid fossa reaching anterior lamina of M3; narrow, forming an angle of about 45° . Incisive foramen ovate. Ventral root of the angular process of the mandible deflected laterally. Upper incisors orthodont.

SIMILAR SPECIES: *P. lamarum* and *P. blainvillii* are similar, medium-sized, drab yellow to yellow-brown spiny rats, but the former has a nearly naked tail and strong and visible spines, while the latter has inconspicuous spines and a longer, hairier tail with a long bushy tuft at tip (fig. 6). *P. blainvillii* also tends to be paler dorsally, with a darker tail. Compared to that of *P. lamarum*, the skull of *P. blainvillii* is longer and narrower, and appears more delicate, with smaller cheekteeth, a more slender zygomatic arch, relatively smaller bullae, and a narrower mesopterygoid fossa. The incisive foramen is smaller and slightly wider and the rostrum tends to be shorter in *P. lamarum*.

Phyllomys nigrispinus (Wagner, 1842)

Loncheres nigrispina Wagner, 1842: 361.

[*Loncheres* (*Loncheres*) *blainvillii*] *nigrispina*: Trouessart, 1881: 177 (as subspecies, name combination).

[*Loncheres* (*Loncheres*)] *nigrispina*: Trouessart, 1897: 604 (name combination).

[*Echimys* (*Echimys*)] *nigrispina*: Trouessart, 1904: 503 (name combination).

[*Nelomys*] *nigrispina*: Thomas, 1916b: 297 (name combination).

Echimys nigrispina: Tate, 1935: 432 (name combination).

Phyllomys nigrispina: Moojen, 1952: 141 (first use of current name combination).

Echimys (*Nelomys*) *nigrispinus*: Eisenberg and Redford, 1999: 488 (name combination).

TYPE MATERIAL: Holotype: NMW B 918, collected by Johann Natterer on 7 June 1819 (date fide von Pelzen, 1883), a male, field number JN 52. A skin, in good condition except tail-tip has been broken off and lost, the legs are bent under the body; no skull. Wagner attributed the name to Natterer.

TYPE LOCALITY: "Ypanema" (Wagner, 1842). The historical Ipanema Farm is now protected as a national forest. Amended locality: Floresta Nacional de Ipanema, 20 km NW Sorocaba, São Paulo, Brazil, $23^\circ 26' S$ $47^\circ 37' W$, elev. 550–970 m (fig. 3, locality 7).

REMARKS: The holotype of *P. nigrispinus* is a close match to animals from São Paulo that have been called by this species epithet in all recent and older works. We find no ambiguity in either the identity of the holotype or in assignment of recent specimens to the taxon (but see comments for *P. kerri* below).

DIAGNOSIS: A medium-sized species (table 1) exhibiting substantial morphological variation within and between populations. Dorsum reddish-brown streaked with black, clothed with relatively narrow (1 mm), medium-length (27 mm), black aristiform hairs, with thin, whiplike tips (fig. 4C). Ventral color extremely variable, ranging from buffy-white to yellowish-gray, hairs usually white at base. Palatine width equal to or larger than tooth width at M1, tooththrows parallel (fig. 9). Supraorbital ridges well developed, interorbital region diverging posteriorly; a postorbital process absent or inconspicuous. Zygomatic arch slender to moderately robust, maximum height between $\frac{1}{4}$ and $\frac{1}{3}$ of jugal length. Postorbital process of zygoma rounded or spinose, formed by jugal or both squamosal and jugal. Mastoid process long, extending below the horizontal midline of the external auditory meatus. Mesopterygoid fossa reaching last laminae of M2 or first of M3; wide, forming an angle of about 60° . Incisive foramen ovate. Ventral root of the angular process of mandible does not deflect laterally (fig. 5). Upper incisors slightly opisthodont.



Fig. 9. *Phyllomys nigrispinus* (MZUSP 175) from Itapetininga, São Paulo.

SIMILAR SPECIES: *Phyllomys kerri* and *P. nigrispinus* are extremely similar in skin and skull morphology and they may be conspecific. Their chief differences are that *P. kerri* has a predominantly orange ventral color, a shorter maxillary tooththrow, a broader rostrum, and a wider interorbital constriction than does *P. nigrispinus*. *Phyllomys nigrispinus* and *P. dasythrix* are similar in size and

color, but the former has well developed spines (fig. 4C), and the latter typically has a soft pelage (fig. 4D). The upper tooththrows are slightly closer to each other and the mastoid process tends to be shorter in *P. dasythrix*, not extending below the midline of the external auditory meatus. In addition, the zygomatic arch is more slender in *P. nigrispinus*. *Phyllomys thomasi* is very close to *P.*

nigrispinus in pelage color, but it is much larger (table 1).

Phyllomys unicolor (Wagner, 1842)

Loncheres unicolor Wagner, 1842: 361.

[*Loncheres (Loncheres) blainvillii*] *unicolor*: Trouessart, 1881: 177 (as subspecies, name combination).

[*Loncheres (Loncheres)*] *unicolor*: Trouessart, 1897: 604 (name combination).

[*Echimys (Echimys)*] *unicolor*: Trouessart, 1904: 503 (name combination).

Nelomys unicolor: Thomas, 1916b: 297 (name combination).

[*Echimys (Phyllomys)*] *unicolor*: Moojen, 1950: 491 (name combination).

Phyllomys unicolor: Moojen, 1952: 142 (first use of current name combination).

TYPE MATERIAL: Holotype: SMF 4319 (old catalog no. VII. T.4.a). Sex unlisted, collected by Johann Freyreiss. The specimen was added to the collection in 1824 by M. von Rothschild, and may have been collected earlier. A mounted skin; the skull, originally inside the mount, was removed and cleaned in 1998. The skin is faded and the skull was originally prepared like a bird mount with the occipital region cut off. The skull is damaged and has been restored by gluing. The skull and teeth are here described for the first time.

TYPE LOCALITY: Wagner (1842) gave only the locality "Brasilia", but the specimen label reads "Prov. Caravelas, Brasilien". Freyreiss was resident in "Leopoldina", today the town of Helvécia. We therefore restrict the type locality to Colônia Leopoldina (now Helvécia), 50 km SW Caravelas, Bahia, Brazil, 17°48'S 39°39'W, elev. 59 m (fig. 3, locality 3).

REMARKS: As noted by Tate (1935), the name *L. unicolor* first appeared in a published museum catalog as a nomen nudum (Rüppell, 1842; cited by Wagner), but the species was formally described later the same year by Wagner, who attributed the name to Rüppell. The type locality was not mentioned in the original description and it was long considered unknown (Cabrera, 1961; Woods, 1993), although it was published by Mertens (1925) and later by Moojen (1952), who correctly assigned the species to *Phyllomys*. Tate (1935) had placed it provisionally in Amazonia and classified it erroneously in his "naked-tailed" group of Amazonian *Echimys*,

although Wagner's description stated "cauda longius pilosa" (long hairy tail).

DIAGNOSIS: The following description is based on the holotype and only known specimen. A large *Phyllomys*, pelage of stiff narrow hairs, no spines at all, hairs short, of even length, less than 2.0 cm on dorsal mid-rump, of uniform color throughout their length. Thick fur on venter with hairs slightly less stiff than on dorsum. Originally described as uniform pale rusty red-brown dorsally ("dilute ferrugineo-brunea"), now faded but the right side of the specimen is still rusty, grading gradually to a buffy venter. There appears to be a pale collar from below the ear to the throat. Tail rust colored, with conspicuous lack of extension of dorsal pelage onto the base; completely covered with hairs quite long, about 0.5 cm, completely hiding scales and becoming longer and perhaps darker towards tip, now broken but apparently originally had a terminal tuft. Feet broad but not long (40.5 mm), with stout claws; yellowish above, unguis tufts to tip of claws, not extending beyond. Remaining mystacial vibrissae short, longest extends when flattened to base of neck, not to shoulder. Superciliary vibrissae to 2.0 cm, genal to 3.0 cm. Ear nearly naked, short (16.2 mm), with tuft on anterior rim. Cranium massively built, flat dorsally in lateral profile (fig. 10); cheekteeth large (maxillary toothrow length = 13.85), toothrows parallel, nasal bones wider distally than at base, rostrum short and robust; supraorbital ridges flared such that interorbital region is widest anteriorly (but supraorbital crests have been cut off). Zygomatic arches broader anteriorly than posteriorly, viewed dorsally. Jugals extremely broad dorsoventrally, jugal fossa deeply concave, with strong, beaded ventral lip; tip of fossa reaches anteriorly into the ventral, maxillary-jugal suture. Prominent foramen on lateral aspect of rostral premaxillary above incisor root. Auditory tympanic bullae conspicuously inflated; auditory tubes short due to this inflation; mastoid process extending to the lower edge of auditory meatus; meatus separated by a wide space from squamosal-mastoid suture. Mesopterygoid fossa reaching to level of posterior edge of first lamina of M3; angle of fossa wide, 60°. Incisive foramen ovate. Mandible without salient ventral pro-



Fig. 10. *Phyllomys unicolor* (SMF 4319, the holotype).

jection at posterior part of symphysis below premolar. Upper incisors broad, orange, orthodont. M3 with four laminae. Mandibular tooththrow at M2–3 without broad shelf on lingual side. Hypoflexids of M1–3 broad, square at internal tips; all posterolophids of P3 M1–2 broadly joined at labial side. Lower incisors strongly curved. Postorbital process of zygoma rounded, formed mainly by jugal. Ventral root of the angular process of mandible deflected laterally.

SIMILAR SPECIES: *Phyllomys unicolor* resembles *P. medius* in having a relatively soft fur but much shorter aristiforms. *Phyllomys unicolor* is larger than *P. medius* (table 1), and the two species have the following cranial differences: *P. medius* has a convex dorsal profile, small tympanic bullae, slender tooththrows, ventral root of angular process of mandible not deflected laterally, mesopterygoid fossa reaching forward to M2, and opisthodont upper incisors; while *P. unicolor* is cranially larger in all dimensions, has the ventral root of the angular process of mandible deflected laterally, a flat skull, inflated bullae, broad teeth, shorter mesopterygoid fossa, and orthodont incisors. *Phyllomys dasythrix* has soft fur similar to that of *P. unicolor* and *P. medius*, but it is a much smaller rat (table 1).

Because the holotype is the only known specimen, we cannot judge the range of variation of *P. unicolor*. The species is the second largest of the genus (table 1) and it has many features in common with *P. medius*. Its type locality is 600 km farther north than any recorded for *P. medius*, and it may represent an isolated peripheral population of the same clade. More specimens are needed before we can better define the relationships between these taxa.

Phyllomys dasythrix Hensel, 1872

Phyllomys dasythrix Hensel, 1872: 49, pl. 1, figs. 11 and 12.

[*Loncheres* (*Loncheres*)] *dasythrix*: Trouessart, 1881: 177 (name combination).

[*Echimys* (*Echimys*)] *dasythrix*: Trouessart, 1904: 503 (name combination).

[*Nelomys*] *dasythrix*: Thomas, 1916a: 240 (name combination).

Echimys dasythrix dasythrix: Cabrera, 1961: 540 (as subspecies).

Echimys (*Nelomys*) *dasythrix*: Eisenberg and Redford, 1999: 487 (name combination).

TYPE MATERIAL: No holotype was designated by Hensel (1872), but the series of syntypes that he mentioned in his description are extant in the museum where he deposited them. Hensel illustrated tooththrows of two individuals, ZMB 38797 (Hensel, 1872: figs. 11a, b) and ZMB 38798 (figs. 12a, b), but as the skulls of these are partly broken, we designate ZMB 38800 as the lectotype, a skull in perfect condition (fig. 12). ZMB 38794, 38795, 38796, 38797, 38798, 38799, 38801, 38802, 38803, 38804, and 11651, and BMNH 1.12.3.1 are paralectotypes.

TYPE LOCALITY: “Rio Grande do Sul, Süd-Brasiliens” (Hensel, 1872). Rio Grande do Sul, where Hensel collected his specimens, is the southernmost state in Brazil. Because . . . “from 1863–1866 he [Hensel] collected in Rio Grande do Sul, especially *Porto Alegre* [our italics] and the German colonies to the north of that city” (Papavero, 1971: 296), and A. Christoff recently collected specimens of *P. dasythrix* in the city of Porto Alegre, we restrict the type locality to: Porto Alegre, Rio Grande do Sul, Brazil, 30°04’S 51°07’W (fig. 3, locality 9).

DIAGNOSIS: A medium-sized species (table 1) with soft pelage. Aristiforms on rump long (26 mm) and very fine (approximately 0.2 mm), paler at the base and blackish distally, with thin whiplike tips (fig. 4D). Tail moderately covered with brown hairs; without a tuft. Cheekteeth large, palatine width usually less than tooth width at M1, and tooththrows parallel (fig. 11). Supraorbital ridges weakly developed, interorbital region slightly divergent posteriorly, sometimes with a small postorbital process. Zygomatic arch robust, maximum height approximately 1/3 of jugal length. Mastoid process short, extending to the horizontal midline of the external auditory meatus. Mesopterygoid fossa narrow, forms an angle of 45–60°, reaches last lamina of M2. Incisive foramen ovate. Ventral root of the angular process of mandible does not deflect laterally. Upper incisors orthodont.

SIMILAR SPECIES: See *P. nigrispinus* and *P. unicolor* above. *Phyllomys dasythrix* is similar to *P. medius* in pelage color and texture, since both have soft fur, but *P. dasythrix* is

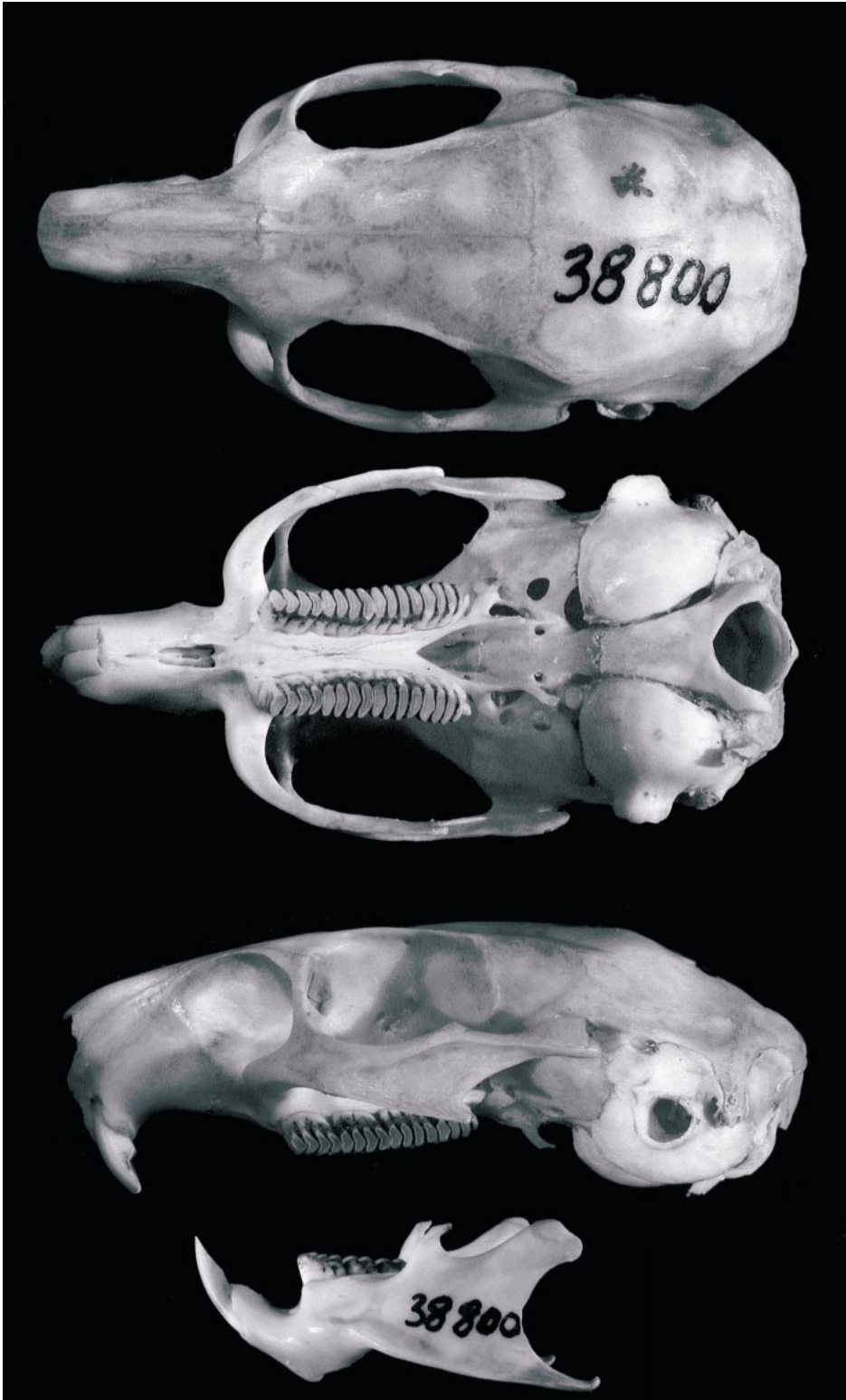


Fig. 11. *Phyllomys dasythrix* (ZMB 38800, the lectotype).

smaller (table 1) with shorter aristiforms (fig. 4D).

Phyllomys thomasi (Ihering, 1897)

Mesomys thomasi Ihering, 1897: 171.

Loncheres nigrispina: Ihering, 1898: 506 (part, not *Loncheres nigrispina* Wagner, 1842).

[*Euryzomatomys*] *thomasi*: Trouessart, 1904: 506 (name combination).

L.[oncheres] thomasi: Thomas, 1909: 239 (name combination).

[*Nelomys*] *thomasi*: Thomas, 1916a: 240 (name combination).

[*Echimys*] *thomasi*: Tate, 1935: 432 (name combination).

Phyllomys thomasi: Moojen, 1952: 138 (first use of current name combination).

Echimys blainvillei thomasi: Cabrera, 1961: 540 (as subspecies).

Echimys (Nelomys) thomasi: Eisenberg and Redford, 1999: 488 (name combination).

TYPE MATERIAL: No holotype was designated by von Ihering, although he stated he was describing the species from the first specimen he received. A series of 10 specimens collected by Bicego in 1896 are extant, 7 of them in MZUSP. We designate MZUSP 47 as the lectotype because it best matches von Ihering's description and original measurements (table 1). Specimens MZUSP 45, 51, 223, 526, 527, 532; FMNH 41360; BMNH 99.8.12.1, and 2.8.25.2, collected in 1896, are paralectotypes.

TYPE LOCALITY: "Ilha de São Sebastião" (Ihering, 1897). We amend this type locality as: Ilha de São Sebastião, São Paulo, Brazil, 23°46'S 45°21'W (fig. 3, locality 6). This is the largest continental island on the Brazilian coast and it is in São Paulo state, not Bahia as listed by Tate (1935), Cabrera (1961), and Woods (1993).

REMARKS: Ihering (1897) based his original description of *P. thomasi* on the fact that the only specimen he examined had no tail. After he inspected the remaining specimens collected in the original series, some with tails and some without, he decided his taxon was conspecific with *P. nigrispinus* (see Ihering, 1898). *Phyllomys thomasi* is however a giant species that is endemic to Ilha de São Sebastião, where it is the only *Phyllomys* species present.

DIAGNOSIS: The largest species in the genus (table 1). Unfortunately, no museum

specimens record external measurements. Olmos (1997) captured and released a female that measured 275 mm in head and body length, 270 mm in tail length, and weighed 432 gr. Dorsal pelage reddish-brown streaked with black, darker on middorsum. Venter cream to light gray, grading gradually from sides. Aristiforms on the rump long (33 mm), relatively narrow (0.7 mm), gray-brown proximally and black distally, with a thin whiplike tip (fig. 4E). Tail robust, covered with dark brown hair to its tip; no terminal tuft. Cheekteeth relatively wide, palatine width equal to or larger than tooth width at M1, toothrows parallel to slightly divergent posteriorly (fig. 12). Supraorbital ledges well-developed; interorbital region nearly parallel, with inconspicuous postorbital processes. Zygomatic arch robust, maximum height more than 1/3 of jugal length. Postorbital process of zygoma usually rounded, formed mainly by jugal. Mastoid process short, extending to the midline of the external auditory meatus. Mesopterygoid fossa wide, forming an angle of about 60°; reaches the posterior lamina of M2. Incisive foramen tear-drop shaped. Ventral root of the angular process of mandible does not deflect laterally. Upper incisors slightly opisthodont.

SIMILAR SPECIES: See *P. nigrispinus* above.

Phyllomys medius (Thomas, 1909)

Loncheres medius Thomas, 1909: 239.

[*Nelomys*] *medius*: Thomas, 1916a: 240 (name combination).

[*Echimys*] *medius*: Tate, 1935: 432 (name combination).

Phyllomys medius: Moojen, 1952: 138 (first use of current name combination).

Echimys blainvillei medius: Cabrera, 1961: 540 (as subspecies).

Echimys blainvillei: Woods, 1993: 791 (part, not *Nelomys blainvillii* Jourdan, 1837).

TYPE MATERIAL: Holotype: BMNH 3.4.1.84, an adult female, collected 18 September 1901 by A. Robert. A skin and skull with mandible, in good condition.

TYPE LOCALITY: "Roça Nova, Serro [sic] do Mar, Parana, S[outh]. Brazil. Alt. 1000 m" (Thomas, 1909). Thomas had previously described the locality as: "situated at an al-



Fig. 12. *Phyllomys thomasi* (MZUSP 47, the lectotype).

titude of about 1000 meters (1902; “930 to 1115” [his quotes]) in the Serro[sic] do Mar of the province of Paraná, and on the railway between Paranaguá and Curitiba”. We

amend this type locality as: Roça Nova, Serra do Mar, Paraná, Brazil, 25°28'S 49°01'W, elev. 1000 m (fig. 3, locality 8).

DIAGNOSIS: One of the largest species in



Fig. 13. *Phyllomys medius* (BMNH 3.7.1.84, the holotype).

the genus (table 1). Dorsal pelage stiff but relatively soft, dark brown sprinkled with black, darkest on middorsum. Aristiforms very long (39 mm), narrow (0.4 mm), black distally, with thin whiplike tip (fig. 4F). Ventral hair distinctly gray-based with fulvus tips. Skull robust and long; auditory tympanic bullae small; incisive foramen tear-drop shaped and small (fig. 13). Teeth narrow, palatine width equal to tooth width at M1; toothrows parallel. Supraorbital ledges well-developed, interorbital region parallel sided or divergent posteriorly, postorbital process absent or inconspicuous. Zygomatic arch robust, maximum height more than $\frac{1}{3}$ of jugal length. Postorbital process of zygoma spinose, formed mainly by jugal. Mastoid process short, extending to the horizontal midline of the external auditory meatus. Mesopterygoid fossa reaching the last lamina of M2 and narrow, forming an angle of about 45° . Ventral root of angular process of mandible does not deflect laterally. Upper incisors opisthodont.

SIMILAR SPECIES: Cabrera (1961) considered *P. medius* to be a subspecies of *P. blainvillii*, but the two species are not similar; however, *P. medius* is very like *P. unicolor*. See *P. unicolor*, *P. nigrispinus*, and *P. dasythrix*, above.

Phyllomys lamarum (Thomas, 1916)

Nelomys lamarum Thomas, 1916b: 297.

[*Echimys*] *lamarum*: Tate, 1935: 431 (name combination).

Phyllomys blainvillii: Moojen, 1952: 139, pl. 19 (not *Nelomys blainvillii* Jourdan, 1837).

Echimys dasythrix lamarum: Cabrera, 1961: 541 (as subspecies).

Echimys (*Nelomys*) *lamarum*: Eisenberg and Redford, 1999: 487 (name combination).

TYPE MATERIAL: Holotype: BMNH 3.9.5.96, an adult female collected by A. Robert, 4 March 1903. A museum skin and skull, both in excellent condition. The British Museum has 12 paratypes, and Thomas sent others to at least three museums: Paris (MNHN), Copenhagen (UZMC), and Chicago (FMNH).

TYPE LOCALITY: "Lamaraõ[sic], Bahia, about 70 miles N.W. of Bahia city [now Salvador]. Alt. 300 mm [sic]." (Thomas, 1916b). We amend it as: Lamarão, about 70

miles NW Salvador, Bahia, Brazil, $11^\circ 47' S$ $38^\circ 53' W$, elev. 300 m (fig. 3, locality 1).

REMARKS: When describing *P. lamarum*, Thomas (1916b) erroneously listed the collection date as "24th May, 1903" instead of 4 March 1903, as is written on the label. The external measurements he published also do not match those of the holotype, but those of a paratype: BMNH 3.9.5.99. The actual external measurements of the holotype according to the skin tag are: 225–216–35–13. This species has often been confused in collections with *P. blainvillii*, perhaps because of their similar, pale coloration; for example, as Moojen (1952) described them, he had the two species reversed. There are a number of specimens apart from the type series: all are highly uniform in appearance and present no taxonomic problems.

DIAGNOSIS: A small- to medium-sized species (table 1) with conspicuous spines. Dorsum yellow-brown with a speckled pattern given by the short (24 mm), broad (1.3 mm) aristiforms (fig. 4G). Spines pale at base, darkening towards tip where they become orange, ending in dark, thin, whiplike tips. Venter pale brown with white patches, to pure white, with fulvus lateral line. Tail relatively slender, slightly shorter than or equal to head and body, thinly covered with pale brown hairs, scales visible to the eye along entire length. Cheekteeth wide, palatine width equal to or shorter than tooth width at M1, toothrows slightly divergent at either end (fig. 14). Supraorbital ledges well developed. Interorbital region almost straight, diverging posteriorly, postorbital process absent or inconspicuous. Zygomatic arch relatively robust, maximum height less than or equal to $\frac{1}{3}$ of jugal length. Postorbital process of zygoma spinose, usually with no contribution from squamosal. Mastoid process short, extending to midline of external auditory meatus. Mesopterygoid fossa reaching last lamina of M2; wide, forming an angle of more than 60° . Incisive foramen ovate. Ventral root of angular process deflected laterally. Ventral spine present near posterior junction of mandibular rami. Upper incisors orthodont.

SIMILAR SPECIES: See *P. blainvillii* and *P. brasiliensis*, above.



Fig. 14. *Phyllomys lamarum* (BMNH 3.9.5.96, the holotype).

Phyllomys kerri (Moojen, 1950)

Echimys (Phyllomys) kerri Moojen, 1950: 489, figs. 1–5.

Phyllomys kerri: Moojen, 1952: 142 (first use of current name combination).

Echimys kerri: Vieira, 1955: 437 (name combination).

Nelomys kerrei: Emmons and Feer, 1990: 274 (name combination and subsequent incorrect spelling).

TYPE MATERIAL: Holotype: MNRJ 6241, collected 13 June 1941 by G. Dutra. An adult female, skin prepared as a museum specimen and skull, both in good condition.

TYPE LOCALITY: “Ubatuba, S[ão]. Paulo, Brasil” (Moojen, 1950). The skin tag gives locality as: “Estação Experimental, Ubatuba”, which was not mentioned in the original description. We therefore restrict the type locality to: Estação Experimental de Ubatuba, Ubatuba, São Paulo, Brazil, 23°25'S 45°07'W (fig. 3, locality 5).

REMARKS: *Phyllomys kerri* is so similar to *P. nigrispinus* that we had difficulty finding diagnostic characters, but we hesitate to synonymize it until more specimens become available and its genetics can be carefully examined. Moojen (1950) considered it to be closest to *P. unicolor* and compared it only with that species, of which he stated that he had a male specimen. Other than the original description of *unicolor* as rust colored, we find no similarities between the two, and we have found no other *P. unicolor* specimen than the holotype.

DIAGNOSIS: A medium-sized species (table 1). Dorsum reddish-brown streaked with black. Aristiform hairs on rump black, 24 mm in length and 1 mm in width, with thin, whiplike tips. Ventral color yellowish-orange, hairs usually gray at base. Skull long and narrow, palatine width equal to or larger than tooth width at M1, toothrows nearly parallel (fig. 15). Supraorbital ridges well-developed, interorbital region diverging posteriorly, with an inconspicuous postorbital process. Zygomatic arch robust, maximum height approximately $\frac{1}{3}$ of jugal length. Postorbital process of zygoma spinose, formed mainly by jugal. Mastoid process short, reaching horizontal midline of external auditory meatus. Mesopterygoid fossa reaching last laminae in M2; wide, forming an angle

of nearly 60°. Incisive foramen ovate. Ventral root of angular process of mandible does not deflect laterally. Upper incisors slightly opisthodont.

SIMILAR SPECIES: See *P. nigrispinus* above.

THE RUSTY-SIDED ATLANTIC TREE RAT

After examining the type material collected by Peter W. Lund at Lagoa Santa, Minas Gerais, we concluded that a species quite common in museum collections, frequently misidentified in the literature as *Phyllomys brasiliensis* (e.g., in Thomas, 1916; Moojen, 1952), is distinct from that species. It was described in Emmons and Feer (1990, 1997) as the rusty-sided Atlantic tree rat, “*Nelomys* sp.” We have discovered no formal name that can be applied to it, and we name and describe it here.

SPECIMENS AND GAZETTEER

We examined 61 specimens of the species we describe below, housed at BMNH, MBML, MNRJ, MZUSP, MVZ, UFPB, UFV, and UZMC. We also examined uncataloged specimens collected by Yuri Leite (YL), Leonora P. Costa (LC), and Gustavo A. B. da Fonseca (GABF), to be deposited at UFMG; Alfredo Langguth (AL) to be deposited at UFPB; and Helena G. Bergallo (HGB), Lena Geise and Rui Cerqueira (initials FS, IG), to be deposited at MNRJ. Specimens are listed by locality, from north to south. Numbers correspond to numbered localities in figure 16. **Estado da Paraíba:** 1) João Pessoa, próximo ao NUPPA, 07°07'S 34°52'W (UFPB 774). **Estado de Pernambuco:** 2) Dois Irmãos, Recife, 08°03'S 34°54'W (MNRJ 8195). **Estado da Bahia:** 3) Fazenda Almada, Ilhéus, 14°39'16"S 39°11'25"W (MNRJ 11253); 4) Aritaguá-Urucutuca, Ilhéus, 14°39'28"S 39°07'31"W (MNRJ 21517); 5) Fazenda Pirataquicê, Ilhéus, 14°50'S 39°05'W (MNRJ 10452, 10453, 11251, 11256, 11257, 11258); 6) Itabuna, 14°48'S 39°16'W (MNRJ 33515); 7) Mata Fortuna, Itabuna, 14°57'S 39°19'W (MNRJ 11254); 8) São Felipe, 14°49'S 41°23'W (MNRJ 22264, 22265); 9) Mangue do Caritoti, Caravelas, Bahia, Brazil, 17°43'30"S 39°15'35"W; at sea level (MNRJ 62391, YL 195, 196); 10) Fazenda Monte Castelo, Ilha da Cassumba, 7



Fig. 15. *Phyllomys kerri* (MNRJ 6241, the holotype; mandible photo reversed).

km SW Caravelas, Bahia, Brazil 17°48'06"S 39°15'49"W (YL 198, 199, 200, 201); **11**) Helvécia, Nova Viçosa, 17°48'30"S 39°39'49"W (HGB 36). **Estado do Espírito Santo:** **12**) Fazenda Santa Terezinha, 33 km NE Linhares, 19°08'S 39°57'W, 50 m (LC

32); **13**) Rio São José, 19°10'S 40°12'W (MNRJ 8276); **14**) Povoação, Linhares, 19°37'S 39°49'W (MBML 1856); **15**) Estação Biológica de Santa Lúcia, Santa Teresa, 19°57'S 40°31'W, 600–900 m (MBML 2011, 2032, 2047); **16**) Reserva Biológica de Duas

Bocas, Cariacica, 20°17'S 40°28'W (MBML 226); **17**) Mata da Torre, Vitória, 20°19'S 40°21'W (MBML 162); **17**) Parque Estadual da Fonte Grande, Vitória, 20°19'S 40°21'W (MBML 316); **18**) Hotel Fazenda Monte Verde, 24 km SE Venda Nova do Imigrante, 20°20'S 41°08'W (UFPB 346). **Estado de Minas Gerais:** **19**) Fazenda Montes Claros, Caratinga, 19°50'S 41°50'W, (GABF 97P); **20**) Silvicultura, Viçosa, 20°45'S 42°53'W (UFV 379); **21**) Mata Paraíso, Viçosa, 20°48'18"S 42°51'32"W, 750 m (UFV 385, 696); **22**) Fazenda Paraíso, Além Paraíba, 21°52'S 42°41'W (MNRJ 10454); **22**) Fazenda São Geraldo, Além Paraíba, 21°52'S 42°41'W (MNRJ 4077). **Estado do Rio de Janeiro:** **23**) Fazenda São José da Serra, 6 km E, 9.2 km N (by rd.), Bonsucesso, Sumidouro, 22°12'S 42°44'W, 1000 m (MVZ 183139); **24**) Nova Friburgo, 22°16'S 42°32'W (MNRJ 31564, 31567); **25**) Fazenda União, Casimiro de Abreu, 22°29'S 42°12'W (MNRJ 42978); **26**) Fazenda Alpina, Teresópolis, 22°25'S 42°50'W (MNRJ 1933); **27**) Fazenda Rosimery, Município de Cachoeiras de Macacu, 22°29'S 42°51'W (FS 11–52); **28**) Teresópolis, 22°26'S 42°59'W (MNRJ 2232, 2237, 2239, 2240); **29**) Saco de São Francisco, Niterói, 22°55'S 43°06'W (MNRJ 6449); **30**) Tijuca, Trapicheiro, Rio de Janeiro, 22°57'S 43°17'W (MNRJ 11252); **31**) Monte São Francisco, Jacarepaguá, Rio de Janeiro, 22°55'S 43°21'W (BMNH 5.4.16.4, 5.4.16.5); **32**) Santa Cruz, estrada Rio-Petrópolis, 22°39'S 43°17'W (MNRJ 21508); **33**) Ilha Grande, 23°09'S 44°14'W (MNRJ 31562, 31566, MZUSP 26718); **33**) Vila Dois Rios, Ilha Grande, 23°09'S 44°14'W (IG 34). **Estado de São Paulo:** **34**) Piquete, 22°36'S 45°11'W (MZUSP 138). **Brazil** (no specific locality): BMNH 51.7.21.25; BMNH 61.12.2.4; UZMC 600. This last specimen was collected by Brandt in 1843 and may be the earliest preserved individual.

Phyllomys pattoni, new species

Loncheres armatus: Burmeister, 1854: 196 (part; not *Nelomys armatus* I. Geoffroy, 1838).

Nelomys brasiliensis: Thomas, 1916b: 297 (not *Phyllomys brasiliensis* Lund, 1840c).

Phyllomys brasiliensis: Moojen, 1952: 141 (not *Phyllomys brasiliensis* Lund, 1840c).

Nelomys sp.: Emmons and Feer, 1990: 220 (“rusty-sided tree rat”).

HOLOTYPE: MNRJ 62391, an adult female collected by Yuri Leite (original number 197) on 14 April 1998. It consists of a study skin, skull, carcass fixed in formalin and preserved in 70% ethanol, and liver sample in 95% ethanol. Table 2 lists selected body and skull measurements of the holotype and adult paratypes.

TYPE LOCALITY: Mangue do Caritoti, Caravelas, Bahia, Brazil, 17°43'30"S 39°15'35"W; at sea level (fig. 16, locality 9).

PARATYPES: There are six paratypes: two from the type locality, YL 195 and YL 196, and four others collected at Fazenda Monte Castelo, Ilha da Cassumba, 7 km SW Caravelas, Bahia, Brazil 17°48'06"S 39°15'49"W (fig. 16, locality 10): YL 198, 199, 200, 201. All consist of study skin, skull, carcass fixed in formalin and preserved in 70% ethanol, and liver sample in 95% ethanol; except YL 195, which is a whole animal fixed in formalin and preserved in 70% ethanol, with liver sample removed and fixed in 95% ethanol. The paratypes will be deposited in MZUSP (YL198, 199, 200, 201), MVZ (YL195), and USNM (YL196).

DISTRIBUTION AND HABITAT: *Phyllomys pattoni* is found chiefly along the coast from the state of Paraíba, northeastern Brazil, to the NE corner of the state of São Paulo, in the southeast; it occurs inland only in Bahia and the eastern portion of the state of Minas Gerais, east of the Rio Doce (fig. 16). It is recorded from sea level to 1000 m elevation, in rainforests and associated coastal habitats such as mangroves. Most of the type series were collected by day, when they were in nests of leaves and twigs in treeholes. They were collected near the town of Caravelas, in areas dominated by mangroves, with sparse, short vegetation (ca. 4 m) and abundant terrestrial and arboreal bromeliads and many palm trees. Laemmert et al. (1946) reported *P. pattoni* (as “*P. brasiliensis*”) from “Old- or primary-type forest” near Ilhéus in southern Bahia (fig. 16, localities 5, 7). They characterized the primary forest as having:

a greater variety of species, and fewer components of each species, while the . . . young-type forest is not so rich in variety of species, but contains proportionally greater numbers of the species present. In addi-

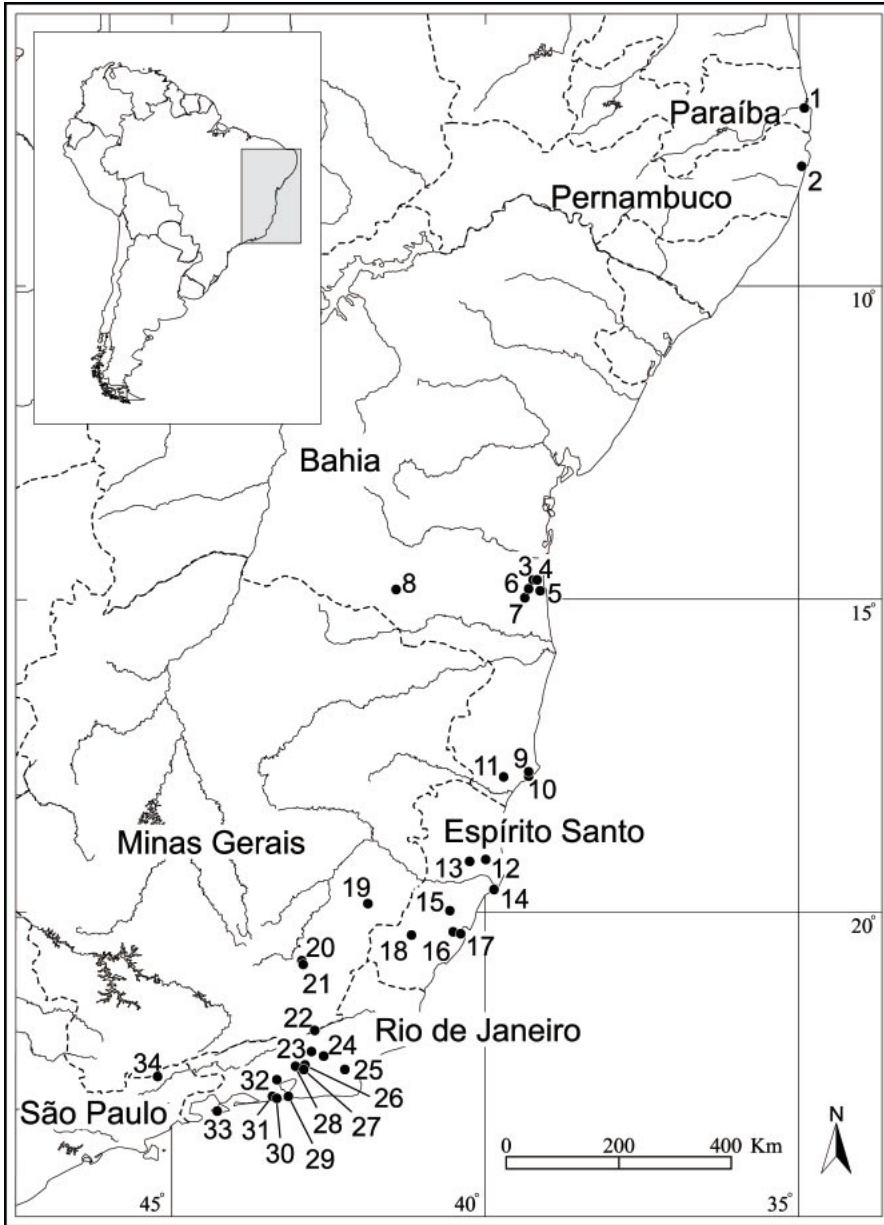


Fig. 16. Map of eastern Brazil showing collecting localities for *P. pattoni*. Numbers correspond to numbered localities in the text.

tion the older forests have a highly and usually more homogeneous and denser canopy of foliage, which creates a more effective shade with the stunting or elimination of undergrowth. Another feature which characterizes and affects the environment in the older forests is the abundance of lianas and epiphytes in or immediately below the foliage canopy.

Fazenda Santa Terezinha, in northern Es-

pírito Santo (fig. 16, locality 12) is a typical lowland primary forest on a sandy-soil coastal plain, with sparse understory, large trees, epiphytes, palm trees, few lianas, and a canopy that reaches 25 m. Recent selective logging is the main disturbance in this small area (ca. 400 ha.), which is contiguous to two

large protected areas: Linhares Forest Reserve (ca. 22,000 ha.) and Sooretama Biological Reserve (ca. 24,000 ha.). At Fazenda Montes Claros (fig. 16, locality 19; 860 ha. of forest), *P. pattoni* was collected in a primary forest with average canopy height of 19 m, tall buttressed emergents, sparse herbaceous stratum, and well developed mid-story (Fonseca and Kierulff, 1989). At Mata Paraíso (fig. 16, locality 21; 192 ha.), a specimen (UFV 696) was collected in a second-growth riparian forest with tall trees (reaching ca. 20 m), dense understory, some palm trees (*Euterpe edulis*), and relatively abundant heliconias (R. Ribón, personal commun.).

ETYMOLOGY: Named in honor of James L. Patton, in recognition of his remarkable contributions to knowledge of the evolution and systematics of Neotropical mammals, especially toward understanding the diversification of echimyid rodents.

DIAGNOSIS: The most heavily spined tree rat in the genus. Dorsal spines light gray at the base, gradually darkening toward black medially, terminating in an orange tip. Most aristiforms on rump lack the characteristic whiplike tip present in all other species of *Phyllomys* (fig. 4H). Dorsum dark brown, with a speckled aspect given by the rusty-tipped spines. Spines conspicuous from the tail base to the head, but longest and most abundant on the rump. Tail slightly shorter to slightly longer than head and body length and covered with fine hair not hiding the scales. Skull robust and relatively broad (fig. 17). Supraorbital ledges well developed, beaded, and extending beyond the postorbital ridge onto the squamosal. Incisive foramen bullet-shaped and long, extending from the base to the midline of the rostrum in ventral view.

KARYOTYPE: Zanchin (1988) reported $2n = 80$ for a specimen of *P. pattoni* (AL 2398 = UFPB 346) identified as "*Echimyis* sp.", collected in the state of Espírito Santo, and Severo (1998) recorded $2n = 80$, FN = 112 for the same specimen, identifying it as "*Echimyis thomasi*". According to L. Geise (personal commun.), specimens from the state of Rio de Janeiro (MNRJ 42978, FS 11–52) have $2n = 72$, FN = 114.

DESCRIPTION: External features—Medium-

sized, heavily-spined tree rat. Dorsum blackish-brown, speckled with rusty-tipped spines. Aristiforms on rump robust, approximately 1 mm wide and 20–25 mm long; most with a blunt tip (fig. 4H). Spines dark on edges; nearly transparent at the base, gradually darkening to blackish-brown medially, tip distinctly orange. Older animals tend to have more orange-tipped aristiforms, especially on the sides for which it was called the rusty-sided Atlantic tree rat by Emmons and Feer (1990, 1997). Young animals are very spiny. Setiforms gray-brown at the base and orange distally, with a short black tip. Setiforms are not evident on the rump, where most are hidden by the aristiforms. Ventral hairs short (5 cm), stiff, varying from cream-white to gray-white. Pure white patches are common on the venter around the throat, chest, and axillary and inguinal regions; some individuals have a continuous narrow white midline extending from the throat to the genitals. External nose, eyelids, and pinna blackish. Pinna thinly covered with fine, dark-brown and black hairs, with 5 mm-long aristiforms abundant near tragus. Mystacial vibrissae long, the longest reaching 6–7 cm. Most emerge in pairs from a single pore: a black, thinner and shorter one and a dark-brown, thicker and longer one. Genal vibrissae blackish-brown, the longest reaching 5 cm; supraciliary vibrissae black, the longest reaching 5 cm. Fore- and hind feet covered dorsally with silver and cream-white hairs. White unguis tufts reach, but rarely exceed claw length. Forefoot with three interdigital pads and coalesced metacarpal pads. Hind foot with four interdigital pads and independent thenar and hypothenar pads. All pads on both hind- and forefeet are surrounded by a ring of small tubercles. Tail gray-brown, darker dorsally, covered with hexagonal scales. Three hairs emerge distally from each scale: a longer and thicker medial one and two shorter and thinner lateral ones. Those hairs are shorter near the base (3.5 mm) lengthening near the tip of the tail where they can reach 2 cm.

Cranium—Skull robust and relatively wide (fig. 17). Rostrum wide; nasal bones widen gradually toward anterior end in dorsal view. Interorbital region diverging posteriorly, with or often without a small postorbital process. Supraorbital ridges well developed, extend-



Fig. 17. *Phyllomys pattoni* (MNRJ 62391, the holotype; original number YL 197). Scale bar = 5 mm.

TABLE 2
 Selected Body and Skull Measurements (in millimeters) of the Holotype and Four Adult Paratypes
 of *Phyllomys pattoni*
 Abbreviations of measurements as in table 1

	Holotype	Paratypes			
	MNRJ 62391 ♀	YL 196 ♀	YL 198 ♂	YL 199 ♂	YL 200 ♀
Total length	409	420 ^a	464	230 ^a	240 ^a
TAIL	200	190 ^a	223	0 ^a	0 ^a
HF	40	41	42	42	42
EAR	16	16	17	18	17
GLS	49.63	54.58	55.04	53.01	55.48
NL	14.57	17.58	16.88	16.94	18.19
RL	17.76	20.82	20.33	19.7	20.48
OL	13.73	14.07	14.84	14.03	14.14
RB	8.17	8.99	9.83	8.79	9.08
IOC	11.81	13.43	13.35	12.89	13.23
MB	21.2	21.25	22.87	21.01	22.72
ZB	24.21	26.36	27.01	25.17	26.32
CIL	44.82	48.38	49.71	47.03	49.6
BaL	39.09	41.99	42.95	40.73	43.76
D	11.12	12.06	13.17	11.4	13.54
MTRL	11.55	11.57	11.64	12.14	11.96
PLb	8.98	9.67	9.25	9.95	9.93
IFL	4.63	4.47	5.12	4.76	5.56
BuL	10.71	10.82	12.19	11.83	11.8
PLa	19.92	21.58	21.79	20.82	22.95
PPL	18.94	21.04	21.09	20.65	20.64
MPF	3.6	3.82	4.44	4.06	4.05
MaxB	8.24	7.72	8.02	7.62	8.64
Occw	9.15	9.4	9.56	8.79	9.54
RD	11.21	11.54	12.32	12.14	12.38
CDM1	14.34	14.78	15.94	14.89	15.79
CD	17.58	21.15	19.67	20.83	18.31

^a Incomplete measurements since tail was naturally broken.

ing posteriorly beyond the postorbital ridge and the frontoparietal suture. Zygomatic arch robust, maximum height approximately $\frac{1}{3}$ jugal length. Postorbital process of zygomatic arch prominent and formed by jugal and squamosal. Lateral jugal fossa deep, originating anteriorly at suture between maxillary and jugal. Suture between jugal and maxillary trapezoidal. Upper incisors orthodont. Lateral margin of the infraorbital foramen forming an angle of 45° to the sagittal plane. Incisive foramen narrow and long, extending from base to midline of rostrum in ventral view; bullet-shaped. Posterolateral margins of incisive foramina flanged with deep grooves extending onto anterior palate, with

a sharp medial ridge. Mesopterygoid fossa wide, forming an angle of nearly 90° , its point reaches anterior lamina in M3 or posterior lamina of M2. Tooththrows slightly divergent posteriorly, palatine width larger than tooth width at M1. All upper molars have four transverse laminae. Upper premolar narrower than molars. Laminar width decreases anteriorly on upper premolar and posteriorly on last molar. Medial flexus often deeper than other two in all cheekteeth. Bullae inflated, with a relatively long tympanic duct. Mastoid process long, extends beyond horizontal midline of external auditory meatus. Occipital and lambdoidal crests well developed. Occipital squared in posterior view,

interparietal not evident. Mandible strong, inferior masseteric fossa well developed. Coronoid and condyloid processes reach approximately the same height. Coronoid process deflected laterally. Ventral root of angular process deflected laterally.

COMPARISONS WITH OTHER SPECIES: *Phyllomys pattoni* has been confused with *P. brasiliensis* for over a century. Although both species share some characters, such as a robust body and skull, they differ strikingly in several other characteristics. The dorsum of *P. brasiliensis* is covered with strong and wide aristiforms, but these have a whiplike tip as in all other *Phyllomys* but *P. pattoni*, and they are largely hidden by orange tipped setiforms, so that *P. brasiliensis* lacks the speckled aspect of *P. pattoni*. Even young *P. pattoni* have strong spines, unlike young of other *Phyllomys* species, which tend to have soft pelage. The skull of *P. pattoni* has longer incisive foramina that are wider proximally than those of *P. brasiliensis*. Externally, *P. pattoni* resembles *P. lamarum*, in that both have a nearly naked tail and a dorsum speckled by orange tipped aristiforms, but the rump aristiforms of *P. lamarum* have the more typical whiplike tips, and *P. lamarum* has more abundant dorsal setiforms and a body color usually paler than that of *P. pattoni*, where the setiforms are hidden by aristiforms. The skull of *P. pattoni* is of similar shape, but larger, wider, and more robust than that of *P. lamarum*, with more marked crests and ridges, such as the supraorbital and lambdoidal. The skull of *P. lamarum* is narrower and more delicate, with smoother angles (fig. 14). The rostrum of *P. pattoni* is larger than that of *P. lamarum*, with longer and wider incisive foramina. The nasal bones of *P. pattoni* widen gradually anteriorly so that their lateral edges are straight in dorsal view; those of *P. lamarum* have a medial constriction; while those of *P. brasiliensis* are parallel-sided proximally, and diverge distally in dorsal view. Another species, *P. unicolor* Wagner, is known from the region of Caravelas, Bahia, but it bears little resemblance to *P. pattoni*. *Phyllomys unicolor* is large, rust colored, has harsh fur but no spines, and its tail is densely furred, whereas *P. pattoni* is heavily spined, with a tail that appears thinly furred and scaly. The cranium

of *P. unicolor* is characterized by greatly inflated auditory tympanic bullae.

Phyllomys pattoni is distinct from all others in terms of morphology, as shown above. In addition, Leite (2001) found substantial genetic differentiation (more than 10%) in DNA sequences of the mitochondrial cytochrome b gene between *P. pattoni* and other taxa, providing support for the significance of the morphological differences presented here. The phylogenetic position of *P. pattoni* is not clear, but it seems to represent one of the oldest lineages within the genus, perhaps the sister group to all other extant forms (Leite, 2001).

REMARKS: This species has been called "*Phyllomys brasiliensis*" in the literature (e.g., Moojen, 1952). Burmeister (1854) was apparently the first author to publish a description of *P. pattoni*. He arrived in Rio de Janeiro in 1850 and went on an expedition to Lagoa Santa, Minas Gerais, where he spent 5 months with Lund and Reinhardt. At Nova Friburgo, his son collected a specimen that matches the description given above. This animal was described in his book (Burmeister, 1854: 196), where he called it "*Loncheres armatus*", associating it with a specimen collected by Natterer in Mato Grosso (a *Makalata didelphoides*). Thomas (1916b) provisionally used the name *brasiliensis* for the specimens of the "Rio de Janeiro region", and was followed by subsequent authors.

CONCLUSIONS

Our investigations of members of the genus *Phyllomys* have revealed all of the named taxa to be valid species with distinctive sets of characters (table 3, species key), but further studies are needed of several species currently represented by few specimens, including *P. unicolor*, *P. dasythrix*, and *P. kerri*. Moreover, among the fossil and subfossil material collected by Lund at Lagoa Santa there are at least two other species that may or may not be the same as currently recognized living forms. The genus comprises a large radiation of species endemic to the eastern forests of Brazil. Forests within the range of members of the genus are greatly reduced and highly fragmented. One species, *P. unicolor*, known only from the holotype

TABLE 3
Selected Characters of Species of *Phyllomys*

Character	<i>P. brasiliensis</i>	<i>P. blainvillii</i>	<i>P. nigripinus</i>	<i>P. unicolor</i>	<i>P. dasythrix</i>
Body-size (greatest skull length)	medium (49–52 mm)	small-medium (47–49 mm)	medium (49–51 mm)	large (? × ? mm)	small-medium (47–51 mm)
Aristiform hairs on rump	medium length, wide (27 × 1.3 mm)	medium length, narrow (24 × 1 mm)	medium length, narrow (27 × 1 mm)	short, thin (20 × ? mm)	medium length, thin (26 × 0.2 mm)
Aristiform tip	whiplike, orange	whiplike, orange	whiplike, black	whiplike, black	whiplike, black
Tail	length ≈HB, nearly naked, tufted tip	length ≥HB, thickly haired, tufted tip	length ≥HB, hairy, no tuft	hairy, tufted tip?	length > HB, hairy, no tuft
Palatine width at M1	≈tooth width	> tooth width	≥tooth width	≤tooth width	< tooth width
Maxillary toothrows	parallel	slightly divergent at either end	parallel	parallel	parallel
Supraorbital ridges	well developed, beaded	well developed	well developed	well developed	weakly developed
Interorbital region	divergent posteriorly	divergent posteriorly	divergent posteriorly	convergent posteriorly?	divergent posteriorly
Postorbital process	present	absent or inconspicuous	absent or inconspicuous ?		inconspicuous
Zygomatic arch	height ≤1/3 jugal length	height ≤1/3 jugal length	height 1/3–1/4 jugal length	height 1/3 jugal length	height ≈1/3 jugal length
Postorbital process of zygoma	spinose, formed by jugal only	usually spinose, formed mainly by jugal	rounded or spinose, formed by jugal or squamosal and jugal	?	rounded or spinose, formed by jugal or squamosal and jugal
Mastoid process	long, extending below midline of EAM ^a	short, extending to midline of EAM	long, extending below midline of EAM	long, extending below midline of EAM	short, extending to midline of EAM
Mesopterygoid fossa	wide, to M2	narrow, to M3	wide, to M2 or M3	wide, to M3	narrow, to M2
Incisive foramen	ovate	ovate	ovate	ovate,	ovate
Ventral root of angular process	deflected laterally	deflected laterally	not deflected laterally	?	not deflected laterally
Ventral mandibular spine	present	absent	absent	absent	absent
Upper incisors	orthodont	orthodont	slightly opisthodont	orthodont	orthodont

collected in 1824 or earlier, was not found during recent extensive collecting efforts, and it might therefore be extinct.

The new species described here, *Phyllomys pattoni*, seems to have a broad habitat tolerance and a relatively large geographic range for members of its genus. Several recent specimens have been collected in protected areas that are adjacent to large forest reserves; the species conservation status would thus appear to be good. On the other hand, remaining populations of most species of *Phyllomys* may be small and patchily distributed. We urge all

naturalists to preserve and record information and specimens that come to hand, and likewise to identify which species are present in protected areas, so that the distribution and status of Atlantic tree rats can become better known and conservation measures can be undertaken where needed.

KEY TO SPECIES OF *PHYLLOMYS*
Specimens of undescribed species can not be identified with the key below.

1. Aristiforms on rump ending in a blunt tip *P. pattoni*

TABLE 3
(Continued)

Character	<i>P. thomasi</i>	<i>P. medius</i>	<i>P. lamarum</i>	<i>P. kerri</i>	<i>P. pattoni</i>
Body-size (greatest skull length)	very large (56–62 mm)	medium-large (50–55 mm)	small-medium (46–48 mm)	medium (51 mm)	medium (49–51 mm)
Aristiform hairs on rump	long, narrow (33 × 0.7 mm)	very long, thin (39 × 0.4 mm)	med. length, wide (24 × 1.3 mm)	med. length, narrow (24 × 1 mm)	med. length, narrow (23 × 1 mm)
Aristiform tip	whiplike, black	whiplike, black	whiplike, orange	whiplike, black	blunt, orange
Tail	length ≈HB, hairy, no tuft	length ≥HB, hairy, no tuft	length ≈HB, nearly naked, no tuft	length ≥HB, hairy, no tuft	length ≈HB, nearly naked, no tuft
Palatine width at M1	≥tooth width	≈tooth width	≤toothwidth	≥tooth width	≥tooth width
Maxillary tooththrows	parallel	parallel	slightly divergent at either end	parallel	slightly divergent posteriorly
Supraorbital ridges	well developed	well developed	well developed	well developed	well developed, beaded
Interorbital region	parallel sided	divergent posteriorly or parallel sided	divergent posteriorly	divergent posteriorly	divergent posteriorly
Postorbital process	inconspicuous	absent or inconspicuous	absent or inconspicuous	inconspicuous	absent
Zygomatic arch	height > 1/3 jugal length	height > 1/3 jugal length	height ≤1/3 jugal length	height ≈1/3 jugal length	height ≈1/3 jugal length
Postorbital process of zygoma	usually rounded, formed mainly by jugal	spinose, formed mainly by jugal	spinose, usually formed by jugal only	spinose, formed mainly by jugal	spinose, formed by jugal and squamosa
Mastoid process	short, extending to midline of EAM	short, extending to midline of EAM	short, extending to midline of EAM	short, extending to midline of EAM	long, extending below midline of EAM
Mesopterygoid fossa	wide, to M2	narrow, to M2	wide, to M2	wide, to M2	wide, to M2
Incisive foramen	tear-drop shaped	tear-drop shaped	ovate	ovate	bullet shaped
Ventral root of angular process	not deflected laterally	not deflected laterally	deflected laterally	not deflected laterally	deflected laterally
Ventral mandibular spine	absent	absent	present	absent	absent
Upper incisors	slightly opisthodont	opisthodont	orthodont	slightly opisthodont	orthodont

^a EAM = External auditory meatus.

- Aristiforms on rump ending in a whiplike tip 2
- 2. Aristiforms on rump black-tipped 3
- Aristiforms on rump orange-tipped 8
- 3. Large: head and body length above 290 mm, greatest skull length more than 56 mm; endemic to island of São Sebastião, off the coast of São Paulo *P. thomasi*
- Medium to small: head and body length below 290 mm, greatest skull length less than 56 mm 4
- 4. Spines conspicuous: aristiforms on rump more than 0.7 mm wide 5
- Spines inconspicuous or absent: aristiforms on rump less than 0.5 mm wide 6
- 5. Longer maxillary tooththrow (length > 11.5 mm); narrower rostrum (rostral breadth < 8 mm) and interorbital constriction (< 11.5 mm) *P. nigrispinus*

- Shorter maxillary tooththrow (length < 11.5 mm); broader rostrum (rostral breadth > 8 mm) and interorbital constriction (> 11.5 mm) *P. kerri*
- 6. Longer pelage: aristiforms on rump more than 26 mm in length, larger body size: head and body length more than 215 mm, hindfoot length more than 40 mm, occipital more than 8.2 mm wide *P. medius*
- Shorter pelage: aristiforms on rump less than 26 mm in length, larger or smaller body size 7
- 7. Larger body size, head and body more than 250 mm, hind foot more than 40 mm; longer maxillary tooththrow (length > 13.0 mm); incisors nearly orthodont *P. unicolor*
- Smaller body size: head and body length less than 215 mm; hindfoot length less than 40 mm; shorter maxillary tooththrow (length < 13.0 mm); incisors opisthodont *P. dasythrix*
- 8. Aristiforms on rump longer than 25 mm; mesopterygoid fossa more than 4.0 mm wide, interorbital constriction more than 12.0 mm *P. brasiliensis*
- Aristiforms on rump shorter than 25 mm; smaller size: mesopterygoid fossa less than 4.0 mm wide; interorbital constriction less than 12.0 mm 9
- 9. Tail thickly haired with a tuft at the tip; aristiforms on rump less than 0.9 mm wide *P. blainvillii*
- Tail nearly naked, with visible scales and no tuft at the tip; aristiforms on rump more than 0.9 mm wide *P. lamarum*

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