The genus *Hylaeamys* Weksler, Percequillo, and Voss 2006 (Rodentia: Cricetidae: Sigmodontinae) in the Brazilian Atlantic Forest: geographic variation and species definition

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The genus *Hylaeamys* Weksler, Percequillo, and Voss 2006 (Rodentia: Cricetidae: Sigmodontinae) in the Brazilian Atlantic Forest: geographic variation and species definition

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Seven species are included in the genus *Hylaeamys*. Their limits and distribution, however, are uncertain. We used morphometric analyses performed in univariate (Dice–Leraas diagrams) and multivariate (size-free principal component analysis) approaches, along with qualitative analysis, as well as information on the karyology, to make an assessment on the status of populations of the genus in the Atlantic Forest. On the basis of the evidence we found, it was possible to corroborate the hypothesis that there are actually 2 species in this biome: *H. oniscus*, a species distributed on the northern bank of the São Francisco River, from the State of Alagoas to the State of Paraíba; and *H. seuanezi*, which occurs on the southern bank of the São Francisco River, from the southern portion of Bahia State to the northern part of Rio de Janeiro State. *Hylaeamys laticeps*, the name formerly used for this entity, was allocated to the synonymy of *H. megacephalus*, a species that inhabits the Cerrado and Amazon Forest biomes. *Hylaeamys oniscus* exhibits a longer and more robust skull, with a longer rostrum and the 1st upper molar narrower, and a karyotype with 2n = 52 chromosomes and fundamental number (FN) = 62 autosomic arms, whereas *H. seuanezi* is smaller and more delicate, with a karyotype of 2n = 48 and FN = 60. The São Francisco River and the associated dry vegetation probably have played an important role in the origin of these species and today may still play a role as a barrier to gene flow between these species.

Key words: cytogenetics, geographic variation, morphology, morphometry, Oryzomyini, South America, taxonomy

Weksler et al. (2006) described the genus *Hylaeamys* for the species formerly associated with the *Oryzomys capito* complex or the *megacephalus* group (genus *Oryzomys*, sensu Musser et al. 1998; Weksler et al. 1999; Patton et al. 2000; Weksler 2006), on the basis of evidence that species of this new genus share a common ancestor on the basis of external and cranial traits, morphometrics, karyotype, and DNA sequences. These authors attributed 7 species to the genus *Hylaeamys*, namely: *H. acritus* (Emmons and Patton 2005), *H. laticeps* (Lund 1840), *H. megacephalus* (Fischer 1814), *H. oniscus* (Thomas 1904), *H. perenensis* (Allen 1901), *H. tatei* (Musser et al. 1998), and *H. yunganus* (Thomas 1902). These species are distributed throughout the moist (evergreen and semievergreen) forests of cis-Andean tropical and subtropical lowlands and foothills (to about 1,500 m above sea level), from Venezuela and Guyana southward through the Amazon, and the Atlantic rain forest from eastern Brazil to eastern Paraguay (Weksler et al. 2006).

In the Brazilian Atlantic Forest, there is an apparent consensus that 2 species of *Hylaeamys* are present, but no agreement regarding the name that should be applied to them: *H. oniscus* (Thomas 1904) and *H. laticeps* (Lund 1840), according to Weksler et al. (2006); or *H. oniscus* (Thomas 1904) and *H. seuanezi* (Weksler et al. 1999), as suggested by Weksler and Percequillo (2011). In fact, for a long time, the taxonomy of samples of *Hylaeamys* from the Atlantic Forest was unstable: for instance, Hershkovitz (1960) has given the name *O. capito* (Olfers 1818; = *O. megacephalus*, sensu Musser et al. 1998) for specimens of *Hylaeamys* from western

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and eastern Amazonia, Cerrado, and Atlantic Forest, and even for species presently allocated in other Oryzomyini genera. Therefore, there are specific epithets that had been consistently applied for the populations that inhabit the Brazilian Atlantic Forest: *laticeps*, *oniscus*, and *seuanezi* (Musser et al. 1998; Weksler et al. 1999, 2006; Weksler and Percequillo 2011; see detailed taxonomic history below). There are other available specific epithets of the species-group taxa that could be assigned to Atlantic Forest taxa, as *megacephalus* (Fischer 1814—considering the broad concept of *O. capito* advocated by Hershkovitz 1960) and *saltator* (Winge 1887).

Considering that the delimitation and distribution of *Hylaeamys* species that occur in the Atlantic Forest are still uncertain, we endeavored to test the current hypothesis (addressed by Weksler et al. 2006 and Weksler and Percequillo 2011) that 2 species of the genus occur in this biome, and to evaluate what should be the available name to be applied to these species. To accomplish this, we performed a thorough comparative analysis of the geographical variation among the populations of *Hylaeamys* in the Atlantic Forest of Brazil.

MATERIALS AND METHODS

Specimens.—We examined specimens deposited in the following collections: The Natural History Museum (BMNH), London, United Kingdom; Zoological Museum of Copenhagen (ZMC), Copenhagen, Denmark; Museu Nacional da Universidade Federal do Rio de Janeiro (MN), Rio de Janeiro, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; National Museum of Natural History (NMNH), Washington, D.C.; Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Brazil; Universidade Federal da Paraíba (UFPB), João Pessoa, Brazil; Universidade Federal de Pernambuco (UFPE), Recife, Brazil; Universidade de Brasília (DZUnB), Brasília, D.F., Brazil; University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan.

Cranial measurements.—We have recorded the following cranial and dental dimensions, following Voss (1988) and Musser et al. (1998), directly from the skull, using a dial caliper to the nearest 0.01 mm. Condylo-incisive length (CIL): measured from the greater curvature of the upper incisor to the articular surface of the occipital condyle, on the same side of the skull. Length of diastema (LD): measured from the crown of the 1st 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 1st upper molar to the posterior surface of the 3rd upper molar, at the crown of the molars. Breadth of 1st upper molar (BM1): breadth of the 1st upper molar, measured on the basal portion of the molar crown, at the level of the paracone–protocone 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 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 nasofrontal 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): shortest distance between the anterior and posterior margins of the inferior zygomatic root or zygomatic plate. Orbital fossa length (OFL): greatest dimension of the orbital fossa between the squamosal and maxillary roots of the zygomatic arch.

Gazetteer.—Localities and geographical coordinates were taken from the original and museum labels attached to specimens; when geographical coordinates were not available, we used other sources (Rodrigues et al. 1989; Paynter and Traylor 1991; U.S. Board on Geographic Names 1994; Geonames 2004; Roda and Santos 2005). The gazetteer, ordered alphabetically by country, state or province, and collection locality, is provided in Appendix I.

Age and sex variation.—We classified specimens in 5 age classes according to the eruption and wear of the occlusal surface of the molars, following Voss (1991) and Percequillo (1998). Age class 1: 1st and 2nd molars with no apparent wear; 3rd molar usually nonerupted or newly erupted with main cusps still closed; labial lophs well developed and isolate; labial and lingual flexus deep and distinct. Age class 2: 1st and 2nd molars with minor wear, with small exposure of dentine, 3rd molar already showing minimal to moderate wear; anteroloph and mesoloph may be connected to paracone, through marginal lophules; posteroloph nearly fused to metacone, marginally. Age class 3: 1st and 2nd molars with moderate wear, 3rd molar with marked wear, and a nearly flat surface; anteroloph and mesoloph fused marginally to paracone, forming long anterofosset and mesofosset, respectively; posteroloph completely fused to metacone, forming a distinct mesofosset. Age class 4: 1st and 2nd molars with heavy wear, indistinct cusps, and massive exposure of dentine; 3rd molar appears quite flat, with major exposure of dentine; anteroloph, mesoloph, and posteroloph indistinct, fused to major cusps. Age class 5: all 3 molars are completely worn away, and the dentine is largely exposed.

To evaluate the sexual dimorphism we applied a *t*-test in populations that had more than 10 adult specimens. To test age variation we used 1-way analysis of variance (ANOVA) comparing the 5 age classes of the larger samples available (Simpson et al. 2003; Hair et al. 2007), namely Murici, Ilhéus, Unacau, and Una.

Geographic variation.—The 37 available samples (Fig. 1) are distributed along a north–south transect in the Atlantic Forest along which all analyses of geographic variation were conducted (Musser 1968; Vanzolini 1970). These samples were grouped to yield more robust samples, following the geographic proximity criterion (Musser 1968; Vanzolini 1970),
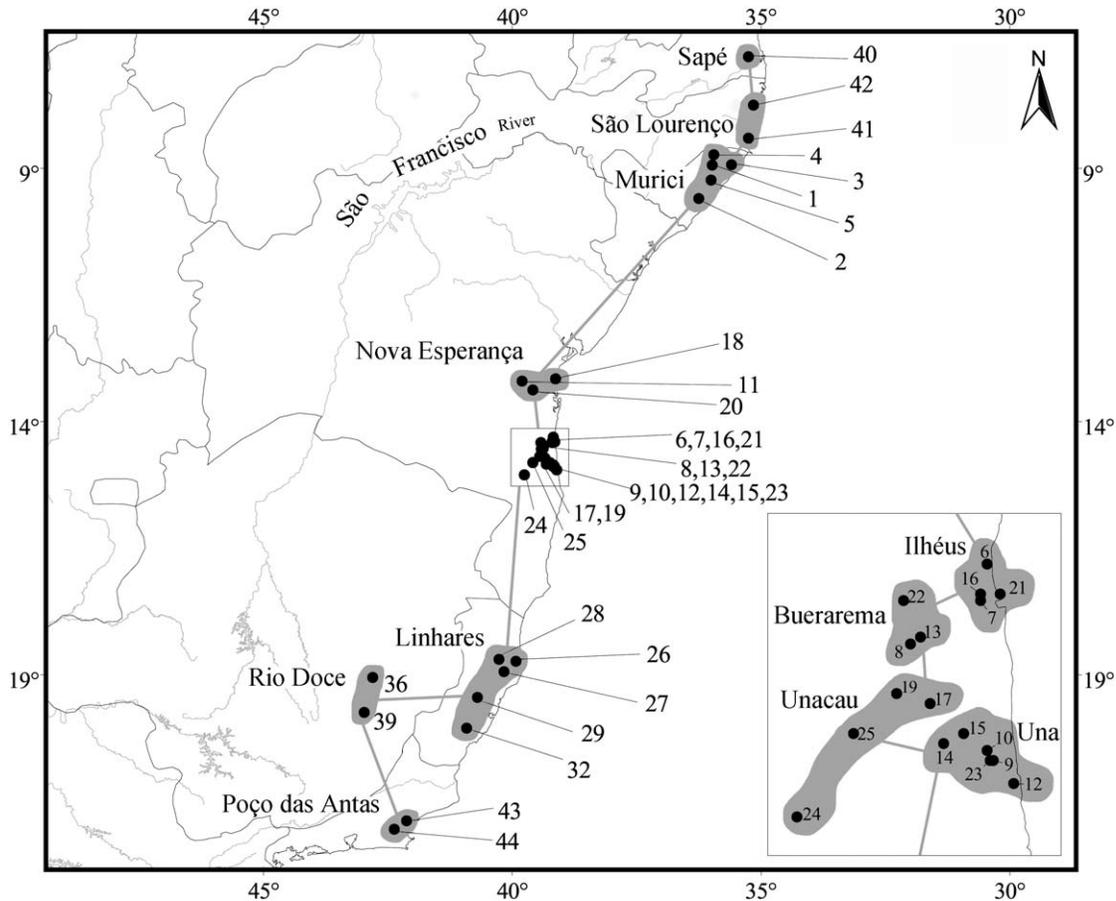
Fɪɢ. 1.—Distribution of the 37 samples of *Hylaeamys* available in the Brazilian Atlantic Forest. Gray areas represent the 11 samples that were pooled and used in qualitative and quantitative comparisons, along a north–south transect, indicated by the gray lines.

the criterion of similarity between the geomorphological characteristics of the samples (riverbanks, mountain slopes, relief), and the similarity between qualitative external characters and cranial characters (see below). On the basis of these criteria, we pooled the 37 samples and established 11 groups (with 4 or more adults) that were used in qualitative and quantitative (univariate and multivariate) comparative analysis, named: Sapé, São Lourenço, Murici, Nova Esperança, Ilhéus, Buerarema, Unacau, Una, Linhares, Rio Doce, and Poço das Antas (Table 1). Sapé was used only in multivariate statistics, since it exhibits only 1 adult specimen.

The geographic variation was assessed quantitatively and qualitatively. For the quantitative comparisons we elaborated Dice–Leraas univariate diagrams, using the mean and confidence intervals (95%) for each cranial variable (Simpson et al. 2003).

We then performed a principal component analysis (PCA) over the within-group variance–covariance matrix of the log-transformed variables to evaluate the multivariate difference between groups. This procedure also allows for the calculation of a common 1st PC that accounts for all variation that can be attributed to size differences (Bookstein 1989). The projection of the original observations on a plane that is orthogonal to this axis of size variation (PC1) produces variables that are size-free

and can be evaluated in subsequent analysis (Burnaby 1966). The resulting size-corrected variables were analyzed through a PCA. Only individuals without missing data were analyzed in this way.

This analysis assumes that this matrix was the same for all presumably 3 species: to compare the species of the Atlantic Forest and to solve nomenclatural issues (e.g., the validity of *laticeps* Lund 1840, *oniscus* Thomas 1904, and *seuanezi* Weksler et al. 1999), we included in this analysis all 11 samples, including type material of the nominal taxa whose type locality occurs in this biome (the holotypes of *oniscus* Thomas 1904; *seuanezi* Weksler et al. 1999), and also samples of *H. megacephalus* (Fischer, 1814) from Paraguay, including the type locality and neotype of this species, and from São Paulo and Minas Gerais, which includes the type material of *Mus laticeps* from Lagoa Santa (the lectotype, ZMC 266, and a topotype, ZMC 389, from the original series obtained by P. Lund; specimens listed in Appendix II). Maps were constructed using ArcView (ArcView GIS 3.4; ESRI 2000), and the statistical analyses were performed on SPSS (SPSS Inc. 2008) and R (R Development Core Team 2008) software packages.

In the qualitative comparisons of the 11 samples studied, and also in samples of *H. megacephalus*, we evaluated the following traits: color of the dorsum, flanks, venter, hind foot,

TABLE 1.—Localities in order of gazetteer, number of adult specimens used in Dice–Leraas, and group to which each locality belongs.

Gazeteer number	Locality	Number of specimens	Group
1	Estação Ecológica de Murici, Murici	36	Murici
2	Fazenda do Prata, 13 km SSW de São Miguel dos Campos	1	Murici
3	Fazenda Santa Justina, 6 km SSE de Matriz de Camaragibe	1	Murici
4	Mata de Coimbra, Usina Serra Grande, Ibateguara	4	Murici
5	Mata do Cedro, Usina Utinga-Leão, Rio Largo	1	Murici
6	Aritaguá, Urucutuca, Ilhéus	1	Ilhéus
7	Banco da Vitória, Pirataquissé, Ilhéus	20	Ilhéus
8	Buerarema, Ribeirão da Fortuna	31	Buerarema
9	EDJAB–CEPLAC, Una	2	Una
10	ESMAI, CEPLAC, Una	2	Una
11	Estação Ecológica Nova Esperança, Wenceslau Guimarães	3	Nova Esperança
12	Fazenda Bolandeira; 10 km S Una	7	Una
13	Fazenda Brejo Grande, 12 km S, 1.7 km W de Itabuna	8	Buerarema
14	Fazenda Dendhevea, Una	1	Una
15	Fazenda Jueirana, Una	1	Una
16	Fazenda Limeira, Ilhéus	1	Ilhéus
17	Fazenda Orion, Serra das Lontras, Arataca	2	Unacau
18	Fazenda Subauma, Cairu	1	Nova Esperança
19	Fazenda Unacau, 8 km SE de São José	45	Unacau
20	Gandu	1	Nova Esperança
21	Ilhéus	30	Ilhéus
22	Parque Zoobotânico da CEPLAC, 6 km E de Itabuna	3	Buerarema
23	Reserva Biológica de Una, Una	35	Una
24	Reserva Biológica Pau-brasil, 15 km NW de Porto Seguro	4	Una
25	RPPN Serra do Teimoso, Jussari	18	Unacau
26	Fazenda Santa Terezinha, 33 km NE de Linhares	4	Linhares
27	F. M. A. Linhares	4	Linhares
28	Linhares	4	Linhares
29	Santa Teresa	3	Linhares
32	Engenheiro Reeve–Matilde, Alfredo Chaves	1	Linhares
36	Parque Estadual do Rio Doce; 13 km E Marliéria	3	Rio Doce
39	Rio Doce	1	Rio Doce
40	Fazenda Pacatuba, 10 km NE de Sapé	1	Sapé
41	Saltinho, Rio Formoso	6	São Lourenço
42	São Lourenço da Mata	5	São Lourenço
43	Fazenda União, Casimiro de Abreu	1	Poço das Antas
44	Reserva Poço das Antas, Silva Jardim	6	Poço das Antas

and tail; the shape of the incisive foramen; the posterolateral palatine perforations; the palatine processes; and the morphology of the interorbital region (Carleton 1980; Voss 1988; Musser et al 1998; Weksler 2006).

We also used cytogenetic data (diploid number, 2n; fundamental number or number of autosomal arms, FN) in the comparative analysis, compiled from the literature (Zanchin et al. 1987; Maia 1990; Geise 1995; Weksler et al. 1999; Andrades-Miranda et al. 2000). On the basis of analyses of the morphologic and cytogenetic variation associated with the examination of the type of material and the original descriptions of all taxa (*M. megacephalus* Fischer 1814; *M. laticeps* Lund 1840; *Calomys saltator* Winge 1887; *O. oniscus* Thomas 1904; and *O. seuanezi* Weksler et al. 1999), we assigned the proper names to each species. These were defined on the basis of unique combinations of diagnostic characters, a procedure that is similar to the phylogenetic species concept advocated by Cracraft (1983), who favors diagnosability: species are the smallest diagnosable cluster of organisms. In the future, as more samples become available, we aim to evaluate if within species diagnosed here there is a parental pattern of ancestry and descent, another corollary of the Cracraft species concept (1983).

RESULTS

Age and sex.—Our analysis suggests that there are no sexual differences in cranial variables (Table 2), and therefore, in subsequent analyses of the geographic variations, we grouped the males and females for all groups (see also Voss 1991; Percequillo et al. 2008; Prado and Percequillo 2011; Abreu-Junior et al. 2012).

In all populations analyzed, young individuals were all similar, having the dorsal pelage thinner and harsher, pale gray, and the venter predominantly lighter gray. Some subadults (age class 2) have the same color as the adults (age classes 3, 4, 5), or are in the process of changing the pelage, which is gradually replaced (on the flanks 1st, then the middle of the dorsum, toward the head and finally toward the tail) by the adult pelage. Among adults, we found a wide variation in the dorsal coloration, which will be described in the geographic variation section; however, it is important to note that sexual differences

TABLE 2.—Results of *t*-tests of 13 cranial and dental measurements of some populations of *Hylaeamys* in Atlantic Forest (M = number of males and F = females from each population). Results in bold when *P* < 0.05.

	Murici M = 20, F = 15		Ilhéus M = 19, F = 14		Unacau M = 32, F = 23		Una M = 26, F = 9	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*
CIL	1.393	0.708	1.158	0.566	0.829	0.544	1.941	0.598
LD	1.246	0.462	1.474	0.839	1.080	0.551	2.266	0.667
CLM1-3	0.192	0.240	0.784	0.539	0.610	0.704	**−0.75**	**0.031**
BM1	0.455	0.982	1.448	0.627	0.799	0.499	1.277	0.337
LIF	1.033	0.796	0.428	0.554	0.454	0.862	1.122	0.496
BIF	1.338	0.165	1.357	0.184	0.609	0.759	0.015	0.335
BR	0.924	0.337	1.502	0.844	1.167	0.514	0.074	0.149
LN	1.316	0.444	0.926	0.542	0.175	0.476	0.590	0.434
LBP	1.679	0.373	1.323	0.906	2.358	0.646	0.087	0.652
IB	0.951	0.502	0.487	0.947	0.341	0.524	0.546	0.196
ZB	0.781	0.385	2.246	0.529	0.581	0.122	1.496	0.450
BZP	1.203	0.491	0.988	0.573	0.563	0.350	0.615	0.831
OFL	1.099	0.417	1.012	0.439	0.181	0.405	2.033	0.635

in the coloration or structure of the pelage were not detected in the young and in the adults. We consider that to be classified as adult, a specimen had to exhibit full adult pelage associated with age classes 3, 4, or 5 (Voss 1991; Musser et al. 1998); ANOVA results (not shown) revealed that specimens of each age class are not significantly different.

Geographic variation.—Univariate analyses of geographic variation using Dice–Leraas diagrams (supplemental material: Supplement 1) revealed, in general, sharp discontinuities: São Lourenço and Murici groups, the only samples on the northern bank of São Francisco River used in univariate analyses, sharply differ from the samples on the southern bank of São Francisco River by their higher mean values.

The size-free PCA revealed a subtle separation between the São Lourenço, Murici, and Sapé clusters in the *x*-axis with respect to the other samples of Atlantic Forest (Fig. 2A), where score values of the 1st PC are presented. This component is responsible for explaining over 33% of the variation and

variables with greater discriminatory power were LIF, BZP, and CLM1-3 (Table 3). The 2nd component explains only 17% of the variation, and together with the 1st component, it totals over 50% of the differences among these samples. This component, which was mostly dependent on the variables LIF, BIF, and BR, revealed some separation among the samples, especially for those samples of São Lourenço, Murici, and Sapé, which are pooled on the superior portion of the scatter plot (Fig. 2A).

Overall, the results of the multivariate analysis revealed that samples of São Paulo, Minas Gerais, and Paraguay, assigned to *H. megacephalus*, are sharply distinct from the samples of the southern bank of São Francisco River (Nova Esperança, Ilhéus, Buerarema, Una, Unacau, Rio Doce, Linhares, and Poço das Antas), although with discrete overlap. The samples of the northern bank of São Francisco River, São Lourenço, Murici, and Sapé are pooled and overlap partially to the other 2 groups. Regarding morphofunctional complexes, the most important
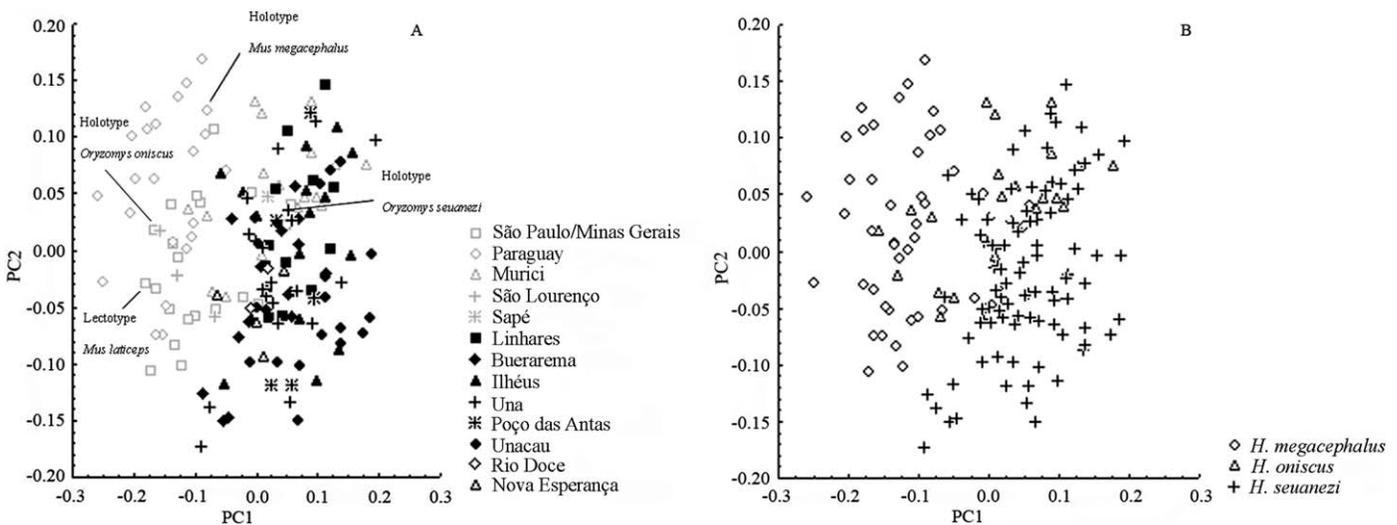

FIG. 2.—Results of size-free principal components analysis (PC1–PC3) of 13 ln-transformed cranial and dental measurements of 11 population samples of *Hylaeamys* from Atlantic Forest, A) grouped by the pooled samples defined in Table 1 and in the text, and indicating the type specimens of *laticeps*, *megacephalus*, *oniscus*, and *seuanezi*; and B) grouped by species, *H. oniscus*, *H. seuanezi*, and *H. megacephalus*.

TABLE 3.—Results of size-free principal components analysis (PC1–PC3) of 13 ln-transformed cranial and dental measurements of 11 geographic samples of *Hylaeamys* from Atlantic Forest and also samples of *H. megacephalus* from São Paulo, Minas Gerais, and Paraguay.

	PC1	PC2	PC3
CIL	0.0944464	0.054032	−0.019907
LD	−0.107462	0.147246	0.122143
CLM1-3	0.2197720	−0.142618	0.051275
BM1	0.0841950	−0.212459	−0.12362
LIF	0.1660317	−0.522261	0.581401
BIF	−0.733157	−0.445879	−0.348957
BR	−0.1424833	0.407003	0.259708
LN	−0.0135932	0.11416	0.131522
LBP	−0.0437784	0.4048892	−0.325748
IB	−0.0081572	0.0837325	0.082991
ZB	−0.0505898	0.1841188	0.037883
BZP	0.5778795	−0.1581433	−0.536229
OFL	−0.0091591	0.1726007	0.1424186
Proportion of variance	0.33486	0.17277	0.13765
Cumulative proportion	0.33486	0.50763	0.64528

variables in PCA are associated with the zygomasseteric complex (BZP) and with the shape of incisive foramina (LIF and BIF), the last being an important feature for discriminating taxa on the genus *Hylaeamys* (see below; Musser et al. 1998; Weksler et al. 1999).

Qualitatively, we observed, in samples of Sapé, São Lourenço, and Murici, a more ochraceous-buffy or ochraceous-orange coloration of the dorsum, weakly and grossly grizzled with brown dorsally, and flanks with a predominantly ochraceous to buffy-orange color. Some specimens are darker, with ochraceous-brown coloration. In samples from Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro, a slightly darker coloration with ochraceous buffy to ochraceous brown, thinly and densely grizzled with dark brown, and the sides are more evenly ochraceous to buffy brown. In the samples from Fazenda Unacau, the back is still quite darker than in other specimens, densely dark ochraceous brown and thinly grizzled with dark brown. In samples of *H. megacephalus* from São Paulo, Minas Gerais, and Paraguay specimens are ochraceous to ochraceous yellow-orange or even yellowish orange, weakly and finely grizzled with brown, with the sides more intensely ochraceous to ochraceous yellow-orange or even yellowish orange. We did not detect any consistent pattern of variation in the coloration of the venter, which in most specimens was grayish white.

Furthermore, the specimens from São Lourenço, Murici, and Sapé have more robust, heavily built skulls with a wider and longer rostrum. Additionally, these specimens exhibit longer diastema that houses relatively longer and narrower incisive foramina, with lateral margins slightly diverging posteriorly. They also share more robust and thick zygomatic arches and palates usually adorned with very robust palatal processes, fused with the maxillary bones. Upper molar series are also narrow. In specimens of the Atlantic Forest south of the São Francisco River, the skulls are usually smaller and more delicate, with rostrums bearing shorter incisive foramina that

are generally shorter and wider posteriorly, with slightly convex margins (in elongated teardrop shape). The palate is less frequently decorated by palatine processes, which are more delicate. The upper molar series are large and robust. In samples of *H. megacephalus*, specimens are even smaller and more delicate, with rostrums and diastema shorter. The incisive foramen is much shorter and wider on its posteriormost portion, with lateral margins convex (teardrop shaped); molars narrow, similar in samples from São Lourenço, Murici, and Sapé. These specimens also exhibit an interorbital region weakly divergent posteriorly, with slightly squared or weakly beaded supraorbital margins, when compared with Atlantic Forest samples, which possess more sharp and squared or beaded supraorbital margins.

A noticeable discontinuity was also observed in the chromosomes. Zanchin et al. (1987) reported, for individuals collected in southern Bahia (Fazenda Unacau), a karyotype with $2n = 48$ chromosomes and the FN = 64. By contrast, Geise (1995) established that the appropriate number of autosomal arms for specimens from southern Bahia is FN = 60; she explained the differences between her result and that of Zanchin et al. (1987) by the mounting of the karyotype. In 1990, Maia found in São Lourenço da Mata, State of Pernambuco, the type locality of *O. oniscus* Thomas 1904, a karyotype with a $2n = 52$ chromosomes and FN = 62. Later, Weksler et al. (1999) described a karyotype with $2n = 48$ and FN = 60 for specimens from Rio de Janeiro (Fazenda União), Minas Gerais (Rio Doce), and southern Bahia (Fazenda Brejo Grande), in agreement with Geise (1995). Andrades-Miranda et al. (2000) mentioned 2 karyotypes for the species of the genus *Hylaeamys* on the Atlantic Forest: $2n = 52$, FN = 62 and $2n = 48$, FN = 60. The 1st karyotype was obtained from specimens collected in Sapé in the State of Paraíba and in Valença, State of Bahia. The 2nd karyotype was found in specimens from the Reserva Ecológica Pau Brazil and the Fazenda Unacau, both in the southern portion of Bahia. However, the original label of the specimen from Valença (AL3426) deposited in the Museu Nacional do Rio de Janeiro under number MN30595 reads Fazenda do Prata, São Miguel dos Campos, Alagoas. There are 2 explanations for the discrepancy: the collecting location on the specimen's label is correct, which means that Andrades-Miranda et al. (2000) made a mistake regarding the collecting locality of MN30595 (AL 3426); or the location shown in the publication by Andrades-Miranda et al. (2000) is correct, i.e., the specimen is from Valença, but there was a mistake when transcribing the information to the museum label. The results published so far (except for the Valença information by Andrades-Miranda et al. 2000) suggest that the karyotype $2n = 52$, FN = 62 is distributed in the states of Paraiba and Pernambuco, and that the karyotype $2n = 48$ and FN = 60 occur in the southern portion of the State of Bahia and in the State of Rio de Janeiro. We believe that it is more likely that Andrades-Miranda et al. (2000) made the mistake, and that the correct location of the specimen is Fazenda do Prata, São Miguel dos Campos, Alagoas. This extends the range of the karyotype $2n = 52$, which is currently restricted to the north of

the São Francisco River, to the state of Alagoas. We hold this belief on the basis of the congruence between the observed morphological variation and the cytogenetic variation (on the basis of analysis of the morphology of specimens karyotyped) in populations of *Hylaeamys* along the Atlantic Forest.

Taxonomic history and name attribution.—Throughout history, various names have been given to the *Hylaeamys* populations of the Atlantic Forest. In 1904, Thomas described *O. oniscus* on the basis of specimens collected in São Lourenço da Mata, State of Pernambuco. In 1952, Moojen identified specimens of *Hylaeamys* collected in the southern portion of the State of Bahia as *H. oniscus*, considerably expanding the distribution of the species. Almost a decade later, Hershkovitz (1960) synonymized various taxa with *O. capito* (= *H. megacephalus*), including *O. oniscus*.

Cabrera (1961), influenced by Hershkovitz (1960), recognized *O. capito* as a valid species, with several subspecies associated to genus *Hylaeamys* on eastern South America: *O. c. capito* (Olfers 1818) for Paraguayan populations, *O. c. laticeps* (Lund 1840) for Cerrado Brazilian populations, *O. c. goeldi* (Thomas 1897) for Eastern Amazonian populations, and *O. c. oniscus* (Thomas 1904) for Atlantic Forest samples from northeastern Brazil, besides other taxa presently allocated to other oryzomyine genera. These nomenclatural changes elaborated by Hershkovitz (1960) were probably responsible for the fact that *O. laticeps* (Lund 1840), as well *O. oniscus* (Thomas 1904), remained a junior synonym of *O. capito* (Olfers 1818) for several decades thereafter (see Honacki et al. 1982; Musser and Carleton 1993). Although Gardner and Patton (1976) re-established the validity of many of the species synonymized by Hershkovitz, e.g., *Euryoryzomys nitidus*, they maintained *H. oniscus* as a junior synonym of *H. megacephalus* (then called *H. capito*).

In 1987, Zanchin et al. described the karyotype of specimens with 2n = 48 chromosomes and FN = 64 autosomal arms, collected in Fazenda Pau Brasil and Unacau, Bahia. They identified these specimens as *Oryzomys* [= *Hylaeamys*] sp. Shortly thereafter, Maia (1990) described the karyotype of specimens collected in São Lourenço da Mata, in Pernambuco, with 2n = 52 chromosomes and FN = 62, showing for the 1st time the existence of cytogenetic differences between *Hylaeamys* populations of the Atlantic Forest. As São Lourenço is the type locality of *O. oniscus* Thomas, 1904, Maia identified his specimens as *O. capito oniscus*.

Later, Musser and Carleton (1993) synonymized all those names under *O. capito* (Olfers 1818), an arrangement that prevailed in the literature until 1998, when Musser et al. published their influential revision on the group *capito* of genus *Oryzomys* and played an important role in solving many problems concerning the definition of *Hylaeamys*. These authors recognized 2 forms in eastern South America: the 1st one widely distributed throughout the Cerrado, semideciduous forests of the interior, and Amazon Forest; and the 2nd restricted to the Atlantic Forest. To the 1st entity they assigned the name proposed by Fischer (1814), *megacephalus*, whose type locality is in the Cerrado areas of eastern Paraguay, listing

the names *capito* (Olfers 1818), *goeldi* (Thomas 1897), *cephalotes* (Desmarest 1819), *velutinus* (Allen and Chapman 1893), *modestus* (Allen 1899) and *perenensis* (Allen 1901) as synonymies. To provide nomenclatural stability to the name, these authors designated a neotype for *megacephalus*, since D. Felix de Azara's original specimens are not known to exist.

For the species of the Atlantic Forest, Musser et al. (1998) applied the name *laticeps* Lund 1840, whose type locality is Lagoa Santa, an area of Cerrado from Minas Gerais, considering *oniscus* a junior subjective synonym and *C. saltator* (Winge 1887) a junior objective synonym (Cabrera 1961:386; Musser et al. 1998:263–266) through the attachment of this name to the lectotype of *M. laticeps*. This was the 1st occasion in history that this name was associated to Atlantic Forest samples of genus *Hylaeamys*, a name consistently applied to Cerrado populations, as a synonym or as subspecies of *O. capito* (Cabrera 1961; Musser and Carleton 1993). Despite the morphological variation observed among the populations of the Atlantic Forest, Musser et al. (1998:42–43) considered these samples as belonging to a single biological entity, *H. laticeps*. In this concept, they included specimens from Pernambuco, Bahia, Espirito Santo, and Minas Gerais. The authors considered the karyotype published by Maia (1990) as being valid for the species and ignored the karyotype variation described for these populations.

A year later, Weksler et al. (1999) found significant differences in populations of *Hylaeamys* in the Atlantic Forest among samples of Pernambuco and samples of Bahia, Espírito Santo, and Rio de Janeiro on the basis of multivariate analysis of skull measurements and cytogenetic analyses. They also determined the karyotype 2n = 48 and FN = 60 for the population of Rio de Janeiro, Espirito Santo, and southern Bahia and established that populations south of the São Francisco River are clearly distinguished from those having the karyotype found by Maia (1990) for specimens collected in São Lourenço da Mata, Pernambuco. Weksler et al. (1999) concluded that the populations on the northern and southern banks of the São Francisco River were distinct species, and named the southern species *O. seuanezi* Weksler, Geise, and Cerqueira 1999, under the assumption that *M. laticeps* was a synonym of *H. megacephalus*.

The karyotype published by Weksler et al. (1999) was obtained from specimens from the states of Bahia, Espírito Santo, and Rio de Janeiro, and did not include the type locality of *M. laticeps*, Lagoa Santa. Therefore, it is not possible to associate any of the karyotypes described (by Maia 1990; Weksler et al. 1999) with *H. laticeps*, nor it is possible to effectively associate the karyotype of 2n = 52 with the type material of *H. oniscus*, only with the type locality.

In the multivariate analysis using the type specimens, the lectotype (ZMC 266) and the topotype (ZMC 389) of *M. laticeps* Lund 1840 appeared among the specimens from the Cerrado and the semideciduous forests of São Paulo, Minas Gerais, and in eastern Paraguay (Fig. 2A). In the present contribution and also in the current literature (e.g., Musser et al. 1998; Weksler et al. 1999), these specimens are often referred
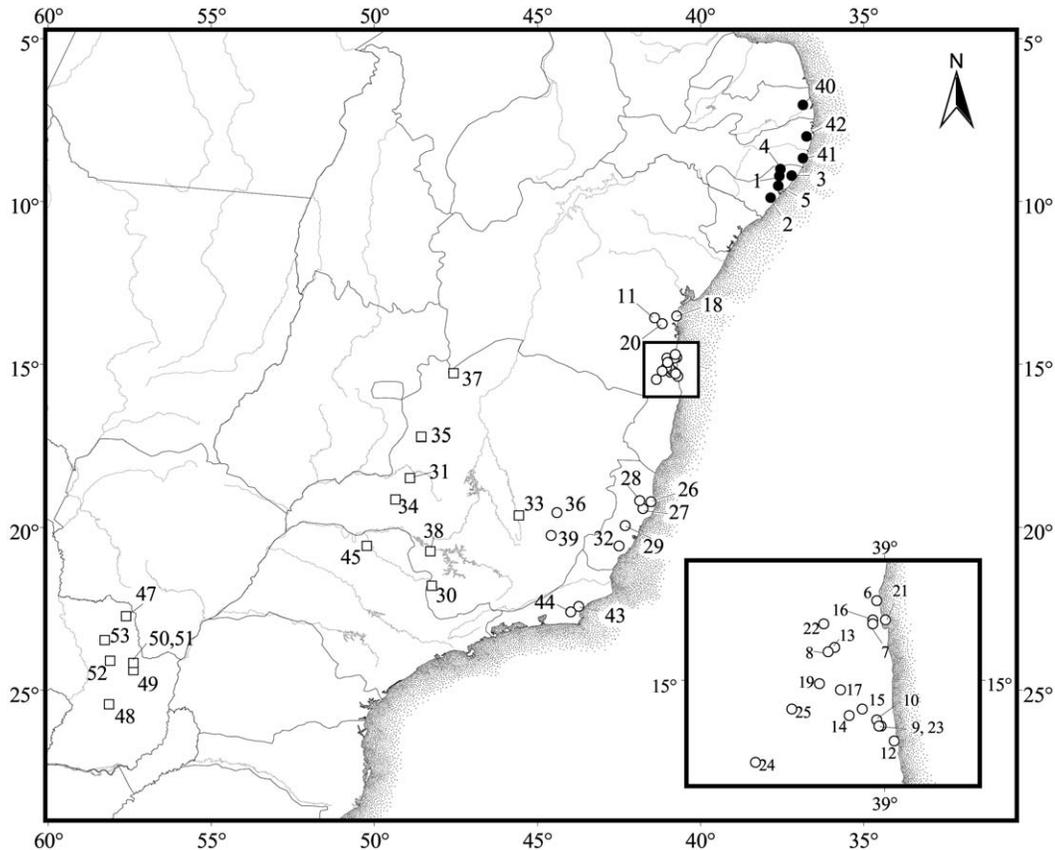
Fig. 3.—Distribution of collecting localities of all specimens examined of *Hylaeamys oniscus* (solid circles) and *H. seuanezi* (open circles). For *H. megacephalus* (open squares) we plotted on this map only the collecting localities that we currently used in the analysis here performed; for an updated distribution for this species, see Prado and Percequillo (2013).

to as *H. megacephalus*, Fischer 1814. The neotype of *M. megacephalus* Fischer 1814, UMMZ 133811, also groups with these specimens, suggesting that both names apply to the same biological entity, for which the name *M. megacephalus*, Fischer 1814 is available (Langguth 1966; Sabrosky 1967, Musser et al. 1998) and has priority over *M. laticeps* Lund 1840. Additional comparisons also revealed that the type series of *M. laticeps* Lund 1840, including the lectotype, exhibits more correspondence on external and qualitative cranial traits to populations of *H. megacephalus* Fischer 1814. Thus, we propose that *M. laticeps* Lund 1840 is a subjective junior synonym of *M. megacephalus* Fischer 1814.

In our opinion, this association between the name *laticeps* and, consequently, the sample of Lagoa Santa with these populations from the gallery forests, cerradão, and semi-deciduous forests of the Cerrado biome in the interior of South America makes more zoogeographical sense. No species typical of the coastal Atlantic Forest penetrates up to Lagoa Santa, which currently has a fauna typical of the Cerrado, with elements such as *Cerradomys*, *Calomys*, and *Necromys* among other taxa. The Atlantic Forest elements recorded by P. Lund and described by him or by H. Winge from Lagoa Santa, such as *Calomys rex* [= *Sooretamys angouya*], *C. anoblepas* [= *Juliomys* sp.] and *Hesperomys molitor* [= *Lundomys molitor*], were obtained only in caves, and probably represent a

testimony of more humid conditions during the late Pleisto-cene/early Holocene (Voss and Carleton 1993; Silva et al. 2003).

Thus, populations of the Atlantic Forest cannot receive the name that had been assigned to them by Musser et al. (1998), but 2 other names are still available and can be applied to 2 distinct populations of this biome. The holotype (MN 42678) and paratypes (MN 42899, 42900, 35904, 31478, 35879) of *H. seuanezi* stand among populations south of the São Francisco River, whereas the holotype of *O. oniscus* (BMNH 3.10.1.42) is placed close to specimens of Alagoas, Pernambuco, and Paraiba, north of the São Francisco River. Although also overlapped to other specimens of *H. megacephalus*, this specimen is qualitatively distinct from typical representatives of this latter species.

On the basis of the quantitative and qualitative analysis of all samples, we assign to the specimens from the populations that are found north of the São Francisco River, represented here by São Lourenço, Murici, and Sapé, the name *H. oniscus* Thomas, 1904. Regarding the specimens from populations distributed south of the São Francisco River, represented here by the localities of Nova Esperança, Ilhéus, Buerarema, Unacau, Una, Linhares, Rio Doce, and Poço das Antas, we apply the name *H. seuanezi* Weksler, Geise, and Cerqueira 1999 (Figs. 2B and 3).

TABLE 4.—Mean ± SD, minimum, maximum, and number of specimens for each measurement of adults of *Hylaeamys oniscus*, *H. seuanezi*, and *H. megacephalus*.

	H. oniscus	H. seuanezi	H. megacephalus
CIL	32.3 ± 1.5 (28.7–34.6) 27	31.3 ± 1.3 (28.5–35) 117	28.9 ± 1.1 (26.5–30.6) 31
LD	9.6 ± 0.7 (7.85–10.8) 28	8.8 ± 0.5 (7.6–10.1) 117	8.2 ± 0.4 (7.3–8.9) 33
CLM1-3	5.16 ± 0.15 (4.92–5.49) 27	5.11 ± 0.18 (4.62–5.53) 117	4.8 ± 0.19 (4.41–5.20) 33
BM1	1.46 ± 0.06 (1.32–1.60) 28	1.50 ± 0.06 (1.39–1.83) 117	1.45 ± 0.07 (1.29–1.58) 34
LIF	5.21 ± 0.33 (4.62–6.08) 29	4.92 ± 0.38 (4.05–5.92) 118	4.41 ± 0.33 (3.77–5.03) 32
BIF	2.53 ± 0.28 (2.11–3.43) 29	2.38 ± 0.19 (1.99–2.83) 118	2.53 ± 0.22 (1.91–2.87) 33
BR	6.22 ± 0.44 (5.14–7.45) 29	5.66 ± 0.32 (4.50–6.43) 118	5.81 ± 0.31 (5.25–6.34) 32
LN	14.4 ± 1 (11.9–16.4) 29	13.30 ± 0.74 (11.8–16.4) 118	12.8 ± 0.7 (11.5–14) 30
LBP	7.49 ± 0.46 (6.40–8.49) 29	7.38 ± 0.42 (6.42–8.43) 118	6.91 ± 0.26 (6.24–7.51) 32
IB	5.31 ± 0.32 (4.71–5.91) 29	5.29 ± 0.21 (4.60–5.85) 118	5.24 ± 0.28 (4.61–5.74) 34
ZB	17.7 ± 1.01 (15.9–19.8) 28	17.1 ± 0.7 (15.3–18.7) 107	16.2 ± 0.9 (14.2–17.5) 23
BZP	4.02 ± 0.33 (3.23–4.77) 28	4.07 ± 0.32 (3.22–4.91) 118	3.53 ± 0.22 (3.16–3.95) 34
OFL	12.2 ± 0.7 (10.9–13.2) 27	11.3 ± 0.5 (10.1–12.3) 118	10.7 ± 0.5 (9.7–11.3) 33

Hylaeamys oniscus (Thomas 1904).

Oryzomys oniscus Thomas 1904:142. *Type locality.*—São Lourenço, Pernambuco.

(*Oryzomys* [*Oryzomys*]) *oniscus*.—Tate 1932:18. Name combination.

Oryzomys laticeps.—Hershkovitz, 1960:544. Footnote; part, not *Mus laticeps* Lund 1840 (= *Hylaeamys laticeps* [Lund 1840]). Name combination.

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

Oryzomys capito.—Hershkovitz 1966:137. Footnote; part, not *Mus capito* Olfers 1818 (= *Hylaeamys megacephalus* [Fischer 1814]).

(*Hylaeamys*) *oniscus*.—Weksler, Percequillo, and Voss 2006:14. First use of current name combination.

Type material.—BMNH 3.10.1.42, a male specimen collected by A. Robert in São Lourenço, in "23. juillet. 05," with the original number 1573; the skin and skull are well preserved.

Type locality.—São Lourenço, Pernambuco; presently São Lourenço da Mata, Pernambuco, Brazil; geographical coordinates: 8°00′S, 35°03′W (locality 42; Fig. 3).

Distribution.—This species inhabits the coastal lowlands on the northern bank of the river São Francisco, in the states of Paraíba, Pernambuco, and Alagoas. Throughout this small distributional range, this species dwells in disturbed and mature evergreen and semideciduous humid forests that form the northern Atlantic Forest, from sea level to nearly 400-m elevation.

Diagnosis.—Dorsal pelage yellowish brown, heavily grizzled with dark brown; ventral pelage markedly whitish, tail bicolor or slightly bicolor, shorter than or the same length of body; skull robust, palatine processes well developed, fused with the mandible in adult specimens; karyotype with $2n = 52$ and $FN = 62$.

Description.—Medium-sized rodent (body mass: 57–95 g, $n = 8$), with short and round ears (20–28 mm, $n = 9$), with tail (135–162 mm, $n = 14$) slightly shorter than or as long as combined head and body (136–162 mm, $n = 14$), feet long (27–35 mm, $n = 14$) and narrow. Dorsal pelage soft and short, wispy; villiform hairs very short, flat, thin (6–7 mm long); setiform hairs medium, fine, and smooth (9–11 mm long); aristiforms long, thick (12–13 mm long). Head pelage usually shorter than on dorsum, with a smaller proportion of aristiform hairs. Dorsal pelage brown to yellowish brown, heavily grizzled with dark brown from head to base of tail; dorsal and ventral coloration clearly separated; ventral coloration gray or grayish white, hairs with basal portion (2 mm) grayish and apical portion white. Ears covered with very short hairs, both internally and externally, entirely brown. Mystacial vibrissae, when facing backward, do not reach beyond apical apex of ear; vibrissae usually white or pigmented. Tail with conspicuous large scales; hairs dark brown, central hair longer, as long as 2 rows of scales, lateral hairs shorter, as long as one and a half scale; tail usually bicolored, with dorsum darker and venter less pigmented, or weakly bicolor with ventral half more pigmented. Fore and hind feet with dorsal surface covered with short hairs, all white; ventral surface of fore and hind feet naked and squamous between interdigital pads; fore feet with 3 interdigital pads and 2 palmar pads, thenar and hypothenar, large and fleshy; hind feet with 4 interdigital pads and 2 plantar pads, thenar and hypothenar, large and fleshy. Epidermal color of ventral surface of fore and hind feet light brown; hind feet with ungual tufts scarce, as long as or shorter than claws; tufts with same color pattern as fingers.

Skull robust, medium sized (Table 4; Fig. 4), rostrum short, ranging from narrow to broad; rostrum flanked by nasolacrimal foramen with wide lumen; capsular projections inflated laterally; rostral fossa shallow and inconspicuous; zygomatic notch shallow and narrow. Interorbital region narrower anteriorly, with supraorbital margins slightly diverging posteriorly and weakly beaded dorsolaterally, but without a distinct crest. Supraorbital border extended posteriorly, configuring weak temporal margin continuous with supraorbital margin; braincase with profile more round; lambdoidal crest conspicuous; nuchal crest smooth. Gnathic process short, slightly surpassing anterior surface of anterior incisors. Zygomatic arches strong, parallel or diverging posteriorly; jugal present; zygomatic plate tall and narrow, with predominantly straight anterior margin, rarely concave, free anterior dorsal margin of

FIG. 4.—Dorsal, ventral, and lateral views of cranium and lateral view of dentary of the specimen UFPB BC195 of *Hylaeamys oniscus*, from Estação Ecológica de Murici, Alagoas, Brazil; specimen with age class = 3, and CIL = 31.29 mm.

plate slightly protruding anteriorly. Anterior portion of alisphenoid projected anteriorly as a blade, hiding the sphenoidal fissure. Alisphenoid strut absent, squamosoalisphenoid foramen and sphenofrontal foramen absent; stapedial foramen wide, posterior opening of alisphenoid canal ample, configuring the circulation pattern type 2 (Voss 1988). Mastoid strongly convex; mastoid fenestra large and always present. Postglenoid foramen broad; subsquamosal fenestra elongated and narrow, slit-shaped. Hamular process of squamosal long and narrow; tegmen tympani laminar, occupying a great portion of the postglenoid foramen and not reaching the squamosal. Tympanic bulla not very globose, with wide external auditory meatus; ectotympanic stapedial process well developed, long and thin, always overlapping the squamosal/alisphenoid. Stapedial dorsal process absent; malleus with orbicular apophysis well developed. Diastema long, with short and narrow incisive foramen occupying, on average, 54.6% of diastema; posterior end of the incisive foramen not reaching the alveoli or the anterocone the M1, anterior and posterior ends of incisive foramen rounded and lateral margins convex,

elongated, teardrop in shape. Bony palate long and wide; posterolateral palatine pits (double or triple) located in shallow or slightly deep palatal depressions; palate with palatine processes highly developed, fused to maxillary bone in adults. Anterior margin of mesopterygoid fossa not reaching the alveoli or the posterior portion of the M3, except in young individuals; mesopterygoid fossa as wide as adjacent parapterygoid plates; anterior margin of fossa rounded, triangular, or, more rarely, with a small posterior median process. Roof of mesopterygoid fossa completely ossified without sphenopalatine vacuities; parapterygoid plate shallow, slightly concave, not contiguous with palate; plate perforated by numerous nutritive foramina. Lacerate foramen wide on average. Transverse channel broad. Posterior opening of the alisphenoid channel wide, with a defined posterior groove. Auditory bulla small and narrow, slightly inflated; eustachian tube short and broad, slightly compressed dorsoventrally; stapedial foramen broad; carotid canal small.

Mandible low, with coronoid process falciform, as tall as or shorter than condyloid process; upper or sigmoid notch shallow. Angular process with rounded profile, located at the same plane as condyloid process; inferior notch shallow; capsular process of lower incisor absent. Upper and lower masseteric ridges present but not pronounced.

Upper incisors narrow, opisthodont with yellow-orange enamel band on anterior surface. Molar series parallel, robust, but with 1st molar proportionally narrow (Table 3); labial and lingual cusps arranged in opposite pairs. Lingual and labial folds overlapping conspicuously in the middle portion of molar.

M1 anterocone not divided by anteromedian flexus; labial and lingual portions of anterocone separated by shallow medial valley; anterocone narrower than paracone/protocone pair. Anterocone connected with anterior wall by a posteromedial enamel bridge. Anteroloph posterior to anterocone and parallel to it; anteroloph linked to labial portion of anterior wall, extended to molar margin. Anterocone and anteroloph separated by a shallow anteroflexus; when these 2 structures wear out, they fuse marginally, forming an enamel island medial to anterocone and to anterofossete, which becomes completely obliterated with increasing age. Protocone connected anteromedially to anterior mure, and separated from anterocone by wide protoflexid and from paracone by paraflexus; the latter also separates paracone from anteroloph. Paracone and protocone interconnected posteromedially by transverse ridge and through it to median mure. Narrow mesololoph connected to median mure medially, and to mesostyle labially; mesoloph separated from paracone by mesoflexus, and from metacone by metaflexus. Mesoloph, even when worn, merges marginally to paracone, forming a mesofosset. Hypocone linked anteriorly to median mure and separated from protocone by hypoflexus and from metacone by metaflexus; this fold also separates hypocone form metacone. Hypocone connected to posteroloph posteromedially, the latter short but extending to labial margin of molar. Metacone connected to posteroloph via posteromedial enamel bridge, defining shallow labial fold, the posteroflexus; when not much

worn, posteroloph connecting to metacone marginally forming posterofosset, 1st structure in the topography of the molar that becomes obliterated with wear. Protocone and hypocone separated by broad hypoflexus.

M2 without anterocone, anteroloph being the only structure reminiscent of procingulum. In a few specimens, small anterolabial cingulum and consequently shallow protoflexus present. Except for these differences, molar topography very similar to that found in M1.

Size of M3 approximately ⅔ of M2. Anteroloph developed, but in some specimens does not reach margin of labial molar; anteroloph connected with posteromedial protocone. Paraflexus deep, distinguishes anteroloph from protocone and protocone from paracone; in some specimens, paraflexus bisects the molar completely, separating protocone from remaining tooth structures. Paracone may be linked to anteroloph by anterolophule forming labial and medial enamel islands. Paracone reduced, connected posteromedially to median mure, which connects via enamel bridge to posterior portion of protocone, also small. Mesoloph very short, originating from median wall and oriented posterolaterally toward the molar margin; mesoloph separated from paracone by shallow mesoflexus and metacone/posteroloph through shallow metaflexus; with wear, mesoloph binds marginally to paracone. Hypocone greatly reduced and separated or not from protocone by hypoflexus, which varies from shallow to deep, and is obliterated after minimal wear. Metacone and hypocone may be fused and indistinguishable from each other and not discernible from posteroloph; posteroflexus absent. Hypocone may be separated from metacone by a flexus, but not necessarily connected to posteroloph, which is short or absent. First upper molar with anterior labial and posterior root, and lingual root, the lingual one posterolateral to anterior lingual root. Second molar with anterior and posterior labial roots, and long lingual root. Third molar with anterior and posterior labial roots, short lingual root, posterior labial root positioned posterolaterally to lingual root.

Lower incisors narrow and long. Molar series with lingual and labial cusps arranged in slightly alternating pairs, linguals anterior to labials. Anteroconid of m1 not divided by anteromedian flexid; anteroconid rounded, labial and lingual conulids not recognizable. Anteroconulid linked to anterior murid by posteromedial enamel bridge. Anterolabial cingulid connected labially to anterior murid, cingulid extended laterally to molar margin and posteriorly to anterolabial margin of protoconid. Cingulid separated from anteroconid by anterior fold of protoflexid and from protoconid by posterior fold of protoflexid. Anterolophid lingually connected to median murid, reaching lingual margin of molar. Anterolophid separated from anteroflexid by anteroconid and from metaconid by metaflexid. Anterior murid connected to protoconid and metaconid through anteromedian end of the metaconid; protoconid and metaconid delimited by mesoflexid, which also separates metaconid from mesolophid. Protoconid linked to median murid, which connects to mesolophid, which extends to the lingual margin of tooth. Mesolophid separated

from entoconid through entoflexid; lingual margins of these structures merge, forming an island, the entofossetid, which is obliterated with increasing wear. Median murid linked to entoconid; hypoconid fused to medial end of entoconid. Metaconid and entoconid delimited by deep flexid, the posteroflexid, also responsible for separating the entoconid from posterolophid. Hypoconid and protoconid discriminated through ample and deep valley, the hypoflexid. On labial edge of the hypoflexid a large ectoestilid is present; with wear, it can fuse with the edge of anterolateral protoconid through ectolophid. Posterolophid emerging directly from hypoconid, reaching lingual edge of molar; with increasing age, lingual portion of posterolophid merging with posterior edge of entoconid, forming the entofossetid.

Topography of m2 very similar to that described for m1, except for the reduced procingulus, the only remaining structure being the anterolingual cingulid, which is well developed and well delimited from protoconid by protoflexid.

Morphology of m3 similar to m2 on anterior portion of tooth, but with cingulid less developed. Mesolophid completely fused to entoconid, which is very small and virtually indistinguishable on the crown of the molar; even in juveniles, the island of enamel that delimits these 2 lophids is not visible. Also fused to entoconid is lingual portion of posterolophid; this is distinct from hypoconid and from entoconid/mesolophid by the presence of enamel island. Hypoconid and protoconid separated by hypoflexid, which is shallower than in m2; ectoestilid present, but never connected with hypoconid by an ectolophid. The 3 molars have only 2 roots, an anterior and a posterior, of the same size.

Specimens examined.—We examined 55 specimens, which are listed in Appendix III.

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 1894:354. Part; name combination.

Oryzomys laticeps laticeps.—Gyldenstolpe 1932:17. Part; name combination.

Oryzomys oniscus.—Moojen 1952:47. Part; name combination.

Oryzomys laticeps.—Hershkovitz 1960:544. Footnote; part; not *Mus laticeps.* Lund 1840 (= *Hylaeamys laticeps* [Lund 1840]).

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 1818 (= *Hylaeamys megacephalus* [Fischer 1814]).

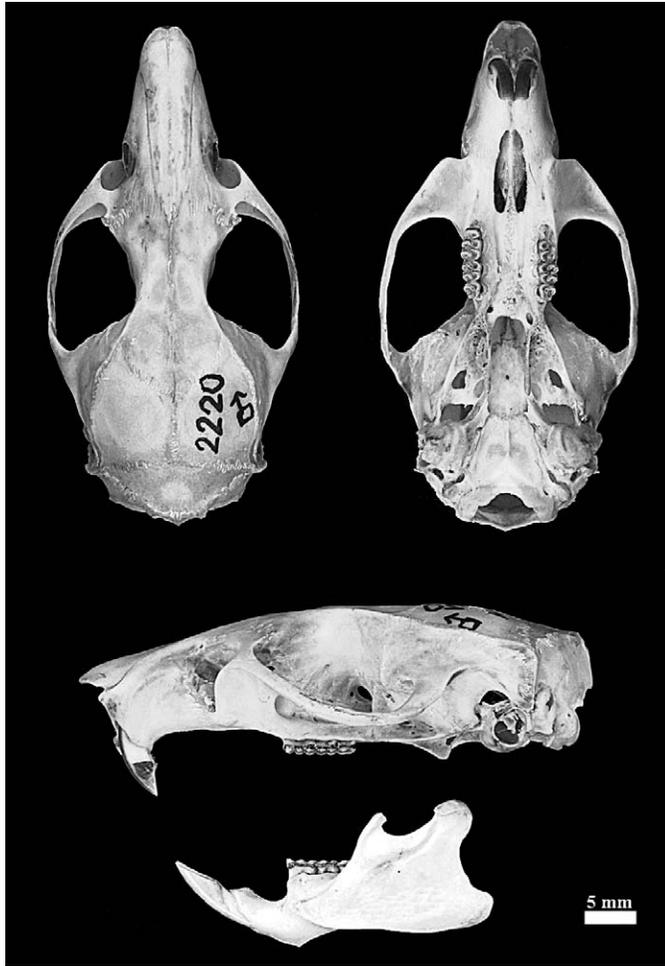*Oryzomys seuanezi.*—Weksler, Geise, and Cerqueira, 1999:454. *Type locality.*—Fazenda União, Município de

FIG. 5.—Dorsal, ventral, and lateral views of cranium and lateral view of dentary of the specimen UFMG 2220 of *Hylaeamys seuanezi*, from ESMAI, CEPLAC, Una, Bahia, Brazil; specimen with age class = 5, and CIL = 33.48 mm.

Casimiro de Abreu, estado do Rio de Janeiro (22°25′S, 42°02′W); 50 m.

(*Hylaeamys*) *laticeps*.—Weksler, Percequillo, and Voss 2006:14. Part; name combination.

Type material.—The holotype is housed at the Museu Nacional da Universidade Federal do Rio de Janeiro, under the number MN 42678, a male specimen collected by M. Weksler, L. Geise, and R. Cerqueira, original number FU11; the specimen is well preserved, with skin and skull in very good condition.

Type locality.—Fazenda União, Casimiro de Abreu, Rio de Janeiro, Brazil. Geographical coordinates: 22°25′S, 42°02′W (locality 43, Fig. 3).

Distribution.—This species occurs throughout the coastal lowlands and the lower slopes of Brazilian coastal highlands, from the southern State of Bahia to the State of Rio de Janeiro, through the State of Espírito Santo, and reaching the oriental portion of the State of Minas Gerais. Olmos (1991) listed *O. capito* (presumably *H. seuanezi*) for the Atlantic Forest in southern São Paulo, at Parque Estadual (then Fazenda)

Intervales; unfortunately, Olmos did not preserve voucher specimens, precluding us to the check the validity of this record. However, extensive sampling performed by other authors at Intervales (Vivo and Gregorin, 2001; samples collected by M. A. Mustrangi housed at the Museum of Vertebrate Zooogy and MZUSP) did not capture this species or even this genus. In fact, we are not aware of any record for the genus *Hylaemys* southward of Rio de Janeiro. On the other hand, *Euryoryzomys russatus* is a fairly common species at Intervales (op. cit.), being similar in size to *H. seuanezi*; therefore, we suspect that Olmos captured *E. russatus*, but misidentified his specimens.

Along this wide distribution, *H. seuanezi* inhabits "cabruca" forests, which are disturbed canopy forests, mixed with cacao plantations (understory is removed and replaced by cacao plants), in southern Bahia; disturbed and mature dense evergreen lowland forests, in Espírito Santo and Minas Gerais, "restinga" forests, which are disturbed; and mature dense evergreen lowland seasonally flooded forests, in Rio de Janeiro. All of these forest types are associated with the southern Brazilian Atlantic Forest.

Diagnosis.—Dorsal pelage yellowish brown to more intense brown, heavily grizzled with dark brown; venter markedly whitish. Tail slightly bicolor, shorter than or the same size as body. Skull smaller, with palatal processes weakly developed, rarely fused to maxillary bones. Karyotype with $2n = 48$ chromosomes and $FN = 60$.

Description.—Qualitatively and quantitatively, this species is very similar to *H. oniscus* and both share many characteristics. Below, we present only the traits that distinguish these 2 species. Medium-sized rodent (body mass: 51–97 g, $n = 92$), with rounded and short ears (20–26 mm, $n = 92$), with tail (106–174 mm, $n = 92$) smaller or the same size as length of the head and body (126–174 mm, $n = 92$), and with long (29–35 mm, $n = 92$) and narrow hind feet. Dorsal pelage soft and short. Skull small, more delicate and less robust than *H. oniscus*, ranging from 31.63 to 37.87 mm (34.70 ± 1.3 mm, $n = 118$). Rostrum narrower (6.61 ± 0.4 mm, $n = 118$) with short nasal bone (13.31 ± 0.73 mm, $n = 118$) and 1st molar wider (1.50 ± 0.06 mm, $n = 118$) than in *H. oniscus* (Table 3; Fig. 5).

Specimens examined.—We examined 244 specimens that are listed in Appendix IV.

DISCUSSION

The evidence presented in this contribution leads us to accept the hypothesis that there are 2 species of *Hylaeamys* in the Atlantic Forest. The available and appropriate name for the species occurring north of the São Francisco River, in the states of Alagoas, Pernambuco, and Paraiba, is *H. oniscus* (Thomas 1904). However, we reject the hypothesis that the name applicable to the species that occurs from Bahia to Rio de Janeiro is *H. laticeps* (Lund 1840), considered here a synonym of *H. megacephalus*. Our results suggest that the most

appropriate name for this species is *H. seuanezi* (Weksler et al. 1999).

Despite their similarities (Figs. 4 and 5), it is possible to differentiate these 2 species of the Atlantic Forest through cranial characteristics. First, the averages of the measurements obtained for the skull of *H. oniscus* are consistently higher than those obtained for *H. seuanezi*. Furthermore, most cranial variables, including ZB and OFL (Table 3), which are associated with the development of the zygomasseteric musculature, exhibit higher mean values in individuals of *H. oniscus*, which leads us to believe that this muscle is probably more developed in this species. Another characteristic associated with mastication that exhibited variation is the 1st molar, which is narrower (BM1), on average, in populations of *H. oniscus* (Table 3). The ecological differentiation between the habitats exploited by both species may have directed the changes associated with the perception of the environment and search and mastication of food. Because the mandible muscles are responsible for different functions, such as chewing, agonistic behavior, vocalization, and respiration (Allen 1880; Herring and Herring 1974), changes in them usually reflect adaptive advantages.

There is a sampling gap between the populations of *H. oniscus* and *H. seuanezi* that corresponds to the State of Sergipe and the entire northern portion of the State of Bahia, which is known as "Recôncavo Baiano," a region with a lowland semideciduous seasonal forest at low elevations along the coast (Thomas and Barbosa 2008). Although sampling has been carried out in Sergipe (material deposited in collections visited), *Hylaeamys* has not been recorded in the state. Similarly, we have not found specimens of this genus from the Recôncavo Baiano in samples of small mammals deposited in the major mammal collections. This distributional gap represents either: a sampling artifact, or the real absence of species of the genus in this vast area, which could mean that, along with the São Francisco River, this gap corresponds to a barrier between the 2 species.

The distribution patterns and the discontinuities reported here for *Hylaeamys* have also been documented for other groups. For instance, according to Kobayashi and Langguth (1999), the São Francisco River limits the distribution of *Callicebus coimbrai*. Similarly, Marinho-Filho and Verissimo (1997) indicated that this river corresponds to the western boundary of *C. barbarabrownae*. Both species, however, occur in the State of Sergipe. Also, geographical variations found in a group of lizards of the genus *Gymnodactylus* along the Atlantic Forest coincides with the existing rivers, including the São Francisco (Pellegrino et al. 2005). Studies on the herpetofauna of the dunes in the São Francisco River region (Rodrigues 1991a, 1991b, 1996) postulate that the last Quaternary marine transgression, together with the paleoclimatic changes in this region, isolated populations of lizards, snakes, and amphibians on either side of the river. This could explain the peculiar herpetological fauna of this region.

Carnaval and Moritz (2008) proposed a climate model in which forest areas that remained intact during these climatic changes served as a refuge for wildlife. In the Caatinga, the habitat locally named "brejos de altitude," islands of humid forest associated with mountains within the Caatinga domain, represent remnants of these events. In the Atlantic Forest, on the other hand, 2 refuge areas, one in the southern region of Bahia and another in a region of forest in the State of Pernambuco, have been identified as fitting this model. Interestingly, these Pleistocene refugia coincide with the distribution of the collection sites of the 2 species of *Hylaeamys* in the Atlantic Forest.

We suspect that the absence of *Hylaeamys* in the Sergipe part of the Reconcavo Baiano is the result of sampling artifact, as these areas harbor suitable vegetation for *Hylaeamys* species (possibly *H. seuanezi*). We also believe that the São Francisco River, as well as the drier vegetation associated with the lower course of this river, has probably played an important role in the origin of these species. Nowadays, it may also play a role as a barrier to gene flow maintaining them as independent evolutionary entities.

Through various studies based on morphology and/or molecules and the distribution of various taxa, it has been possible to trace a connection between the evolutionary history of taxa and the biogeographical areas they inhabit (Patton et al. 1997, 2000; Patton and da Silva 1998; Costa 2003; Leite 2003). However, any statement about the evolutionary processes that led to diversification patterns within *Hylaeamys* in the Atlantic Forest remains purely speculative, and requires additional phylogenetic evidence. Studies on the distribution of species, geographic variation, and phylogenetic relationships are important aspects (Patton et al. 1997), and together they provide a solid foundation for the comprehension of the biological diversity and its origin.

Resumo

Atualmente, sete espécies estão alocadas no gênero *Hylaeamys*, mas as suas delimitações e respectivas distribuições ainda permanecem incertas, principalmente na Floresta Atlântica brasileira. Através de análises morfométricas, realizadas através de abordagens univariadas (diagramas de Dice-Leraas) e multivariadas (análise canônica discriminante), somadas a análises qualitativas e a informações citogenéticas avaliamos a variação existente entre as populações do gênero ao longo da Floresta Atlântica. Foi possível corroborar a hipótese de que existem duas espécies do gênero neste bioma: *H. oniscus*, que encontra-se distribuída na margem norte do Rio São Francisco, na Floresta Atlântica ao norte do Rio São Francisco, desde o Estado de Alagoas até o Estado da Paraíba, e *H. seuanezi*, que se distribuí na margem sul do Rio São Francisco, desde o sul do Estado da Bahia até o norte do Estado do Rio de Janeiro. *Hylaeamys laticeps*, o nome empregado anteriormente para esta entidade, foi alocado à sinonímia de *H. megacephalus*, uma espécie que habita os biomas Cerrado e Floresta Amazônica. A primeira espécie possui um crânio maior e mais robusto, com rostro mais longo e o primeiro molar superior mais estreito, e um cariótipo com 2n = 52 cromossomos e NF = 62 braços autossômicos, quando

comparada a *H. seuanezi*, que é uma espécie menor, com rostro mais curto e molares levemente mais largos e cariótipo com 2n = 48 cromossomos e NF = 60 braços autossômicos. O Rio São Francisco, bem como a vegetação mais seca associada à foz deste rio, pode ter desempenhado um papel importante na origem destes táxons, ou pode desempenhar um papel de barreira ao fluxo gênico para as populações atuais, mantendo-as como unidades evolutivas independentes.

Palavras - Chave: América do Sul, citogenética, morfologia, morfometria, Oryzomyini, Taxonomia, variação geográfica.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Dice–Leraas Diagrams.
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APPENDIX I

GAZETTEER

BRAZIL

Alagoas

1. Estação Ecológica de Murici, Murici. *Hylaeamys oniscus,* 9°13′S, 35°53′W.

2. Fazenda do Prata, 13 km SSW de São Miguel dos Campos. *Hylaeamys oniscus,* 09°53′S, 36°09′W.

3. Fazenda Santa Justina, 6 km SSE Matriz de Camaragibe. *Hylaeamys oniscus,* 09°12′S, 35°30′W.

4. Mata de Coimbra, Usina Serra Grande, Ibateguara. *Hylaeamys oniscus,* 9°00′S, 35°51′W.

5. Mata do Cedro, Usina Utinga-Leão, Rio Largo. *Hylaeamys oniscus,* 9°31′S, 35°54′W.

Bahia

6. Aritaguá, Urucutuca, Ilhéus. *Hylaeamys seuanezi*, 14°42′S, 39°05′W.

7. Banco da Vitória, Pirataquissé, Ilhéus. *Hylaeamys seuanezi,* 14°47′S, 39°06′W.

8. Buerarema, Ribeirão da Fortuna. *Hylaeamys seuanezi,* 14°56′S, 39°19′W.

9. Estação Experimental Djalma Bahia (EDJAB), Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC) Una. *Hylaeamys seuanezi,* 15°17′S, 39°04′W.

10. Estação Experimental Lemos Maia (ESMAI), Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC), Una. *Hylaeamys seuanezi,* 15°15′S, 39°05′W.

11. Estação Ecológica Nova Esperança, Wenceslau Guimarães. *Hylaeamys seuanezi,* 13°34′S, 39°42′W.

12. Fazenda Bolandeira; 10 km S Una. *Hylaeamys seuanezi,* 15°21′S, 39°0′W.

13. Fazenda Brejo Grande, 12 km S–1.7 km W Itabuna. *Hylaeamys seuanezi,* 14°55′S, 39°17′W.

14. Fazenda Dendhevea, Una. *Hylaeamys seuanezi,* 15°14′S, 39°13′W.

15. Fazenda Jueirana, Una. *Hylaeamys seuanezi,* 15°12′S, 39°9′W.

16. Fazenda Limeira, Ilhéus. *Hylaeamys seuanezi,* 14°47′S, 39°02′W.

17. Fazenda Orion, Serra das Lontras, Arataca. *Hylaeamys seuanezi,* 15°07′S, 39°15′W.

18. Fazenda Subauma, Cairu. *Hylaeamys seuanezi,* 13°31′S, 39°02′W.

19. Fazenda Unacau, 8 km SE São José. *Hylaeamys seuanezi,* 15°05′S, 39°21′W.

20. Gandu. *Hylaeamys seuanezi,* 13°44′S, 39°29′W.

21. Ilhéus. *Hylaeamys seuanezi,* 14°47′S, 39°02′W.

22. Parque Zoobotânico da CEPLAC, 6 km E de Itabuna. *Hylaeamys seuanezi,* 14°48′S, 39°20′W.

23. Reserva Biológica de Una, Una. *Hylaeamys seuanezi,* 15°17′S, 39°4′W.

24. Reserva Biológica Pau-brasil, 15 km NW de Porto Seguro. *Hylaeamys seuanezi,* 15°27′S, 39°39′W.

25. Reserva Particular do Patrimônio Natural (RPPN) Serra do Teimoso Jussari. *Hylaeamys seuanezi,* 15°12′S, 39°29′W.

Espírito Santo

26. Fazenda Santa Terezinha, 33 km NE de Linhares. *Hylaeamys seuanezi,* 19°12′S, 39°50′W.

27. F. M. A. Linhares. *Hylaeamys seuanezi,* 19°10′S, 40°10′W.

28. Linhares. *Hylaeamys seuanezi,* 19°25′S, 40°04′W.

29. Santa Teresa. *Hylaeamys seuanezi,* 19°56′S, 40°36′W.

Minas Gerais

30. Alto da Consulta, Poços de Caldas. *Hylaeamys megacephalus*, 21°47′′S, 46°33′W.

31. Coromandel (includes Fazenda da Barra and Fazenda Marques). *Hylaeamys megacephalus*, 18°28′S, 47°13′W.

32. Engenheiro Reeve–Matilde, Alfredo Chaves. *Hylaeamys seuanezi*, 20°33′S, 40°49′W.

33. Lagoa Santa. *Hylaeamys megacephalus*, 19°37′S, 43°53′W.

34. Nova Ponte (includes Fazenda do Sr. Vasco Naves and Mata Península). *Hylaeamys megacephalus*, 19°08′S, 47°40′W.

35. Parque Acangau, Paracatú. *Hylaeamys megacephalus*, 17°13′S, 46°52′W.

36. Parque Estadual do Rio Doce, 13 km E Marliéria. *Hylaeamys seuanezi*, 19°32′S, 42°32′W.

37. Parque Nacional Grande Sertão Veredas, Formoso. *Hylaeamys megacephalus*, 15°16′S, 45°52′W.

38. Passos. *Hylaeamys megacephalus*, 20°43′S, 46°36′W .

39. Rio Doce. *Hylaeamys seuanezi*, 20°14′S, 42°53′W.

Paraíba

40. Fazenda Pacatuba, 10 km NE de Sapé. *Hylaeamys oniscus*, 07°02′S, 35°09′W.

Pernambuco

41. Saltinho, Rio Formoso. *Hylaeamys oniscus*, 8°40′S, 35°09′W.

42. São Lourenço da Mata. *Hylaeamys oniscus*, 8°00′S, 35°03′W.

Rio de Janeiro

43. Fazenda União, Casimiro de Abreu. *Hylaeamys seuanezi*, 22°25′S, 42°02′W.

44. Reserva Poço das Antas, Silva Jardins. *Hylaeamys seuanezi*, 22°35′S, 42°17′W.

São Paulo

45. Barretos. *Hylaeamys megacephalus*, 20°33′S, 48°33′W.

46. Teodoro Sampaio. *Hylaeamys megacephalus*, 52°10′S, 22°31′W.

PARAGUAY

Amambay

47. 28 km SW from Pedro Juan Caballero. *Hylaeamys megacephalus*, 22°43′S, 55°56′W.

Caaguazu

48. 22.5 km N Coronel Oviedo. *Hylaeamys megacephalus*, 25°25′S, 56°27′W.

Canediyu

49. 13.3 km N Curuguaty. *Hylaeamys megacephalus*, 24°22′S, 55°42′W.

50. Colonia Chupa Pou. *Hylaeamys megacephalus*, 24°09.380′S, 55°42.300′W.

51. Estancia Felicidad. *Hylaeamys megacephalus*, 24°09.380′S, 55°42.300′W

San Pedro

52. Ganadera La Carolina. *Hylaeamys megacephalus*, 24°05.698′S, 56°24.439′W.

Paraguari

53. Tacuati, Aca Poi. *Hylaeamys megacephalus*, 23°27′S, 56°35′W.

APPENDIX II

Hylaeamys megacephalus specimens examined (M = male, F = female, I = unknown sex):

BRAZIL: Minas Gerais: **Coromandel:** Fazenda da Barra: **M**, UFMG 3 skin and skull; **F**, UFMG 2 skin and skull. Fazenda Marques: **M**, UFMG 59 skin and skull, UFMG 40 skin and skull; **F**, UFMG 32 skin and skull. **Lagoa Santa: M**, ZMC 268 skin and skull; **F**, BMNH 881282 skin and skull, ZMC 269 skin and skull, ZMC 389

skin and skull; **I**, ZMC 266 skin and skull. **Nova Ponte:** Fazenda do Sr. Vasco Neves: **M**, UFMG 02 skin and skull; **F**, UFMG 19 skin and skull, UFMG 1 skin and skull. Mata do Vasco: **M**, UFMG 44 skin and skull; **F**, UFMG 45 skin and skull. Mata Península: **M**, UFMG 27 skin and skull; **F**, UFMG 24 skin and skull. **Paracatu:** Parque Acangau: **M**, DZUnB 1016 skin and skull, DZUnB 1026 skin and skull. **Formoso:** Parque Nacional Grande Sertão Veredas: **M**, MZUSP M97140 skin and skull, MZUSP M97126 skin and skull; **F**, MZUSP M97123 skin and skull, MZUSP M97033 skin and skull. **Passos: M**, UFMG 19 skin and skull, UFMG 33 skin and skull. **Poços de Caldas:** Alto da Consulta: **M**, UFMG 11 skin and skull, UFMG 6 skin and skull, UFMG 36 skin and skull, UFMG 9 skin and skull, UFMG 4 skin and skull. São Paulo: **Barretos: F**, MZUSP 1428 skin and skull. **Teodoro Sampaio: M**, MZUSP 25163 skin and skull, MZUSP 25164 skin and skull, MZUSP 25165 skin and skull, MZUSP 24994 skin and skull, MZUSP 24050 skin and skull; **F**, MZUSP 24046 skin and skull, MZUSP 8855 skin and skull. PARAGUAY: Amambay: **Pedro Juan Caballero: M**, UMMZ 125233 skin and skull, UMMZ 125234 skin and skull; **F**, UMMZ 125454 skin and skull, UMMZ 125455 skin and skull. Caagazu: **Coronel Oviedo: M**, UMMZ 124499 skin and skull. Canadiyu: **Coruguaty: M**, UMMZ 133811 skin and skull, UMMZ 126010 skin and skull, UMMZ 133801 skin and skull, UMMZ 133802 skin and skull, UMMZ 133803 skin and skull, UMMZ 133804 skin and skull, UMMZ 133808 skin and skull, UMMZ 133811 skin and skull, UMMZ 137010 skin and skull, UMMZ 137011 skin and skull; **F**, UMMZ 133807 skin and skull. **Colonia Chupa Pou: M**, GD 463 skin and skull. **Estancia Felicidad: M**, GD 411 skin and skull, GD 440 skin and skull. Paraguari: **Tacuati:** Aca Poi: **F**, NMNH 293148 skin and skull. San Pedro: **Ganadera de la Carolina: M**, GD 383 skin and skull, GD 384 skin and skull; **F**, GD 381 skin and skull, GD 382 skin and skull.

APPENDIX III

Hylaeamys oniscus 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 PBG76 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.

APPENDIX IV

Hylaeamys seuanezi 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. **Jussarí:** RPPN Serra do Teimoso, Jussarí: 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. ESMAI, 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: **Marliéria:** Parque Estadual do Rio Doce; 13 km E Marliéria: 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 Jardim:** Reserva Poço das Antas, Silva Jardim: 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.