Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.89-112, jan./mar.2005
ISSN 0365-4508

A NEW GENUS FOR *LONCHERES GRANDIS* WAGNER, 1845, WITH TAXONOMIC COMMENTS ON OTHER ARBOREAL ECHIMYIDS (RODENTIA, ECHIMYIDAE) [1]

(With 14 figures)

GILSON E. IACK-XIMENES [2, 4]
MARIO DE VIVO [2]
ALEXANDRE R. PERCEQUILLO [3]

ABSTRACT: A study of arboreal echimyids in Brazilian and European collections revealed a number of morphological traits supporting the recognition of *Loncheres grandis* Wagner, 1845, currently included in *Makalata* Husson, 1978, as a full genus. Our proposition of a new genus for *L. grandis* changed the species content of *Makalata*, what led us to reformulate the generic diagnosis for this genus and other arboreal echimyids as well. The new genus can be distinguished by several external characters including its color pattern, striking differences in tail pilosity, and palmar and plantar pad morphology. Osteological distinguishing traits includes the shape of nasals, the structure of the postorbital process of the zygomatic arch, petrosal morphology, the presence of a posterior maxillary foramen, the crown pattern of molariform teeth, and *baculum* morphology.

Key words: Rodentia, Hystricognathi, Echimyidae, *Loncheres grandis*, *Makalata, Phyllomys, Echimys.*

RESUMO: Novo gênero para *Loncheres grandis* Wagner, 1845, com comentários taxonômicos sobre outros equimídeos arborícolas (Rodentia, Echimyidae).

O estudo de equimídeos arbóreos em coleções brasileiras e européias revelou diversas características morfológicas sustentando o reconhecimento de *Loncheres grandis* Wagner, 1845, atualmente incluído em *Makalata* Husson, 1978, como um gênero válido. Nossa proposta de um novo gênero para *L. grandis* alterou o conteúdo específico de *Makalata*, o que nos levou a reformular a diagnose genérica para este gênero, assim como para outros equimídeos arbóreos. O novo gênero pode ser distinguido através de várias características externas tais como seu padrão de coloração, uma notável distinção da pilosidade caudal e a morfologia das almofadas das patas anteriores e posteriores. Características osteológicas distintivas incluem a forma dos nasais, a estrutura do processo pós-orbital do arco zigomático, a morfologia do petroso, a presença de um foramen maxilar posterior, a morfologia da coroa dos dentes molariformes e a forma do báculo.

Palavras-chave: Rodentia, Hystricognathi, Echimyidae, *Loncheres grandis*, *Makalata, Phyllomys, Echimys.*

INTRODUCTION

TATE (1935) created a broad concept for *Echimys* Cuvier, 1809, in which the genus occurred in all of the tropical South America to the east of the Andes, and included all species presently placed within the genera *Makalata* Husson, 1978, *Phyllomys* Lund, 1839, *Callistomys* Emmons & Vucetich, 1998, and *Echimys* itself. Despite MOOJEN's (1948, 1952) attempt to break *Echimys* by recognizing *Phyllomys* from eastern Brazil as a distinct genus, most authors (CABRERA, 1961; WOODS, 1993; NOWAK, 1999) simply continued to follow TATE (1935). HUSSON (1978) opened the way to a better understanding of the systematics of arboreal echimyids by creating *Makalata* to include *Echimys armatus* I. Geoffroy, 1838.

Since Husson's contribution several important steps have followed, all of them resulting in a much more refined view of groups of species within Tate's broad concept of *Echimys*: the separation of southeastern Brazilian species first under *Nelomys* Jourdan, 1837 (EMMONS & FEER, 1990) and later *Phyllomys* Lund, 1839 (LEITE, 2001; EMMONS *et al.*, 2002)

[1] Submitted on June 18, 2004. Accepted on January 25, 2005.
[2] Museu de Zoologia da Universidade de São Paulo, Mastozoologia. Av. Nazaré, 481, Ipiranga, 04263-000, São Paulo, SP, Brasil.
[3] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Mastozoologia. Caixa Postal 5133, João Pessoa, 58051-970, PB, Brasil.
[4] E-mail: giliackx@yahoo.com.

and the erection of *Callistomys* by EMMONS & VUCETICH (1998) to include *Echimys pictus* from the coastal forests of the Brazilian State of Bahia.

Here we propose a new genus for *Loncheres grandis* Wagner, 1845. This species was part of the species content of TATE's (1935) *Echimys* and was later transferred to *Makalata* by EMMONS & FEER (1997). We believe that *Loncheres grandis* does not belong to neither *Makalata* nor *Echimys*, and in fact to no other currently available arboreal echimyid genus. The recognition of this new genus led us to a redefinition of the species content of both *Echimys* and *Makalata* and their generic diagnostic features.

BRIEF TAXONOMIC HISTORY, WITH SPECIAL REFERENCE TO *LONCHERES GRANDIS* WAGNER, 1845

WAGNER (1845) described *Loncheres grandis* based on a specimen collected by J. Natterer in Brazil, attributing his placement of the new species in *Loncheres* Illiger, 1811, on its "affinities" with *L. cristatus* (a junior synonym of *Echimys chrysurus*). A few years later, WAGNER (1850) distinguished two groups of species in *Loncheres*, the first including all species with hairy tails, namely *L. grandis*, *L. nigrispina*, and *L. unicolor* (the latter two species currently in *Phyllomys* Lund, 1839), and the second group including the naked-tailed species *L. macrura* and *L. armata* (both currently in *Makalata* Husson, 1978).

PELZELN (1883), in his contribution dealing with the material obtained by J. Natterer, was able to restrict the type locality of *L. grandis* as Manaqueri, Solimões River, Amazonas. This decision had some importance because *Loncheres* was a broad genus, containing arboreal echimyid species from the entire South American continent. The increase in knowledge on the geographic distribution of its species eventually led to the avoidance of errors such as that by TROUESSART (1880), who included *L. grandis* under *L. blainvillei* (*sic*; currently in *Phyllomys*).

ALLEN (1899), acting as first reviewer, fixed *Myoxus chrysurus* Zimmermann, 1780 as type species of *Loncheres* and *Echimys spinosus* Desmarest, 1817 as type species of *Echimys*. This act was intended to keep both genera as distinct and valid, however the fixation of the type species of *Echimys* was not made according to the rules of the zoological nomenclature (article 30 of the International Commitee of Zoological Nomenclature, see TATE, 1935), and TATE (1935) corrected this by fixing *Myoxus chrysurus*, as the type species of *Echimys*. This act made *Loncheres* definitely a synonym of *Echimys*.

Even before Tate's solution to the question of the validity of *Loncheres* and *Echimys*, authors begun to group many species of arboreal echimyids in the genus *Echimys*. TROUESSART (1905) was the first to transfer species that he had formerly (TROUESSART, 1880) placed in *Loncheres* to the genus *Echimys* Cuvier, 1809, and THOMAS (1916) included *L. grandis* in *Echimys*. Later, THOMAS (1928) described *E. saturnus* and compared it with *E. chrysurus* and *E. grandis*.

At the time of Tate's publication of the taxonomic history of "hystricoid" rodents (TATE, 1935), the genus *Echimys* included 24 valid species, which that author decided to distribute in two species groups, his "hairy" and "naked-tailed" groups. This division does not correspond to any of the currently recognized genera, but certainly indicates that Tate was aware of the diversity within *Echimys*. ELLERMAN (1940) also tried to group species within *Echimys*, but despite his employment of a number of external and cranial characters, his species groups were also heterogeneous by current standards.

MOOJEN (1948, 1952) was the first to group a number of species previously under *Echimys* in the genus *Phyllomys* Lund, 1839, but subsequent authors, notably CABRERA (1961), ignored his opinion. The recognition that *Echimys* was a heterogeneous assemblage of species became widely accepted only after HUSSON (1978) erected *Makalata* to contain *Echimys armatus* I. Geoffroy, 1838. This led to further studies of the many species contained in the genus *Echimys*. EMMONS & FEER (1990, 1997) adopted *Nelomys* Jourdan, 1837 for several eastern Brazilian species, an usage that was later corrected by EMMONS *et al.* (2002) through the use of *Phyllomys* for the same group of species. An additional consequence of the same trend was the creation of the genus *Callistomys* EMMONS & VUCETICH, 1998 for *Nelomys pictus* Pictet, 1838.

Evidently, changing the species content of *Echimys* by creating or revalidating genera to contain subsets of its species, made the definition of those an important issue, that it is still under progress. EMMONS & FEER (1997) included *E. grandis* in *Makalata* without offering justification. In our opinion this happened due to improper characterization of both *Echimys* and *Makalata*. We believe that *Echimys grandis* belong in a separate genus, which we describe bellow. Additionally we provide comparisons between our new monotypic genus and other genus level taxa which species were previously included within *Echimys*.

METHODS

We examined 317 specimens (Appendix I) of *Echimys*, *Makalata*, *Loncheres grandis* and *Phyllomys* deposited in the following collections: Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional - Rio de Janeiro (MN); The Natural History Museum, London (BMNH); Museum für Naturkunde, Berlin (MNK); Naturhistorika Riksmuseet, Stockholm (NRM); Zoologische Staatsammlung, München (ZSM); Naturhistorisches Museum, Wien (NMW); Zoological Museum, University of Copenhagen (ZMUC), and Musée Nationale d´Histoire Naturelle, Paris (MNHN). Locality records for specimens examined can be found in Appendix II.

We have recorded the external measurements from the specimen's tags as follows: 1) head and body length (HB); 2) tail length (T); 3) ear length (E); and 4) hind foot length (HF). When the alternative "total length" was given instead of "head and body length", we have subtracted the tail length values from the total length.

We have recorded 15 skull measurements directly from skulls to the nearest 0.01mm. Measurements were based on PATTON & ROGERS (1983), and their definitions, as employed in this study are: 1) Skull length (SL): from the tip of the nasals to the posteriormost part of the occipital region; 2) Zygomatic breadth (ZB): largest distance across the external sides of the zygomatic arches; 3) Frontal constriction (FC): the smaller distance across the orbital border of frontals; 4) Nasal length (NL): greatest distance from the tip to the posteriormost part of nasals; 5) Squamosal breadth (SB): distance across the external projection of the squamosal crest taken at the level of the external auditory meatus; 6) Rostrum breadth (RB): distance across both sides of the rostrum at the premaxilar-maxilar suture; 7) Bullar length (BL): greatest length of the bulla, from anteriormost portion to the posterior border nearest to the paraoccipital process; 8) Postpalatal length (PPL): from the anteriormost border of the foramen magnum to the anteriormost edge of the mesopterygoid fossa; 9) Palatal length (PL): from the alveolar edge of incisors to the anteriormost edge of the mesopterygoid fossa; 10) Maxillary toothrow length (TRL): largest distance from the anteriormost border of the fourth premolar to the posteriormost border of the third molar; 11) Maxillary breadth (MB): greatest distance across the fourth premolars taken from their alveolar borders; 12) First molar breadth (M1B): greatest distance from lingual to buccal borders of the first upper molar at tip of crown level; 13) Braincase width (BW): taken across the outermost borders of parietals at their contact with the squamosals; 14) Mandible length (MBL): from the lingual border of the incisor's alveolus to the posteriormost border of the postcondyloid process; 15) Mandible height (MH): shortest distance taken vertically from the uppermost part of the condyloid process to a plane passing from the lower edge of the symphiseal suture to the lowermost edge of the angular process.

We recognized three dental age classes, based on the eruption of the maxillary teeth: 1) young: specimens with third upper molar unerupted; 2) subadult: specimens with the third upper molar in the process of eruption; 3) adult: specimens with all maxillary teeth erupted.

We employed WAHLERT (1974, 1983, 1985) and WOODS & HOWLANDS (1979) for the nomenclature of cranial foramina. Dental nomenclature (Fig.1) is modified from LAVOCAT (1976) with further considerations of BUTLER (1985), JAEGER *et al.* (1985), FLYNN *et al.* (1986), JAEGER (1989), BRYANT & MCKENNA (1995), and CANDELA (1999a, b; 2002). We employed DIDIER (1962) and PATTON (1987) for *baculum* nomenclature.

RESULTS

Order Rodentia Bowdich, 1821
Suborder Hystricognathi Tullberg, 1899
Family Echimyidae Gray, 1825

Toromys gen.nov.

Loncheres: Wagner, 1845:145, part.
Echimys: Trouessart, 1905:504, part.
Makalata: Emmons & Feer, 1997:236, part.

Type-species: *Loncheres grandis* Wagner, 1845.

Geographic distribution – Known records of *Toromys grandis* are depicted in figure 2. The species was previously known to occur along both banks of the Rio Amazonas (EMMONS & FEER, 1990, 1997; EISENBERG & REDFORD, 1999). Here we extend its distribution to include the species' type locality, Manaqueri, at the lower Rio Solimões (Amazonas, Brazil) and the mid to lower sections of the Rio Tapajós (Pará, Brazil). EMMONS & FEER (1997) suggested that this rodent prefers the proximity of water, particularly the seasonally flooded forest ("várzea"), and the distribution here presented supports this claim. We believe that further collecting may demonstrate the presence of *Toromys* along other tributaries of Rio Amazonas.

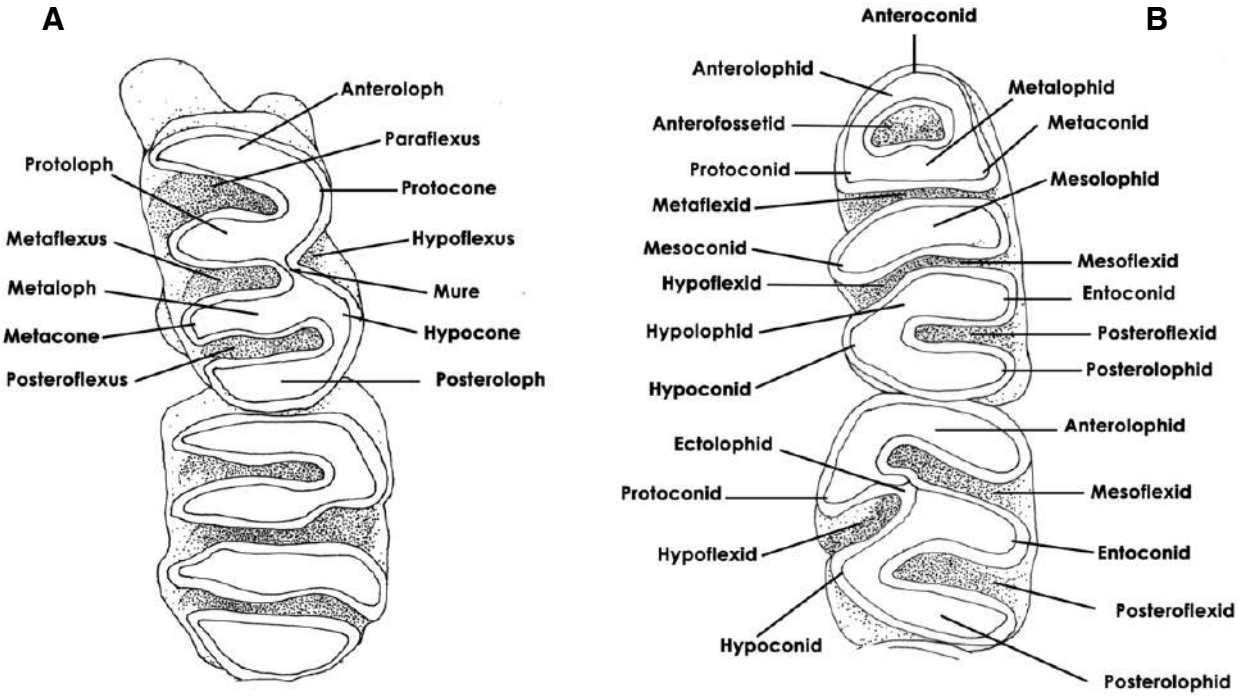

Fig.1- Dental nomenclature for the molariforms: (A) upper molariforms, (B) lower molariforms.

Etymology – "Toro" (= local name in Amazon region to arboreal echimyids) + "mys" (= rat). Arboreal Amazonian echimyins are locally known as "rato-toró" or "toró", which is the onomatopoeic Portuguese for the vocalizations of these rodents. *Toromys grandis* is specifically known as "Toró preto" (black Toró).

The genus is masculine.

Species included – Only the type species, *Loncheres grandis* Wagner, 1845 is currently included in the genus.

Diagnosis – *Toromys* is identifiable by its color pattern of body with golden and black upper parts, blackish head sprinkled with gold, and black tail; body covered with setiforms and aristiforms as soft spines (definition of "soft spines" is made under "Comparisons", below); tail fully covered by hairs (scales not visible) but without a distal hair tuft; small tubercular rugosities between plantar and palmar pads in hands and feet; nasals medially constricted; external auditory meatus of *Toromys* is separated from squamosal bone by a thin ridge of petrosal bone; posterior maxillary foramen present; upper molariform teeth with protoloph and metaloph connected by a slender mure.

Description

External Measurements: A large Echimyinae rodent with head and body length ranging from 275 to 354mm (mean=303mm, n=45), tail frequently shorter than head and body length ranging from 244 to 361mm (mean=285mm, n=42); ear round and short, from 15 to 25mm (mean=19.5mm, n=27); and hind foot length varying from 40 to 65mm (mean=52.8mm, n=45).

Pelage and coloration: Head darker than body; dorsally and laterally black sprinkled with gold; quantities of black and gold varying individually, from black slightly mottled with gold to uniformly sprinkled with gold and black; variation related to the number of monochromatic black hairs to black hairs with subterminal gold bands. Mystacial vibrissae thick and long, entirely black, reaching or extending beyond the pinnae. Mental region and throat lighter than sides and dorsum of head, with variable amounts of straw yellow. Ears round, hairs black; external face of pinnae slightly hirsute, with short black hair; internal face of pinnae slightly hirsute, with longer black hairs in the outer border of pinnae. Dorsal and lateral pelage of body composed largely by narrow and soft spines; general coloration from black sprinkled with gold to gold sprinkled with black; mid dorsum slightly darker; hairs from entirely black to black with a subterminal golden band; the amount of black and gold varying individually relatively to the amount of unicolored

black hairs and black hairs with subterminal gold band and to the width of the gold band; lateral parts of body similar to dorsum but slightly lighter. Shoulders and proximal parts of limbs indistinct from sides of the body; limbs ventrally less hirsute, proximally grading to the general ventral color. Hands and feet varying from black or dark brown mottled with gold to sprinkled with black and gold; two kinds of hair present: unicolored black hair and black hair with subterminal gold band. Ventrum gold yellowish to straw yellow, sometimes with a median gold yellowish line; hair bicolored, light brown at base and yellow to gold terminally. Tail fully haired; the color pattern of the posterior dorsum extends to the basal 1/6 portion of tail, which hairs are longer than in the remainder of the tail; distal 5/6 of tail covered with relatively shorter hairs; tail with basal one-sixth mottled with black and copper, the remainder jet-black; scales not visible covered by tail hairs; longest middle hair of the tail scale triad covers from 20 to 22 rows of scales at the base of tail, approximately 15 rows in the middle, and nine to 11 at the tip; tail tuft absent.

Cranial anatomy: Skull large and robust (SL range: 60.8-72.9mm); slender rostrum; nasals constricted medially. Lateral wings of frontal well-developed forming a roof over the orbital region. Postorbital process of zygoma formed by jugal and squamosal. Incisive foramina variable, generally moderately long and narrow, but in some individuals wide and short; septum of incisive foramina formed mainly by premaxillae. Palatal region long and slender; palatine extending up to M1. Mesopterygoid fossa with slit-shaped lateral openings. Alisphenoid region wide; alisphenoid canal incomplete, formed only by posterior opening; buccinator and masticator foramina separated from each other; foramen ovale medium sized; maxillary vein pass through foramina; transverse canal well-developed. Bullae with tiny styliform process, tegmen timpani short and wide; external auditory meatus separated from squamosal bone by a thin ridge of petrosal bone.

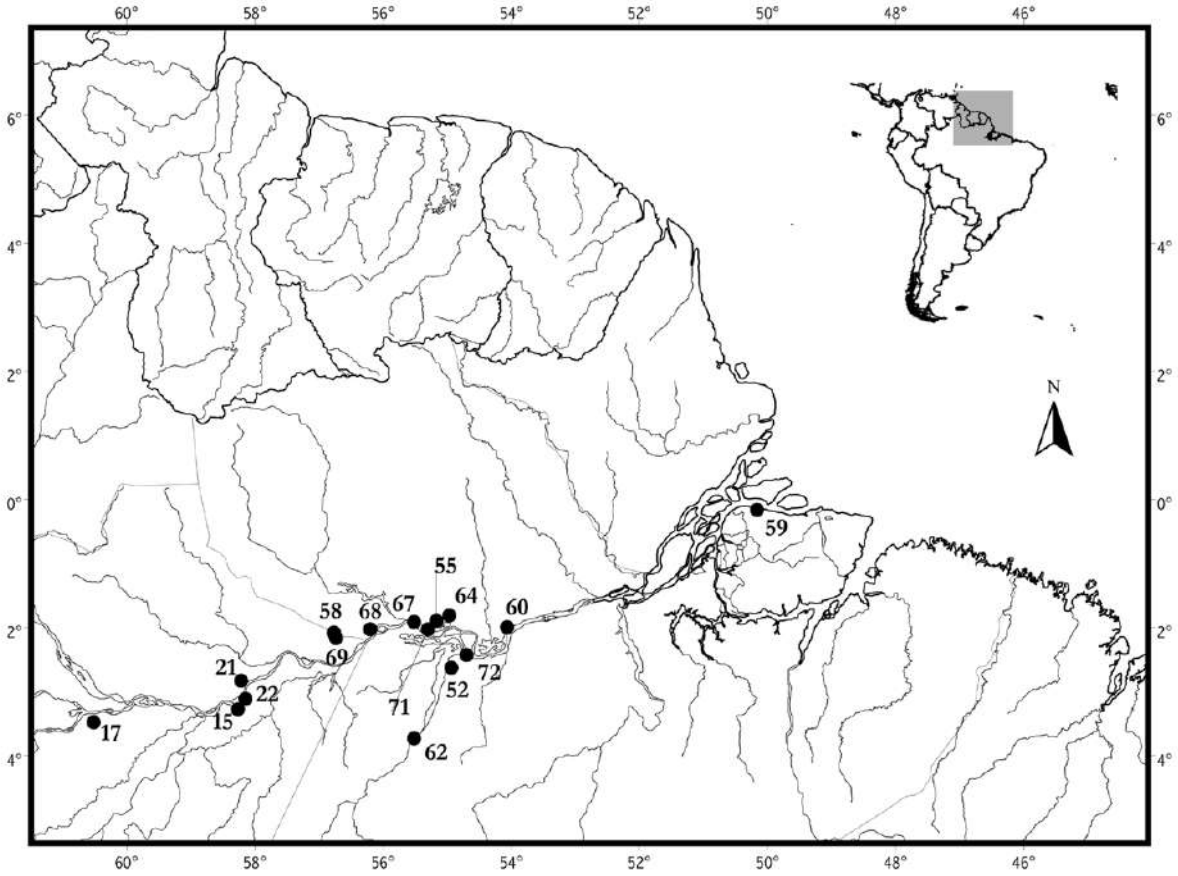

Fig.2- Geographic distribution of *Toromys grandis*. For localities names and geographical coordinates, see Appendix II.

Dental morphology: Upper molariforms tetralophodont; anteroloph, protoloph, and metaloph connected by slender mure. Lower dp4 tetralophodont, metalophid absent, mesolophid isolated; lower molars trilophodont. The holotype of *Loncheres grandis* (NMW B920) and two other specimens (NRM A587187, A597188) have a particular M3 morphology compared to other specimens: the M3 in the above cited material is smaller and trilophodont, but this seems to be anomalous and with no geographic or taxonomic significance.

Baculum: Baculum elongate (greatest length: 7.69mm; n=1; Fig.3) with a broad and thick shaft. Proximal end of baculum round, broader and thicker than distal end, which is pointed. The shaft does not present any dorsoventral curvature and apical wings are absent.

Fig.3- *Baculum* of *Toromys grandis* (MZUSP4722). Scale bar =2mm.

COMPARISONS

Table 1 presents the most relevant distinguishing characters of *Toromys*, *Echimys*, *Makalata*, and *Phyllomys*. More detailed morphological comparisons follow.

Body size and proportions: Head and body length and tail length distinguish *Toromys* and *Echimys* from *Makalata* and *Phyllomys*; *Toromys* and *Echimys* have larger body and tail lengths than the latter (Tabs.1-2). In *Makalata*, tail length ranges from 145 to 234mm, while in *Echimys* it ranges from 270 to 415mm, and in *Toromys* from 244 to 361mm. Tail length in *Phyllomys* is similar to that of *Makalata*, ranging from 180 to 275mm. Aside from absolute size, *Toromys* and *Makalata* have tails shorter than head and body length (89% and 94%, respectively); *Echimys* and *Phyllomys* generally have tails longer than head and body (118% and 106%, respectively). Thus, *Toromys* has a large body size and proportionally shorter tail; *Echimys* is also a large bodied form, but with a longer tail. On the other hand, *Makalata* and *Phyllomys* are small bodied forms of Echimyinae, but they do differ on tail size: the former having the tail shorter than head and body, and the latter a longer tail. Hind foot is smaller in *Makalata* and *Phyllomys* (HF range: 30-48mm, and 30-50mm, respectively) than in *Echimys* and *Toromys*. These have long and wide feet, ranging from 40 to 65mm in *Toromys* and from 45 to 60mm in *Echimys*.

Chromogenetic fields: *Toromys* and *Phyllomys* have three basic chromogenetic fields (as defined by HERSHKOVITZ, 1977) – 1- head, body (including limbs and fore and hindfeet) and proximal part of tail; 2- ventral region; 3- most of the tail except for its proximal region. In the three genera, coloration of each chromogenetic field is mostly uniform, sometimes gradually darkening or becoming lighter, but without clear-cut regional differentiation. *Makalata* is essentially similar to *Toromys* and *Phyllomys*, but with an additional field in the muzzle; all of its known species have reddish muzzles. These three genera have the head and body chromogenetic fields expressing their particular colors as "sprinkled" patterns, i.e. the hairs usually present two or more distinct bands of pigmentation, except for an additional field in the muzzle. *Echimys* differs from all of the

former in two important aspects; its chromogenetic fields are more complex, and they express color as uniformly monochromatic; the hairs have a single color throughout their length. The additional chromogenetic fields in *Echimys* include its complex head pattern, with long eye stripes and a distinctive stripe from the rostrum extending medially to the crown, up to the pinnae. Additionally, the tail is tricolored, with the proximal region similar to the dorsum and a middle section distinct from the distal third.

Body hair patterns: Echimyins possess two main basic types of body hair in upper and lateral surfaces: aristiforms and setiforms (MOOJEN, 1948), both with flattened shape. Aristiforms are wide and strong, and the dorsal margins are raised pronouncedly, forming a wide and shallow longitudinal groove. This type of hair is flat throughout its length and has thick borders, except at the tips. It also presents different degrees of hardness, and this characteristic is directly related to the width of the hair: broad aristiforms form hard spiny pelage and narrow aristiforms form a more flexible and soft pelage. The setiforms are narrower than aristiforms, and flattened with moderately raised margins; the longitudinal groove and the thick marginal borders are present with varied length along the setiforms; the width of the groove varies from a narrow groove to a slight indentation.

In *Toromys*, the body is covered by setiforms and aristiforms, the latter as narrow and soft spines (total length=30.44mm, maximum width=0.32mm); the setiforms (total length=34.13mm, maximum width=0.17mm) are longer than aristiforms, the

Table 1. Comparisons between *Toromys* , *Echimys*, *Makalata*, and *Phyllomys*.

	Toromys	*Echimys*	*Makalata*	*Phyllomys*
Tail/ Head and body ratio	94%	118%	88.08%	106%
Tail: tuft	absent	present	absent	present
Tail: chromogenetic fields	basal and distal	basal, medial and distal	basal; bicolored dorso-ventrally	basal
Palmar and plantar surface between pads	with small rugosities	smooth	smooth	smooth
Dorsal pelage	narrow and soft spines; hairs present	wide and hard spines; hairs totally concealed	spines and hairs equally distributed	spines and hairs equally distributed
Body chromogenetic fields	head, dorsal and ventral	mask and crown stripe on head	muzzle	none
Nasal shape	external margins strongly concave and sharpen angles	external margins concave	external margins straight, tapering posteriorly	external margins straight, slightly tapered posteriorly
Passage of maxillary vein	Passing through a foramen	Passing through a maxillary notch	Passing through a maxillary notch	Passing through a maxillary notch
External auditory meatus/squamosal	thin blade of petrosal	wide crest of petrosal	wide crest of petrosal	wide crest of petrosal
Teeth occlusal pattern	anteroloph, protoloph, and metaloph connected by a slender mure; dp4 tetralophodont	metaloph isolated from protoloph by a continuous hypoflexus-metaflexus; dp4 pentalophodont	metaloph isolated from protoloph by a continuous hypoflexus-metaflexus; dp4 pentalophodont or tetralophodont	lophs isolated; dp4 pentalophodont

longitudinal groove and the thick marginal borders are present almost along the entire setiforms, the basal portion is slightly wider than distal part which tapers to a short filamentous tip. *Makalata* and *Phyllomys* share the broader and harder aristiforms (*Makalata* total length=24.25-30.88mm, maximum width=0.89-1.66mm; *Phyllomys* total length=22-36mm, maximum width=0.4-1.6mm; LEITE, 2003) and thin short setiforms over the body (*Makalata* total length=21.55mm, maximum width=0.15mm; *Phyllomys* total length=22.83mm, maximum width=0.18mm), relative amounts of each kind of hair varying within different species. In these two genera the width of the aristiforms also varies among species. The morphology of setiforms of *Toromys*, *Makalata*, and *Phyllomys* are similar, but in *Makalata* and *Phyllomys* the setiforms are shorter than aristiforms. In *Toromys*, *Makalata*, and *Phyllomys* setiforms and aristiforms are evident on inspection. The relative amounts of aristiforms and setiforms vary among species in *Makalata* and *Phyllomys*. In *Echimys* the aristiforms are well developed (total length=30.59mm, maximum width=2.67mm), wide and hard. The setiforms in *Echimys* are shorter than aristiforms (total length=25.79mm) and they have a wide basal portion (maximum width=0.62mm) with a longitudinal groove, abruptly tapering in a long filamentous distal portion (maximum width=0.11mm); setiforms can be seen only under magnification.

Caudal hair patterns: The patterns of hair coverage, chromogenetic fields, and scale size of tails may easily distinguish the four genera. All genera possess well furred tails, but in *Toromys* and *Echimys* tails are entirely covered by long hairs, in such a way that visualization of scales is difficult. On the other side, the caudal hairs of *Makalata* and *Phyllomys* are shorter and thinner, and scales are more clearly visible through the fur. However, the tail hairs of *Echimys* and *Phyllomys* become increasingly longer from the base to the tip of the tail, thus forming distinct distal tufts, while the opposite occurs in *Toromys* and *Makalata*, which lack tufts. In *Toromys*, the longest middle hair of the tail scale triad covers from 20 to 22 rows of scales at the base of tail, approximately 15 rows in the middle, and 9 to 11 at the tip of tail. In *Echimys* and most species of *Phyllomys*, the longest hair covers 10 to 12 rows at the base of tail, reaching approximately 30 rows at the tip. In *Makalata*, hairs are present along the entire tail, but they are much shorter than in the previous genera; the number of scale rows covered by the longest hairs is 5 to 6 at the base of tail and 3 to 4 at the tip. In *Phyllomys* the development of the tuft is variable and in *P. dasythrix*, tuft is absent.

The coloration of posterior end of dorsum continues until the base of tail in the four genera. This chromogenetic field covers at least 10% of the entire tail in *Toromys* and *Echimys* and is shorter in *Makalata* and *Phyllomys*. In *Toromys* there is only one additional chromogenetic field for the remaining part of tail (hair entirely black in the only known species). In *Echimys* there are two additional chromogenetic fields, dividing the remaining part of the tail in two areas. The first begins posteriorly to the base and covers at least half of the tail and is dark brown in color; the second one extends to the tip, and its color is whitish or yellowish. There is no color differentiation in the dorsal and ventral regions of the tail. *Makalata* also presents two additional chromogenetic fields in the tail besides that of the base, but they express themselves dorso-ventrally, with a lighter tone below and a darker one above (countershading pattern). However, since the tail hair is short in *Makalata*, visualization of the pattern is not obvious. In *Phyllomys* the tail is variable, generally unicolored, but in *P. lundi* a weak countershading pattern occurs (LEITE, 2003).

Palmar and plantar morphology: *Toromys* presents a very distinct morphology of plantar and palmar surfaces relatively to *Echimys*, *Phyllomys*, and *Makalata*. In the latter three, the pads are relatively smooth, as is the skin between the pads. In *Toromys* the pads are likewise smooth, but the skin between the pads present small but distinct rugosities (Fig.4).

Cranial anatomy. There are few diagnostic qualitative cranial traits for the genera studied here. They all share a basic morphologic plan, with a remarkable differentiation on skull size and robustness. The most conspicuous traits that distinguish these genera are the nasal shape, the presence of maxillary foramen, and morphology of the bullae.

Toromys presents concave external margins of nasals; in *Echimys* the external margins of the nasals are also concave, but distinctly less so than in *Toromys*; *Makalata* presents external margins of the nasals almost longitudinally parallel, while *Phyllomys* presents them converging posteriorly (Fig.5). In *Toromys* the maxillary vein pass through a foramen formed by maxillar palatine and alisphenoid bones, the posterior maxillary foramen. The other genera have a posterior maxillary notch

Table 2. Descriptive statistics of *Toromys*, *Echimys*, *Makalata*, and *Phyllomys*. (N) $\bar{x}$ ± *s.d.* *Min.* - *Max.*

	Toromys	*Echimys*	*Makalata*	*Phyllomys*
HB	(45) 303 ± 15.58 275 - 354	(8) 280.63 ± 25.70 250 - 310	(39) 220.56 ± 27.90 168 - 294	(62) 212.58 ± 18.53 160 - 262
T	(42) 285.12 ± 22.06 244 - 361	(9) 330.55 ± 47.20 270 - 415	(29) 196.72 ± 20.86 145 - 234	(47) 226.55 ± 22.44 180 - 275
F	(45) 52.78 ± 4.71 40 - 65.00	(9) 52.89 ± 14.04 45 - 60	(39) 38.15 ± 4.73 30 - 48	(68) 37.08 ± 3.55 30 - 50
E	(27) 19.48 ± 2.01 15 - 25	(4) 20.50 ± 6.87 19 - 23	(20) 13.50 ± 2.09 10 - 17	(61) 15.54 ± 2.78 9 - 20
SL	(41) 67.15 ± 2.38 60.78 - 72.90	(9) 62.20 ± 16.17 59 – 65.89	(50) 53.54 ± 2.6 47.23 – 59.30	(42) 50.02 ± 3.12 41.03 – 58.25
ZB	(41) 32.31 ± 1.32 30.33 - 36.69	(11) 30.41 ± 5.67 25.96 - 33.33	(49) 25.65 ± 1.46 21.55 - 28.20	(49) 24.22 ± 1.74 20.93 - 29.41
FC	(45) 18.69 ± 1.25 15.570 - 21.36	(13) 15.29 ± 1.60 12.46 - 18.50	(54) 13.29 ± 0.97 11.35 - 15.08	(54) 11.28 ± 1.04 9.29 - 13.97
NL	(41) 22.24 ± 1.22 19.40 - 24.28	(12) 18.50 ± 2.42 16.20 - 21.96	(52) 16.47 ± 1.27 13.28 - 19.20	(44) 14.81 ± 1.94 10.38 - 21.34
BW	(43) 21.93 ± 1.35 18.40 - 24.72	(10) 21.44 ± 3.36 19.69 - 22.38	(55) 18.99 ± 1.15 16.40 - 21.43	(51) 18.26 ± 0.74 16.69 - 19.63
SB	(38) 25.62 ± 1.13 23.55 - 28.31	(9) 23.81 ± 4.53 21.59 - 24.83	(248) 21.04 ± 1.25 18.80 - 23.99	(46) 19.72 ± 1.14 17.86 - 23.77
RB	(43) 10.87 ± 0.67 9.60 - 12.48	(13) 10.51 ± 1.14 8.64 - 11.81	(55) 8.31 ± 0.68 6.49 - 9.70	(53) 7.46 ± 0.88 6.41 - 10.58
PL	(44) 28.65 ± 1.32 26 - 33.12	(11) 24.39 ± 4.03 21.60 - 27.34	(55) 20.97 ± 1.36 17.48 - 25.58	(53) 19.21 ± 1.81 15.27 - 26.02
PPL	(42) 25.23 ± 1.17 23.35 - 27.44	(9) 24.63 ± 4.78 21.80 - 26.17	(51) 20.22 ± 1.44 16.92 - 23.61	(49) 19.68 ± 1.49 16.02 - 23.84
TRL	(43) 15.56 ± 0.51 14.25 - 16.71	(11) 13.51 ± 1.05 12.65 - 14.89	(50) 11.26 ± 0.68 9.53 - 12.63	(51) 11.45 ± 1.09 10.19 - 15.10
M1B	(45) 3.24 ± 0.15 2.97 - 3.62	(13) 2.96 ± 0.25 2.53 - 3.55	(53) 2.28 ± 0.22 1.79 - 2.75	(54) 2.37 ± 0.21 1.88 - 2.96
MB	(45) 8.40 ± 0.44 7.60 - 9.21	(12) 8.92 ± 1.03 7.77 - 9.85	(55) 6.74 ± 0.62 5.50 - 9.44	(56) 6.48 ± 0.62 5.60 - 8.39
BL	(42) 13.00 ± 0.66 11.42 - 13.46	(11) 12.47 ± 0.71 11.42 - 13.46	(54) 11.36 ± 0.58 10.11 - 12.84	(51) 11.02 ± 0.93 9.40 - 13.17
MBL	(44) 36.51 ± 1.46 33.40 - 40.37	(10) 32.80 ± 6.75 27.60 - 35.30	(50) 27.56 ± 2.57 14.52 - 33.17	(50) 27.66 ± 2.38 22.04 - 35.69
MH	(45) 17 ± 1.04 15.23 - 19.77	(8) 16.21 ± 2.77 12.63 - 16.88	(49) 12.88 ± 1.23 9.86 - 15.43	(49) 13.01 ± 1.29 10.54 - 16.79

(N) number of specimens, ($\bar{x}$) average, (s.d.) standard deviation, (Min.-Max.) minimum and maximum.

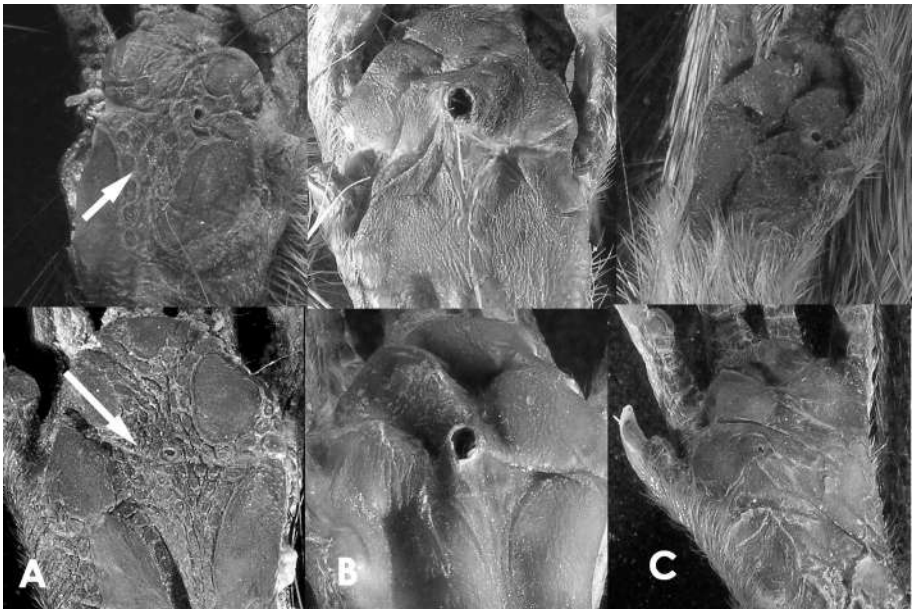

Fig.4- Palmar (upper) and plantar regions: (A) *Toromys grandis* (MZUSP4488; foot length=54mm), (B) *Echimys chrysurus* (foot: MZUSP4548; hand: MZUSP4558), (C) *Makalata didelphoides* (foot: MZUSP4559; foot length=44mm; hand: MZUSP24488), (→) rugosities between the pads.

embracing the maxillary vein (Fig.6). The external auditory meatus of *Toromys* is separated of the squamosal bone by a thin ridge of petrosal bone; *Phyllomys*, *Makalata*, and *Echimys* have the external auditory meatus separated by a well-developed crest of petrosal bone (Fig.7). The postorbital process of the zygoma in *Toromys* and *Makalata* is formed by the squamosal and the jugal; in *Echimys* and most species of *Phyllomys*, only by the jugal (Fig.8). The alisphenoid canal in *Toromys* is incomplete, usually appearing as a short canal with only the posterior opening differentiated; only the posterior opening is present in *Makalata*, while in *Echimys* the development of the alisphenoid canal is variable: most species have a complete canal with well developed anterior and posterior openings. In *Phyllomys* the alisphenoid canal is incomplete, formed by the posterior foramen and with a gutter extending through the sphenoidal fissure (Fig.9). In *Toromys*, the buccinator and masticator foramina are separated, while in *Echimys* and *Phyllomys* both foramina merge, and in *Makalata* this character is polymorphic but, in general, the buccinator and masticator foramina merge (Fig.9).

Cranial size: *Toromys* possess the largest and most robust skull of all Echimyinae rodents (Tab.2). The average skull length and molar toothrow length observed in *Toromys* exceed values found in all other genera. When compared to *Makalata* and *Phyllomys*, the differences are substantial (Fig.10; Tab.2); even relatively to *Echimys*, there are also obvious quantitative differences. *Phyllomys* is the smallest genus in almost all cranial variables.

Dental morphology: Figure 11 depicts upper and lower toothrows for the taxa here discussed. The upper molariforms of *Toromys* present the anteroloph, protoloph, and metaloph connected by a slender mure; in *Makalata* and *Echimys* the metaloph is isolated from the protoloph by a continuous hypoflexus-metaflexus. In *Phyllomys* all lophs are isolated from each other. *Toromys* has a tetralophodont lower fourth premolar (dp4), with an isolated mesolophid and lacking a metalophid. *Makalata* presents two distinct dp4 morphologies: the first is similar to the one just described for *Toromys*. The mesolophid may connect labially or lingually to the anterolophid in old individuals, a condition most easily found in the tetralophodont *Makalata*, but also present in very old *Toromys*. The second dp4 morphology found in *Makalata* is shared with *Phyllomys* and *Echimys*. In *Echimys* and pentalophodont *Makalata* the anterolophid is connected both lingually and labially with metalophid forming an anterofossetid, while in *Phyllomys* the anterolophid is connected labially to the metalophid.

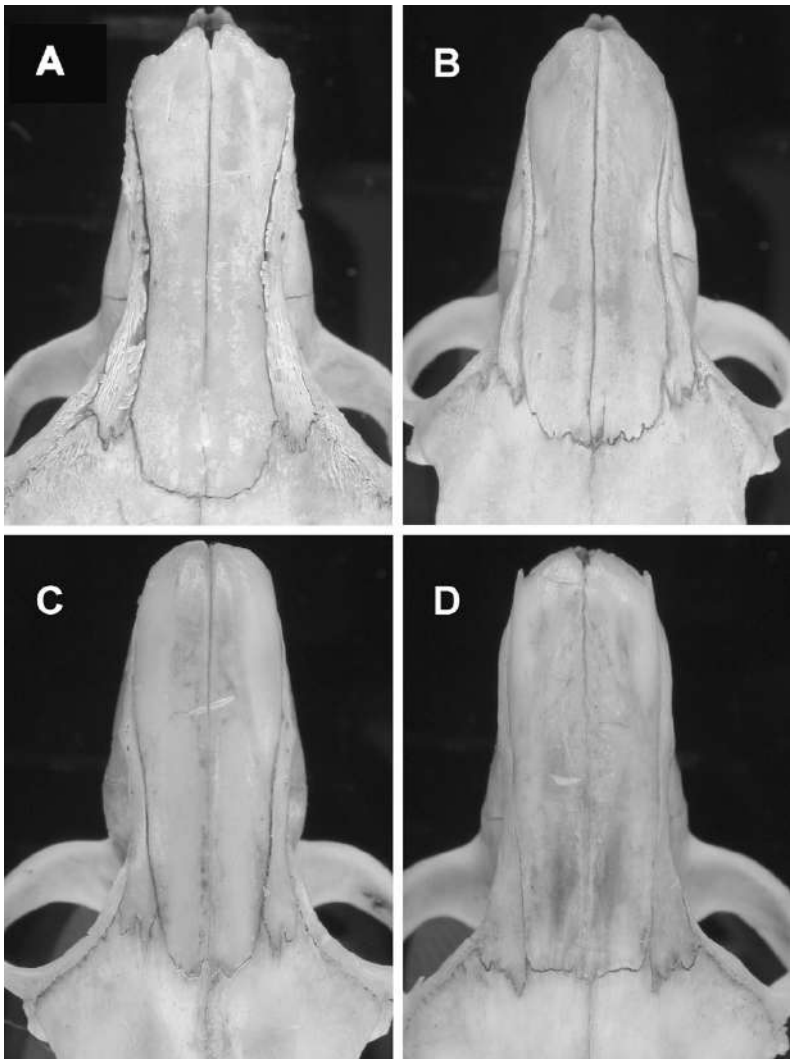

Fig.5- Shape of the nasals in dorsal view: (A) *Toromys grandis* (MZUSP4722; NL=21.6mm), (B) *Echimys chrysurus* (MZUSP4548; NL=18.3mm), (C) *Phyllomys nigrispinus* (MZUSP25858; NL=15.75mm), (D) *Makalata didelphoides* (MZUSP899; NL=15.4mm). Photos: C.Moreira.

Baculum: As bacula of *Echimys* and *Makalata* were not available for study, we limited our comparisons to Didier's descriptions of *Makalata* (DIDIER, 1962), and LEITE's (2003) description of *Phyllomys*.

DIDIER (1962) described and illustrated three quite different bacula for *Makalata* (treated as *Echimys* by that author), all three types notably differing from that of *Toromys* as follows: 1) the general shape of the *baculum* body (ventral view) is claviform in *Toromys grandis* and *M. semivillosus*; pyriform elongate in *M. rhipidurus* and straight with a wider proximal end in *M. didelphoides* (*E. armatus*, *sensu* DIDIER, 1962); 2) in *Toromys* the shaft is elongate, straight, thick, and broad; in *M. rhipidurus* the shaft is similar to that of *Toromys* except that it has a lateral indentation at the proximal end, which narrows abruptly distally; in *M. didelphoides* the shaft is elongate, straight and thin with a sinoidal curvature in lateral view; in *M. semivillosus* the shaft is elongate and thin with a lateral indentation at both proximal and distal extremities; 3) Proximal end of baculum is irregularly rounded, thick and broad in *Toromys*; in *M. didelphoides* the proximal end is V-notched; in *M. rhipidurus* the proximal end is evenly rounded; the *baculum* of *M. semivillosus* is fusiform proximally, with a slender median

depression; 4) The distal end of the baculum is pointed in *Toromys*; in *M. didelphoides* it is concave with apical wings and a median depression; in *M. rhipiddurus* it is evenly rounded; the distal extremity of the baculum of *M. semivillosus* is straight. *Phyllomys* has a baculum with a straight terminal extremity, the shaft is straight and slender from the distal to the middle portion, widening in the proximal third in an obovate shape, abruptly changing into a straight proximal extremity (LEITE, 2003).

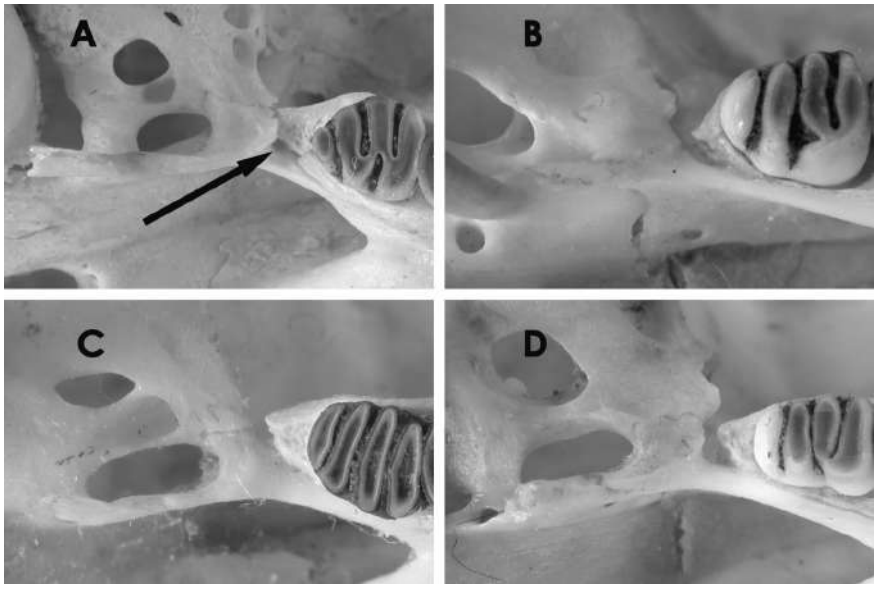

Fig.6- Passage of maxillary vein: (A) *Toromys grandis* (MZUSP4722; TL=62.7mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm), (C) *Phyllomys nigrispinus* (MZUSP666; TL=48.82mm), (D) *Makalata didelphoides* (MZUSP899; TL=52.4mm), (→) passage of the vein in the postmaxillary foramen. Photos: C.Moreira.

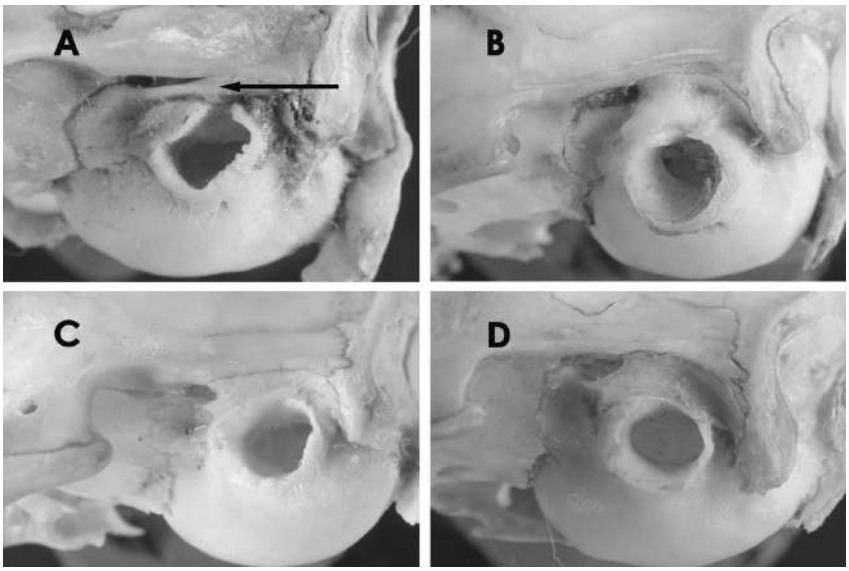

Fig.7- Bullar and petrosal morphology: (A) *Toromys grandis* (MZUSP4720; BL=13.3mm), (B) *Echimys chrysurus* (MZUSP4551; BL=12.2mm), (C) *Phyllomys nigrispinus* (MZUSP 25858; BL=10.53mm), (D) *Makalata didelphoides* (MZUSP899; BL=11.4mm), (→) external appearance of the petrosal bone. Photos: C.Moreira.

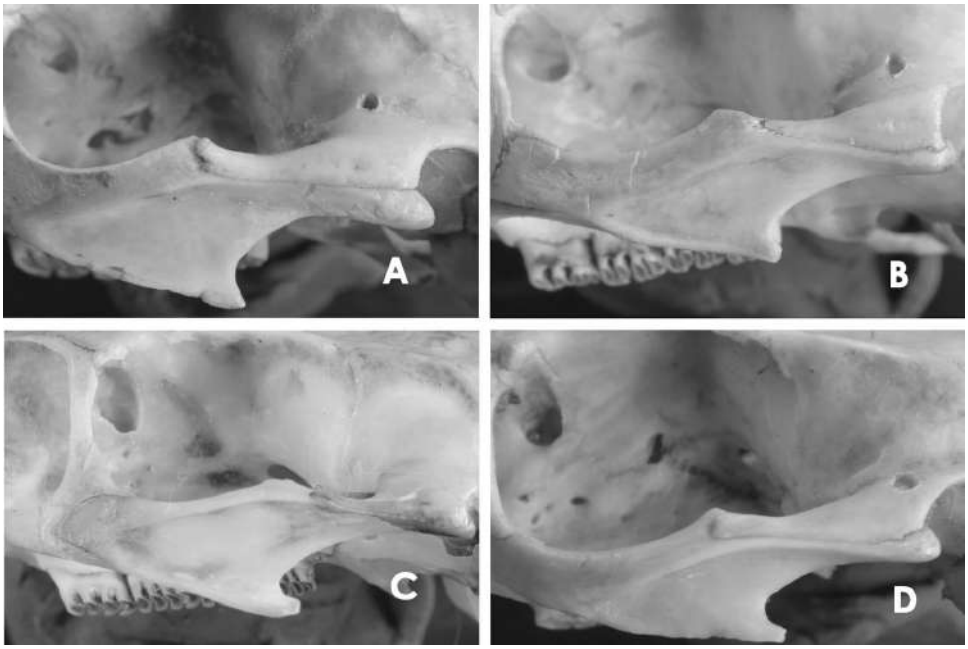

Fig.8- Postorbital process of zygoma: (A) *Toromys grandis* (MZUSP4720; TL=65.4mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm), (C) *Phyllomys nigrispinus* (MZUSP 25858; TL=50.73mm), (D) *Makalata didelphoides* (MZUSP4546; TL=56.9mm). Photos: C.Moreira.

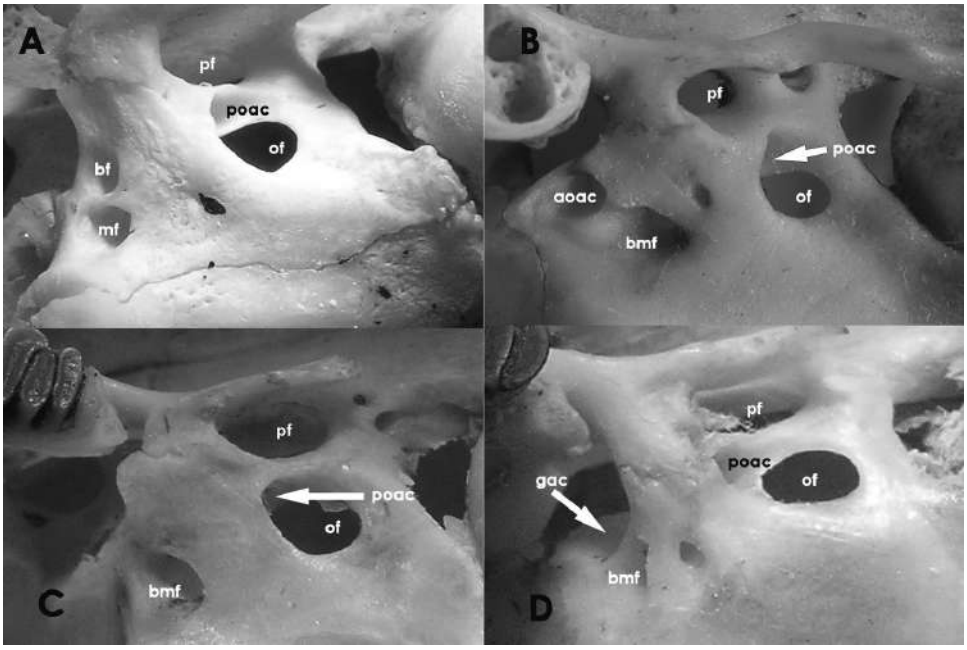

Fig.9- Alisphenoid region: (A) *Toromys grandis* (MZUSP4722), (B) *Echimys chrysurus* (MZUSP4642), (C) *Phyllomys thomasi* (MZUSP3197), (D) *Makalata didelphoides* (MZUSP899). Abbreviations for foramina and other structures: (bf) buccinator foramen, (mf) masticator foramen, (bmf) buccinator masticator foramina confluents, (of) oval foramen, (aoac) anterior opening of alisphenoid canal, (poac) posterior opening of alisphenoid canal, (gac) gutter of alisphenoid canal, (pf) pterygoid fossa.

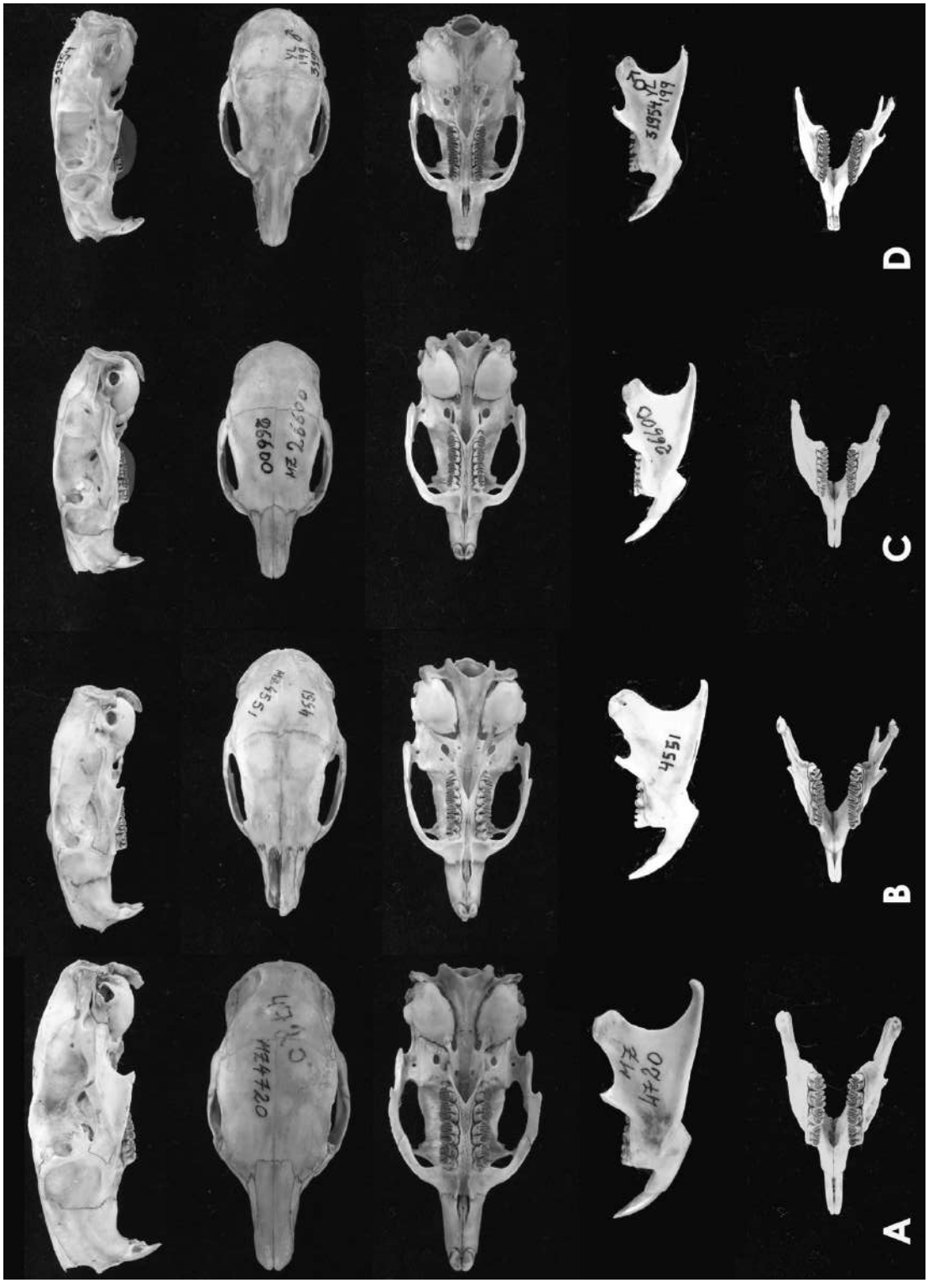

Fig.10- Skulls and mandibles: (A) *Toromys grandis* (MZUSP4720; TL=65.4mm; MBL=36.6mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm, MBL=31.2mm), (C) *Makalata didelphoides* (MZUSP26600; TL=53mm, MBL=27.6mm), (D) *Phyllomys pattoni* (MZUSP31954; TL=53.3mm, MBL=26.6mm). Photos: C.Moreira.

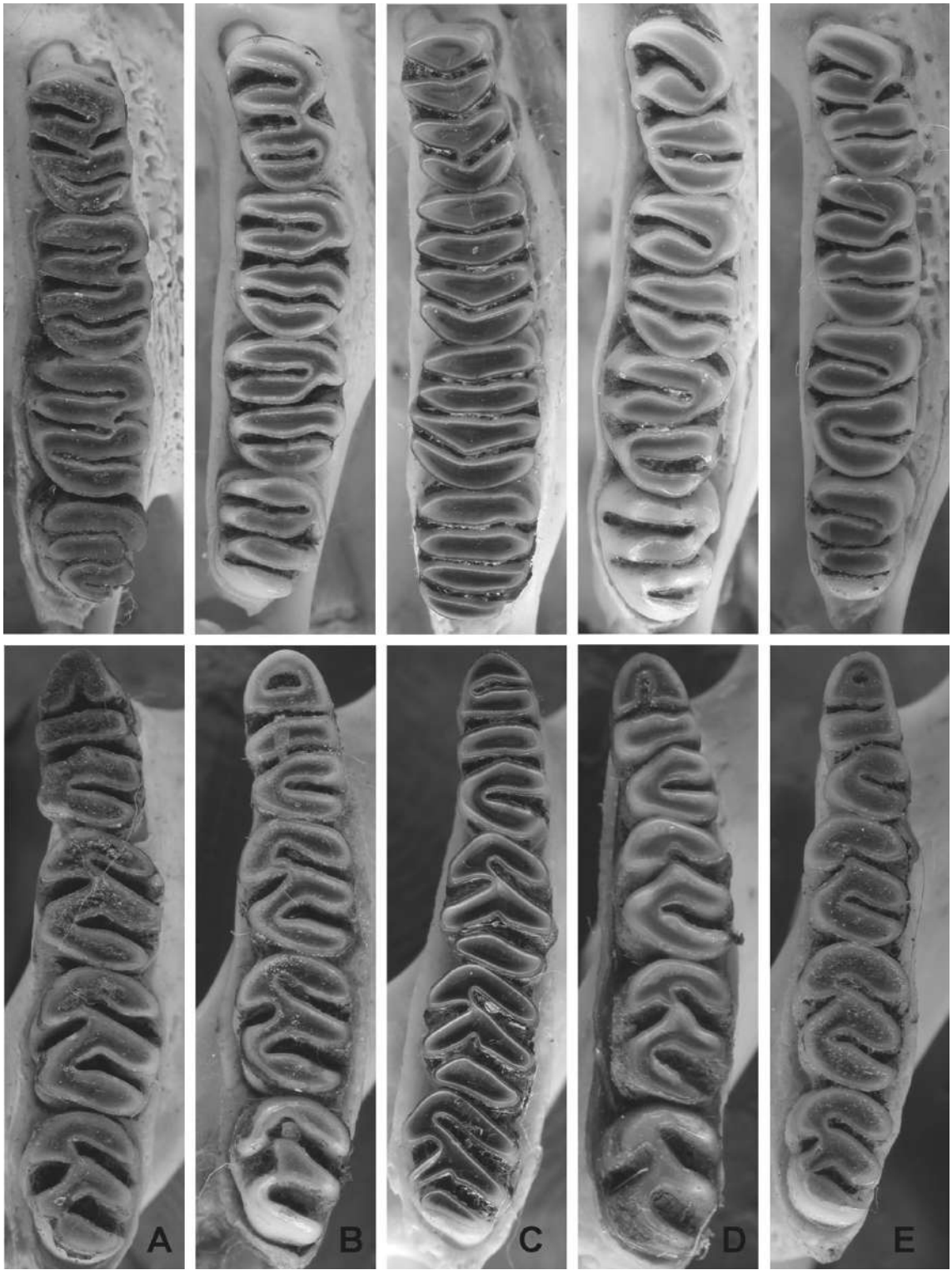

Fig.11- Toothrows: (A) *Toromys grandis* (MZUSP 4489; TRL=14.7mm), (B) *Echimys chrysurus* (MZUSP4551; TRL=12.9mm), (C) *Phyllomys nigrispinus* (MZUSP25858; TRL=12.92mm), (D) *Makalata* with pentalophodont dp4 (MZUSP899; TRL=11.4mm), (E) *Makalata* with tetralophodont dp4 (MZUSP22930; TRL=11.8mm). Photos: C.Moreira.

CHARACTERIZATION OF *ECHIMYS*, *MAKALATA*, AND *PHYLLOMYS*

The creation of *Toromys* for *Loncheres grandis* changes the species content of both *Echimys* and *Makalata*, since that species was alternatively placed in one or other genus (WOODS, 1993; EMMONS & FEER, 1997; EISENBERG & REDFORD, 1999; CARVALHO & SALLES, 2004). Additionally, since we make many comparisons with *Phyllomys* as well, we furnish emended diagnosis for the three genera bellow. Each generic diagnosis is followed by a list of species currently recognized as valid and their synonyms.

Genus *Echimys* Cuvier, 1809

Type-species – *Myoxus chrysurus* Zimmermann, 1780.

Diagnosis – A large sized echimyine with a long tricolored tail and with the white distal portion of tail extending over more than one third of tail length. Head with a black mask extending from the muzzle to above and bellow the eyes. Differentiated chromogenetic field extending from immediately behind the muzzle to the region between the ears. Septum of incisive foramen formed only by premaxillar; dp4 with anterolophid developed and connected to metalophid evenly both lingually and labially; upper molars with protoloph connected to protocone, deep groove formed by continuous hypoflexus and metaflexus; metaloph connected with posteroloph by hypocone; postorbital process of zygoma formed by jugal.

Distribution – Amazon basin and Guiana region (Fig.12).

Species included – *E. chrysurus* (Zimmermann, 1780); *E. paleaceus* (Olfers, 1818); and a third, new species (IACK-XIMENES *et al.*, in press). Synonym: *E. cristatus* Desmarest, 1817.

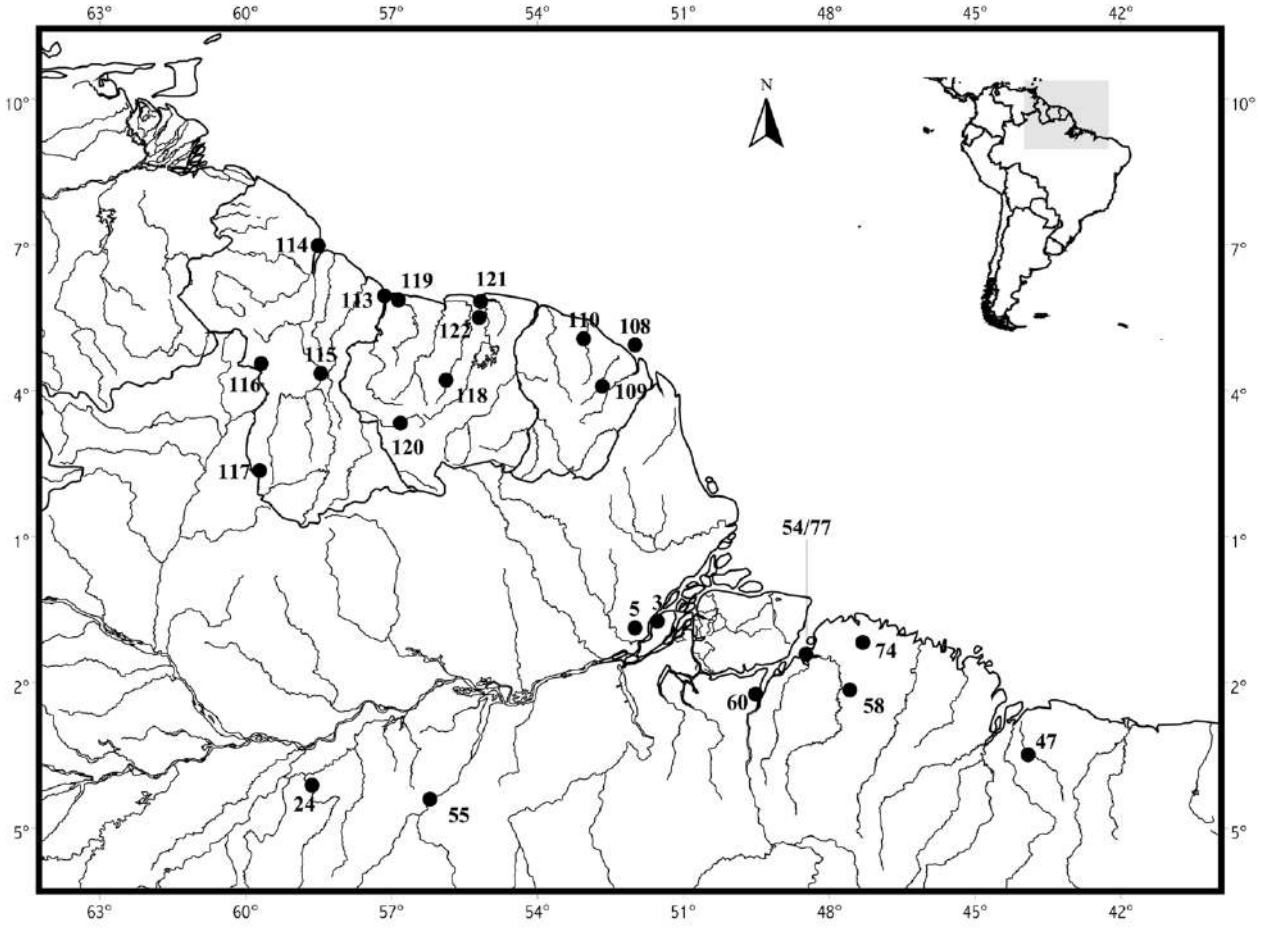

Fig.12- Geographic distribution of *Echimys*. For localities names and geographical coordinates, see Appendix II.

Genus *Makalata* Husson, 1978

Type-species – *Nelomys armatus* Geoffroy, 1838.

Diagnosis – An echimyid with mystacial region pheomelanic (rusty, from red to orange), tail with short hair, making scales plainly visible; postorbital process of zygoma formed mostly by jugal, squamosal projects below the postorbital process.

Distribution – Amazon basin, Northeastern Brazil and the Guiana region (see figure 13).

Species included – *M. didelphoides* (Desmarest, 1817); *M. macrura* (Wagner, 1842); *M. obscura* (Wagner, 1840); *M. occasius* (Thomas, 1921); *M. rhipidurus* (Thomas, 1928); *M. semivillosus* (I.Geoffroy, 1838). Synonyms: *Nelomys armatus* I. Geoffroy, 1838; *Loncheres carrikeri* Allen, 1911; *Loncheres castaneus* Allen and Chapman, 1897; *Loncheres flavidus* Hollister, 1914; *Loncheres guianae* Thomas, 1888; *Echimys longirostris* Anthony, 1921; *Loncheres punctatus* Thomas, 1899.

Genus *Phyllomys* Lund, 1839

Type-species – *Phyllomys brasiliensis* Lund, 1840.

Diagnosis – An echimyid with alisphenoid canal incomplete, formed by posterior foramen and a gutter extending until the sphenoidal fissure; upper molariformes formed by isolated lophs; dp4 pentalophodont with anterolophid and metalophid connected labially.

Distribution – East Brazil (Fig.14).

Species included: *P. blainvilii* (Jourdan, 1837); *P. brasiliensis* Lund, 1840; *P. dasythrix* Hensel, 1872; *P. kerri* (Moojen, 1950); *P. lamarum* (Thomas, 1916); *P. lundi* Leite, 2003; *P. mantiqueirensis* Leite, 2003; *P. medius* (Thomas, 1909); *P. nigrispinus* (Wagner, 1842); *P. pattoni* Emmons, Leite, Kock and Costa, 2002; *P. thomasi* (Ihering, 1897); *P. unicolor* (Wagner, 1842). Synonym: *Loncheres braziliensis* Waterhouse, 1848.

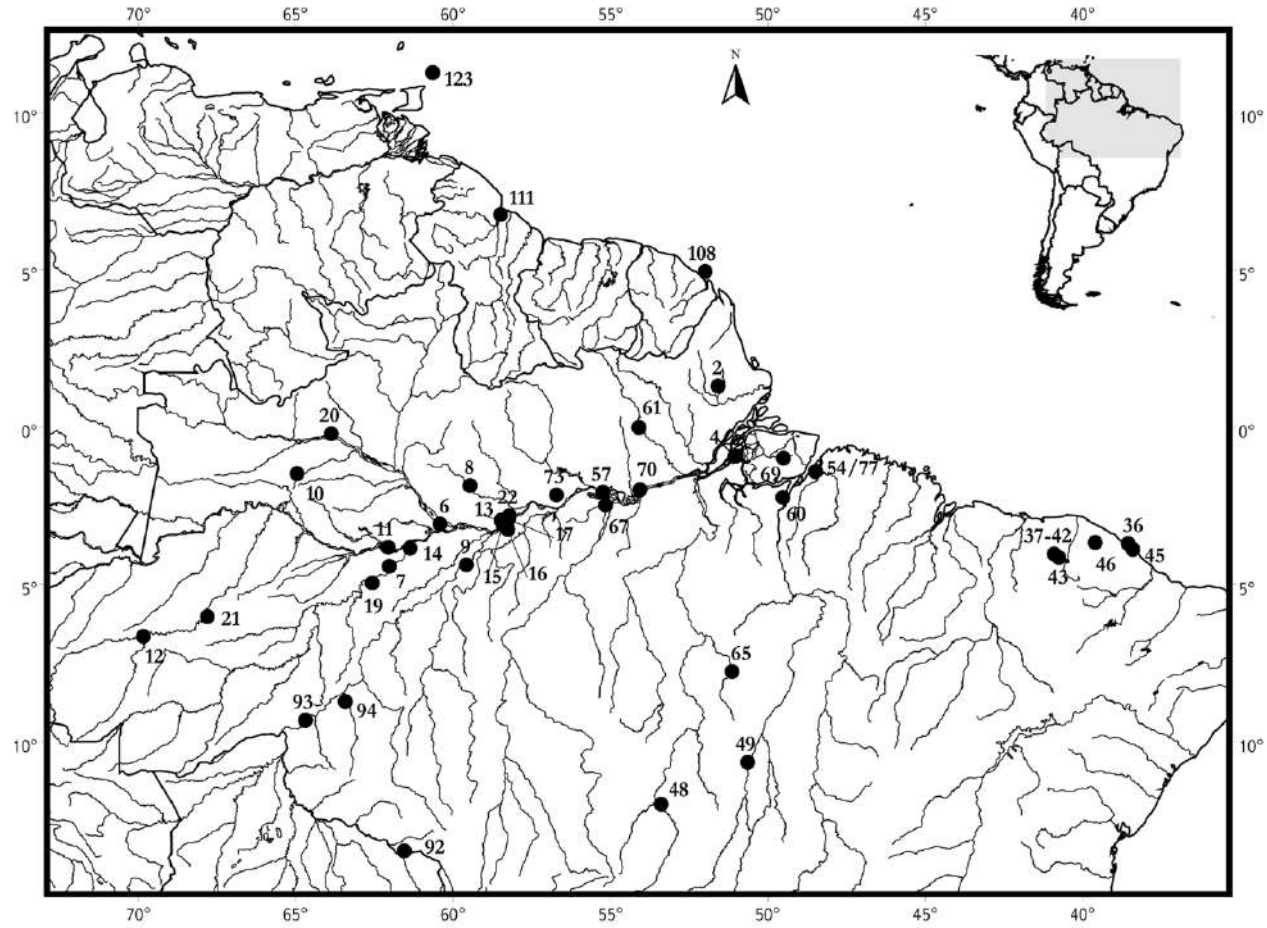

Fig.13- Geographic distribution of *Makalata*. For localities names and geographical coordinates, see Appendix II.

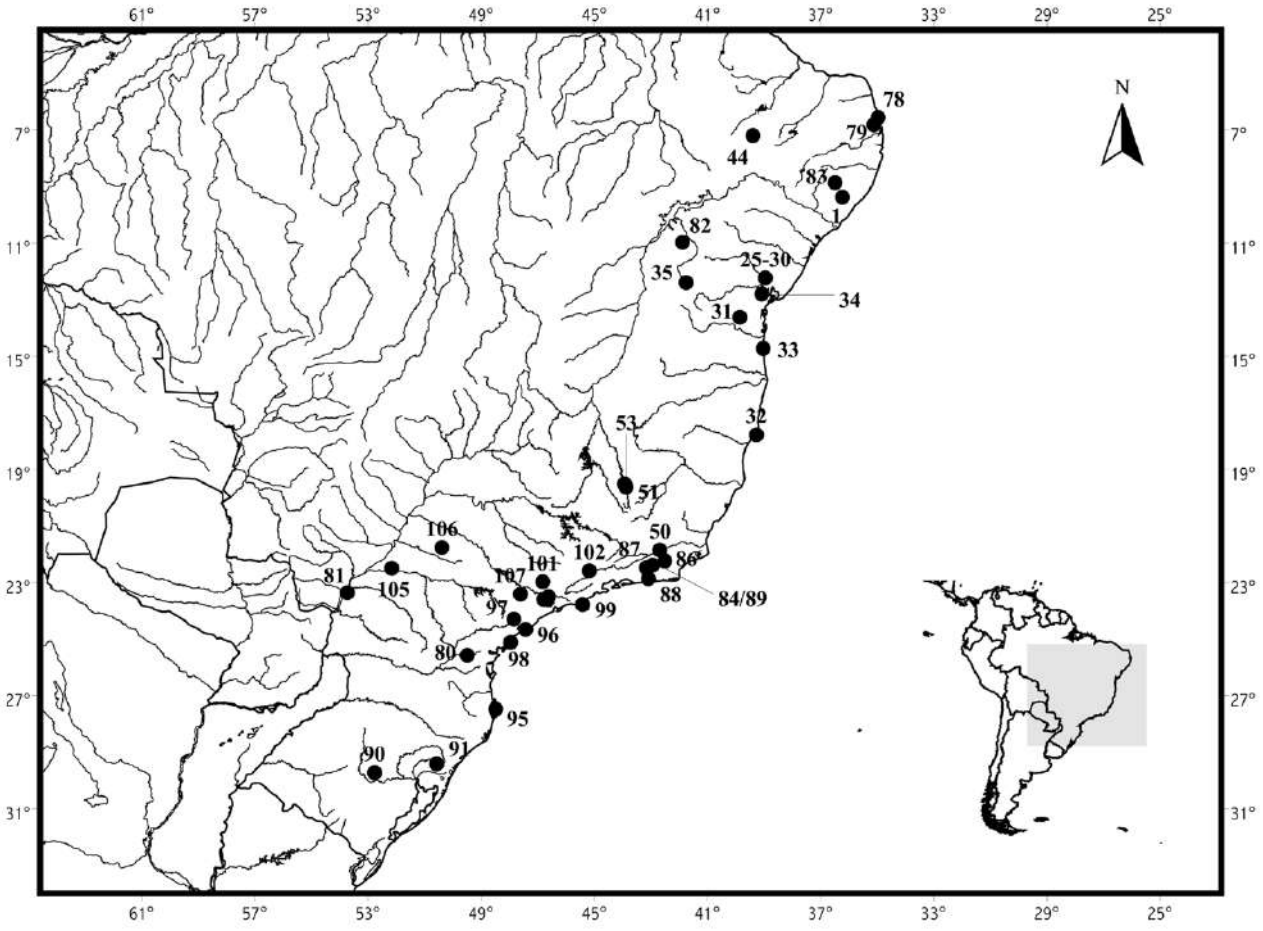

Fig.14- Geographic distribution of *Phyllomys*. For localities names and geographical coordinates, see Appendix II.

ACKNOWLEDGEMENTS

We are indebted to the curators of the several museums visited for their permission to study specimens under their care, namely Dr. João A. Oliveira (Museu Nacional - Rio de Janeiro); Dr. Paula Jenkins and Dr. Daphne Hills (Natural History Museum, London), Dr. Peter Giere (Museum für Naturkunde, Berlin), Dr. Olavi Grönwall (Naturhistorika Riksmuseet, Stockholm), Dr. Barbara Herzig, Dr. Friederike Spitzenberger, and Alexander Bibl (Naturhistorische Museum Wien), Dr. Richard.Kraft (Zoologische Staatsammlung München), Dr. Hans Jørgen Baagøe and Dr. Andersen Mogens (Zoological Museum University of Copenhagen), and Dr. Christiane Denys (Museum Nationale D´Histoire Naturelle, Paris). Research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (Biota Program 98/05075-7; G.E. Iack-Ximenes – grant 99/07973-5; A.R. Percequillo – grant 98/12273-0). We would particularly like to thank Dr. M.G.Vucetich for advice concerning dental nomenclature and Cristiano R. Moreira for photographs.

LITERATURE CITED

ALLEN, J.A. 1899. The generic names *Echimys* and *Loncheres*. **Bulletin of the American Museum of Natural History**, New York, **115**:257-264.

BRYANT, J.D. & MCKENNA, M.C., 1995. Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia; Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. **American Museum Novitates**, New York, **3156**:1-42.

BUTLER, P.M., 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent morphology. In: LUCKETT, W.P. & HARTENBERGER, J.L. [Eds.] **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York and London: Plenum Press. p.381-401.

CABRERA, A., 1961. Catálogo de los mamíferos de América del Sur. Volume II. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, Buenos Aires, **4**:309-732.

CANDELA, A.M., 1999a. **Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva y biogeográfica**. 357p. Ph.D. Dissertation, Facultad de Ciências Naturales y Museo.

CANDELA, A.M., 1999b. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino, 1904. **Palaeovertebrata**, Montpellier, **28**:53-73, figs.1-8.

CANDELA, A.M., 2002. Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): evolutionary significance. **Acta Paleontologica Polonica**, Warszaw, **47**(4):717-723.

CARVALHO, G.A.S & SALLES, L.O., 2004. Relationships among extant and fossil echimyids (Rodentia, Hystricognathi). **Zoological Journal of the Linnean Society**, London, **142**:445-477.

CARVALHO, J.C.M., 1955. Notas de viagem ao Rio Paru do Leste. **Publicações Avulsas do Museu Nacional**, Rio de Janeiro, **14**:1-82, figs.1-18.

CUVIER, G.F., 1809. Extrait des premiers Mémoires de M.F.Cuvier, sur les dents des mammifères considérés comme charactères génerics. **Nouveau Bulletin des Sciences, par la Société Philomathique**, Paris, **1**(24):394-395.

CUVIER, G.F., 1812. Essai sur de nouveaux caractères pour les genres des mammifères. **Annales du Muséum d'Histoire Naturelle**, Paris, **19**:268-295.

DESMAREST, A.G., 1817. **Nouveau Dictionnaire d'Histoire Naturelle, appliquée aux arts, a l'Agriculture, à l'Économie rurale et domestique, à la Médecine, etc**. *EAL-EZE*. Par une société de Naturalistes et d'Agriculteurs. Nouvelle Édition. Paris: Abel Lanoir Imprimerie. Tome X. 591p.

DIDIER, R., 1962. Note sur l'os penien de quelques rongeurs de l'Amerique du Sud. **Mammalia**, Paris, **26**(3):408-430.

EMMONS, L.H., 1993. On the identity of *Echimys didelphoides* Desmarest, 1817 (Mammalia: Rodentia: Echimyidae). **Proceedings of Biological Society of Washington**, Washington, **106**(1):1-4.

EMMONS, L.H. & FEER, F., 1990. **Neotropical Rainforest Mammals: A field Guide**. Chicago: The University Chicago Press. 281p.

EMMONS, L.H. & FEER, F., 1997. **Neotropical Rainforest Mammals: A field Guide**. 2.ed. Chicago: The University Chicago Press, 307p.

EMMONS, L.H.; LEITE, Y.R.; KOCK, D. & COSTA, L.P., 2002. A review of the named forms of *Phyllomys* (Rodentia, Echimyidae), with the description of a new species from coastal Brazil. **American Museum Novitates**, New York, **3380**:1-40.

EMMONS, L.H. & VUCETICH, M.G., 1998. The identity of Winge's *Lasiuromys villosus* and the description of a new genus of echimyid rodent (Rodentia: Echimyidae). **American Museum Novitates**, New York, **3223**:1-12.

EISENBERG, J.F. & REDFORD, K.H., 1999. **Mammals of the Neotropics. The Central Tropics. Ecuador, Peru, Bolivia, Brazil**. v.3. Chicago: The University of Chicago Press, 609p.

ELLERMAN, J.R., 1940. **The families and genera of living rodents with a list of named forms**.v.1. London: British Museum of Natural History, 689p.

FLYNN, L.J.; JACOBS, L.L. & CHEEMA, I.U., 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. **American Museum Novitates**, New York, **2891**:1-25.

GEOFFROY, I., 1838. Notices sur les rongeurs épineux désignés par les auteurs sous les noms d' *Echimys*, *Loncheres*, *Heteromys* et *Nelomys*. **Revue Zoologique**, Paris, **1**:99-101.

GEOFFROY, I., 1840. Notices sur les rongeurs épineux désignés par les auteurs sous les noms d' *Echimys*, *Loncheres*, *Heteromys* et *Nelomys*. **Magasin de Zoologie 2nd Serie**, Paris, **2**:1-57.

HUSSON, A.M., 1978. **The Mammals of Suriname**. Zoologische Monographieën van het Rijksmuseum van natuurlijke historie 2. Leiden: E.J.Brill. xxxiv, 569p., il.

IACK-XIMENES, G.E.; DE VIVO, M. & PERCEQUILLO, A.R. (in press) A new species of *Echimys* Cuvier, 1809 (Rodentia, Echimyidae) from Brazil. **Papéis Avulsos de Zoologia, São Paulo**, São Paulo.

JAEGER, J.J., 1989. L'évolution de la pentalophodontie chez les rongeurs caviomorphes (Mammalia, Rodentia) In: DAVIS-DOMERGES, J.L.; CHALINE, J. & LAURIN, B. (Eds.) **Ontogenèse et évolution**. Geobios, Mémoire Spéciale 12. Lyon: Elsevier Ed. p.235-244.

JAEGER, J.J.; DENIS, C. & COIFFAIT, B., 1985. New Phiomorpha and Anomaluridae from the late Eocene of North-West Africa: phylogenetics implications. In: LUCKETT, W.P. & HARTENBERGER, J.L. (Eds.) **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York: Plenum Press, p.685-712.

JOURDAN, C., 1837. Mémoire sur quelques mammifères nouveaux. **Comptes Rendus Hebdomadaires des Sceànces de L'Academie des Sciences**, Paris, **15**:521-524.

LAVOCAT, R., 1976. Rongeurs caviomorphes de l'Oligocène de Bolivie. II Rongeurs du Bassin Deseadien de Salla-Luribay. **Palaeovertebrata**, Montpellier, **7**(3):15-90.

LEITE, Y.L.R., 2003. Evolution and systematics of the Atlantic tree rats, genus *Phyllomys* (Rodentia, Echimyidae) with description of two new species. **University of California Publications, Zoology**, Berkeley, **132**:1-118.

LUND, P.W., 1839. Nouvelles observations sur la faune fossile du Brésil; extraits d'une lettre adressée aux redacteurs par M.Lund. **Annales des Sciences Naturelles, ser.2**, Paris, **12**:205-208.

MAUFFREY, J.F. & CATZEFLIS, F., 2003. Ecological and isotopic discrimination of syntopic rodents in a neotropical rain forest of French Guiana. **Journal of Tropical Ecology**, Cambridge, **19**:209-214.

MOOJEN, J., 1948. Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications, Museum of Natural History**, Kansas, **1**(19):301-406.

MOOJEN, J., 1952. **Os Roedores do Brasil**. Rio de Janeiro: Instituto Nacional do Livro. Biblioteca Científica Brasileira, Série A-II., 214p., il.

NOWAK, E.M., 1999. **Walker's Mammals of the World**. 6.ed., v.2. Baltimore and London: The John Hopkins University Press. 1936p., il.

OLIVEIRA, T.G. & MESQUITA, E.R.L., 1998. Notes on the distribution of the white faced tree rat, *Echimys chrysurus* (Rodentia, Echimyidae) in northeastern Brazil. **Mammalia**, Paris, **62**(2):305-306.

PATTON, J.L., 1987. Species groups of spiny rats genus *Proechimys* (Rodentia: Echimyidae). **Fieldiana Zoology, n.s.**, Chicago, **39**:305-345.

PATTON, J.L. & ROGERS, M.A., 1983. Systematic implications of non-geographic variation in the spiny rat genus *Proechimys* (Echimyidae). **Zeitschrift für Saugertierkunde**, Jena, **48**:363-370.

PELZELN, A., 1883. Brasilische Säugerthiere. Resultate von Johann Natterers Reise in den Jahren 1817 bis 1835. **Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien**, Wien, **33**:1-140.

TATE, G.H.H., 1935. The taxonomy of the genera of Neotropical hystricoid rodents. **Bulletin of the American Museum of Natural History**, New York, **68**:295-447.

THOMAS, O., 1910. Mammals from the River Supinaam, Demerara, presented by Mr. F.V.McConnell to the British Museum. **Annals and Magazine of Natural History**, London, **8**(6):111-14.

THOMAS, O., 1916. Some notes on the Echimyinae. **Annals and Magazine of Natural History**, London, **8**(18):294-301.

THOMAS, O., 1928. A new *Echimys* from Eastern Ecuador. **Annals and Magazine of Natural History**, London, **10**(2):409-410.

TROUESSART, E.L., 1881[1888]. Catalogue des mammifères vivants et fossiles. Ordre des rongeurs. **Bulletin de la Société d'Etudes Scientifiques D'Angers**, Angers, **10**(1):58-144; (2):145-212 [for 1880].

TROUESSART, E.L., 1905. **Catalogum mammalium tam viventium quam fossilium**. Suppl. Pts. 3 & Ungulata to Monotremata. Berlin: Friedländer, 929p.

VANZOLINI, P.E., 1992. **A Supplement to the Ornithological Gazetteer of Brazil**. São Paulo: Museu de Zoologia, Universidade de São Paulo, 252p.

UNITED STATES BOARD ON GEOGRAPHICAL NAMES, 1993. **Gazetteer. Guyana**. Official Standard Names. Washington: Office of Geography, Department of the Interior, 123p.

WAGNER, J.A., 1845. Diagnosen einiger neuer Arten von Nagern und Handflüglern. **Archiv für Naturgeschichte**, München, **11**:145-149.

WAGNER, J.A., 1850. Beiträge zur Kentniss der Säugethiere Amerika's. **Abhandlungen der Königlichen Akademie der Wissenschaft**, München, **5**(2):271-332.

WAHLERT, J.H., 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. **Bulletin of the Museum of Comparative Zoology**, Cambridge, **113**:113-214.

WAHLERT, J.H., 1983. Relationships of Florentiamyidae (Rodentia, Geomyidae) based on cranial and dental morphology. **American Museum Novitates**, New York, **2769**:1-23.

WAHLERT, J.H., 1985. Cranial foramina of rodents. In: LUCKETT, W.P. & HARTENBERGER, J.L. (Eds.) **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York: Plenum Press, p.311-333.

WATERHOUSE, G.R., 1848. **A Natural History of the Mammalia II**. London: Hyppolyte Bailliere Publisher, 500p., il.

WOLFHEIM, J.H., 1983. *Alouatta seniculus*. In: **Primates of the World - Distribution, Abundance, and Conservation**. Seattle and London: University of Washington Press. 831p.

WOODS, C.A., 1993. Hystricognathi. In: WILSON, D.E. & REEDER, D.A. (Eds.) **Mammals Species of the World. A taxonomic and geographic reference**. 2.ed. Washington: Smithsonian Institution Press. p.771-806.

WOODS, C.A. & HOWLANDS, E.B., 1979. Adaptative radiation of capromyid rodents: anatomy of the masticatory apparatus. **Journal of Mammalogy**, Provo, **60**(1):95-116.

ZIMMERMANN, E.A.W., 1780. **Geographische Geschichte des Menschen und der viersüßigen Thiere. Zweiter Band Enthalt ein vollständiges verzeichniß aller bekannten Quadrupeden von E. A. W Zimmermann**. Leipzig. In der Weygandschen Buchhandlung 1780.

APPENDIX I

Specimens examined (Abreviations: s&s = skin & skull, ♂ = males, ♀ =females, Faz.=Fazenda, Sit.=Sítio):

Echimys (N= 29): *Echimys chrysurus* (N= 27) – BRAZIL - PARÁ: Aurá, Belém, MN3847 (s&s); Cametá, Rio Tocantins: MZUSP4510, 4547, 4548, 4551, 4642, MN21504, NRM A587194-A587196 (♂, s&s), 4557, 4558 (♂, skin); Pará: MZUSP25809 (♂, skin), MNK1181 (♂, s&s, holotype of *Loncheres paleaceus*); Peixe-Boi: BMNH14.6.10.1 (♂, s&s); Utinga, Belém: MZUSP25810 (♂, skin); Rodovia BR-010 km 87-94: MZUSP26200 (skull); AMAPÁ - Rio Amapari: MN21505 (♀, s&s); Serra do Navio: MN20411 (s&s); GUYANA: Potaro Highlands, 1300ft.: BMNH7.6.10.4 (♂, skin); Supinaam river: BMNH10.5.4.21 (♂, skin); Upper County [Upper Corentyn]: BMNH43.8.19.14 (♀, s&s); SURINAM: Surinam: MNK1182 (♂, s&s); FRENCH GUIANA - Cayenne: MNHN 1995-1398 (♂, s&s, holotype of *Echimys cristatus*); rive droite du Petit Saut, Programme Faune Sauvage: MNHN1999-1082 (skin & skeleton); No locality: MZUSP4011 (skull); MN60538 (skeleton). *Echimys* sp. (N=2) – BRAZIL - PARÁ: Barreirinhas, Tapajós River: MZUSP26650 (♂, s&s); AMAZONAS: Virgem Guajará, Rio Madeira: MN67549 (alcohol).

Makalata (N= 93): *Makalata didelphoides* (N= 45) – BRAZIL - AMAPÁ: Igarapé do Braço, Rio Araguari: IEPA: 0174 (♂, s&s); AMAZONAS: Ayapua, Rio Purús, MNK35816, 35817 (♂, s&s); Balbina: MN26925 (♂, s&s); Igarapé Anibá, N. bank Rio Amazonas: MZUSP4641, 26553 (♀, s&s), 4549 (♂, s&s); Lago do Batista, Rio Amazonas: MZUSP4509, 4550, 26554, 26599 (♀, s&s), 4546, 4559, 26600 (♂, s&s), 26601 (s&s); Rio Juruá: MZUSP: 896 (skull), 899 (♂, s&s); Silves: MZUSP: 4553 (♂, s&s); 40km up to mouth of Rio Ariaú, right bank of Rio Negro: MN30487 (skull), 30475 (skull); Codajás, Rio Solimões (N): NRM A59 8016 (♀, s&s); Igarapé do Castanha, Rio Purús: NRM A591144, A591148 (♀, s&s); Itacoatiara, Rio Amazonas (N): NRM A581433 (♀, s&s); João Pessôa, Rio Juruá: NRM2117, 2163 (♂, s&s), 2333 (♀, s&s); Lago do Canaçari, Rio Amazonas (N): NRM A621453 (♂, s&s); Redempção, Rio Purús: NRM A591176 (♀, s&s); PARÁ: Boiuçu, N. bank Rio Amazonas: MZUSP4481, MN6450 (♀, skin); 26593 (♀ skull); Rio Ererê: MN6151 (♀ s&s); Irocanga, Rio Tapajós (W): NRM A588045, A598209 (♀, s&s), A608046 (♂, s&s); Paraná de Faro: MNK38814 (♂, s&s); FRENCH GUIANA: Cayenne: MNK1183 (♂, s&s, holotype of *Nelomys armatus*:); Environs immédiate du barrage de Petit Saut (Programme Faune Sauvage): MNHN1999-1082 (♀, s&s); GUIANA: Guiana: MNK8345 (♂, skull); BONASICA: Essequibo river: NRM1 (♂, s&s); DEMERARA: Plantation Providence: NRM2 (♂, s&s); No locality: MZUSP25854, ZSM54a (skulls); MN31530 (♀, skull); *Makalata castaneus* (N= 1): TOBAGO: ZMUC: CN2307 (s&s); *Makalata macrura* (N=2) – BRAZIL - AMAZONAS: Borba: NMW B921 (♀, skin, holotype:); Carvoeiro, próximo à boca do Rio Branco: NMW923 (♂, s&s); *Makalata* sp. (N= 45) – BRAZIL - AMAPÁ: Rio Tracajatuba: MN20412 (♂, skull), 20413 (♀, skull); AMAZONAS: Balbina: MZUSP22757, 22933, 22936, 22937, 26923, 26924 (♂, s&s), 22930, 22931, 22934, MN26922 (♀, s&s); CEARÁ: Fortaleza: MN8279 (♀, skin); Sit. Piraquara, São Benedito: MN21488, 21494 (♀, s&s), 21495 (♂, s&s); Sit. Macapá, São Benedito: MN21489 (♀, s&s), 21499 (♂, s&s); Sit. Cinta do S. José, São Benedito: MN21490 (♂, s&s); Sit. Guaribas do Amaral, São Benedito: MN21491 (♂, skin), 21500 (♀, s&s), 21501 (♂, skull); Sit. São José da Boa Vista, São Benedito: MN21496 (♀, s&s); Sit. Barra, São Benedito: MN11101 (♂, s&s), 21492 (♀, s&s); Sit. Trairuçu, Itapagé, Ceará: MN31541 (♀, skin) Sit. Trairuçú (córrego no litoral da praia) Aguiráz: MN21493 (♂, s&s); 31541 (♀, skull); Sit. Mazagão, Guaraciaba do Norte: MN21497 (♂, s&s); 21498 (♀, skin); Ceará: MNI p267 (♀, skull); MATO GROSSO: Jacaré, baixo Rio Kuluene, Alto Xingú: MN10394 (♂, s&s); Rio Tapirapé: MN6152 (♂, skin); PARÁ: Cametá, Rio Tocantins: MN4080 (♂, s&s); Coatacoará, Rio Parú do Leste, Almeirim: MN21502 (♀, skin); Gorotire, Rio Fresco: MZUSP25824 (♀, s&s); Monte Alegre: MN1929 (skull); 1971, 1972 (♂, skins); Marajó: MNK38813, 43570 (♀, s&s); Utinga, Belém: MN19619 (♀, s&s); RONDÔNIA: UHE Samuel: MZUSP27446 (♂, s&s); Campo dos Veados, Rio Guaporé: NMW ST182 (♀, s&s); Pedra de Amolar, Salto do Girão, Rio Madeira: NMW917 (♂, skin).

Phyllomys (N= 137): *Phyllomys blainvilii*: (N=39) BRASIL - ALAGOAS: Viçosa: MN21513 (♂, s&s); BAHIA: Lapa: MN4125-4127, 4132, 4137, 4140, (♂, s&s), 4133 (♂, skin), 4128, 4131 (♀, s&s), 4136 (s&s); Várzea da Canabrava, Seabra: MN21626, 21628, 21630, 21635, 21627, 21638, 21639,

21650 (♂, s&s), 31544 (♂, skull), 21631-21634, 21636, 21640, 21643-21645, 21649 (♀, s&s), 2P1641, 2P1647, 2P1664 (♀, skull); CEARÁ: Sit. Serra Bebida Nova, Crato: MN21572, 21574 (s&s), 21599, 21601 (♂, s&s); PERNAMBUCO: Sit. Barquinho, Garanhuns: 21516 (♂, s&s), No locality: NMW B1101 (♂, s&s); *Phyllomys brasiliensis* (N=3): BRAZIL: MINAS GERAIS: Rasquão do Azude: ZMK CN83 (♀, s&s); Lagoa Santa: ZMK81 (♀, s&s); Sumidouro: ZMK CN83 (♂, skeleton); *Phyllomys dasythrix*: (N= 2) BRAZIL - RIO GRANDE DO SUL: Pinheiros, Candelária: MN6238 (♂♂, s&s); São Francisco de Paula: MN21503 (♂, s&s). *Phyllomys* aff. *dasythrix*: (N= 1) BRAZIL - SÃO PAULO: Teodoro de Sampaio, Serra do Diabo: MZUSP8885 (♀, s&s). *Phyllomys lamarum*: (N=16) BRAZIL - BAHIA: Faz. Morro, Feira de Santana: MN21654 (♀, s&s); Faz. Estiva, Feira de Santana: MN21655 (♀, s&s), 21656 (♀, s&s); Faz. Salgado Quarta, Feira de Santana: MN21661 (♂, skin); Faz. Estrada Nova, Feira de Santana: MN21660 (♂, skull); Faz. Quituba, Feira de Santana: MN21662 (♀, skin), 21663 (♀, skin), 21664 (♂, s&s); Faz. Feira Nova 2ª, Feira de Santana: MN21667 (♂, skin), 21668 (♂, skin); PARAÍBA: Camaratuba, Mamanguape: MZUSP8413 (♀, s&s), 8415 (♂, s&s), 8416 (♂, s&s), 8417 (♂, s&s), 8418 (♀, skull); Uruba, Mamanguape: MZUSP8414 (♂, s&s).

Phyllomys medius: (N= 6) BRAZIL - PARANÁ: Porto Camargo, Rio Paraná: MZUSP7716 (♀ s&s); SANTA CATARINA: Florianópolis: MN31568, 31570-31572 (skins); SÃO PAULO: Barra do Onça Parda: MZUSP 10629 (♀, s&s); *Phyllomys nigrispinus*: (N=29) BRAZIL - PARANÁ: Guajuvira: MN6431 (skin); SÃO PAULO: Barra do Icaparra: MZUSP25862, 25863 (♀, s&s); Itatiba: MZUSP664, 666 (s&s), 665, 25819 (♂, s&s); São Paulo: MZUSP: 1949, 1952, 1953 (♀, s&s); Interlagos, São Paulo: MZUSP10311, 10312, 10316-10318, 25854-25857 (♀, s&s), 10319, 10320, 25853, 25858-25861 (♂, s&s); Taboão da Serra: MZUSP26652 (♀, s&s); Vanuire: MZUSP3738 (♀, s&s); Ypanema: NMW B918 (♂, skin, holotype). *Phyllomys pattoni*: (N= 26) BRAZIL - BAHIA: faz. Monte Castelo, ilha da Cassumba, 7km SW Caravelas: MZUSP 31953-31956 (♂, s&s, all paratypes); Pirataquissé, Ilhéus: MN10453, 11258 (♂, s&s), 11256, 11257, 21517 (♀, s&s); São Felipe: MN22264 (s&s); MINAS GERAIS: Faz. São Geraldo, Além Paraíba: MN4077 (♂, s&s); PERNAMBUCO: Dois Irmãos, Recife: MN8195 (s&s); RIO DE JANEIRO: São Francisco, Niterói: 6449 (♀, s&s); Teresópolis: MN2232 (skull), 2239 (♀, skull), 2240 (skull), 6440 (♂, skull), 6443 (♂, skull), 6742 (♂, s&s); Faz. Alpina, Teresópolis: MN: 1933 (s&s), 31522 (skull); Nova Friburgo: MN31564 (♂, skin), 31567 (♂, skin); Ilha Grande: MN31566 (s&s); Santa Cruz, Petrópolis: MN21508 (♂, s&s); SÃO PAULO: Piquete: MZUSP138 (alcohol); *Phyllomys thomasi*: (N=14) BRAZIL: SÃO PAULO: Ilha de São Sebastião: MZUSP45 (♂ skin), 47 (♂, s&s, holotype), 51 (♂, skin), 223 (♂, skull), 526 - 528 (♂, skull), 532 (♂, skin), 535 (♂, s&s), 2151 (♂, s&s), 3197 (♂, s&s), 3199 (♂, s&s), 6433 (♂, s&s), 27755 (♀♀, s&s); *Phyllomys* sp. (N=1) No locality: MN1930 (♂, skin).

Toromys (N= 57): *Toromys grandis* – BRAZIL - AMAZONAS: Lago Batista, N. bank Rio Amazonas: MZUSP4790 (♀, s&s), NRM A587189-A587193 (♂, s&s); Manaqueri im Mündungsbereich des Rio Solimões: NMW: B920 (s&s, holotype); Silves: MZUSP4487 (♀, s&s), 4488, 4489 (♂, s&s); Urucurituba, Rio Amazonas: NRM A587184-A587186 (♂, s&s); 556 (♂, skin); PARÁ: Belterra, Santarém: MN5751 (♂, s&s); Bravo, N. bank Rio Amazonas: MZUSP4719, 4720, 4722, 4723 (♂, s&s); Faz. Recreio, Ilha Caviana: MZUSP: 25815 (♀, s&s); Facienda Paraiso bei Faro: MNK38812 (♂, s&s); Lago Cuiteua, N. bank Rio Amazonas: MZUSP4786 (♀, s&s); Paraná do Bom Jardim, Paissandú, Nhamundá: MZUSP8960 (♂, s&s); 8961 - 8963 (♀, s&s); 25817 (♂, s&s); Paraná de Faro: MNK38811 (♀, s&s); BMNH11.12.22.12 (♂, s&s); Santarém: MN11922-11924, 11926, 11928, 11929, 11940, 11941 (♀, s&s); 11925, 11927, 11930-11939 (♂, s&s), BMNH: 5.6.3.4 (♂, skull); Igarapéassú, Santarém: MN11584 (♀, s&s); Faz. São Pedro, Monte Alegre: MN1944 (♂, s&s), 1945 (♀, s&s); Óbidos: MN5968 (♂, s&s); Santa Rita, Rio Amazonas: NRM A58 7187-A59 7188 (♂, s&s); Jardim Zoológico, Santarém: BMNH5.6.3.1 (♀, s&s).

APPENDIX II

Gazetteer

BRAZIL - ALAGOAS: 1- Viçosa 09°24'S 36°14'W. AMAPÁ: 2- Igarapé do braço, Rio Araguari 01°17'02"N 51°35'20"W; 3- Rio Amapari. 00°45'N 51°32'W; 4- Rio Tracajatuba 00°56'N 51°00' W; 5- Serra do Navio 00°53'44"N 52°00'08"W. AMAZONAS: 6- 40km up to mouth of Rio Ariaú right bank of Rio Negro *c.* 03°06'S 60° 26'W; 7- Aiapuá, Rio Purus 04°27'S 62°03'W; 8- UHE Balbina, Rio Uatumã 01°53'S 59°28'W; 9- Borba, Rio Madeira 04°24'S 59°35'W; 10- Carvoeiro, near mouth of Rio Branco 01°26'S 62°01'W; 11- Codajás, Rio Solimões 03°50'S 62°05'W; 12- Eirunepé (=João Pessôa), Rio Juruá 06°40'S 69°52'W; 13- Igarapé Anibá, N. bank Rio Amazonas 02°59'S 58°29'W; 14- Igarapé do Castanho, Rio Purús 3°52'S 61°23'W; 15- Itacoatiara Rio Amazonas, N. bank 03°08'S 58°25'W; 16- Lago do Batista, Rio Amazonas 03°17'S 58°16'W; 17- Lago do Canaçari 02°57'S 58°15'W; 18- Manaqueri, Rio Solimões 03°29'S 60°31'W; 19- Redenção, Rio Purús 04°58'S 62°35'W; 20- Rio Ererê, left bank Rio Negro 00°14'S 63°53'W; 21- Rio Xiruã, afl. right bank Rio Juruá 06°03'S 67°50'W; 22- Silves 02°50'S 58°13'W. 23- Urucurituba, Rio Amazonas 02°46'S 57° 49'W; 24- Virgem Guajará, Borba, Rio Madeira 04°19'44"S 59°42'26"W. BAHIA: Feira de Santana 12°15'S 38°57'W (includes 25- Faz. Estiva, 26- Faz. Estrada Nova, 27- Faz. Feira Nova 2ª, 28- Faz. Morro, 29- Faz. Quituba, 30- Faz. Salgado Quarta); 31- Lapa 13°39'S 39°51'W; 32- Faz. Monte Castelo, ilha da Cassumba, 7km SW Caravelas 17°48'06" 39°15'49" W; 33- Pirataquissé, Banco da Vitória, Ilhéus *c.* 14°45'S 39°04'W; 34- São Felipe 12°50'50" S 39°05'22"W; Seabra 12°25'S 41° 46'W (includes 35- várzea da Cana Brava, Seabra). CEARÁ: 36- Fortaleza 03°43'02"S 38°32'35"W; São Benedito 04°03'S 40°53'W (includes: 37- Sit. Barra; 38- Sit. Cinta do S. José, 39- Sit. Guaribas do Amaral, 40- Sit. Macapá, 41- Sit. Piraquara; 42- Sit. São José da Boa Vista); Guaraciaba do Norte 04°10' 01" S 40°44'51"W (includes 43- Sit. Mazagão, Guaraciaba do Norte); 44- Sit. Serra Bebida Nova, Crato 07°14'03"S 39°24'34"W; 45- Sit. Trairuçú (córrego no litoral da praia), Aquiráz 03°54'05"S 38°23'28"W; 46- Sit. Trairuçú, Itapagé 03°41'S 39°35'W. MARANHÃO: 47- Vargem Grande 03°30'S 43°55'W (Locality from OLIVEIRA & MESQUITA, 1998; Four specimens were collected). MATO GROSSO: 48- Jacaré, baixo Rio Kuluene, Alto Xingú 12°00'S 53°24'W; 49- Rio Tapirapé 10°40'54"S 50°39'22"W. MINAS GERAIS: Além Paraíba 21°52'S 42°41'W (includes 50- faz. São Geraldo, Além Paraíba); 51-Lagoa Santa 19°38'S 43°53'W; 52- Rasquão do Azude (not located; probably near to Lagoa Santa); 53- Sumidouro 19°32'28"S 43°56'28"W. PARÁ: Belém 01°26'S 48°29'W (includes 54- Aurá, Belém; 77- Utinga, Belém); 55- Barreirinhas, Rio Tapajós 04°25'S 56°13'W; 56- Belterra, Santarém 02°38'S 54° 56'W; 57- Boiuçu, N. bank Rio Amazonas 02°05'S 55°14'W; 58- BR-010 km 87-94 *c.* 02°10'S 47°35'W. 59- Bravo, N. bank Rio Amazonas 01°54'S 55°10'W; 60- Cametá, Rio Tocantins 02°15'S 49°31'W; 61- Coatacoará, Rio Parú do Leste, Almeirim 00°02'48"S 54°06'48"W (coordinates based on CARVALHO [1955] itinerary); 62- Faz. Paraíso, Faro, Rio Amazonas 02°05'S 56°46'W; 63- faz. Recreio, ilha Caviana 00°10'N 50°10'W; 64- Faz. São Pedro, Monte Alegre: See Monte Alegre; 65- Gorotire, Rio Fresco 07°47'S 51°08'W; 66- Igarapé Açú, left bank of Rio Tapajós, Santarém 03°44'S 55°31'W; 67- Iroçanga, Rio Tapajós 02°30'S 55°10'W; 68- lago Cuiteua, N. bank Rio Amazonas 01°49'S 54° 58'W; 69- Marajó 01°00'S 49°30'W; 70- Monte Alegre 02°00'28"S 54°04'09"W; 71- Óbidos 01°55'S 55°31'W; 72- Paraná de Bom Jardim, Nhamundá, Paissandú 02° 02'S 56°12'W (VANZOLINI , 1992); 73- Paraná de Faro 02°10'S 56°44'W; 74- Peixe-Boi 01°11'32"S 47°18'50"W; 75- Santa Rita, Rio Amazonas 02°02'S 55° 18'W (Paraná do Bom Jardim, near Bom Jardim (or Santa Rita) island. Located on map SA21 of Hispanic America); 76- Santarém 02° 26' S 54° 42' W. PARAÍBA: 78- Camaratuba, Mamanguape 06°35'32" S 34°58'12"W; 79- Mamanguape 06°50'19"S 35°07'34"W (includes Uruba, Mamanguape). PARANÁ: 80- Guajuvira 25°35'51"S 49°30'59"W; 81- Porto Camargo, Rio Paraná 23° 22'05"S 53°44'35"W; PERNAMBUCO: Recife 11°00'35"S 41°53'23"W (includes 82- Dois Irmãos, Recife); Garanhuns 08°53'25"S 36°29'34"W (includes 83- Sit. Barquinho, Garanhuns). RIO DE JANEIRO: 84- Faz. Alpina, Teresópolis 22°19'S 42°59'W; 85- Ilha Grande 23°09' S 44°14'W; 86- Nova Friburgo 22°16'55"S 42°31'52"W; Petrópolis 22°30'18"S 43° 10'43" W (includes 87- Santa Cruz, Petrópolis); Niterói 22°53'00"S 43°06'13"W (includes 88- São Francisco, Niterói); 89- Teresópolis 22°24'44"S 42°57'56"W. RIO GRANDE DO SUL: 90- Candelária 29°40'09"S 52°47'20"W (includes Pinheiros, Candelária 29°44'S 52°46'W); 91- São Francisco de Paula 29°26'53"S 50°35'01"W. RONDÔNIA: 92-

Campo dos Veados Rio Guaporé 13º 29' S 61º 34' W; 93- Pedra de Amolar Salto do Girão Rio Madeira 09º20'S 64º43'W; 94- UHE Samuel 08°45'S 63°27'W. SANTA CATARINA: 95- Florianópolis 27°29'S 48°29'W. SÃO PAULO: 96- Barra de Icaparra 24º41'S 47º26'W; 97- Barra do Onça Parda 24º 19'S 47º51'W (ribeirão Onça Parda); 98- Ilha do Cardoso 25º08'S 47º58'W; 99- Ilha de São Sebastião 23°48'S 45°25'W; 100- Interlagos, São Paulo (see São Paulo); 101- Itatiba 23º00'21"S 46º50'20"W; 102- Piquete 22°36'S 45º10'W; 103- São Paulo 23°32'S 46°37'W; 104- Taboão da Serra, 23º37'34"S 46º47'30"W; 105- Teodoro de Sampaio, near Serra do Diabo 22°31'57"S 52°10'03"W; 106- Vanuire, posto indígena 21°47'S 50º23'W; 107- Ypanema (currently Floresta Nacional de Ipanema, 20km NW Sorocaba) 23º26 07"S 47º37'41"W.

FRENCH GUIANA: 108- Cayenne 04º56'N 52º00'W; 109- Nouragues 04º05'N 52º40'W (MAUFFREY & CATZEFLIS, 2003); 110- rive droite du Petit Saut (Programme Faune Sauvage) 05º04'N 53º03'W.

GUYANA - DEMERARA-MAHAICA: 111- Bonasika creek, Essequibo River 06º45'N 58º30'W; 112- Plantation Providence (not located); 113- East Berbice Corentyne Upper County (here as Upper Corentyne Local Government Distric 5º57'N 57º09'W; Collected by Sir R. Schomburgh; According THOMAS (1916), the specimen of Sir Schomburgh came from Upper Corenty). POMEROON-SUPENAAM: 114- Supinaam river, 1300ft 06º59'N 58º31'W (Collected by McConnell/Cozier. In USBGN, 1976 as Supenaam River; see also THOMAS (1910) and WOLFHEIM (1983). POTARO-SIPARUNI: 115- Kabukalli, landing Iwokrama forest Potaro-Siparuni (not located, here as Akramukra falls 04º21'S 58º28'W; based on specimen ROM111578); 116-Potaro Highlands, 1300ft. (not located, here as Kowa Mountain 04º51'N 59º 41'W). UPPER TAKUTU-UPPER-ESSEQUIBO: 117- Tamton 02º21'N 59º43'W (based on specimen ROM36840).

SURINAM: (Localities based on 8 specimens examined by Husson, 1978) BROKOPONDO: 118- Bedoti, south of Gansee on West Bank of Suriname River, locality now submerged by the Brokopondo Lake 04º13'N 55º53'W. NICKERIE: 119- Groot Henarpolder South east of Nieuw Nickerie, northwestern Nickerie district 05º52'N 56º52'W; 120- Zuid River, near Kayserberg Airstrip, southern Nickerie District 3º20'N 56º49'W. PARA: 121- Republiek, about 35km South of Paramaribo 5º30'N 55º12'W. PARAMARIBO: 122- Agricultural Experimental Station (Cultuurtuin) 05º50'N 55º10'W.

TOBAGO: 123- Tobago 11º15'N 60º40'W.