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The phylogenetic position of the enigmatic Atlantic forest-endemic spiny mouse *Abrawayaomys* (Rodentia: Sigmodontinae)

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Abstract

Background: The phylogenetic position of the sigmodontine genus *Abrawayaomys*, historically assigned to the tribe Thomasomyini or considered a sigmodontine incertae sedis, was assessed on the basis of nuclear and mitochondrial DNA sequences obtained from four individuals from different localities in the Atlantic forest of Brazil. Sequences of *Abrawayaomys* were analyzed in the context of broad taxonomic matrices by means of maximum-likelihood (ML) and Bayesian analyses (BA).

Results: The phylogenetic position of *Abrawayaomys* differed depending on the gene analyzed and the analysis performed (interphotoreceptor retinoid-binding protein (IRBP) ML: sister to Thomasomyini; IRBP BA: sister to Akodontini; cytochrome (Cyt) *b* ML: sister to *Neotomys*; and Cyt *b* BA: sister to Reithrodontini). With the sole exception of the BA based on Cyt *b* sequences, where the *Abrawayaomys-Reithrodon* clade had strong support, all sister-group relationships involving *Abrawayaomys* lacked any significant support.

Conclusions: As such, *Abrawayaomys* constitutes the only representative so far known of one of the main lineages of the sigmodontine radiation, differing from all other Atlantic forest sigmodontine rodents by having a unique combination of morphological character states. Therefore, in formal classifications, it should be regarded as a Sigmodontinae incertae sedis.

Keywords: Akodontini; Atlantic forest; Cricetidae; Phylogeny; Thomasomyini

Background

With about 86 living genera, cricetids of the subfamily Sigmodontinae are one of the most diversified and taxonomically complex groups of mammals. Predominantly distributed in South America, sigmodontines also reach Central and North America, and one extant genus is endemic to the Galapagos Islands (D'Elía 2003a). Remarkably, new sigmodontine genera are still being erected on the basis of both revisionary museum work and from newly discovered species (e.g., Pardiñas et al. 2009a; Percequillo et al. 2011; Pine et al. 2012; Alvarado-Serrano and D'Elía 2013; see comments in D'Elía and Pardiñas 2007). Similarly, statuses of several sigmodontine taxonomic forms at

the species level are unclear (e.g., Alarcón et al. 2011; Bonvicino et al. 2012).

Sigmodontine genera have been arranged into different groups, most of which have been given the formal rank of tribes (e.g., Reig 1980). In the last two decades, phylogenetic analyses using either morphological or molecular data or both were used to set the limits and contents of these groups and determine the timing of their diversification (e.g., Braun 1993; Smith and Patton 1999; Steppan 1995; D'Elía 2003b; Pacheco 2003; Weksler 2003; D'Elía et al. 2003; D'Elía et al. 2006a, b; Martínez et al. 2012; Parada et al. 2013; Salazar-Bravo et al. 2013). Those studies caused a number of major reconsiderations on the limits and contents of these groups. Currently, 12 extant genera are considered as Sigmodontinae incertae sedis (see the most recently published classification in D'Elía et al. (2007) and the modification prompted by the description of a new

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genus by Alvarado-Serrano and D'Elía (2013)); one of these is *Abrawayaomys* Cunha and Cruz 1979.

Abrawayaomys is a poorly known sylvan sigmodontine genus that stands out within the sigmodontine radiation due to its spiny pelage and unusual craniodontal morphology. It is found in the Atlantic forest of Argentina and Brazil and is known from a handful of trapped specimens and a few osteological remains gathered from owl pellets (Pardiñas et al. 2009b). Two species are recognized: the type species *Abrawayaomys ruschii* Cunha and Cruz 1979 and the recently described *Abrawayaomys chebezi* (Pardiñas et al. 2009a, 2009b).

Abrawayaomys displays a striking combination of morphological features that was referred by Musser and Carleton (2005, p. 1,088) in the following terms 'Diagnostic traits seem to combine aspects of *Neacomys*, *Oryzomys*, and *Akodon*, and both Reig (1987) and Smith and Patton (1999) acknowledged the enigmatic affinities of *Abrawayaomys* as uncertain.' Recently, Pardiñas et al. (2009b) evaluated the morphology of *Abrawayaomys* in detail and noted a certain resemblance to the bauplan of the tribe Akodontini but also to the thomasomyine genera *Chilomys* and *Rhagomys*. Similarities with Akodontini were regarded as convergences since *Abrawayaomys* was assigned to Thomasomyini given that independent sets of data placed *Chilomys* and *Rhagomys* in Thomasomyini (D'Elía et al. 2006a; Salazar-Bravo and Yates 2007) and because morphology-based phylogenetic analyses placed *Abrawayaomys* in this tribe (Pacheco 2003; Salazar-Bravo and Yates 2007). The lack of molecular data for *Abrawayaomys* has prevented an assessment of its position within the available comprehensive sigmodontine trees generated on the basis of mitochondrial and nuclear DNA sequences (e.g., Engel et al. 1998; Smith and Patton 1999; D'Elía 2003b; Weksler 2003; D'Elía et al. 2006a, b).

In recent fieldwork in the states of Rio de Janeiro (Pereira et al. 2008), Minas Gerais (Passamani et al. 2011), and São Paulo (see below) in southeastern Brazil, four specimens referred to as *A. ruschii* were collected. Based on mitochondrial and nuclear DNA sequences gathered from these specimens, we present the first phylogenetic analyses to test previous hypotheses concerning the placement of *Abrawayaomys* within the sigmodontine radiation. In addition, we provide some taxonomic judgments based on the resulting phylogeny and comments on the evolution of some morphological traits.

Methods

DNA sequences corresponding to the cytochrome (Cyt) *b* gene and the first exon of the nuclear interphotoreceptor retinoid-binding protein (IRBP) gene were used as evidence. We sequenced four specimens of *A. ruschii* deposited in the following Brazilian collections: Museu Nacional, Univ. Federal do Rio de Janeiro (MN 67557; Brazil, Rio

de Janeiro, Aldeia Sapucaí) (Pereira et al. 2008); Museu de Zoologia, Univ. de São Paulo (MZUSP 32319; Brazil, São Paulo, Biritiba-Mirim; BO 27; Brazil, São Paulo, Estação Ecológica de Boracéia); and Coleção de Mamíferos da Univ. Federal de Lavras (CMUFLA 906; Brazil, Minas Gerais, Caeté) (Passamani et al. 2011). Sequences were gathered following the protocol of Pardiñas et al. (2003) and D'Elía et al. (2006b). We found minor differences among Cyt *b* sequences (see 'Results' below), but in the phylogenetic analyses, we used that of specimen MN 67557 because it was the only complete one (i.e., 1,140 bp; the other being 801 bp long). We found no variation in IRBP sequences of the four specimens analyzed, and therefore, *Abrawayaomys* was represented by a single terminal (MN 67557) in the phylogenetic analyses. New sequences were submitted to GenBank [GenBank: JX949182 to JX949189].

To appraise the phylogenetic position of *Abrawayaomys* within the radiation of the Sigmodontinae, we sought to ensure that sigmodontine diversity was represented as comprehensively as possible. According to the current classification, our sampling only lacked for both matrices the incertae sedis genera *Phaenomys* and *Wilfredomys*; the akodontines *Gyldenstolpia* and *Podoxymys*; the ichthyomyines *Anotomys*, *Chibchanomys*, *Neusticomys*, and *Ichthyomys*; and the oryzomyine *Mindomys*. In addition, the IRBP matrix lacked the thomasomyine *Chilomys*. Meanwhile, the ichthyomyine *Rheomys*, the oryzomyine *Microakodontomys*, and the thomasomyine *Aepeomys* were also missing from the Cyt *b* matrix. Therefore, both the IRBP (1,181 characters) and Cyt *b* (1,134 characters) matrices respectively included representatives of 76 and 74 sigmodontine genera (including sequences of the recently described genus *Neomicroxus*). The IRBP matrix lacked a sequence for *Neusticomys* available in GenBank [GenBank: EU649036] because a recent inspection of it indicated that it may be in fact a composite of an ichthyomyine and an oryzomyine sequence. Although the monophyly of the Sigmodontinae is well corroborated (e.g., Engel et al. 1998; Steppan et al. 2004; Parada et al. 2013), the identity of its sister group is unclear. Therefore, we integrated the outgroup with two representatives of each of the other four main lineages that, together with the Sigmodontinae, compose the family Cricetidae: arvicolines (*Arvicola* and *Microtus*), cricetines (*Cricetulus* and *Phodopus*), neotomines (*Neotoma* and *Scotinomys*), and tylomyines (*Nyctomys* and *Tylomys*). All taxa represented in the analyses, along with the GenBank accession numbers of their DNA sequences, are listed in Table 1.

Alignment was done with Clustal X (Thompson et al. 1997) using default parameters for all alignment parameters. Uncorrected genetic distances (*p* distances) with pairwise deletions were computed using MEGA 5 (Tamura et al. 2011). Each matrix was subjected to maximum-likelihood (ML) (Felsenstein 1981) and Bayesian analyses (BA)

Table 1 List of taxa and the DNA sequences of which were included in the phylogenetic analyses

Tribe	Species	IRBP	Cyt b
Abrotrichini	<i>Abrothrix longipilis</i>	AY163577	U03530
Abrotrichini	<i>Chelemys macronyx</i>	AY277441	U03533
Abrotrichini	<i>Geoxus valdivianus</i>	AY277448	AY275116
Abrotrichini	<i>Notiomys edwardsii</i>	AY163602	U03537
Abrotrichini	<i>Pearsonomys annectens</i>	AY851749	AF108672
Akodontini	<i>'Akodon' serrensis</i>	EF626799	AY273908
Akodontini	<i>Akodon azarae</i>	AY163578	DQ444328
Akodontini	<i>Bibimys chacoensis/labiosus</i>	AY277435	DQ444329
Akodontini	<i>Blarinomys breviceps</i>	AY277437	AY275112
Akodontini	<i>Bucepattersonius soricinus</i>	AY277439	AY277486
Akodontini	<i>Deltamys kempii</i>	AY277444	AY195862
Akodontini	<i>Juscelinomys huanchacae</i>	AY277453	AF133667
Akodontini	<i>Kunsia tomentosus</i>	AY277455	AY275120
Akodontini	<i>Lenoxus apicalis</i>	AY277456	U03541
Akodontini	<i>Necomys lasiurus</i>	AY277459	AY273912
Akodontini	<i>Oxymycterus nasutus</i>	AY277468	EF661854
Akodontini	<i>Scapteromys tumidus</i>	AY163637	AY275133
Akodontini	<i>Thalpomys cerradensis</i>	AY277481	AY273916
Akodontini	<i>Thaptomys nigrita</i>	AY277482	AF108666
Ichthyomyini	<i>Rheomys raptor</i>	AY163635	-
Incertae sedis	<i>Abrawayaomys ruschii</i>	JX949185	JX949189
Incertae sedis	<i>Andinomys edax</i>	JQ434400	AF159284
Incertae sedis	<i>Chinchillula sahamae</i>	JQ434409	JQ434422
Incertae sedis	<i>Delomys sublineatus</i>	AY163582	AF108687
Incertae sedis	<i>Euneomys chinchilloides</i>	AY277446	AY275115
Incertae sedis	<i>Irenomys tarsalis</i>	AY163587	U03534
Incertae sedis	<i>Juliomys pictipes</i>	AY163588	AF108688
Incertae sedis	<i>Neomicroxus latebricola</i>	QCAZ4160	QCAZ4160
Incertae sedis	<i>Neotomys ebriosus</i>	HM061605	HM061604
Incertae sedis	<i>Punomys kofordi</i>	JQ434414	JQ434426
Oryzomyini	<i>Aegialomys xantheolus</i>	GQ178247	EU579479
Oryzomyini	<i>Amphinectomys savamis</i>	AY163579	EU579480
Oryzomyini	<i>Cerradomys scotti</i>	EU649040	EU579482
Oryzomyini	<i>Drymoreomys albimaculatus</i>	EU649042	EU579487
Oryzomyini	<i>Eremoryzomys polius</i>	AY163624	EU579483
Oryzomyini	<i>Euryoryzomys macconnelli</i>	AY163620	EU579484
Oryzomyini	<i>Handleyomys intectus</i>	AY163584	EU579490
Oryzomyini	<i>Holochilus brasiliensis</i>	AY163585	EU579496
Oryzomyini	<i>Hylaeamys megacephalus</i>	AY163621	EU579499
Oryzomyini	<i>Lundomys molitor</i>	AY163589	EU579501
Oryzomyini	<i>Melanomys caliginosus</i>	EU649052	EU340020
Oryzomyini	<i>Microakodontomys transitorius</i>	EU649054	-
Oryzomyini	<i>Microryzomys minutus</i>	AY163592	AF108698
Oryzomyini	<i>Neacomys spinosus</i>	AY163597	EU579504

Table 1 List of taxa and the DNA sequences of which were included in the phylogenetic analyses (Continued)

Oryzomyini	<i>Nectomys squamipes</i>	AY163598	EU340012
Oryzomyini	<i>Nephelomys albigularis</i>	EU649057	EU579505
Oryzomyini	<i>Nesoryzomys fernandinae</i>	EU649058	EU579506
Oryzomyini	<i>Oecomys bicolor</i>	AY163604	EU579509
Oryzomyini	<i>Oligoryzomys fulvescens</i>	AY163611	DQ227457
Oryzomyini	<i>Oreoryzomys balneator</i>	AY163617	EU579510
Oryzomyini	<i>Oryzomys palustris</i>	AY163623	EU074639
Oryzomyini	<i>Pseudoryzomys simplex</i>	AY163633	EU579517
Oryzomyini	<i>Scolomys ucayalensis</i>	AY163638	EU579518
Oryzomyini	<i>Sigmodontomys alfari</i>	AY163641	EU340016
Oryzomyini	<i>Sooretamys angouya</i>	AY163616	EU579511
Oryzomyini	<i>Tanyuromys aphrastus</i>	JF693878	JF693877
Oryzomyini	<i>Transandinomys talamancae</i>	AY163627	EU579514
Oryzomyini	<i>Zygodontomys brevicauda</i>	AY163645	EU579521
Phyllotini	<i>Andalgalomys pearsoni</i>	EU649038	AF159285
Phyllotini	<i>Auliscomys pictus</i>	AY277434	JQ434420
Phyllotini	<i>Calomys lepidus</i>	AY163580	EU579473
Phyllotini	<i>Eligmodontia typus</i>	AY277445	AF108692
Phyllotini	<i>Galenomys garleppi</i>	JQ434410	JQ434423
Phyllotini	<i>Graomys griseoflavus</i>	EU649037	EU579472
Phyllotini	<i>Loxodontomys micropus</i>	AY277457	AY275122
Phyllotini	<i>Phyllotis xanthopygus</i>	AY163632	AY275128
Phyllotini	<i>Salinomys delicatus</i>	JQ434415	EU377608
Phyllotini	<i>Tapecomys primus</i>	JQ434416	AF159287
Phyllotini	Phyllotini n. gen.	JQ434417	JQ434425
Reithrodontini	<i>Reithrodon auritus</i>	AY163634	EU579474
Sigmodontini	<i>Sigmodon alstoni</i>	EU635698	AF293397
Thomasomyini	<i>Aepeomys lugens</i>	DQ003722	-
Thomasomyini	<i>Chilomys instans</i>	-	AF108679
Thomasomyini	<i>Rhagomys longilingua/rufescens</i>	DQ003723	AY206770
Thomasomyini	<i>Rhipidomys macconnelli</i>	AY277474	AY275130
Thomasomyini	<i>Thomasomys aureus</i>	AY277483	U03540
Wiedomyini	<i>Wiedomys pyrrhorhinos</i>	AY163644	EU579477
Outgroup	<i>Arvicola terrestris</i>	AY277407	AY275106
	<i>Cricetus cricetus</i>	AY277410	AY275109
	<i>Microtus socialis</i>	FM162055	AY513830
	<i>Neotoma albigula</i>	AY277411	AF108704
	<i>Nyctomys sumichrasti</i>	AY163603	AY195801
	<i>Phodopus sungorus</i>	AY163631	JN015007
	<i>Scotinomys xerampelinus</i>	AY277416	AF108706
	<i>Tylomys nudicaudus</i>	AY163643	DQ179812

Sequences of the genera *Bibimys* and *Rhagomys* of each gene were gathered from different species. GenBank accession numbers for each gene (IRBP and Cyt b) are indicated in the last two columns. Tribal assignments follow D'Elia et al. 2007 (see also D'Elia and Pardiñas 2007) and results of the present study.

(Rannala and Yang 1996). The ML analysis was conducted in Treefinder (Jobb et al. 2004; Jobb 2008). The best fitting models of nucleotide substitution (IRBP: TVM[Optimum, Empirical]:G[Optimum]:5; Cyt *b*: GTR[Optimum, Empirical]:G[Optimum]:5) (see Jobb 2008) were selected with the Akaike information criterion in Treefinder using the 'propose model' routine. The best tree was searched under the model of nucleotide substitutions previously selected using search algorithm 2 implemented in Treefinder version March 2011; nodal support was estimated with 1,000 bootstrap pseudoreplicates (BS). The BA was conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) by means of two independent runs with three (IRBP) or seven (Cyt *b*) heated and one cold Markov chains each. Considering the model selected by Treefinder and models specified in MrBayes, a model with six categories of a base substitution, a gamma-distributed rate parameter, and a proportion of invariant sites was specified for both matrices; all model parameters were estimated using MrBayes. Runs were allowed to proceed for 20 million (IRBP) and 28 million (Cyt *b*) generations, and trees were sampled every 1,000 (IRBP) and 2,000 (Cyt *b*) generations. Log-likelihood values were plotted against the generation time to check that runs converged on a stable log-likelihood value. The first 25% of sampled trees were discarded as burn-in; the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

Results

Cyt *b* gene sequences of *Abrawayaomys* gathered from the three specimens collected in the states of São Paulo and Rio de Janeiro varied by 0.5% ~ 0.7%; while comparisons involving the Cyt *b* sequence of the specimen from Minas Gerais ranged 2.6% ~ 3.0%. As mentioned above, IRBP sequences of the four specimens analyzed were identical.

Abrawayaomys, as represented by sequences of specimen MN 67557, was highly divergent from all compared sigmodontines for both analyzed genes. For the Cyt *b* gene, observed pairwise values involving *Abrawayaomys* ranged 19.0% ~ 25.9% for comparisons with *Neotomys* and *Lundomys*. For the IRBP gene, observed pairwise values involving *Abrawayaomys* ranged 3.42% ~ 6.65% for comparisons with *Brucepattersonius* and *Rheomys*.

Phylogenetic analyses recovered general results congruent with those of previous IRBP- and/or Cyt *b*-based studies (e.g., D'Elia et al. 2006a, b; Percequillo et al. 2011; Martínez et al. 2012; Parada et al. 2013; Salazar-Bravo et al. 2013). For descriptions and discussions of these findings (e.g., a strongly supported Sigmodontinae, a strongly supported Oryzomyalia, the polyphyly of the *Reithrodon* group, and differences between gene trees), we refer the reader to those studies because herein we focus on the phylogenetic position of *Abrawayaomys*.

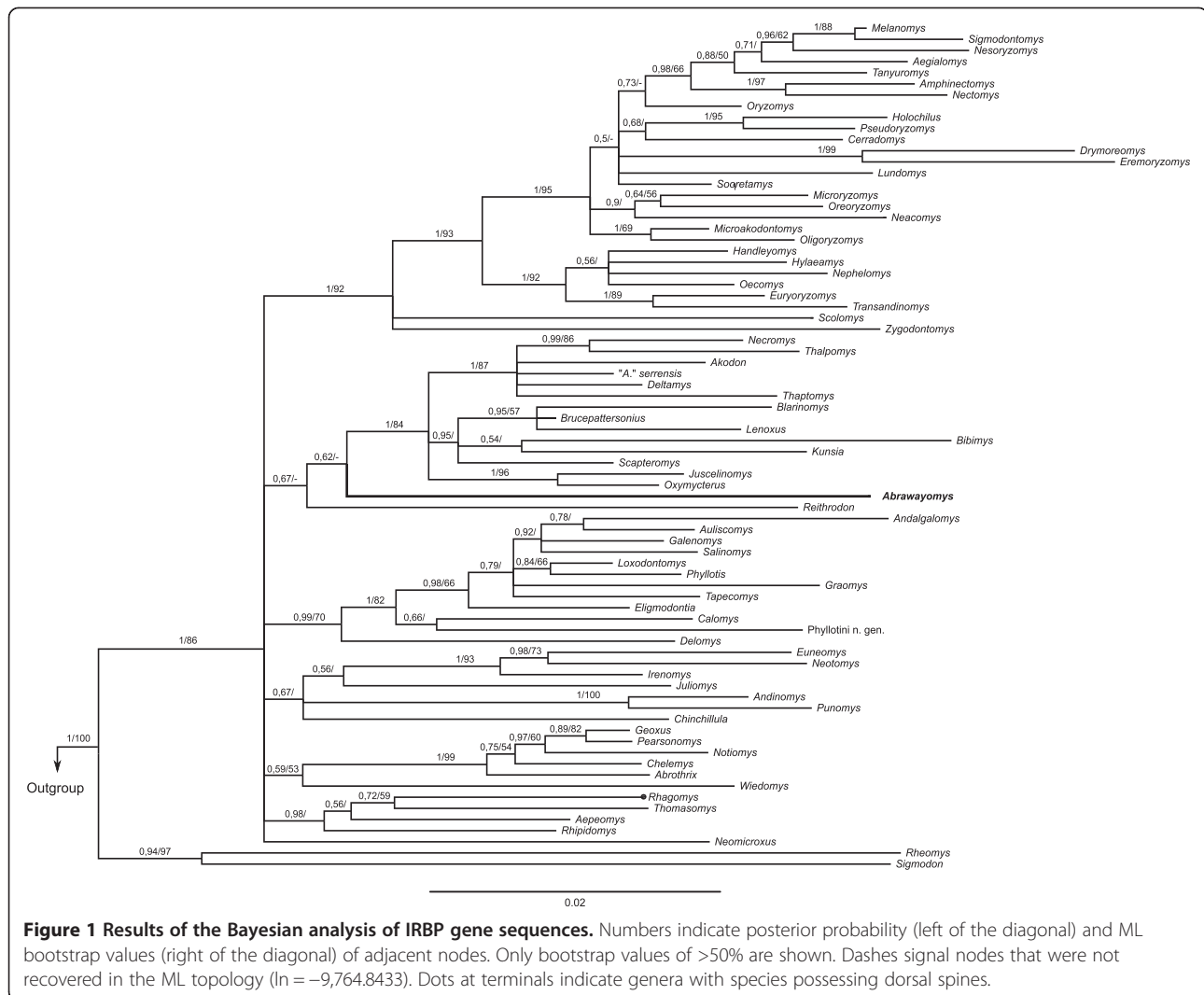
Depending on the gene analyzed, the phylogenetic position of *Abrawayaomys* varied from being sister to Akodontini (IRBP BA; PP = 0.62; Figure 1), sister to Thomasomyini (IRBP ML; BS < 50), sister to Reithrodontini (Cyt *b* BA; PP = 0.98; Figure 2), or sister to *Neotomys* (Cyt *b* ML; BS < 50). As noted, with the sole exception of the BA based on Cyt *b* sequences, where the *Abrawayaomys*-*Reithrodon* clade had strong support, all sister-group relationships involving *Abrawayaomys* lacked any significant support. The most inclusive and well-supported clade containing *Abrawayaomys* was that corresponding to Oryzomyalia (*sensu* Steppan et al. 2004).

Discussion

The diversity of sigmodontine forms has long captivated students of New World mammals, but at the same time, it has seriously defied those attempting to classify them according to their evolutionary history. Problems range from species boundaries to relationships among species and genera, and limits and contents of higher taxa (e.g., tribes). These issues have direct implications for the study of the history of the diversification of the group, which in turn arguably constitutes one of the most controversial debates in muroid systematics (Voss 1993; D'Elia 2003b).

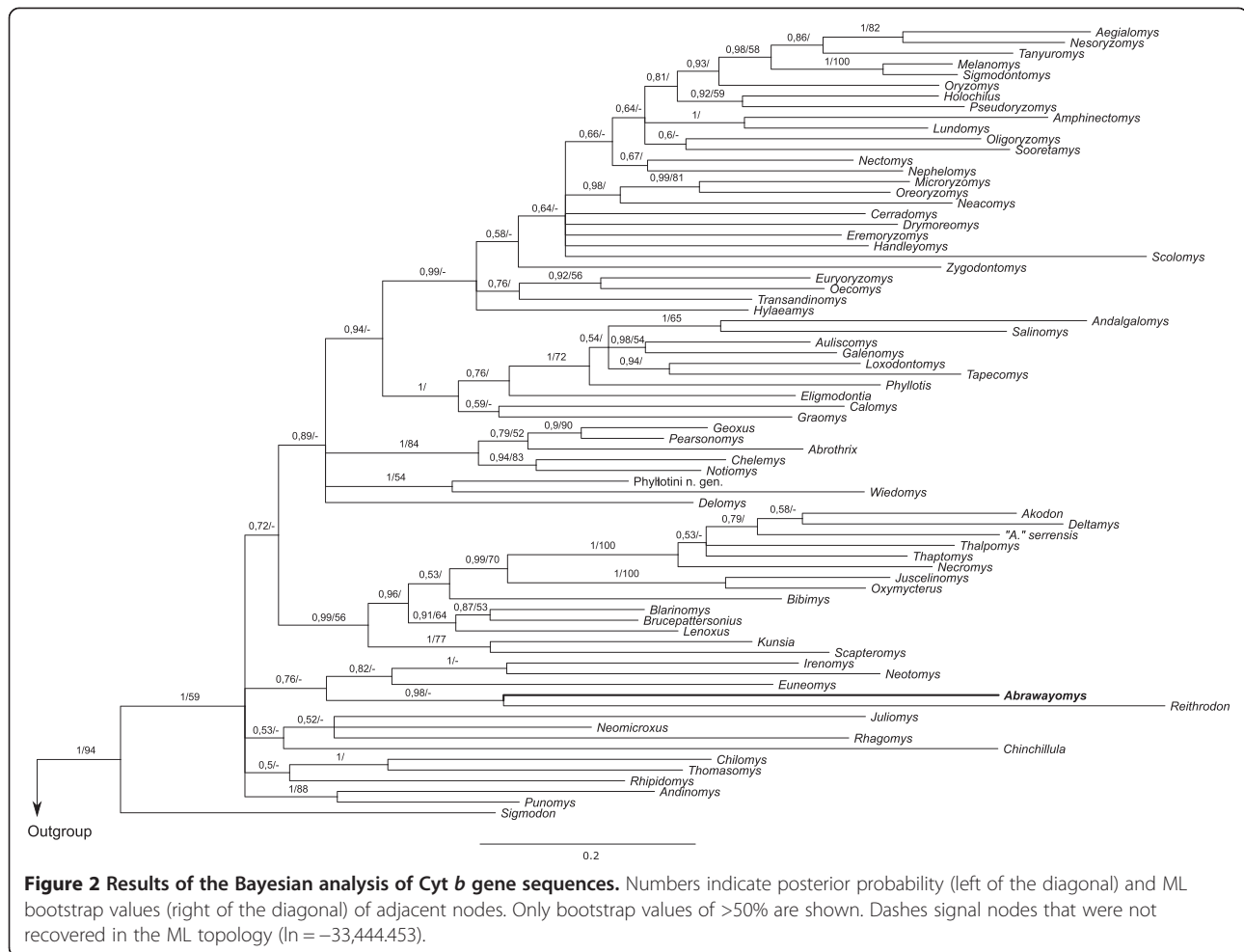
Herein, we showed that the phylogenetic position of *Abrawayaomys* varies from being sister to Akodontini, Thomasomyini, Reithrodontini, or *Neotomys*, depending on the gene analyzed (IRBP or Cyt *b*) and the analysis performed (ML or BA). Given that previous studies showed discrepancies between the topologies of different sigmodontine gene trees (e.g., Feijoo et al. 2010; Teta et al. 2011), the fact that different datasets (i.e., IRBP or Cyt *b* matrices with slightly different taxonomic sampling) provide different relationships for *Abrawayaomys* is not unexpected. Importantly, with the exception of the BA based on Cyt *b* sequences (sister to Reithrodontini), no sister relationship involving *Abrawayaomys* was recovered that had good support. In light of the analytical results, *Abrawayaomys* cannot be placed with certainty in any more inclusive clade than that of Oryzomyalia (*sensu* Steppan et al. 2004).

Pacheco (2003, p. 130), in a phylogenetic analysis based on morphological characters, found the genus *Abrawayaomys* to be sister to *Rhagomys* within the Thomasomyini clade. This relationship was supported by the following character states: a broad zygomatic plate, an interorbital region convergent with the supraorbital margins squared or weakly beaded, a long jugal, the absence of mesolophids (but see below), a masseteric crest anterior to the procingulum of the first lower molar, and a deeply excavated retromolar region of the mandible. Pacheco (2003) highlighted the retromolar region condition, i.e., broad and fenestrated, as a synapomorphy of *Abrawayaomys* + *Rhagomys*. We agree with Pacheco



(2003) (see Musser and Carleton 2005) in the general resemblance between *Abrawayaomys* and *Rhagomys* and to a lesser extent to the remainder of the Thomasonyini, but we suggest that this similarity is not remarkable and more important and that these shared character states are not synapomorphies of a putative *Abrawayaomys* and *Rhagomys* clade. Almost all of those character states listed by Pacheco (2003) are also present in many sigmodontines, indicating the large amount of homoplasy existing within this group. In addition, we assert that the molar morphologies of both genera are quite distinct, having only the widespread brachyodont condition in common. *Rhagomys* has very well-developed mesoloph/phids (*cf.* Luna and Patterson (2003) vs. Pacheco (2003)), procingula of the first upper molars clearly crossed by a deep anteromedian flexus, well-developed posterolophs, a slightly reduced third lower molar with respect to the second lower molar, and several other traits found among taxa displaying the dental bauplan of the pentalophodont type

(*sensu* Hershkovitz 1962), which is clearly distinguishable from the unequivocally tetralophodont molar of *Abrawayaomys* (*cf.* Pardiñas et al. 2009b). Additional differences between these two genera are more than trenchant, including incisive foramina and palate extensions, parapterygoid plate morphology, and carotid circulatory pattern (Table 2) (see also Pardiñas et al. 2009b, Table three). Similarly, several trenchant character states are present in *Abrawayaomys* and representatives of other sigmodontine tribes. The external morphology of *Abrawayaomys* resembles that of many akodonts (*cf.* Pereira et al. 2008, Figure one), although it has a moderately longer tail, at least in some individuals. A morphological description of the stomach (Finotti et al. 2003) suggests a hemiglandular-unilocular type, a widespread condition among sigmodontines (Carleton 1973). Finally, Pacheco (2003) also indicated that *Abrawayaomys* has a peculiar genal vibrissa (called genal vibrissa 2), which is also present in the oryzomyine *Oecomys* and



the akodontine *Kunsia*, and a reduced fifth pedal digit. Similarly, karyotypic evidence sheds no conclusive light on the phylogenetic position of *Abrawayaomys*, as the diploid number of $2n = 58$ (Pereira et al. 2008) found in *A. ruschii* is also present in several distantly related oryzomyine species, such as *Euryoryzomys lamia* (Andrades-Miranda et al. 2000), *Holochilus brasiliensis* (Yonenaga-Yassuda et al. 1987), *Nectomys squamipes* (Yonenaga-Yassuda et al. 1987), *Oecomys trinitatis* (Patton et al. 2000), *Oligoryzomys chacoensis* (Myers and Carleton 1981), and *Sooretamys angouya* (Andrades-Miranda et al. 2000). Taking all this evidence as a whole, *Abrawayaomys* cannot be placed with certainty in any clade less inclusive than the large clade Oryzomyalia (see also Voss 1993). Therefore, in light of all of the evidence at hand, in formal classifications, *Abrawayaomys* should be kept as an incertae sedis sigmodontine (D'Elía et al. 2007). Results of future phylogenetic analyses, especially those including sequences of two other Atlantic forest inhabitants, *Phaenomys* and *Wilfredomys*, which were also considered part of the tribe Thomasomyini (e.g., Pacheco 2003) and are now regarded as Sigmodontinae incertae sedis

(e.g., D'Elía et al. 2007), may prompt changes in this classification.

The prevailing biogeographic view is that the Andes played a major role in sigmodontine diversification, in which the main sigmodontine lineages originated there and later colonized lowlands of South America (Reig 1984, 1986; see also Salazar-Bravo et al. 2013). However, *Abrawayaomys*, an Atlantic forest endemic, is the sole living representative of one of the main sigmodontine lineages (i.e., those classified at the tribal rank in formal classifications or those genera that do not belong to any recognized tribe). A similar scenario was found for two other Atlantic forest endemics, the genera *Delomys* and *Juliomys* (Figures 1 and 2) (Voss 1993; D'Elía et al. 2006a; see also the classification in D'Elía et al. 2007). The other main sigmodontine lineages are distributed outside the Atlantic forest (e.g., Abrotrichini and Sigmodontini) or, even when present in this biome, are not endemic to it (e.g., Akodontini and Oryzomyini). As mentioned above, the Atlantic forest-endemic *Phaenomys* and mostly Atlantic forest-resident *Wilfredomys* have not been included in any molecular-based phylogenetic analysis. Until their

Table 2 Morphological comparisons among *Abrawayaomys* and other members of the Sigmodontinae

Character	<i>Abrawayaomys</i>	<i>Rhagomys</i> ^b	<i>Phaenomys</i> ^d	<i>Thomasomys</i> ^f	<i>Aepeomys</i> ^g	<i>Akodon</i>	<i>Reithrodon</i>
Plantar pads	6	6	6	6	6	6	4
Hindfoot surface	Smooth?	Smooth	Squamated	Smooth	Smooth	Squamated	Squamated
Mammae	6a	6	8	6	6	8	8
Spines	Present	Present ^c	Absent	Absent	Absent	Absent	Absent
Relation of tail length (LT) to head-body length (HB)	LT < = > HB	LT ≤ HB	LT > > HB	LT < = > HB	LT > HB	LT ≤ HB	LT < < HB
Rostrum	Short	Short	Long	Long	Long, rostral tube developed	Moderate	Moderate
Interorbit	Hourglass-shaped or slightly convergent, with rounded margins	Convergent, with beaded margins	Hourglass-shaped ^e , with beaded margins	Hourglass-shaped, with rounded margins	Hourglass-shaped, with rounded margins	Hourglass-shaped, with rounded margins	Symmetrically constricted, with parallel margins
Palate	Typically short	Long	Short	Short	Short	Short	Long
Mesopterygoid fossa	Not fenestrated	Not fenestrated	Not fenestrated	Not fenestrated	Not fenestrated	Fenestrated	Fenestrated
Alisphenoid strut	Typically present	Present	Absent	Present	?	Typically present	Present
Tegmen tympani	Overlaps squamosal	Overlaps squamosal	Overlaps squamosal	Overlaps squamosal	Overlaps squamosal	Overlaps squamosal	Does not overlap squamosal
Carotid circulation	Pattern 1	Pattern 3	Pattern 1	Pattern 1	Pattern 1	Pattern 1	Pattern 3
Capsular process	Present	Present	Absent	Absent	Absent	Typically present	Present
Retromolar fossa	Enlarged	Enlarged	Not enlarged	Not enlarged	Not enlarged	Not enlarged	Not enlarged
Molar design	Intermediate to alternate, crested	Opposite, crested	Opposite, crested	Opposite, crested	Opposite, crested	Intermediate, crested to terraced	Alternate, plane
Anteromedian flexus	Patent	Patent	Patent	Patent	Patent	Patent	Not patent
Mesoloph on M1	Present, small	Present, large	Present, large	Present, large	Present, large	Present, small	Absent
M3 reduction to M2	Much reduced	Moderately	Weakly	Moderately	Moderately to reduced	Much reduced	Weakly
Incisors	Orthodont to proodont	Orthodont	Opisthodont	Opisthodont	Opisthodont	Typically opisthodont	Opisthodont
Incisive foramina	Reaching anterior face M1	Very short	Reaching anterior face M1	Reaching anterior face M1	Reaching anterior face M1	Reaching protocone M1	Reaching protocone M1
Subsquamosal foramen	Present	Present	Absent	Present	Present	Present	Present
Number of ribs	12	13	12	13	13	13	12
Gall bladder	Absent	Absent	Present	Present	Present	Typically present ^h	Present

^aInguinal, abdominal, and postaxial pairs (Pardiñas, unpublished data). ^bBased on *Rhagomys longilingua*, after Luna and Patterson (2003). ^c*Rhagomys rufescens* lacks spines (cf. Luna and Patterson 2003). ^dData from Voss et al. (2002) and Pardiñas (unpublished data). ^eScored as 'convergent' by Pacheco (2003, p. 43). ^fVariation in this genus is remarkable (cf. Pacheco 2003); herein, we follow Voss (1993). ^gBased on *Aepeomys lugens*, after Voss et al. (2002). ^h*Akodon montensis* lacks gall bladder (cf. Geise et al. 2004).

phylogenetic position is assessed, it is unclear whether they in fact represent additional main sigmodontine lineages almost endemic to the Atlantic forest or simply constitute additional genera belonging to other already identified main lineages of the Sigmodontinae either already known from the Atlantic forest or not. Whatever this result is, the finding that at least three unrelated main sigmodontine lineages, those currently represented by *Abrawayaomys*, *Delomys*, and *Juliomys*, are endemic to the southern Atlantic forest supports early claims (Smith and Patton 1999; D'Elia 2003b; see also Salazar-Bravo et al. 2013) highlighting the role of the Atlantic forest in harboring sigmodontine phylogenetic diversity. Future studies should be designed to test if these lineages originated in the Atlantic forest or simply invaded it after originating elsewhere.

Spines of varying hardness and architectures are present in several rodents (Chernova and Kuznetsov 2001) and are conspicuous in some Neotropical groups, such as porcupines (Erethizontidae) and spiny rats (Echimyidae). The vast majority of sigmodontine rodents have soft fur, but a few genera and species have dorsal spines. These spines are present in both species of *Abrawayaomys*, both species of *Scolomys*, all eight species of *Neacomys*, but only in one of the two species of *Rhagomys*. *Rhagomys longilingua* from the Andes has spiny fur, but *Rhagomys rufescens* from the Atlantic forest has soft fur (Luna and Patterson 2003). Considering the phylogeny portrayed here, we concluded that these spines are the result of evolutionary convergence, and this trait evolved at least four times in sigmodontines (Figure 1). None of these four genera are sister groups, and each one of them shares a more recent common ancestor with soft-furred genera or species (in the case of *Rhagomys*). The functional significance of spines remains unknown. Unlike porcupine quills, spines of muroid or echimyid rodents are insufficiently rigid to provide much protection against predators, including snakes, birds, and mammals, which are known to prey heavily on many spiny species (Hoey et al. 2004). Patterson and Velasco (2008) suggested a thermoregulatory interpretation based on the geographic distribution of echimyid rodents: the spiniest members occur in tropical lowland forests, while many of the softest-haired members of the family range into high elevations or latitudes, but they also noted several exceptions. The same pattern does not occur in sigmodontine rodents, since soft-furred taxa occur at all latitudes and elevations throughout the Neotropics. Regarding spiny taxa, both *Neacomys* and *Scolomys* are lowland forest genera found at lower latitudes (Patton et al. 2000); *Abrawayaomys* also occurs in lowland forests, but at higher latitudes in the Atlantic forest (Pardiñas et al. 2009b); and the spiny *R. longilingua* is found in Andean cloud forests at 1,900 ~ 2,100 m in elevation (Luna and Patterson 2003), while the soft-furred *R.*

rufescens occurs mostly in montane Atlantic forest at 500 ~ 1,000 m in elevation (Steiner-Souza et al. 2008). Therefore, we still lack robust hypotheses for the ecological role, if any, of spiny fur in sigmodontine rodents, but the character distribution mapped on a phylogenetic tree presented here is the first step toward understanding its evolutionary importance.

Conclusions

Phylogenetic analyses show that *Abrawayaomys* constitutes the single representative so far known of one of the main lineages of the radiation of Sigmodontinae. In addition, it differs from all other Atlantic forest sigmodontine rodents by having a unique combination of morphological character states. Therefore, in formal classifications, it should be regarded as a Sigmodontinae incertae sedis.

Finally, the observed variation of the four *Cyt b* sequences analyzed and their geographic pattern, where the one gathered from the northernmost-collected specimen (in the state of Minas Gerais) was the most divergent, are enticing to further explore variation of a larger sample of *A. ruschii* sequences. Such a study would clarify into which of the already known phylogeographic patterns of Atlantic forest mammals (e.g., Colombi et al. 2010; Ventura et al. 2012; Valdez and D'Elia 2013; see reviews in Martins 2011; Costa and Leite 2012) would *A. ruschii* fit, or if this species presents a so far undescribed pattern. Similarly, such a study would help assess the alpha diversity of *Abrawayaomys* (Pardiñas et al. 2009b). Now, that *A. ruschii* is becoming more frequent in specimen collections, such a study seems feasible.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

KV and GD conceived and coordinated the study. KV, MJJS, LG, YLRL, and YY-Y gathered the DNA sequences. UFJP and YLRL performed the morphological assessment. GD carried out the phylogenetic analyses. GD, KV, and UFJP drafted the manuscript. All authors read and approved the final manuscript.

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