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The genus *Abrawayaomys* Cunha and Cruz, 1979 (Rodentia: Cricetidae: Sigmodontinae): geographic variation and species definition

Alexandre Reis Percequillo,* Caryne Aparecida de Carvalho Braga, Marcus Vinicius Brandão, Edson Fiedler de Abreu-Júnior, Juliana Gualda-Barros, Gisele M. Lessa, Maria Rita Silvério Pires, and Erika Hingst-Zaher

Laboratório de Mamíferos, Departamento de Ciências Biológicas, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo, Av. Pádua Dias 11, Caixa Postal 9, 13418-900 Piracicaba, São Paulo, Brazil (ARP, EFAJ)
Programa de Pós-Graduação em Ecologia, Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho 373, 21941-590 Rio de Janeiro, Rio de Janeiro, Brazil (CACB)
Universidade Federal de São Carlos, Campus Sorocaba, Departamento de Biologia, Laboratório de Diversidade Animal, Rodovia João Leme dos Santos km 110, Itinga, 18052-780 Sorocaba, São Paulo, Brazil (MVB)
Coleção de Mamíferos, Departamento de Vertebrados, Museu de Zoologia da Universidade de São Paulo, Av. Nazaré 481, Ipiranga, 04263-000 São Paulo, São Paulo, Brazil (JGB)
Museu de Zoologia João Moojen, Departamento de Biologia Animal, Universidade Federal de Viçosa, Vila Gianetti 32, 36570-000 Viçosa, Minas Gerais, Brazil (GML)
Programa de Pós-Graduação em Diversidade Biológica e Conservação, Instituto de Ciências Exatas e Biológicas, Departamento de Biodiversidade, Evolução e Meio Ambiente, Laboratório de Zoologia dos Vertebrados, Universidade Federal de Ouro Preto, Campus Universitário Morro do Cruzeiro, Rua Quatro 786, 35400-000 Ouro Preto, Minas Gerais, Brazil (MRSP)
Museu Biológico do Instituto Butantan, Av. Vital Brazil 1500, Butantã 05503-900, São Paulo, São Paulo, Brazil (EHZ)

* *Correspondent: percequillo@usp.br*

Abrawayaomys is a genus endemic to the Atlantic Forest with unique craniodental attributes within the radiation of sigmodontine rodents. Recent data hypothesized the existence of 2 species of *Abrawayaomys*, namely *A. ruschii* (from the Brazilian states of Espírito Santo, Rio de Janeiro, and São Paulo) and *A. chebezi* (from the Argentinean province of Misiones and the Brazilian state of Paraná), as well as a possible undescribed species (from the Brazilian state of Minas Gerais). Herein, based on a large series of recently collected specimens, we assessed the congruence between morphologic and molecular characters to search for discontinuities on these features across geography to delimit species within the genus, testing the aforementioned hypothesis. Morphological analyses, both qualitative and quantitative, showed that all characters are polymorphic throughout the geographic range of the genus. Results from phylogenetic analyses of cytochrome *b* (*Cytb*) data showed the topology (Misiones (Minas Gerais (São Paulo, Rio de Janeiro))), which is better explained as geographic rather than taxonomic variation, based on low values of genetic divergence observed between all specimens. Therefore, we reject the hypothesis of a polytypic *Abrawayaomys*, synonymizing *A. chebezi* to *A. ruschii*, and do not recognize specimens from Minas Gerais state as representing a distinct species.

Abrawayaomys é um gênero endêmico da Floresta Atlântica que apresenta características crânio-dentais exclusivas dentre os roedores sigmodontíneos. Dados recentes sugerem a existência de duas espécies distintas de *Abrawayaomys*, *A. ruschii* (com ocorrência nos estados brasileiros do Espírito Santo, Rio de Janeiro e São Paulo) e *A. chebezi* (ocorrendo na Província de Misiones, Argentina, e no Estado do Paraná, Brasil), além de uma possível espécie não descrita (espécimes do Estado de Minas Gerais, Brasil). No presente estudo, com base em uma série expressiva de espécimes recentemente coletados, avaliamos a congruência entre caracteres morfológicos e moleculares buscando encontrar possíveis descontinuidades discretas associadas à geografia, a fim de delimitar

as espécies do gênero com base na hipótese taxonômica acima mencionada. As análises morfológicas qualitativas e quantitativas mostraram que todos os caracteres são polimórficos ao longo da geografia e não apresentam descontinuidades discretas que favoreçam o reconhecimento de distintas entidades taxonômicas. Os resultados das análises filogenéticas a partir de sequências de cytb mostraram a seguinte topologia (Misiones (Minas Gerais (São Paulo, Rio de Janeiro))), que é melhor explicada como uma variação geográfica e não taxonômica, com base nos baixos valores de divergência genética observados entre todos os espécimes. Portanto, nós rejeitamos a hipótese de um gênero *Abrawayaomys* politípico, reconhecendo *A. chebezi* como sinônimo júnior de *A. ruschii* e não reconhecendo os espécimes de Minas Gerais como uma nova espécie.

Key words: Atlantic Forest, geographic variation, morphology, morphometry, phylogeny, Ruschi's spiny mouse, South America, taxonomy

Cunha and Cruz (1979) described the genus *Abrawayaomys* with a sole species, *A. ruschii*, based on a single specimen obtained in the state of Espírito Santo, southeastern Brazil. Cunha et al. (1978) had previously reported the existence of a new genus and species, "close to *Neacomys*" (as both present spiny fur), that would be described later by Cunha and Cruz honoring J. P. "Abrawaya" [*sic*] and A. Ruschi, respectively. Leite (Y. Leite, Universidade Federal do Espírito Santo, pers. comm.) stated that the correct spelling of the generic patronymic is Abravaya and that Cunha and Cruz (1979) consistently misspelled the name throughout the text. Leite also argued "that the name should stay as it is written in the original description given that incorrect original spellings must be corrected only if there is clear evidence of error in the original publication itself, without recourse to any external source of information (ICZN 1999, Art. 32.5.1)."

Nearly a decade later a second specimen of *Abrawayaomys* was captured in Minas Gerais, Brazil (Stallings 1989), and a third one was obtained from owl pellets in Misiones, Argentina (Massoia et al. 1991). More recently, new records of *A. ruschii* from Brazil, collected in the states of Rio de Janeiro (Cunha and Rajão 2007; Pereira et al. 2008), Minas Gerais (Pardiñas et al. 2009; Passamani et al. 2011), São Paulo (Vivo et al. 2011; Ventura et al. 2013), Paraná (Cerboncini et al. 2014), and Santa Catarina (Cherem et al. 2011; Maestri et al. 2015), were published.

However, as the samples so far available are still quite few, knowledge of the morphological variation and geographic distribution for this genus is minimal. Pardiñas et al. (2009) granted the status of species to specimens from Misiones, Argentina, based on their qualitative and quantitative variation, describing *A. chebezi*. Pardiñas et al. (2009) also provided an update on the morphological variation in *Abrawayaomys*, with some comments on its putative phylogenetic relationships. Furthermore, as a consequence of such paucity of information, Pardiñas et al. (2009, 2016) and Ventura et al. (2013) suggested that specimens from Minas Gerais (that represent the northernmost record of the species distribution) might exhibit distinct morphological traits that would warrant them to be recognized as a new species.

The availability of several recently collected specimens in Brazilian scientific collections compelled us to provide a reappraisal of the morphological and molecular variation and the geographic distribution of *Abrawayaomys*. Moreover, these specimens allowed us to test Pardiñas et al.'s hypothesis in which *Abrawayaomys* comprises 3 distinct species: *A. chebezi* restricted to Argentina and southwestern Brazil, Paraná state; *A. ruschii* occurring in the coastal portion of Brazilian Atlantic Forest, in the states of Espírito Santo, Rio de Janeiro, and São Paulo; and an undescribed species restricted to the forests of Minas Gerais state. The present contribution assesses the definition of this enigmatic genus and its species, providing additional data that will endow a solid basis for future studies on the relationships within Sigmodontinae.

Materials and Methods

Specimens.—The material we examined consisted of skins, skulls, skeletons, and tissue samples of *Abrawayaomys* housed in the following zoological collections: Coleção de Mamíferos da Universidade Federal de Lavras (CMUFLA; Lavras, Minas Gerais, Brazil); Departamento de Zoologia, Universidade Federal do Paraná (DZUP; Curitiba, Paraná, Brazil); Coleção do Laboratório de Mamíferos da Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo (LMUSP; Piracicaba, São Paulo, Brazil); Coleção do Laboratório de Zoologia dos Vertebrados da Universidade Federal de Ouro Preto (LZV-UFOP; Ouro Preto, Brazil); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN; Buenos Aires, Argentina); Museu Nacional, Universidade Federal do Rio de Janeiro (MN; Rio de Janeiro, Brazil); Museu de Zoologia da Universidade Federal de Viçosa (MZUFV; Viçosa, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP; São Paulo, Brazil); Universidade Federal de Minas Gerais (UFMG; Belo Horizonte, Brazil); National Museum of Natural History, Smithsonian Institution (USNM; Washington, D.C., United States). For morphological analyses, we also obtained qualitative and quantitative information from the literature, especially for Argentinean samples of *A. chebezi* (Pardiñas et al. 2009, 2016). For molecular analyses, we obtained additional sequences of specimens of *Abrawayaomys* in GenBank; we also included sequences of specimens representing the 9 tribes of Sigmodontinae and 2 genera *incertae sedis*—due to the controversial phylogenetic position of the genus (see Ventura et al. 2013). Specimens included in morphological and molecular analyses are reported in the Supplementary Data SD1 and SD2. This study is in conformity with the ASM guidelines for the use of wild mammals in research and education (Sikes et al. 2016).

Qualitative morphological analyses.—To describe qualitative external, cranial, and dentition characters and their variation, we employed the terminology proposed by Reig (1977), Voss (1988, 1993), Carleton and Musser (1989), Voss and Carleton (1993), Steppan (1995), and Pacheco (2003). We classified specimens in 3 age classes based on enamel wear of upper molars: age class 1, no or minute wear, with minimal exposition of dentine restricted to upper portion of main cusps (young); age class 2, medium to moderate wear, with some exposition of dentine on isolated main cusps (paracone and median mure still isolated by enamel; protocone and hypocone connected by narrow dentine bridge; subadult); age class 3, moderate to heavy wear, with large exposition of dentine, and wider connection between cusps (posterior limit of paracone largely connected to median mure; protocone and hypocone largely connected medially by wide dentine basin; adult). For all subsequent analyses, we used adults only to avoid comparisons among distinct semaphoronts (except for molar descriptions and comparisons, and for some selected traits, as informed in the comparisons). Quantitative comparisons were performed with adults pooled in geographic samples (arranged by state or province), with character state frequencies presented through the text (Musser 1968; Chiquito et al. 2014).

Quantitative morphological analyses.—We obtained the following external measurements from original specimen labels: head and body length (HB); tail length (T); ear length (E); hind foot length (HF); and body mass (M). Cranial measurements were obtained with digital calipers, with data recorded to the nearest 0.01 mm. We employed the following measurements (see Voss 1988; Percequillo et al. 2011): occipito-nasal length (ONL); condylo-incisive length (CIL); length of diastema (LD); length of rostrum (LR); length of nasals (LN); breadth of rostrum (BR); length of incisive foramina (LIF); breadth of incisive foramina (BIF); length of palatal bridge (LPB); length of palate (LP); breadth of bony palate across the first upper molars (BBP); bullar length (BL); crown length of maxillary toothrow (CLM1–3) from molar 1 (M1) to molar 3 (M3); greatest crown breadth of first upper molar (BM1); breadth of anterocone of first upper molar (BM1ant); greatest zygomatic breadth (ZB); interorbital breadth (IB); length of orbital fossa (LOF); breadth of zygomatic plate (BZP); braincase breadth (BRB); braincase height (BRH); length of frontal (LF); length of parietal (LPa); length of interparietal (LIP); breadth of interparietal (BIP); mandible length (ML); mandible heigth (MH), crown length of mandibular toothrow (CLm1–3); and breadth of first inferior molar (Bm1). Dimensions are given in millimeters (mm), and the body mass in grams (g).

As our sample is small, we did not perform analyses of sexual dimorphism, assuming that this component is not a major source of variation in sigmodontines (Voss 1991; Percequillo et al. 2008; Abreu-Júnior et al. 2012). Univariate descriptive statistics and principal component analyses (PCA) were used to compare geographic samples. The PCA was performed over a subset of 13 dimensions (LR, BR, LIF, BIF, LPB, LP, LMS, BM1S, ZB, BZP, IB, LOF, BRH) including adults only (age class 3) with complete measurements (n = 17, 41.3% of the sample). Principal components were extracted from a variance-covariance matrix and computed by using the craniodental variables after transformation to their base 10 logarithms. Statistical analyses were performed with the program STATISTICA 10 (StatSoft, Inc., Tulsa, Oklahoma).

Molecular analyses.—Genomic DNA of 2 *Abrawayaomys* specimens (see Supplementary Data SD2) was extracted using DNeasy Blood and Tissue kit, following the manufacturer's protocol (Qiagen, Inc., Valencia, California). We amplified the mitochondrial cytochrome *b* (*Cytb*) gene using the primers MUS14095 (Anderson and Yates 2000) and ORYZO1 (Percequillo et al. 2011). Amplifications were performed as 35 µl reactions, using Platinum Taq DNA polymerase with recommended concentrations of primers and reagents (Life Technologies Corp., Carlsbad, California). Amplifications occurred in 35 PCR cycles of denaturation at 92°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 60 s. PCR products were purified using ExoSap-IT (Affymetrix, Inc., Santa Clara, California) and sequenced in both directions using amplification primers and BigDye Terminator (Life Technologies Corp., Carlsbad, California), on ABI3130 sequencer (Applied Biosystems Corp., Foster City, California). Sequences were edited and assembled using Geneious 6.1.4 (Biomatters Ltd., Auckland, New Zealand). Multiple sequence alignments were performed using MUSCLE (Edgar 2004) implemented on Geneious. The best-fitting nucleotide substitution model was GTR+I+G, as recommended by the Akaike Information Criterion (AIC) in jModelTest 2.1.2 (Guindon and Gascuel 2003; Darriba et al. 2012).

For phylogenetic reconstructions, we applied Maximum Likelihood (ML) and Bayesian Inference (BI) methods, and we used *Tylomys nudicaudus* as an outgroup according to the sister-group relationship of Sigmodontinae and Tylomyinae (Leite et al. 2014; Vilela et al. 2014). ML analysis was performed in RaxML 7.0.3 (Stamatakis 2006) with 20 independent searches, from which we chose the topology with the best likelihood score; nodal support was obtained by running 1,000 bootstraps replicates using the GTRGAMMAI model and the "thorough standard bootstrap" optimization option. BI analysis was performed in MrBayes 3.2.0 (Ronquist et al. 2012) by 2 independent runs with 4 chains each (Markov Chain Monte Carlo [MCMC]), proceeding for 2×10^6 generations and sampled every 1,000 generations; nodal support was obtained as posterior probability. The results of MCMC runs were verified in Tracer 1.5 (Rambaut and Drummond 2007). The first 25% of trees were discarded as burn-in. Trees were edited in FigTree 1.4.0 (Rambaut 2012). We also calculated mean sequence divergence between *Abrawayaomys* specimens using *p*-distances and pairwise deletion of missing sites in Mega 6.0 (Tamura et al. 2013). To verify the correlation between geographic and genetic distances under an isolation by distance model, we conducted a Mantel test (Mantel 1967; Smouse et al. 1986). The genetic distances between specimens were accessed through pairwise comparisons of *p*-distances in Mega 6.0 (Tamura et al. 2013). The geographic distances between specimens' localities were obtained in kilometers through the

function "earth.dist" from the "fossil" package (Vavrek 2011) in RStudio 0.99.903 (RStudio Inc. 2016). The Mantel test was performed with 5,000 permutations over the function "mantel" from the "vegan" package (Oksanen et al. 2016) in RStudio 0.99.903 (RStudio Inc. 2016).

Species definition.—Through analyses of the variation in the metrics described above, we evaluated the existence of morphological and molecular discontinuities throughout the species distribution: species were defined and recognized based on the congruence of discontinuities with qualitative, quantitative, and molecular markers (see Musser 1968; Chiquito et al. 2014). We considered this variation under Cracraft's (1983) phylogenetic species concept, whose criteria involve the diagnosability and the ancestral-descent hierarchical pattern of the lineages: populations without unique morphological traits and retrieved as non-monophyletic were not considered as discrete species.

Results

Qualitative morphological analyses.—Several traits exhibited qualitative geographic variation. On the external morphology, the ratio of tail/head and body length (T/HB), the presence and color of the apical tuft on tail, and the ventral coloration were the features that exhibited the most conspicuous variation. The T/HB ratio varied from 1.05 to 1.19 in samples from Minas Gerais, 1.24–1.34 in samples from São Paulo, around 1.19 in the sole adult from Paraná, 1.15–1.36 in samples from Santa Catarina (Maestri et al. 2015), and about 1.1 in the specimen from Misiones.

The apical tuft apparently exhibited some level of age variation, as in the sample from São Paulo (the larger sample available), specimens of young individuals exhibited inconspicuous or very short tuft and brown tail tip, subadults had moderately long and grayish tail tips (a mix of brown and gray hairs), and adults had long and predominantly whitish tufts (Fig. 1). Nevertheless, throughout geography, the apical tuft was also variably present in adults, but this condition was not homogeneously recorded because the tip of the tail was missing in several specimens, including the holotype of *A. ruschii* and specimens from Rio de Janeiro. Specimens from Minas Gerais had the apical tuft present, which ranged from short (around 4 mm in length; $n = 1$), moderately long (7 mm in length; $n = 1$), or long (9 [$n = 1$] and 10 [$n = 2$] mm in length). In this sample, color of the apical tuft was gray ($n = 1$), brown ($n = 3$), or a mix of brown and white ($n = 1$). One adult from São Paulo did not present the tuft, but this structure was present in other specimens, being short (2.8 mm) and mixed brownish-whitish ($n = 1$) or long (9.8 [$n = 1$] and 18 [$n = 1$] mm in length) and whitish in color; specimens from Paraná exhibited moderately long (7.9 mm; $n = 1$) or long (11.9 mm; $n = 1$) brown tufts; the holotype of *A. chebezi*, an adult from Argentina, exhibited a moderately long (8 mm; $n = 1$) and brown tuft.

Ventral body color varied randomly without any evident pattern. Specimens from Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and Misiones exhibited a buffy-grayish venter; the specimen from Espírito Santo exhibited an ochraceous chest; 3 specimens from Ouro Branco, Minas Gerais, had a rich buffy venter; 1 specimen from Rio Doce State Park (Espírito Santo) presented an ochraceous gray venter; specimens from São Paulo, Paraná, and Misiones had grayish, buffy-grayish, or predominantly buffy ventral regions. The 2 females from São Paulo and Minas Gerais exhibited 4 pairs of mammae distributed in the inguinal, abdominal, thoracic (nearly postaxial), and pectoral positions.

Fig. 1.—Distal portion of the tail of 3 specimens of *Abrawayaomys* from São Paulo state, detailing the development of the apical tuft. From left to right: young with no trace of apical tuft (MZUSP 34718); young adult or subadult with small tuft of white hairs (MZUSP 34721); and adult with well-developed tuft of white hairs (MZUSP 35268).

The skull also presented noticeable variation in the shape of the nasofrontal suture, lateral expansion of the nasals, interorbital region, incisive foramina, alisphenoid strut, as well as in some dental characters, such as the orientation of the incisors and the presence of an anteromedian flexus and flexid. Other traits were also variable, as the mesopterygoid fossa and the development of the mesoloph and the mesolophid, which we discuss later due to its usage as diagnostic by Pardiñas et al. (2009, 2016). The nasal bones tapered gradually toward their caudal extremities in all examined specimens (Fig. 2). Nevertheless, the caudal end of nasal bones can vary in shape, ranging from narrow and acute (defining a nasofrontal suture V-shaped, in specimens from Espírito Santo [$n = 1$], Minas Gerais [$n = 5$], São Paulo [$n = 2$], and Misiones [$n = 1$]); moderately narrow and acute (forming a suture nearly V-shaped, observed in specimens from São Paulo [$n = 3$] and Paraná [$n = 1$]); and blunt and squared (defining a suture nearly square-shaped [Fig. 2], in individuals from Minas Gerais [$n = 1$], São Paulo [$n = 3$], and Paraná [$n = 1$]). On the other hand, there was some variation on the rostral portion of the nasal, with some specimens exhibiting the rostral end of the nasals expanded laterally (Fig. 2): slightly expanded, in specimens from Espírito Santo ($n = 1$), Minas

Gerais (n = 3), and São Paulo (n = 5), or largely expanded in specimens from Minas Gerais (n = 1 [see also Pardiñas et al. 2009: figure 9]) and São Paulo (n = 1). Alternatively, 9 specimens had the nasal bone without lateral expansion of their rostral portion: 4 from Minas Gerais, 2 from São Paulo, 2 from Paraná, and 1 from Argentina.

The interorbital region was quite polymorphic in all samples (Fig. 3), with no discernible geographic pattern of discontinuity, as for all traits so far evaluated. The shape of this region can be hourglass in specimens from Minas Gerais (n = 2), São Paulo (n = 5), and Misiones (n = 1); convergent to moderately convergent posteriorly in specimens from Minas Gerais (n = 5), Rio de Janeiro (n = 1), São Paulo (n = 2), and Paraná (n = 2); or strongly convergent posteriorly in specimens from Minas Gerais (n = 2), with nearly squared supraorbital margins (all other specimens exhibited rounded, smooth supraorbital margins).

The incisive foramina were moderate in size (see qualitative analyses), with some variation on the position of the posterior margins (Fig. 4), which can reach the alveolus of M1, in the same level of the alveolus, not penetrating between upper molar series in specimens from Minas Gerais (n = 1) and São Paulo (n = 1); reach the alveolus of M1, slightly penetrating between upper molar series in specimens from São Paulo (n = 1); or, not reach the alveolus, being variably distant from the molar series in specimens from Minas Gerais (n = 7), Rio de Janeiro (n = 1), São Paulo (n = 6), Paraná (n = 1), and Misiones (n = 1). The lateral margins were also variable, being more frequently wider or slightly wider anteriorly in samples from Espírito Santo (n = 1), Minas Gerais (n = 5), Rio de Janeiro (n = 1), and São Paulo (n = 6); slightly wider medially in 1 specimen from Minas Gerais and 1 from Paraná; or parallel, in specimens from Minas Gerais, São Paulo, Paraná, and Misiones (n = 1 for these 4 samples).

The presence of the alisphenoid strut also varied randomly without any clear geographic pattern: 1 specimen from Espírito Santo exhibited the strut; 5 specimens from Minas Gerais presented this bony strut—in 1 specimen (UFMG 2492) mentioned

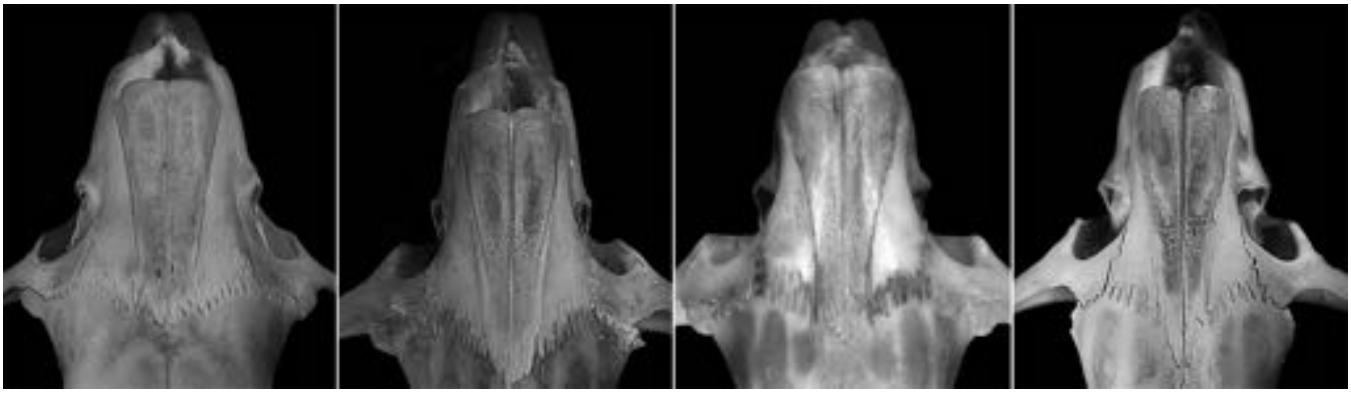

Fig. 2.—Detail of the rostral region of the skull of 4 specimens of *Abrawayaomys* from São Paulo and Minas Gerais states, showing variation in the shape and extent of posterior margins of nasals and the lateral expansion of the anterior portion of nasals. From left to right: nasofrontal suture blunt and squared, not surpassing the lacrimal level (MZUFV 3590); nasofrontal suture V-shaped, with posterior margin of nasal bones moderately narrow and acute, surpassing the lacrimal level (MZUSP 34720); nasofrontal suture blunt and squared, aligned to the lacrimal (UFGM 2492); nasofrontal suture V-shaped, with posterior margin narrow and acute, largely surpassing the lacrimal level (LZV-UFOP 206 R). Also note the anterior portion of nasals expanded laterally (UFGM 2492 and LZV-UFOP 206 R).

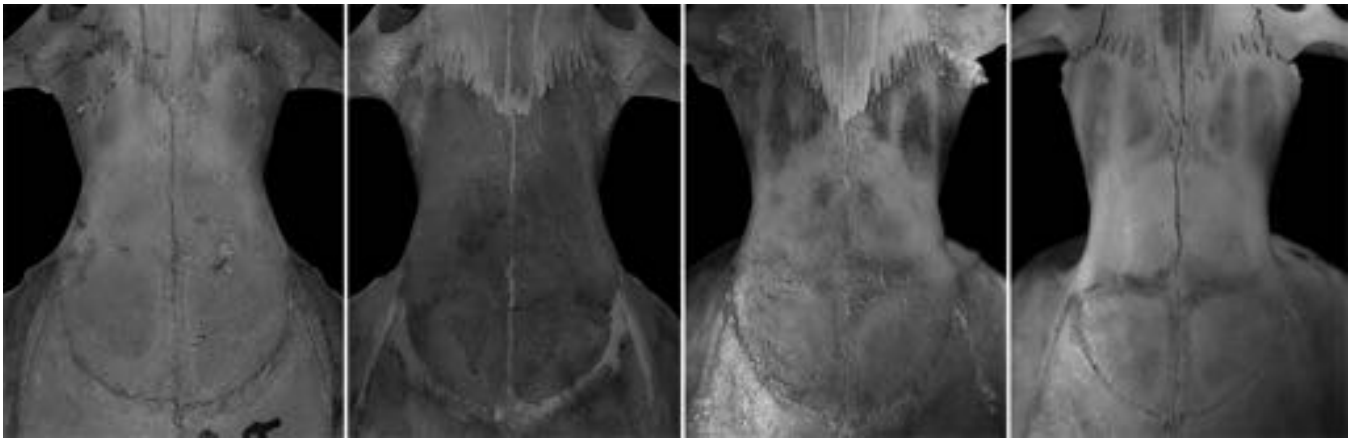

Fig. 3.—Detail of the interorbital region of the skull of 2 specimens of *Abrawayaomys*. From left to right: interorbital region hourglass shaped, with rounded supraorbital margins (MZUSP 32319); interorbital region slightly divergent posteriorly, with squared supraorbital margins (MZUSP 35268); interorbital region convergent posteriorly, with nearly squared supraorbital margins (LZV-UFOP 206 R); interorbital region strongly convergent posteriorly, with squared supraorbital margins (MZUSP 34720).

by Pardiñas et al. (2009, 2016) the structure was absent, leading these authors to hypothesize that such structure would not be present in samples from Minas Gerais, and that this absence, along with other traits, would define a new species from this state; and in another (LZV-UFOP 354 R) its presence was asymmetric, being small and delicate on the right side, and a little more robust on the left side (a specimen of a young individual from Minas Gerais was also asymmetric, with the strut small and delicate on the right side, and absent on the left side [LZV-UFOP 326 R]); the individual from Rio de Janeiro and all but 1 specimen from São Paulo presented the strut; both specimens from Paraná lacked the strut; and the Misiones specimen also exhibited this bony bar.

The anterior margin of the mesopterygoid fossa was variable, not reaching the molar series or penetrating between the molar series. In specimens from Espírito Santo, the fossa reached the alveolus of M3; in Minas Gerais, the fossa reached the alveolus of M3 in 4 specimens, and the posteroloph of M3 in 2 specimens; in the specimen from Rio de Janeiro, the fossa was leveled with the alveolus of M3; in São Paulo, the anterior margin of the fossa was distant from molar series in 4 specimens, reached the alveolus of M3 in 2 specimens and the posteroloph of M3 in 1 specimen; specimens from Paraná also presented anterior margins of the mesopterygoid fossa distant from M3, a feature also shared with the specimen from Misiones.

Proodont or orthodont upper incisors occurred randomly throughout the geographic samples (Fig. 5). The proodont condition was observed in specimens from Espírito Santo (n = 1), Minas Gerais (n = 4; being 2 slightly proodont, and 2 more pronounced proodont), Rio de Janeiro (n = 1), São Paulo (n = 7; slightly proodont in 4), and Paraná (n = 2) and Misiones (n = 1). Orthodont incisors were present in samples from Minas Gerais (n = 3) and São Paulo (n = 1).

The anteromedian flexus was also highly variable in all available samples (Fig. 6): in Espírito Santo the flexus was present; in the samples from Minas Gerais the flexus was

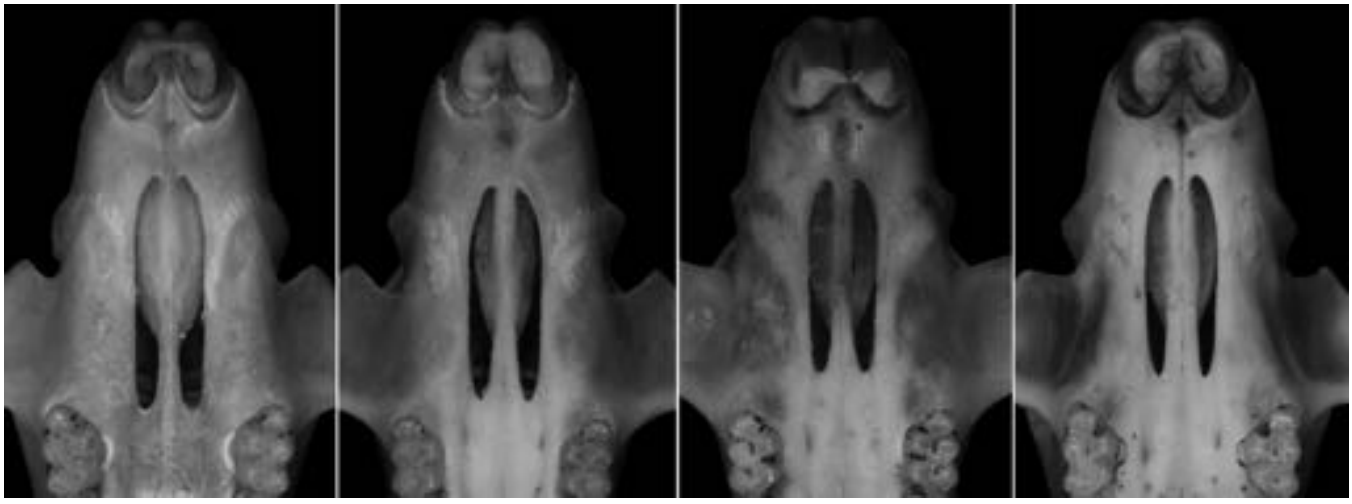

Fig. 4.—Detail of the ventral view of the skull of *Abrawayaomys*, illustrating variation in the length and width of the incisive foramina. On length, from left to right: posterior margin penetrating between upper molar series (MZUSP 32328); posterior margin not reaching, but close, to the alveolus of M1 (MZUSP 35268); posterior margin not reach the alveolus, being variably distant from the molar series (UFMG 2492 and LZV-UFOP 206 R). On width, from left to right: lateral margins parallel (MZUSP 32328 and MZUSP 35268); slightly wider anteriorly (UFMG 2492); slightly wider medially (LZV-UFOP 206 R).

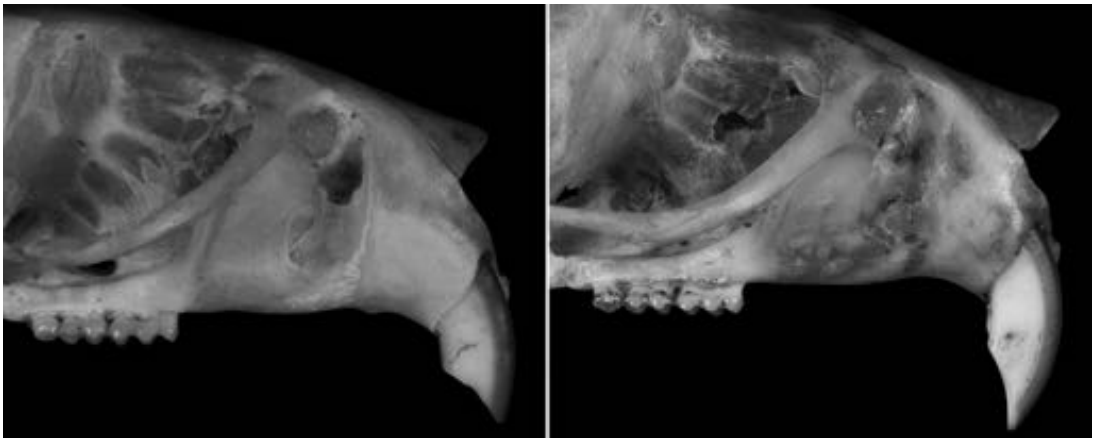

Fig. 5.—Orientation of upper incisors of 2 specimens of *Abrawayaomys*. From left to right: proodont (MZUSP 35268) and orthodont (UFMG 2492).

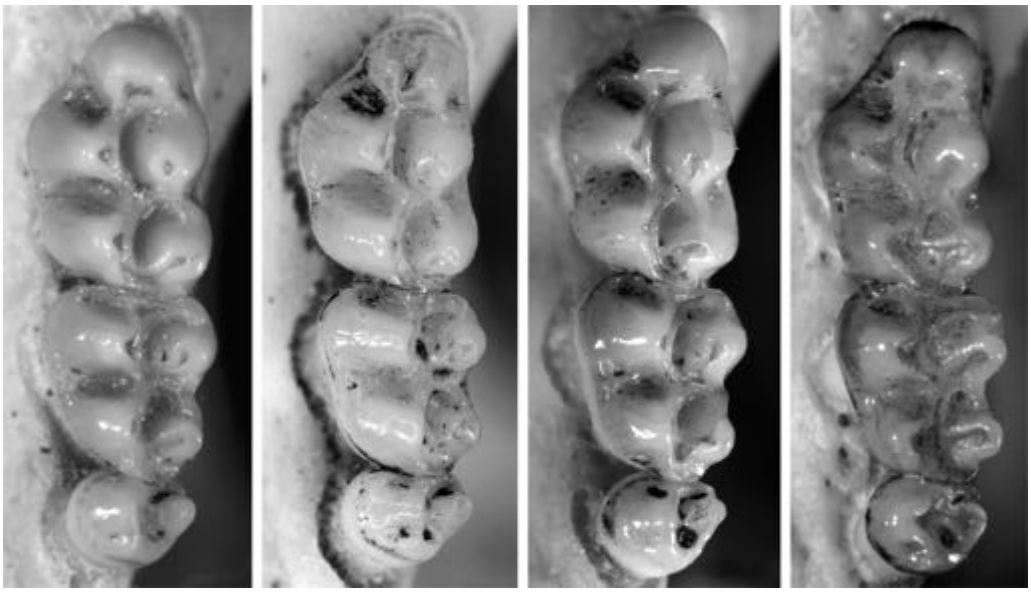

Fig. 6.—Upper molar series, in occlusal view, of 4 specimens of *Abrawayaomys*. From left to right: MZUSP 35267, MZUSP 32327, MZUSP 34717 (all age class 1), and MZUSP 32319 (age class 2). Note: the presence (MZUSP 32327 and MZUSP 32319) and absence (MZUSP 35267 and MZUSP 34717) of the anteromedian flexus on the procingulum; the presence of a well-developed protoloph (MZUSP 34717), a small protoloph (MZUSP 32319), a small protosyle (MZUSP 35267), and the absence of both (MZUSP 32327); the small mesoloph on M1, fused to the anteromedial surface of the metacone, not reaching the labial margin (all specimens, except MZUSP 35267, that presents this mesoloph more labially positioned); the more developed mesoloph on M2, more labially positioned, reaching the labial margin (all specimens).

present in 7 specimens (absent in 3 individuals); in the only available specimen from Rio de Janeiro the flexus was absent; in São Paulo the flexus was present in 2 specimens (absent in 3 specimens; asymmetric in 1 specimen); specimens from Paraná exhibited too much wear, and the condition was not clear (as in some specimens from São Paulo); and the specimen from Misiones presented the flexus. Considering the anteromedian flexid (Fig. 7), almost the same specimens that exhibited the flexus also possessed the flexid, with few exceptions: the specimen from Espírito Santo had the flexus, but lacked the flexid, since the procingulum is very narrow; some specimens from Minas Gerais exhibited the flexid (n = 5; 2 of them presented the flexus, without the flexid; 1 of them exhibited a very shallow flexid, with the labial conulid smaller and lower than the lingual), some specimens lacked it (n = 5); the specimen from Misiones lacked the anteroflexid, although presented the flexus.

Nevertheless, there were some specimens in which the identification of these structures was not trivial. In the MZUSP 34717, from São Paulo, there was a small projection of enamel on both left and right molars that apparently crosses the procingulum diagonally and could be interpreted as a small and shallow anteromedian flexus, now obliterated by wear; moreover, this specimen presented a well-developed protoloph (a small loph positioned between the procingulum and protocone on the lingual margin of molar, dividing the protoflexus in 2, an anterior anteroprotoflexus and a posteroprotoflexus) that could be confounded with a small lingual anterocone. In the MZUSP 35469, from São Paulo, the left M1 exhibited a well-marked and visible anteromedian flexus, clearly defining anterolabial and anterolingual conules; the protoloph was absent on this tooth; on the other hand, the right M1 showed a large and high anterolabial conule, a shallow and incipient anteromedian flexus, and a very reduced and low structure, bisected medially by a very superficial notch, with the lingual portion more developed and reaching the margin of the molar; we do not know if these structures are remnants of the anterolingual conule and the protoloph.

The mesoloph was highly variable, and uncorrelated with geography. In general, the mesoloph of M1 was fused to the paracone, which was an isolated cusp, not connected to the median mure or to the protocone; this cusp was only in contact to the mesoloph in unworn molars, but with moderate wear the paracone appeared to be connected to a structure formed by the fusion of the median mure and mesoloph (Fig. 6, specimen MZUSP 32319). In addition, there was a loph emerging from this paraloph-mesoloph that was oriented posteriorly and fused to the labial portion of the metacone or the mid-portion of the metacone: this loph could be the mesoloph or a paralophule. The mesostyle appears to be absent, since no style is observed on the labial margin of the paraflexus; alternatively, this lophule could be a more medial mesostyle. One specimen from São Paulo exhibited the mesoloph of M1 free from the paracone: it was a short mesoloph, fused to the anterior portion of metacone; the paracone was connected to the median mure. In this specimen the posterior-oriented loph that emerges from the paraloph-mesoloph seems to be the mesoloph.

The mesoloph of M2 was also variable, as in some specimens it was similar to M1; in other specimens (see Fig. 6, MZUSP 34717) the mesoloph was an independent loph, connected to the median mure and connected labially to the paracone and to

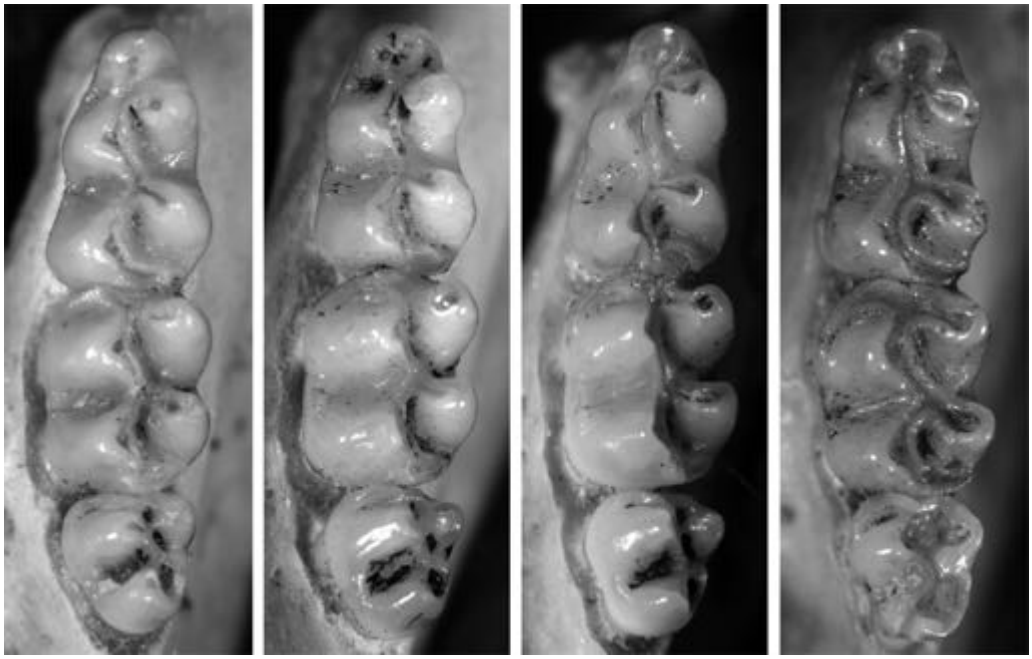

Fig. 7.—Lower molar series, in occlusal view, of 4 specimens of *Abrawayaomys*. From left to right: MZUSP 35267, MZUSP 32327, MZUSP 34717 (all age class 1), and MZUSP 32319 (age class 2). Note: the anteroconid constricted medially, apparently divided by a narrow anteromedian flexid (MZUSP 32327); the very narrow anteroconid (all specimens, even MZUSP 32327); the absence of a mesolophid on m1 (all specimens); the presence of a small mesolophid or lophulid on m2 (all specimens).

the metacone (similar to the M1 described above); the paracone was connected to the median mure and also to the metacone by a small and delicate anteromedial paralophule; the main difference with the M1 is that this loph (mesoloph, paralophule, mesoloph plus paralophule) was more labially positioned in all specimens examined.

The mesolophid was more consistently absent on the m1 of most specimens, as well as the mesostylid; few individuals from São Paulo (MZUSP 32319, MZUSP 35266) and Minas Gerais (CMUFLA 906, LZV-UFOP 58 R) exhibited a very small lophid, as a small ridge on the wide entoflexid, emerging from either the median murid or from the junction between the median murid and the entoconid; in these individuals the entostylid was always absent. The same pattern was observed in the m2, but this lophid was more commonly observed (Fig. 7).

Quantitative morphological analyses.—Our sample was comprised of 8 young (age class 1), 6 subadults (age class 2), and 23 adults (age class 3). Some of these adults lacked some measurements because the skulls were broken, which made the sample size smaller and precluded any objective comparison based on age, sex, and geography.

The scatterplot (Fig. 8) of the individual scores along the 1st and 2nd principal components (PC1, PC2) showed that specimens from different geographical samples overlapped throughout the multivariate space: specimens from Minas Gerais (the largest sample available for statistical analysis) were the most widespread, overlapping with several specimens from São Paulo. The type specimen of *A. ruschii* (MN 23075; specimen ES) was retrieved close to the specimen from Paraná; the holotype of *A. chebezi* (MACN 20253; specimen MIS), from Argentina, was slightly isolated

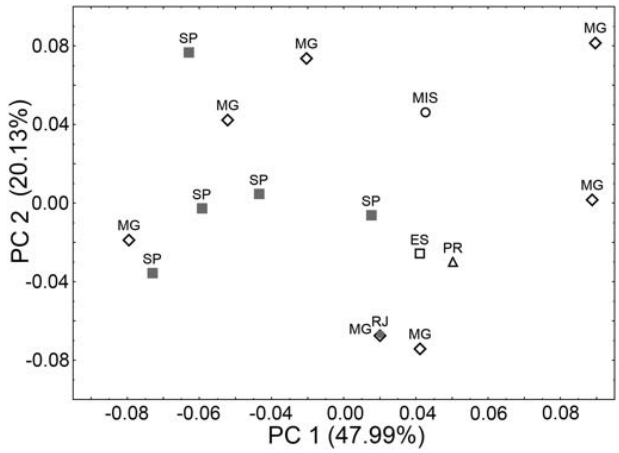

Fig. 8.—Scatterplot of the individual scores along the first 2 principal components obtained through 13 log-transformed craniodental measurements of 17 adult *Abrawayaomys*. PC1, PC2 = 1st and 2nd principal components. For abbreviations, see Table 2.

from other specimens, but similar in size to specimens from Minas Gerais, São Paulo, Espírito Santo, and Paraná. The variables that explained most of the variation along PC1 are breadth of the zygomatic plate (BZP), length of the incisive foramina (LIF), and length of the palate (LP). Along PC2, the most important variables were length of the palatal bridge (LPB) and length of the orbital fossa (LOF), which are associated with the antero-posterior axis of the skull. PC1 accounted for 48% and PC2 for 20% of the total variation (Table 1; Fig. 9). Interestingly, these traits were also qualitatively variable, and did not allow us to recognize discrete clusters of individuals associated with the geographic samples. The descriptive statistics for these geographic samples (Table 2)

suggest that *Abrawayaomys* exhibit short and narrow molars; a short rostrum; a short (the length of the incisive foramina occupies 63–67% of the length of the diastema) and narrow incisive foramina in a short diastema; and a robust, deep, and wide braincase.

Molecular analyses.—ML and BI analyses retrieved *Abrawayaomys* as monophyletic with full support (Figs. 10a and 10b, respectively). *Neotomys* was the sister group in both analyses. However, no significant support was obtained in BI (Fig. 10b), and weak support was obtained in ML (Fig. 10a). Furthermore, most relationships outside *Abrawayaomys* lacked significant support, with a few exceptions, such as the sister-group relationship between *Wiedomys* and *Abrothrix*. Our samples of *Abrawayaomys* presented an overall mean distance of 2.11%, with pairwise distances ranging from 0.14% to 4.51%. The 1st split within *Abrawayaomys* was between the specimen from Misiones, Argentina, and all Brazilian specimens. The mean sequence divergence between them was 4.32%. The following event of divergence occurred between the specimen of Minas Gerais, Brazil, and the remaining Brazilian specimens (São Paulo and Rio de Janeiro) that showed a mean sequence divergence of 2.90%. The Mantel test showed a significant correlation between genetic and geographic distances ($r = 0.88$, $P = 0.01$), consistent with an isolation by distance model.

Discussion

Species definition.—We observed a different pattern of pelage in the samples of *Abrawayaomys* when compared to that described by Pardiñas et al. (2009) for the Argentinean samples of the genus, named *A. chebezi*. Our specimens exhibit 3 distinct hair types: thin and wavy wool hairs; long and distally flattened cover hairs; and longer, wider, and grooved guard hairs (2 types, 1 narrower and another wider; spines). We did not observe the unique kind of hair described by Pardiñas et al. (2009) in any of the examined specimens. Moreover, these unique hairs were not observed in specimens from Paraná and Santa Catarina, as would be expected if they were *A. chebezi* as hypothesized by Pardiñas et al. (2016). Therefore, we believe that these specimens are not *A. chebezi* (as our analyses revealed) and this trait could be either an individual variation of MACN 20253 (holotype of *A. chebezi*) and CNP3631, or could be an apomorphy for these samples from Misiones.

The tail is also longer than the head and body in the adults examined, confirming the general trend observed by Pereira et al. (2008) and Pardiñas et al. (2009). We observed a remarkable variation in the presence and length of the white caudal tip and tuft (Fig. 1): some adults presented a wide white band on the tip of tail (15 mm in length) and a long white tuft of white hairs (20 mm in length [e.g., MZUSP 34720, MZUSP 35268]), whereas younger specimens (e.g., MZUSP 34718–9, MZUSP 35265–7) usually exhibited dark-tipped tails and very short tufts, or no tufts whatsoever. This suggests the existence of an age variation associated with this trait, and this assumption is supported by the fact that in 2 subadults (MZUSP 34721, MZUSP 35264) the apex of the tail presented a mixture of brown and white hairs, forming a very short tuft (3 mm in length). Specimens from Santa Catarina exhibited apical tufts (Maestri et al. 2015); however, information on the length of these tufts was not made available by the authors and the color of the tufts is controversial, since authors mentioned that apical tufts are "whitish" (Maestri et al. 2015:2) but depict a specimen with brownish coloration (Maestri et al. 2015:3).

The alisphenoid strut was frequently observed in the genus but also was polymorphic among samples. This observation is partially in accordance with data reported by Pardiñas et al. (2009). However, our data show that this variation apparently does not have any geographic or taxonomic value, considering its polymorphism in the samples studied, mainly from São Paulo and Minas Gerais.

Table 1.—Results of the principal component analysis, employing the covariance matrix for 13 log-transformed craniodental measurements of 17 adults of *Abrawayomys* arranged in geographic samples. PC1, PC2 = 1st and 2nd principal components. Bold values indicate variables most correlated to the respective PC.

	PC1	PC2
LR	–0.08	–0.18
BR	0.00	–0.21
LIF	**–0.54**	–0.06
BIF	–0.27	–0.06
LPB	0.11	**–0.75**
LP	**–0.34**	–0.32
LMS	–0.06	–0.05
BM1S	–0.14	–0.06
ZB	–0.11	–0.16
BZP	**–0.67**	0.23
IB	–0.07	–0.13
LOF	–0.05	**–0.35**
BRH	–0.07	–0.18
Eigenvalue	0.006	0.003
% Variance	47.99	20.13

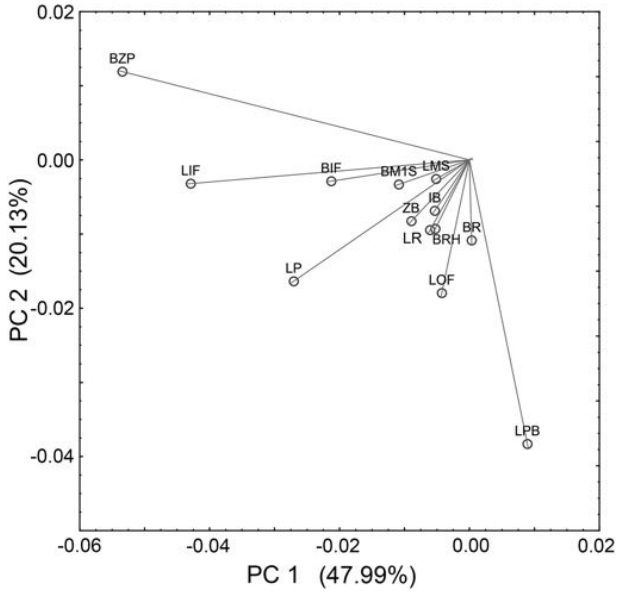

Fig. 9.—Vectors of 13 log-transformed craniodental measurements of 17 adult *Abrawayaomys* corresponding to the magnitude and direction of their loadings along the first 2 principal components. PC1, PC2 = 1st and 2nd principal components.

Table 2.—Descriptive statistics (mean ± *SD*, variation range, and sample size) for 29 craniodental measurements of adults (males and females grouped) of *Abrawayaomys*. Brazilian states: MG = Minas Gerais, SP = São Paulo, PR = Paraná, ES = Espírito Santo, RJ = Rio de Janeiro; Argentinean state: MIS = Misiones; NA = not available.

	MG	SP	PR	ES	RJ	MIS
ONL	26.94 ± 1.9	27.18 ± 1.59	28.51	28.48	NA	27.75
	23.53–29.42 (6)	27.54–29.24 (6)				
CIL	28.55 ± 1.40	29.53 ± 0.84	28.55	27.71	NA	27.52
	26.14–30.48 (8)	28.36–30.77 (6)				
LD	8.31 ± 1.74	7.91 ± 0.40	8.62	7.64	NA	7.26
	6.47–12.25 (8)	7.49–8.50 (6)				
LR	8.60 ± 0.47	8.52 ± 0.32	8.25 ± 0.10	8.28	8.7	8.11
	8.07–9.23 (8)	8.21–9.10 (7)	8.18–8.32 (2)			
LN	8.65 ± 0.80	8.86 ± 0.47	8.44 ± 0.26	7.83	9.25	8.96
	7.77–9.90 (8)	8.06–9.46 (7)	8.25–8.62 (2)			
BR	4.17 ± 0.21	4.36 ± 0.42	4.80 ± 0.04	4.07	4.84	4.28
	3.75–4.46 (8)	3.80–5.10 (7)	4.77–4.83 (2)			
LIF	5.02 ± 0.63	5.38 ± 0.29	4.92 ± 0.49	5.06	5.39	4.51
	4.21–5.95 (8)	5.01–5.74 (7)	4.57–5.27 (2)			
BIF	1.68 ± 0.15	1.81 ± 0.14	1.57 ± 0.08	1.71	1.71	1.65
	1.45–1.84 (8)	1.66–2.06 (7)	1.51–1.62 (2)			
LPB	5.34 ± 0.56	5.11 ± 0.40	5.50 ± 0.24	5.71	5.66	5.15
	4.47–6.04 (8)	4.28–5.49 (7)	5.33–5.67 (2)			
LP	12.05 ± 0.91	12.91 ± 0.71	12.39 ± 0.20	11.74	12.39	10.94
	10.45–13.27 (8)	12.11–14.22 (7)	12.25–12.53 (2)			
BBP	2.95 ± 0.18	2.93 ± 0.11	2.65 ± 0.29	2.93	3.15	2.85
	2.76–3.26 (8)	2.82–3.10 (6)	2.44–2.85 (2)			
BL	4.38 ± 0.25	4.39 ± 0.21	NA	4.41	NA	4.4
	4.05–4.86 (7)	4.10–4.73 (6)				
LMS	4.34 ± 0.16	4.40 ± 0.15	3.95	4.42	4.22	3.89
	4.06–4.56 (7)	4.29–4.67 (6)				
BM1S	1.40 ± 0.07	1.35 ± 0.07	1.19	1.36	1.34	1.20
	1.27–1.48 (8)	1.25–1.45 (6)				
BM1ant	0.82 ± 0.09	0.77 ± 0.12	0.77	0.89	0.94	0.68
	0.65–0.92 (8)	0.64–0.91 (6)				
ZB	16.99 ± 0.92	16.78 ± 0.33	17.19 ± 0.54	16.66	17	16.74
	14.98–17.86 (8)	16.39–17.35 (7)	16.81–17.57 (2)			
BZP	3.61 ± 0.57	3.98 ± 0.35	3.39 ± 0.08	3.21	3.17	3.76
	2.91–4.37 (8)	3.30–4.34 (7)	3.33–3.45 (2)			
IB	6.05 ± 0.25	6.17 ± 0.18	6.00 ± 0.40	6.31	6.27	6.05
	5.81–6.47 (8)	6.02–6.49 (7)	5.72–6.28 (2)			
LOF	10.21 ± 0.61	10.25 ± 0.23	10.81 ± 0.57	10.26	11.2	9.89
	9.11–10.77 (8)	9.84–10.53 (7)	10.41–11.21 (2)			
BRB	13.24 ± 0.38	13.18 ± 0.24	13.15	13.85	NA	12.88
	12.74–13.97 (8)	12.75–13.43 (7)				
BRH	9.94 ± 0.49	9.80 ± 0.23	10.13	10.06	10.16	10.35
	8.85–10.46 (8)	9.45–10.16 (7)				
LF	9.59 ± 0.71	10.00 ± 0.64	10.63 ± 1.42	9.74	9.63	9.17
	8.85–10.96 (8)	8.8–10.82 (7)	9.62–11.63 (2)			
LPa	6.10 ± 0.35	5.99 ± 0.37	6.93	6.12	6.68	5.97
	5.55–6.43 (8)	5.58–6.51 (7)				
LIP	2.42 ± 0.63	2.27 ± 0.33	2.92	3.38	NA	2.08
	1.68–3.59 (8)	1.87–2.69 (6)				
BIP	4.20 ± 0.70	4.26 ± 0.79	4.88	3.82	NA	6.39
	3.22–5.26 (8)	3.34–5.64 (6)				
LMAN	17.08 ± 1.03	17.05 ± 0.76	13.24 ± 0.13	17.14	17.57	13.73
	15.1–18.45 (8)	15.49–17.71 (7)	13.14–13.33 (2)			
HMAN	9.81 ± 0.72	10.36 ± 0.33	9.77 ± 0.13	9.95	10.25	9.01
	8.49–10.74 (8)	9.84–10.76 (6)	9.68–9.86 (2)			
LMI	4.50 ± 0.22	4.49 ± 0.07	4.22	4.67	4.67	4.27
	4.21–4.88 (8)	4.42–4.62 (6)				
BM1I	1.05 ± 0.08	1.10 ± 0.16	0.93	1.17	1.15	1.05
	0.90–1.14 (8)	0.93–1.30 (6)				

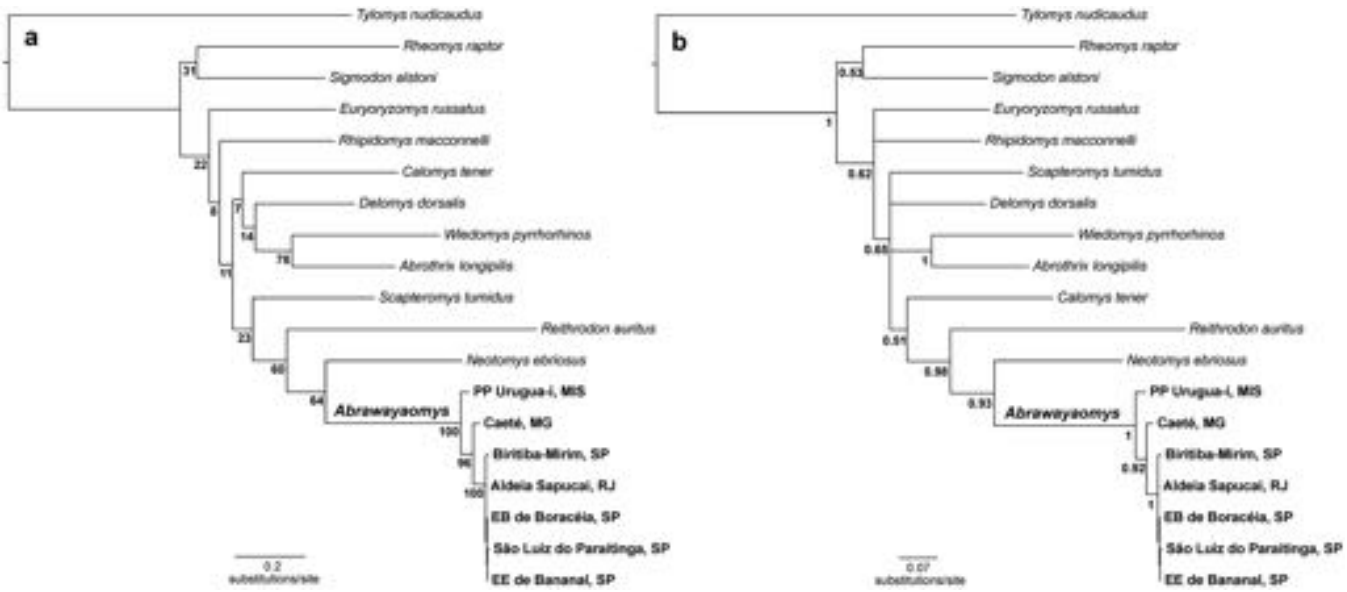

Fig. 10.—Phylogenetic reconstructions including 7 specimens of *Abrawayaomys* and 11 specimens representing most other sigmodontine lineages, with *Tylomys nudicaudatus* (Tylomyinae) as outgroup. a) ML topology of *Cytb* sequences (likelihood −5542.513628), with nodal support presented as bootstrap replicates; b) BI topology for *Cytb* sequences, with nodal support presented as posterior probabilities. *Cytb* = cytochrome *b*; BI = Bayesian Inference; ML = Maximum Likelihood.

The interorbital region was also variable in the examined specimens (Fig. 3), with some specimens with supraorbital margins hourglass shaped, with rounded margins (MZUSP 32319, 35264, 35265, 35267), and some specimens with margins slightly to strongly divergent posteriorly, and slightly squared or with squared borders (MZUSP 32278, 35266, 35268, LZV-UFOP 206 R). Apparently, there is no age variation related to these differences, as the specimens MZUSP 32278, 32319, 35268, and LZV-UFOP 206 R are all adults and possess distinct interorbital regions.

Regarding the presence of an anteromedian flexus, the sample we studied provides further important evidence on the morphological variation of *Abrawayaomys*. Some examined specimens (MZUSP 32319, 32327, 32328, 34717, 34720, 34721, MZUFV 3562, 3590; Fig. 6) exhibited a shallow depression more lingually positioned on the procingulum (slightly larger anterolabial conule), probably the remnant of an anteromedian flexus. Other specimens examined (including young specimens, being 2 with the M3 erupting) did not exhibit any trace of the flexus. Moreover, we suspect that in some of the specimens (e.g., MZUSP 34717) that apparently exhibited a division of the anterocone, the smaller anterolingual conule could be in fact a well-developed protoloph, and the flexus would be a protoflexus instead of an anteroflexus. This uncertainty arose from the observation of specimens showing a flexus and small protolophs, and specimens without a flexus and protoloph. Our data suggest that this variation is neither sex- nor age-related, and apparently also not resultant from taxonomic variation. This evidence suggests that the morphology of the anterocone is highly polymorphic, but more specimens are necessary to fully understand this variation.

We believe that the differences observed in external and cranial traits (tail, interorbital region, alisphenoid strut, occlusal molar morphology) in the available samples as well as in the literature (Pereira et al. 2008; Pardiñas et al. 2009) could be interpreted as individual variation and do not represent sharp discontinuities favoring taxonomic recognition. The topology recovered in the molecular phylogenetic analyses suggest some level of geographic structure; however, considering the level of qualitative and quantitative polymorphism, this structure is better explained as geographic rather than taxonomic variation. Moreover, the values of genetic divergence in *Cytb* sequences obtained for *Abrawayaomys* are quite similar to, and sometimes lower than, the values that have been observed for other Atlantic Forest sigmodontine species with similar geographic distribution. The mean sequence divergence between *Abrawayaomys* clades ranged from 2.9% to 4.3%. For the akodontine *Akodon cursor*, Geise et al. (2007) found a divergence of 3.6% between 2 geographic groups corresponding to samples from north and south of the Jequitinhonha River. For *Blarinomys breviceps*, also an akodontine, Ventura et al. (2012) reported values of pairwise sequence divergence among specimens varying between 4.9% and 8.4%, comparing samples from São Paulo, Rio de Janeiro, Minas Gerais, Espírito Santo, and Bahia; and Gonçalves and Oliveira (2014) detected genetic divergence ranging from 3.7% to 4.8% among the main clades of *Delomys dorsalis*, which are related to Serra da Mantiqueira, Serra do Mar, and the southern portion of the Atlantic Forest. These genetic divergences were not considered evidence for these authors to recognize new species, especially as they also exhibited a mosaic quantitative variation, the same pattern we observed with samples of *Abrawayaomys*. Additionally, we found a pattern of isolation by distance, showing that there was not a sharp discontinuity across *Abrawayaomys* samples. The divergence observed between Argentinean and Brazilian populations more likely reflected the lack of geographic intermediary

samples rather than an actual genetic break (see Moreira and Oliveira 2011). According to De Queiroz and Good (1997), a significant correlation between genetic and geographic distances is associated with genetically cohesive populations (i.e., populations that exchange genes), which also supports the recognition of 1 single species of *Abrawayaomys*.

Therefore, based on the analyses aforementioned, we reject the hypothesis raised by Pardiñas et al. (2009, 2016) and Ventura et al. (2013) that northern samples of the genus represent a distinct species. The qualitative, quantitative, and molecular variation exhibited by the available samples does not allow us to recognize sharp discontinuities or unambiguous and unique combinations of characters that would be diagnostic. Additionally, except for the tufted hairs, our analysis showed that most diagnostic traits proposed for *A. chebezi* by Pardiñas et al. (2009, 2016) are present in the variation of the Brazilian samples from Santa Catarina, Paraná, São Paulo, Rio de Janeiro, Minas Gerais, and Espírito Santo. Thus, we propose a hypothesis that only 1 species should be assigned to the genus, for which the name *Abrawayaomys ruschii* should be applied as the oldest available name for this entity. Nevertheless, it is likely that further samples could falsify our hypothesis that only 1 species inhabits the Atlantic Forest.

As demonstrated above, specimens of the genus are similar in external and cranial morphology, including the specimens already described in the literature (Pereira et al. 2008; Pardiñas et al. 2009, 2016). However, since our concept of *A. ruschii* is distinct from that of previous authors (including *A. chebezi* as a junior synonym), and since the specimens here reported represent the largest series available from eastern populations of the genus *Abrawayaomys*, below we provide an account for the species based on the information we retrieved from samples analyzed throughout the species distribution.

Abrawayaomys ruschii Cunha and Cruz, 1979

Abrawayaomys ruschii Cunha and Cruz, 1979:2; type locality "Forno Grande, município de Castelo, ES, Brasil."

Abrawayaomys chebezi Pardiñas, Teta, and D'Elía, 2009:41; type locality "Argentina: Province of Misiones, Department of Iguazú, conjunction Arroyo Mbocaí and route 12 (-25.680115° S, - 54.508060° W)."

Morphological description.—Head and body moderate in size (HB: 104–140 mm; T: 123–153 mm; E: 16–21 mm; HF: 29–32 mm; M: 40–63 g); dorsal pelage dense and stiff, spinous, consisting of short and dense underfur, with thin and numerous wool hairs (length: 8–10 mm), with 9/10 basal length grayish and 1/10 apical portion with a buffy subterminal band and a brownish terminal band, long and stiff overfur, with cover and guard hairs; cover hairs long (10–13 mm) and numerous, with 2/3 basal portion thin and cylindrical and 1/3 apical portion flattened and wide, with a basal brown band, a subterminal buffy to orange-buffy band and a terminal brownish band; guard hairs longer (13–16 mm), modified in spines, wide, flattened, and grooved through its entire length; there are wide spines, entirely grayish-brownish, and narrow spines with subterminal buffy to orange-buffy band and apical brownish band. Dorsal body color buffy, densely grizzled with black. Anterior half of head (on eyes level) covered with gray-based and buffy-tipped hairs, very similar to posterior half of head and dorsal body color. Ventral pelage consisted by wool and cover hairs (distally flattened) grayish-based and white- or buffy-tipped hairs, configuring grayish, buffy, or yellowish tones slightly grizzled, distinctively lighter than dorsal pelage. Lateral surface less grizzled with brown. Mystacial vibrissae short and scarce, not surpassing ears when laid back. Tail length generally slightly longer than head and body (~105–134% of head and body length); tail not bicolored or only slightly bicolored dorsoventrally (in younger specimens), covered with sets of 5 short brown hairs per scale (the central one noticeably longer and the lateral ones decreasing in length); some individuals (MZUSP 35268) exhibit a distinct white-tipped tail (10–15 mm) and a long apical tuft of white hairs (up to 20 mm in length; Fig. 1). Manus moderately wide and short, terrestrial type, with claws moderately long and robust; digit I very reduced; digit V slightly shorter; digits II–IV similar in size; plantar surface naked; manual pads larger than pedal pads, particularly the thenar and hypothenar 2 carpals. Pes moderately wide and long (~28–29% of head and body length), terrestrial-fossorial type, with claws long and robust; digit I very short, with the claw reaching only the base of the 1st phalanx of digit II; digit V short, with claw reaching the middle of the 1st phalanx of digit IV; digits II–IV similar in size; interdigital and plantar pads small and delicate; thenar small and rounded, and hypothenar small and elongated; ventral surface of pes densely covered with squamae; ungual tufts scarce and shorter than claws in digits II–V and absent from digit I; dorsal surface of pes grayish, covered with short hairs, with 3/4 distal portion white and basal 1/4 grayish or washed brown and with entirely brownish hairs; ventral surface naked, unpigmented. Pinnae rounded and very small (~19% of head and body length); pinnae covered internally with short hairs with 3/4 basal portion brown and 1/4 apical portion yellowish or golden and externally with glossy dark brown hairs. Females exhibit 8 mammae in inguinal, abdominal, thoracic (nearly postaxial), and pectoral positions.

Skull (Fig. 11) with very narrow and short rostrum in dorsal view (Table 2; Fig. 2); nasals with squared terminal extremities, very short and abrupt, exposing the dorso-rostral component of premaxillaries, the short gnathic process and the incisors; nasals tapering posteriorly; apical one-third of nasals expanded laterally (slightly 45%, or largely expanded 10%) or not (45%; n = 20); nasofrontal suture aligned with premaxilar-frontal suture (11%) or surpassing the level of lacrimals in some specimens (89%; n = 18); lacrimal bones long and narrow, contacted both to premaxilar and frontal bones; rostrum with discrete to inflated nasolacrimal capsules, flanked by shallow to moderately deep and narrow to moderately wide zygomatic notches. Interorbital region variable, hourglass shaped, slightly divergent posteriorly, slightly convergent posteriorly, or even strongly convergent posteriorly (Fig. 3), with rounded, slightly squared, or squared supraorbital margins. Frontoparietal suture concave, continuous to fronto-squamosal suture. Zygomatic

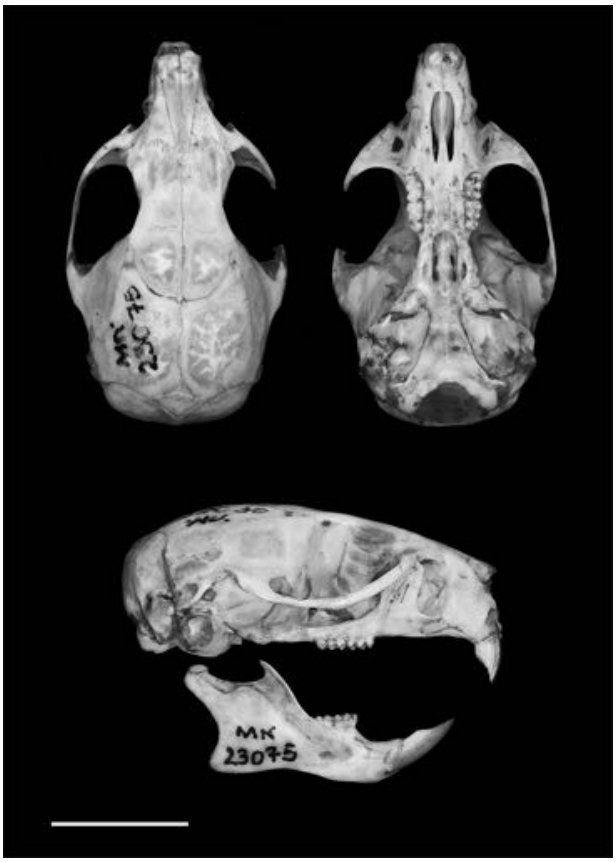

Fig. 11.—Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype of *Abrawayaomys ruschii* (MN 23075), from Reserva Biológica de Forno Grande, Castelo, Espírito Santo, Brazil. Scale = 10 mm.

arches expanded laterally, with parallel margins; zygomatic arches thin and delicate; jugal present. Braincase elongated and rounded, with rounded and weakly developed temporal ridges; lambdoidal and nuchal crests weakly developed; interparietal very short and narrow; parietal projected ventrally, widely contributing to the lateral wall of braincase. Rostrum short (in lateral view), with gnathic process very reduced. Zygomatic plate narrow, with a straight or slightly concave anterior margin, without a spinous anterodorsal process, and a posterior margin that reaches the anterior alveolus of M1. Alisphenoid strut present in most specimens (78%; $n = 18$), configuring discrete oval accessory and buccinators-masticatory foramina. Large stapedial foramen, squamoso-alisphenoid groove, and sphenofrontal foramen present, configuring the carotid circulatory pattern 1 (Voss 1988). Parietals projected ventrally, on the lateral surface of the braincase. Auditory bullae small, with moderate external auditory meatus; stapedial process long and wide, overlapped to squamosal; tegmen tympanyi large and long, conspicuously overlapped to the suspensory process of squamosal; posglenoid foramen large; subsquamosal fenestra very large and rounded; hamular process of squamosal slender; mastoid rounded, not completely ossified, perforated by small to large fenestra; malleus with large orbicular apophysis. Incisive foramina medium, reaching (in young individuals) or not the alveolus or the anterocone of M1, with slightly convergent posteriorly (wider anteriorly) or nearly parallel lateral margin, and rounded or acute anterior-posterior margins. Palatal bridge wide and short, with mesopterygoid fossa penetrating anteriorly between the molar series, reaching (or not) the posterior or medial alveoli of M3 in older specimens; palate smooth, without palatal excrescencies; posterolateral palatal pits small and puntiform at palatal level. Mesopterygoid fossa narrow; bony roof of mesopterygoid fossa imperforated (19%) or perforated by small and narrow sphenopalatine vacuities in most specimens (81%; $n = 16$). Parapterygoid fossae very narrow and deeply excavated; posterior opening of alisphenoid canal small; parapterygoid process long and slender. Foramen lacerum medium much reduced or nearly absent in some specimens. Auditory bullae large, flask-shaped, with very short Eustachian tube; periotic partially exposed posteriorly between ectotympanic and basioccipital, but not extending anteriorly to carotid canal; carotid canal small. Paraoccipital process short and narrow.

Mandible dorsoventrally very deep proportionally to its length, with weakly to moderate falciform or subtriangular coronoid process; coronoid process lower than or equal in height to the condyloid process; angular process noticeable short, not reaching the condyloid process; capsular process of lower incisor strongly developed posteriorly to the base of coronoid process; superior and inferior notches shallow. Superior and inferior masseteric ridges converge anteriorly as open chevron.

Upper incisors deep, ranging from orthodont to proodont; anterior surface of incisors smooth and rounded (Fig. 5). Molar series nearly parallel to slightly convergent posteriorly; upper molars (Fig. 6) tetra or pentalophodont, moderately high-crowned; cusps obliquely oriented, the labial cusps arranged posteriorly to lingual cusps; labial and lingual flexus very wide and deep, do not interpenetrate at median molar plane; lingual cusps higher than labial ones. M1 with anterocone much narrower than paracone-protocone pair and more labially positioned; anterocone variable in morphology: not divided (48%) or divided (52%; $n = 25$) by an oblique, deep, and narrow anteromedian flexus, defining a small anterolingual and a slightly larger anterolabial conule; in some specimens (e.g., MZUSP 34717) the anterocone seems to be undivided, and a small lingual loph may represent a well-developed protoloph; in other specimens (e.g., MZUSP 34720) the flexus is present, the anteroconules are similar in size, and the protoloph is small; and in some specimes (e.g., MZUSP 35266) the anterocone is undivided and the protoloph is indistinct on molar topography, with a small protostyle on the lingual margin; protoloph present and well developed in most specimens (63%; $n = 19$); anteroloph fused to anterolabial conule, with no flexus apparent; paracone-protocone pair wider than metacone-hypocone pair; paracone connected to the median mure or to a inconspicuous mesoloph; paracone rarely connected to protocone posteromedially (in a few specimens, e.g., MZUSP 35266, the paracone is also connected to the median mure by an enamel bridge); paracone and metacone divided by a wide and deep paraflexus; mesoloph present (not discernible in some specimens, as, e.g., MZUSP 34717 [Fig. 6], in which a long paralophule is present

on the more medial surface of paracone); mesoloph small, usually not extending to the labial margin (mesoloph eroded with minimum wear, and paracone, median mure, and mesoloph became indistinct); mesostyle absent; mesoloph (or the paralophule) connected to the anterolateral or anteromedial surface of metacone (sometimes forming a wide and deep metafosset) and to the posterolateral surface of paracone (no trace of a mesofosset is observable); hypocone connected medially to median mure; protocone and hypocone connected posteromedially; posteroloph small; lingual cingula absent. M2 with large anteroloph; anterolingual cingulum developed, forming a deep protoflexus; similar to M1; mesoloph usually present (but in some specimens, e.g., MZUSP 35264, 35265, 35267, there is a shallow depression, distinct from a usual mesoflexus, separating the paracone from a small and low loph that occupies the same topographic position of the mesoloph; Fig. 6), usually connected to the anterolateral surface of metacone through a long and oblique loph or lophule (forming a wide and deep, parabola-shaped, metafosset) and to the posterolateral surface of paracone (forming a narrow and small mesofosset, obliterated with light wear); metacone connected more medially to the protocone; posteroloph long (rapidly obliterated by light wear). M3 very reduced, peg-like; narrow anteroloph and shallow protoflexus present; paracone-protocone pair reduced; mesoloph, metacone-hypocone pair, hypoflexus, and posteroloph absent.

Lower molar series nearly parallel (Fig. 7); molars tetralophodont, high-crowned; labial cusps arranged slightly posteriorly to lingual cusps; labial and lingual flexids wide and deep, do not interpenetrate at median molar plane (mainly hypoflexid and meso-entoflexid). The m1 has a very narrow anteroconid, medially oriented; anteroconid not divided by anteromedian flexid (the MZUSP 32327 exhibit the anteroconid constricted medially, apparently divided by a narrow anteromedian flexid [Fig. 4], and the MZUFV 3562 present a deep anteromedial flexid, forming equally sized anterolabial and anterolingual conulids; $n = 21$); anteroconid without small internal fold; anterolophid and protolophid absent (some specimens exhibit a small protostylid); metaconid and protoconid connected anteromedially to anterior murid; metaconid connected to median murid by a narrow enamel bridge; mesolophid and mesostylid absent; entoconid-hypoconid pair wider; wide posteroloph connected to hypoconid; labial cingula absent; small lingual cingulid present. The m2 has developed anterolabial cingulum; narrow protoflexid; mesolophid present or absent; mesolophid or small lophulid originating on mediam murid (oriented obliquely and connected to the posterolateral surface of metaconid); mesostylid apparently absent. The m3 is very reduced; anterolabial cingulum present; metaconid-protoconid pair developed, but small; mesolophid small; deep hypoflexid present; entoconid-hypoconid pair and posterolophid fused.

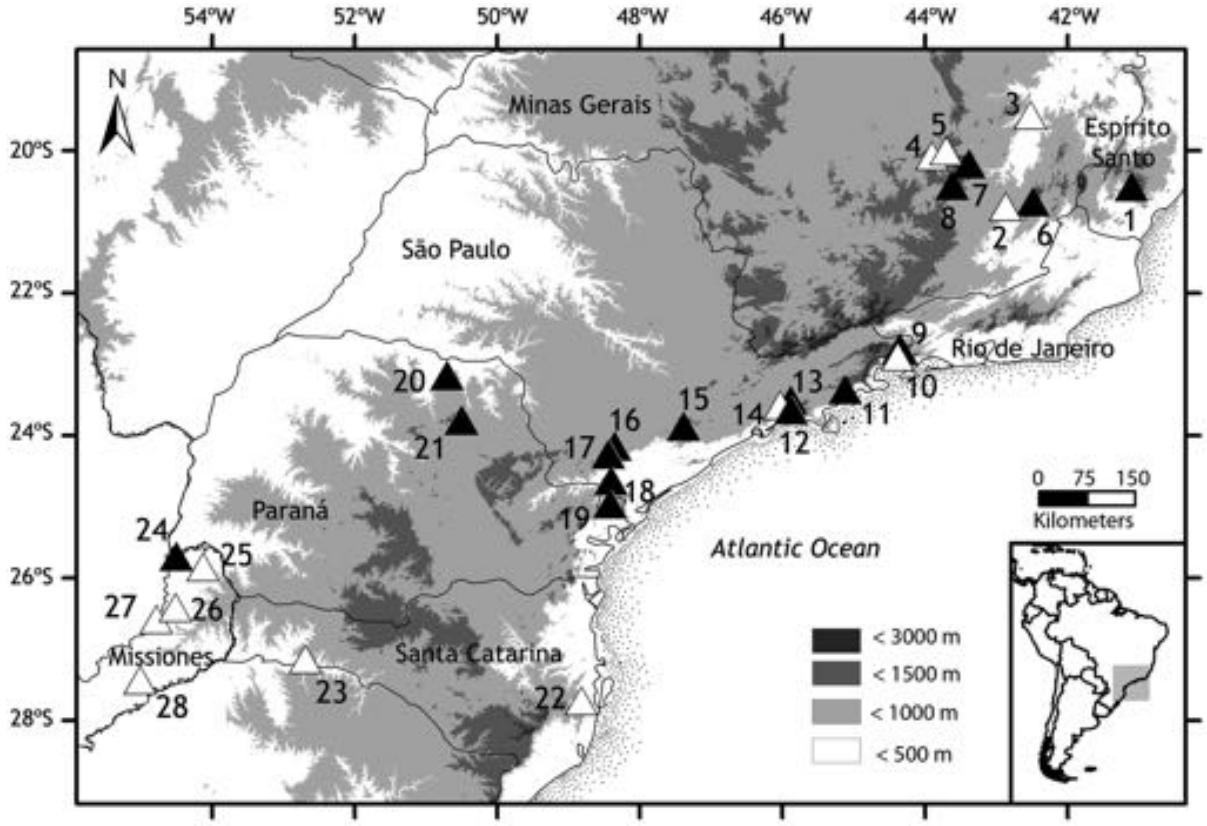

Fig. 12.—Known collection localities of *Abrawayaomys*. White triangles indicate literature records (specimens not examined here) and black triangles indicate localities of specimens examined here. Detailed information is provided in Supplementary Data SD1, where numbers on the map correspond to numbers of the collection localities.

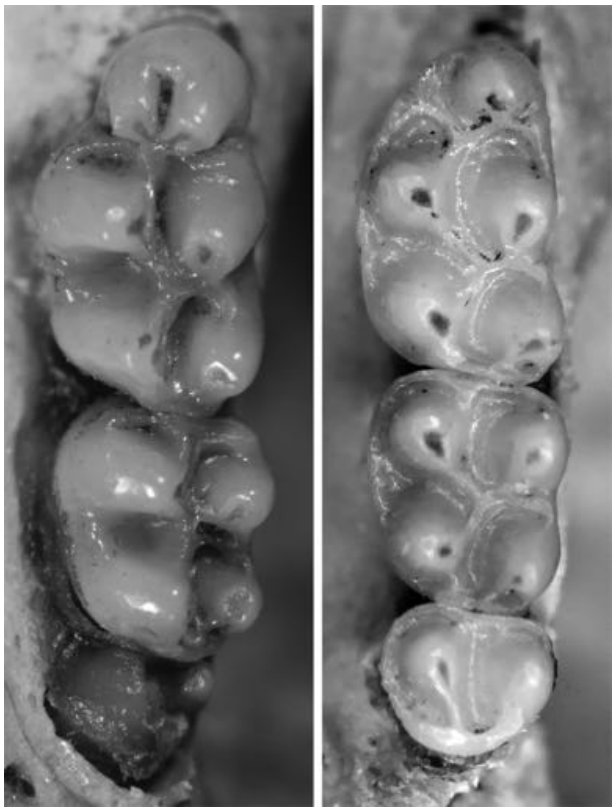

Fig. 13.—Upper molar series, in occlusal view, of 1 specimen of *Abrawayaomys ruschii* (LZV-UFOP 58 R, left) and 1 specimen of *Rhagomys longilingua* (MJ 550, right). Note: the narrower procingulum; the resemblance between the shape and pattern of connection of the M1 main cusps; the development of the mesoloph; the exposition of dentine restricted to the apical portions of the main cusps.

Postcranial axial skeleton formed by 7 cervical, 12–13 thoracic, 7–6 lumbar, 4 sacral, and 35 caudal vertebrae ($n = 4$); the 2nd cervical vertebra exhibits a long neural apophysis; hemal arches with (or without; $n = 2$) distinct posterior process present between 2nd and 3rd and between 3rd and 4th caudal vertebrae; anapophysis on the 17th thoracolumbar vertebra absent; sternum formed by 6 elements, the xyphoid process very long and narrow; supratrochlear foramen of humerus present; deltoid tuberosity well developed.

Geographic distribution.—Abrawayaomys ruschii occurs in eastern South America, mostly in the Atlantic Forest sensu lato, from the Brazilian state of Espírito Santo to the Argentinean Province of Misiones (Stallings 1989; Pereira et al. 2008; Pardiñas et al. 2009, 2016; Cherem et al. 2011; Passamani et al. 2011; Cerboncini et al. 2014). The new collecting localities reported here (Fig. 12), as well as the previously known localities, are presented in Supplementary Data SD1.

The records from São Paulo are distributed from the northernmost portion of the state (near the border with Rio de Janeiro state, at the Estação Ecológica de Bananal) to the southernmost area (near the border with Paraná state, at the Parque Estadual de Jacupiranga). The collection localities of Minas Gerais specimens are distributed on the eastern slope of Serra do Espinhaço and on the Serra do Brigadeiro, on the southeastern portion of the state. Although these records do not extend the known geographical distribution of the species, they fill in part of the large distributional gap (about 700 km) between the previously registered localities in the states of Espírito Santo, Rio de Janeiro, Paraná, Santa Catarina, and Argentina.

Habitat.—Collection localities of *A. ruschii* are distributed along part of the most preserved remnants of Atlantic Forest in Brazil, some of them in legally protected areas (see Supplementary Data SD3 for a detailed description of the new collection localities from São Paulo and Minas Gerais). In summary, throughout the new localities here reported, the genus *Abrawayaomys* inhabits lowland and montane humid forests in the Serra do Mar and Serra do Espinhaço, from 230 m to nearly 1,250 m, in secondary and disturbed forests, as well as in mature forests.

Concluding Remarks

Abrawayaomys ruschii is the only Atlantic Forest sigmodontine presenting the body covered with spines. Only 3 genera distributed in the Amazon forest present such external morphological trait, among them all known species of *Neacomys* and *Scolomys*, and *Rhagomys longilingua*. Nevertheless, these 3 genera and *Abrawayaomys* are not phylogenetically related (D'Elía 2003; Weksler 2003, 2006; Percequillo et al. 2011), indicating independent origins for this trait, as also suggested by Ventura et al. (2013).

It is noteworthy that the number of mammae in *Abrawayaomys* was not described in the literature until recently, since the only female specimens previously recorded were the holotype (Cunha and Cruz 1979) and those reported by Passamani et al. (2011) and Maestri et al. (2015), and they do not exhibit apparent mammae. Ventura et al. (2013) described 6 mammae in inguinal, abdominal, and postaxial positions. However, 2 females observed by us (MZUSP 35268 and LZV-UFOP 57 R) revealed the presence of 8 mammae in inguinal, abdominal, thoracic, and pectoral positions (sensu Pacheco 2003), as exhibited by *A. ruschii*, which is also the modal number found in sigmodontine rodents (Steppan 1995).

Regarding its phylogenetic relationships, *Abrawayaomys* still exhibits uncertainties. Based on molecular data, Ventura et al. (2013) obtained 4 hypothetical scenarios, but only 1 was statistically supported: the sister-group relationship between *Abrawayaomys* and *Reithrodon* on BI analysis based on *Cytb* sequences. Ventura et al. (2013) also reported similar results with *Cytb* sequences on a ML analysis, and they also did not obtain strong support. Salazar-Bravo et al. (2016) also recovered this sister-group relationship, with strong support only on the BI analysis for a data set composed by *Cytb* and IRBP genes. Based on morphological characters, some authors suggest a close relationship of *Abrawayaomys* with *Rhagomys* and other Thomasomyni genera (Pacheco 2003), or alternatively to *Chilomys* (Salazar-Bravo and Yates 2007). The molars of *Abrawayaomys* are quite similar to those of *Rhagomys* (Fig. 13): both genera present molar crowns predominantly

covered by enamel, with dentine exposition mainly associated with the apex of the main cusps. Considering the M1, similarities are even more noticeable: the paracone-protocone pair is wider than the procingulum and the metacone-hypocone pair (in some specimens the paracone-protocone pair is quite wider than the procingulum, that can be highly variable in width in *Rhagomys*; see Percequillo et al. 2011); the paracone is seldom connected to the median mure, being more associated to the mesoloph; the mesoloph is oriented posteriorly, and connected to the anterior or anteromedial surface of the metacone the labial and lingual flexus are quite wide and deep.

Considering morphology, the skull of *Abrawayaomys* is unique in the sigmodontine radiation, with its short and blunt rostrum, procumbent incisors, strong braincase, and divergent molar toothrows. These features seem to be adaptations to semifossorial-fossorial life (also observed in other fossorial and semifossorial rodents, such as sigmodontine *Kunsia*, *Ctenomys*, and the echimyids *Carterodon* and *Euryzygomatomys*), thus precluding the recognition of similarity with another members of the tribe Thomasomyini, which is composed mainly of arboreal and scansorial forms. On the other hand, some traits exhibited by the genus (and not related to digging) are shared with akodontine rodents (an aspect also highlighted by Pardiñas et al. [2009]), as the concave frontoparietal suture (similar to *Necromys*); large postglenoid foramen and subesquamosal fenestra (similar to *Akodon* and *Necromys*); narrow and delicate parapterygoid plates (similar to *Necromys*); small posterolateral palatal pits (most akodontine genera); tegmen typmani overlapped to the posterior suspensory process of squamosal; delicate or reduced mesoloph and reduction of mesolophid (several genera of open and transitional habitats).

These comparisons indicate similarity among these lineages, but a more comprehensive phylogenetic approach employing morphologic traits still needs to be performed to evaluate if these similarities represent synapomorphies or homoplasies. So far, the position of *Abrawayaomys* in morphologic phylogenies is conflicting, different from the molecular phylogenies that suggest its position among the thomasomyines; however, it merits attention the fact that most of these results employ the same database (*Cytb* and IRBP genes), which can be misleading. Voss (1993) considered this species as a member of a plesion called "Neotropical plesiomorphic murid," along with other Atlantic Forest endemic species such as the species of *Delomys*, and *Phaenomys ferrugineus* and *Rhagomys rufescens*. Reig (1986) and Smith and Patton (1999) considered *Abrawayaomys* as Sigmodontinae *incertae sedis*, a position still held by D'Elía and Pardiñas (2015).

The distributional records presented here provide compelling evidence that this species is homogeneously distributed in the Atlantic Forest, and that the previously described distribution (Pardiñas et al. 2009; Maestri et al. 2015) was a collecting artifact due to inappropriate sampling efforts (e.g., exclusive use of live-traps without the complementary use of pitfall traps). The records of *A. ruschii* are still sparse and, therefore, knowledge of the distributional limits of this species is still incomplete. Intensive sampling with pitfall traps in the current realm of this species could recover additional specimens of this and other rare genera of small mammals that eventually will provide valuable insights on the systematics of these groups.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—List of known collection localities of *Abrawayaomys*.

Supplementary Data SD2.—Catalog numbers and GenBank access taxa included in the phylogenetic analyses.

Supplementary Data SD3.—Habitat data for collection localities of *Abrawayaomys ruschii*.

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