**University of São Paulo
“Luiz de Queiroz” College of Agriculture
Center for Nuclear Energy in Agriculture**

**The genus *Hylaeamys* (Weksler, Percequillo and Voss, 2006): species
definition and phylogeny of the forest clade of Oryzomyini tribe**

Pamella Gusmão de Góes Brennand

Thesis presented to obtain the degree of Doctor in
Science. Area: Applied Ecology

**Piracicaba
2015**

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Bachelor in Biological Sciences

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To the best scientist and women I ever met, my Mom!

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“Nothing in life is to be feared,
it is only to be understood.
Now is the time to understand more,
so that we may fear less.”
Marie Curie

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RESUMO

O gênero *Hylaeamys* (Weksler, Percequillo and Voss, 2006): definição de espécies e filogenia do clado florestal da tribo Oryzomyini

Padrões faunísticos atuais de diversidade, distribuição geográfica, relações filogenéticas e biogeográficas constituem uma ferramenta para a compreensão da história evolutiva dos táxons. As delimitações destes táxons e suas respectivas relações filogenéticas nos revelam eventos de especiação e consequentemente nos permitem levantar hipóteses gerais de diversificação de um determinado grupo. O gênero *Hylaeamys* está inserido na tribo Oryzomyini, a mais diversa da subfamília Sigmodontinae. Possui atualmente sete espécies descritas: *H. acritus*, *H. laticeps*, *H. megacephalus*, *H. oniscus*, *H. perenensis*, *H. tatei*, e *H. yunganus*. Estas espécies se distribuem pelas florestas tropicais e subtropicais sempre verdes cisandinas, do nível do mar até uma altitude de 1500 metros, desde a Venezuela e as Guianas, passando pela Amazônia e pela Floresta Atlântica, até o norte do Paraguai. A distribuição dos táxons dentro do gênero eram confusas e as relações filogenéticas entre estas espécies, também, foram pouco exploradas, assim como o posicionamento do gênero dentro do clado B da tribo Oryzomyini e consequentemente seu grupo irmão. Portanto, minha proposta foi reavaliar as espécies atualmente descritas abordando de forma integrativa os dados morfológicos e moleculares para melhor explorar a diversidade dentro do gênero, assim como as relações de parentesco dentro do gênero *Hylaeamys* e do clado onde este se encontra inserido. Como resultado, obtive uma diversidade maior do que a descrita atualmente. Análises morfológicas puderam auxiliar na delimitação dos taxa, porém não traduziu toda a diversidade filogenética encontrada dentro do gênero, podendo o gênero apresentar espécies crípticas. O gênero se mostrou monofilético e uma nova espécie de *Hylaeamys*, relacionada às populações de *H. yunganus* do leste da América do Sul foi reconhecida, assim como, ficou evidente a estruturação geográfica presente dentro da espécie *H. megacephalus*, onde as amostras ao norte do Rio Amazonas se mostraram geneticamente distintas das amostras ao sul do Rio Amazonas. Porém nas análises morfológicas não foi observado esse padrão. As espécies da Floresta Atlântica se mostraram filogeneticamente mais próximas das espécies do oeste Amazônico. *Hylaeamys* se mostrou grupo irmão de um clado contendo gêneros Cis e Trans- Andinos, sendo eles, *Oecomys*, *Euryoryzomys* e *Transandinomys*, indicando que a dispersão para áreas trans-andinas se deu após a diversificação do gênero na América do Sul.

Palavras-chave: Diversidade; Rodentia; Cricetidae; Sigmodontinae; Morfometria; América do Sul

ABSTRACT

The genus *Hylaeamys* (Weksler, Percequillo and Voss, 2006): species definition and phylogeny of the forest clade of Oryzomyini tribe

Current patterns of faunal diversity, geographic distribution, phylogenetic relationships and biogeography constitute a tool for understanding the evolutionary history of taxa. The boundaries of these taxa and their phylogenetic relationships reveal speciation events and therefore allow us to raise general hypotheses about the diversification of a particular group. Into the Oryzomyini, one of the most diverse tribe of Sigmodontinae subfamily, we can found the genus *Hylaeamys*. Currently seven species were described to that genus: *H. acritus*, *H. seuanezi*, *H. megacephalus*, *H. oniscus*, *H. perenensis*, *H. tatei* and *H. yunganus*. These species are distributed throughout the tropical and subtropical evergreen cis-andinean forests, from sea level to an altitude of 1500 meters, from Venezuela and Guyana, through the Amazon and the Atlantic Forest, to the north of Paraguay. The distribution of taxa within the genus were confusing and phylogenetic relationships among these species have been little explored, as well as the positioning of the genus within the clade B of Oryzomyini tribe and consequently his sister group. So my proposal was to reassess the species currently described through morphometric and molecular data to better explore the diversity within the genus, and the relations within the genus *Hylaeamys* and clade where it is inserted. My results showed a greater diversity than the currently described. Morphometric analysis could be helpful in the delimitation of taxa, however did not translate all the phylogenetic diversity found within the genus, witch may present cryptic species. The genus is monophiletic and a new species of *Hylaeamys* related to *H. yunganus* populations, from eastern South America was recognized. The results, also highlighted a geographical structure present within *H. megacephalus*, so, samples from north of the Rio Amazonas showed to be genetically distinct to those samples in southern of Rio Amazon. But this pattern was not observed in morphometric analysis. The species of the Atlantic Forest were closer to the western amazonian species. *Hylaeamys* showed as a sister group of a clade containing Cis and Trans Andean genera: *Oecomys*, *Euryoryzomys* and *Transandinomys*, indicating that the dispersion for trans-Andean areas occurred after the diversification of the Forest clade in South America.

Keywords Diversity; Rodentia; Cricetidae; Sigmodontinae; Morphometric; South America

1 INTRODUCTION

The Order Rodentia is the most diverse group of mammals, and one of its subgroups is the subfamily *Sigmodontinae*, which comprises around 10% of all mammal species and 20% of all rodents (MUSSER; CARLETON, 2005). The members of that subfamily are distributed throughout South and Central America, extending northwards into southern North America (PARDIÑAS et al., 2002; D'ELÍA, 2003).

One of the most controversial questions about the *Sigmodontinae* lineage is when they arrived at South America and how much lineages arrived into the new continent. Stepan et al. (2004) using nuclear genes, proposed that only one lineage reached the South America continent around 6 Mya., before the formation of the Panama isthmus in agreement with Marshalls (1979) models of lower sea level. In 2013, Schenk and collaborators demonstrated that the *Sigmodontinae* diversification in South America is due to an ecological opportunity process. Leite et al. (2014) suggest that the diversification of *Sigmodontinae* involve paleogeographic changes at the continental and global scales, which makes possible a first invasion of northwestern region of Colombia in the middle to late Miocene.

At present, the diversity of the subfamily is distributed in nine tribes: *Abrotrichini*, *Akodontini*, *Ichthyomyini*, *Oryzomyini*, *Phyllotini*, *Reithrodontini*, *Sigmodontini*, *Thomasomyini* and *Wiedomyini*; plus some genera without tribal position defined, named *Sigmodontinae incertae sedis* (MUSSER; CARLETON, 2005; D'ELIA et al., 2007).

The tribe *Oryzomyini* is the most specious tribe of the subfamily *Sigmodontinae*, with 36 genera and 130 species (MUSSER; CARLETON, 2005; WEKSLER; PERCEQUILLO, 2011; PINE et al., 2012). Prado and Percequillo (2013) presented three general patterns of distribution for this tribe: the Trans-Andean group (distributed in low to moderate altitudes in the western Andean Cordillera), the Cis-Andean group (also distributed in low to moderate altitudes, but in the eastern Andean Cordillera) and the Andean Cordillera group (genera distributed in montane and elfin forest and paramo habitats). Prado et al. (2014) detected the northwestern South America as an area with high endemism score for *Oryzomyini* tribe, followed by the Brazilian Atlantic Forest, the Guyana Shield and Galapagos archipelago.

Besides its wide distribution on the South American continent, we can also attribute to this tribe a noticeable ecological variation between genera, since they can be found in almost all South America biomes (PRADO; PERCEQUILLO, 2013). Some of them are restricted to forested areas as Atlantic and Amazon forest, others are found within dry forests, such as Cerrado and Caatinga forests (Central Brazil), and some of them are semi-aquatic species, and consequently living close related to water bodies (in tropical and dry forests). This diversity is

also remarkable through the morphological variation observed among their taxa (BONVICINO; MOREIRA, 2001; WEKSLER, 2006; WEKSLER; PERCEQUILLO, 2011; PERCEQUILLO et al., 2011; PAGLIA et al., 2012), for example, in morphological variation as body mass, (which can vary from 14g (*Oligoryzomys*) to 400g (*Nectomys*)); dorsal and ventral fur with (*Neacomys* and *Scolomys*) or without grooved spines; number of mammae (8 or 6 pairs) and tail length (tail can be shorter, longer or same size as head and body) (WEKSLER; PERCEQUILLO, 2011).

In the last decades, a significant number of new species and genera belonging to *Oryzomyini* tribe were described (VOSS; CARLETON, 1993; VOSS et al., 2002; LANGGUTH; BONVICINO, 2002; WEKSLER et al., 2006; PERCEQUILLO et al., 2008, PERCEQUILLO et al., 2011, TAVARES et al., 2011, PINE et al., 2012) using morphologic, cytogenetic, phylogenetic and morphometric data. However, a lot of South American biomes have either been poorly sampled or not yet inventoried (PRADO; PERCEQUILLO, 2013). The description and classification of this diversity shed some light on the evolutionary history of the *Oryzomyini* tribe and the *Sigmodontinae* subfamily (STEPPAN, 1995; SMITH; PATTON, 1999; D'ELIA, 2003; D'ELIA et al., 2006; WEKSLER, 2006; WEKSLER et al., 2006, PINE et al., 2012; SCHENK et al., 2013).

In this sense, Weksler et al. (2006) proposed an important change in the diversity of the tribe when they described ten new genera. Even though the description of these ten genera was a taxonomic arrangement for species already described and classified as *Oryzomys*, these taxonomic changes also have an important implication for biogeography, character evolution and conservation assessments of the *Sigmodontinae* group (D'ELIA; PARDIÑAS, 2007).

Some phylogenetic hypothesis at the genera level have been made using different methodologies (including morphological data, mitochondrial and nuclear genes, karyotype data) in an attempt to reflect the different levels of variations found within this group, comprehend the phyletic relationships among these genera, and to provide new nomenclatural insights for the tribe. (VOSS; CARLETON, 1993; WEKSLER, 2003, 2006; D'ELIA et al., 2007;).

More recently, phylogenetic hypothesis were proposed for the tribe (PERCEQUILLO et al., 2011; PINE et al., 2012), but although the trees obtained have similar structure to previous phylogenetic results from Weksler (2006).

The phylogenetic hypotheses proposed by Weksler (2003, 2006) confirmed the tribe *Oryzomyini* as a monophyletic lineage, with representatives of the tribe arranged in 4 clades.

Subsequent hypotheses (PERCEQUILLO et al., 2011; PINE et al., 2012) consistently recovered the same 4 clades which were named A, B, C and D (Figure 1).

The clade A includes the genera *Scolomys* (2 species) and *Zygodontomys* (2 species). Clade B includes the most diverse genera of the tribe, *Euryoryzomys* (6 species), *Oecomys* (14 species), *Handleyomys* (2 species), *Hylaeamys* (7 species), *Transandinomys* (2 species) and *Nephelomys* (14 species; *sensu* MUSSER et al., 2005; PERCEQUILLO, 2015). Clade C includes few genera with numerous species: *Microryzomys* (2 species), *Oreoryzomys* (1 species), *Neacomys* (7 species) and *Oligoryzomys* (22 species). Clade D exhibits several monotypic genera, being formed by *Eremoryzomys* (1 species), *Drymoreomys* (1 species), *Cerradomys* (7 species), *Sooretamys* (1 species), *Lundomys* (1 species), *Holochilus* (6 species), *Pseudoryzomys* (1 species), *Oryzomys* (4 species), *Amphinectomys* (1 species), *Nectomys* (4 species), *Aegialomys* (2 species), *Nesoryzomys* (5 species), *Tanyuromys* (1 species), *Melanomys* (3 species) and *Sigmodontomys* (1 species).

The genus *Mindomys* (1 species) is an *insertae sedis* and have never been used in molecular analysis, only in morphological ones or combines molecular and morphology dataset phylogenies. The genus is sometimes included in clade B, closely related to the genus *Oecomys* or *Euryoryzomys* and sometimes it is placed as the first split in *Oryzomyini* (WEKSLER, 2006; PERCEQUILLO et al., 2011; PINE et al., 2012). It is important to notice that the relationships between *Oryzomyini* genera are highly variable in the aforementioned phylogenies.

Recently, Machado et al. (2014) proposed a phylogeny for *Oryzomyini* clade D. They found that tetralophodont forms of clade D are paraphyletic and the trans-Andean taxa mostly dispersed from the cis-Andean region. The migrations routes were most likely in extreme northern South America and the Andes should operate as a post-dispersal barrier.

The relationship between the different genera in clade B (hereafter named the Forest clade), who includes trans and cis-Andean genera associated with evergreen or semi-deciduous lowland, highland and mountain forests, is still unclear. The Forest clade represents the most specialized forest-dweller taxa of the entire tribe, and exhibit different patterns of distribution in South American forests. Two genera (*Hylaeamys* and *Euryoryzomys*) are widely distributed throughout cis-Andean forests; *Nephelomys* is widely distributed throughout the Andes (northern, center-north and center-south); *Handleyomys* and *Mindomys* (if considered to be in this clade) are restricted to northern Andes; *Transandinomys* is widely distributed through the trans-Andean region; and *Oecomys* occurs throughout South and Central America, inhabiting both sides of Andes (PRADO; PERCEQUILLO, 2013).

Figure 1 - Bayesian tree of *Oryzomyini* tribe obtained with nuclear, mitochondrial and morphological characters by Pine et al. (2012, p. 855, fig. 1)

As said, the genera that comprise the Forest clade of *Oryzomyini* are distributed in all South America biomes, in both sides of the Andean Cordillera, so, a better understanding about the relationship between these taxa can bring some biogeographic insights about patterns of diversification in the South America rodents.

Even though some new taxa were described or revalidated in the past few years for the Forest clade genera (PATTON et al., 2000; VOSS et al., 2001, EMMONS; PATTON, 2005; WEKSLER et al., 2006; CARLETON et al., 2009; BRENNAND et al., 2013); some clades still needs revision, as the genus *Oecomys* for example, once its species delimitations remains unclear.

Included into this taxonomic and phylogenetic scenario, the genus *Hylaeamys* was described by Weksler, Percequillo and Voss (2006) for the species formerly associated with the *Oryzomys* “capito complex” or to the *megacephalus* group (genus *Oryzomys*, *sensu* MUSSER et al., 1998; WEKSLER et al., 1999; PATTON et al., 2000; WEKSLER, 2006). The species that currently comprise the genus *Hylaeamys* were synonymized with *Oryzomys capito* by Herschkovitz (1960) and posteriorly recognized as subspecies of *Oryzomys capito* by Cabrera (1961), besides other taxa presently allocated into other Oryzomyini genera. Musser et al. (1998) reviewed the *Oryzomys* “capito complex”, and they recognized two different species groups that would be later recognized as genus *Hylaeamys*: the “yunganus group” with *O. yunganus* and *O. tatei* as belonging species; and “*megacephalus* group”, including *O. megacephalus* and *O. laticeps*. Subsequently, other species were described and assigned to the *O. “capito complex”* (*sensu* MUSSER et al., 1998). *O. seuanezi* was described by Weksler et al. (1999) in the eastern Atlantic Forest in Brazil, Patton et al. (2000) designated the western Amazon populations of *O. megacephalus* as *O. perenensis* and *O. acritus* was described by Emmon and Patton (2005) in eastern Bolivia. Weksler et al. (2006) attributed seven species to the genus *Hylaeamys*, named: *H. acritus* (Emmons and Patton, 2005), *H. laticeps* (Lund, 1841), *H. megacephalus* (Fischer, 1814), *H. oniscus* (Thomas, 1904), *H. perenensis* (Allen, 1901), *H. tatei* (Musser, Carleton, Brothers and Gardner, 1998) and *H. yunganus* (Thomas, 1902). More recently, Brennand et al. (2013) provided a new arrangement for the Atlantic Forest species of the genus. They formally recognized *H. oniscus* and revalidated *H. seuanezi* (Weksler, Geise and Cerqueira, 1999), for the species from the eastern Brazilian Atlantic Forest, assigning *laticeps* (Lund, 1841) as a junior synonym of *H. megacephalus*. However, despite a relatively good understanding of the taxonomy of the genus, Percequillo (2015) pointed out the fact that the delimitation and distribution of the species, as well the geographic variation within the genus remains unclear.

The phylogenetic relationship between *Hylaeamys* species has not been properly tested (BONVICINO; MOREIRA, 2001; WEKSLER, 2003, 2006; PERCEQUILLO et al., 2011). Musser et al. (1998) presented the first phylogeny for the group (Figure 2) using cytochrome b (cyt b) gene, and they showed that *H. yunganus* has an average sequence divergence of 18%

from *H. megacephalus* and *H. laticeps*, and treated them as two different species group (as mentioned above).

Figure 2 - Maximum Parsimony tree presented by Musser et al. (1998, p.27, Fig. 6) with *O. capito* complex species showing the average percent sequence divergence in the top of the nodes

Patton et al. (2000) considered *O. yunganus* and *O. megacephalus* as “*megacephalus* group” and formally denominated the western populations of *H. megacephalus* as *H. perenensis*, which they recognized as different in their phylogenetic analysis (Figure 3). Costa (2003) analyzes the patterns of diversification in Brazilian Atlantic Forest, using the mitochondrial gene *cyt b* from different small mammals taxa. For the genus *Hylaeamys*, the author demonstrated (Figure 4) that the species from Atlantic Forest (*H. laticeps*) are more closely related to the species from central Brazil (*H. megacephalus*) than to species from western Amazonian (*H. perenensis*). Costa (2003) also showed two structured clades within *H. megacephalus*, one clade from northern Amazon forest populations and another for southern and central Brazil populations.

Figure 3 - Maximum Parsimony tree presented by Patton et al. (2000, p. 142, Fig. 97) with *O. megacephalus* group showing the average percent sequence divergence in the top of the nodes. The authors applied the name *O. perenensis* to the western populations of *O. megacephalus*

Figure 4 - Phylogeographical relationship and geographical distribution of *Hylaeamys* species obtained by Costa (2003, p. 79, Fig. 7)

In the description of a new species of the genus from Bolivia, *H. acritus*, Emmons and Patton (2005) includes five species of the genus and proposed a phylogenetic hypothesis (Figure 5). The species described by these authors appears as a sister group of *H. perenensis*, and with the Atlantic Forest species (*H. laticeps*) they form a clade, in a pattern very different from those presented by Costa (2003). Therefore, there is no congruence in the phylogenetic analyses of the genus, and the inclusion of all taxa of the genus along with a comprehensive molecular and morphologic dataset would be necessary to obtain a robust phylogenetic hypothesis.

Figure 5 - Maximum Parsimony tree presented by Emmons and Patton (2005, p. 3, Fig. 1) when they describe *H. acritus*

In the morphologic phylogeny proposed by Weksler (2006) were used samples of *H. megacephalus* and *H. yunganus* and the genus appeared paraphyletic (Figure 6). But, in subsequent trees, using nuclear or combined datasets (molecular and morphological characters) the genus appeared as monophyletic. However the relationship between the genera within the Forest Clade were not clear, since the author obtained a polytomy using only the molecular dataset. Subsequently, when the genus *Hylaeamys* was described, (WEKSLER et al., 2006, p. 16), the authors suggested that the monophyly of the genus should be tested.

Figure 6 - Maximum Parsimony tree using morphological character presented by Weksler (2006, p. 62, Fig. 34)

Percequillo et al. (2001) showed through Parsimony analysis (Figure 7) using molecular and morphologic characters that *Hylaeamys* was the sister group of a clade formed by *Transandinomys* and *Euryoryzomys*. In the other hand, in their molecular phylogeny the sister group of *Hylaeamys* was *Handleyomys* (Figure 8).

Figure 7 - Partial most Parsimonious tree show by Percequillo et al. (2011, p. 337, Fig. 7) using molecular and morphological combined dataset

Figure 8 - Partial Likelihood tree presented by Percequillo et al. (2011, p. 374, Fig. 8) using only molecular dataset

The most recently phylogenies proposed for the Forest clade of Oryzomyini (PERCEQUILLO et al., 2011; PINE et al., 2012) exhibited quite distinct topologies. As the genus *Hylaeamys* is included in this clade (WEKSLER, 2006; WEKSLER et al., 2006; PERCEQUILLO et al., 2011; PINE et al., 2013) a better resolution of the entire clade could

be important to establish the monophyly of the genus and its relationship with the other genera into the clade. It would also allow advancing hypotheses on the evolutionary and biogeographic history of this clade. It is likely that more comprehensive datasets would be extremely useful to establish robust phylogenetic hypotheses for *Hylaeamys* genus and the Forest Clade members.

Along the years, the methods used for taxonomists to recognized species varied a lot. The concept of species has been central in Biology and the species still considered the fundamental unit of biological studies in many different aspects as anatomy, behavior, genetics, molecular biology, physiology, phylogeny, systematics, and paleontology (SOKAL; CROVELO, 1970; WIENS; PANKROT, 2002; SITES; MARSHALL, 2003, 2004; DE QUEIROZ, 2005). The biological species concept was first proposed based on evolutionary theory with the contribution of Theodosius Dobzhanski, Ernest Mayr and George Gaylord Simpson in the 1930's and 1940's. In this concept, the species is defined as a group of interbreeding natural populations, reproductively isolated from other groups, thus constituting a reproductive entity (MAYR, 1964; FUTUYMA, 1992). According to Mayr (1963, 1964), all differences between species are subject to geographic variation, and these differences, whether morphological, physiological or ecological, are mechanisms potentially insulators that reinforce the discontinuity between two populations. Geographic variation is then capable of producing the two components of speciation: the development and the establishment of divergence between different forms of discontinuity. Also according to this author, the speciation phenomenon is not abrupt but gradual and continuous, and we can find in nature all levels.

For a long time, biologist recognized species based in morphological methods only. Sokal and Crovelo (1970) argued that the decisive criterion of the biological species concept proposed by Mayr (1963) is not the fertility of individuals but the reproductive isolation of populations. In that way, the existence of gaps in the pattern of phenetic diversity can be taken as evidence for reproductive isolation, and species could be delimited based in morphological discontinuities (SOKAL; CROVELO, 1970; SITES; MARSHALL, 2004, ZAPATA; JIMENEZ, 2012). By this mean, geographic variation is then capable of producing the two components of speciation: the development and the establishment of divergence between different forms of the discontinuity.

According to Cracraft (1989), the biological species concept is presented as an obstacle to the description and the interpretation of evolutionary patterns and processes of differentiation. In the 70s, Henning Willig offers the speciation process vision diagnosed by

monophyletic groups, not through reproductive barriers (ALEIXO, 2007). However, it was inevitable that the classification of organisms, according to their morphological similarities, combined with aspects of its ontogenetic development and their geographical distribution, have been, sooner or later associated with the discovery of their different degrees of phylogenetic relationship and thus, the evolutionary theory (HENNING, 1965). Through the process of speciation, a population has one or more evolutionary novelties, which can be fixed from the genetic level to morphological, biochemical and behavioral (CRACRAFT, 1989).

Using the phylogenetic species concept, the species becomes the entity of evolutionary theory and the basis for historical patterns of taxonomic diversity (CRACRAFT, 1989). Several criticisms of the phylogenetic species concept have been suggested based on the uncomfortable adjustment between its theoretical basis and its applicability (COLLAR, 1997; AGAPOW et al., 2004). Based on this discrepancy between theory and their ability to be really tested, Queiroz (1998) draws a distinction between specie concept and specie criterion. The author emphasizes that the conceptual differences that highlighted the distinctions between the different species concepts are related only to the emphasis that each one of them draws from a different phenomenon accompanying the cladogenesis process, and there is a conflict related to the type of entity to which they refer.

We should then consider the temporal aspect of cladogenesis process in microevolutionary level, culminating in the production of species whose genomes no longer mix, so, the reproductive isolation should be a consequence, and not the cause of the cladogenesis process. Despite long and historical discussions about the kind of concept and regardless of which of these concepts is used, the similarities and morphological differences found in the most diverse taxa are used as a tool for evolutionary understanding. Currently, morphological and molecular characteristics are used to delimit species, whatever its definition. However, when employing morphological and molecular characteristics in the same taxon in an attempt to delimit species, the results may be different (WIENS; PENKROT, 2002; STEPPAN, 1998; SERB et al., 2001). This difference does not mean that one hypothesis is not valid. The disagreement may indicate that the selection of characters does not reflect the real divergence between taxa, which may have been promoted by different evolutionary processes (PADIAL et al., 2009). According to Smith and collaborators (1997), gene flow and the selective pressures can result in high levels of morphological divergence in some populations, but, in other cases, genetic drift can promote rapid genetic differentiation, and no morphological differences.

Considering the actual recognized species into the genus *Hylaeamys*, and the phylogenetic relationship between them, the first hypotheses I tested here was if there is seven species into *Hylaeamys* genus and for answer that I used morphometrics and phylogenetics methods. The second hypothesis was if the genus *Hylaeamys* is monophyletic, using a phylogenetic approach for the Forest clade of the tribe Oryzomyini.

2 OBJECTIVES

Based on these hypotheses above cited, I proposed to answer the following questions: How many groups can I recognized inside the genus *Hylaeamys* using skull morphometric data? Can I recuperate theses morphometric groups using phylogenetic methods? Is *Hylaeamys* a monophyletic group? Who is the sister group of *Hylaeamys* into the Forest clade? These morphometric and phylogenetic groups corresponded to the current species?

For answer these questions I established the following objectives:

- Describe the morphometric variation between skull samples, in order to establish the discontinuities among populations of *Hylaeamys*;
- Stablish geographical limits distribution for the morphometric groups;
- Test the monophyly of the genus *Hylaeamys*;
- Recover the relationship between the genera of the Forest clade of the tribe Oryzomyini;
- Compare groups founded with morphometrical approach to those founded in the phylogenetic approach;
- Associate the morphometric and phylogenetic groups with the current taxonomic arrangement;

3 METHODS

3.1 Sampling

3.1.1 Specimens

I analyzed the skins, skulls, of 2.411 and some skeletons and carcasses preserved in fluid of specimens of genus *Hylaeamys*, deposited in the following collections:

AMNH - American Museum of Natural History (New York, USA)

BMNH – The Natural History Museum (London, England)

FM - Florida Museum of Natural History, University of Florida (Gainesville, USA)

FMNH – The Field Museum (Chicago, USA)

INPA - Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil)

MN - Museu Nacional da Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil)

MNHN – Musée National d'Histoire Naturelle de Paris (Paris, France)

MPEG - Museu Paraense Emilio Goeldi - Material under the supervision of Professor Claudia Nunes at Universidade Federal do Pará (Campus Bragança, Brazil)

MPEG – Museu Paraense Emilio Goeldi (Belém, Brazil)

MVZ – Museum of Vertebrate Zoology, University of California (Berkeley, USA)

MZUSP – Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil)

UFMG - Universidade Federal de Minas Gerais (Belo Horizonte, Brazil)

UFPB – Universidade Federal da Paraíba (João Pessoa, Brazil)

UFPE – Universidade Federal de Pernambuco (Recife, Brazil)

UnB – Universidade de Brasília (Brasília, Brazil)

UNEMAT - Universidade Estadual do Mato Grosso (Nova Xavantina, Brazil)

UNMSM - Universidad Mayor de San Marco (Lima, Peru)

USMN - National Museum of Natural History, Smithsonian Institution (Washington, USA)

UZM – Universitets Zoologisk Museum (Copenhagen, Denmark)

A list of specimens examined is provided in the species account. The list is organized in alphabetic order by country, state or province and locality of collection. Uppercase letters proceeding museums numbers refer to sex of voucher specimens: M for males, F for females and I for no sexed specimens.

3.1.2 Measurements

Specimens were measured following cranial and dental dimensions adapted from Voss (1988) and Musser et al. (1998) using a digital caliper to the nearest 0.01 mm. The following measurements were taken:

Occipital Nasal length (ONL): measured from the anteriormost end of the nasal to the occipital bone;

Length of diastema (LD): measured from the crown of the first upper molar to the inner side of the base of the upper incisor, on the same side of the skull;

Crown length of maxillary toothrow (CLM1-3): measured from the anterior surface of the first upper molar to the posterior surface of the third upper molar, at the crown of the molars;

Breadth of first upper molar (BM1): breadth of the first upper molar, measured on the basal portion of the molar crown, at the level of the paracone-protcone pair;

Length of incisive foramina (LIF): the greatest length measured from the anterior to the posterior edge of the incisive foramen;

Breadth of incisive foramina (BIF): the greatest internal breadth, measured on the lateral margins of the incisive foramen;

Breadth of bony palate (BBP): the greatest breadth of bony palate measured across the third upper molar;

Breadth of rostrum (BR): measured across the rostrum at the posterior extremity of the upper edge of the infraorbital foramen;

Length of nasals (LN): measured from the anteriormost end of the nasal to the naso-frontal suture;

Length of bony palate (LBP): measured from the posterior margin of the incisive foramen to the anterior margin of the mesopterygoid fossa;

Interorbital breadth (IB): shortest distance through the frontals in the orbital fossa;

Greatest zygomatic breadth (ZB): greatest external distance of the zygomatic arches, close to the squamosal roots, measured across the skull;

Breadth of zygomatic plate (BZP): the shortest distance between the anterior and posterior margins of the inferior zygomatic root or zygomatic plate.

Limits of these measurements are presented in Figure 9. External measurements used as body length (BL), tail length (TL), hind foot length (FL), ear lengths (EL) and bodies mass (BM) are those made by collectors and recorded in the museums' labels.

Figure 9 - Dorsal, ventral and lateral views of a skull of a specimen of *Hylaeamys* (UFPB BC195), from Murici, Alagoas state, Brazil, showing the limits of cranial and dental dimensions measured in the specimens studied (see text for definitions and abbreviations)

3.1.3 Sexual dimorphism

Previous studies suggest that the sexual variation in *Oryzomyini* rodents does not appear to be an important component of the variation on the cranial and dental dimensions

(CARLETON; MUSSER, 1989, 1995; MUSSER et al., 1998; CARMADILLA et al., 1998; PRADO; PERCEQUILLO, 2011; ABREU-JUNIOR et al., 2012; BRENNAND et al., 2013). Therefore, females and males are combined in all subsequent morphologic and morphometric analyzes.

3.1.4 Age criteria

I employed five different age classes defined based in eruption and wear of superior molars, following Voss (1991) and Percequillo (1998). The classes are described as follows and only adults were used in the morphometric and morphological comparisons, but all age classes were used to described the valid species:

Age class 1 (AC1): first (M1) and second (M2) superior molars with no apparent wear. Anteroloph, mesoloph and posteroloph are distinct and easily recognizable. The third superior molar (M3) are not erupted or newly erupted with main cusps still closed, labial lophs well developed and isolated, labial and lingal flaxus deep and distinct (Figure 10A).

Age class 2 (AC2): M1 and M2 with a small tooth wear, exhibiting a small part of dentine between cusps. M3 already showing minimal to moderate wear; anteroloph and mesoloph may be connected to paracone, through marginal lophules, posteroloph nearly fused to metacone marginally (Figure 10B).

Age class 3 (AC3): M1 and M2 with moderate wear. M3 with marked wear and a nearly flat surface, anteroloph and mesoloph fused marginally to paracone forming a long anterofosset end a mesofosset respectively; posteroloph completely fused to metacone forming a distinct mesofosset (Figure 10C).

Age Class 4 (AC4): M1 and M3 with a heavy wear, showing indistinct and massive exposure of dentine. M3 appears quite flat, with major exposition of dentine; anteroloph, mesoloph and posteroloph indistinct and fused to major cusps (Figure 10D).

Age Class 5 (AC5): M1, M2 and M3 completely worn away with the dentine largely exposed (Figure 10E).

Figure 10 - Five different age classes (AC1, AC2, AC3, AC4 and AC5 respectively), based on molar eruption and wear; root exposition is also useful to determine age, with classes 4 and 5 with moderate and large exposition of dentine, respectively

3.1.5 Anatomy

Anatomical terminology used in this study follow different authors. I followed Hershkovitz (1977), Voss (1988), Carleton and Musser (1989) for external features, and Hill (1935), McDowell (1958), Wahlert (1974, 1985), Voss (1988), Bugge (1970), Guthrie (1963) and Steppan (1995) for cranial and dental terms.

3.1.6 Gazetteer

Localities and geographical coordinates were taken from the original and museum labels attached to specimens; when geographical coordinates were not available, I used other sources (GEONAMES, 2004; PAYNTER; TRAYLOR, 1991; U.S. BOARD ON GEOGRAPHIC NAMES, 1994). The gazetteer is ordered alphabetically by country, state or province and collection locality. All maps produced in this study using QGIS 1.8 (2012) are numbered according this gazetteer. The gazetteer is presented in Appendix A.

3.2 Assessment of geographical variation

3.2.1 *Hylaeamys* Groups of species

For a better explanation and presentation of the statistical results, the genus was split into 2 groups of specimens (MUSSER et al., 1998). First group called “*yunganus* group” included specimens with two fossettes (a labial and a medial fossette) and a short paraflexus in the second upper molar. The second group, called “*megacephalus* group” includes all other *Hylaeamys* specimens (Figure 11).

Figure 11 - Occlusal views of right upper molar rows from species of *Hylaeamys* adapted from Musser et al. (1998, p. 77, Figure 30) showing labial (lf) fossettes and paraflexus (p) in the second molar. A: *H. yunganus* (AMNH23166) from Peru (CLM1-3 = 5 mm). B: *H. perenensis* (AMNH 231655) from Peru (CLM1-3 = 5 mm)

These samples were grouped to yield more robust samples by increasing the number of specimens per group. I delimited some sub-groups based on the geographic proximity criterion, karyotype information, the criterion of similarity between the geomorphological characteristics of the samples (riverbanks, mountain slopes, relief), the similarity between qualitative external characters and cranial characters; morphological and genetic differences reported in the literature (MUSSEY, 1968; VANZOLINI, 1970).

I applied multivariate tests among these groups. As the genus is widely distributed in South America biomes, I started the comparisons between the groups by biomes. For the Amazon Forest, I also used the large rivers as a tool for delimited the internal groups. Moreover I did a specific comparison for groups in sympatric areas, such as Bolivia.

3.2.2 Karyotype variation

I used the karyotype information available in the literature for all population of specimens attributed to the genus *Hylaeamys*. This information was also used to compound the group of specimens used in geographical variation tests.

3.2.3 Statistics Analyses for Cranial Morphometric variation

The samples are distributed in all Cis-Andean South America biomes and all analyses of geographic variation were conducted in pooled samples within and between those two groups (see 3.2.1 for more details).

Standard descriptive statistics (mean, standard deviation and observed range) have been calculated for all groups with more than five adults. Dice-Leraas univariate diagrams using mean and confidence intervals (95%) for each cranial and dental variable was used to assess geographic variation comparisons between samples.

A Principal Component Analysis (PCA) over the within-group variance-covariance matrix and a Discriminant Functions Analysis (DFA) were computed using the cranial and dental log-transformed variables between groups. The first two or three principal components and discriminant function were plotted in a scatterplot graphic, providing visual observance of the patterns. SPSS (SPSS, 2008) was used to perform all statistics analysis.

3.3 Phylogeny

3.3.1 Extractions and Hybrid enrichment

The DNA was extracted using Invitrogen PureLink Pro 96 kit, following the kit recommended procedures. For DNA from skin samples some changes in the digestion step were done, adding more 20uL of protease, computing a total of 40ul of protease, 5ul of DTT and the time of digestion were overnight or more than 16 hours. The DNA was quantifying using nanodrop, and only samples with a minimum of 10ng/μl could be submitted to Library preparation.

The Hybrid enrichment consists in the development of probes that will be hybridized to a DNA library, isolating the targets from the genome prior to high-throughput sequencing (LEMMON; LEMMON, 2013; McCOMACK et al., 2013). The procedure was made at Center For Anchored Phylogenomics at Florida State University following the methods developed by Lemmon, Emme and Lemmon (2012). It consists in a mix of probes that capture a conserved DNA region flanked by less conserved region across the genome and generating up to 3000 bp per locus. After enrichment, samples were sequencing on Illumina HiSeq2000 at the Florida State University Translational laboratory.

3.3.3 Alignment and Phylogenetic analysis

The assembling and the consensus sequences obtained from the final assemble were made according to procedures described by Lemmon et al. (2012). Each locus was aligned

using MUSCLE (EDGAR, 2004), implemented in Geneious 5.1 (DRUMMOND et al., 2012). Alignments were manually inspected and all ambiguous regions or missing sites were denoted as character sets using MacClade 4.08 (MADDISON; MADDISSON; 2005) and excluded from phylogenetic analysis.

For phylogenetics analysis, only one of the alleles alignments was used. The alignment has 7.24% of proportion of gaps. The Maximum Likelihood tree was obtained using RaxML-HPC 8.0 (STAMATAKIS, 2014) implemented in CIPRES science gateway. A GTR GAMMA model of rate heterogeneity was estimated using 322 data partitions with join branch length optimization and 1000 bootstrat were performed.

Samples from clade D of Oryzomyini tribe were used as outgroup and a sample of *Abrawayomys ruschii* was used to root the tree. The trees were edited using FigTree 1.4 (STAMATAKIS, 2014).

3.4 Species Delimitation

To recognize and define diagnosable groups and test their reciprocal monophyly, and formalize hypothesis about the species of the genus *Hylaeamys*, I combined the results of geographical variation among samples and karyotype information available in the literature, altogether with the phylogenetic trees. All this information was the core evidence to support my taxonomic decisions and delimitations of the taxa. In this sense, I employed the integrative approach to establish these species, that although is not a formal species concept, it considers the use of different methods to recovery a lineage, applying the criteria of diagnostic characters and reciprocal monophyly to recognize species. (DE QUEIROZ, 1998, 2007; COLLAR, 1997; CRACRAFT, 1989; PADIAL et al., 2009)

3.4.1 Species Account

I formally present my hypothesis about the number of species that compound the genus *Hylaeamys* and their distribution. I presented the following informations for each species: a plate with dorsal, ventral and lateral view of the skull and a lateral view of the mandibula; the synonym; the map of distribution with the type locality based in the gazetteer showed in Appendix I; the karyotype; a diagnose with morphological and morphometric description of the variation founded into each species.

4 RESULTS

4.1 The “yunganus group”

The samples of this group included specimens with two fossettes (a labial and a medial fossette) and a short paraflexus in the second upper molar (Figure 11). Presently, two species are recognized into this group: *H. tatei* (Musser, Carleton, Brothers and Gardner 1998) and *H. yunganus* (Thomas 1902). These two species are sympatric with others forms of group “megacephalus” of genus *Hylaeamys*: *H. yunganus* presents a wide distribution in the northern portion of South America in both banks of Rio Amazonas, and part of central Brazil and Bolivia, while *H. tatei* exhibits a restricted distribution in few localities of central Ecuador, on the eastern slope of Eastern Andean Cordillera (Figure 13; see detailed maps with localities numbers in the topic Species Account, associated to each recognized species).

Figure 12 - Distribution of all samples of “yunganus group” analyzed. Open circles are samples presently named as *H. yunganus*, dark circles are samples presently named as *H. tatei*

4.1.1 Morphometric variation

As all samples from this group are distributed predominantly in the Amazon Forest and also in some transitional areas between Amazon Forest and Cerrado biome, I employed two approaches to pool geographic samples and conduct subsequent morphometric analysis. In

both approaches, I also considered the karyotype information (topic 4.1.2) and previous molecular results published elsewhere (MUSSE et al., 1998; PATTON et al., 2000; JORGE-RODRIGUES, 2011) to delimit the pooled samples.

At first, I pooled the samples through the geographic proximity criteria and assembled 17 groups with at least 4 individuals per group: these groups were listed in the Table 1, in the column labelled group 1 (they are also represented in Figure 14). Secondly, these 17 previous groups were pooled according to the following criteria: the margin of the Rio Amazonas, the geographic distance between them and the morphology of specimens (Figure 14). These nine new groups of samples, labelled group 2 (on Table 1) were named as: NEastAmaz, NCentralAmaz, NWestAmaz and Ecuador for samples in the north of Rio Amazonas; SEastAmaz, Xavantina, Bolivia, Madeira, SWestAmaz for samples in the south of Rio Amazonas (Figure 13). Specimens from Xavantina were placed in a separated group because represents a transitional area between Amazon Forest and Cerrado biome.

To be able to better analyze the geographic variation within “*yunganus* group”, I performed the statistic analysis using only the group 2 of samples once this groups had a larger number of individuals and consequently showed more robust statistics results.

Figure 13 - Map of “*yunganus* group” samples (Group 1 and 2 from Table 1) used in morphometric analysis

The Bolivia sample will be used in a subsequent analysis with others samples from that geographic region (topic 4.2.1.1) with the objective to better identify and delimit the discontinuities among *Hylaeamys* samples from this area. The samples from localities 251 (Mera, Pastaza, Ecuador) and 260 (Palmera, Tungurahua, Ecuador) were joined and labeled as Ecuador because this population presents specific cranial and dental characteristics that distinguished them to the others samples, and were formally recognized as *O. tatei* (MUSSE et al., 1998).

Table 1 - Pooled localities (Groups 1 and 2) and their respective localities number and total number of specimens of “*yunganus* group” used in morphological and morphometric analysis. The localities numbers are those from the Gazetteer presented in Appendix I

Group 1	Group 2	Localities	Number of specimens in group 1
SerraNavio	NEastAmaz	67, 68	16
Paracou	NEastAmaz	265	7
Auyantepui	NCentralAmaz	386, 391	7
Guaicaramo	NWestAmaz	234, 236, 237, 238	6
Yasuni	NWestAmaz	233, 243, 244, 247, 252, 255	16
Conchaguaya	SWestAmaz	326, 327, 360	4
Chinchao	SWestAmaz	314, 348, 352, 354	12
Potaro	NCentralAmaz	269, 279	6
BaixoJurua	SWestAmaz	53, 54, 55, 56, 59	24
MedJurua	SWestAmaz	73, 76, 78, 82, 85, 86, 91	20
SenaMadu	SWestAmaz	52, 57, 362	14
Cuzco	SWestAmaz	306, 310, 311, 312	6
Bolivia	Bolivia	1, 11, 35, 37, 49, 221	8
Madeira	Madeira	37, 49, 221	5
Xavantina	Xavantina	140	15
Altamira	SEastAmaz	185, 190, 194 197	7
Ecuador	Ecuador	251, 260	7

To explore data, I performed error bar diagrams, to compare the means between all samples simultaneously. I did not include the samples Bolivia and Madeira in the graphics because they had a small number of specimens, who influenced the confidence interval, but these groups were used in the multivariate tests. For the variables ONL, CLM1-3, BBP, ZB and BZP we could observe tree distinct groups: Ecuador, Eastern Amazon Forest and Western Amazon Forest (Figure 14). In the other hand, for the variable BM1 (Figure 14) the sample from Ecuador have the largest mean value, but the differences between the means from Eastern and Western samples are not quite distinct.

Figure 14 - Comparison of variables ONL, CLM1-3, BBP, ZB and BZP between samples of “*yunganus* group”.

Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

For the variable LD the samples from Ecuador and West Amazon Forest had similar mean values, but they had a very distinct mean from samples of East Amazon (Figure 15). For the others variables the differences between East and West samples are less prominent. However, in the variables LN, BIF and LIF (figure 16) we can see a significant difference in the mean of samples between NEastAmaz and NWestAmaz.

Figure 15 - Comparison of variable LD between samples of “*yunganus* group”. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 16 - Comparison of variables LN, BIF and LIF between samples of “*yunganus* group”. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

In the other hand, in the variables IB and LBP (Figure 17) the samples from Xavantina showed the lowest means and the samples from Ecuador showed the highest mean values, but in the variable BR (Figure 17) Xavantina exhibited the lowest mean value.

Figure 17 - Comparison of variables IB, LBP and BR between samples of “*yunganus* group”. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

In the most of the variables, we could observe that the samples from both sides of Amazon River had the same mean and the differences were more conspicuous between Eastern and Western populations, instead of Northern and Southern populations of Amazon Forest.

In the PCA analysis, the first component was responsible for 45% of the variation, the second component was responsible for 14.99%, and the third component was responsible for 12.6% of the observed variation (Table 2). Together, these three components were responsible for more than 70% of the total variation. The variables that had the highest score in the first component were: (+) ZB, (+) ONL and (+) CLM1-3. The variables that had the highest score in second component were (-) LFI, (-) BIF and (+) LBP, and for the third component, the variables that showed the highest scores were (-) BM1, (+) LD and (+) BR (Table 2). I used the group 2 from Table 1 to label the scores into the scatterplot graphic (Figures 18 and 19).

Table 2 - Values of first (PC1), second (PC2) and third (PC3) components resulted from a Principal Component Analysis of log transformed cranial and dental variables of *Hylaeamys* “*yunganus* group”. Variables with highest scores are in bold

Variables	PC1	PC2	PC3
ONL	0.882	0.067	0.351
LD	0.711	0.065	0.510
CLM1-3	0.803	0.057	-0.318
BM1	0.643	0.038	-0.699
LIF	0.506	-0.716	0.031
BIF	0.493	-0.653	0.158
BBP	0.763	-0.079	-0.306
BR	0.540	-0.004	0.496
LN	0.639	0.075	0.384
LBP	0.639	0.075	0.384
IB	0.595	0.285	0.137
ZB	0.892	0.001	0.116
BZP	0.705	0.338	-0.189
Eigenvalue	0.005	0.002	0.001
% Variance	45	14.99	12.6

I also performed a Discriminant Function Analysis (Figure 21) with the groups defined in the error bars and in the PCA. In this analysis, three distinct groups were obtained, one group with sample from Ecuador, one group with samples from Eastern Amazonian Forest and finally, a group with samples from Western Amazonian Forest, the same pattern observed on the PCA analysis. Moreover, samples from Madeira River came from the right bank of the river and appeared morphometric similar to the eastern populations. The population from Ecuador is morphometric different from all others samples. The first discriminant score was responsible for 89% of the variation and the variables (+) ZB, (+) BM1 and (+) ONL, respectively, had the highest values of the first Discriminant Scores (Table 3). For the second Discriminant score the following variables had the highest values: (+) BM1, (-) ZB and (-) LD.

Figure 18 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and second principal components (PC1 and PC2) extracted from analysis of samples of “*yunganus* group” listed in Table 1 and labeled as group 2

Figure 19 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and second principal components (PC1 and PC3) extracted from analysis of samples of “*yunganus* group” listed in Table 1 and labeled as group 2

Table 3 - Values of first (DS1), second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* “*yunganus* group”. Variables with highest discriminant score are in bold

Variables	DS1	DS2
ONL	0.474	-0.593
LD	0.273	-0.641
CLM1-3	0.449	0.096
BM1	0.611	0.793
LIF	0.242	-0.103
BIF	0.208	-0.127
BBP	0.333	0.124
BR	0.356	-0.426
LN	0.300	-0.370
LBP	0.146	-0.349
IB	0.183	-0.250
ZB	0.736	-0.677
BZP	0.396	-0.036
Wilk's Lambda	0.000	0.000
Eigenvalue	4.525	0.558
% Variance	89	11

Figure 20 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurements extracted from a discriminant function analysis with covariance matrix of samples of “*yunganus* group” listed in Table 3 and labeled as group 2 of Table 1

4.1.2 Karyotypic variation of “*yunganus* group”

Gardner & Patton (1976) described three different karyotypes for *Hylaeamys* populations from Peru. One was assigned to *Oryzomys capito* (see Karyotype of “*megacephalus* group” (topic 4.2.1 for more details) and two were assigned to *Oryzomys yunganus*. The authors named these specimens according to skull characteristics and comparisons with the holotype of *O. yunganus* deposited at The Natural History Museum (British Museum).

The first karyotype is $2n = 60$ and $FN = 66$, comprising four pairs of metacentric, 25 pairs of acrocentrics, and two sex chromosomes: a large acrocentric X and a medium or small acrocentric Y. This karyotype was found in populations of Ayacucho department, (locality San José, Rio Santa Rosa). The second karyotype is $2n = 58$ and $FN = 62$ and is identical in form to the previous one except for the absence of one pair of small metacentric chromosomes. This karyotype was found in populations of Loreto department (at the locality of Balta, Rio Curanja).

In 1983, Koop and colleagues described chromosomal polymorphism from a unique and small population (10 individuals) of “*Oryzomys*” from a single locality at the top of a table mountain (the Tafelberg) in the Guiana Shield in Surinam. At that moment, the authors

could not really identify at specific level but they attribute that polymorphism to a *macconnelli-capito* complex. However, what intrigued the researchers was the fact that each individual has a unique karyotype and concludes that the Tafelberg sample represented the greatest amount of chromosomal polymorphism thus far identified in a single naturally occurring mammalian population.

Kerridge and Baker (1990) documented that the sample from Tafelberg consisted of two different species: *Oryzomys capito* and *Oryzomys yunganus*. The *O. capito* samples had FN = 58 - 59 and the FN for *O. yunganus* ranged from 64 to 67. But the authors also emphasized that the removal of two specimens of *O. capito* in that sample reduces the variation in FN but all the fusions identified by G-bands remain assigned to one species, *O. yunganus*, and the polymorphism is still greater than that described of any other occurring population of mammals. The observation of the absence of *O. capito* alleles in the samples of chromosomally polymorphic *O. yunganus* is not compatible with the hypothesis that chromosomal polymorphism resulted from recent hybridization between the *O. capito* and an unidentified species.

In their manuscript about the “*Oryzomys capito* complex”, Musser et al (1998) presents the karyotype $2n = 58$ and FN = 62, obtained in the Brazil (in Juruá River, a tributary of Amazon River in northwestern Brazil) for the *O. yunganus* populations. This karyotype was more detailed by Patton et al. (2000) in their manuscript about small mammals of the Juruá River. The karyotype of this population from the western part of Amazon Forest agree with those previously described by Gardner and Patton (1976) for the populations from Peru. Patton et al. (2000) describe this karyotype as 25 pairs of large to small acrocentric, 3 pairs of small metacentric and two sex chromosomes: a medium large acrocentric X and a small acrocentric Y.

In 2000, Volobouev and Aniskin presented a karyotype of a female *O. yunganus* from Loreto department in Peru as a tree pairs of small metacentrics, 25 pairs of acrocentrics decreasing in size and a couple of medium size acrocentric X, resulting in $2n = 58$ and FN = 62. This karyotype agrees with those previously described by Gardner and Patton (1976) from Ayacucho department, also in Peru and those described by Patton et al. (2000) from northwestern Brazil.

In this same year, Andrades-Miranda et al. (2000) showed a karyotype with $2n=60$ and FN=64, constituted of 26 acrocentric pairs and 3 small biarmed pairs plus an X acrocentric from Niquelândia, central Brazil.

So, the karyotype diversity registered for this group is compounded by the following different karyotypes (Figure 21): $2n=60$, $FN=66$ from Peru; $2n=58$, $FN=62$ from Peru and northwestern Brazil; $2n=60$, $FN=62$ from central Brazil and $2n=52-59$; $FN=64-67$ from Suriname.

Figure 21 - Distribution of the karyotypes described for populations of *Hylaeamys* “*yunganus* group”

Unfortunately, the karyotypes for most part of the samples that I analyzed were not available in the literature. In addition, I did not have access to the specimens from Niquelândia with karyotype $2n = 60$, $FN = 62$, so, these specimens were not included into the morphometric analysis, and have not their identity checked.

4.1.3 Summary of variation in “*yunganus* group”

The pattern observed in the karyotype and morphometric results were not totally congruent, once we had two distinct karyotype associated to the western populations and a lot of different karyotype in a single population from eastern amazon forest. More karyotype informations from populations of eastern amazon forest and south of Rio Amazonas should be necessary for a better understanding about the karyotype diversity in that group os species.

The morphometric analyses of variation showed sharp differences in the skull size, revealing gaps between eastern (NEastAmaz, SEastAmaz, Xavantina and part of the specimens of the sample Madeira) and western (NCentralAmaz, NWestAmaz, SWestAmaz, Bolivia and part the specimens from Madeira) populations from both sides of Amazon River, and finally and most noticeably, regarding the Ecuador pooled sample. For a better definition and classification of samples from Madeira, this sample will be included as an independent group in subsequent morphometric comparisons (Bolivia samples, and Amazon Forest groups).

Musser et al. (1998) were the first to highlight the morphometric geographic variation observed into this “*yunganus* group”. These authors also described the species *H. tatei*, based in some specimens collected in Ecuador, more exactly, in two localities: Mera (locality number 251 in the Gazetteer in Appendix I) and Palmera (locality number 260 in the Gazetteer in Appendix I). Despite the restricted distribution of the taxa in only central and northern Ecuador, these authors presented morphological and morphometric differences between *H. tatei* and *H. yunganus*. They also highlighted the occurrence of geographic variation among populations of *H. yunganus*.

In my results I was able to analyze more material than Musser *et al.* (1998), and, consequently, increase the number of specimens and localities employed in the analysis. With larger samples, the discontinuities between eastern and western populations appeared more conspicuous, as well as the differences between those and the sample that I labelled as Ecuador.

These specimens from Ecuador showed morphometric difference in the total size (length and breadth) of the skull, as well as in the breadth of M1 and length of maxillary tooth row (Figure 14). These characteristics were also visible in qualitative aspects, along with other traits, as more robust skulls; posterior part of zygomatic plate positioned more perpendicular to the anterior - posterior axis of the skull; supraorbital margins sharp and moderately beaded. However, no information was founded in the literature about karyotype for that sample.

The sample I named as Ecuador, were in fact, the sample used by Musser et al. (1998) to described the specie they named as *H. tatei*. In that case, all morphometric analysis supported the hypotheses that this is a singular population of *Hylaeamys*. That population occurred in the highest elevation that the genus could be founded. These two localities are situated in the eastern foothills of the Andes, between 1140m and 1300m of elevation.

However, for the others samples of “*yunganus* group” the morphometric analyzes highlighted an important geographic variation. Populations from eastern Amazon Forest presented difference from the populations on the western part of the Biome. The eastern populations represented by populations from NAmazEast, SAmazEast and Xavantina showed a delicate skull and the smallest means for the variables related to length and breadth of the skull, as well as the breadth of M1 and length of maxillary tooth row (Figure 14). Samples from Madeira had a smaller and more gracile skull, more similar to eastern population samples.

Jorge-Rodrigues (2013), in a previous analysis of *Hylaeamys yunganus*, also showed morphological and morphometric difference between population from Guiana and populations from Rio Juruá and western Amazon Forest. The author considered those differences as geographical variation of this species, as well as Musser et al (1998). I think that the variation between those samples from east and west of Amazon Forest are really expressive, and depending upon the results of the phylogenetic analysis, can be translated to the recognition of a new biological entity in the group.

4.2 The “*megacephalus* group”

The samples of this group included specimens with one fossette and a long paraflexus in the second upper molar (Figure 11). At the present, five species are recognized into this group: *H. acritus* (Emmons and Patton 2005), *H. laticeps* (Lund 1841), *H. megacephalus* (Fischer 1814), *H. oniscus* (Thomas 1904), *H. perenensis* (Allen 1901). They are distributed into the north part of Cis-Andean South America, going eastern until the Brazilian coast through the entire central Brazil and going south until Paraguay (Figure 21).

4.2.1 Cranial morphometric variation of “*megacephalus* group”

As this group has a wide distribution and to discriminate local, regional and continental geographic variation, I compartmentalize the morphometric analysis in four different levels: At first I analyzed all samples from Bolivia (including those of “*yunganus* group”), since there is not a consensus in the literature (MUSSEr et al., 1998; EMMONS; PATTON, 2005; WEKSLER; PERCEQUILLO, 2011; PRADO; PERCEQUILLO, 2013) about which species of *Hylaeamys* occurred there; secondly, I performed the analysis between samples within the same biome; thirdly, I conducted morphometrical analysis between all groups identified in the previous analysis among different biomes; and, finally, I conducted an analysis with groups of *Hylaeamys* recovered in the previous analysis and samples from Atlantic Forest.

Figure 21 - Distribution of the known collection localities of all samples of “*megacephalus* group”

4.2.1.1 Bolivia samples

Into his Bolivian list of mammals, Anderson (1997) recognized 6 different species and one undetermined species of the genus *Oryzomys*. From this six species, two of them are today attributed to the *Hylaeamys* genus: *Oryzomys capito* and *O. yunganus*. Emmons and Patton described, in 2005, a new species of *Hylaeamys* from Bolivia, which they named as *H. acritus*. The species is restricted to a small area of the western basin of the Río Itenez (Figure 23) and sympatric to other forms of *Hylaeamys*. The authors showed some morphological and genetic difference between the species described and western Amazon samples of “*megacephalus* group”. Patton et al. (2000) analyzed samples from the Rio Juruá and some localities in Peru and suggested that *H. perenensis* were the appropriate name for these populations. Prado and Percequillo (2013) mapped the distribution of Oryzomyini rodents, and for the populations of Bolivia they considered tree species: *H. megacephalus*, *H. acritus* and *H. yunganus*. Percequillo (2015) pointed that the limits of distribution between *H. megacephalus* and *H. perenensis* are still unclear. He argued that the Madeira - Guaporé Rivers could be the limit to *H. perenensis* and includes that specie in the north part of Bolivia.

Therefore, it is not quite clear how many species occur in Bolivia, nor their geographic distribution.

I made some morphometric analysis with all samples from Bolivia, including specimens of “*yunganus* group” from Bolivia to analyze the variation into the skull size of that populations. I also used samples from close localities from Central Brazil and Paraguay, and samples from Madeira River and Peru (Table 4) to better understood the variations of the Bolivian samples (Figure 22) and to propose a better delimitation of the taxa in that region.

Table 4 - Grouped localities and their respective localities number (numbers correspond to gazetteer in Appendix I) and total number of specimens of *Hylaeamys* used in morphometric analysis of Bolivia samples

Groups	Localities	Number of specimens in each group
Bodoquena	164, 165, 166	14
Baures	10	6
Centenela	8, 12, 14	9
CostaMarq	15	15
Elrefugio	17, 18	7
EBBeni	13, 19, 26	7
Madeira	221	8
OppCostaMarq	3, 9, 24	17
Paraguay	281, 282, 283, 287, 288	20
Paranatinga	144, 137	12
PNKempf	42, 44, 45	8
RioPitasama	2, 27, 39, 41, 46, 47, 49	10
PuertoSiles ¹	4, 5, 22	3
yunganus	1, 37, 35, 41, 40	5

1. Samples from Puerto Siles were not included into univariate analysis because of the small number of specimens

To explore the data I performed error bar diagrams for all variables. In these diagrams we can see the mean and 95% of confidence interval. I could not include the samples from

PuertoSiles and from “*yunganus* group” into the graphics because they had a small number of specimens (Table 4) that influenced the confidence interval.

Figure 22 - Distribution of the samples of *Hylaeamys* groups in Bolivia, Brazil and Paraguay, employed in the quantitative analyses of variation

For the variables ONL, LD, LFI and LN, samples from Baures, EBBeni and RioPitasama showed the lowest mean values (Figure 23). For the variable BBP, sample from PNKempf also showed the lower mean, as well as Baures and EBBeni for the variable BIF.

For two variables, CLM1-3 and ZB, the sample EBBeni showed the lowest mean value (Figure 24). On the other hand, for the variables BM1 and BR the sample from CostaMarq showed the highest averages (Figure 24). For the variable IB, samples from EBbeni and RioPitasama showed the highest one and for BZP they showed the lowest one. The variable LBP did not show any pattern of geographic variation, with means varying in mosaic (Figure 25).

Figure 23 - Comparison of variables ONL, LD, LFI, LN, BBP and BIF between samples from Bolivia. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 24 - Comparison of variables CLM1-3, ZB, BM1 and BR between samples from Bolivia. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 25 - Comparison of variables IB, BZP and LBP between samples from Bolivia. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

I performed multivariate analyses only using samples from Bolivia, including together samples of “*megacephalus*” and “*yunganus*”. In the PCA analysis, the first component was responsible for 44.78% of the variation, the second component was responsible for 14.86%, and the third component was responsible for 10.58% of the observed variation (Table 5). Together, these three components were responsible for more than 70% of the total variation. The variables that had the highest score in the first component were: (+) ZB, (+) LN and (+) LIF. The variables that had the highest score in second component were (+) BBP, (-) BZP and (+) BIF, and for the third component, the variables that showed the highest scores were (+) BIF, (+) BR and (+) ZB (Table 5). The scores are showed in two scatterplot graphic (Figure 26 and 27).

Table 5 - Values of first (PC1), second (PC2) and third (PC3) components resulted from a Principal Component Analysis of log transformed cranial and dental variables of *Hylaeamys* from Bolivia. Variables with highest scores in each component are in bold

Variables	PC1	PC2	PC3
ONL	0.924	-0.041	-0.098
LD	0.893	0.036	-0.130
CLM1-3	0.428	-0.029	0.041
BM1	0.141	0.029	0.024
LIF	0.729	0.069	0.323
BIF	0.606	0.445	0.571
BBP	0.366	0.742	-0.390
BR	0.504	-0.066	0.425
LN	0.805	0.063	-0.401
LBP	0.614	-0.154	-0.186
IB	-0.090	-0.018	0.416
ZB	0.885	0.061	-0.045
BZP	0.709	-0.622	-0.022
Eigenvalue	0.003	0.001	0.001
% Variance	44.78	14.86	10.58

Figure 26 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and second principal components (PC1 and PC2) extracted from analysis of *Hylaeamys* samples from Bolivia

Figure 27 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and third principal components (PC1 and PC3) extracted from analysis of *Hylaeamys* samples from Bolivia

In the Discriminant Function Analysis, the first discriminant function was responsible for 80.6% of the variation and the variables (+) BBP, (-) BZP, and (+) LN showed the highest scores (Table 6). For the second discriminant function, which was responsible for 19.4% of the variation, the following variables had the highest values: (+) BZP, (+) ONL, (+) ZB. The scores are presented in a scatterplot graphic (Figure 28).

Table 6 - Values of first (DS1) and second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* from Bolivia. Variables witch must influence each discriminant score are in bold

Variables	DS1	DS2
ONL	-0.011	0.650
LD	-0.002	0.567
CLM1-3	0.002	0.257
BM1	0.128	-0.027
LIF	-0.039	0.437
BIF	0.104	-0.090
BBP	0.866	0.501
BR	-0.034	0.450
LN	0.178	0.588
LBP	-0.074	0.417
IB	0.014	-0.090
ZB	0.090	0.613
BZP	-0.388	0.922
Wilk's Lambda	0.000	0.000
Eigenvalue	1.245	0.299
% Variance	80.6%	19.4%

Figure 28 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurements extracted from a discriminant function analysis with covariance matrix of *Hylaeamys* samples from Bolivia

The dispersal of scores on the multivariate space showed some level of structure between Bolivia samples, with three main clusters recognized; one, including samples from EBBeni, RioPitasama and *yunganus* groups; another cluster, formed by the samples from Centenela, CostaMarq and ElRefugio; and one last cluster, that exhibit the samples from OppCostaMarq, PNKempf, PuertoSiles and Baures.

Despite the morphometric difference between samples of the first and second clusters, no qualitative trait was found for each cluster, except for the presence of the two parafoesets on the specimens of the “*yunganus* group” samples. On the other hand, morphological characters, as a single complete dermal ring on digit I, and a notch in the rim of auditory meatus, were observed only in specimens of the last group.

With the objective to further understand the variation of this samples from Bolivia, I performed other multivariate analysis, including samples from others localities close to Bolivia, as samples from Madeira River, Paraguay and Cerrado of cenral Brazil. In the PCA analysis, the first component was responsible for 42.51% of the variation and the second component was responsible for 16.05%, of the observed variation (Table 7). Together, these two components were responsible for more than 58% of the total variation. The variables that had the highest score in the first component were: (+) ONL, (+) LD and (+) ZB. The variables

that had the highest score in second component were (+) BIF, (+) BZP and (-) CLM1-3. The scores are showed into the scatterplot graphic (Figure 29).

Table 7 - Values of first (PC1) and second (PC2) components resulted from a Principal Component Analysis of log transformed cranial and dental variables of *Hylaeamys* from Bolivia, Paraguay, Madeira River and nearby Central Brazil. Variables with highest scores in each component are in bold

Variables	PC1	PC2
ONL	0.922	0.099
LD	0.890	0.157
CLM1-3	0.575	-0.236
BM1	0.257	-0.018
LIF	0.748	0.018
BIF	0.583	0.672
BBP	0.006	0.161
BR	0.298	0.197
LN	0.708	0.128
LBP	0.728	0.083
IB	0.015	0.164
ZB	0.845	0.162
BZP	0.776	-0.574
Eigenvalue	0.003	0.001
% Variance	42.51	16.05

Figure 29 - Scatterplot of first and third Canonical Score of log-transformed value of 13 cranial and dental measurement extracted from a discriminant function analysis with covariance matrix of *Hylaeamys* samples from Bolivia, nearby central Brazil, Madeira River and Paraguay

In the Discriminant Function Analysis the first discriminant score was responsible for 54% of the variation and the variables (+) BZP, (+) LBP, and (+) CLM1-3 showed the highest scores (Table 8). For the second discriminant score, which was responsible for 24% of the variation, the following variables had the highest values: (-) LBP, (+) BZP and (-) LD. The scores are presented in a scatterplot graphic (Figures 30).

Table 8 - Values of first (DS1) and second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* from Bolivia. Variables witch must influence each discriminant score are in bold.

Variables	DS1	DS2
ONL	0.424	-0.208
LD	0.466	-0.366
CLM1-3	0.477	0.154
BM1	0.095	0.227
LIF	0.276	0.266
BIF	0.083	-0.088
BBP	-0.305	-0.305
BR	-0.205	0.097
LN	0.136	-0.174
LBP	0.507	-0.508
IB	-0.141	-0.026
ZB	0.278	-0.140
BZP	0.539	0.413
Wilk's Lambda	0.000	0.000
Eigenvalue	2.099	0.948
% Variance	54%	24%

Figure 30 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurement extracted from a discriminant function analysis with covariance matrix of *Hylaeamys* samples from Bolivia, nearby central Brazil, Madeira and Paraguay

These results showed that samples from Bodoquena, Paraguay, Paranatinga and Madeira (some specimens) were morphometrically distinct from the specimens from Bolivia. It is also visible that specimens from OppCostaMarq, PNKempf, PuertoSiles and Baures were more similar, being clustered, although with some overlap to other Bolivian samples. On the other hand, the variation among the first and second cluster described above was much less pronounced. Such results lend me to hypothesize that, aside from specimens of the yunganus group, in Bolivia there are two additional clusters (one from OppCostaMarq, PNKempf, PuertoSiles and Baures; the other from EBBeni, RioPitasama, Centenela, CostaMarq and ElRefugio), both distinct among them and also distinct to other close geographic samples from Brazil, as demonstrated above.

4.2.1.2 Amazon Samples

The samples used in this group extend from the mouth of the Amazon River to the Cis-Andean regions of Amazon Forest, including samples from Trinidad and Tobago archipelago. As the samples were widely distributed, I pooled them in two ways (see Table 9): firstly, I pooled samples by geographic proximity (Group 1, Table 9). To achieve a larger number of

cases for statistics analysis and, very likely, more robust comparisons between samples, I grouped samples from group 1 according to the north and south margins of Amazon River (Figure 31), and previous analysis performed with some specimens as those from Rio Jurua (PATTON et al. (2000)). These samples were labeled as indicated in Group 2 of Table 9.

As the samples from Bolivia showed to be a unique morphometric unity when compared with others samples I decided, in a first moment, to consider them as a unique sample. In a second moment, I splitted them into 2 different groups according to the results founded when I analyse only Bolivian samples. That way I could better compare the variation founded into Bolivia with all others samples from Amazon Forest.

Figure 31 - Pooled samples of *Hylaeamys* in Amazon Forest Biome, as defined in Table 9.

Table 9 - Grouped localities and their respective localities number (numbers correspond to gazetteer in Appendix I) and total number of specimens of “*megacephalus* group” from Amazon Forest used in morphological and morphometric analysis

Group 1	Group 2	Localities	number of specimens in group 1
Altamira	SEAmaz	184, 185, 187, 188	42
UpperJurua	Jurua	78, 92	6
Aripuanã	Aripuana	142	6
LowerJurua	SWAmaz	53, 54, 56	13
Balta	SWAmaz	362	15
Baures	Bolivia	9, 10, 21	11
Curicha	Bolivia	4, 5, 8, 12, 14, 22	17
Chodikar	NEAmaz	275, 277	7
CollpaSalv	NWAmaz	327, 334	19
Conchaguaya	SouthWestAmaz	326, 234, 238, 363	12
CostaMarq	Bolivia	3, 15, 16, 24	53
Cundinamarca	NWAmaz	234, 238	6
EEBeni	Bolivia	7, 13, 19, 26, 29, 30	13
ElRefugio	Bolivia	17, 18, 25	11
Paracou	NEAmaz	265, 269, 272, 276	5
Itaituba	SEAmaz	197, 199, 203, 204	45
Jau	NCentralAmaz	83, 89	13
Manaus	NEAmaz	69, 84	17
Manu	SWAmaz	303, 339, 341, 343	21
Marcapata	SWAmaz	310, 356	12
Mecaya	NWAmaz	239	13
CentralJurua	Jurua	70, 71, 72, 80, 85, 73, 76, 86, 91	56
Napo	NWAmaz	241, 242, 243, 245, 246, 247, 248	43
Negro	NEAmaz	75, 81, 201, 207, 208	20
Pasco	SWAmaz	35, 318, 322, 346, 347, 350, 352	16
ReservaCuzco	SWAmaz	337, 338, 340, 342, 345	45
RioApurimac	SWAmaz	289, 302, 304, 306, 307, 320, 353	23
RioBiata	Bolivia	11, 31	6
RioPitasama	Bolivia	2, 27, 46, 47, 49	12
RioSamiria	NWAmaz	330, 332, 336	10
RioTocantins	SEAmaz	186, 189, 195, 200, 202	35
Sarayacu	NWAmaz	250, 253, 256, 257	6
SerraNavio	NEAmaz	67, 68,	43
Finisanti	NEAmaz	365, 369, 370, 372	8
Kaiser	NEAmaz	373, 368, 376	10
Trinidad	Trinidad	378, 379, 380, 381, 382,	20
Tseasim	NWAmaz	261, 291, 293, 297, 294, 355	28
CerroNeblina	NCentralAmaz	90, 388, 385	6
Auyantepui	NCentralAmaz	391, 392, 393	16
MonteDuida	NCentralAmaz	384, 387, 389	7

The error bar diagrams for the variables ONL, LD and LBP, showed that samples were arranged in two clusters: one with the samples of Bolivia, Jurua, NWAmaz and SWAmaz, that exhibit the highest averages; and another cluster formed by NCentralAmaz, NEAmaz, SEAmaz and Trinidad, presenting low mean values (Figure 32).

Figure 32 - Comparison of variables ONL, LD and LBP between samples of “*megacephalus* group” from Amazon Forest. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

For the variables BM1 and ZB we can identify 3 groups: Bolivia, Juruá, NWAmaz and SWAmaz, present higher mean values; NCentralAmaz, SEAmaz and Trinidad, with intermediate mean values; and the sample NEAmaz, with the lower average. Similar results were observed in the variable CLM1-3, but for this trait the samples from NCentralAmaz showed an intermediate mean value, when compared with all others samples (Figure 33).

Figure 33 - Comparison of variables BM1, ZB and CLM1-3 between samples of “*megacephalus* group” from Amazon Forest. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

For the variables BBP and IB, the Trinidad samples showed intermediate average between two groups, one formed by Jurua, NWAmaz and SWAmaz, and the second group formed by Bolivia, NCentralAmaz, NEAmaz and SEAmaz with the lowest means (Figure 34). For the variables LIF, BIF, LN and BR, I did not found a pattern of geographic variation among the samples (Figure 35).

Figure 34 - Comparison of variables BBP and IB between samples of “*megacephalus* group” from Amazon Forest. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 35 - Comparison of variables LIF, BIF, LN and BR between samples of “*megacephalus* group” from Amazon Forest. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

In the PCA analysis, three components (PC1, PC2 and PC3) totalized more than 70% of the variation. The first component was responsible for 48.75% of the variation, the second component was responsible for 12.37% and the third component was responsible for 9.65% (Table 8). The variables that had the highest score in the first component were: (+) ONL, (+) LD and (+) ZB. The variables that had the highest score in second component were (+) BIF, (+) LIF and (-) LBP, and for the third component, the variables that showed the highest scores were (+) BBP, (-) BZP and (+) BM1 (Table 10). The individual scores are showed into the scatterplot graphics (Figures 36 and 37).

Table 10 - Values of first (PC1), second (PC2) and third (PC3) components resulted from a Principal Component Analysis of log transformed cranial and dental variables of *Hylaeamys* from Amazon Forest. Variables with highest scores in each component are in bold

Variables	PC1	PC2	PC3
ONL	0.930	0.045	-0.038
LD	0.874	0.160	-0.063
CLM1-3	0.710	-0.240	0.260
BM1	0.626	-0.275	0.299
LIF	0.484	0.625	-0.168
BIF	0.323	0.776	0.136
BBP	0.609	0.048	0.634
BR	0.665	0.073	0.082
LN	0.577	0.272	-0.189
LBP	0.803	-0.330	0.063
IB	0.420	-0.190	0.383
ZB	0.868	0.047	0.058
BZP	0.823	-0.185	-0.447
Eigenvalue	0.005	0.001	0.001
% Variance	48.75	12.37	9,65

Figure 36 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and second principal components (PC1 and PC2) extracted from analysis of *Hylaeamys* samples from Amazon Forest Biome

Figure 37 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and third principal components (PC1 and PC3) extracted from analysis of *Hylaeamys* samples from Amazon Forest Biome

In the Discriminant Function Analysis, the first discriminant score was responsible for 71.4% of the variation and the variables (+) CLM1-3, (+) BZP and (+) ZB showed the highest scores. For the second discriminant score, which was responsible for 18.5% of the variation, the following variables had the highest values: (+) IB, (-) BZP and (+) BBP (Table 11). The individual scores are presented in a scatterplot graphic (Figure 38).

Table 11 - Values of first (DS1) and second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* from Amazon Forest. Variables which must influence each discriminant score are in bold

Variables	DS1	DS2
ONL	0.522	0.008
LD	0.504	0.083
CLM1-3	0.621	0.112
BM1	0.375	0.083
LIF	0.175	0.114
BIF	0.001	-0.037
BBP	0.307	0.405
BR	0.226	0.158
LN	0.113	-0.110
LBP	0.467	0.008
IB	0.302	0.558
ZB	0.555	-0.119
BZP	0.561	-0.421
Wilk's Lambda	0.000	0.000
Eigenvalue	2.297	0.597
% Variance	71.4%	18.5%

Figure 38 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurements extracted from a discriminant function analysis with covariance matrix of group 2 of table 7 of *Hylaeamys* samples from Amazon Forest

Considering all analysis with Amazon samples of the “*megacephalus* group”, I was able to identify, although with some overlap among marginal specimens, at least two morphometric units, one assembling samples from the western portion of Amazon basin (Bolivia, Juruá, NWAmaz and SWAmaz); and a second one, gathering specimens from eastern Amazon (NCentralAmaz, NEAmaz, SEAmaz and Trinidad). A similar pattern of morphometric variation was observed in “*yunganus* group”, and in both groups eastern samples are smaller than western populations. Despite the boundaries of this segregation between east and west in the north portion of Rio Amazonas, being differently with samples from NCentralAmaz of “*yunganus* group” more similar to western samples, once the NCentralAmaz of “*megacephalus* group” was more similar to eastern samples; the pattern is consistent, and also supported by karyotypic data related to each group of species. Therefore, in Amazon basin I recognize the existence of two groups, discriminated by size.

4.2.1.3 Central Brazil and Paraguay Samples

Into this topic, I made morphometric comparison between all samples into the Cerrado biome, as well as some samples on the transition with Amazon Forest, as Claudia (Figure 39, Table 12). The group SP/MG was not used into this exploratory analysis because of its small number of specimens (Table 12).

Table 12 - Grouped localities and their respective localities number (numbers correspond to gazetteer in Appendix I) and total number of specimens of “*megacephalus* group” from central Brazil and Paraguay used in morphological and morphometric analysis

Group	Localities	Number of specimens
Claudia	138, 157	28
Xavantina	137, 140, 150	25
Rio Manso	144, 153, 158, 161, 162	30
Barra Garça	134, 139, 146, 149, 151	18
Peixe	229, 232	9
DFederal	116, 117, 118, 119, 125, 131, 132, 133, 178	27
Coromandel	127, 128, 169, 170, 175, 176, 180	30
TSampaio	226, 227, 228,	9
SP/MG	173, 222, 223, 225	5
Paranatinga	144, 137	12
Paraguay	281, 282, 283, 287, 288	20
Bodoquena	164, 166	13

Figure 39 - Samples and pooled samples of *Hylaeamys* groups from central Brazil and Paraguay

For the most part of variables, I did not observe a pattern of geographic variation. The differences were in mosaic; for instance, for three variables, ONL, LD and LBP, Paraguayan sample showed the highest mean (Figure 40), as well as Bodoquena sample for LN, BBP and BZP variables (Figure 41).

On the other hand, for the variables CLM1-3, LIF and ZB, the sample from Claudia showed the lower mean values (Figure 42). Only for the variable BIF, I observed a difference not only in the mean, but in the confidence interval as well, between samples from Coromandel, Paraguay and TSampaio, with the highest means, and the others samples (Figure 43).

Figure 40 - Comparison of variables ONL, LD and LBP between samples of “*megacephalus* group” from central Brazil and Paraguay. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 41 - Comparison of variables LN, BBP and BZP between samples of “*megacephalus* group” from central Brazil and Paraguay. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 42 - Comparison of variables CLM1-3, LIF and ZB between samples of “*megacephalus* group” from central Brazil and Paraguay. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

Figure 43 - Comparison of variables BIF, BM1, BR and IB between samples of “*megacephalus* group” from central Brazil and Paraguay. Open circles are the mean and error bar diagrams showing 95% of confidence interval for each group

In the PCA analysis, three components (PC1, PC2 and PC3) totalized 69.81% of the variation. The first component was responsible for 46.73% of the variation, the second component was responsible for 14.38% and the third component was responsible for 8.7% (Table 13). The variables that had the highest score in the first component were: (+) ONL, (+) LN and (+) ZB. The variables that had the highest score in the second component were (-) LIF, (+) BZP and (-) BM1, and for the third component, the variables that showed the highest scores were (-) BZP, (+) LBP and (-) LFI (Table 13). The individual scores are showed into the scatterplot graphics (Figures 44 and 45).

Table 12 - Values of first (PC1), second (PC2) and third (PC3) components resulted from a Principal Component Analysis of log transformed cranial and dental variables of *Hylaeamys* from central Brazil and Paraguay. Variables with highest scores in each component are in bold

Variables	PC1	PC2	PC3
ONL	0.916	-0.012	0.203
LD	0.835	-0.177	0.215
CLM1-3	0.487	0.126	0.060
BM1	0.489	0.509	-0.009
LIF	0.645	-0.582	-0.343
BIF	0.727	-0.361	-0.093
BBP	0.644	0.325	-0.008
BR	0.706	0.308	0.035
LN	0.841	-0.020	0.194
LBP	0.629	0.331	0.439
IB	0.561	0.185	0.210
ZB	0.814	-0.132	0.263
BZP	0.532	0.546	-0.576
Eigenvalue	0.004	0.001	0.001
% Variance	46.73%	14.38%	8.7%

Figure 44 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and third principal components (PC1 and PC2) extracted from analysis of *Hylaeamys* samples from central Brazil and Paraguay

Figure 45 - Samples score, based on log-transformed mean value of 13 cranial and dental measurement projected onto the first and third principal components (PC1 and PC3) extracted from analysis of *Hylaeamys* samples from central Brazil and Paraguay

I also performed a Discriminant Function Analysis. In this analysis, the first discriminant score was responsible for 65.8% of the variation and the variables (+) ZB, (+) ONL and (+) LN showed the highest scores. For the second discriminant score, which was responsible for 32.1% of the variation, the following variables had the highest values: (+) IB, (+) BZP and (+) BR (Table 14). The individual scores are presented in a scatterplot graphic (Figure 46).

Table 14 - Values of first (DS1) and second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* from central Brazil and Paraguay. Variables which must influence each discriminant score are in bold

Variables	DS1	DS2
ONL	0.472	0.384
LD	0.428	0.291
CLM1-3	0.198	0.262
BM1	0.161	0.335
LIF	0.275	0.105
BIF	0.255	0.160
BBP	0.262	0.410
BR	0.226	0.489
LN	0.463	0.266
LBP	0.109	0.357
IB	0.420	0.849
ZB	0.797	0.264
BZP	-0.226	0.594
Wilk's Lambda	0.000	0.000
Eigenvalue	0.872	0.439
% Variance	65.8%	32.1%

Figure 46 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurement extracted from a discriminant function analysis with covariance matrix of group 2 of table 7 of *Hylaeamys* samples from central Brazil and Paraguay

The performed analysis did not show any congruent pattern of geographical variation in the skull size between samples of central Brazil and Paraguay. Therefore, the samples from this region were considerate as a unique group in the morphometric analysis between *Hylaeamys* species group.

4.2.1.4 Morphometric variation between “*megacephalus* group” samples

Based on the results obtained in the previous analyses, I performed a Discriminant Function Analyses between all *Hylaeamys* groups. Samples from Amazon Forest were splitted into two distinct groups: EasternAmaz comprising samples from NcentralAmaz, NEAmaz, SEAmaz (including Madeira samples); and WesternAmaz were I grouped samples from SWAmaz and NWAmaz. Central Brazil and Paraguay samples were labeled as Cerrado. Although I considered the Bolivia samples as a unique morphometric unity in previous analysis, I decided to separate it in two different groups, once they can be diferenciaded through morphological characters: samples from EEBeni, RioPitasama, Centenela, CostaMarq and El Refugio I labeled as Bolivia, and samples from Baures, PNKempf, Puerto Siles and OppCostaMarq are labeled as PNKempf. Samples from Atlantic Forest were also included,

and splited into two diferentt groups, according to Brennand et al. (2013): Samples from north of Rio São Francisco were labeled as NortheasternAF; and, samples from South of Rio São Francisco were labeled as SoutheasternAF.

The first discriminant score was responsible for 58.3% of the variation and the variables (+) ONL, (+) BZP and (+) CLM1-3 showed the highest scores (Table 15). For the second discriminant score, witch was responsible for 22.9% of the variation, the following variables had the highest values: (+) LD, (+) LBP and (+) ZB. The scores are presented in a scatterplot graphic (Figure 47).

Table 15 - Values of first (DS1) and second (DS2) Discriminants Scores resulted from a Canonical Discriminant Analysis of cranial and dental log transformed variables of *Hylaeamys* from all Amazon Forest. Variables witch must influence each discriminant socre are in bold

Variables	DS1	DS2
ONL	0.638	-0.036
LD	0.442	0.360
CLM1-3	0.560	0.051
BM1	0.407	-0.159
LIF	0.364	-0.089
BIF	0.031	0.060
BBP	0.162	0.000
BR	0.163	0.021
LN	0.227	-0.165
LBP	0.439	0.313
IB	0.255	-0.045
ZB	0.476	0.175
BZP	0.579	-0.102
Wilk's Lambda	0.000	0.000
Eigenvalue	2.705	1.063
% Variance	58.3%	22.9%

Figure 47 - Scatterplot of first and second Canonical Score of log-transformed value of 13 cranial and dental measurements extracted from a discriminant function analysis with covariance matrix of group 2 of table 7 of *Hylaeamys* samples from Amazon Forest, Cerrado and Atlantic Forest biomes.

These results reinforce the results that the specimens from eastern and western portion of Amazonia are distinct in size, clustering in different sections of the multivariate space. Bolivia, WesternAmaz and PNKempf are overlapped, as specimens from Cerrado and EasternAmaz, even including specimens from the Atlantic Forest. These are similar among themselves, with wide overlap of individual scores, but quite distinct from the samples from Amazonia.

4.2.2 Karyotype variation in “*megacephalus* group”

Three different karyotypes were described by Gardner and Patton (1976) for *Hylaeamys* populations of the Ayacucho, Loreto, and Junín departments in Peru, assigned as *Oryzomys capito*. The karyotype of diploid number (2n) was 52 and the fundamental number (FN) was 62, comprising six pairs of medium to small metacentric or submetacentric, 18 large to small pairs of acrocentric, one very large acrocentric, and two sex chromosomes: a large acrocentric X and a small acrocentric Y. Two different karyotypes were described for the

specimens named *Oryzomys yunganus*. See Karyotype of “*yunganus* group” (topic 4.1.1) for more details.

Leitão and Barros (1977) and Barros (1978) described a karyotype with $2n = 54$ and $FN = 62$ for specimens from Para and Amazon States in north Brazil. Despite the fact that the karyotype was described for specimens from the type locality of *Oryzomys goeldi* (Itaituba, Para), the authors named them as *Oryzomys capito*.

Perez-Zapata et al. (1985) analyzed the karyotype of some *Oryzomys* samples from Venezuela. The karyotype $2n=54$, $FN=62$ found in San Ignacio de Yuruni, in Bolivar state in eastern Venezuela, was considered by them as *Oryzomys capito*.

In 1988, Zanchin analyzed samples from the southeastern Brazil, in the south of Bahia state. He found $2n = 48$ and $FN = 64$ karyotype and attributed it to a new species related to *Oryzomys capito* complex, more precisely related to the *O. capito* form with $FN=52$, also from Brazilian Atlantic Forest. The author considered that difference between both forms was due to a Robertsonian translocation.

Maia (1990) described the karyotype of two females and one male from São Lourenço da Mata, Pernambuco State, in northeastern of Brazil. The following karyotype was described: $2n = 52$ and $FN = 62$, composed of 19 acrocentric pairs and 6 biarmed. The X chromosome was acrocentric sized and the chromosome Y was a small acrocentric. This karyotype is very similar to this one described by Gardner and Patton (1976) for *O. capito* from Peru but Maia (op.cit.) named them as *O. capito oniscus* because theses specimens was collected in the type locality of *O. oniscus* described by Thomas (1904) and considered a subspecies of *O. capito* by Cabrera (1961).

Svartman and Almeida (1992) collected specimens from Goiás State in central Brazil and obtained the karyotype $2n=54$ and $FN=62$ composed of 21 acrocentric autosomal pairs, 5 biarmed autosomal pairs, a large acrocentric X, and a medium acrocentric Y. P. Hershkovitz identified the specimens as *O. capito laticeps*, and have the same karyotype of those described in Amazonas and Para State in north Brazil (LEITÃO; BARROS, 1977; BARROS, 1978) and differed from those from Brazilian Atlantic Forest (ZANCHIN, 1988; MAIA, 1990). According to the authors, this difference in the diploid number was due to a Robertsonian rearrangement. The authors also emphasized the fact that these different karyotypes were related to two different subspecies of *O. capito* and these two forms did not occur in sympatry.

Silva (1994) described the same karyotype as Leitão and Barros (1977), Barros (1978) and, Svartman and Almeida (1992) for samples from Manaus, north of Brazil.

Perez-Zapata and Aguilera (1996) used banding technique to suggest that the two *Oryzomys* forms from Venezuela, *O. capito* and *O. talamancae*, described earlier (Perez-Zapata et al., 1985) were two distinct karyological forms with very different karyotypes related through Robertsonian fusions and confirm that the karyotype previous described by Perez-Zapata et al. (1985) were attributed to a species from “*megacephalus* group”.

In 1998, Musser and collaborators revised the *Oryzomys capito* complex and for the “*megacephalus* group” forms they presented the karyotype $2n=54$, $FN=62$ for the populations of eastern Paraguay and north Brazil. They recognized these populations as *O. megacephalus*. Despite the karyotype differences in the Atlantic forest forms, the authors synonymized these populations under the name *O. laticeps*.

Weksler et al. (1999) described new species in Brazilian Atlantic Forest, from Bahia to Rio de Janeiro States. The new species was named *O. seuanezi* and its karyotype was $2n=48$, $FN=60$. The authors considered this species as a sister taxa of *O. oniscus* forming an Atlantic Forest clade. The authors also compared their results with the previous karyotype found by Zanchin (1988) for populations from Bahia state, northeastern Brazil. The two karyotypes were different only in the number of arms; $FN=60$ for this study and $FN=64$ for Zanchin (1988). The author argued that Zanchin misidentified two pairs of acrocentrics as metacentric or submetacentric; and that the correct fundamental number for the samples is 60.

Patton et al. (2000) recognized as new specie the western population of *O. megacephalus* and named it as *O. perenensis*. This new specie has the karyotype $2n=52$, $FN=62$ consistent with 25 acrocentric chromosome grading in size from large to small and six pairs of small metacentric or submetacentric, a medium large acrocentric X and a small acrocentric Y. This karyotype was previously found in populations from eastern (GARDNER; PATTON, 1976) and central Peru and eastern Ecuador (MUSSER et al., 1998).

In this same year, Andrades-Miranda et al. (2000) found the following karyotypes for the “*megacephalus* group”: $2n=54$, $FN=62$ for central Brazil samples and, two karyotypes for Atlantic Forest samples: $2n=52$, $FN=62$ for northeastern samples and $2n=48$, $FN=64$ for southeastern samples. The fundamental number of the karyotypes in the southeastern samples agrees with Zachin (1988) but not with Weksler et al. (1999).

So, for the “*megacephalus* group” we had the following karyotypes described in the literature (Figure 48): $2n=52$; $FN=62$ to samples from Peru, Ecuador, and Brazilian Atlantic Forest; $2n=54$; $FN=62$ to samples from Venezuela, north, northeastern and central Brazil and Paraguay, and, finally, $2n=48$, $FN=60$ or 64 for southeastern Brazil.

Figure 48 - Distribution of the karyotypes described for populations of *Hylaeamys* “*megacephalus* group”

4.2.3 Summary of variation in “*megacephalus* group”

Morphometric results are in agreement with karyotype informations for “*megacephalus* group” despite some overlapping between groups. When morphometrics analyses were applied in samples from closed geographic area, for example, analysis between Bolivia samples and between Atlantic Forest samples, the method was able to recovery size difference, in skull variable, between samples with different karyotypes.

Samples with larger and robust skull, as northeastern Atlantic Forest and western Amazon Forest samples also shared the same karyotype, $2n = 52$; $FN = 62$. As well as samples with smaller and gracile skull, as central Brazil and Paraguay, and samples from eastern Amazon forest, both with $2n = 54$; $FN = 62$.

4.3 Phylogeny of the genus *Hylaeamys*

In a first moment, I focused in relationship between the samples of the genus *Hylaeamys*, and I labeled the terminals with the same names that I employed to the samples and pooled samples that I employed in the morphometric analyses (Figure 49), in order to be

able to compare both results, and test if size discontinuities are consistent with phyletic relationship throughout the geography.

The tree recovered revealed that the genus is monophyletic, as well as the “yunganus group” (red and dark gray branches; Figures 49) and the “megacephalus group” (remaining branches). The split between these two groups was the first split inside the genus.

For “*yunganus* group”, specimens from western Ecuador were not included in the analysis. The available specimens from eastern Amazon (Guyana) and from Western Amazon (Rio Juruá) form a monophyletic clade, with both samples from Guyana nesting on a clade, reciprocally monophyletic to the western populations of “*yunganus* group”. The morphological analyses revealed that eastern and western samples are distinct, and the phylogenetic results obtained sustain that specimens may represent distinct evolutionary lineages. The inclusion of additional samples will allow further testing to this pattern of relationship, but so far, I address the hypothesis that eastern and western samples of the yunganus group represent “phylogenetic” species.

For samples of the “*megacephalus* group”, the phylogenetic approach showed two distinct clades, one clade with samples from western Amazonia (blue and pink clades; Figure 49), and Atlantic Forest (brown and orange branches; Figure 49); and a second clade with samples from eastern Amazonia, including samples from Rio Madeira and Cerrado. These two clades corroborated with the morphometric results showed previously. In the western clade there are two reciprocally monophyletic groups, one with samples from western Amazon and other with samples from eastern Bolivia (pink clade; Figure 49) and Atlantic Forest. The fact that samples from Atlantic Forest did not show reciprocal monophyly, corroborates the hypothesis that the sample from northeastern Atlantic Forest (brown branch of Figure 49) was a distinct lineage regarding samples from southeastern Atlantic Forest (orange branch of Figure 49), as proposed by Brennand, Langguth and Percequillo (2013). These results also contradict the hypothesis advocated by Costa (2003), who argued that Atlantic Forest lineages of genus *Hylaeamys* were closely related to Cerrado samples; however, the geographic and taxonomic sampling employed by this author was less robust than the studied here.

Figure 49 - Maximum Likelihood consensus tree of Forest clade of Oryzomyini focusing in the genus *Hylaeamys* with terminals labeled as morphological groups. Number next to nodes is the bootstrap value. Locality of each sample is showed in brackets

Into the eastern clade, samples from north of Rio Amazonas (light blue branch of Figure 49) were sister group of a clade composed by two other groups: one with samples from central Brazil, a Cerrado area (green branch of Figure 49), and Southeastern amazon (yellow branch) and the other with samples from Rio Madeira (light grey branch of Figure 49). That difference between samples from north and south samples of Rio Amazonas were first proposed by Patton et al. (2000) and sustained by Costa (2003), but a distinct clade from Rio Madeira was not expected and should be more investigated.

4.4 Species definitions

Combining the results of geographical variation among samples, karyotype information available in the literature, together with the phylogenetic trees to support my taxonomic decisions and delimitations of the taxa. I formally present my hypothesis about the number of species that compound the genus *Hylaeamys* and their distribution

I was able to establish discontinuities among samples of the genus *Hylaeamys*, recognizing 8 groups: Central Ecuador, from Mera and Palmera; Eastern Amazon, from Serra do Navio, Paracou, Xavantina and Altamira; and Western Amazon, from Venezuelan tepuis until Ecuador, and then in Peru and Bolivia, all belonging to yunganus group; Northern

Atlantic Forest, from Paraíba, Pernambuco and Alagoas; Southern Atlantic Forest, inhabiting from Bahia to Rio de Janeiro states; Western Amazon, from Colombia to Bolivia, passing through Ecuador and Peru; and Eastern Amazon, from Venezuela to Para state of Brazil and transional areas between Amazon Forest and Cerrado Biome, all from the megacephalus group. Moreover, molecular phylogenetic approach also recovered most of these groups as monophyletic entities. Therefore, I believe that my results are concordant with the conceptual framework of the integrative species concept, regarding the diagnosis and monophyly of these morphologic groups, and I hypothesize that these eight groups represents eight species of the genus *Hylaeamys* in western South America (Figure 50).

For the “*yunganus* group”, I recognized three different species: For samples from Ecuador group I applied the name *Hylaeamys tatei*, once this samples include the type specimen and the type locality of this species, in the Ecuadorean Andes. Although I did not include specimens of this species on the phylogenetic analysis, the morphologic hypothesis is consistent and will be tested in the future, with forthcoming samples. For samples from western Amazon Forest (Bolivia, SWestAmaz, NWestAmaz and NCentralAmaz groups), that is coincident with the morphology of the type specimen and whose distribution includes the type locality of this species, Charuplaya, Bolívia, I applied the name *Hylaeamys yunganus* Thomas, 1902. And finally, the samples from eastern Amazon Forest and transitional areas between Amazon Forest and Cerrado Biome (NEastAmaz, SEastAmaz and Xavantina groups) I recognized as a new species; as there are no known synonyms for *Hylaeamys yunganus* and available names for this species, herein I report this new species as *Hylaeamys* sp. nov.

For the “*megacephalus* group”, I recognized five species. Two species from Atlantic Forest, two species from western Amazon Forest and one species from eastern Amazon Forest and central Brazil and Paraguay. For the samples from Atlantic Forest, I applied the name *Hylaeamys onicus* Thomas, 1904, for northeastern samples, on the northern bank of Rio São Francisco, once contains the type specimen and type locality of this species, São Lourenço da Mata, Pernambuco; I applied the name *Hylaeamys seuanezi* Weksler, Geise, Cerqueira, 1999, for southeastern samples, located on the southern margin of Rio São Francisco, since the morphological variation of this species included the phenotype of the type specimen of this species, and the geographic distribution of known collection localities includes the type locality of this species.

For samples from western Amazon, I recognized two species. One restricted to eastern Bolivia (OppCostaMarq, Baures, PNKempf, Puerto Siles samples from Bolivia), which received the name *Hylaeamys acritus* Emmons and Patton (2005), once the type specimen

was included in the analysis and exhibit great similarity with the variation observed on samples from northeastern Bolivia and type locality is among the samples that I analyzed of this species; the second species, more widely distributed through western Amazon Forest, including all others samples from Bolivia, SWAmaz, Juruá and NWAmaz, I propose to employ the name *H. perenensis* Allen, 1901, as there is conformity with the type specimen and type locality of this species.

Lastly, a name should be applied to the samples from eastern Amazon Forest (NCentralAmaz, NEAmaz and SEAmaz), central Brazil and Paraguay. Although slightly smaller than other samples in some variables, specimens from Paraguay (the type locality is Curuguaty, in Paraguay) are similar to these samples in most analysis, and as samples from northern and southern bank of Rio Amazonas are reciprocally monophyletic, I adopt a conservative posture and consider these samples as a single species, to which the name *H. megacephalus* Fischer, 1814, should be applied.

Despite the fact that only one sample of *H. oniscus* was included into the analysis, the species from Atlantic Forest did not appear as sister group: *H. oniscus* is closely related to *H. acritus* than to *H. seuanezi*. This result was in accordance with the karyotype attributed to these species, although no information about karyotype was available to *H. acritus*, the two Atlantic Forest species had difference in diploid number as well as in fundamental number. *H. acritus* and *H. perenensis* occurred as sympatric specie in eastern Bolivia, and the phylogenetic results support the fact that they are two different lineages as proposed by Emmons and Patton (2005). The phylogeny also showed a level of geographic structure between *H. megacephalus* populations, as the differences between populations from northern and southern margins of Rio Amazonas were highlighted. As I did not have an estimated dating for that split, I could not argue if the Rio Amazonas acted as an effective barrier or only maintained that divergence among those samples. Considering that Patton et al. (2000) concluded that the Rio Juruá was not a barrier to *H. perenensis* populations, the most plausible scenario was that the Rio Amazonas also was acting as a maintainer of this divergence, but that hypothesis should be better tested. Therefore, I decided not to consider two different species once the morphological (results not show) and morphometric variation between these two populations still overlap in a lot of aspects. *H. megacephalus* is the most plastic species inside the genus and more evidence should be taken into account before to make the taxonomic decision of split into two different species. The hypothesis of two cryptic species was not dropped but need more evidence.

Figure 50 - Maximum Likelihood consensus tree of Forest clade of Oryzomyini focusing in the genus *Hylaeamys* with terminals labeled as the recognized species. Number next to nodes is the bootstrap value. Locality of each sample is showed in brackets

On the other hand, I decided to recognize the samples of “*yunganus* group” from Guyana as a new species (*Hylaeamys* sp.nov). Morphometric and morphological aspect showed that the variations between samples from eastern and western “*yunganus* group” were more consistent than the divergence between *H. megacephalus* of north and south Rio Amazonas. Musser *et al.* (1998) has proposed that this difference were a geographic variation, but frequency in external morphological character as hipotenar pad (already mentioned by Musser *et al.* (1998)) and the morphometric variation showed in previous results, as well as the general aspect of the skull, contributed to my taxonomic decision.

4.4.1 Species Account

Hylaeamys acritus (Emmons and Patton, 2005)

Oryzomys capito: Anderson, 1997:399; part; not *Mus capito* Olfers (= *Hylaeamys megacephalus* [G. Fischer]).

Oryzomys megacephalus: Musser, Carleton, Gardner, and Brothers, 1998:32; part; not *Mus capito* Olfers (= *Hylaeamys megacephalus* [G. Fischer]).

Oryzomys acritus Emmons and Patton, 2005:14; new species.

[*Hylaeamys*] *acritus*: Weksler, Percequillo, and Voss, 2006:14; first use of current name combination.

HOLOTYPE: MNK 3628, a specimen collected by Louise H. Emmons (LHE 1540), in November 6, 1998; the specimen, an adult male, is preserved as skin, skull and tissue sample in ethanol.

TYPE LOCALITY: “Bolivia, Departamento de Santa Cruz, Provincia Velasco, Parque Nacional Noël Kempff Mercado, El Refugio Huanchaca, an outpost with a few buildings and an airstrip on private property, but within the park (14°42.553'S, 061°2.034'W [WGS 84]; elev. 170 m)”; for further details, see the original description (Emmons; Patton, 2005: 14).

DESCRIPTION: This species is characterized externally by a tail much shorter than head and body length (average about 81%), long dorsal (ranging from 9-10 mm in length) and ventral hairs (about 3-4 mm in length), a whitish venter, and a large and fleshy hypothenar pad, one ring of squamae on the digit I of the pes, a notch in rim of meatus. The skull is robust and with strongly developed palatal excrescencies, a very large foramen ovale, M2 with a short paraflexus and a single labial fossete (mesoflexus), and m2 with a short hypoflexid.

DISTRIBUTION: Most known records of *Hylaeamys acritus* are distributed on northeastern Bolivia, on the west bank of the Río Iténez (= Río Guaporé, in Brazil), in the departments of Santa Cruz and El Beni. In this study, we added new localities on the distribution of this species, Puerto Siles, Baures and Opposit Costa Marques, extending the distribution westwards, approximately 400 km upriver on Río Iténez (Figure 51). Although Paglia et al. (2012) recorded the species in Brazil, there were no known confirmed records or vouchers for this táxon and the samples from Opposit Costa Marques (locality number 3 in the gazetteer), Rondônia state were considered as *H. perenensis*.

Figure 51 – Known collection localities of *H. acritus*, in northeastern Bolivia and adjacent Brazil. Number of localities according to Gazetteer in Appendix A

NATURAL HISTORY: Most information on the natural history data of *H. acritus* are from Emmons and Patton (2005), regarding populations of the Parque Nacional Noel Kempff Mercado. At this site, specimens were captured on ground level, in several forested habitats, as evergreen riverine (gallery) forests, deciduous and semideciduous upland (“terra firme”) forests, and seasonally flooded forests on the edge of seasonally flooded pampa. Two main physiognomies are observed on these forests, a “seasonally deciduous emergent canopy, sparse understory and midstory varying in deciduousness depending both on the location and on the dryness of the particular year,” or liana forests, exhibiting “low canopies and dense lianas at all levels” (EMMONS; PATTON 2005). The elevation ranges from 170 to 700 meters. This species occurs in sympatry with *H. perenensis* in eastern Bolivia.

COMMENTS: This species was diagnosed and described by Emmons and Patton (2005), who provided molecular, morphometric, and morphological evidence to support their hypothesis. The morphologic and multi-loci molecular analysis conducted in this contribution also recognizes the samples from northeastern Bolivia on the banks of Río Iténez as a distinct and diagnosable monophyletic lineage that should be named *H. acritus*, and consequently, my

hypothesis agrees with the one advocated by original authors (EMMONS; PATTON, 2005). On a nomenclatural point of view, the history of this species is quite simple and clear: prior to the coinage of the new name, specimens from this region of Bolivia were named *capito* and *megacephalus* (ANDERSON, 1997 and MUSSER et al., 1998, respectively). Morphologically, it resembles to *H. perenensis*, and can be distinguished by external and cranial characters, but the morphometric variation founded in *H. acritus* samples are comprised into the morphometric variation of *H. perenensis*, and carefully analysis should be done to differentiate them. Phylogenetically, and despite the similarity with and geographic proximity with *H. megacephalus*, *H. perenensis* and *H. yunganus*; *H. acritus* is the sister-species of *H. oniscus*, and this clade is sister to *H. seuanezi*. Therefore, this species from western Amazon is deeply nested in an Atlantic Forest clade (see Geographic distribution below in Figure 51). *Hylaeamys acritus* is sympatric to *H. yunganus*, as well as with several other species of small mammals from Cerrado and Amazon forest in Bolivia (Anderson, 1997; Emmons and Patton 2005).

SPECIMENS EXAMINED: (M = Male. F = female. I = unknow sex). BOLIVIA: EL BENI: **Curicha: M**, USMN 551653, USMN 551654. **San Joaquin: F**, USMN 460272, USMN 460738, USMN 460429. **Baures: M**, FMNH 117115, FMNH 117116, AMNH 209953; **F**, AMNH 209952, AMNH 209959, AMNH 209957, AMNH 210018, AMNH 209948, AMNH 210017, AMNH 209961, AMNH 209950; **I**, AMNH 209960, AMNH 209955. **4 km Opposite Costa Marques: F**, AMNH 209996, AMNH 209992, AMNH 209990, AMNH 209974, AMNH 29992, AMNH 209993, AMNH 209971, AMNH 209989, AMNH 209990, AMNH 209991, AMNH 209995, AMNH 209996, AMNH 24614; **M**, AMNH 246139, AMNH 209999, AMNH 209980, AMNH 29984, AMNH 209966, AMNH 209970, AMNH 209965, AMNH 209997, AMNH 209962, AMNH 210361, AMNH 209989, AMNH 209983, AMNH 209979, AMNH 246139, AMNH 210270, AMNH 209966, AMNH 209970, AMNH 209966, AMNH 209970, AMNH 209980, AMNH 209984, AMNH 209988, AMNH 209997, AMNH 210361, AMNH 209983. **Puerto Siles: F**, AMNH 211748. **Palmira: F**, AMNH 262946. **Yutiales: F**, USNM 460429. **Rio Itenez, Pampa de Meio: M**, AMNH 210011, AMNH 210008; **F**, AMNH 210022.

Figure 51 - Dorsal, ventral and lateral views of the skull and mandible of *Hylaeamys acritus*, USNM 597567, from Parque Nacional Kempf Mercado, Bolivia

Hylaeamys megacephalus (G. Fischer, 1814)

Mus megacephalus G. Fischer, 1814:71; no type locality given; based on Azara's (1801, 1802) "*Rat Second ou Rat a Grosse Tête*" and "*Del Cola Igual al Cuerpo*".

Mus ? *Capito* Illiger, 1815:70; *nomem nudum*.

? *Mus capito*: Olfers, 1818:209; redescription of *Mus Capito* Illiger; based on Azara's (1801, 1802) "*Rat Second ou Rat a Grosse Tête*" and "*Del Cola Igual al Cuerpo*."

Mus cephalotes Desmarest, 1819d:63; based on Azara's (1801, 1802) "*Rat Second ou Rat a Grosse Tête*" and "*Del Cola Igual al Cuerpo*."

Mus laticeps Lund, 1839a:233; *nomen nudum*.

Mus laticeps Lund, 1840b [1841c:279]; type locality "Rio das Velhas's Floddal" (Lund 1841c:292, 294), Lagoa Santa, Minas Gerais (see also Musser et al. 1998).

H[esperomys] cephalotes: Wagner, 1843:542; name combination.

Hesperomys laticeps: Burmeister, 1854:171; part; name combination.

Calomys cephalotes: Fitzinger, 1867b:87; part; name combination.

Hesperomys (Calomys) laticeps: Thomas, 1882:102; part; name combination.

Hesperomys (Oryzomys) laticeps: Thomas, 1884:452; part; name combination.

Calomys saltator Winge, 1887:48, plate I, figs. 16 and 17; plate III, fig. 7; renaming of *Mus laticeps* Lund.

Oryzomys velutinus J. A. Allen and Chapman, 1893:214; type locality "Princetown [= Princes Town], Trinidad," Trinidad and Tobago.

Oryzomys Goeldi Thomas, 1897c:494; type locality "Itaituba, Rio Tapajós," Pará, Brazil.

[*Oryzomys*] *cephalotes*: Trouessart, 1897:526; name combination.

Oryzomys modestus J. A. Allen, 1899b:212; type locality "Campo Alegre, Sucre, Venezuela."

[*Oryzomys (Oryzomys)*] *goeldi*: Tate, 1932e: 7; part; name combination.

[*Oryzomys (Oryzomys)*] *cephalotes*: Tate, 1932a:18; part; name combination.

- [*Oryzomys (Oryzomys)*] *saltator*: Tate, 1932a:18; part; name combination.
- Oryzomys angouya*: Vieira, 1953:137; part; not *Mus angouya* G. Fischer (= *Sooretamys angouya* [G. Fischer]).
- Oryzomys capito*: Hershkovitz, 1959b:339; part; name combination.
- Oryzomys* [(*Oryzomys*)] *capito capito*: Cabrera, 1961:385; name combination.
- Oryzomys* [(*Oryzomys*)] *capito goeldii*: Cabrera, 1961:385; name combination.
- Oryzomys (Oryzomys) laticeps* cf. *modestus*: Carvalho, 1962:290; part; name combination.
- Oryzomys capito goeldi*: Carvalho and Toccheton, 1969:290; part.
- [*Oryzomys*] *megacephalus*: Langguth, 1966b:287; name combination.
- Oryzomys oniscus*: Alho, 1981:225; part; not *Oryzomys oniscus* Thomas (= *Hylaeamys oniscus* [Thomas])
- Oryzomys macconnelli*: Koop, Baker, Haiduk, and Engstrom, 1984:201, fig. 1; part; not *Oryzomys macconnelli* Thomas (= *Euryoryzomys macconnelli* [Thomas]).
- [*Hylaeamys*] *megacephalus*: Weksler, Percequillo, and Voss, 2006:14: first use of current name combination.

NEOTYPE: UMMZ 133811, a “young adult male” specimen collected by P. Myers (PM 4186), on July 18, 1979 (Musser et al., 1998:236). The specimen is preserved as skin, skull, carcass in fluid and chromosome preparation; the specimen is also in very good condition.

TYPE LOCALITY: “Paraguay east of the Río Paraguay, Departamento de Canendiyu, 13.3. km (by road) N Curuguaty (24°31'S/ 55°42'W), 255 m”, based on designation of a neotype (MUSSEr et al., 1998).”

DESCRIPTION: This species exhibits a smaller to medium body size (head and body length range, 80-158 mm, mean, 121.9, n=151), a tail shorter than head and body length (range, 90-138 mm; mean, 115.4, n=145), small hind feet with small plantar pads (especially the hypothernar), and sparse unguis tufts that are shorter than the claws. The dorsal fur is short, dense, and slightly harsh, colored overall with ochraceous, yellow, or orange tones weakly to moderately grizzled with dark brown. The ventral fur is comparatively shorter and predominantly grayish, often with small white patches on gular and inguinal regions. The tail

may be dorsoventrally uniform, weakly bicolored, or completely bicolored. The ears are sparsely covered with either entirely brown or banded hairs that are brown basally but white or golden distally. The skull is small and delicate (greatest length range, 27.2-34.8 mm), with very short and wide tear-drop shaped incisive foramina (length range, 3.5-5.4 mm; width range, 1.9-3.1mm), an interorbital region that diverges slightly posteriorly, with rounded to weakly beaded supraorbital margins, a palate with complex and multiple posterolateral palatal pits recessed in shallow palatine depressions and palatal excrescences varying from small projections to large bone struts fused to the maxilla, and short and narrow molar tooth rows (length range, 3.7-5.2 mm; M1 width range, 1.1-1.6 mm) (Figure 53).

DISTRIBUTION: *Hylaeamys megacephalus* exhibits the widest known distribution of collecting localities in the genus, with samples recorded “throughout the forested areas of the Cerrado and Chaco in central Paraguay, the Cerrado and semideciduous forests in southeastern and central Brazil, the Amazonian forest of the eastern [and central] Brazil, the Guianan region and southern Venezuela, as well forested areas within the Venezuelan Llanos, extending to the coastal island of Trinidad” (PERCEQUILLO, 2015, Figure 54). Altitudinally, *H. megacephalus* is distributed from nearly the sea level, on the Amazonian lowlands (Itaituba, Pará state at 15 m above sea level), to approximately 1,100 m on the central Brazilian highlands (Brasília, Distrito Federal) and on the Venezuelan Tepuis (Monte Duida, La Esmeralda).

NATURAL HISTORY: As a species widely distributed, *H. megacephalus* inhabits a wide range of habitats biomes and exhibits varied life histories, as summarized by Percequillo (2015).

Figure 53 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys megacephalus* (MZUSP 27149) from Rio Xingú, Para State, Brazil

Figure 54 – Known collection localities of *H. megacephalus* in South America. Number of localities are provided in the Gazetteer in Appendix A.

COMMENTS: As one of the first “species” of rat to be recognized in South America, both informally (by AZARA, 1801, 1802) and formally (by FISCHER, 1814), and as one the most geographically widespread entity, *Hyleamys megacephalus* received several names of the species group throughout its history, presenting a long and confuse taxonomic history, full of name combinations and subjective synonyms (as can be appreciated in the synonymic list above). Nevertheless, Musser et al. (1998) and Percequillo (1998, 2015) had told most of this history and clarified the nomenclatural issues associated to this name.

The concept of *H. megacephalus* that I employ here is resultant from the morphologic and molecular analysis performed and from the species concept adopted. I identified some morphologic discontinuities or gaps throughout the geographic samples of *megacephalus*, and such geographic groups appear as reciprocally monophyletic lineages in the recovered phylogenies: the clades from the northern and southern bank of Solimões/Amazonas rivers (this clade also exhibit some level of structuration, with specimens from Amazonia in a

distinct clade from the specimens of Cerrado and transition areas), and also the clade from the upper Rio Madeira. I did not acknowledge them species status, once qualitative traits were not recovered for these 3 clades, consequently not attending the prerogatives of the species concept (fonte), concerning the criteria of diagnosis. I believe that a clear diagnosis should bring autapomorphies or apomorphic exclusive combinations of character states, and not only size differences. If further analysis recover such traits, I believe that to these clades should be warranted the specific status: for the clade of southern bank, the name *megacephalus* is the oldest available and should be applied; for the northern clade, the names *Oryzomys velutinus* Allen and Chapman (1893) and *Oryzomys modestus* Allen (1899) are available, the first one exhibiting precedence over the second, being the appropriate name for this species.

Regarding the clade from upper Rio Madeira, some arguing is necessary since some relevant morphologic variation was observed. Sorting the nine specimens from this locality, I was able to discriminate two diagnosable groups: one, with a paraflexus divided in two enamel islands on M2 formed by specimens MJ222, MJ201 and MJ219 a typical feature of species of group *yunganus*; and other group, with most specimens (MJ191, MJ160, MJ257, MJ244, MJ226 and MJ236), without this enamel island. These specimens with two islands were *a priori* allocated and analyzed along with specimens of the *yunganus* group on the geographic variation approach, but the results of these analyses showed the specimens of upper Rio Madeira greatly dispersed across the multivariate space and overlapped to specimens from both *yunganus* and *megacephalus* groups. In addition to the fact that all specimens of this region nested in the clade sister to the *megacephalus* from the southern bank of Rio Amazonas, I considered most parsimonious that this sample of Rio Madeira should be assigned to this species. Awkwardly, the specimens MJ222, MJ201 and MJ219 are the only known specimens with two enamel islands presently allocated to *H. megacephalus*.

In this concept, *Hylaeamys megacephalus* can be discriminated from other species of the genus, by its smaller body size (head and body length ranges from 80 to 158 mm), smaller cranial size (greatest skull length, 27.2 to 34.9 mm), short tear-drop shaped incisive foramina (incisive foramina length, 3.4 to 5.4 mm), shorter tooth row (toothrow length, 3.7 to 5.2 mm), and a karyotype with $2n = 54$ and $FN = 62$.

There are few current records of this species in eastern coastal Brazil, and the most relevant are those from Amapá and Ceará states (PRADO; PERCEQUILLO, 2013). Specimen from Maranguape, Ceará (UFC M 101) is a subadult, and was not included in the analyses of geographic variation (see above); but preliminary Principal Component analyses (results not shown) performed with subadults and adults revealed that this specimen is clustered with

other specimens of *H. megacephalus* from the southern margin of Rio Amazonas. The records from Ceará are noteworthy, since they represent the easternmost record of this species: these specimens from Maranguape considerably extends the distribution of *H. megacephalus*, nearly 975 km eastwards of the nearest record in eastern Pará, Paragominas, and approximately 980 km northeast of the nearest record in southern Maranhão, Alto Parnaíba. To the best of my knowledge, there are no known records of this species to the Cerrado biome of the southern portion of Piauí.

Zoogeographically, this is a very interesting record: Serra de Maranguape is an area of humid forest surrounded by open formations and more drier, xerophytic and semi-arid, more typical of the Caatinga, a “brejo de altitude” (ANDRADE-LIMA, 1982; AB'SABER, 1992; BORGES-NOJOSA; CARAMASCHI, 2003). Along the coast, between Pará and Ceará states, there are extensive lines of coastal sandy dunes, such as those observed in the “Parque Nacional dos Lençóis Maranhenses” and in the “Delta do Rio Parnaíba”, open areas with drier vegetation (HUECK, 1972). Although there are no published inventories for these areas, the habitat is probably not suitable for this species, which apparently prefers forested environments (CARMIGNOTTO, 2004). The presence of *H. megacephalus* in “brejo de Maranguape” could be considered a testimony and another piece of evidence favoring the model that suggests a past connection between eastern Amazon Forest and Atlantic Forest, due to the expansion of forests associated to more humid climate during the interglacial cycles of Quaternary (HAFFER, 1979; VANZOLINI; WILLIAMS, 1970; VANZOLINI, 1981; CLAPPERTON, 1993; VIVO, 1997; BORGES-NOJOSA, 2002; BORGES-NOJOSA; CARAMASCHI, 2003; BORGES-NOJOSA, 2007; COSTA, 2003; VIVO; CARMIGNOTTO, 2004).

The Refuge model could be the explanation for the occurrence of various taxonomic groups of presumed Amazon and Atlantic origins, that over the years have been found in these formations: invertebrates (LOURENÇO, 1988), amphibians (HOOGMOED; BORGES; CASCON, 1994; CARNAVAL; BATES, 2007), lizards and snakes (NASCIMENTO; LIMA-VERDE, 1989; RODRIGUES; BORGES 1997, BORGES-NOJOSA; LIMA, 2001; BORGES-NOJOSA; CARAMASCHI, 2003; BORGES-NOJOSA et al., 2006; BORGES-NOJOSA, 2007) and others. Recent evidence has demonstrated that these forest remnants are repositories of distinct and independent phylogenetic lineages, and exhibit a complex biogeographic history. Carnaval and Bates (2007), studying frogs of the genera *Proceratophrys* and *Ischnocnema* suggest that populations of “brejos” represent independent evolutionary lineages (possibly unique species) that do not share a common ancestor. Similar

results were observed by Campos (2009) that recognized several distinct lineages of the genus *Rhipidomys* for various “Brejos de Altitude” of Paraíba, Pernambuco and Ceará, while each of these species shows affinities with groups of the Amazon, Cerrado and Atlantic Forest. Thus, the record of *H. megacephalus* in Maranguape represents an important advance in the comprehension of the diversity of mammals of Ceará, but also provides another piece of evidence for the complex biogeographic history of the “Brejos de Altitude” of Northeastern Brazil. Despite this evidence, the precise eastern distributional limits remain unknown, and this record from Ceará attests that much fieldwork still needs to be done for a better comprehension of the geographic distribution of this species. However, it is likely that the eastern limit of this species is concordant with the limits of the Cerrado Biome. Considering that the samples from upper Rio Madeira are (for now) assigned to *H. megacephalus*, it is probable that this river represents the western limit of this species and the boundary between *H. perenensis* and *H. megacephalus*, instead of the lower Rio Tapajós, as stated by Musser et al. (1998; see also PERCEQUILLO, 2015).

Western Amazonia, more precisely Bolivia border, in the upper course of Rio Madeira and Rio Mamoré (Iténez) basins, harbors several species of the genus *Hylaeamys*, namely *H. acritus*, *H. megacephalus* and *H. perenensis*, as well as *H. yunganus*.

SPECIMENS EXAMINED: (M = Male. F = female. I = unknow sex). BRASIL: AMAPA: **Serra do Navio:** Rio Amapari, Serra do Navio: **M**, MNRJ 20296, MNRJ 20290, MNRJ20493. Serra do Navio: **M**, MNRJ 20284, MNRJ 20287, MNRJ 20291, USMN 393943, USMN 393945, USMN 393948, USMN 393954, USMN 393957, USMN 393959, USMN 393963, USMN 393964, USMN393958; **F**, MNRJ 14629, MNRJ 20292, MNRJ 20295, MNRJ 20298, USMN 393933, USMN 393940. Serra do Navio, C3 e C11: **F**, MPEG 15060. Serra do Navio, C3 e C8: **M**, MPEG 15054. Serra do Navio, C3 e C9: **M**, MPEG 15125. Serra do Navio, ICOMI: **F**, MPEG 15070. Serra do Navio, Km. 190 EFA: **M**, MPEG 15069. Terezinha, Rio Amapari, Serra do Navio: **M**, MPEG 15050, MPEG 15024, MPEG 15028, MPEG 15035, USMN 393887, USMN 393867; **F**, MPEG 15124, MPEG 15049, MPEG 15027, MPEG 15044, MPEG 15039, MPEG 15030, MPEG 15032, MNRJ 20501, USMN 393891, USMN 393903, USMN 393885. AMAZONAS: **Lago do Meduinin:** Lago do Meduinin, left bank rio Negro: **M**, JLP 16813, JLP 16791, MNFS 2124, YL 164, JLP 16815; **F**, MNFS 1989, MNFS 1990, MNFS 2115, LC 173. **Macaco:** Macaco, left bank rio Jáú: **M**, LC 129, VCSV 33, VCSV 13, YL 119; **F**, YL 148, VCSV 16, LC 152, YL 140, YL 134, YL 145, JLP 16731. Rio Uatumã: Margem direita do rio Uatumã, próximo a foz do Igarapé Caititu: **M**, INPA 1215, INPA 1214, INPA 1213, INPA 1208, INPA 1216, INPA 1209.

Manaus: 80 km N Manaus, INPA/WWF-US MCSE Project (PDBFF), Reserva 34 2R11: **M**, NMNH 580003, INPA 1822; **F**, NMNH 554848. Manaus, Estrada Manaus-Itacoatiara: **M**, MPEG 7173, MPEG 7168, MPEG 7196, MPEG 7186, MPEG 7183, MPEG 7179, MPEG 7178, MPEG 7171, MPEG 7187, MPEG 7172; **F**, MPEG 7185, MPEG 7177, MPEG 7175, MPEG 7174. **Rio Jaú:** Right bank rio Jaú, above mouth: **M**, JLP 16773; **F**, JLP 16777, JLP 16757. **Rio Katana-ú:** rio Katana-ú, 2,7km NNE Missão Marari, Barcelos: **M**, MNRJ56825. **Rio Pitinga:** Próximo foz igarapé Água Branca, margem esquerda rio Pitinga: **M**, INPA 1217. DISTRITO FEDERAL: **Brasília:** Centro de instrução e adestramento de Brasília (CIAB), Brasília: **M**, MZUSP M968563, MZUSP M976295/29515. Parque Nacional de Brasília: **M**, DZUnB 323, DZUnB 319; **F**, DZUnB 332, DZUnB 325. **Reserva Biológica de Águas Emendadas:** Reserva Biológica de Águas Emendadas: **M**, DZUnB 540, DZUnB 490, DZUnB 598; **F**, DZUnB 589, DZUnB 600. **Rio Capetinga:** Rio Capetinga (Fazenda Água Limpa): **F**, UFPB 1930. GOIAS: **Anápolis:** Anápolis: **M**, MNRJ 4312; **F**, MNRJ 4319, MNRJ 34192. **Baliza:** Baliza, Fazenda Bandeirantes, Rio Lageado: **M**, DZUnB 1155, DZUnB 1167. **Catalão:** Catalão, Fazenda Cassiano, vereda: **F**, UFMG 19. Catalão, Vau da Cruz: **F**, UFMG 24.24. **Davinópolis:** Davinópolis, Cerrado alto: **M**, UFMG 99. Davinópolis, Fazenda Nenzinha: **M**, UFMG 101, UFMG 92. **Pouso Alto:** Pouso Alto, Fazenda Taquari (atualmente Piracanjuba, Fazenda Taquari): **M**, MNRJ 5327. **Serra da Mesa:** rio do Peixe, rio Maranhão, Serra da Mesa: **M**, MNRJ 37290, MNRJ 37354, MNRJ 37390; **F**, MNRJ 37263. Rio Tocantinzinho, Serra de Mesa: **F**, MNRJ 36519, MNRJ 36487. Serra Negra, rio Bagagem, Serra da Mesa: **M**, MNRJ 35972; **I**, MNRJ 36065, MNRJ 35996, MNRJ 36169, MNRJ 36152. MATO GROSSO: **Alta Floresta:** Reserva Biológica (ou Ecológica) Cristalino, 40 Km N Alta Floresta: **F**, LC 557, LC 567. **Aripuanã:** Aripuanã, Cidade Laboratório de Humboldt: **M**, MPEG 12647; **I**, MZUSP APC1022, MZUSP APC1064, MZUSP APC1014, MZUSP APC1033, MZUSP APC1029. **Barra do Bugres:** Estação Ecológica Serra das Araras, 65 km S de Barra do Bugres, Barra do Bugres: **M**, MZUSP APC870, MZUSP APC872; **I**, MZUSP APC1076, MZUSP APC1047, MZUSP MRT3899, MZUSP APC1046, MZUSP APC1043. **Barra do Garças:** Fazenda Lagoa Bonita, 36 Km N Barra do Garças: **M**, LC 403; **F**, LC 444. Fazenda São Luis, 30 Km N Barra do Garças: **M**, LC 419, LC 427, LC 433, LC 492; **F**, LC449. **Chapada dos Guimarães:** Chapada dos Guimarães, Rio Manso, UHE Manso: **M**, DZUnB 629, DZUnB 753, DZUnB 607, DZUnB 755, DZUnB 636, DZUnB 673, DZUnB 857, DZUnB 675, DZUnB 887, DZUnB 854; **F**, DZUnB 754, DZUnB 666, DZUnB 605, DZUnB 657, DZUnB 614, DZUnB 619, DZUnB 633, DZUnB 621. **Claúdia:** 30 km SSW Claúdia: **M**, MZUSP M97145, MZUSP 183, MZUSP M000026, MZUSP M000077, MZUSP

M97128, MZUSP M97127, MZUSP M97132, MZUSP M97019, MZUSP M000033, MZUSP M97017, MZUSP M97119; **F**, MZUSP M97080, MZUSP M97121, MZUSP M97122, MZUSP M97131, MZUSP M97146, MZUSP M97006, MZUSP M97041, MZUSP M000003, MZUSP M97139, MZUSP M000071, MZUSP M000028, MZUSP APC937, MZUSP APC898, MZUSP M97015, MZUSP APC941. **Cocalinho**: 40 km ao redor de Cocalinho: **M**, MZUSP M97078. **Juruena**: Juruena: **M**, MZUSP M97179; **F**, MZUSP M97185. **Ouro Preto**: Vila Rica, Ouro Preto: **M**, MZUSP M97042; **F**, MZUSP M968585. **Paranatinga**: 30 km ao redor de Gaúcha do Norte, Paranatinga: **F**, MZUSP M97178; **I**, MZUSP MRT3869, MZUSP MRT3873, MZUSP JEM13, MZUSP JEM65. **Ponte Branca**: Ponte Branca, Fazenda Altamira: **M**, DZUnB 1182; **F**: DZUnB 1184; **I**, DZUnB 1186. **Ribeirão Cascalheira**: Fazenda Noirumbá, 34 Km NW Ribeirão Cascalheira: **M**, LC 761; **F**, LC 786, LC 785. **Salto do Utuary**: Rio Papagaio, Salto do Utuary: **I**, MNRJ 2526. **Serra do Roncador**: 264 km N Xavantina, Serra do Roncador: **M**, BMNH 81505, BMNH 81550, BMNH 81551, BMNH 81557, BMNH 81558, BMNH 81560, BMNH 81587, BMNH 861144; **F**, BMNH 81508, BMNH 81512, BMNH 81528, BMNH 81529, BMNH 81530, BMNH 81559, BMNH 861145, BMNH 81506. MATO GROSSO DO SUL: **Bodoquena**: Fazenda Califórnia, Morraria do Sul, Bodoquena: **M**, MZUSP 29738, MZUSP APC732, MZUSP 29601; **F**, MZUSP 29774, MZUSP APC998, MZUSP 29691, MZUSP APC721, MZUSP APC783; **I**, MZUSP APC731, MZUSP APC1071, MZUSP APC1059, MZUSP APC1084. **Dourados**: Fazenda Maringá, 54 Km W Dourados: **M**, LC 625. **Porto Faya**: Porto Faya: **M**, MZUSP 1700. MINAS GERAIS: **Coromandel**: Coromandel, Fazenda da Barra: **M**, UFMG 3. Coromandel, Fazenda Marques: **M**, UFMG 59, UFMG 40, UFMG 32. Coromandel, Fazenda da Barra: **F**, UFMG 2. **Lagamar**: Lagamar, Fazenda Caxambú: **I**, UFMG 153. **Lagoa Santa**: Lagoa Santa: **M**, ZMC 268; **F**, BMNH 881282, ZMC 269; **I**, ZM 266. **Nova Ponte**: Nova Ponte, Fazenda do Sr. Vasco Naves: **M**, UFMG 2; **F**, UFMG 19, UFMG 1. Nova Ponte, Mata do Vasco: **M**, UFMG 44; **F**, UFMG 45. Nova Ponte, Mata Península: **M**, UFMG 27; **F**, UFMG 24. **Paracatu**: Paracatu, Parque Acangau: **M**, DZUnB 1026, DZUnB 1016; **F**, DZUnB 1017, DZUnB 1030. **Parque Nacional Grande Sertão Veredas**: Parque Nacional Grande Sertão Veredas (PNGSV): **M**, MZUSP M97140, MZUSP M97126; **F**, MZUSP M97033. **Pedrinópolis**: Pedrinópolis, Mata dos Adolfos: **M**, UFMG 11, UFMG 6, UFMG 36, UFMG 9, UFMG 4; **F**, UFMG 25. **Perdizes**: Perdizes, Cerrado João Alonso: **M**, UFMG 19, UFMG 33. PARA: **Altamira**: 18 Km. S e 19 Km. W de Altamira (Agrovila da União): **M**, MPEG 15341, MPEG 15281, MPEG 15290, MPEG 15283, MPEG 15286, NMNH 521523, NMNH 521524; **F**, MPEG 15340, MPEG 15316, NMNH 521443, NMNH 521446, NMNH 521522. Rio Xingu,

east bank 52 km SSW Altamira: **M**, NMNH 549542, NMNH 549544; **F**, NMNH 549545, NMNH 549548, NMNH 549543. **Belém**: Utinga, Belém: **M**, MPEG 2608, MPEG 8273, MPEG 2613, MPEG 2606, MPEG 2604, MPEG 2599, MPEG 2609, MPEG 8393, MPEG 2475, USMN 393929. **Bragança**: Bragança, Jandiaí, Caratatena [= Caratateua]: **M**, NMNH 543343. **Capim**: Capim, BR 14, Kms. 93/94/87: MPEG 8391, MPEG 8264, MPEG 8421; **F**, MPEG 8390, MPEG 8416. **Chiqueirinho**: Chiqueirinho, margem direita Rio Tocantins, 70 Km. S de Tucuruí: **M**, MPEG 12257. **Itaituba**: Itaituba: MPEG 15077, MPEG 15080, MPEG 15081, MPEG 12648; **F**, BMNH 97411, MPEG 15079. Itaituba, BR 230 Km. 25, Rio Tapacurazinho: **M**, MPEG 8664. Itaituba, BR165, Santarém-Cuiabá, Zona Sul, Km. 447: **F**, MPEG 12673. Itaituba, Itaituba-Jacareacanga, Km. 212, Flexal: MPEG 12665, MPEG 12662, MPEG 13175, MPEG 12686, NMNH 461943, MPEG 12680; **F**, MPEG 10663, MPEG 12669, MPEG 13174, MPEG 15083, NMNH 461944. Itaituba, Rodovia Transamazônica, Km. 19, Itaituba-Jacareacanga: **M**, MPEG 8650, NMNH 461745; **F**, NMNH 461746. Itaituba, Rodovia Transamazônica, trecho Itaituba-Jacareacanga, Km. 200: **M**, NMNH 461937, NMNH 461938; **F**, NMNH 461936, NMNH 461940. **Marabá**: 20 Km. N e 30 Km. W de Marabá (perto Itupiranga): **M**, MPEG 13353, NMNH 519748; **F**, MPEG 15350. 73 Km. N e 45 Km. W de Marabá (perto Jatobal), Gleba 29, Lote 3: **M**, NMNH 519747, NMNH 519767, NMNH 521436, NMNH 519756; **F**, NMNH 519754, NMNH 519757, NMNH 519761, MPEG 15364. 80 Km. N e 45 Km. W de Marabá (perto Jatobal), Gleba 29, Lote 3: **F**, NMNH 521448, NMNH 521518. Floresta Nacional Tapirapé-Aquiri, Marabá – Área do Companhia Vale do Rio Doce em Carajás: **M**, INPA 2804, INPA 2803, INPA 2799, INPA 2800; **F**, INPA 2802, INPA 2801. **Oriximiná**: Oriximiná, Porto Trombetas, Rio Sacarazinho (Km. 43); 23.171 no km.8: **F**, MPEG 10475. Oriximiná. Cachoeira Porteira, Km. 23: **M**, NMNH 545306. **Paragominas**: 8 Km. N e 75 Km. W Paragominas: **M**, MPEG 15464; **F**, MPEG 15466. Paragominas: **M**, MPEG 15455; **F**, MPEG 15017, MPEG 15450, MPEG 15456. **Rio Tocantins**: Ilha Tocantins, Rio Tocantins, 75 Km. S e 18 Km. E de Tucuruí: **M**, MPEG 12513, MPEG 12518, MPEG 12489, MPEG 12516, MPEG 12522, MPEG 12523, MPEG 12524, MPEG 12520; **F**, MPEG 12517, MPEG 12491, MPEG 12512, MPEG 12519, MPEG 12490, MPEG 12521, MPEG 12492. **Rio Trombetas**: Foz do Igarapé Tramalhetinho, margem direita do rio Trombetas: **M**, INPA 618; **F**, INPA 621. **Santarém**: 44 Km S e 40 Km. E de Santarém (Curuá-Una): **M**, MPEG 15384, MPEG 15380, MPEG 15379. BR 165, KM 216, Santarém - Cuiaba, Santarém: **M**, USMN 544582, USMN 544584, USMN 544588, USMN 544596, USMN 544600, USMN 544591, USMN 544598, USMN 544624, USMN 544626, USMN 544587, USMN 544594, USMN 544629, USMN 544579, USMN 544580,

USMN 544627. Santarém, Estrada Santarém-Cuiabá BR 165, Km. 84: **M**, NMNH 461752, NMNH 461765; **F**, NMNH 461774, NMNH 461775. **Tiriós-Óbidos**: Tiriós-Óbidos, 12 Km da Guiana Holandesa: **F**, NMNH 392053. SÃO PAULO: **Barretos**: Barretos: **F**, MZUSP 1428. **Itapura**: Itapura: **M**, MZUSP 1699. **Ituverava**: Ituverava: **M**, MZUSP 2954. **Mogi Guaçu**: Mogi Guaçu, Faz. Sete Lagoas: **M**, MZUSP 25759. **Paranã**: Paranã, Palma: **M**, MZUSP M000068, MZUSP APC000175/29519; **F**, MZUSP M000002. **Peixe**: Rio Santa Teresa, 20 Km NW Peixe: **M**, LC 697, LC 702; **F**, LC 701, LC 713, LC 696, LC 717. **Presidente Prudente**: Presidente Prudente: **I**, MZUSP 10221. **Rio Feio**: Rio Feio: **I**, MZUSP 1946. Teodoro Sampaio: Teodoro Sampaio: **M**, MZUSP 25163, MZUSP 25164, MZUSP 25165, MZUSP 24994, MZUSP 24050; **F**, MZUSP 24046, MZUSP 8855. COLOMBIA: META: **Villavicencia**: Villavicencia: AMNH 136360, AMNH 136358, AMNH 136364. **Guaicaramo**: Guaicaramo: USMN 251966, USMN 251964. GUYANA: BARIMA-WAINI: Kwabanna, Barima-Waini: **M**, ROM 98752, ROM 100976, ROM 98870, ROM 98907; **F**, ROM 101072, ROM 98827. RUPUNUNI: Potaro-Siparuni, Iwderama (ou Iwohrama) Reserve, Gorge Camp, 40 km SSW Hurupuhari (ou Kurupuhari): **F**, ROM 108802, ROM 111607. Upper Takuku-Upper Essequibo, Kamo River, 50 km SWW Gunn's Strip: **M**, ROM 106683, ROM 106682; **F**, ROM 106569, ROM 106681, ROM 106680. EAST DEMERARA-WEST COAST BERBICE: Geogetown: FMNH 18543. FRENCH GUIANA: Paracou, near Sinnamary: **M**, AMNH 266508, AMNH 266533; **F**, AMNH 266494, AMNH 266518, AMNH 267018. PARAGUAY: AMAMBAY: **Pedro Juan Caballero**: 28 Km Sw de Pedro Juan Caballero: **M**, UMMZ 125233; **F**, UMMZ 125455, UMMZ 125454. CAAGUAZU: **Coronel Oviedo**: 22.5 Km S N Coronel Oviedo, by road: **M**, UMMZ 124499. **Curuguaty**: 13.3 Km N de Curuguaty: **M**, UMMZ 126010, UMMZ 133801, UMMZ 133803, UMMZ 133804, UMMZ 133808, UMMZ 133811, UMMZ 137010, UMMZ 137011, UMMZ 133811, UMMZ 133802, UMMZ 133807. PARAGUARI: **Tacuati**: Tacuati, Aca Poi: **F**, NMNH 293148. SAN PEDRO: **Ganadera La Carolina**: Ganadera La Carolina: **M**, GE 384, GE 383; **F**, GE 382. SURINAME: BROKOPONDO: **Finisanti**: Finisanti, Saramacca River: **M**, FMNH 95615; **F**, FMNH 95619. **Loksie Hatti**: Loksie Hatti, Saramacca River: **F**, FMNH 95612. NICKERIE: **Kaiserberg airstrip**: Kaiserberg airstrip, Zuid River (ou Kaiser Gebergte Airstrip): **F**, FMNH 93287, FMNH 93289. **Wilhelmina**: Wilhelmina Mts., West River: **F**, FMNH 95632. Paloemeu airstrip-Tapahoni River: **F**, FMNH 94035, FMNH 94055, FMNH 94057, FMNH 94067, FMNH 94070, FMNH 94054; **I**, FMNH 94027. SARACACCA: **Dirkshoop**: Dirkshoop: **F**, FMNH 95626, FMNH 95628. **La Poule**: La Poule: **M**, FMNH 95623, FMNH 95624; **F**, FMNH 95677. TRINIDAD & TOBAGO: Trinidad: Bush Bush forest, Nariva Swamp: **M**,

AMNH 186786, AMNH 186831, AMNH 188426; **F**, AMNH 186809, AMNH 186829, AMNH 188473, AMNH 189354, AMNH 188472. Caparo: **F**, AMNH 7718. Caura: **M**, AMNH 7724. Maingot Estate, 5 miles from Sangre Grande: **M**, AMNH 174061, AMNH 174062, AMNH 174013, AMNH 174014, AMNH 174064; **F**, AMNH 174056; **I**, AMNH 174036, AMNH 174239. Princetown: **M**, AMNH 5949, FMNH 5355; **F**, AMNH 5950. VENEZUELA: AMAZONAS: **Caipibara**: Caipibara, 106 km SW Esmeralda, Brazo Casiquiare: **F**, USMN 409873. **Cerro Neblina**: Cerro Neblina Base Camp, 140 m., Rio Mawarinuma: **M**, NMNH 559193; **F**, NMNH 560647. Clearwater Stream, ca. 2 km. SE Cerro Neblina Base Camp.: **F**, NMNH 560646, USMN 560646. Neblina Base Camp, Rio Mawarinuma: **F**, USMN 560647. **Tamatama**: Tamatama, Rio Orinoco: **M**, USMN 409870; **F**, NMNH 409873. BOLIVAR: **Auyantepui**: Auyantepui: **M**, AMNH 131134, AMNH 131021, AMNH 130972, AMNH 130945, AMNH 130938, AMNH 130964, AMNH 130973, AMNH 130977; **F**, AMNH 130982, AMNH 130980, AMNH 130978, AMNH 130966, AMNH 30957. **El Manaco**: El Manaco, 59 km SE El Dorado, Km 74: **M**, USMN 495350. **Esmeralda**: Monte Duida, Esmeralda: **M**, AMNH 77325, AMNH 77322; **F**, AMNH 77323, AMNH 77318. **San Ignacio de Yuruani**: San Ignacio de Yuruani: **M**, USMN 448587, NMNH 448587.

Hylaeamys oniscus (Thomas, 1904)

Oryzomys oniscus Thomas, 1904b:142; type locality “São Lourenço [= São Lourenço da Mata],” Pernambuco, Brasil.

[*Oryzomys* (*Oryzomys*)] *oniscus*: Tateb, 1932e:18; name combination.

Oryzomys laticeps: Hershkovitz, 1960:544, footnote; part; not *Mus laticeps* Lund (= *Hylaeamys laticeps* [Lund]).

Oryzomys [(*Oryzomys*)] *capito oniscus*: Cabrera, 1961:387; part; name combination.

Oryzomys capito: Hershkovitz, 1966:137, footnote; part; not *Mus capito* Olfers (= *Hylaeamys megacephalus* [G. Fischer]).

[*Hylaeamys*] *oniscus*: Weksler, Percequillo, and Voss, 2006:14; first use of current name combination.

HOLOTYPE: BMNH 3.10.1.42, an adult male, collected in July 23, 1905, by Alphonse Robert, original number 1573. The specimen is preserved as skin and skull, and both are in good conditions.

TYPE LOCALITY: “São Lourenço [= São Lourenço da Mata]; 28 a 60 m”, Pernambuco, Brasil;

DESCRIPTION: *Hylaeamys oniscus* is large in body size (head and body length range, 140-162 mm; mean, 147.2, n = 8), has a tail equal to shorter than head and body length (range, 135-162 mm; mean, 146.8, n = 8), robust hind feet with fleshy and large plantar pads, and sparse ungual tufts that are shorter than the claws. The dorsal fur is short and harsh, with overall yellowish to buffy color tones intensely grizzled with dark brown. The ventral fur is comparatively shorter and predominantly grayish. The tail is dorsoventrally bicolored basally and uniformly colored distally. The ears are sparsely covered with reddish-brown hairs (more dorsally) or yellowish (more ventrally). The skull is large and robust (skull length range, 33.7-37.6 mm), with long and wide tear-drop shaped incisive foramina (length range, 4.9-5.8 mm; width range, 2.3-3.4mm), a slightly and posteriorly divergent interorbital region with squared to beaded supraorbital margins, a palate with complex and multiple posterolateral palatal pits recessed in shallow to moderately deep palatine depressions and palatal excrescencies varying from small projections to large and robust bone struts fused to maxilla, and molar tooth rows long and wide (length range. 4.9-5.3 mm; M1 width range, 1.4-1.6 mm) (Figure 55).

DISTRIBUTION: *Hylaeamys oniscus* is an endemic species of the Atlantic forest of northeastern Brazil, with all known localities on the northern margin of Rio São Francisco, in the states of Alagoas, Pernambuco, and Paraíba (Figure 56).

Figure 55 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys oniscus* (UFPB BC195), from Estação Ecológica de Murici, Alagoas State, Brazil

Figure 56 – Known collection localities of *H. oniscus* in northeastern Brazil, on the northern margin of Rio São Francisco. Number of localities as provided in the Gazetteer in Appendix A.

NATURAL HISTORY: Currently, there is no information on the natural history or ecology of this species, aside from information obtained by A.R. Percequillo team during field trips to Estação Ecológica de Murici, the largest Atlantic Forest remnant on the north of Rio São Francisco. Two field trips were conducted in November and December, 2006, and August, 2007, on the dry and rainy season, respectively. Similar efforts were performed in similar areas within the station, but the team only trapped *H. oniscus* on the rainy season: during 10 days, employing Sherman and pitfall traps, the team captured 159 specimens of additional 11 species, namely *Nectomys squamipes*, *Oecomys* cf. *catherinae*, *Akodon* cf. *cursor*, *Cerradomys langguthi*, *Oligoryzomys nigripes*, *Marmosa murina*, *Marmosa (Micoureus) demerarae*, *Marmosops incanus*, *Monodelphis* gr. *americana*, *Didelphis aurita*, *Gracilinanus microtarsus*. By far, *H. oniscus* was the most abundant species, consisting of 42.1% of the captures. The 67 specimens consisted of adults, but also of subadults and young specimens; adults were reproductively active, with males with scrotal testis and with females pregnant and also with developed lactant mammae.

COMMENTS: *Hylaeamys oniscus* has a quite simple taxonomic history, being recognized as a valid taxon, as a species or subspecies, or as a synonym of *H. megacephalus*.

Musser et al. (1998) assigned this taxon as a junior synonym of *laticeps* (here recognized as *H. seuanezi*; see below), but the analysis of geographic variation conducted by Brennand et al. (2013) identified sharp gaps between *seuanezi* and *oniscus*, warranting valid species status to the latter species. The results presented here show that *oniscus* is clearly diagnosed from other congeneric forms, but also represent a distinct monophyletic lineage, being therefore a phylogenetic species (*sensu* CRACRAFT, 1985).

Phylogenies performed recovered that this species is more closely related to *H. acritus*, a western Amazon species, than to *H. seuanezi*, another Atlantic Forest species that is distributed on the Atlantic Forest of Bahia, Espírito Santo and Rio de Janeiro.

SPECIMENS EXAMINED (M = male, F = female, I = unknown sex): BRAZIL: PARAÍBA: **Sapé:** Fazenda Pacatuba, 10 km NE de Sapé: **M**, UFPB 1931 skin and skull. PERNAMBUCO: **Rio Formoso:** Saltinho, Rio Formoso: **M**, UFPB 1989 skin and skull, UFPB 1990 skin and skull, UFPB 1996 skin and skull; **F**, UFPB 446 skin and skull, UFPB 811 skin and skull; **I**, UFPB 1991 skin and skull. **São Lourenço da Mata:** São Lourenço da Mata: **M**, BMNH 310142 skin and skull, BMNH 310143 skin and skull, BMNH 310144 skin and skull, BMNH 310146 skin and skull; **F**, BMNH 310153 skin and skull. ALAGOAS: **Ibateguara:** Mata de Coimbra, Usina Serra Grande, Ibateguara: **M**, UFPE 1645 skin and skull, UFPE 1649 skin and skull; **F**, UFPE 1646 skin and skull, UFPE 1647 skin and skull. **Matriz de Camaragibe:** Fazenda Santa Justina, 6 km SSE de Matriz de Camaragibe: **F**, UFPB 978 skin and skull. **Murici:** Estação Ecológica de Murici, Murici: **M**, UFPB BC67 skin and skull, UFPB BC124 skin and skull, UFPB BC133 skin and skull, UFPB BC135 skin and skull, UFPB BC180 skin and skull, UFPB BC209 skin and skull, UFPB BC89 skin and skull, UFPB BC130 skin and skull, UFPB BC132 skin and skull, UFPB BC142 skin and skull, UFPB BC190 skin and skull, UFPB BC191 skin and skull, UFPB BC192 skin and skull, UFPB BC199 skin and skull, UFPB PGB74 skin and skull, UFPB PGB75 skin and skull, UFPB PGB76 skin and skull; **F**, UFPB AF16 skin and skull, UFPB AF17 skin and skull, UFPB BC68 skin and skull, UFPB BC72 skin and skull, UFPB BC74 skin and skull, UFPB BC96 skin and skull, UFPB BC125 skin and skull, UFPB BC140 skin and skull, UFPB BC189 skin and skull, UFPB BC196 skin and skull, UFPB PGB82 skin and skull; **I**, UFPB AF4 skin and skull, UFPB BC89 skin and skull, UFPB BC94 skin and skull, UFPB BC95 skin and skull, UFPB BC136 skin and skull, UFPB BC144 skin and skull, UFPB BC195 skin and skull, UFPB BC200 skin and skull. **Rio Largo:** Mata do Cedro, Usina Utinga-Leão, Rio Largo: **M**, UFPE 1305 skin and skull. **São Miguel dos Campos:** Fazenda do Prata, 13 km SSW de São Miguel dos Campos: **F**, MN 30595 skin and skull.

Hylaeamys perenensis (J. A. Allen, 1901)

Oryzomys perenensis J. A. Allen, 1901c:406; type locality “Perené, Department of Junin, Peru; altitude 800 m,” defined as “Valle Perené, Colonia del Perené; a coffee plantation at junction of ríos Pauacartambo and Chanchamayo, 1000 m” (Stephens and Traylor 1983:161).

[*Oryzomys* (*Oryzomys*)] *perenensis*: Trouessart, 1904:419; name combination.

Oryzomys laticeps perenensis: Gyldenstolpe, 1932:18; part; name combination.

Oryzomys [(*Oryzomys*)] *capito nitidus*: Cabrera, 1961:386; part; name combination.

Oryzomys megacephalus: Musser, Carleton, Brothers, and Gardner, 1998:251; name combination.

[*Hylaeamys*] *perenensis*: Weksler, Percequillo, and Voss, 2006:14; first use of current name combination.

HOLOTYPE: BMNH 0.7.7.25, an adult male, captured by P.O. Simmons, original number 930, in 11.April.1900, preserved as skin and skull. The skin is in good condition, but the skull presents some damage on the zygomatic arches.

TYPE LOCALITY: “Perené, Peru; 800 m”.

DESCRIPTION: *Hylaeamys perenensis* is medium in body size (head and body length range, 81-169 mm; mean, 135.7, n=337), with a tail shorter than head and body length (tail range, 94-154 mm; mean, 122.9, n=339), and moderately robust feet with medium sized hypothenar pads. Coloration of the dorsal pelage ranges from ochraceous buffy weakly to intensely grizzled with dark brown or reddish brown; that of the ventral pelage is predominantly grayish. The dorsal surfaces of the hind feet are grayish to whitish; ungual tufts are short, whitish in color, but sparse; and the tail is unicolored or only weakly bicolored. The skull is large and robust (greatest skull length range, 29.5-37.9 mm), has long and narrow ‘tear-drop’ incisive foramina (length range, 3.6-6.0 mm; width range, 1.5-2.9 mm), long and robust molars (length range, 4.5-5.6 mm), and a completely ossified mesopterygoid fossa (in more than 90% of specimens from the Rio Juruá in Amazonas and Acre states, Brazil;

PATTON et al., 2000). The lower second molar has a distinct entoflexid or entofossetid and short hypoflexid in most specimens (Figure 57).

Figure 57 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys perenensis*, ESALQ 204, from ESEX Chico Mendes, Acre State, Brazil

NATURAL HISTORY: Recently, Hice and Velazco et al. (2012) provided some data on the abundance and reproduction of this species in Peru, informing that this is a common species, reproductively active year round, and confirming information available in the literature for other sites in western Amazonia (information summarized by PERCEQUILLO, 2015).

COMMENTS: The morphologic and multi-*loci* molecular analyses suggest that *H. perenensis* is a distinct species from *H. megacephalus* and *H. acritus*, confirming previous results obtained by other studies (PATTON et al., 2000; COSTA 2003; EMMONS; PATTON, 2005). Moreover, *perenensis* and *megacephalus* are not even sister taxa: the former species is sister to a clade formed by (*seuanezi*(*oniscus*, *acritus*)), while the latter is sister to the clade (*perenensis*(*seuanezi*(*oniscus*, *acritus*))). Cyt b tree (EMMONS; PATTON, 2005) recovered *perenensis* as sister to *acritus*, and these two taxa sister to *latipes* (= *seuanezi* plus *oniscus*).

The nomenclatural history of this species is simple: the most conspicuous entry on the synonymic history is the employment of *Oryzomys capito nitidus* by Cabrera (1961). A reason for this erroneous name use is unknown, but is probably due to the proximity of the type localities of both taxa (Amable Maria, the type locality of *nitidus*, is quite close to Perené).

Specimens of *H. perenensis* can be distinguished from those of *H. megacephalus* by their larger body size, larger skull, longer tear-drop shaped incisive foramina, more robust molars, and a $2n = 52$, $FN = 62$ karyotype (GARDNER; PATTON, 1976, as *Oryzomys capito*).

SPECIMENS EXAMINED: (M = Male. F = female. I = unknown sex). BOLIVIA: COCHABAMBA: **Villa Tunari**: 2 km E of Villa Tunari: **M**, AMNH 247778; **F**, AMNH 247780. EL BENI: **Arruda**: Arruda: **M**, FMNH 117106, FMNH 117104, FMNH 117105; **F**, FMNH 117103. **El Refugio**: El Refugio Pampa 3 km. NE (from Camp): **M**, LHEmmons & partners 1524, LHEmmons & partners 16, LHEmmons & partners 1508; **F**, LHEmmons & partners 10. El Refugio: **M**, LHEmmons & partners 1552, LHEmmons & partners 4, LHEmmons & partners 55, LHEmmons & partners 1536; **F**, LHEmmons & partners 1543, LHEmmons & partners 11, LHEmmons & partners 1535. **Estacion Biologica de Beni**: Estacion Biologica de Beni: **M**, AMNH 262022, AMNH 262023; **F**, AMNH 262047. **Exaltacion**: 8 km N Exaltacion: **F**, AMNH 211747. **Itenez**: Itenez, Curicha: **M**, NMNH 551654, NMNH 551653. Totaisal, 1 km SW of Estacion Biologica de Beni: **M**, AMNH 262022, AMNH 262023. **Lago Victoria**: Lago Victoria: **M**, FMNH 117108; **F**, FMNH 117109, FMNH 117107, FMNH 117112. **Rio Biata**: Boca del Rio Biata: **M**, AMNH 262953, AMNH 262959; **F**, AMNH

262956, AMNH 262959. **Rio Curicker:** Curicker River mouth: **F**, AMNH 210006. **Rio Itenez:** Bahia de los casara, 20 km W Laranjeira, Rio Itenez: **F**, AMNH 210272. Costa Marquez, Rio Itenez: **M**, AMNH 210004, AMNH 210005, AMNH 210019, AMNH 210021, AMNH 246140; **F**, AMNH 210003, AMNH 210002, AMNH 210020, AMNH 210000. Rio Itenez: **M**, AMNH 210007. Rio Itenez, 20 km. W Larangeira, Bahia de Los Casara: **F**, AMNH 210272. Rio Itenez, circa 4km. above Costa Maquez: **M**, AMNH 210004, AMNH 210005, AMNH 210019, AMNH 210021; **F**, AMNH 210002, AMNH 210003, AMNH 210020. **Rio Mamore:** Mamore River, 7 km. N Lagionka: **F**, AMNH 211714. Mamore River, Lado E, em frente a Cascajal: **M**, AMNH 211743. **San Joaquin:** Camino Vildes, San Joaquin: **M**, FMNH 117091, FMNH 117092, FMNH 117093; **F**, FMNH 117089, FMNH 117117. Centenela, Rio Machupo, 1 mi E of S. Joaquim: **M**, FMNH 117097, FMNH 117099, FMNH 117100, FMNH 117096; **F**, FMNH 117098, FMNH 117101. Yutiales, 3 leagues S San Joaquin: **F**, NMNH 460429. **Santa Rosita:** Santa Rosita, 3 km. SW Warnes: **F**, NMNH 588193. **Velasco:** Velasco Province, Serrania Huanchuca, Bosque Huanchuca: **F**, NMNH 588192. **Yacuma:** 45 KM by road N Yacuma: **F**, AMNH 262053, AMNH 262055. Campamento Busurucucu, Yacuma: **M**, AMNH 263502. LA PAZ: **Alcoche:** 4 km. NW by road Alcoche: **M**, UMMZ 126773. 5 km. NW by road Alcoche: **F**, UMMZ 126774. 6 km. NW by road Alcoche: **M**, UMMZ 126776. **La Emboscada:** 1 km. E La Emboscada, Estancia La Cabaña: **F**, UMMZ 155886. **Rio Madidi:** 8 Km from mouth of Rio Madidi: **I**, AMNH 262118. PANDO: **La Cruz:** La Cruz: **F**, AMNH 262944. **Santa Rosa:** Santa Rosa: **F**, AMNH 262966. SANTA CRUZ: **Rio Chapare:** 2 Km N Chapare river mouth: **M**, AMNH 211739, AMNH 211740, AMNH 211744. **Rio Pitasama:** Rio Pitasama, 4,5 Km N and 1,5 Km E of Cerro Amboro: **M**, AMNH 262080; **F**, AMNH 262941, AMNH 262021. **Rio Saguay:** Rio Saguay, 3 Km W of San Rafael de Amboro: **I**, AMNH 262084, AMNH 262086. **San Rafael de Amboro:** San Rafael de Amboro: **M**, AMNH 262020; **F**, AMNH 262015, AMNH 262016, AMNH 262019. BRAZIL: ACRE: **Nova Vida:** Nova Vida, right bank rio Juruá: **M**, INPA 3273, INPA 3278, INPA 3198, INPA 3276, INPA 3277; **F**, INPA 3197, INPA 3272. **Porongaba:** Opposite Porongaba, left bank rio Juruá: **M**, INPA 3253, INPA 3254, INPA 3236, INPA 3237; **F**, INPA 3256. Porongaba, right bank rio Juruá: **M**, INPA 3245, INPA 3228, INPA 3230, INPA 3246; **F**, INPA 3227, INPA 3234, INPA 3231, INPA 3232, INPA 3233. **Sena Madureira:** Segundo Distrito (Niterói), Sena Madureira: **M**, NMNH 545299. Sena Madureira, BR 364, Manuel Urbano Km. 8: **M**, NMNH 545301, NMNH 545305, NMNH 545298, NMNH 545295; **F**, NMNH 545303. **Sobral:** Sobral, left bank rio Juruá: **M**, INPA 3257, INPA 3259; **F**, INPA 3260, INPA 3261, INPA 3265. AMAZONAS: **Altamira:**

Altamira, right bank Rio Juruá: **M**, MVZ 190525, MVZ 190523, MVZ 190527; **F**, MVZ 190522, MVZ 190524, MVZ 190520, MVZ 190521. Opposite Altamira, left bank rio Juruá: **M**, MVZ 190526. **Barro Vermelho**: Barro Vermelho, left bank of rio Juruá: **M**, MVZ 190503, MVZ 190512, MVZ 190507, INPA 3339, MVZ 190501, MVZ 190502, MVZ 190505, MVZ 190508, INPA 3326, INPA 3338, MVZ 190509, INPA 3309, INPA 3310, MVZ 190496, MVZ 190504, MVZ 190510, MVZ 190499, MVZ 190506; **F**, MVZ 190500, MVZ 190498, MVZ 190511, INPA 3892, MVZ 190497. **Boa Esperança**: Boa Esperança, right bank rio Juruá: **M**, INPA 3343, INPA 3345. Condor: Condor, left bank rio Juruá: **M**, MVZ 190485, MVZ 190488, MVZ 190490, MVZ 190492, MVZ 190493, MVZ 190494; **F**, MVZ 190486, MVZ 190489, MVZ 190491, MVZ 190487. **Condor**: Opposite Condor right bank Rio Juruá: **F**, MVZ 190495. Sacado (Condor), right bank of rio Juruá: **M**, INPA 3305, INPA 3306, INPA 3307; **F**, INPA 3308. **Igarapé Nova Empresa**: Igarapé Nova Empresa, left bank rio Juruá: **M**, MVZ 190480, MVZ 190481, INPA 3211, MVZ 190484, INPA 3225, MVZ 190483, INPA 3226, INPA 3195, INPA 3200; **F**, INPA 3194, MVZ 190482, INPA 3202, INPA 3196. **Lago Vai Quem Quer**: Lago Vai Quem Quer, right bank rio Juruá: **M**, MVZ 190528. **Penedo**: Penedo, right bank of rio Juruá: **M**, MVZ 190470, INPA 3296, MVZ 190464, MVZ 190458, MVZ 190477, MVZ 190462, MVZ 190463, MVZ 190465, MVZ 190466, MVZ 190467, MVZ 190459, MVZ 190460, MVZ 190469, MVZ 190475, MVZ 190476, INPA 3297, INPA 3301, INPA 3300; **F**, INPA 3303, INPA 3299, MVZ 190468, MVZ 190461, MVZ 190471, INPA 3298. **Viravolta**: Ilhazinha, Viravolta, left bank rio Juruá on igarapé Arabidi, affluent of Paraná Breu: **M**, INPA 3221, MVZ 190548, MVZ 190546, INPA 3214, INPA 3217; **F**, MVZ 190547, INPA 3218, INPA 3222, INPA 3213, INPA 3293, MVZ 190545, MVZ 190543, INPA 3223, INPA 3220, MVZ 190544. Jainú: Jainú, right bank rio Juruá: **M**, INPA 3318, MVZ 190519, INPA 3313, INPA 3311, INPA 3321, INPA 3315, INPA 3316; **F**, MVZ 190518, INPA 3314, INPA 3319, INPA 3312. Viravolta, left bank rio Juruá on igarapé Arabidi, affluent of Paraná Breu: **M**, MVZ 190529, MVZ 190532, MVZ 190537, MVZ 190539, MVZ 190534, INPA 3210, MVZ 190536, MVZ 190538, MVZ 190541, MVZ 190542, INPA 3206, INPA 3208, INPA 3205, INPA 3209, INPA 3215, MVZ 190533, MVZ 190535, INPA 3219; **F**, INPA 3207, MVZ 190530, INPA 3216, MVZ 190531, MVZ 190540, INPA 3204, INPA 3212. RONDONIA: **Rio Itenez**: Costa Marques, rio Itenez: **M**, AMNH 210363. COLOMBIA: CUNDINAMARCA: **Guaicaramo**: Guaicaramo: **F**, NMNH 251966, NMNH 251964. META: **El Parque La Macarena**: El Parque La Macarena: **M**, FMNH58777. PUTUMAYO: **Rio Cuyabano**: Laguna Grande, Rio Cuyabano: **F**, FMNH 125063. **Rio Mecaya**: Rio Mecaya: **M**, FMNH 72037, FMNH 72038, FMNH 72039, FMNH

72040, FMNH 72046, FMNH 72047, FMNH 72043; **F**, FMNH 72054, FMNH 72055, FMNH 72056, FMNH 72091, FMNH 72049, FMNH 72050. **San Jose de Payamino:** San Jose de Payamino: **M**, FMNH 125052, FMNH 125054, FMNH 125059. ECUADOR: NAPO: **Aguarico:** Intillama, Rio Napo, Aguarico, Napo-Pastaza: **M**, UMMZ 80101. San Francisco, Rio Napo, Aguarico, Napo-Pastaza: **M**, UMMZ 80116; **F**, UMMZ 80121, UMMZ 80120, UMMZ 80119. **Limocha:** Limocha: **M**, USMN 528353, USMN 528355, USMN 513442. **Limoncocha:** Limoncocha: **M**, NMNH 513542, NMNH 528353, NMNH 528355; **F**, NMNH 513540, NMNH 513541, LSUMZ 17207, LSUMZ 17028. **Rio Napo:** Llunchi, Rio Napo: **M**, UMMZ 80085, UMMZ 80091, UMMZ 80104, UMMZ 80109, UMMZ 80110, UMMZ 80114; **F**, UMMZ 80088, UMMZ 80090, UMMZ 80103. **Rio Suno Abajo:** Rio Suno Abajo: **M**, AMNH 68075, AMNH 68069, AMNH 68051, FMNH 31080; **F**, AMNH 68061, AMNH 68093, AMNH 68096, AMNH 68111, AMNH 68114, AMNH 68055, AMNH 68112, AMNH 68088, AMNH 68094, AMNH 68095, AMNH 68074, AMNH 68108, AMNH 68097, FMNH 31082. **San José Abajo:** San José Abajo, San José Nuevo: **M**, AMNH 68084, AMNH 68085, AMNH 68087; **F**, AMNH 68047, AMNH 68048, AMNH 68086, AMNH 68104, AMNH 68107, AMNH 68060. PASTAZA: **Canelos:** Canelos: **M**, AMNH 67373. **Oriente:** Oriente, Avila: **M**, NMNH 267501. Rio Copotaza, Oriente: **M**, FMNH 53334. **Tiguino:** Provincia Tiguino, 130 km. S of Coca: **F**, NMNH 574568. **Sarayacu:** Sarayacu: **M**, AMNH 67400; **F**, AMNH 67353, AMNH 67352. ZAMORA-CHINCHIPE: **Zamora:** Zamora: **F**, AMNH 36570, AMNH 36569, AMNH 36566. PARAGUAY: LA PAZ: Iturralde: Ixiamas, 13 km SW, Iturralde Province: **F**, USMN 579254. PERU: AMAZONAS: **Albergue:** Albergue: **M**, MVZ 168963, MVZ 168937; **F**, MVZ 168964. **Bagua:** Bagua, Imaza, Imacita, Comunidad Aguaruna: **F**, MUSM 12056, MUSM 12055. **Chiriaco:** 43 rd Km NE Chiriaco: **F**, LSUMZ 21869, LSUMZ 21871. **Condorcanqui:** Condorcanqui, Nieva, Pto Tunduzza: **M**, MUSM 16260, MUSM 16271, MUSM 16257, MUSM 16262, MUSM 16266, MUSM 16263; **F**, MUSM 16259, MUSM 16267, MUSM 16269, MUSM 16268. **La Poza:** La Poza, Rio Santiago: **M**, MVZ 157809, MVZ 157807, MVZ 157808. **Rio Alto Madre de Dios:** Hacienda Eika, Rio Alto madre de Dios, opposite Selvation: **F**, MVZ 166675. **Rio Cenepa:** Huampami, Rio Cenepa: **M**, MVZ153522. Shimpants, Rio Cenepa: **F**, MVZ153527. Tseasim, (Aguaruna Village) head wafers Rio Huampam, north of Huampami, Rio Cenepa: **I**, MVZ 153520. Vicinity of Huampami, Rio Cenepa: **M**, MVZ 154941, MVZ 154969, MVZ 154966, MVZ 154965, MVZ 154971, MVZ 154940, MVZ 154942, MVZ 154951, MVZ 154956, MVZ 155009, MVZ 154938, MVZ 154945, MVZ 154949, MVZ 154954, MVZ 154955, MVZ 154958, MVZ 154963; **F**, MVZ 154961, MVZ 154944, MVZ 154948, MVZ 154957, MVZ

154939, MVZ 154952, MVZ 154967, MVZ 154943, MVZ 154946, MVZ 154947, MVZ 154950, MVZ 154953, MVZ 154959, MVZ 154960, MVZ 154962, MVZ 154964, MVZ 154970. **Rio Kagka:** Headwaters of Rio Kagka (of Rio Cenepa): **F**, MVZ 154975, MVZ 154973. AYACUCHO: **Rio Apurimac:** Rio Apurimac, Hacienda Luisiana: **M**, LSUMZ 16664, LSUMZ 16666; **F**, LSUMZ 16679. CUSCO: **Armihuari:** La convención, Camisea, Armihuari: **M**, MUSM 14267, MUSM 14266, MUSM 14280, MUSM 14352, MUSM 14289, MUSM 14285, MUSM 14293; **F**, MUSM 14269, MUSM 14273, MUSM 14875, MUSM 14287; **I**, MUSM 14878. **Catarata:** Catarata: **M**, MUSM 21463; **F**, MUSM 21469, MUSM 21464. **Huyro:** Bosque Aputinye, above Huyro: **F**, LSUMZ 19279. **Pauacartambo:** 72 Km. NE Pauacartambo (by rd, Km. 152): **M**, FMNH 84305; **F**, FMNH 84307, FMNH 84306. **Rio Urubamba:** Kiteni, Rio Urubamba: **M**, MVZ 166677.08, MVZ 166676.08, MVZ 166678.08. **Rio Marcapata:** E. Quince Mil on Rio Marcapata: **M**, LSUMZ 19272, LSUMZ 19273; **F**, LSUMZ 19270, LSUMZ 19271, LSUMZ 19274. HUANUCO: **Rio Cayumba:** Rio Cayumba, Hacienda Exito: **F**, FMNH 24558. **Tingo Maria:** 35 Km. NE Tingo Maria, Hacienda Santa Ekna: **M**, LSUMZ 17722. Tingo Maria: **F**, MUSM 2411. JUNIN: **Capitiri:** Capitiri: **M**, MUSM 35544; **I**, MUSM 35693, MUSM 35543, MUSM 35691. **Chalhuapuquio:** Chalhuapuquio: **F**, MUSM 22002. **Naranjal:** Naranjal: **F**, MUSM 22003. **Perené:** Perené: **M**, BMNH 7725. **Poyeni:** Poyeni: **F**, MUSM 35694; **I**, MUSM 35547, MUSM 35548. **San Ramón:** San Ramón: **M**, FMNH 20897. LORETO: **Rio Amazonas:** Boca Rio Peruete, Rio Amazonas: **M**, FMNH 88922. **Lagunas:** Lagunas, lower Huallag: **F**, FMNH 19640. **Nauta:** Nauta, 1 km. above Rio Tigrillo: **M**, FMNH 122980, FMNH 122982; **F**, FMNH 122981. Nauta, Rio Samiria, Santa Elena: **M**, FMNH 87191, FMNH 87194; **F**: FMNH 87192, FMNH 87193. Nauta, Rio Samiria: **M**, FMNH 122973, FMNH 122978, FMNH 122971, FMNH 22976; **F**, FMNH 122977. **Quebrada Agua Negra:** Quebrada Agua Negra: **M**, MUSM 24440. **Rio Curanja:** Balta, Rio Curanja: **M**, LSUMZ 12353, LSUMZ 12354, LSUMZ 12355, MVZ 136583, MVZ 136580, LSUMZ 12348, LSUMZ 12349, LSUMZ 12350, LSUMZ 12356, LSUMZ 16680, MVZ 136577, MVZ 136582, MVZ 136589, LSUMZ 14358, LSUMZ 16692, MVZ 136584, MVZ 136575, MVZ 136579, LSUMZ 12352, LSUMZ 16684; **F**, MVZ 136586, LSUMZ 12351. **Rio Curaray:** Margen derecho do rio Curaray, a 50 km SO de la Base Militar Arica: **F**, MUSM 24604. **Rio Pucacuro:** Dto Tigre, Rio Pucacuro, Collpa Salvador, margen derecha: **M**, MUSM 17591, MUSM 17566, MUSM 17626, MUSM 17687, MUSM 17646, MUSM 17647; **F**, MUSM 17576, MUSM 17617, MUSM 17625, MUSM 17648, MUSM 17708. Dto. Tigre, Rio Pucacuro, Collpa Salvador: **M**, MUSM 17574, MUSM 17635, MUSM 17632; **F**, MUSM 17677; **I**, MUSM 17644, MUSM 17636, MUSM 17710,

MUSM 17707, MUSM 17582, MUSM 17628, MUSM 17634, MUSM 17614, MUSM 17667, MUSM 17613, MUSM 17654, MUSM 17618, MUSM 17619. **Sierra de Contamana:** Sierra de Contamana, Cerros de Canchaguaya: **M**, MUSM 17914, MUSM 7986, MUSM 18023; **F**, MUSM 17969, MUSM 17909, MUSM 17920. **Ullpayacu:** Ullpayacu, aprox. 5 kms ao NO de la Boca del Rio: **F**, MUSM 16437; **I:** MUSM 16432. **Yurimagas:** Yurimagas, Yaneyaku: **M**, FMNH19639. MADRE DE DIOS: **Albergue:** Albergue: **M**, FMNH 139868. **Alto Rio Madre de Dios:** Alto Rio Madre de Dios, Hacienda Amazonia: **M**, FMNH139869; **F**, FMNH 139865. **Boca Inambari:** Boca Inambari: **F**, FMNH 84313, FMNH 84317. Itahuania: Itahuania: **F**, FMNH 84308. **Manu:** Manu, Altamira: **M**, FMNH 98057. Manu, Blanquillo: **M**, MUSM 8419, MUSM 8424, MUSM 8417; **F**, MUSM 8412. Manu, Pakitza: **M**, MUSM 7143, MUSM 7124, MUSM 7026, MUSM 7052, MUSM 7051, MUSM 7050; **F**, MUSM 7045, MUSM 7059, MUSM 7060. Manu: **F**, FMNH 84309, FMNH 84312. Mouth of Quebrada Juliaca on Rio Heath, ca 50 Km S Pto. Pardo, elev. 525, Pampas de Heath, ca 50 Km S Puerto Pardo: **M**, LSUMZ 22684, LSUMZ 22689. **Reserva Cusco Amazónico:** Reserva Cusco Amazónico, 15 km NE de Puerto Maldonado: **M**, MUSM 6379, MUSM 6383, MUSM 6384, MUSM 6408, MUSM 6417, MUSM 6420, MUSM 6426, MUSM 6427, MUSM 6386, MUSM 6397, MUSM 6403, MUSM 6404, MUSM 6421, MUSM 6428, MUSM 6429, MUSM 6380, MUSM 6382, MUSM 6385, MUSM 6388, MUSM 6409, MUSM 6412, MUSM 6430, MUSM 6433, MUSM 6329, MUSM6344, MUSM6353, MUSM6370, MUSM6376, MUSM 6389, MUSM 6405, MUSM 6326, MUSM 8310, MUSM 6394, MUSM 6343, MUSM 8309; **F**, MUSM 6378, MUSM 6377, MUSM 6391, MUSM 6396, MUSM 6401, MUSM 6411, MUSM 6392, MUSM 6413, MUSM 6418, MUSM 6422, MUSM 6425, MUSM 6431, MUSM 6398, MUSM 6399, MUSM 6414, MUSM 6419, MUSM 6424, MUSM 6338, MUSM 6355, MUSM 6358, MUSM 6372, MUSM 6374, MUSM 8308, MUSM 6436, MUSM 6416, MUSM 6356, MUSM 6400, MUSM 6342, MUSM6395; **I**, MUSM 6423, MUSM 6335. **Rio Manu:** Rio Manu, Parque Nacional del Manu, Puesto de Vigilancia da Pakitza: **M**, MUSM 9239, MUSM 9240; **F**, MUSM 9246. PASCO: **Huancabamba:** Huancabamba: **M**, MUSM 432. **Oxapampa:** Cordillera El Sira, Oxapampa: **M**, MUSM 9406, MUSM 9404; **F**, MUSM 9403. **Pozuzu:** Pozuzu: **M**, FMNH 24564, FMNH 24566, FMNH 34253, FMNH 126695; **F**, FMNH 24561, FMNH 24567, FMNH 126696, FMNH 126698, FMNH 126703, FMNH 126705. PUNO: **Carabaya:** Carabaya, Puente Candamo: **M**, MUSM 11577, MUSM 11590, MUSM 11589, MUSM 11580; **F**, MUSM 11579, MUSM 11585, MUSM 11588, MUSM 11583, MUSM 11586. SAN MARTIN: **Moyobamba:** Moyobamba: **F**, FMNH 19391. TUMBES: **Zarumilla:** P-V- Cotrina, Campo Verde, Zarumilla,

Z-R-Tumbes: **F**, MUSM 10729. UCAYALI: **Yarinacocha**: Yarinacocha, R Ucayali: **M**, MUSM 2366.

Hylaeamys seuanezi (Weksler, Geise and Cerqueira, 1999)

Hesperomys (*Calomys*) *laticeps*: Thomas, 1882:102; part; name combination.

Hesperomys (*Oryzomys*) *laticeps*: Thomas, 1884:452; part; name combination.

O[ryzomys]. *laticeps*: Thomas, 1894b:354; part; name combination.

[*Oryzomys* (*Oryzomys*)] *laticeps laticeps*: Tate, 1932a:18; part; name combination.

Oryzomys laticeps laticeps: Gyldenstolpe, 1932:17; name combination.

Oryzomys oniscus: Moojen, 1952b:47; part; name combination.

Oryzomys laticeps: HersHKovitz, 1960:544, footnote; part; not *Mus laticeps* Lund (= *Hylaeamys laticeps* [Lund]).

Oryzomys [(*Oryzomys*)] *capito laticeps*: Cabrera, 1961:386; part; name combination.

Oryzomys [(*Oryzomys*)] *capito oniscus*: Cabrera, 1961:387; part; name combination.

Oryzomys capito: HersHKovitz, 1966:137, footnote; part; not *Mus capito* Olfers (= *Hylaeamys megacephalus* [Fischer]).

Oryzomys seuanezi Weksler, Geise, and Cerqueira, 1999:454. sp.n.

[*Hylaeamys*] *laticeps*: Weksler, Percequillo, and Voss, 2006:14; part; name combination.

Hylaeamys seuanezi: Brennand, Langguth, and Percequillo, 2013:1356; first use of current name combination.

HOLOTYPE: MN 42678, an adult male, captured by M. Weksler, L. Geise and R. Cerqueira (original number FU11).

TYPE LOCALITY: “Fazenda União, Casimiro de Abreu municipality, Rio de Janeiro state (22°25'S, 42°02'W); 50 m.”

DESCRIPTION: This is a large bodied species (range of length of head and body, 122-174 mm) with a short tail (range, 100-157 mm), robust hind feet with fleshy hypothernar pads, and with ungual tufts that are sparse and shorter than the claws. The dorsal fur is very short

and harsh, colored buffy, yellowish, or grayish-brown densely grizzled with dark brown. The ventral fur is shorter and predominantly grayish in color. The tail is dorsoventrally bicolored, basally and uniformly colored distally. The ears are sparsely covered with reddish-brown hairs. The skull is robust and large (greatest skull length range, 31.8-37.6 mm), with short, narrow, and tear-drop shaped incisive foramina (length range, 4.3-5.9 mm; width range, 2.1-2.9 mm). The interorbital region diverges slightly posteriorly, with squared or weakly to moderately beaded supraorbital margins. The palate has complex, multiple posterolateral palatal pits recessed in shallow palatine depressions and developed palatal excrescencies. The molar tooth rows are robust (length range, 4.6-5.5 mm; M1 width range, 1.4-1.8 mm) (Figure 59).

DISTRIBUTION: Known collecting localities of *Hylaeamys seuanezi* are distributed from southern Bahia to northern Rio de Janeiro states, throughout coastal lowland forests and eastern-forested foothills of the Serra do Mar. The elevational range of this species extends from near sea level at Casimiro de Abreu, Rio de Janeiro (17 m) to approximately 300 m at Parque Estadual do Rio Doce, Minas Gerais (Figure 60).

Figure 59 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys seuanezi*, UFMG 2220, from Una, Bahia State, Brazil

Figure 60 – Known collection localities *H. seuanezi* in southeastern Brazil, on the southern margin of Rio São Francisco. Lower inset: detail of the gray box on the large map, with the collection localities of central Bahia. Number of localities in accordance with Gazetteer in Appendix A.

NATURAL HISTORY: Brennand et al. (2013) and Percequillo (2015) recently summarized published data on the natural history of this species.

COMMENTS: The name *laticeps*, presently recognized as a synonym of *H. megacephalus*, was tentatively associated to the species nowadays named *H. seuanezi* through much of its history. Only Musser et al. (1998) formally proposed the use of *laticeps* for the Atlantic Forest samples, based on type species exam and comparisons of series of specimens, a procedure followed by several authors (WEKSLER et al., 2006; WEKSLER; PERCEQUILLO, 2011). Nevertheless, Brennand et al. (2013) analyzing larger series of specimens, concluded that the type of *laticeps* is morphologic, morphometric and zoogeographically more akin to Cerrado samples that are named *megacephalus*, therefore re-establishing the synonymy of *laticeps* under *megacephalus*, and revalidating *seuanezi*.

Hylaeamys seuanezi can be differentiated from *H. megacephalus* by its thinner and coarser pelage; dark, grayish or blackish brown dorsal body coloration; larger cranial size;

more robust molars; larger and wider palatal excrescences; diploid number $2n = 48$ and fundamental number $FN = 60$ (in contrast to $2n = 54$ and $FN = 62$ in *H. megacephalus*), and geographical distribution (while the former is restricted to eastern Brazilian Atlantic forest, the latter has a more widespread range that extends from the Cerrado throughout eastern Amazonia).

SPECIMENS EXAMINED: (M = male, F = female, I = unknown sex). BRAZIL: BAHIA: **Arataca**: Fazenda Orion, Serra das Lontras, Arataca: **M**, UFMG 2109 skin and skull; **F**, UFMG 2108 skin and skull. **Buerarema**: Buerarema, Ribeirão da Fortuna: **M**, MN 9010 skin and skull, MN 9193 skin and skull, MN 9259 skin and skull, MN 9264 skin and skull, MN 9309 skin and skull, MN 9333 skin and skull, MN 9513 skin and skull, MN 9529 skin and skull, MN 9569 skin and skull, MN 9577 skin and skull, MN 9585 skin and skull, MN 9640 skin and skull, MN 9644 skin and skull, MN 9651 skin and skull; **F**, MN 9070 skin and skull, MN 9186 skin and skull, MN 9219 skin and skull, MN 9227 skin and skull, MN 9230 skin and skull, MN 9255 skin and skull, MN 9372 skin and skull, MN 9400 skin and skull, MN 9542 skin and skull, MN 9555 skin and skull, MN 9571 skin and skull, MN 9575 skin and skull, MN 9642 skin and skull, MN 9645 skin and skull, MN 9653 skin and skull, MN 9654 skin and skull, MN 9655 skin and skull. **Cairú**: Fazenda Subauma, Cairú: **F**, UFMG 2115 skin and skull. **Gandú**: Gandú: **M**, UFPB 979 skin and skull. **Ilhéus**: Aritaguá, Urucutuca, Ilhéus: **M**, MN 9561 skin and skull. Banco da Vitória, Pirataquissé, Ilhéus: **M**, MN 9015 skin and skull, MN 9110 skin and skull, MN 9232 skin and skull, MN 9314 skin and skull, MN 9386 skin and skull, MN 9360 skin and skull, MN 9494 skin and skull, MN 9502 skin and skull, MN 10512 skin and skull, MN 10994 skin and skull; **F**, MN 9111 skin and skull, MN 9217 skin and skull, MN 9253 skin and skull, MN 9402 skin and skull, MN 9545 skin and skull, MN 9548 skin and skull, MN 9552 skin and skull, MN 9619 skin and skull, MN 9629 skin and skull, MN 9634 skin and skull. Ilhéus: **M**, MN 10747 skin and skull, MN 10756 skin and skull, MN 10758 skin and skull, MN 10763 skin and skull, MN 10764 skin and skull, MN 10773 skin and skull, MN 10774, skin and skull MN 10781 skin and skull, MN 10795 skin and skull; **F**, MN 10796 skin and skull, MN 10803 skin and skull, MN 10805 skin and skull; **I**, MN 1783 skin and skull, MN 10791 skin and skull, MN 10793 skin and skull, MN 1799 skin and skull, MN 10802 skin and skull, MN 10807 skin and skull, MN 10815 skin and skull, MN 10824 skin and skull, MN 10827 skin and skull, MN 10831 skin and skull, MN 10843 skin and skull, MN 10845 skin and skull, MN 10851 skin and skull, MN 10852 skin and skull, MN 10856 skin and skull, MN 10860 skin and skull, MN 10872 skin and skull, MN 10877 skin and skull. Fazenda Limeira, Ilhéus: **F**, UFMG 36 skin and skull. **Itabuna**:

Fazenda Brejo Grande, 12 km S - 1.7 km W Itabuna: **M**, MN 31415 skin and skull, MN 31420 skin and skull, MN 31453 skin and skull, MN 31456 skin and skull, MN 31457 skin and skull, MN 31420 skin and skull, MN 31453 skin and skull, MN 31420 skin and skull, MN 31453 skin and skull; **F**, MN 35893 skin and skull. Parque Zoobotânico da CEPLAC, 6 km E de Itabuna: **M**, MN 31416 skin and skull, MN 31418 skin and skull; **F**, MN 31419 skin and skull. **Jussari**: RPPN Serra do Teimoso, Jussari: **M**, MZUSP 29601 skin and skull, MZUSP 29636 skin and skull, MZUSP 29637 skin and skull, MZUSP 29732 skin and skull, MZUSP 29780 skin and skull, MZUSP 29790 skin and skull, MZUSP 29794 skin and skull, MZUSP 29795 skin and skull, MZUSP 29803 skin and skull, MZUSP 29808 skin and skull, MZUSP 29820 skin and skull; **F**, MZUSP 29691 skin and skull, MZUSP 29742 skin and skull, MZUSP 29781 skin and skull; **I**, MZUSP 26793 skin and skull, MZUSP 29595 skin and skull, MZUSP 29797 skin and skull, MZUSP 29817 skin and skull. **Porto Seguro**: Reserva Biológica Pau-Brasil, 15 km NW de Porto Seguro: **M**, UFPB 557 skin and skull, UFPB 558 skin and skull, UFPB 559 skin and skull, UFPB 574 skin and skull. **São José**: Fazenda Unacau, 8 km SE de São José: **M**, UFPB 468 skin and skull, UFPB 470 skin and skull, UFPB 475 skin and skull, UFPB 476 skin and skull, UFPB 477 skin and skull, UFPB 478 skin and skull, UFPB 480 skin and skull, UFPB 484 skin and skull, UFPB 486 skin and skull, UFPB 487 skin and skull, UFPB 489 skin and skull, UFPB 491 skin and skull, UFPB 492 skin and skull, UFPB 497 skin and skull, UFPB 499 skin and skull, UFPB 500 skin and skull, UFPB 504 skin and skull, UFPB 508 skin and skull, UFPB 511 skin and skull, UFPB 512 skin and skull, UFPB 515 skin and skull; **F**, UFPB 467 skin and skull, UFPB 471 skin and skull, UFPB 472 skin and skull, UFPB 473 skin and skull, UFPB 474 skin and skull, UFPB 479 skin and skull, UFPB 483 skin and skull, UFPB 485 skin and skull, UFPB 488 skin and skull, UFPB 493 skin and skull, UFPB 494 skin and skull, UFPB 495 skin and skull, UFPB 496 skin and skull, UFPB 498 skin and skull, UFPB 502 skin and skull, UFPB 503 skin and skull, UFPB 507 skin and skull, UFPB 509 skin and skull, UFPB 510 skin and skull, UFPB 513 skin and skull; **I**, UFPB 469 skin and skull, UFPB 490 skin and skull, UFPB 501 skin and skull, UFPB 505 skin and skull. **Una**: EDJAB - CEPLAC, Una: **M**, UFMG 42 skin and skull, UFMG 2225 skin and skull. ESMAL, CEPLAC, Una: **M**, UFMG 2220 skin and skull, UFMG 2221 skin and skull. Fazenda Bolandeira; 10 km S Una: **M**, UFMG 11 skin and skull, UFMG 2049 skin and skull, UFMG 2875 skin and skull, UFMG 2879 skin and skull; **F**, UFMG 2876 skin and skull, UFMG 2880 skin and skull; **I**, UFMG 2050 skin and skull. Fazenda Dendhevea, Una: **M**, UFMG 2210 skin and skull. Fazenda Jueirana, Una: **M**, UFMG 2034 skin and skull. Reserva Biológica de Una, Una: **M**, UFMG 2037 skin and skull, UFMG 2038 skin and skull;

F, UFMG 2035 skin and skull; **I**, UFMG 2121 skin and skull, UFMG 2120 skin and skull. Una: **M**, MZUSP RP34 skin and skull, MZUSP RP106 skin and skull, MZUSP RP128 skin and skull, MZUSP RP 169 skin and skull, MZUSP RP180 skin and skull, MZUSP RP190 skin and skull, MZUSP RP250 skin and skull, MZUSP RP260 skin and skull, MZUSP RP 413 skin and skull, MZUSP SL10 skin and skull; **F**, MZUSP RP12 skin and skull, MZUSP RP158 skin and skull, MZUSP RP367 skin and skull, MZUSP RP385 skin and skull, MZUSP RP927 skin and skull, MZUSP SL6 skin and skull; **I**, MZUSP RP5 skin and skull, MZUSP RP 27 skin and skull, MZUSP RP66 skin and skull, MZUSP RP 80 skin and skull, MZUSP RP240 skin and skull, MZUSP RP340 skin and skull, MZUSP RP347 skin and skull, MZUSP RP354 skin and skull, MZUSP RP380 skin and skull, MZUSP RP467 skin and skull, MZUSP RP555 skin and skull, MZUSP RP1115 skin and skull, MZUSP SL1 skin and skull, MZUSP SL2 skin and skull. **Wenceslau Guimarães**: Estação Ecológica Nova Esperança, Wenceslau Guimarães: **M**, UFMG 2112 skin and skull, UFMG 2114 skin and skull; **F**, UFMG 2113 skin and skull. ESPÍRITO SANTO: **Alfredo Chaves**: Engenheiro Reeve - Matilde, Alfredo Chaves: **F**, BMNH 39456 skin and skull. Linhares: Fazenda Santa Terezinha, 33 km NE de Linhares: **M**, UFMG 4 skin and skull, UFMG 37 skin and skull; **F**, UFMG 33 skin and skull, UFMG 36 skin and skull. F. M. A. Linhares: **M**, MN 32668 skin and skull; **F**, MN 32639 skin and skull, MN 32641 skin and skull, MN 32643 skin and skull. Linhares: **M**, MN 34497 skin and skull; **F**, MN 32638 skin and skull; **I**, MN 34493 skin and skull, MN 32648 skin and skull. Santa Teresa: **M**, DZUnB 1247 skin and skull; **F**, DZUnB 1265 skin and skull, DZUnB 1285 skin and skull. MINAS GERAIS: Marliéira: Parque Estadual do Rio Doce; 13 km E Marliéira: **M**, UFMG 111 skin and skull; **F**, UFMG 382 skin and skull, UFMG 2874 skin and skull. Rio Doce: **M**, UFMG 5 skin and skull. RIO DE JANEIRO: **Casimiro de Abreu**: Fazenda União, Casimiro de Abreu: **M**, MN 42678 skin and skull. Silva Jardins: Reserva Poço das Antas, Silva Jardins: **M**, MN 42866 skin and skull, MN 42872 skin and skull, MN 42873 skin and skull, MN 42883 skin and skull; **F**, MN 42867 skin and skull, MN 42874 skin and skull.

Hylaeamys tatei (Musser, Carleton, Brothers, and Gardner, 1998)

Oryzomys tatei Musser, Carleton, Brothers, and Gardner, 1998:100; type locality “Palmera (01°25'S/78°12'W;...), at 4000 ft (1220 m), Provincia del Tungurahua, Ecuador.”

[*Hylaeamys*] *tatei*: Weksler, Percequillo, and Voss, 2006:14; first use of current name combination.

DESCRIPTION: This species is diagnosed by the presence of a long and deep mesoflexus on first and second upper molar (moderate wear forms either a long medial mesofossette or small labial and a long medial mesofossettes), and a robust ectolophid on m1 and m2 (Figure 61).

DISTRIBUTION: *Hylaeamys tatei* is known from three localities along the upper Río Pastaza on eastern slope of the Ecuadorean Andes (Figure 62).

NATURAL HISTORY: Musser et al. (1998) provided information on the natural history of this species, and no additional information was published ever since.

COMMENTS: *Hylaeamys tatei* is conspicuously distinct from other congeneric forms, but especially from *H. yunganus*, by its large body size and cranial dimensions, shorter incisive foramina (length 4.2 to 4.9 mm in *H. tatei*; length 3.9 to 5.8 mm in *H. yunganus*), and longer and wider molar tooththrow (length 5.5 to 5.7 mm and breadth range 1.7 to 1.9 mm in *H. tatei*; length 3.9 to 5.5 mm and breadth 1.3 to 1.7 mm in *H. yunganus*).

SPECIMENS EXAMINED: (M = Male. F = female. I = unknown sex). ECUADOR: PASTAZA: Mera: **M**, AMNH 67366, AMNH 67367. TUNGURAHUA: Palmera: **M**, AMNH 67358, AMNH 67351, AMNH 67363, AMNH 67376, AMNH 67359, AMNH 67360; **F**, AMNH 67362, AMNH 67364, AMNH 67365.

Figure 61 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys tatei*, AMNH 67358, from Palmera, Ecuador

Figure 62 – Known collection localities of *H. tatei* in Ecuadorean Andes. Number of localities as provided in Gazetteer in Appendix A.

Hylaeamys yunganus (Thomas, 1902)

Oryzomys yunganus Thomas, 1902b:130.

[*Oryzomys* (*Oryzomys*)] *yunganus*: Trouessart, 1904:419; name combination.

Oryzomys [(*Oryzomys*)] *capito yunganus*: Cabrera, 1961:387; name combination.

[*Hylaeamys*] *yunganus*: Weksler, Percequillo, and Voss, 2006:14; part; first use of current name combination.

HOLOTYPE: BMNH 2.1.1.39, an adult male collected by P.O. Simmons (original number 1475), in 19.June.1901, “In woods”, and preserved as skin and skull; the skin is well preserved, but the skull shows some damage in the incisive foramina, roof of mesopterygoid fossa, and hamular process of pterygoid.

TYPE LOCALITY: “Charuplaya, 1350 m,” indicated by Thomas (1902b:126) to be “...on the [Río] Securé, just north of 16 S.,” Cochabamba, Bolivia. Musser et al. (1998:269-271) commented on the actual placement of the type locality, stating that the appropriate collecting

site is located on the Río Santa Elena about 10 km down the river valley north of Langunillas, at 1,300 to 1,400 m, and not in the headwaters of Río Sécure, on the coordinates 16°36'S, 66°37'W.

DESCRIPTION: *Hylaeamys yunganus* has a moderate body size with the tail equal to or shorter than the length of the head and body. Dense, velvety dark fur covers the upperparts (brownish tawny to brownish black); underparts are dark grayish white. The tail is monocolored or with ventral basal half either unpigmented or mottled. Dorsal surfaces of front and hind feet are whitish, the claws sparsely covered by ungual tufts, and the plantar surfaces lack hypothenar pads in some specimens. Superciliary, genal, and mystacial vibrissae are not exceptionally long, extending only to ears. Cranial shape is similar to that of *H. perenensis*, but the zygomatic plate is much wider relative to other cranial dimensions, and lengths of bony palate, incisive foramina, and molar row are each longer relative to occipitonasal length. Posterior margins of the dentary are shallowly concave between condyloid and angular process (compared with more deeply concave margin of *H. perenensis*); the molars are chunky and wide. M2 has a short paraflexus and labial and medial fossettes are present; m2 has a conspicuous entoflexid, short hypoflexid that extends only to medial plane of tooth, and a single fossettid (Figure 63).

DISTRIBUTION: *Hylaeamys yunganus* is widely distributed in northern and western Amazon basin, inhabiting the lowland Amazonian rainforest of western Brazil, northern and central Bolivia, Peru, Ecuador, Central Colombia and southern and eastern Venezuela. Throughout this region, *H. yunganus* occupies a wide elevational range, from 1200, in Île de Cayenne to nearly 2,000 m on the eastern Andean slopes of Peru (Yambra and Yambrasbamba) (Figure 64).

Figure 63 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys yunganus*, USMN 393868, from San Pedro, Loreto, Peru

Figure 64 – Known collection localities of *H. yunganus* in western and northern Amazonia . Number of localities in accordance to Gazetteer in Appendix A.

NATURAL HISTORY: Percequillo (2015) recently compiled available information on the natural history of *Hylaeamys yunganus*, but his concept included populations from eastern Amazon (from Guiana shield) that are presently allocated to a new species of the genus (*Hylaeamys* sp.n.; see next account). The “apparent geographical variation in habitat preferences”, in fact, reflects species level differences. While in Rio Juruá, in western Brazilian Amazonia, specimens of *H. yunganus* were trapped “in primary and secondary flooded and non-flooded forests, as well as abandoned and active garden plots and *Heliconia* thickets” (PATTON et al., 2000), in Paracou, French Guiana, specimens of *Hylaeamys* sp.n. were “limited to primary forest, most frequently in moister sites, such as swampy and creek side forest formations, where specimens were captured under or besides logs, around the bases of trees, in dense undergrowth unsheltered by woody objects, in tangled dead branches, among fallen palm fronds, and within the stilt roots of standing trees” (PERCEQUILLO, 2015; based on VOSS et al., 2001). Patton et al. (2000) also reported that *H. yunganus* is more frequently associated with *terra firme* forests than sympatric *H. perenensis*, being also less

abundant than the latter species. Percequillo (2015) provided data on reproduction, for typical *H. yunganus*.

COMMENTS: Percequillo (2015) stated, “whether these differences warrant taxonomic recognition must remain for future analyses”, when referring to size and karyological differences (see above) observed among eastern and western samples of *H. yunganus*. Analyses performed in the present contribution, allowed me to hypothesize that these differences, along with the topology recovered on phylogenetic analysis, were adequate to acknowledge the status of a new species for the eastern samples of Brazil, Guyana, Surinam and French Guiana.

The nomenclatural history of *H. yunganus* is not confusing, with only some variation on the species concept: until Musser et al. (1998), the concept was narrower, including only Bolivian samples, but latter several authors adopted their wider concept (PATTON et al., 2000; VOSS et al., 2001; WEKSLER et al., 2006; PERCEQUILLO, 2015).

SPECIMENS EXAMINED: (M = Male. F = female. I = unknown sex). BOLIVIA: BENI: **Rio Biata**: Boca del rio Biata: **M**, AMNH 262952; **F**, AMNH 262957, AMNH 262951, AMNH 262950. COCHABAMBA: **Charuplaya**: Charuplaya: **M**, BMNH 21139. PANDO: **Las Piedras**: Las Piedras: **M**, AMNH 262736. **Santa Rosa**: Santa Rosa: **F**, AMNH 262947. SANTA CRUZ: **Rio Pitasama**: 4.5 km N, 1.5 km E Cerro Amboro, Rio Pitasama: **F**, AMNH 262079, AMNH 262081. **Rio Saguayo**: Rio Saguayo, 3 Km W of San Rafael de Amboro: **I**, AMNH 262085. BRAZIL: ACRE: **Nova Vida**: Nova Vida, right bank rio Juruá: **F**, INPA 3372, INPA 3375. **Ocidente**: Occidente, right bank rio Juruá: **M**, INPA 3361. **Porongaba**: Opposite Porongaba, left bank rio Juruá: **M**, INPA 3371, INPA 3368, MPEG 1244, MPEG 1346, INPA 3366, MPEG 1246, MPEG 1341, MPEG 1348, MPEG 1391, MPEG 1408; **F**, MPEG 1390, INPA 3370, MPEG 1334, MPEG 1335, MPEG 1243. Porongaba, right bank rio Juruá: **M**, MPEG 1421, INPA 3363, MPEG 1115, MPEG 1227, INPA 3362, MPEG 1148, MPEG 1206, MPEG 1400, INPA 3364, MPEG 1173, MPEG 1268, INPA 3367, MPEG 1204; **F**, MPEG 1422, MPEG 1144, MPEG 1146, MPEG 1168, MPEG 1418, MPEG 1423, INPA 3365. **Sena Madureira**: Bairro do Triângulo, Sena Madureira: **M**, MPEG 10754, MPEG 10751, MPEG 10756, MPEG 10763, MPEG 10767, MPEG 10750, MPEG 10764, MPEG 10765, MPEG 10745; **F**, MPEG 10766, MPEG 10748. Segundo Distrito (Niterói), Sena Madureira: **F**, MPEG 13181. Sena Madureira, BR 364, Manuel Urbano Km. 8: **M**, NMNH 545304, MPEG 13180, NMNH 545300, MPEG 10603, MPEG 10594, MPEG 10599, NMNH 545302; **F**, MPEG 13178, NMNH 545297, MPEG 10602; **I**, MPEG 10611. **Sobral**: Sobral, left bank rio Juruá: **M**, MPEG 1466; **F**, MPEG 1436, MPEG 216. AMAPA: **Serra do Navio**: Rio Amapari,

Terezinha, Serra do Navio: **M**, USMN 393866, USMN 393868, USMN 393872; **F**, USMN 393869, USMN 393878. AMAZONAS: **Altamira**: Altamira, right bank Rio Juruá: **M**, MVZ 190588; **F**, MVZ 190589. Opposite Altamira, left bank rio Juruá: **M**, MPEG 868, MPEG 917, MPEG 952, INPA 3394; **F**, MPEG 897. **Boa Esperança**: Boa Esperança, right bank rio Juruá: **M**, MPEG 190. **Condor**: Condor, left bank rio Juruá: **M**, MVZ 190580, INPA 3391, MVZ 190579, INPA 3390, MVZ 190582, MVZ190581, MVZ 190583; **F**, INPA 3392, MVZ 190584. Igarapé Nova Empresa: Igarapé Nova Empresa, left bank rio Juruá: **M**, INPA 3201, MVZ 190577. Sacado (Condor), right bank of rio Juruá: **M**, MPEG 174, MPEG 587, MPEG 633; **F**, MPEG 635, MPEG 656, MPEG 175, MPEG 588, MPEG 621, MPEG 634, MPEG 657. **Ilhazinha Viravolta**: Ilhazinha Viravolta, left bank rio Juruá on igarapé Arabidi, affluent of Paraná Breu: **M**, MPEG 551, MPEG 510; **F**, MPEG 474. **Jainú**: Jainú, right bank rio Juruá: **F**, INPA 3393, MVZ 190585. **Lago Vai Quem Quer**: Lago Vai Quem Quer, right bank rio Juruá: **M**, MPEG 394; **F**, MPEG 295. **Manaus**: Manaus, Estrada Manaus-Itacoatiara: **M**, MPEG 7196. **Penedo**: Penedo, right bank of rio Juruá: MVZ 190572, INPA 3381, MVZ 190565, MVZ 190567, MVZ 190570, INPA 3382, MVZ 190551, MVZ 190559, MVZ 190562, MVZ 190566, MVZ 190569, INPA 3378, INPA 3380, MPEG 420, MPEG 421, MVZ 190560; **F**, MVZ 190549, MVZ 190561, MVZ 190563, MVZ 190568, MVZ 190571, MVZ 190564, INPA 3379, MVZ 190555. Sacado (Condor), right bank of rio Juruá. RONDONIA: **Abunã**: Margem direita do Rio Madeira, Abunã, UHE Jirau: **I**, MZUSP MJ201, MZUSP MJ222, MZUSP MJ219. COLOMBIA: CAQUETÁ: **Rio Caquetá**: Rio Caquetá, La Taqua, Tres Troncos: **M**, FMNH 72036; **F**, FMNH 72051. CUNDINAMARCA: **Guaicaramo**: Guaicaramo: **M**, AMNH 71328. META: **El Parque La Macarena**: El Parque La Macarena, camp Izawa, in caño near camp: **M**, FMNH 58778, FMNH 58779. **Serrania de La Macarena**: Serrania de La Macarena, Pico Renjifo: **M**, FMNH 87969; **F**, FMNH 87970. **Villavicencia**: Villavicencia: **M**, AMNH 136361. ECUADOR: NAPO: **Llunchi**: Llunchi, Rio Napo: UMMZ 80095, UMMZ 80106. **Pompeya**: PN Yasuni, 42 km S, 1 km E Pompeya: **M**, ROM 104054; **F**, ROM 104047. PN Yasuni, El Saladero, 76 km S Pompeya Sur: **M**, ROM 104561, ROM 105259, ROM 105288; **F**, ROM 105320. **Rio Napo**: Near the River Napo: **M**, UMMZ 65181. **San José Abajo**: San José Abajo, na realidade San José Nuevo: **M**, AMNH 68049, AMNH 68082, AMNH 68115; **F**, AMNH 68059, AMNH 68106. PASTAZA: **Rio Curaray**: Boca Rio Curaray: **F**, AMNH 71570. **Oriente**: Rio Capahuari, Oriente: **M**, FMNH 43271, FMNH 43270. Rio Yana-Rami, Oriente: **F**, FMNH 43265. ZAMORA-CHINCHIPE: **Zamora**: Zamora: AMNH 47830. PERU: AMAZONAS: **Uscho**: Uscho, about 50 miles E of Chachapoyas, NE Peru: **F**, AMNH 73182. AYACUCHO: **San Jose**: Rio Santa Rosa, San Jose:

F, LSUMZ 16685. CUSCO: **Cashiriari**: La convención, Camisea, Cashiriari: **F**, MUSM 14278. **Consuelo**: Consuelo, 15.9 km SW Pilcopata: **M**, MUSM 19999. **Marcapata**: Hacienda Cadena, Marcapata: **M**, FMNH 68631, FMNH 68630; **F**, FMNH 66399. **Quince Mil**: Quince Mil: **M**, FMNH 75272, FMNH 75259, FMNH 75264; **F**, FMNH 75253, FMNH 75254, FMNH 75261, FMNH 75263, FMNH 75262. **Santa Ana**: Santa Ana: **M**, NMNH 194887. HUANUCO: **Chinchao**: Chinchao, Hacienda Buena Vista: **M**, FMNH 24546, FMNH 24551; **F**, FMNH 24549. Chinchao: **M**, FMNH 23721, FMNH 23722. LORETO: **Balta**: Balta, Rio Curanja: **M**, MVZ 136587, MVZ 136585. **Rio Pucacuro**: Dto Tigre, Rio Pucacuro, Collpa Salvador, margen derecha: **F**, MUSM 17567. Dto. Tigre, Rio Pucacuro, Cocha Coconilla, margen izquierda: **I**, MUSM 17724. Dto. Tigre, Rio Pucacuro, Collpa Salvador: **I**, MUSM 17561. **Rio Santiago**: Boca Rio Santiago: **M**, AMNH 98257. **Requena**: Requena, Centro de Invertigaciones Jenaro He: **M**, MUSM 16009, MUSM 16010. **Sierra de Contamana**: Sierra de Contamana, Cerros de Canchaguaya: **F**, MUSM 17961, MUSM 17998, MUSM17972, MUSM 17905. **Ullpayacu**: Ullpayacu, aprox. 5 km NO de la Boca del Rio: **M**, MUSM 16441. PASCO: **Delfin**: Delfin: **M**, MUSM 12709, MUSM 12973, MUSM 12706, MUSM 12148; **F**, MUSM 12705, MUSM 12708. **Pozuzu**: Pozuzu: **M**, FMNH 126707. **Shiringamazu**: Shiringamazu, carretera a Iscosazin: **M**, MUSM 10452. SURINAME: **Nickerie**: Kaiserberg airstrip, Zuid River: **M**, FMNH 93284; **F**, FMNH 93286. VENEZUELA: BOLIVAR: Auyán-Tepuí: Auyán-Tepuí: **M**, AMNH 131125; AMNH 130898, AMNH 130906, AMNH 130914, AMNH 130960; **F**, AMNH 131126, AMNH 130940, AMNH 130941, AMNH 130901, AMNH 130955, AMNH 130959, AMNH 130905, AMNH 130916, AMNH 130933. AMAZONAS: **Agüita**: Mt. Duida, Agüita, Tyler Duida Expedition: **F**, AMNH 77337. **Tamatama**: Tamatama, Rio Orinoco: **F**, USMN 409869, NMNH 409869.

Hylaeamys sp.n.

DESCRIPTION: *Hylaeamys* sp.n. has a small body size with the tail equal to or shorter than the length of the head and body. Dense, velvety dark fur covers the upperparts (brownish tawny to brownish black); underparts are dark grayish white. The tail is monocolored or with ventral basal half either unpigmented. Dorsal surfaces of front and hind feet are whitish, the claws sparsely covered by ungual tufts, and the plantar surfaces lack hypothenar pads in most part of specimens. Superciliary, genal, and mystacial vibrissae are not exceptionally long, extending only to ears. Cranial shape is similar to that of *H. megacephalus*, but the zygomatic plate is much wider relative to other cranial dimensions, and lengths of bony palate, incisive foramina, and molar row are each longer relative to occipitonasal length. The molars are

chunky and wide. M2 has a short paraflexus and labial and medial fossettes are present; m2 has a conspicuous entoflexid, in most part of specimens, a shorter hypoflexid than *H. yunganus*, not extending to medial plane of tooth, and a single fossettid (Figure 65).

DISTRIBUTION: The known collection localities of this new species are distributed on the eastern Amazon, on the northwestern border of Central Brazilian Shield and on the easternmost portion of the Guianan shield, in Brazil, French Guiana, Surinam and Guyana (Figure 66).

NATURAL HISTORY: Voss et al. (2001) provided all available information on some aspects of natural history of this species. See account of *Hylaeamys yunganus* above for further information.

COMMENTS: Musser et al. (1998) were the first to highlight the morphometric geographic variation observed into “*yunganus* group”. The new species showed a delicate skull and the smallest means for the variables related to length and breadth of the skull, as well as the breadth of M1 and length of maxillary tooth row when compared to *H. yunganus*.

SPECIMENS EXAMINED: BRAZIL: Amapá, Macapá, Rio Amapari (MPEG 6686); Mato Grosso, 264 km N Xavantina, Serra do Roncador (BM 81.470); Pará, Agrovila da União, 18 km S & 19 km W Altamira, (USNM 521519). FRENCH GUIANA: Cayenne, Kaw (MNHN 1986-322). GUYANA: Barima-Waini, Santa Cruz (ROM 98719).

Figure 65 - Dorsal, ventral and lateral views of the skull and lateral view of mandible of *Hylaeamys* *sp. nov.*, UF 30545, Rio Amapari, Amapá State, Brazil

Figure 66 – Known collection localities of *Hylaeamys* sp. nov. in Eastern Amazonia. Number of localities according to Gazetteer in Appendix A.

4.5 Phylogenetic relationship of Forest clade of Oryzomyini tribe

In the present study, the first split into the Forest clade appeared between *Nephelomys* and all other genera. That first split between Andean species and all other taxa into the clade was highly supported in all previous results (WEKSLER, 2006; PINE et al. 2012).

The next significant event is the cladogenesis between the genus *Hylaeamys* (red clade; Figure 67), and a clade composed by genera *Oecomys*, *Euryoryzomys* and *Transandinomys* (blue, gay and yellow clades, respectively; Figure 67), and *Oecomys* showed as sister to a clade formed by *Euryoryzomys* and *Transandinomys*. That arrangement is variable in the literature and always showed a lower support (>50%). In Percequillo et al. (2011) *Hylaeamys* and *Handleyomys* were sister groups. However, in the phylogeny showed by Pine et al (2012), *Hylaeamys* is the sister group of a clade that contained *Oecomys*, *Transandinomys* and *Euryoryzomys*, but despite these authors presented the same topology as the results showed here, they had a support lower than 50%.

The relationship between genera of the Forest clade varied a lot in previous phylogenetic trees. Weksler (2006) obtained a good support for the clades inside Oryzomyini, but not internal to each one of the four recognized clade. The author suggested that separate analysis of each clade with denser taxa sampling would enable a better resolution of this internal clades. My results, with denser taxonomic sampling and a more robust dataset, recovered a more stable topology, with much higher support for the internal nodes obtained.

The Andean taxon *Nephelomys* is sister to all other genera, including cis and trans Andean lineages. This suggests that the hypothesis advocated by Reig (1986) that the Andes is the Area of Original Differentiation of the tribe Oryzomyini is not totally out of context. Maybe it is not for the entire tribe, but the Andes may represent the ancestral area for the taxa on this Forest clade.

Nephelomys is the only Andean genus inside the forest clade (PRADO; PERCEQUILLO, 2013), the Trans-Andean genus, *Transandinomys*, showed as sister group of *Euryoryzomys*, a Cis-Andean genus. Machado et al. (2013) showed a similar result for the clade D of Oryzomyini. They suggested that the trans-andean taxa dispersed to cis-andean region, crossing the Andes through the extreme northern of South America continent. As the tree was not dated, I could not make any statement about this, but I should highlight that both clades of Oryzomyini tribe, forest clade and clade D, showed a similar phylogenetic pattern, where trans - Andean genera is sister group of cis-Andean genera. The hypothesis about the time and mode of dispersal to Trans-Andean areas by Oryzomyini tribe should be examined.

The genus *Hylaeamys* appeared as a monophyletic lineage, in agreement with Weksler, Voss and Percequillo (2006). These authors suggested that the pattern of carotid circulation (VOSS, 1988) was the morphological synapomorphy of the genus. Brace et al. (2015) investigating the diversification in Antillean Oryzomyine using mitochondrial DNA, proposed that the fossil genus *Antillomys* was the sister group of *Hylaeamys*. They estimated the mean divergence between *Antillomys* and *Hylaeamys* at 6.3 Ma. Machado et al. (2011) investigated the phylogeny of clade D, a clade with pentalophodont and tatalophodont species. The authors proposed that the crown age of diversification of the clade D was 3.31 Ma. Machado et al (2011) argued that the cis-Andean area was the ancestral area of diversification of tetralophodont species (diversification inside the clade D). According to the results showed here, the first split inside the forest clade was between an Andean lineage, *Nephelomys*, and cis and tras-Andean lineages, but without dating these cladogenetics events, we can think about two distinct scenarios: First, the ancestral of the Forest clade was already in South

America and disperse to Caribbean Islands, or, the ancestor arrived in South America through the Caribbean Islands, and diversificate there, before reach South America continent.

Figure 67 - Maximum Likelihood consensus tree of Forest clade of Oryzomyini. Number next to nodes is the bootstrap value. Locality of each sample is showed in brackets

5 CONCLUSIONS

Morphometric methods were not the most adequate tool to delimit the monophyly of the lineages of the genus *Hylaeamys*, but they were essential on the establishment of gaps throughout the geography and, hence, on the delimitation of taxa. Thus, they are and can be a powerful tool for species recognition, for samples that molecular data are not available. Moreover, cytogenetic and skull morphological characters can, also, be very efficient. Species of the genus *Hylaeamys* are quite polymorphic and can be better recognized by the application of multiple methods. Thus, I hypothesize that the genus is monophyletic and presents eight valid, diagnosable and monophyletic species; thus, rejecting the current hypothesis that the genus presents seven species.

Multi-loci molecular datasets represented a powerful method for the recognition of the genetic diversity observed in the genus. The molecular phylogenetic tree supported the monophyly of the genus, and also revealed more monophyletic lineages than presently recognize species. In respect to *Hylaeamys megacephalus*, recovered topology may reveal that its internal clades may have experimented cryptic differentiation (maybe speciation?): there is solid genetic variation on the geography (regarding samples from northern and southern bank of Rio Amazonas, and also samples from Rio Madeira); however, cytogenetic or morphologic were conservative within this clade, difficulting to diagnosis that genetic variation. Thus, there is still hidden diversity in the genus, that should be further tested to evaluate if it merits or not species recognition.

The analysis into the Forest clade, showed that the first split into the clade occurred between *Nephelomys*, the Andean genus of Forest clade, and all other genera. The second split put apart the genus *Hylaeamys* and all other genera, so, its sister group is a clade that contain cis and trans - Andean genera. These results showed that dispersions toward Andes Cordillera occurred after the clade pass through a first speciation process in South America.

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APPENDIX

Appendix A

Gazetteer of all *Hylaeamys* samples.

BOLIVIA

Cochabamba

- 1) Charuplaya, 1350 m, (MUSSE *et al.*, 1998). Type locality of *Oryzomys yunganus*, 16°36'S, 66°37'W.
- 2) 2 km E Villa Tunari. Not located; we used the geographic coordinates of Villa Tunari. *Hylaeamys perenensis*. 16°58'27''S, 65°25'15''W.

El Beni

- 3) 4 km opposite Costa Marques, Rio Iténez [= Rio Guaporé]. *Hylaeamys acritus*, 12°29'S, 64°15'W.
- 4) 7 km N Lagoinha, Rio Mamoré. *Hylaeamys acritus*, 11°53'S, 65°06'W.
- 5) 8 km N Exaltacion. Not located; we used the geographic coordinates of Exaltation. *Hylaeamys acritus*. 13°16'43''S, 65°14'24''W.
- 6) 17 km NNW of Nuevo Berlin. *Hylaeamys perenensis*, 12°41'S, 65°06'W.
- 7) 45 km by road N Yacuma. *Hylaeamys perenensis*. 14°42'S, 67°04'W.
- 8) Arruda [= Ríncon de Arruda]. *Hylaeamys perenensis*, 13° 03'S, 64° 47'59''W
- 9) Bahia de Los Casara, 20 km W Larangeiras, Rio Iténez. *Hylaeamys acritus*, 13°13'S, 62°21'W.
- 10) Baures [Includes Baures river mouth]. *Hylaeamys acritus*, 13°35'S, 63°35'W.
- 11) Boca do Rio Biata, 170 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 11°44'S, 66°47'W.
- 12) Camino Vildes, San Joaquin. Not located; we used the geographic coordinates of San Joaquin. *Hylaeamys perenensis*, 13°04'S, 64°48'W.
- 13) Campamento Busurucucu, Yacuma. *Hylaeamys perenensis*. 14°39'S, 66°17'W
- 14) Centenela [= Puerto Centenela ou Centinela], Rio Machupo, 1 mi E of San Joaquin. *Hylaeamys perenensis*, 13° 04'S, 64° 50'W.
- 15) Costa Marquez, Río Itenez. *Hylaeamys perenensis*. 12°29'S, 64°17'W
- 16) Curicha [= Çuricha], Iténez. *Hylaeamys acritus* and *Hylaeamys perenensis*. 12°37'S, 63°31'W.
- 17) El Refugio Pampa, 3 km NE from Camp. *Hylaeamys perenensis*. 14°44'35''S, 61°01'20''W.

- 18) El Refugio. *Hylaeamys perenensis*. 14°46'S, 61°01'05''W.
- 19) Estación Biológica de Beni, 300 m. *Hylaeamys perenensis*, 14°51'S, 66°21'W.
- 20) Lado E opposite Cascajal, Rio Mamoré. *Hylaeamys perenensis*, 12°13'S, 65°13'W
- 21) Lago Victoria, Iténez. *Hylaeamys perenensis*, 13°46'S, 63°30'W
- 22) Puerto Siles. *Hylaeamys acritus*. 12°48'38''S, 65°06'54''W.
- 23) Remanso [= Remansos], Rio Iténez. *Hylaeamys perenensis*, 13°34'S, 61°54'W
- 24) Rio Iténez. Pampa de Meio, *Hylaeamys acritus*, 12°30' S, 64°19' W.
- 25) Serrania Huachuca, Bosque Huachuca, Velasco Province. *Hylaeamys perenensis*. 14°31'23''S, 60°44'22''W.
- 26) Totaizal [= Totalisal], 1 km SW of Porvenir, Estação Biológica de Beni. *Hylaeamys perenensis*. 14°51'S, 66°21'W.
- 27) Warnes [Inlcudes Santa Rosita, 3 km SW de Warnes]. *Hylaeamys perenensis*. 18°31'43''S, 64°05'25''W
- 28) Yutioles, 3 leagues S San Joaquin. *Hylaeamys perenensis* and *Hylaeamys acritus*, 13° 15'S, 64° 48'W.

La Paz

- 29) 1 km E La Embocada [= Emboscada], Estância La Cabaña. *Hylaeamys perenensis*, 15°03'S, 67°00'W
- 30) 4 km NW by road of Alcoche. *Hylaeamys perenensis*. 15°40'S, 67°42'W.
- 31) 8 km from mouth of Rio Madidi. 240m. *Hylaeamys perenensis*. 12°34'S, 67°00'W.

Pando

- 32) Gargantua. *Hylaeamys perenensis*, 12°23'S, 68°35'W.
- 33) Independencia. *Hylaeamys perenensis*, 11°26'S, 67°34'W.
- 34) La Cruz. *Hylaeamys perenensis*, 11°24'S, 67°13'W.
- 35) Las Piedras, 170 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 11°02'S, 66°07'W.
- 36) Palmira. *Hylaeamys perenensis*, 11°42'S, 67°56'W.
- 37) Santa Rosa. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 12°13'S, 68°24'W.
- 38) West bank Rio Beni, before Hamburgo. *Hylaeamys perenensis*, 11°01'S, 66°06'W.

Santa Cruz

- 39) 2 km SW Las Cruces. *Hylaeamys perenensis*. 17°47'S, 63°22'W.
- 40) 3 km N San Rafael de Amboró, Rio Saguayo. *Hylaeamys perenensis*, 17°34'S, 63°42'W.
- 41) 4,5 km N and 1.5 km E Cerro Amboró, Rio Pitasama, 620 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 17°45'S, 63°40'W.
- 42) El Refugio, Parque Nacional Kempff Mercado, Provincia Velasco. *Hylaeamys acritus*. 14°46'02''S, 61°02'02''W.
- 43) El Refugio, Rio Paraguá/Tarvo [= Rio Turvo], right bank, Provincia Velasco, 200 m. *Hylaeamys perenensis*, 14°46'01''S, 61°02'02''W.
- 44) Lago Caiman, Provincia Velasco. *Hylaeamys acritus*, 13°35'S, 60°54'W
- 45) Los Fierros, Provincia Velasco. *Hylaeamys acritus*, 14°33'S, 60°55'W
- 46) Rio Mamoré, 2 km N of the Rio Chapare mouth. *Hylaeamys perenensis*, 15°57'S, 64°41'W.
- 47) Rio Pitasama, 4,5 km N and 1,5 km E of Cerro Amboro. *Hylaeamys perenensis*. 17°45'S, 63°40'W.
- 48) San Martín. *Hylaeamys acritus*, 14°19'S, 62°25'W
- 49) San Rafael de Amboró [Includes Río Sangayo]. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 17°36'S, 63°36'W
- 50) Toledo, Provincia Velasco. *Hylaeamys acritus*, 14°42'S, 61°09'W.
- 51) Urubicha, Rio Negro, Provincia Guarayos. *Hylaeamys acritus*, 14°58'S, 62°36'W

BRAZIL

Acre

- 52) BR 364, km 8, Manuel Urbano, Sena Madureira,. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 08°53'S, 69°18'W.
- 53) Igarapé Porongaba, right bank Rio Juruá. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 08°40' S, 72°47' W.
- 54) Nova Vida, right bank Rio Juruá. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 08°40'S, 72°49'W.
- 55) Ocidente, right bank Rio Juruá. *Hylaeamys yunganus*, 08°34' S, 72°48' W.

- 56) Oposite Igarapé Porongaba, left bank Rio Juruá. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 08°40' S, 72°47' W.
- 57) Sena Madureira [Includes Segundo Distrito (Niterói) and Bairro do Triângulo]. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 09°04'S, 68°40'W.
- 58) Seringal Triunfo, Plácido de Castro. *Hylaeamys perenensis*, 09°54'S, 66°38'W.
- 59) Sobral, left bank Rio Juruá. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 08°40'S, 72°49'W.

Alagoas

- 60) Estação Ecológica de Murici, Murici. *Hylaeamys oniscus*, 9°13'S, 35°53'W
- 61) Fazenda do Prata, 13 km SSW of São Miguel dos Campos. *Hylaeamys oniscus*. 09°53'S, 36°09'W.
- 62) Fazenda Santa Justina, 6 km SSE of Matriz de Camaragibe. *Hylaeamys oniscus*. 09°12'S, 35°30'W.
- 63) Mata de Coimbra, Usina Serra Grande, Ibateguara. *Hylaeamys oniscus*, 9°00'S, 35°51'W.
- 64) Mata do Cedro, Usina Utinga-Leão, Rio Largo. *Hylaeamys oniscus*, 9°31'S, 35°4'W.

Amapá

- 65) Calçoene, km 26, mata "Calçoene". *Hylaeamys megacephalus*, 02°30' N, 50°57'W.
- 66) Macapá, Rio Amapari. *Hylaeamys megacephalus*, 00°02'N, 51°03'W.
- 67) Serra do Navio. [Includes ICOMI; Igarapé do Ouro; C3; C5 and Km 190 Estrada de Ferro Amapá]. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 00°59'N, 52°04'W.
- 68) Terezinha, Rio Amapari, Serra do Navio. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 00°58'N, 52°02'W.

Amazonas

- 69) 80 km N Manaus, Projeto INPA/WWF-US MCSE (PDBFF), Reserva 34 2R11. *Hylaeamys megacephalus*, 02°25'S, 59°50'W.
- 70) Altamira, right bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°35'S, 68°54'W.
- 71) Barro Vermelho, left bank Rio Juruá. *Hylaeamys perenensis*, 06°28'S, 68°46'W.

- 72) Boa Esperança, right bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°32'S, 68°55'W.
- 73) Condor, left bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°45'S, 70°51'W.
- 74) Fazenda Esteio, acampamento florestal, 80 km N Manaus, INPA/WWF-US MCSE Project (PDBFF). *Hylaeamys megacephalus*, 02°30' S, 60°00' W.
- 75) Foz Igarapé Caititu, right bank Rio Uatumã [= Igarapé Caititu, right bank Rio Uatumã, near the mouth and right bank Rio Uatumã, near the mouth of the Igarapé Caititu]. Not located; we used the geographic coordinates of Rio Uatumã. *Hylaeamys megacephalus*, 02°35'S, 57°51'W.
- 76) Igarapé Nova Empresa, left bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°48' S, 70°44' W.
- 77) Ilha Paxiúba, right bank Rio Juruá. *Hylaeamys perenensis*, 03°19'S, 66°00' W.
- 78) Ilhazinha, Viravolta, left bank Rio Juruá in Igarapé Arabidi, tributary of the Paraná Breu [= Ilhazinha, Vira-Volta, left bank Lago Arabidi, left bank tributary Paraná Breu, left bank Rio Juruá]. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 03°17'S, 66°14' W.
- 79) Imediações da Comunidade Tambor, Parque Nacional do Jaú, left bank Rio Jaú. *Hylaeamys megacephalus*, 02°13'S, 62°26'W.
- 80) Jainú, right bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°28'S, 68°46'W.
- 81) Lago do Meduinin, left bank Rio Negro. *Hylaeamys megacephalus*, 01°47'S, 56°23'W.
- 82) Lago Vai Quem Quer, right bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 03°19' S, 66°01'W.
- 83) Macaco, left bank Rio Jaú. *Hylaeamys megacephalus*, 02°05'S, 62°07'W.
- 84) Manaus [Includes Estrada Manaus - Itacoatiara]. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 02°25'S, 59°50'W.
- 85) Oposite Altamira, left bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°35'S, 68°54'W.
- 86) Penedo, right bank Rio Juruá. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 06°50'S, 70°45'W.

- 87) Próximo a foz Igarapé Água Branca, left bank Rio Pitinga. Not located; we used the geographic coordinates of the mouth of Rio Pitinga. *Hylaeamys megacephalus*, 01°04'S, 59°34'W.
- 88) Reserva Ducke, Manaus. *Hylaeamys megacephalus*, 02° 52' S, 59° 59' W.
- 89) Rio Jaú right bank, above the mouth. *Hylaeamys megacephalus*, 01°57'54"S, 61°29'14"W.
- 90) Rio Katana-ú, 2,7km NNE Missão Marari, Barcelos. *Hylaeamys megacephalus*, 01°12'31''N, 64°47'21''W.
- 91) Sacado (Condor), right bank Rio Juruá. *Hylaeamys perenensis*, 06°45' S, 70°51'W.
- 92) Viravolta, left bank Rio Juruá in Igarapé Arabidi, tributary of Paraná Breu [= Vira-Volta, left bank Lago Arabidi, left bank tributary Paraná Breu, left bank Rio Juruá]. *Hylaeamys perenensis*, 03°17'S, 66°14'W.

Bahia

- 93) Companhia Agropecuária Sul Bahia, Fazenda Bulandeira Bradesco, Una. Not located; we used the geographic coordinates of Una. *Hylaeamys seuanezi*, 15°17'S, 39°04'W
- 94) Estação Ecológica Nova Esperança, Wenceslau Guimarães. *Hylaeamys seuanezi* 13°34'S, 39°42'W
- 95) Fazenda Almada, Rio do Braço, Ilhéus. Não encontrado. Foi utilizada a coordenada geográfica do Rio do Braço. *Hylaeamys seuanezi*, 14°41'S, 39°15'W.
- 96) Fazenda Bolandeira, 10 km S Una. *Hylaeamys seuanezi*, 15°21'S, 39°0'W
- 97) Fazenda Brejo Grande, 12 km S 1.7 km W of Itabuna by road, Itabuna. *Hylaeamys seuanezi*, 14°55'S, 39°17'W.
- 98) Fazenda Dendhevea, Una. *Hylaeamys seuanezi*, 15°14'S, 39°13'W.
- 99) Fazenda Jueirana, Una. *Hylaeamys seuanezi*, 15°12'S, 39°09'W.
- 100) Fazenda Limeira, Ilhéus. Not located; we used the geographic coordinates of Ilhéus. *Hylaeamys seuanezi*, 14°47'S, 39°02'W.
- 101) Fazenda Orion, Serra das Lontras, Arataca. *Hylaeamys seuanezi*, 15°07'S, 39°15'W.
- 102) Fazenda Subauma, Cairu. *Hylaeamys seuanezi*, 13°31'S, 39°02'W.
- 103) Fazenda Unacau, 8km SE São José. *Hylaeamys seuanezi*, 15°05'S, 39°21'W.
- 104) Gandu. *Hylaeamys seuanezi*, 13°44'S, 39°29'W.
- 105) Ilhéus. *Hylaeamys seuanezi*, 14°47'S, 39°02'W.
- 106) Mucugê. *Hylaeamys seuanezi*, 13° 00'19''S, 41° 22'15''W.

- 107) Parque Zoobotânico da Comissão Executiva do Plano de Lavoura Cacaueira (CEPLAC), 6km E of Itabuna by road, Itabuna [includes EDJAB – CEPLAC (Comissão Executiva do Plano de Lavoura Cacaueira); ESCAN; ESMAI – CEPLAC]. *Hylaeamys seuanezi*, 14°48'S, 39°20'W.
- 108) Pirataquissé, Banco da Vitória, Ilhéus. Not located; we used the geographic coordinates of Banco da Vitória. *Hylaeamys seuanezi*, 14°47'S, 39°06'W.
- 109) Reserva Biológica Pau-brasil, 15km NW de Porto Seguro [includes Fazenda Água Santa]. *Hylaeamys seuanezi*, 15°27'S, 39°39'W.
- 110) Reserva Biológica de Una, Una. *Hylaeamys seuanezi*, 15°17'S, 39°04'W.
- 111) RPPN [abbreviation of Reserva do Patrimônio Particular Nacional] Serra do Teimoso, Jussari. *Hylaeamys seuanezi*, 15°12'S, 39°29'W.
- 112) Ribeirão da Fortuna, Buerarema. Not located; we used the geographic coordinates of Buerarema. *Hylaeamys seuanezi*, 14°56'S, 39°19'W.
- 113) Urucutuca, Aritaguá, Ilhéus. Not located; we used the geographic coordinates of Aritaguá. *Hylaeamys seuanezi*, 14°42'S, 39°05'W.

Ceará

- 114) Serra de Maranguape, 919m. *Hylaeamys megacephalus*, 3°54'S, 38°43'W.

Distrito Federal

- 115) Brasília. *Hylaeamys megacephalus*, 15°47'S, 47°53'W.
- 116) Centro de Instrução e Adestramento de Brasília – Brasília, 1000-1170m. *Hylaeamys megacephalus*, 16°01'S, 47°57'W.
- 117) Parque Nacional de Brasília. *Hylaeamys megacephalus*, 15°40'S, 48°00'W.
- 118) Reserva Biológica de Águas Emendadas. *Hylaeamys megacephalus*, 15°33'S, 47°37'W.
- 119) Rio Capetinga, Brasília (Fazenda Água Limpa). *Hylaeamys megacephalus*, 15°49'S, 48°12'W.

Espírito Santo

- 120) Engenheiro Reeve - Matilde, Alfredo Chaves. *Hylaeamys megacephalus*, 20°33'S, 40°49'W.
- 121) Fazenda Santa Terezinha, 33 Km. NE of Linhares. *Hylaeamys seuanezi*, 19°12'S, 39°50'W.

- 122) Linhares [includes F. M. A Linhares]. *Hylaeamys seuanezi*, 19°25'S, 40°04'W.
 123) Santa Teresa. *Hylaeamys seuanezi*, 19°56'S, 40°36'W.

Goiás

- 124) 3 km east of Mambai. *Hylaeamys megacephalus*, 14°29' S, 46°08' W.
 125) Anápolis. *Hylaeamys megacephalus*, 16°19' S, 48°58' W.
 126) Cascatinha (SAMA), Minaçu. Not located; we used the geographic coordinates of Minaçu. *Hylaeamys megacephalus*, 13° 32' S, 48°13' W.
 127) Cerrado Alto, Catalão [includes Fazenda Cassiano, Vereda; UHE Bocaina; Fazenda Mancha Velha; Vau da Cruz]. Not located; we used the geographic coordinates of Catalão. *Hylaeamys megacephalus*, 18°10' S, 47°57' W.
 128) Davinópolis [Includes Cerrado Alto and Fazenda Nenzinha]. *Hylaeamys megacephalus*, 18°10'S, 47°35'W.
 129) Fazenda Bandeirantes, Rio Lageado, Baliza. Not located; we used the geographic coordinates of Baliza. *Hylaeamys megacephalus*, 16°15'W, 52°25'W.
 130) Fazenda Fiandeira, Parque Nacional de Chapada dos Veadeiros, 65 km SSW of Cavalcante. *Hylaeamys megacephalus*, 14°19'S, 47°45'W.
 131) Fazenda Taquari, Pouso Alto. Not located; we used the geographic coordinates of Pouso Alto [=Piracanjuba]. *Hylaeamys megacephalus*, 17°18'S, 49°01'W.
 132) Rio do Peixe, Rio Maranhão, Serra da Mesa. *Hylaeamys megacephalus*, 14°00'15''S, 48°23'40''W.
 133) Rio Tocantinzinho, Serra de Mesa. Not located; we used the geographic coordinates of Serra da Mesa. *Hylaeamys megacephalus*, 13°83'42''S, 48°18'15''W.
 134) Serra Negra, Rio Bagagem, Serra da Mesa. *Hylaeamys megacephalus*, 16°19'43''S, 52°18' 20''W.

Maranhão

- 135) Alto Parnahyba (=Alto Parnaíba), 400-600m. *Hylaeamys megacephalus*, 09°06'S, 45°57'W.
 136) Imperatriz. *Hylaeamys megacephalus*, 05°32'S, 47°29'W.

Mato Grosso

- 137) 30 Km ao redor de Gaúcha do Norte, Parantina, 460m. *Hylaeamys megacephalus*, 13°05'S, 53°17'W.
- 138) 30 km SSW Cláudia, 368m. *Hylaeamys megacephalus*, 11°35'S, 55°10'W.
- 139) 40 km ao redor de Cocalinho, 241m. *Hylaeamys megacephalus*, 14°16'S, 50°59'W.
- 140) 264 km N Xavantina, Serra do Roncador, 400 m. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 12°49'S, 51°46'W.
- 141) Cáceres. *Hylaeamys megacephalus*, 16°04'S, 57°41'W.
- 142) Cidade Laboratório de Humboldt, Aripuanã. *Hylaeamys megacephalus*, 09°10'S, 60°38'W.
- 143) Campus UNEMAT [abbreviation of Universidade Estadual do Mato Grosso], Nova Xavantina. *Hylaeamys megacephalus*, 14°43'S, 52°21'W.
- 144) Estação Ecológica Serra das Araras – Porto Estrela [= Serra das Araras, 65 km S of Barra do Bugres]. *Hylaeamys megacephalus*. 15°39'S, 57°12'W.
- 145) Estrada de acesso Fazenda Iberê [includes MT 242], Nova Ubiratã. *Hylaeamys megacephalus*, 13°05'49''S, 54°32'41''W.
- 146) Fazenda Altamira, Ponte Branca. Not located; we used the geographic coordinates of Ponte Branca. *Hylaeamys megacephalus*, 16°43'S, 52°47'W.
- 147) Fazenda Alto Cuiabá, Rosário Oeste. *Hylaeamys megacephalus*, 14°17'20''S, 55°02'14''W.
- 148) Fazenda Iberê, Nova Ubiratã. *Hylaeamys megacephalus*, 13°06'39''S, 54°25'50''W.
- 149) Fazenda Lagoa Bonita, 36 km N Barra do Garças, Barra do Garças, 331m. *Hylaeamys megacephalus*, 15°34'S, 52°21'W.
- 150) Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira, Ribeirão Cascalheira, 297m. *Hylaeamys megacephalus*, 12°38'S, 51°55'W.
- 151) Fazenda São Luis, 30 km N Barra do Garças, Barra do Garças, 389m. *Hylaeamys megacephalus*, 15°38'S, 52°21'W.
- 152) Fazenda Volpec, Cocalinho. *Hylaeamys megacephalus*, 12°57'41''S, 50°52'15''W.
- 153) Juruena. *Hylaeamys megacephalus*, 12°51'S, 58°55'W.
- 154) Mineração Caraíba, Nova Xavantina. *Hylaeamys megacephalus*, 14°37'31''S, 52°29'30''W.
- 155) Palmeiras (Monte Alegre). *Hylaeamys megacephalus*, 15°53'S, 55°24'W.
- 156) PCH Jesuíta, Rio Juruena. *Hylaeamys megacephalus*, 11°26'48''S, 58°39'W.

- 157) Reserva Biológica (ou Ecológica) Cristalino, 40 km N Alta Floresta, Alta Floresta, 360m. *Hylaeamys megacephalus*, 09°35'S, 55°55'W.
- 158) Salto do Utiarity, Rio Papagaio. *Hylaeamys megacephalus*, 13°02'S, 58°17'W.
- 159) Tapirapuan [=Itapirapuan]. *Hylaeamys megacephalus*, 14°51' S, 57°45' W.
- 160) UHE [abbreviation of Usina Hidrelétrica] Manso, 100 km N de Cuiabá. *Hylaeamys megacephalus*, 14°42'S, 56°02'W.
- 161) UHE [abbreviation of Usina Hidrelétrica] Manso, Rio Manso, Chapada dos Guimarães. *Hylaeamys megacephalus*, 14°52'S, 55°57'W.
- 162) Vila Rica, northeast of Mato Grosso. *Hylaeamys megacephalus*, 10°01'S, 51°07'W.

Mato Grosso do Sul

- 163) Balança Velha, 55 km W Dourados, Dourados, 518m. *Hylaeamys megacephalus*, 22°20'S, 55°18'W.
- 164) Fazenda Califórnia, Morraria do Sul, Bodoquena 520m. *Hylaeamys megacephalus*, 20°42'S, 56°52'W.
- 165) Fazenda Maringá, 54 km W Dourados, Dourados, 427m. *Hylaeamys megacephalus*, 22°16'S, 55°18'W.
- 166) Porto Faia. *Hylaeamys megacephalus*, 18°28'S, 57°22'W.
- 167) Salobra. *Hylaeamys megacephalus*, 20°11'S, 56°28'W.

Minas Gerais

- 168) Alto da Consulta, Poços de Caldas. *Hylaeamys megacephalus*, 21°47'S, 46°33'W
- 169) Coromandel [includes Cerrado do Gato Mourisco; Fazenda da Barra; Fazenda Marques; Mata da Abadia, ponte sobre o Rio Parnaíba]. *Hylaeamys megacephalus*, 18°28'S, 47°13'W.
- 170) Fazenda Caxambú, Lagamar. Not located; we used the geographic coordinates of Lagamar. *Hylaeamys megacephalus*, 18°10'S, 46°48'W.
- 171) Fazenda do Grotão, Araguari, Piracaíba. Not located; we used the geographic coordinates of Piracaíba. *Hylaeamys megacephalus*, 18°29'S, 48°26'W.
- 172) Ibiá BR 262, km 580. *Hylaeamys megacephalus*, 19°29'S, 46°32'W.
- 173) Lagoa Santa, 760m. Type locality of *O. laticeps*. *Hylaeamys megacephalus*, 19°37'S, 43°53'W.

- 174) Mata dos Adolfos, Pedrinópolis. Not located; we used the geographic coordinates of Pedrinópolis. *Hylaeamys megacephalus*, 19°30'S, 47°28'W.
- 175) Nova Ponte [includes Fazenda do Sr. Vasco Naves (Fazenda Varginha), Mata do Vasco e Mata Península]. *Hylaeamys megacephalus*, 19°08'S, 47°40'W.
- 176) Parque Acangau, Paracatú. Not located; we used the geographic coordinates of Paracatú. *Hylaeamys megacephalus*, 17°13'S, 46°52'W.
- 177) Parque Estadual do Rio Doce, 13 km E of Marliéria [=Parque Florestal Estadual do Rio Doce]. *Hylaeamys seuanezi*, 19°32'S, 42°32'W.
- 178) Parque Nacional Grande Sertão Veredas – Formoso, 700-800m. *Hylaeamys megacephalus*, 15°16'S, 45°52'W.
- 179) Passos. *Hylaeamys megacephalus*, 20°43'S, 46°36'W.
- 180) Perdizes [includes mata de galeria João Alonso e Cerrado João Alonso]. *Hylaeamys megacephalus*, 19°20'S, 47°17'W.
- 181) Rio Doce. *Hylaeamys seuanezi*, 20°14'S, 42°53'W.
- 182) Teófilo Otoni. *Hylaeamys megacephalus*, 17°52'S, 41°30'W.
- 183) Unaí. *Hylaeamys megacephalus*, 16°23'S, 46°53'W.

Pará

- 184) 8 km N and 75 km W Paragominas (Fazenda Uraim). *Hylaeamys megacephalus*, 02°55'S, 48°12' W.
- 185) 18 km S and 19 km W de Altamira (Agrovila da União). *Hylaeamys megacephalus*, 03°22'S, 52°23'W.
- 186) 20 km N and 30 km W of Marabá (near Itupiranga) [Includes 26 km N and 30 km W of Marabá, near Itupiranga, Gleba 5, lote 5]. *Hylaeamys megacephalus*, 05°07'S, 49°25'W.
- 187) 44 km S and 40 km E of Santarém (Curuá-Una). *Hylaeamys megacephalus*, 02°50'S, 54°22'W.
- 188) 52 km SSW Altamira, Rio Xingú, east bank [= Cachoeira do Espelho, Rio Xingú; Includes 54 km S, 150 km W of Altamira, Altamira (Gleba 61, Lote 02)]. *Hylaeamys megacephalus*, 03°39'S, 52°22'W.
- 189) 73 km N and 45 km W of Marabá (near Jatobal), Gleba 29, Lote 3. *Hylaeamys megacephalus*, 04°41'S, 49°32'W.
- 190) Belém. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 01°27'S, 48°29'W.

- 191) Bragança, Jandiaí, Caratatená [= Caratateua]. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 00°59'S, 46°43'W.
- 192) Bragança, Santa Maria [Includes Tracuateua [= Tracuatena]]. *Hylaeamys megacephalus*, 01°02'S, 46°54'W.
- 193) Capim [= São Domingos do Capim], BR 14, km 87. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 02°06'S, 47°34'W.
- 194) Capim [= São Domingos do Capim], BR 14, km 93 and 94. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 02°10'S, 47°35'W.
- 195) Chiqueirinho, right bank Rio Tocantins, 70 km S of Tucuruí. *Hylaeamys megacephalus*, 04°33'S, 49°28'W.
- 196) Coqueiral [Belém neighborhood], Belém. *Hylaeamys megacephalus*, 01°27'S, 48°29'W.
- 197) Estrada Santarém-Cuiabá, BR165, km 84, Santarém (includes km 217). *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 04°09'S, 55°40'W.
- 198) Extremo Sul Ilha Tocantins, Rio Tocantins, Tucuruí. *Hylaeamys megacephalus*, 04°28'S, 49°32'W.
- 199) Flexal, Itaituba-Jacareacanga, km 212, Itaituba [includes Itaituba, Itaituba-Jacareacanga, km 213, Flexal]. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°45'S, 57°23'W
- 200) Floresta Nacional Tapirapé-Aquiri, Marabá; área da Companhia Vale do Rio Doce em Carajás. *Hylaeamys megacephalus*, 05°48'S, 50°30'W.
- 201) Foz do Igarapé Tramalhetinho, right bank Rio Trombetas = Reserva Biológica do Rio Trombetas. *Hylaeamys megacephalus*, 01°11'19''S, 56°40'15''W.
- 202) Ilha Tocantins, Rio Tocantins, 75 km S and 18 km E of Tucuruí. *Hylaeamys megacephalus*, 04°24'S, 49°32'W.
- 203) Itaituba [Includes BR165, Santarém-Cuiabá, Zona Sul, km 446]. *Hylaeamys megacephalus*, 04°17'S, 55°59'W.
- 204) Itaituba, Rodovia Transamazônica, trecho Itaituba-Jacareacanga, km 200, near Flexal. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°45'S, 57°23'W.
- 205) Itaituba-Belomonte, Itaituba, km 52c. *Hylaeamys megacephalus*, 03°05'S, 51°46'W.
- 206) Monte Dourado. *Hylaeamys megacephalus*, 00°52'S, 52°31'W.
- 207) Oriximiná, Cachoeira Porteira, km 23. *Hylaeamys megacephalus*, 01°02'S, 57°09'W.

- 208) Oriximiná, Porto Trombetas, Rio Sacarazinho (km 43). Not located; we used the geographic coordinates of Porto Trombetas. *Hylaeamys megacephalus*, 01°28'S, 56°24'W.
- 209) Paragominas. *Hylaeamys megacephalus*, 02°56'S, 47°31'W.
- 210) Rio Tapacurazinho [= Rio Itapacurazinho], Itaituba, BR 230, km 25. *Hylaeamys megacephalus*, 04°16'S, 55°55'W.
- 211) Rodovia Transamazônica, km 19, Itaituba-Jacareacanga, Itaituba. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 04°20'S, 56°10'W.
- 212) Tiriós-Óbidos, 12 km of Guiana Holandesa. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 02°30'N, 56°W.
- 213) Utinga [Belém neighborhood], Belém. *Hylaeamys megacephalus*, 01°27'S, 48°29'W.

Paraíba

- 214) Fazenda Pacatuba, 10 km NE of Sapé. *Hylaeamys oniscus*, 07°02'S, 35°09'W.

Pernambuco

- 215) Saltinho, Rio Formoso [Includes EFLEX de Saltinho]. *Hylaeamys oniscus*, 8 °40'S, 35°09'W
- 216) São Lourenço [=São Lourenço da Mata], 28 to 60 m. Type locality of *Oryzomys oniscus*, 08°00'S, 35°03'W.

Rio de Janeiro

- 217) Fazenda União, Casimiro de Abreu. Type locality of *Hylaeamys seuanezi*, 22°25'S, 42°02'W
- 218) Reserva Biológica de Poço das Antas, Silva Jardim. *Hylaeamys seuanezi*, 22°35'S, 42°17'W.

Rondônia

- 219) Cachoeira Nazaré, left bank Rio Ji-Paraná. *Hylaeamys megacephalus*, 10°51'S, 61°56'W.
- 220) UHE [abbreviation of Usina Hidrelétrica] Samuel, [includes Rio Jamari, UHE Samuel, Samuel]. *Hylaeamys megacephalus*, 08°46'S, 63°24'W.

- 221) Margem direita do Rio Madeira, Abunã, UHE [abreviação de Usina Hidrelétrica] Jirau, Porto Velho. *Hylaeamys yungannus*, *Hylaeamys megacephalus* and *Hylaeamys perenensis*, 9°42'S, 65°21'W.

São Paulo

- 222) Barretos. *Hylaeamys megacephalus*, 20°33'S, 48°33'W.
 223) Fazenda Sete Lagoas, Mogi Guaçu. *Hylaeamys megacephalus*, 22°13'S, 47°11'W.
 224) Itapura. *Hylaeamys megacephalus*, 20°38'S, 51°30'W.
 225) Ituverava. *Hylaeamys megacephalus*, 20°21'S, 47°46'W.
 226) Presidente Prudente. *Hylaeamys megacephalus*, 22°07'S, 51°23'W.
 227) Rio Feio. Also spelled Rio Aguapeí; specimens collected near Cancã. *Hylaeamys megacephalus*, 22°01'S, 49°39'W.
 228) Teodoro Sampaio. *Hylaeamys megacephalus*, 52°10'S, 22°31'W.

Tocantins

- 229) Paranã, *Hylaeamys megacephalus*, 12°36'58''S, 47°53'01''W.
 230) Peixe. *Hylaeamys megacephalus*, 12°03'S, 48°32'W.
 231) Rio da Palma right bank, upstream of the confluence of the rivers Palma e Paranã, Paranã. *Hylaeamys megacephalus*, 12°35'S, 47°52'W.
 232) Rio Santa Teresa, 20 km NW Peixe, Peixe, 205 m. *Hylaeamys megacephalus*, 11°50'S, 48°38'W.

COLOMBIA

Caquetá

- 233) Rio Caquetá, La Taqua, Tres Troncos, 185 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 00°08'N, 74°41'W.

Cundinamarca

- 234) Guaicaramo, 600-700 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 04°43'N, 73°02'W.
 235) Mámbita. *Hylaeamys perenensis*, 04°46'N, 73°19'W.

Meta

- 236) El Parque La Macarena [Parque Nacional Natural La Macarena], 0.5 km W of Cabaña Duda, 200 m [includes Camp Izawa]. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 02°33'N, 74°02'W.
- 237) La Macarena [Serrania de], Pico Renjifo, 4500 ft. *Hylaeamys yunganus*, 03°06'N, 73°55'W.
- 238) Villavicencio, 500m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 04°09'N, 73°37'W.

Putumayo

- 239) Rio Mecaya, 185 m. *Hylaeamys perenensis*, 00°28'N, 75°20'W.

ECUADOR

Napo

- 240) Avila. *Hylaeamys perenensis*, 00°38'S, 77°25'W
- 241) Laguna Grande, Rio Cuyabano, 210 m. *Hylaeamys perenensis*, 00°00'S, 76°11'W.
- 242) Limóncocha. *Hylaeamys perenensis*, 00°25'S, 76°38'W.
- 243) Llunchi, 250 m. *Hylaeamys yunganus* e *Hylaeamys perenensis*, 00°37'S, 76°46'W.
- 244) Parque Natural (PN) Yasuni, [includes 42 km S, 1 km E Pompeya Sur and El Saladero, 76 km S Pompeya]. *Hylaeamys yunganus*, 1°05'S, 75°55'W.
- 245) Rio Suno Abajo [includes abajo Loreto]. *Hylaeamys perenensis*, 00°48'S, 77°25'W.
- 246) San Francisco, Aguarico, 200m [includes Intillama]. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 00°30'S, 76°22'W.
- 247) San Jose Abajo [also spelled San José Nuevo; see Musser et al., 1998], 250 m. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 00°26'S, 77°20'W
- 248) San Jose de Payamino, 300 m. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 00°30'S, 77°19'W.
- 249) Volcán Sumaco. *Hylaeamys yunganus*, 00°34'S, 77°38'W.

Pastaza

- 250) Canelos (530 m). *Hylaeamys perenensis*, 01°35'S, 77°45'W
- 251) Mera, 1140 m. *Hylaeamys tatei*, 01°28'S, 78°08'W.
- 252) Río Capahuari, [see Musser et al., 1998]. *Hylaeamys yunganus*, 01°55'S, 77°20'W.

- 253) Río Copotaza, Oriente. *Hylaeamys perenensis*, 2°07'15''S, 77°25'49''W.
 254) Río Tigre, 1000 and 2000 ft. *Hylaeamys yunganus*, 02°07'S, 76°04'W.
 255) Río Yana Rumi [= Río Yanarumiyacu]. *Hylaeamys yunganus*, 01°38'S, 76°59'W.
 256) Sarayacu. *Hylaeamys perenensis*, 01°44'S, 77°29'W.
 257) Oriente, Avila. *Hylaeamys perenensis*, 2°00'S, 77°00'W.
 258) Provincia Tiguino, 130 km. S of Coca. *Hylaeamys perenensis*. 01° 07'S, 76° 57'W.

Tungurahua

- 259) Mirador, 15 mi E Baños, 5000 ft. *Hylaeamys tatei*, 01°26'S, 78°15'W.
 260) Palmera, 4000 ft [1300 m]. *Hylaeamys tatei*, 01°25'S, 78°12'W.

Zamora-Chinchipe

- 261) Zamora, 3250 ft. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 04°04'S, 78°58'W.

FRENCH GUIANA

Cayenne (Arrondissement)

- 262) Cacao, 24 m. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 04°35'N, 52°28'W.
 263) Île de Cayenne, sea level [includes Rorota]. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 04°50'N, 52°20'W
 264) Kaw, 100 m. *Hylaeamys yunganus* e *Hylaeamys megacephalus*, 04°29'N, 52°02'W.
 265) Paracou (Domaine Experimental Paracou), 15 km by road SSE Sinnamary and 5km by road WNW Kourou, 10 - 45 m. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°17'N, 52°55'W.
 266) Río Arataye, 30 m. *Hylaeamys megacephalus*, 04°00'N, 52°40' S.
 267) Säul. *Hylaeamys megacephalus*, 03°37'N, 53°12'W.

GUYANA

Barima-Waini

- 268) Baramita, Old World. *Hylaeamys megacephalus*, 07°22'N, 60°29'W.
 269) Kwabana. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 07°34'N, 59°09'W.

270) Santa Cruz. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 07°40'N, 59°14'W.

271) Waikerebi. *Hylaeamys megacephalus*, 07°31'N, 59°23'W.

Mazaruni-Potaro

272) Kartabu Point. *Hylaeamys megacephalus*, 06°23'N, 58°41'W.

273) Minehaha Creek, 500 ft. *Hylaeamys megacephalus*, 05°08'N, 59°07'W.

Upper Takuku-Upper Essequibo

274) 50 km SWW Gunn's Strip, Rio Kamoá. *Hylaeamys megacephalus*, 01°32'N, 58°50'W.

275) 55 km SW Gunn's Strip, Rio Chodikar. *Hylaeamys megacephalus*, 01°22'N, 58°46'W.

Upper Demerara-Berbice

276) Georgetown. *Hylaeamys megacephalus*, 06°48'N, 58°10'W.

Potaro-Siparuni

277) 30 km NE Surama [Includes 40 km SSW Hurupuhari (or Kurupuhari), Gorge camp, Reserva Iwderama], Rupununi. *Hylaeamys megacephalus*, 04°20'N, 58°51'W.

278) Kabukalli, Floresta Iwokrama. *Hylaeamys megacephalus*, 04°17'N, 58°31'W.

279) First plateau camp (1130 m). *Hylaeamys yunganus*. 05°07'N, 59°49'W.

PARAGUAY

Amambay

280) 4 km by road SW Cerro Corá. *Hylaeamys megacephalus*, 25°15'S, 55°59'W.

281) 28 km SW of Pedro Juan Caballero. *Hylaeamys megacephalus*, 22°43'S, 55°56'W.

Caaguazu

282) 22.5 km N Coronel Oviedo by road [Coronel Oviedo]. *Hylaeamys megacephalus*, 25°25'S, 56°27'W.

Canediyu

- 283) 13.3 km N of Curuguaty, by road. Type locality of *Mus megacephalus*, *Hylaeamys megacephalus*, 24°22'S, 55°42'W.
- 284) Colônia Chupa Pau [Includes Estancia Felicidad]. *Hylaeamys megacephalus*, 24°09'S, 55°42'W.
- 285) Igitimi. *Hylaeamys megacephalus*, 24°05'S, 55°30'W.

San Pedro

- 286) Ganadera Jelvi, 1.8 km SE of las casas. *Hylaeamys megacephalus*, 24°07'S, 56°25'W.
- 287) Ganadera La Carolina, 745 m of las casas. *Hylaeamys megacephalus*, 24°05'S, 56°25'W.

Paraguari

- 288) Tacuati, Aca Poi. *Hylaeamys megacephalus*, 23°27'S, 56°35'W.

PERU

Amazonas

- 289) 43 Km NE Chiriaco (by rd, ca cl. 1050 ft). *Hylaeamys perenensis*, 13°41'24''S, 73°29'18''W.
- 290) Comunidad Aguaruna, Imaza, Imacita, Bagua. Not located; we used the geographic coordinates of Imaza. *Hylaeamys perenensis*, 04°59'35''S, 78°23'08''W.
- 291) Headwaters of Rio Kagka, Rio Cenepa. *Hylaeamys perenensis*. 04°16'S, 78°10'W.
- 292) Huampami (includes Vicinity of Huampami), Rio Cenepa. *Hylaeamys perenensis*, 4°14'26''S, 78°5'37''W.
- 293) La Poza, Rio santiago (180 m). Not located; we used the geographic coordinates of Rio Santiago. *Hylaeamys perenensis*, 3°48'39''S, 77°53'15''W.
- 294) Pto Tunduza, Nieva, Condorcanqui, Amazonas, PE. Not located; we used the geographic coordinates of Nieva. *Hylaeamys perenensis*, 4°50'44''S, 77°55'49''W.
- 295) Rio Santiago mouth. *Hylaeamys yunganus*, 04°27'S, 77°38'W.
- 296) Shimpants (shimpants), Rio Cenepa. Not located; we used the geographic coordinates of Rio Cenepa. *Hylaeamys perenensis*, 4°39'02''S, 78°08'46''W
- 297) Tseasim, (Aguaruna Village) head wafers Rio Huampanm, north of Huampami, Rio Cenepa. *Hylaeamys perenensis*, 4°27'24''S, 78°10'06''W.

298) Yambra, 10 m N de Corosha, 6500 ft. *Hylaeamys yunganus*, 05°50'S, 77°54'W.

299) Yambrashamba, 6500 ft. *Hylaeamys yunganus*, 05°45'S, 77°54'W.

Ayacucho

300) San José, on Rio Santa Rosa, 3300 ft. *Hylaeamys yunganus*, 12°44'S, 73°46'W.

301) Santa Rosa, on Rio Santa Rosa, 800 m. *Hylaeamys yunganus*, 12°42'S, 73°44'W.

302) Hacienda Luisiana, Rio Apurimac, (600 m). Not located; we used the geographic coordinates of Rio Apurimac. *Hylaeamys perenensis*, 12°15'52''S, 73°58'21''S.

Cuzco

303) 72 Km. NE Paucartambo (by rd, Km. 152), 1460 m. *Hylaeamys perenensis*, 13°10'S, 71° 25'W.

304) Bosque Aputinye, above Huyro; 6000 ft. *Hylaeamys perenensis*, 13° 00'S, 72° 31'48''W.

305) Cadena, 1000 m. *Hylaeamys yunganus*, 13°24'S, 70°43'W.

306) Camisea, La convención, [includes Armihuari, Cashiriari, Konkariari, Pagoreni, San Martin e Segakiato]. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 11°43'02''S, 72° 56'43''W.

307) Catarata. *Hylaeamys perenensis*, 12°32'10''S, 73°46'13''W.

308) Consuelo, 15.9 km SW Pilcopata. *Hylaeamys yunganus*, 13°01'25''S, 71°29'30''W.

309) Kiteni, Rio Urubamba. *Hylaeamys perenensis*, 12°20' S, 72°50' W.

310) Marcapata [Inlcudes Hacienda Cadena and Road KM E. Quincemil]. *Hylaeamys yunganus*, 13°38'23''S, 70°54'46''W.

311) Quincemil, 680 m. *Hylaeamys yunganus*, 13°16'S, 70°38'W.

312) Santa Ana, 3500 ft. *Hylaeamys yunganus*, 12°52'S, 72°43'W.

Huánuco

313) Cerros del Sira, 1120 m. *Hylaeamys yunganus*, 09°28'S, 74°46'W.

314) Chinchao, 5700 ft. *Hylaeamys yunganus*, 09°38'S, 76°04'W.

315) Hacienda Exito, Rio Cayumba, (3000 ft.). *Hylaeamys perenensis*, 9°26'S, 70°00'W.

- 316) Rio Chinchao, Hacienda Buena Vista, 3500 ft. *Hylaeamys yunganus*, 09°30'S, 75°56'W.
- 317) Rio Pachitea. *Hylaeamys yunganus*, 08°46'S, 74°32'W.
- 318) Hacienda Santa Ekna, 35 Km. NE Tingo Maria. Not located; we used the geographic coordinates of Tingo Maria. *Hylaeamys perenensis*, 9° 17'46''S, 75° 59'54''W.

Junin

- 319) Amable María. *Hylaeamys perenensis*, 11°10'S, 75°10'W.
- 320) Capitiri. *Hylaeamys perenensis*, 11° 05'50''S, 73° 42'55''W.
- 321) Naranjal. *Hylaeamys perenensis*, 11°08'45''S, 75°26'42''W.
- 322) Perené, 800m. Type locality of *Oryzomys perenensis*, 10°58'S, 75°13'W.
- 323) San Ramón. *Hylaeamys perenensis*, 11°09'25''S, 75°24'18''W.

Loreto

- 324) 1 km. above Rio Tigrillo, Nauta. *Hylaeamys perenensis*, 4°33'16''S, 74°56'38''W.
- 325) Boca Rio Peruato, Rio Amazonas (90m). *Hylaeamys perenensis*, 3° 42'S, 78° 28'59''W.
- 326) Cerros de Canchaguaya, Sierra de Contamana. *Hylaeamys perenensis* and *Hylaeamys yunganus*. 7°11'20''S, 74°56'53''W.
- 327) Collpa Salvador margen derecha del Rio Pucacuro, Departamento Tigre. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 2°37.93'S, 75°08.65'W.
- 328) Cocha Coconilla, margen izquierda del Rio Pucacuro, Departamento Tigre. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 2°42.28'S, 75°05.94'W.
- 329) Huachi. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 03°25'S, 76°20'W.
- 330) Lagunas, lower Huallaga. *Hylaeamys perenensis*, 4°41'16''S, 75°57'45''W.
- 331) Margen derecho do rio Curaray, a 50 km SO de la Base Militar Arica. Not located; we used the geographic coordinates of Arica. *Hylaeamys perenensis*, 1°35'22''S, 75°11'47''W.
- 332) Rio Samiria, Nauta, Santa Elena (1300 m). *Hylaeamys perenensis*, 4°43'15''S, 74°21'22''W.
- 333) Rio Curaray mouth, 140 m. *Hylaeamys yunganus*, 02°22'S, 74°05'W.

- 334) Quebrada Agua Negra. *Hylaeamys perenensis*, 3°06'53''S, 74°48'48''W.
- 335) Requena, Centro de Inverigaciones Jenaro Herrera. *Hylaeamys yunganus*, 5°19'42''S, 73°52'56''W.
- 336) Ullpayacu, aprox. 5 kms ao NO de la Boca del Rio Pastaza. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 4°38'51''S, 76°35'10''W.
- 337) Yaneyaku, Yurimaguas, Not located; we used the geographic coordinates of Yurimaguas. *Hylaeamys perenensis*. 5°54'07''S, 76°07'20''W.

Madre de Dios

- 338) Albergue, 200 m. elev. (includes albergue 20 Km E de Puerto Maldonado). Not located; we used the geographic coordinates of Puerto Maldonado. *Hylaeamys perenensis*, 12°35'36''S, 69°11'21''W.
- 339) Alto Rio Madre de Dios [includes Hacienda Amazonia, Hacienda Eika] (ridge above 825 m). *Hylaeamys perenensis*, 12°17'S, 70°52'W.
- 340) Boca Rio Inambari. *Hylaeamys perenensis*, 12° 30'S, 69° 05'W.
- 341) Itahuania. *Hylaeamys perenensis*, 12° 37'53''S, 71° 13'41''W.
- 342) Mouth of Quebrada Juliaca, Rio Heath, 50 Km S Pto. Pardo (525 m) [includes Pampas de Heath]. Not located; we used the geographic coordinates of Rio Heath. *Hylaeamys perenensis*, 12°31'S, 68°38'W.
- 343) Parque Nacional del Manu [includes Puesto de Vigilancia Blanquillo e Pakitza]. *Hylaeamys perenensis*, 11°51'23''S, 71°43'17''W.
- 344) Reserva Cuzco Amazónico, 200 m. *Hylaeamys yunganus*, 12°33'S, 69°03'W.
- 345) Reserva Cusco Amazónico, 15 km NE de Puerto Maldonado. *Hylaeamys perenensis*, 12°35'S, 69°05'W.

Pasco

- 346) Chalhuapuquio. *Hylaeamys perenensis*, 10°29'21''S, 76°34'34''W.
- 347) Cordillera El Sira, Oxapampa. *Hylaeamys perenensis*, 10°05'S, 74°27'W.
- 348) Delfin, Oxapampa. 810 m. *Hylaeamys yunganus*. 10°06'48.6''S, 75°32'21.5''W.
- 349) Eneñas, 5000 ft. *Hylaeamys yunganus*, 10°45'S, 75°14'W.
- 350) Huancabamba. *Hylaeamys perenensis*, 10° 26'49''S, 75° 36'40''W.
- 351) Nevati Mission, San Pablo. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 10°27'S, 74°52'W.

352) Pozuzo, 1000 m. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 10°04'S, 75°32'W.

353) Poyeni. *Hylaeamys perenensis*, 11°15'24''S, 73°40'05''W.

354) Shiringamazu, carretera a Iscosazin. *Hylaeamys yunganus*, 10°15'40''S, 75°07'41''W.

Puno

355) Moyobamba, 2800 ft. *Hylaeamys yunganus* and *Hylaeamys perenensis*, 06°03'S, 76°58'W.

356) Puente Candamo, Carabaya. Not located; we used the geographic coordinates of Carabaya. *Hylaeamys perenensis*, 13° 50'S, 70° 15'W.

357) Rio Inambari, 1000 m. *Hylaeamys yunganus*, 13°53'S, 69°40'W.

San Martín

358) Puca Tambo, 5100 ft. *Hylaeamys yunganus*, 06°10'S, 77°16'W.

359) Rioja, 842 m. *Hylaeamys yunganus*, 06°05'S, 77°09'W.

360) Uscho [=Uchco], 50 m E Chachapoyas, 5000 ft. *Hylaeamys yunganus*, 06°11'S, 77°13'W.

Tumbes

361) P-V- Cotrina, Campo Verde, Zarumilla. *Hylaeamys perenensis*, 3°49'S, 80°11'W.

Ucayali

362) Balta, Rio Curanja, 300 m. *Hylaeamys perenensis* and *Hylaeamys yunganus*, 10°06'S, 71°14'W.

363) Yarinacocha, Ucayali. *Hylaeamys perenensis*, 8°14'55''S, 74°39'24''W.

SURINAME

Brokopondo

364) Loksie Hatti, Rio Saramacca. *Hylaeamys megacephalus*, 05°09'N, 55°28'W.

365) Finisanti, Rio Saramacca. *Hylaeamys megacephalus*, 05°09'N, 55°28'W.

Marowijne

366) 4 km N, 10 km W Albina. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°30'N, 54°03'W.

367) Mongotapoe, bank Wia-wia. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°35'N, 54°15'W.

368) Rio Paloemeu airstrip-Tapanahoni. *Hylaeamys megacephalus*, 03°19'N, 55°22'W.

Para

369) Groot Poika, Acarami Creek. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 05°25'N, 55°30'W.

Saramacca

370) La Poule. *Hylaeamys megacephalus*, 05°46'N, 55°25'W.

371) Lelydorpplan. *Hylaeamys megacephalus*, 05°37'N, 55°12'W.

372) Dirkshoop. *Hylaeamys megacephalus*, 05°46'N, 55°28'W.

Sipaliwini

373) Kaiser Gebergte (Kaiserberg) Airstrip, Rio Zuid. *Hylaeamys megacephalus* and *Hylaeamys yunganus*, 03°06'N, 56°28'W.

374) Lawa Mision. *Hylaeamys megacephalus*, 02°01'N, 56°07'W..

375) Tafelberg, below Geyskes Creek [Includes SE of Arrowhead Valley, Augustis Creek]. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 03°56'N, 56°11'W.

376) Wilhelmina Mts. *Hylaeamys megacephalus*, 03°45'N, 56°30'W.

Surinam

377) Powakka. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 05°27'N, 55°04'W.

TRINIDAD & TOBAGO

Trinidad

378) Bush Bush forest, Nariva swamp. W. G. Downs (col.). October 1960. AMNH. *Hylaeamys megacephalus*, 10°24'N, 61°03'W.

379) Caparo. *Hylaeamys megacephalus*, 10°27'N, 61°19'W.

380) Caura. *Hylaeamys megacephalus*, 10°22'N, 61°21'W.

- 381) Maingot Estate, 5 miles of Sangre Grande. *Hylaeamys megacephalus*, 10°34'N, 61°04'W.
- 382) Princetown. *Hylaeamys megacephalus*, 10°16'N, 61°22'W.
- 383) San Rafael. *Hylaeamys megacephalus*, 10°34'N, 61°16'W.

VENEZUELA

Amazonas

- 384) Brazo Casiquiare (250 m) of El Merey. *Hylaeamys megacephalus*, 03°05'N, 65°55'W.
- 385) Base camp of Cerro Neblina, 140 m, Rio Mawarinuma. *Hylaeamys megacephalus*, 00°50'N, 66°10'W.
- 386) Cerro Duida, Agüita (3250 ft). *Hylaeamys yunganus*. 3°25'S, 65°40'W.
- 387) Monte Duida, La Esmeralda. *Hylaeamys megacephalus*. 03°09'53''S, 65°33'05''W.
- 388) Rio Clearwater, 2 km SE base camp of Cerro Neblina. *Hylaeamys megacephalus*, ca. 00°49'N, 66°10'W.
- 389) Tamatama, Rio Orinoco, 135 m. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 03°10'N, 65°49'W.

Bolivar

- 390) Arabopó. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 05°06'N, 60°44'W.
- 391) Auyán Tepui. *Hylaeamys yunganus* and *Hylaeamys megacephalus*, 05°45'N, 62°30'W.
- 392) El Manaco, 59 km Se El Dorado. *Hylaeamys megacephalus*. 06°17'N, 61°19'W.
- 393) San Ignacio de Yuruani; 850 m. *Hylaeamys megacephalus*, 05°02'N, 61°08'W.

Sucre

- 394) Campo Alegre. Type locality of *O. modestus*. *Hylaeamys megacephalus*, 10°10'N, 63°45'