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CONTRIBUIÇÕES À SISTEMÁTICA E DISTRIBUIÇÃO PREDITIVA DOS ROEDORES *JULIOMYS* (CRICETIDEA, SIGMODONTINAE)

PAULO TOMASI SARTI

PROFA. ORIENTADORA: DRA. LARISSA ROSA DE OLIVEIRA

PROF. CO-ORIENTADOR: DR. ALEXANDRE UARTH CHRISTOFF

SÃO LEOPOLDO, JANEIRO DE 2016

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Orientadora: Dra. Larissa Rosa de Oliveira

Co-orientador: Dr. Alexandre Uarth Christoff

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“Daria tudo que sei pela metade do que ignoro.”

René Descartes

ÍNDICE

1. AGRADECIMENTOS

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2. RESUMO

Os roedores *Juliomys* possuem tamanho diminuto e hábito arborícola. Desde seu estabelecimento no ano 2000, o gênero vem sendo estudado e novas informações tem sido apresentadas. Entretanto, devido ao pequeno intervalo de tempo desde então, muitas perguntas ainda esperam por respostas acerca da biologia geral, relações ecológicas, distribuição geográfica, riqueza de espécies e posição filogenética dentro dos Sigmodontinae. Especificamente, estudos morfométricos e genéticos são ferramentas importantes a serem exploradas. O objetivo geral deste estudo foi analisar a morfologia bem como os marcadores genéticos, a fim de subsidiar dados relevantes para a sistemática e biogeografia das espécies de *Juliomys*. Utilizamos métodos de análise morfológica, morfométrica e molecular para a definição do novo táxon, que conta com alto suporte. Produzimos mapas de potencial ocorrência das espécies de acordo com o as preferências ambientais. Testamos também o monofiletismo do gênero dentro de Sigmodontinae através do estudo de um marcador molecular. Assim, corroborando os estudos anteriores, descrevemos e propomos uma nova espécie para o gênero. Já a modelagem de distribuição das espécies revelou padrões interessantes, com distribuições desiguais ao longo do bioma Mata Atlântica. Evidenciamos ainda que *Juliomys* trata-se de um clado monofilético, apesar das diferenças morfológicas; dados fundamentais no embasamento de abordagens de distribuição. Ressaltamos que coleções de história natural ou coleções de Museu são fontes essenciais de informações da fauna, pois foram imprescindíveis neste estudo. A conservação da fauna toma os pressupostos da sistemática e biogeografia, como os aqui apresentados, para alicerçar suas ações.

3. ABSTRACT

The *Juliomys* are small-sized arboreal rodents. Since its establishment in 2000, the genus has been studied, and new information has been presented progressively. However, due to the short time period, many questions are still awaiting for answers related about general biology, ecological relationships, geographic distribution, species richness, and phylogenetic position within the Sigmodontinae. Morphometric and genetic studies are important tools to explore these lines. The aim of this study was to analyze the morphology and the genetic markers in order to subsidize the systematic and biogeography of *Juliomys* species. We use methods of morphologic, morphometric, and molecular analyses to define the new taxon. We produce maps of potential occurrence of the species according to the environmental preferences. Finally, we tested the monophyly of the genus within Sigmodontinae through the study of a molecular marker. Corroborating previous studies, we describe and propose a new species for the genus. The species distribution modeling revealed interesting patterns with unequal distributions along the Atlantic Forest biome. We endorse that *Juliomys* it is a monophyletic clade, despite the morphological differences. Studies grounded phylogenetically as well as monophyletic clades should be based delivery approaches. It is notorious that natural history museum collections are essential sources of wildlife information, which was crucial to this study. The conservation of fauna takes the systematic and biogeography assumptions, as those presented in this study, to underpin their actions.

4. PRÓLOGO

A tese que apresento a seguir é fruto de várias etapas de um estudo e de colaboração entre diversos pesquisadores. Neste estudo buscou-se aprimorar o conhecimento sobre um grupo específico, que ainda carece de informações importantes: os roedores. Rodentia é a ordem mais diversa entre os Mammalia, englobando mais de 42% do total de suas espécies (MUSSER; CARLETON, 2005). Mais especificamente, o objeto deste estudo foi um pequeno grupo de roedores neotropicais do gênero *Juliomys* pertencente a subfamília Sigmodontinae.

O estudo dos Sigmodontinae conta com várias abordagens e através delas sua diversidade ainda vem sendo aos poucos revelada (e.g., HERSHKOVITZ, 1955, 1962; REIG 1984, 1987; SMITH; PATTON, 1999; WEKSLER, 2003; D'ELIA et al., 2007; LEITE et al., 2008; SALAZAR-BRAVO et al., 2013). Há ainda carência de informações sobre a sistemática destes roedores, sobretudo aqueles que habitam um dos biomas mais ameaçados e fragmentados do planeta, a Mata Atlântica (MYERS et al. 2000; BRITO, 2004). Os pequenos roedores arborícolas *Juliomys* são um grupo recentemente estabelecido pelo zoólogo uruguaio Enrique M. González em 2000 (Fig. 1). Desde então, o gênero vem sendo estudado e novas informações tem sido apresentadas (e.g. PAVAN; LEITE, 2011). Entretanto, por ser um táxon recentemente descrito muitas perguntas ainda esperam por respostas acerca da biologia geral, riqueza de espécies, distribuição geográfica, sistemática, e ainda sobre suas relações ecológicas.

Fig. 1. *Juliomys pictipes.* Localidade: Dois Irmãos/RS. Foto: Paulo Tomasi.

González (2000) propôs este novo gênero atribuindo a este novo gênero a espécie *Wilfredomys pictipes* (Osgood, 1933). Atualmente são reconhecidas três espécies viventes de *Juliomys*: *J. ossitenuis, J. pictipes* e *J. rimofrons;* além da extinta *J. anoblepas* (OLIVEIRA; BONVICINO, 2002; COSTA et al., 2007; PARDIÑAS et al., 2008; PARDIÑAS; TETA, 2011; GONZÁLEZ et al., 2015). Recentemente um novo cariótipo para o gênero foi descrito por Paresque et al. (2009), sugerindo a possibilidade da existência de uma quarta espécie (doravante apresentada como *Juliomys* sp.1). Tal fato evidencia que a composição deste grupo ainda carece de investigações mais aprofundadas. Uma recente contribuição de González et al. (2015) resume o atual estado do conhecimento sobre o gênero. Entretanto, no âmbito filogenético há incertezas. Diversos estudos têm inferido a posição dos *Juliomys* em relação aos demais Sigmodontinae, porém a cada nova reconstrução sua posição tem variado (D'ELÍA, 2003; WEKSLER, 2003; MARTÍNEZ et al., 2012; PARADA et al., 2013; SALAZAR-BRAVO et al., 2013), sendo assim o gênero tem sido reportado como *incertae sedis* (D'ELÍA, 2015). Contudo, em todas as reconstruções filogenéticas apresentadas, somente uma espécie do gênero tem sido utilizada: *J. pictipes.* Os diferentes táxons que compõe o grupo de espécies apresentam diferenças morfológicas entre si (GONZÁLEZ et al., 2015), e entre elas se destaca o diferente padrão de circulação cariotídica craniana, que diverge entre *J. pictipes* e as demais. Mudanças tão profundas na morfologia muitas vezes estão relacionadas a origens evolutivas distintas (AMORIM, 2002). Neste âmbito, o estabelecimento das espécies deste gênero como um grupo monofilético dentro de Sigmodontinae nunca foi proposto ou analisado.

As incertezas sobre as espécies de *Juliomys* seguem também no âmbito geográfico. Os escassos registros das espécies deste gênero conhecidos na literatura estão restritos do sudeste ao sul do Brasil, e do nordeste da Argentina ao extremo leste do Paraguai (BONVICINO et al., 2008; PAVAN; LEITE, 2011; GONZÁLEZ et al., 2015). Os registros do potencial novo táxon (PARESQUE et al., 2009) restringem-se ao extremo sul da área conhecida de distribuição para o gênero (nordeste do Rio Grande do Sul), ambiente de formação florestal de Mata de Araucária, bioma Mata Atlântica. O conhecimento atual de ocorrência das espécies deste gênero os associa sempre às formações de mata e acredita-se que *Juliomys* são considerados endêmicos das formações florestais do bioma Mata Atlântica (PAVAN; LEITE, 2011). As espécies do gênero parecem ser pouco abundantes nas comunidades, apresentando hábito essencialmente arborícola, e aparentando preferência por ambientes de interior de mata (CADERMATORI et al., 2008). Há registros de simpatria entre as espécies (PAVAN; LEITE 2011), porém os requerimentos de nicho dos taxa em relação as condições ambientais são pouco conhecidas. Além disso, dados ecológicos são praticamente inexistentes, bem como informações da biologia e fisiologia destes animais. Tais fatos somados à aparente baixa densidade populacional (GRAIPEL, 2006) e consequentemente a coleta e tombamento em coleções científicas de poucos indivíduos com identificação correta dificultam o conhecimento da real distribuição das espécies deste gênero. Os componentes de nicho para cada espécie *Juliomys* são desconhecidos, o que potencialmente poderia evidenciar as área de distribuição das espécies. A Mata Atlântica, vem sofrendo intensa degradação ao longo dos séculos, restando hoje aproximadamente 5% de sua cobertura original (CAMPANILI; BERTOLDO, 2010), consequentemente também é importante diagnosticar suas áreas de ocupação neste bioma.

Metodologias atuais, como modelos de predição, tem se mostrado boas soluções para inferência da distribuição geográfica de espécies mesmo que utilizando dados pontuais (PEARSON et al., 2007). Estudos recentes utilizando sistemas geográficos de informação tem desenvolvido bons modelos preditivos de distribuição de espécies, como por exemplo Maxent (PHILLIPS, 2006). Estes modelos utilizam regressão logística, algoritmos e preferências de nicho para produzir modelos (mapas) de distribuição preditiva (STOCKWELL; PETERS, 1999; Austin, 2007) que nos permitem predizer a potencial área de ocorrência das espécies com base na teoria do nicho e através da análise dos registros de ocupação do meio-ambiente. Estes modelos tem como pressuposto as definições taxonômicas, os locais de coleta dos indivíduos e suas variáveis ambientais (importantes para a construção dos modelos) (ELITH; LEATHWICK, 2009), produzindo mapas de potencial ocorrência das espécies de acordo com o as preferências ambientais das espécies.

Segundo Barros (2015) “abordagens puramente morfológicas têm sido ultimamente consideradas, por vezes, insuficientes para o entendimento da complexidade taxonômica de algumas espécies”. Neste sentido, estudos morfométricos e genéticos são ferramentas importantes a serem exploradas. Um aprofundado entendimento sistemático (taxonomia investigativa) é chave para inferências biogeográficas e conservacionistas (Barros 2015). Com base neste olhar, o objetivo geral deste estudo foi analisar a morfologia bem como os marcadores genéticos, a fim de obter subsídios a inferências na sistemática e biogeografia das espécies do gênero *Juliomys*. Assim, os objetivos específicos propostos foram: A) examinar características morfológicas e medidas morfométricas diagnósticas entre as espécies do gênero; B) identificar e descrever possíveis novos taxa; C) gerar modelos de distribuição geográfica preditiva das espécies; D) testar a hipótese monofilética para o gênero dentro de Sigmodontinae.

A coleta de dados teve duração de dois anos e meio, iniciada em Março de 2013 e finalizada em Setembro de 2015, quando foram visitadas 14 coleções científicas (Tabela 1) onde foram examinados morfologicamente 217 indivíduos de *Juliomys* (Tabela 2) através de caracteres anatômicos e medidas lineares (Figs. 2 e 3). Adicionalmente, durante o exame dos espécimes nas coleções científicas coletamos amostras de tecido (n = 60) com o objetivo de identificar as espécies de *Juliomys* através da análise de sequências com sítios diagnósticos de determinados marcadores moleculares usados em análises filogenéticas (SCHLÖTTERER, 2004). A abordagem integrada, combinando métodos de identificação morfológica com dados moleculares, tem sido considerada melhor estratégia de definição taxonômica e filogenética atualmente (e.g. OLIVEIRA; BONVICINO, 2002; COSTA et al., 2007; OLIVEIRA et al., 2008).

Tabela 1. Instituições consultadas e número de espécimes de *Juliomys* analisados.

Instituição	Total de espécimes	Data da consulta
Museu de Ciências Naturais da Universidade Luterana do Brasil (MCNU)	17	1 a 15/3/2013
Laboratório de Mamíferos Aquáticos da Universidade Federal de Santa Catarina (LAMAQ-UFSC)	40	2 a 6/12/2013 e 14 a

		17/4/2014
Coleção Mastozoológica da Universidade Federal do Espírito Santo (UFES)	8	14 a 16/102013
Museu de Biologia Prof. Mello Leitão (MBML)	3	17 a 18/10/2013
Museu Nacional da Universidade Federal do Rio de Janeiro (MN)	25	21 a 25/10/2013
Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M)	10	28 a 31/10/2013
Coleção Mastozoológica da Universidade Federal de Minas Gerais (UFMG)	16	6 a 8/11/2013
Museu de Zoologia da Universidade de São Paulo (MZUSP)	26	12 a 15/5/2014
Coleção Zoológica da Universidade Regional de Blumenau (CZFURB)	35	9 a 12/6/2014 e 8/9/2015
Coleção Mastozoológica da Universidade Federal de Santa Maria (UFSM)	5	28 a 31/10/2014
Coleção Mastozoológica da Universidade Regional Integrada do Alto Uruguai e das Missões (URI)	1	31/10/2014
Coleção Mastozoológica da Escola Superior de Agricultura Luiz de Queiroz da Universidade de São Paulo (ESALQ-USP)	23	2 a 4/3/2015
Coleção Mastozoológica da Universidade Federal do Paraná (DZUP)	8	9/9/2015
Coleção Mastozoológica da Universidade Federal da Paraíba (UFPB)	1	30/9/2015
	217	

Tabela 2. Sexo e classe etária dos indivíduos de *Juliomys* analisados (n = 217).

Taxa	Sexo			Idade			
	Macho	Fêmeas	Indefinido	Adultos	Jovens	Indefinido	Total
Juliomys sp.1	4	0	0	4	0	0	4
J. cf. ossitenuis	17	15	1	32	1	0	33
J. cf. rimofrons	4	1	1	5	0	1	6
J. cf. pictipes	41	28	21	76	6	8	90
Juliomys spp.	32	35	17	68	2	12	84
Total	98	79	40	187	9	21	217

O presente trabalho traz informações pertinentes a representantes muito pouco conhecidos da fauna Neotropical, contribuindo para o conhecimento aprofundado da biologia dos mamíferos. Este, positivamente relacionado aos estudos taxonômicos, especialmente em regiões de biota megadiversa e ameaçada como a Mata Atlântica. Visto que os roedores compõem parte importante de diversas teias alimentares e são essenciais para o funcionamento dos ecossistemas (FELDHAMER et al., 2007), sua conservação é fundamental e depende do entendimento de sua diversidade e uso do ambiente. Com esta contribuição pretendemos fomentar as bases de dados dos Rodentia neotropicais, embasando futuros estudos ecológicos, biogeográficos e conservacionistas.

Fig. 2. Morfologia externa dos táxons analisados neste estudo. Visão dorsal: A) *Juliomys* sp.1 (MCNU 869), B) *J. pictipes* (MZUSP 3171), C) *J. ossitenuis* (MN 69752), D) *J. rimofrons* (MN 61647). Visão ventral: E) *Juliomys* sp.1 (MCNU 869), F) *J. pictipes* (MZUSP 3171), G) *J. ossitenuis* (MN 69752), H) *J. rimofrons* (MN 61647). Escala = 1 cm. Fotos: Paulo S. Tomasi.

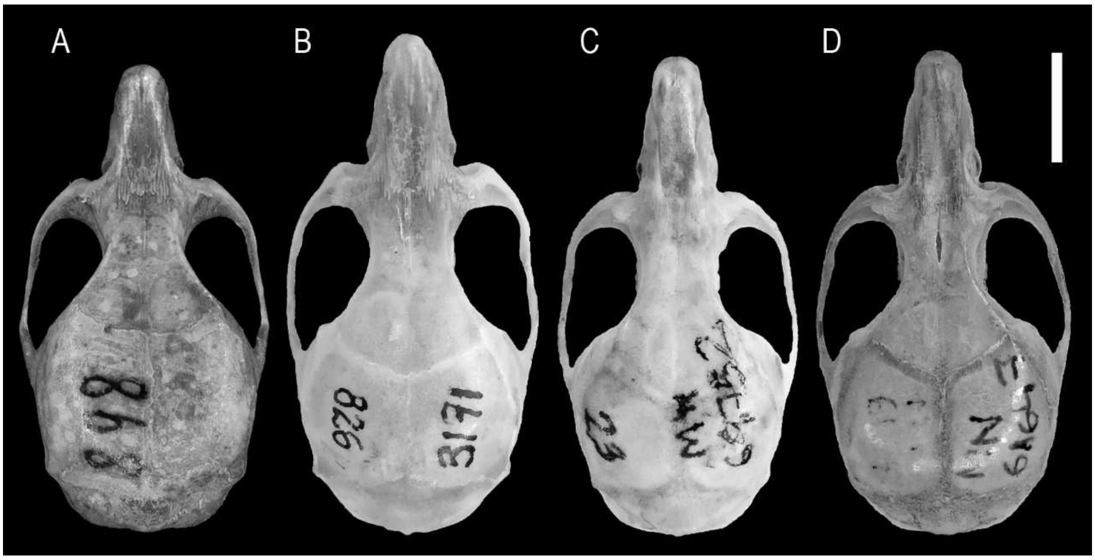

Fig. 3. Visão dorsal do crânio das diferentes taxa. A) *Juliomys* sp.1 (MCNU 869), B) *J. pictipes* (MZUSP 3171), C) *J. ossitenuis* (MN 69752), D) *J. rimofrons* (MN 61647). Escala = 5mm. Fotos: Paulo S. Tomasi.

A tese está dividida em três capítulos que abrangem a referida problemática acerca dos *Juliomys*. No primeiro capítulo descrevemos e propomos uma nova espécie para o gênero com base em dados cariotípicos, moleculares e morfológicos. O título deste capítulo é “A new species of *Juliomys* (Rodentia, Cricetidae, Sigmodontinae) from the Atlantic Forest of Southern Brazil” e encontra-se em revisão “aceito” no periódico *Journal of Mammalogy*. O segundo capítulo aliou a diagnose anatômica e análises morfométricas a fim de ampliar a identificação dos espécimes depositados nas coleções científicas como *Juliomys* sp. Após esta reclassificação e através da análise conjunta com a informação sobre suas respectivas localidades conhecidas, realizamos a modelagem preditiva da distribuição geográfica de cada uma das espécies do gênero. Este capítulo foi intitulado “Predictive distribution of the mice *Juliomys* (Rodentia, Cricetidae, Sigmodontinae) based on morphometric and taxonomic review of specimens” está em preparação para submissão no periódico *Mammal Review*. No terceiro e último capítulo trazemos contribuições sobre o monofiletismo das espécies do gênero dentro de Sigmodontinae, através de uma abordagem molecular. Este capítulo intitulou-se "Monophyletic evidence for the genus *Juliomys* (Rodentia, Cricetidae, Sigmodontinae)" e está em preparação para submissão no periódico *Mammal Research* (Acta Theriológica).

É importante salientar que apesar dos manuscritos estarem formatados para seus respectivos periódicos de submissão, as figuras e as tabelas estão inseridas ao longo do texto para propiciar melhor leitura da tese.

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5. CAPÍTULO I

A NEW SPECIES OF *JULIOMYS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) FROM THE ATLANTIC FOREST OF SOUTHERN BRAZIL

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Contact information for the corresponding author:
Alexandre U. Christoff
Departamento de Biologia, Museu de Ciências Naturais, Universidade Luterana do Brasil, Av. Farroupilha 8001, Canoas, Rio Grande do Sul CEP 92.425-900, Brazil.
E-mail: *auchrist@ulbra.br*

RH: NEW SPECIES OF *JULIOMYS* FROM BRAZIL

A new species of *Juliomys* (Rodentia, Cricetidae, Sigmodontinae) from the Atlantic Forest of Southern Brazil

Alexandre U. Christoff*, Emerson M. Vieira, Larissa R. Oliveira, Juliana W. Gonçalves, Victor H. Valiati, Paulo S. Tomasi

Departamento de Biologia, Museu de Ciências Naturais, Universidade Luterana do Brasil, Av. Farroupilha 8001, Canoas, Rio Grande do Sul CEP 92.425-900, Brazil (AUC)

Departamento de Ecologia, Laboratório de Ecologia de Vertebrados, Universidade de Brasília, Campus Universitário Darcy Ribeiro, Brasília, Distrito Federal CEP 70.910-900, Brazil (EMV)

Laboratório de Ecologia de Mamíferos, Universidade do Vale do Rio dos Sinos, Av. Unisinos 950, São Leopoldo, Rio Grande do Sul CEP 93.022-000, Brazil (LRO, PST)

Laboratório de Biologia Molecular, Universidade do Vale do Rio dos Sinos, Av. Unisinos 950, São Leopoldo, Rio Grande do Sul CEP 93.022-000, Brazil (JWG, VHV)

*Correspondent: *auchrist@ulbra.br*

Abstract

Sigmodontinae is a very rich clade of rodents that is widespread throughout the Neotropics. The arboreal mice *Juliomys* comprise a poorly known branch, with incomplete information about species richness, phylogenetic position, and geographic distribution. Based on a sample from the Atlantic Forest of Southern Brazil, we name and describe a new species for the genus. This new species can be distinguished from others in the genus by its karyotype, morphological traits, and cytochrome *b* gene sequence. It has a unique karyotype (2n = 32, FN = 48), and forms a well-supported monophyletic haplogroup, which is phylogenetically distant from the remaining species of *Juliomys*. The genetic differentiation ranges from 11.1 to 19.7%, and there are 24 molecular autopomorphies in the cytochrome *b* gene. The new species can be distinguished from *J. pictipes* by morphological and morphometric analyses. However, we consider the new species as cryptic, not easily recognized by morphological characteristics of other species of *Juliomys* and not easily distinguished from the other species. This taxon seems to be endemic to the Brazilian Araucaria Forest in the Atlantic Forest biome, occurring in sympatry with its congeneric species *J. ossitenuis* and *J. pictipes*. In this research, we describe a new species for the genus, and extend species distributions in the Atlantic Forest.

Key words: Brazil, Cricetidae, cytochrome *b*, Neotropics, taxonomy, tree mouse

Resumo

Sigmodontinae é um clado de roedores muito diverso com espécies distribuídas por toda a região Neotropical. Dentre esses, as espécies de roedores arborícolas inclusos em *Juliomys* formam um ramo pouco conhecido, com informações incompletas sobre a sua riqueza, posição filogenética e distribuição geográfica. A partir de uma amostra proveniente da porção sul do Bioma Mata Atlântica, nomeamos e descrevemos uma nova espécie para o gênero, a qual pode ser distinguida das demais pelo seu cariótipo, características morfológicas e sequência do gene citocromo *b*. Essa apresenta um cariótipo único (2n = 32, FN = 48) e forma um haplogrupo monofilético com bom suporte, sendo filogeneticamente distante das espécies restantes de *Juliomys*. A diferenciação genética dessa espécie em relação as demais varia de 11,1% a 19,7%, possuindo 24 autapomorfias moleculares no gene do citocromo *b*. A nova espécie pode ser distinguida de *J. pictipes* por caracteres morfológicos e análises morfométricas. No entanto, consideramos a nova espécie como críptica, não facilmente reconhecida, pelos caracteres morfológicos, das demais que compõem *Juliomys*. Esse novo táxon parece ser endêmico da Floresta com Araucária no Bioma Mata Atlântica, ocorrendo em simpatria com as espécies congenéricas, *J. ossitenuis* e *J. pictipes*. Nesse estudo, descrevemos uma nova espécie para o gênero, e estendemos a distribuição das espécies na Mata Atlântica.

Sigmodontinae is the most diverse subfamily of Cricetidae in number of species (Jansa and Weksler 2004; Musser and Carleton 2005). The group is widely distributed in the Neotropical region, with species occurring in a wide diversity of habitats. Sigmodontinae represents a highly diverse group of rodents that has been extensively studied (e.g., Hershkovitz 1955, 1962; Reig 1984, 1987; Smith and Patton 1999; Weksler 2006; D'Elía et al. 2007; Salazar-Bravo et al. 2013). Although the study of these rodents has used a variety of systematic approaches, their species diversity and distribution ranges in South America remain poorly documented.

The Atlantic Forest harbors certain unique forms of Sigmodontinae, such as the arboreal species of the genus *Juliomys*, recently established by González (2000) based on the type species *Thomasomys pictipes* (Osgood, 1933). Three living species are currently recognized: *J. pictipes* (type locality in Argentina, Misiones, Río Paraná, elevation 100 m); *J. rimofrons* Oliveira and Bonvicino, 2002, (type locality in Brazil, Minas Gerais, Itamonte, Brejo da Lapa, elevation 2,000 m); and *J. ossitenuis* Costa, Pavan, Leite and Fagundes, 2007 (type locality in Brazil, Minas Gerais, Parque Estadual da Serra do Brigadeiro, 20 km W Fervedouro, elevation 1,300 m). In addition, 1 extinct sigmodontine from the Pleistocene of Lagoa Santa, Brazil—*Calomys anoblepas* Winge, 1887—was reallocated to *Juliomys* (Pardinãs and Teta 2011). Paresque et al. (2009) described a new karyotype for the genus ($2n = 32$, $FN = 48$), suggesting a possible 5th species that is discussed here. The generic composition has increased considerably since 2000, underscoring our inadequate understanding of muroid biodiversity. The phylogenetic position of this genus is still uncertain. Different phylogenetic approaches have recovered different relationships for *Juliomys* (Smith and Patton 1999; D'Elía 2003; Weksler 2003; Martínez et al. 2012; Parada et al. 2013; Salazar-Bravo et al. 2013). Presently, there is no consensus and the genus has been considered as *insertae sedis* (D'Elía 2015).

Some recent studies have extended species distributions (Fonseca et al. 2013; Cerboncini et al. 2014), and reported sympatry among their species (Aguieiras et al. 2013). Currently, *Juliomys* occurs from the states of Espírito Santo to Rio Grande do Sul (eastern to southern Brazil), westward to eastern Paraguay and northeastern Argentina (Pavan and Leite 2011), reaching the southernmost portion of the Atlantic Forest (see Rizzini 1997; Galindo-Leal and Câmara 2005). This biome has a unique biota, with many endemic species, and is recognized as one of the world's most important biodiversity hotspots (Myers et al. 2000).

The southern portion of the Atlantic Forest is characterized by the subtropical Mixed Ombrophilous Forest (or Brazilian Araucaria Forest). The diversity of Sigmodontinae is still poorly known in this region, and further still, new species have been found in recent years (e.g., Leite et al. 2008; Abreu et al. 2014). The Araucaria Forest is one of the most threatened vegetation types of the Brazilian territory (Guerra et al. 2002), experiencing major impacts from logging, monoculture implementation, cattle raising, and urban development, all with potential deleterious effects on small mammal communities (Reeder et al. 2007). Landscape changes together with the paucity of taxonomic studies, including the paucity of basic field inventory, limit our faunistic knowledge. The Atlantic Forest is a heterogeneous biome, which necessarily still requires several studies for the complete understanding of its faunal patterns. Effective conservation efforts for this forest depend on the knowledge of the taxonomy and systematics of its associated organisms. Besides providing the identification of these organisms such knowledge is an essential tool for more practical actions towards the conservation of the Atlantic Forest (Reeder et al. 2007). In the present study, we propose a new species of *Juliomys*, and we extend southward the geographic distribution of the genus in the Atlantic Forest.

MATERIALS AND METHODS

Specimens examined.—We compared representatives of the new species (*Juliomys* sp.; *n* = 4) with museum specimens of *J. pictipes* (*n* = 98), *J. ossitenuis* (*n* = 46), *J. rimofrons* (*n* = 6), and *Oligoryzomys flavescens* (*n* = 2; see Appendix I). Among them, for each taxon we selected a subsample for the morphometric analyses. These subsamples were restricted to those specimens confidently identified based on the presence of diagnostic characters, including karyotype and/or molecular markers (Appendix I). We assembled a molecular data set with the following 21 ingroup taxa including 5 new sequences generated for this study, and 16 sequences available in GenBank (Appendix II): 3 *Juliomys* sp. (KT749862, KT749863, KT749864); 6 *J. pictipes* (FJ026733, EU157764, AF108688, EF127513, EF127514, EF127515); 2 *J. rimofrons* (AY029476, AY029477); 10 *J. ossitenuis* (AF108689, EF127516, EF127517, EF127518, EF127520, EF127519, EF127521, EF127522, KT749865, KT749866). Outgroups included *Rhagomys rufescens* (AY206770), and *Oligoryzomys microtis* (AY439000).

Specimens are deposited in the following collections: The Museum of Vertebrate Zoology (MVZ), Berkeley, University of California, Berkeley; Field Museum (FMNH), Chicago, USA; Universidade Federal do Espírito Santo (UFES), Vitória, Brazil; Museu de Biologia Prof. Mello Leitão (MBML), Santa Tereza, Brazil; Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Brazil; Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M), Belo Horizonte, Brazil; Museu Nacional, Universidade Federal do Rio de Janeiro (MN), Rio de Janeiro, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu de Zoologia da Universidade Estadual de Campinas (ZUEC-MAM), Campinas, Brazil; Universidade Federal do Paraná (DZUP), Curitiba, Brazil; Museu de História Natural do Capão da Imbuia (MHNCI), Curitiba, Brazil; Universidade

Regional de Blumenau (CZFURB), Blumenau, Brazil; Universidade Federal de Santa Catarina (UFSC), Florianópolis, Brazil; Museu de Ciências Naturais (MCNU), Universidade Luterana do Brasil, Canoas, Brasil; Universidade Nacional de Assunción (CZ), Assunción, Paraguay; Museo de Historia Natural de La Plata (MLP), Buenos Aires, Argentina; Centro de Investigaciones Ecológicas Subtropicales (CIES), Puerto Iguazú, Argentina; Centro Nacional Patagónico (CNP), Puerto Madryn, Argentina.

Morphological and morphometric analyses.—We followed Tribe (1996) for age classes, Reig (1977) for dental characterization, Bugge (1970) for artery and vein identification, Wahlert (1974, 1985) for cranial foramina, Pocock (1914) for vibrissae, and Hershkovitz (1990) for bristle banding. We transcribed the external body measurements according to the information on the museum collection tags: total length (TotL), tail length (Tail), hind foot length (HF) and ear length (Ear). We recorded body weight from museum labels or field notes. Additionally, we took 29 craniodental measurements following Tribe (1996). They were taken to the nearest 0.01 mm using a digital caliper (see Table 1), as following: occipto-nasal length (ONL), palatal length (PL), post-palatal length (PPL), molar row–crown length (MRC), 1st molar breadth (M1B), palatal bridge length (PBL), temporal fossa length (TFL), upper diastemal length (DL), incisive foramen length (IFL), incisive foramen breadth (IFB), palatal breadth at 1st molar (PB1), palatal breadth at 3rd molar (PB3), mesopterygoid fossa breadth (MFB), breadth across incisor tips (BIT), bullar width (BW), bullar length (BL), braincase breadth (BCB), skull height (SH), rostral height (RH), rostral breadth (RB), rostral length (RL), nasal length (NL), zygomatic plate length (ZPL), condyle-incisive length (CIL), interorbital breadth (IOB), zygomatic breadth (ZB), greatest length of mandible (GLM), mandibular molar row–alveolar length (MMR), and depth of ramus (DR). The research conforms to the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

For subsamples confidently identified on the basis of reliable markers (n = 41), we calculated the following descriptive statistics parameters (only adult specimens): mean ($\overline{X}$), maximum (Max), minimum (Min), and standard deviation (*SD*) for the 29 craniodental and 4 external measurements. After this, to test the significance of differences, we performed a 1-way analysis of variance (1-way ANOVA) for each individual measurement and Tukey's post-hoc test. We tested sexual dimorphism within species using a univariate analysis (Student's *t*-test with Bonferroni correction) of the cranial and external measurements. To explore multivariate differences among samples, we performed a principal component analysis (PCA [Neff and Marcus, 1980]) using the variance-covariance matrix of the logarithms, and considering of all measurements. For all morphological analyses, we used the software SPSS version 17.0.

Karyological analysis.—We used results of a previous work (Paresque et al. 2009) that described the karyotype of 3 of the *Juliomys* sp. specimens listed above.

Molecular methods and phylogenetic analyses.—The primers used to amplify the complete cytochrome *b* gene (Cyt*b*) were MVZ05 and MVZ14 (Smith and Patton 1993). We used the following conditions for the amplifications: 2 min at 94º C (initial denaturation), followed by 30 cycles of 60 s denaturation at 94º C, annealing s at 45º C for 40s, and extension at 72º C for 90s, with a final extension step at 72º C for 7 min. We carried out all PCR amplifications in 25 µl volumes containing 50 ng of template DNA, 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM of each primer, and 1 U Taq polymerase (Invitrogen). We visualized PCR-amplified products on agarose gels and performed the DNA sequencing using only the primer MVZ05 and at least 3 products of independent PCRs, combined to form a consensus sequence for each individual, while avoiding the incurrence of errors. We sequenced the samples using an automated 3730XL DNA sequencer by Advancing through Genomics MACROGEN (South Korea). We analyzed a final molecular data set that included the first 800-bp of the mitochondrial Cyt*b* gene from the 21 ingroup and 2 outgroup taxa available in GenBank (Appendix II). We visually inspected the chromatogram quality in Chromas Pro 1.5 (http://www.technelysium.com.au), aligned using ClustalW implemented into Mega 5 (Tamura et al. 2011), and performed manual editing using Bioedit 7.0.9.0 (Hall 1999). We examined the amino acid translation to ensure that no gaps or stop codons were present in the alignment. We subjected the alignment to a saturation test using the DAMBE program (Xia and Xie 2001), which indicated that the transitions and transversions remained informative, with no clear evidence of multiple nucleotide substitutions or loss of phylogenetic signal. We performed phylogenetic analyses based on the maximum likelihood (ML) with PHYML 2.4.4 (Guindon and Gascuel 2003) and Bayesian inference (BI) using MrBayes (Ronquist et al. 2012). The model of nucleotide substitution was elected by jModelTest 2.1.1 software (Darriba et al. 2012) according to the Akaike Information Criterion (AIC) (Akaike 1974). The best-fit substitution models were General Time Reversible model with gamma distributed rate variation among sites (GTR+G+I). We constructed the maximum likelihood tree using a heuristic search to find the most probable topologies based on the substitution models and statistical support was determined using 1,000 bootstrap pseudoreplicates (Felsenstein 1985). We performed the Bayesian inference of phylogeny with default priors and 3 heated and 1 cold Markov chains were run from 2 random starting points. Each run was conducted with 3×10^6 generations and sampled every 1,000 generations. When the log-likelihood scores were found to stabilize (average standard deviation of split frequencies less than 0.01 was considered convergence of the 2 simultaneous runs), a consensus tree was calculated after omitting the first 25% of the trees as burn-in. We considered significantly supported nodes with bootstrap values > 70 (ML) and Bayesian posterior probabilities (BI) > 0.95. We calculated pairwise nucleotide distances between all sequences according to Kimura's 2-parameter model and 1.000 bootstraps (Kimura 1980) using MEGA version 5.1 (Tamura et al. 2011). In addition, we also analyzed the dataset in PAUP*4.0b10 (Swofford 2002) to test, verify, and calculate the consistency index (CI) of each character using heuristic parsimony analysis, with 100 random stepwise additions of taxa (tree-bisection-reconnection [TBR] branch swapping) under ACCTRAN and DELTRAN optimization.

RESULTS

Morphometric analyses.—We did not find sexual dimorphism within species, so we were able to use the entire morphometric sample in the interspecific analyses. The descriptive statistics are presented in Table 1. Seven variables (RB, IOB, MFB, TFL, CIL, BW, RH) presented little overlap among species, with 3 measurements (TFL, BW, RH) significantly different (ANOVA 1-way: $F = 9,706$, $d.f. = 3$, $P < 0.0001$). Among them, *Juliomys* sp. differs from *J. pictipes* and *J. rimofrons* in the temporal fossa length (TFL; Tukey's test: $P < 0.004$, $P < 0.031$, respectively); and also from *J. pictipes* in the bullar width (BW; $P < 0.012$), and in the rostral height (RH; $P < 0.008$).

TABLE 1.—Body and skull measurements (mm) of the *Juliomys* species. $\overline{X}$, mean; Max, maximum; Min, minimum; and *SD* standard deviation. TotL, total length; Tail, tail length; HF, hind foot length; Ear, ear length; ONL, occipto-nasal length; PL, palatal length; PPL, post-palatal length; MRC, molar row–crown length; M1B, first molar breadth; PBL, palatal bridge length; TFL, temporal fossa length; DL, diastema length; IFL, incisive foramen length; IFB, incisive foramen breadth; PB1, palatal breadth at first molar; PB3, palatal breadth at third molar; MFB, mesopterygoid fossa breadth; BIT, breadth across incisor tips; BW, bullar width; BL, bullar length, BCB, braincase breadth; SH, skull height; RH, rostral height, RB, rostral breadth; RL, rostral length, NL, nasal length; ZPL, zygomatic plate length; CIL, interorbital breadth; IOB, interorbital breadth; ZB, zygomatic breadth; GLM, greatest length of mandible; MMR, mandibular molar row–alveolar length; DR, depth of ramus.

	Juliomys sp.					*J. ossitenuis*					*J. rimofrons*					*J. pictipes*				
	Mean	Max	Min	SD	*n*	Mean	Max	Min	SD	*n*	Mean	Max	Min	SD	*n*	Mean	Max	Min	SD	*n*
TotL	194.00	205.00	181.00	12.12	4	189.00	213.00	165.00	17.37	9	193.00	214.00	175.00	19.67	3	192.56	238.00	171.00	16.22	17
Tail	106.00	113.00	101.00	6.24	4	104.63	116.00	89.00	9.97	8	101.67	121.00	85.00	18.15	3	104.69	138.00	95.00	9.88	17
HF	20.50	22.00	19.50	1.32	4	18.81	22.00	14.00	2.98	9	22.00	22.00	22.00	0.00	2	19.76	26.00	11.10	4.11	16
Ear	15.33	16.00	15.00	0.58	4	14.78	21.00	10.00	2.99	8	15.33	18.00	13.00	2.52	3	15.04	19.00	13.00	1.62	17
NL	8.55	9.00	7.98	0.44	4	8.34	9.35	7.10	0.69	9	8.50	9.07	7.73	0.56	4	8.74	9.88	7.24	0.60	23
RL	7.37	7.74	7.01	0.35	4	7.43	8.58	6.41	0.62	9	7.41	7.83	7.08	0.38	4	7.87	8.61	7.25	0.33	23
RB	4.27	4.38	4.21	0.08	4	4.40	5.02	3.83	0.35	9	4.17	4.49	4.00	0.22	4	4.56	4.91	4.23	0.17	24
IOB	4.02	4.12	3.94	0.07	4	3.76	3.96	3.58	0.12	9	3.77	3.86	3.61	0.11	4	4.01	4.36	3.68	0.16	24
ZB	13.17	13.51	12.38	0.53	4	13.05	14.06	12.17	0.62	9	13.66	14.40	13.00	0.61	4	13.63	14.51	12.65	0.51	23
BCB	10.73	10.83	10.65	0.08	4	10.07	10.88	8.52	0.77	9	10.74	11.12	10.41	0.29	4	10.04	11.32	8.93	0.78	19
BIT	1.50	1.62	1.33	0.14	4	1.66	1.89	1.43	0.15	9	1.66	1.77	1.51	0.12	4	1.73	2.04	1.54	0.14	24
DL	5.82	6.13	5.21	0.41	4	6.10	7.01	5.38	0.47	9	6.30	6.58	5.77	0.38	4	6.19	6.95	5.57	0.38	24
IFL	4.81	5.11	4.22	0.42	4	4.59	5.14	4.13	0.28	9	5.11	6.27	4.38	0.82	4	4.49	5.00	3.92	0.28	24
IFB	1.69	1.93	1.57	0.17	4	1.75	2.03	1.32	0.22	9	1.71	1.81	1.48	0.15	4	1.63	1.82	1.43	0.10	24
M1B	1.04	1.07	0.99	0.04	4	1.08	1.14	1.02	0.04	9	1.08	1.12	1.04	0.03	4	1.09	1.19	0.98	0.05	24
PB1	2.44	2.61	2.25	0.15	4	2.49	2.71	2.23	0.15	9	2.68	2.87	2.41	0.19	4	2.39	2.82	2.16	0.14	24

PB3	2.70	2.94	2.55	0.17	4	2.70	3.01	2.39	0.19	9	3.02	3.36	2.66	0.29	4	2.87	3.04	2.52	0.13	24
PBL	3.55	3.70	3.39	0.13	4	3.58	3.86	3.40	0.14	9	3.62	3.74	3.41	0.14	4	3.94	4.54	3.42	0.23	24
PL	10.73	11.11	10.2	0.43	4	11.06	12.29	9.83	0.73	9	11.35	11.73	10.72	0.45	4	11.66	12.87	10.81	0.51	24
TFL	7.07	7.33	6.61	0.34	4	7.49	8.80	6.48	0.72	9	7.98	8.28	7.52	0.34	4	7.88	9.16	6.79	0.70	24
MFB	1.41	1.56	1.23	0.14	4	1.70	2.03	1.47	0.16	9	1.71	1.83	1.59	0.10	4	1.74	2.02	1.54	0.13	24
CIL	24.07	24.95	22.72	0.98	4	23.18	25.39	20.81	1.35	9	24.79	25.77	23.29	1.07	4	25.63	26.90	23.99	0.79	21
ONL	22.73	23.26	21.7	0.72	4	24.34	26.72	22.08	1.39	9	23.46	24.25	22.02	1.02	4	23.83	25.68	22.14	0.83	21
PPL	8.29	8.71	7.68	0.46	4	8.78	9.98	7.65	0.66	9	8.53	8.93	7.88	0.46	4	9.32	10.62	8.40	0.58	21
BW	4.26	4.41	4.09	0.17	4	3.82	4.24	2.87	0.39	9	4.08	4.17	3.97	0.08	4	3.60	4.12	2.84	0.34	22
BL	4.87	5.06	4.60	0.21	4	4.72	4.97	4.35	0.23	9	5.04	5.61	4.75	0.39	4	4.59	5.74	3.39	0.58	22
RH	4.35	4.47	4.13	0.15	4	4.62	5.26	4.12	0.33	9	4.77	4.87	4.64	0.10	4	5.06	6.03	4.64	0.33	24
SH	8.11	8.22	7.94	0.12	4	7.80	8.07	7.27	0.24	9	8.06	8.39	7.88	0.23	4	7.98	8.45	7.32	0.27	24
ZPL	2.26	2.41	2.11	0.14	4	2.22	2.55	1.67	0.29	9	2.16	2.26	1.96	0.14	4	2.38	2.87	2.03	0.20	24
MRC	3.88	4.00	3.77	0.10	4	3.82	4.10	3.63	0.14	9	3.83	3.87	3.75	0.05	4	3.93	4.56	3.61	0.21	24
MMR	4.16	4.27	4.05	0.10	4	3.94	4.15	3.78	0.12	9	3.98	4.02	3.91	0.05	4	4.02	4.22	3.74	0.13	24
GLM	12.48	12.81	11.76	0.49	4	12.71	14.07	11.98	0.65	9	13.05	13.66	12.45	0.50	4	13.39	14.40	12.19	0.57	24
DR	2.86	2.99	2.79	0.09	4	2.85	3.04	2.64	0.15	9	3.12	3.25	2.84	0.19	4	3.13	3.45	2.90	0.15	24

The first 3 principal components explain 72.93% of the total variance, with PC1 accounting for 49.83%, PC2 for 16.65%, and PC3 7.45% of the total variation (Supporting Information S1). PCA scores allow us to recognize 3 groups, but with some overlap along PC1 and PC2 (Fig. 1). The scores for specimens of *Juliomys* sp. do not overlap with those from *J. rimofrons*; but show small overlap with *J. pictipes* and *J. ossitenuis* that have negative scores for PC2. The variables most related to PC1 are RL, ZB, BIT, DL, PL, ONL, CIL, PPL, and GLM; while those most related to PC2 are IFB, PB1, BW, and BL (Table 2).

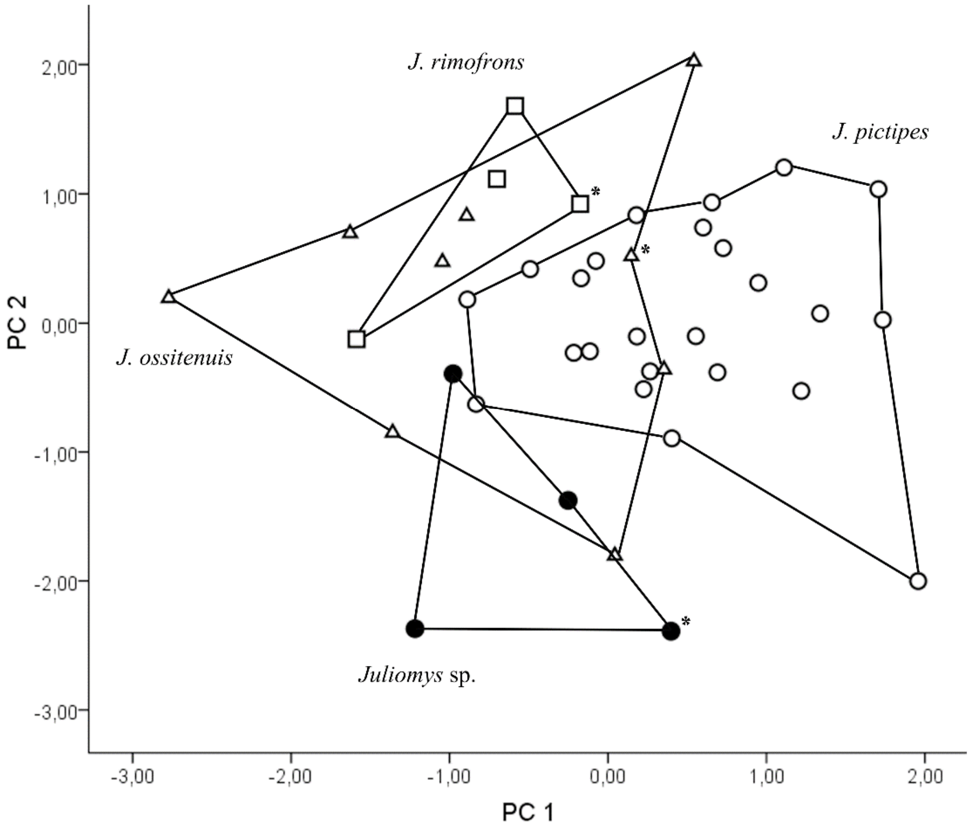

FIG. 1.—Principal component analysis, components 1 and 2, of the 29 log-transformed craniodental measurements of *Juliomys* species; *n* = 41. * Holotype.

Karyology.—Paresque et al. (2009) described the karyotype 2n = 32, FN = 48 for the specimens we are treating here as *Juliomys* sp. Among the autosome complement, chromosome pair 1 is a large submetacentric, pairs 2–9 are meta/submetacentric, and pairs 10–15 are acrocentrics. Sexual chromosomes include a large submetacentric X and medium acrocentric Y. This karyotype distinguishes *Juliomys* sp. from all other species in the genus (Table 2).

Molecular and phylogenetic analyses.—We detected a total of 198-bp (24.6%) variable nucleotide sites in the Cyt*b* gene (out of a total of 800-bp nucleotide sites included in the analyses). Moreover, there was no indication of pseudogenes, numts, or stop codons, which indicates an evolution for normal protein coding mtDNA genes. Pairwise distance among combination of 21 specimens of 4 lineages inside the genus *Juliomys* presents the mean divergence of 10.3%, with a range of 0% to 19.7% (Table 3). The measures of intraspecific variation ranged from 0% to 1.4% and interspecific variation from 11.1% to 19.7%, more than 10 times higher for intraspecific comparisons.

Bayesian and ML analyses recovered a strongly supported monophyletic group of *Juliomys* (*PP* = 1; bootstrap > 90%) that included 4 clades (the 3 currently recognized species and *Juliomys* sp. [Fig. 2]), with the following relationship retrieved: *J. ossitenuis* (*J. pictipes* (*J. rimofrons*, *Juliomys* sp.)). The basal divergence from the remaining *Juliomys* is *J. ossitenuis* (*PP* = 1; bootstrap = 99). Among those specimens confirmed as *J. ossitenuis*, there are 2 vouchers from São Francisco de Paula (KT749865, KT749866), which extends southward the species distribution in Brazil. Another highly supported group (*PP* = 1; boostrap = 98) is composed by *J. pictipes* that is sister to the clade formed by *J. rimofrons* and *Juliomys* sp. (2n = 32, NF = 48). As aforementioned, *Juliomys* formed a well-supported monophyletic haplogroup, where species in this genus share 96 molecular synapomorphies. In addition, 24 molecular autapomorphies were identified for *Juliomys* sp. (Supporting Information S2). Based on this background, we describe below a new species of *Juliomys* (until here referred as *Juliomys* sp.), and extend southward the geographic distribution of the genus in the Atlantic Forest.

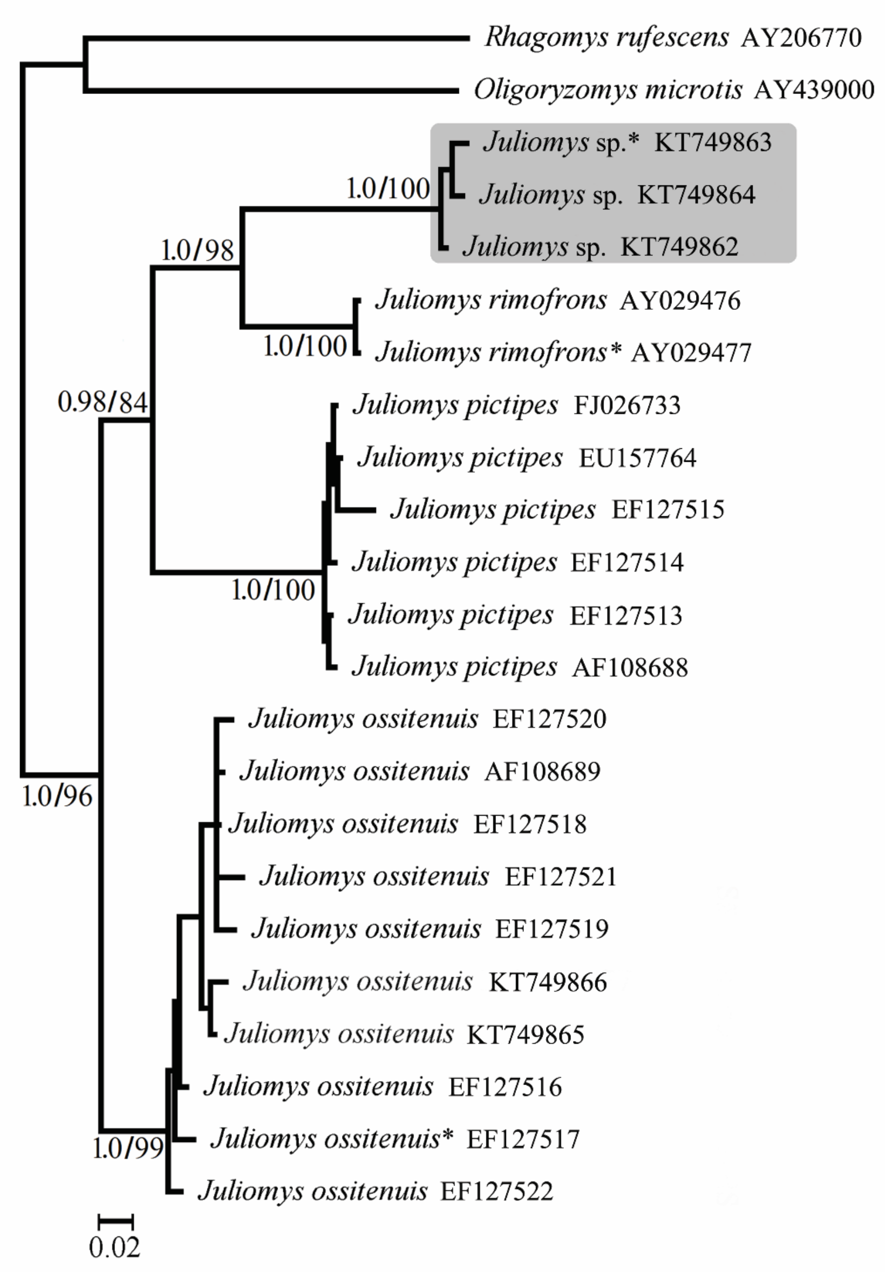

FIG. 2.—Phylogenetic relationships among *Juliomys* species based on Bayesian inference (BI) using 801 base pairs of Cytb gene under GTR + I + G model of sequence evolution. BI posterior probabilities (>0.95) and bootstrap support values (>70%) from Maximum Likelihood are indicated in the nodes. The scale bar indicates the number of changes per site. Specimens are followed by GenBank accession number, holotypes are followed by asterisk. *Juliomys* sp. group is highlighted.

TABLE 2. —Comparative characters among the species of *Juliomys*. Adapted from Costa et al. 2007.

Character	*Juliomys* sp.	*J. pictipes*	*J. ossitenuis*	*J. rimofrons*
Nose	orange	orange	orange	brown
Dorsal pelage	orange-brown	orange-brown	orange-brown	dark-brown
Ventral pelage	cream-white	white	cream-white	light-brown
Dorsal pelage of hindfeet	light-orange	orange	light-orange	dark-orange
Interorbital region	broad; hourglass shaped	broad; convergent anteriorly	narrow; hourglass shaped	narrow; hourglass shaped
Rostral height	small	large	medium	medium
Interfrontal fontanelle	absent	absent	usually absent	present
Zygomatic plate	orthogonal in relation to molar series	projected anteriorly	projected anteriorly	orthogonal in relation to molar series
Zygomatic notch	shallow	deep	shallow	shallow
Temporal fossa	narrow	broad	broad	broad
Coronal suture	U-shaped	V-shaped	V-shaped	V-shaped

Tympanic bullae	medium	small	large	large
Carotid arterial supply	pattern 1 (Voss 1988)	pattern 2 (Voss 1988)	pattern 1 (Voss 1988)	pattern 1 (Voss 1988)
Sphenopalatine vacuities	absent or large	absent or minute	large	large
Posterolateral palatine pits	small	large	small	large
Squamosal-alisphenoid groove	present	absent	present	present
Ectolophid/ectostylid of m1-m2	conspicuous	minute or absent	conspicuous	small
Karyotype	2n = 32 NF = 48	2n = 36 NF = 34	2n = 20 NF = 36	2n = 20 NF = 34

TAXONOMY

Juliomys ximenezi, new species

(Table 1 and 2; Figs. 5a–c)

Araucaria Forest tree mouse

Juliomys sp.: Paresque et al., 2009:302.

Holotype.—MCNU 868, adult male, collected by Rafael Becker on January 2004. The holotype consists of a round skin, skull, and postcranial skeleton with the glans penis and stomach preserved in ethanol (all parts in good condition).

Type locality.—Parque Nacional de Aparados da Serra (Aparados da Serra National Park), municipality of Cambará do Sul, Rio Grande do Sul State, Brazil (29°09′36″S, 50°06′00″W; Fig. 4). Elevation of 800 m, in Mixed Ombrophilous Forest dominated by the Araucaria "pine" *Araucaria angustifolia* (Araucariaceae; Fig. 3). The climate of the region has marked seasons and is of the Cfb type, according to Köppen classification (Kuinchtner and Buriol 2001): subtropical, with a dominant influence of the territorial pattern; humid, with uniform precipitation throughout the year with mild summers.

FIG. 3.—Brazilian Araucaria Forest, a view of Parque Nacional de Aparados da Serra, type locality of *Juliomys* sp.1. Photo by Paulo S. Tomasi.

Paratypes.—Three specimens, adult males collected by Emerson M. Vieira in February 2003 (MCNU 464 and MCNU 870) and Rafael Becker in January 2004 (MCNU 869), all at the type locality. MCNU 464 consists of skin, skull, postcranial skeleton, and tissue preserved in ethanol; MCNU 869 and MCNU 870 include skin, skull, and postcranial skeleton.

Distribution.—*J. ximenezi* is known from type locality, at the northeast of Rio Grande do Sul, Southern Brazil (Fig. 4).

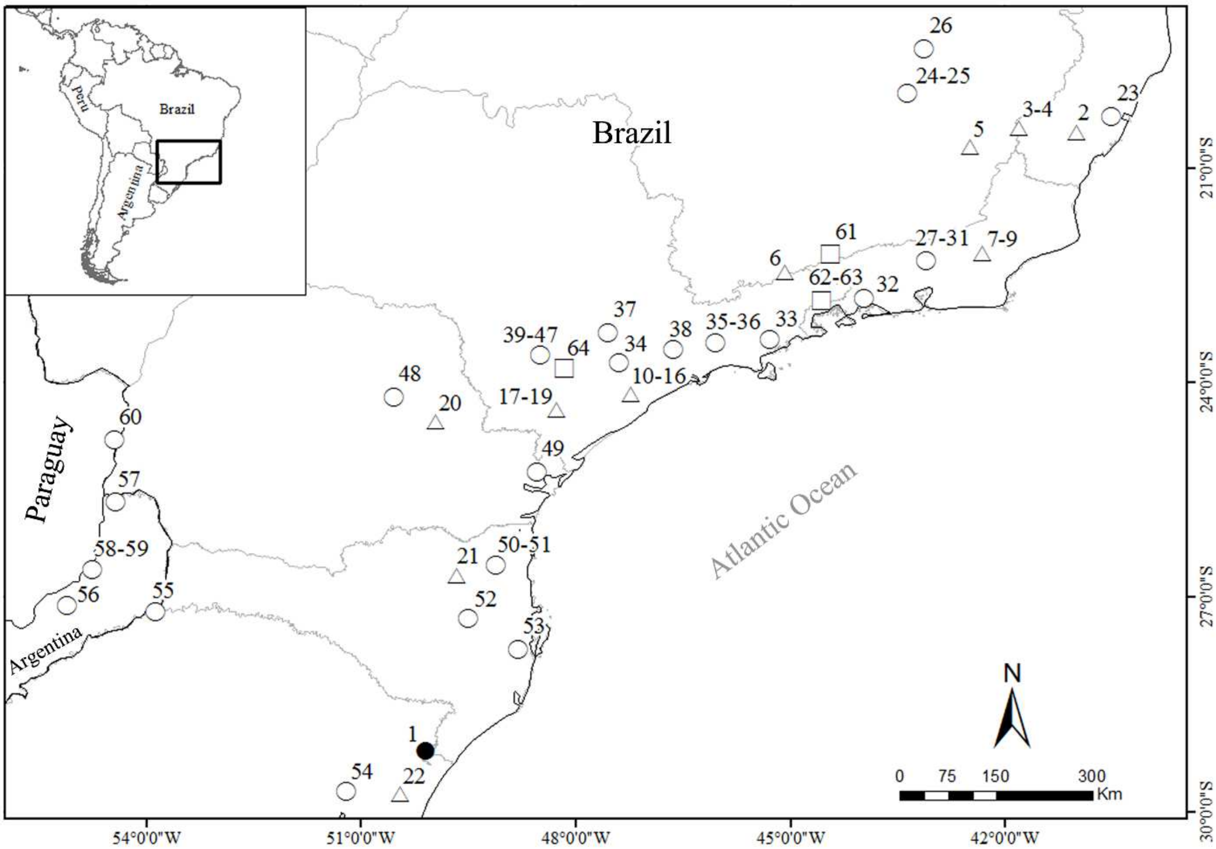

FIG. 4.—Sampling localities of *Juliomys* sp.1 (black circle), *J. ossitenuis* (triangles), *J. pictipes* (white circles) and *J. rimofron*s (squares). Numbers correspond to the localities listed in Appendix I. Map by Diogo Tobolski.

Etymology.—The name is a tribute to the Juan Alfredo Ximenez Trianón, one of the pioneers of mammalogy in Brazil.

Nomenclatural statement.—A life number was obtained for the new species *Juliomys ximenezi*: urn:lsid:zoobank.org:pub:BBF04CF6-B098-40C8-BF51-80844443D739.

Morphological description.—Pelage (see Figs. 5a–c) soft and dense, with a slightly orange rostrum and orange lateral line sharply demarcating dorsal and ventral colors. Anterior dorsum nut-brown to yellowish, grading to a slightly orange over the rump;

ventral pelage cream-white. Dorsal aristiform hairs 11–13 mm long over middle dorsum and blackish (eumelanin); dorsal setiform hairs shorter (9–10 mm) with basal portion dark gray (eumelanin), middle band yellowish (pheomelanin), and terminal portion light brown; ventral setiforms (8–9 mm) dichromatic, their basal portion gray (eumelanin) and terminal portion yellowish to cream (pheomelanin). Pinnae sparsely covered by dicromatic hairs (2–3 mm), with basal portion dark (eumelanin) and terminal portion orange. Mystacial vibrissae dark at base and becoming lighter toward the tip, abundant, and projecting beyond the dorsal rim of the pinnae; superciliary vibrissae sparse and long; submental very short and inconspicuous; 1 or 2 genal short vibrissae. Tail long, approximately 1.5x the length of head-and-body, and hirsute with terminal brush; bicolored hair (dorsal brown, ventral yellowish); individual caudal hairs longer than 3 scales. Forefeet small (Fig. 5e) with yellowish (pheomelanin) dorsal pelage; hindfeet small (Fig. 5d), covered dorsally with orange hairs (pheomelanin), with digits bearing yellowish (pheomelanin) ungual tufts; hypothenar pads large and elongated, interdigital pads 1 and 4 larger than 2 and 3.

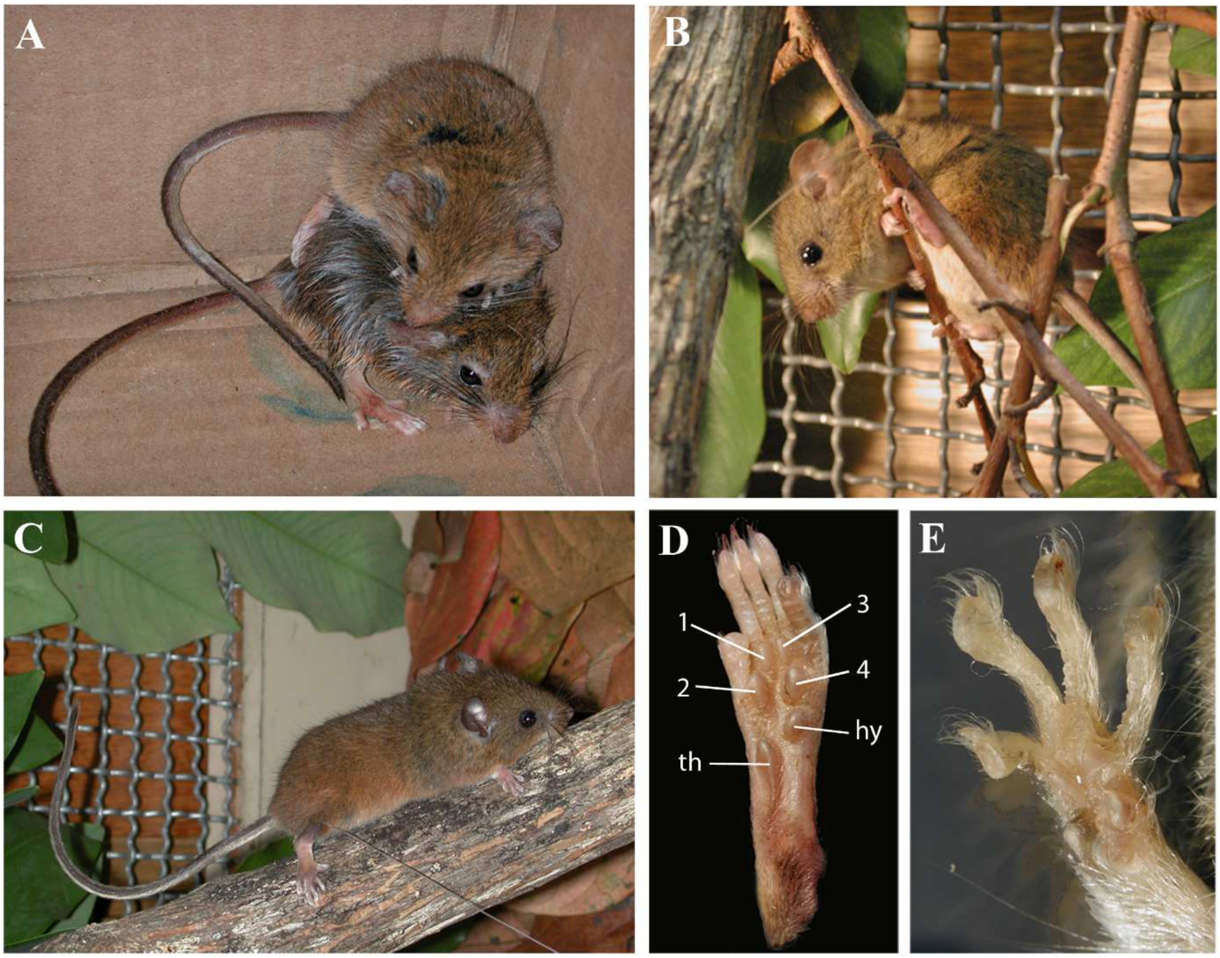

FIG. 5.—External morphology of *Juliomys* sp.1. A-C) Individuals MCNU 868 and MCNU 869, D) hind foot (1-4, interdigital pads; th, tenar pad; hy, hypotenar pad), and E) front foot. Photos by Alexandre U. Christoff.

Rostrum (Figs. 6a-c) short, approximately one third of the skull length (*ca* 30% of ONL); nasals extending beyond the forward edge of the incisors, their posterior margins rounded or squarish, never acute; gnathic process conspicuous, but rostral tube absent, little penetration at the frontals. Lacrimals variable in size, contacting the maxillary and frontal bones.

Zygomatic arches (Fig. 6a; Figs. 7a-c) are parallel, with elongated jugal bone near the squamosal root. Zygomatic plate with a straight anterior borders and posterior to nasolacrimal capsule. Zygomatic notch shallow. Nasofrontal suture markedly denticulate between the frontals; nasolacrimal foramen not inflated in dorsal view with lumen short and narrow.

Interorbital region hourglass-shaped (Fig. 5e; Figs. 6a-c), with its edges rounded and constriction approximately half the length of the frontal, with central depression over their suture. The interfrontal fontanella is absent. Orbital fossa with sphenopalatine foramen present at the level of M2; sphenofrontal foramen is also present.

Braincase region (Figs. 6a-c; Fig. 7e) slightly rounded with inconspicuous lambdoid crests, contributing to a perception of a rounded aspect. Frontoparietal suture (= Coronal suture, U-shape) continuous with the frontosquamosal suture. Parietals expanded onto the lateral surface of the braincase. Interparietal wider than the NL, and without contact with squamosal; Lambdoidal crest inconspicuous. Squamosal hamular process long and not so slender. Postglenoid foramen smaller than subsquamosal fenestra.

Palatal region (Figs. 6b-c) has a long incisive foramen (*ca* 80% of DL); Palate short and wide; fossa mesopterygoid wide U-shaped or slightly biconcave, reaching the M3 metacone, with parallel sides or with extremity of hamular process of pterygoid slightly divergente; sphenopalatine vacuity is either present or absent. Parapterygoid plates as wide as mesopterygoid fossa; posterolateral palatal pits present.

Otic capsules (Figs. 6b-c; Fig. 7f) are small, the ectotympanic covers the anterior portion of periodic, which do not contribute conspicuously to form the cariotid canal that extends along the medial portion of eustachian tube, and is slightly developed. Bony eustachian tube short and relatively broad. Stapedial foramen is small near the posterior end of the petrotympanic fissure. Cephalic circulation pattern is primitive (Pattern 1, Voss 1988) with a visible and pronounced squamosal-alisphenoid groove (Fig. 7b). Alisphenoid strut absent, masticatory-buccinator and oval foramen are confluent. Mastoid is proportionally large and squarish, perforated by a small fenestra which can sometimes be absent. Stylomastoid foramen is present. Paraoccipital process developed.

Lower jaw (Fig. 6d) is short and compact with well-developed upper and lower masseteric ridges. Mental foramen is in front of m1. Coronoid process is large. Concavity of the angular notch is deep.

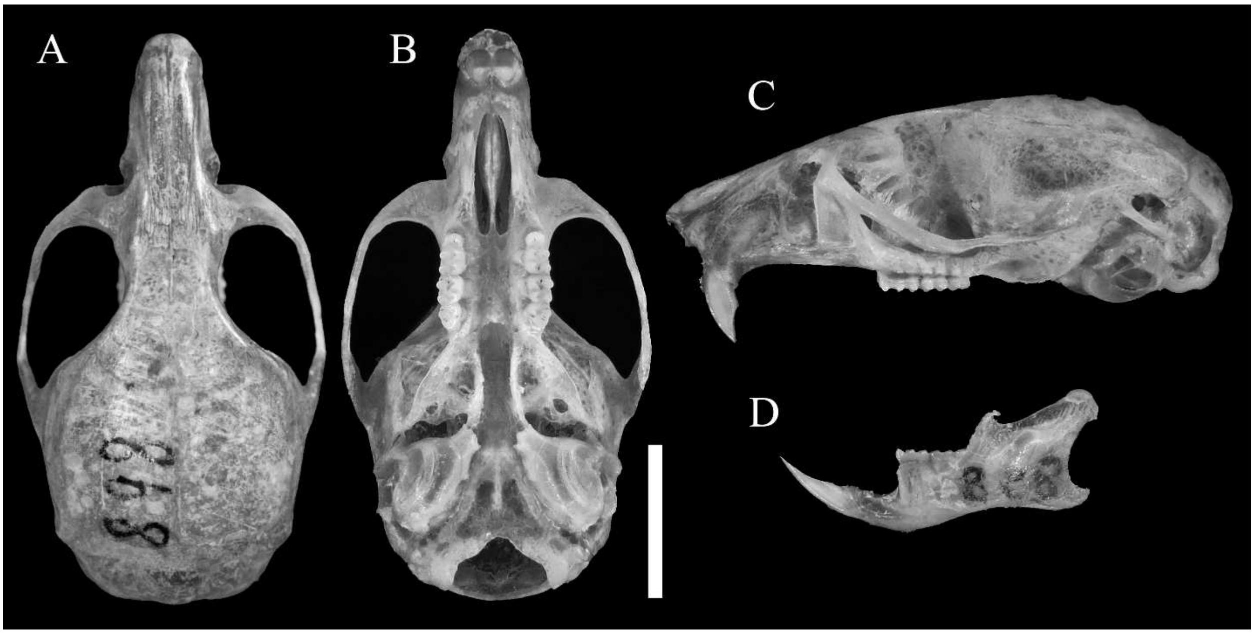

FIG. 6.—Skull, mandible and molar series views of the holotype *Juliomys* sp.1 MCNU 868, where A) dorsal B) ventral, C) lateral, and D) mandible (lateral view). Scale bar = 5 mm. Photos by Paulo S. Tomasi.

Upper incisors are opisthodont (Fig. 6c) with enamel pigmented yellow to orange. Molars (Fig. 7c) brachyodont and crested, more squared than elongated. Upper molar rows slightly convergent anteriorly or parallel with coronal hypsodonty; labial and lingual main cusps about the same size and are oppositely paired. Protocone, paracone, hyponoce, metacone are well defined. M1 presents procingulum divided into anterolingual and anterolabial conules by a large and deep anteromedian flexus from the crown basis; anterolabial conule is bigger than the anteroligual conule; anteroloph well-developed and paraflexus is present; protosyle and protoflexus are also present. Mesoloph present and very developed, mesoflexus and metaflexus are deep, enterostyle is present as well. Posteroloph narrow, posteroflexus inconspicuous. Hypoflexus broad. Morphology of M2 is very similar to the main cuspides of M1. M3 is the smallest upper tooth about 40% of M1 in length, with only protocone and paracone cusps well defined. Lower molars (Fig. 7d) m1 with procingulum divided into anterolingual and anterolabial conulids by the anteromedian flexid. Anterolophid is present, anteroflexid and metaflexid are deep, mesolophid present, well developed and projected lingually, hypoflexyd broad, ectolophyd is present with ectostylid conspicuous (m1 and m2). Morphology of m2 very similar to the main cuspides of m1, about 30% shorter than m1; m3 similar in size to m2.

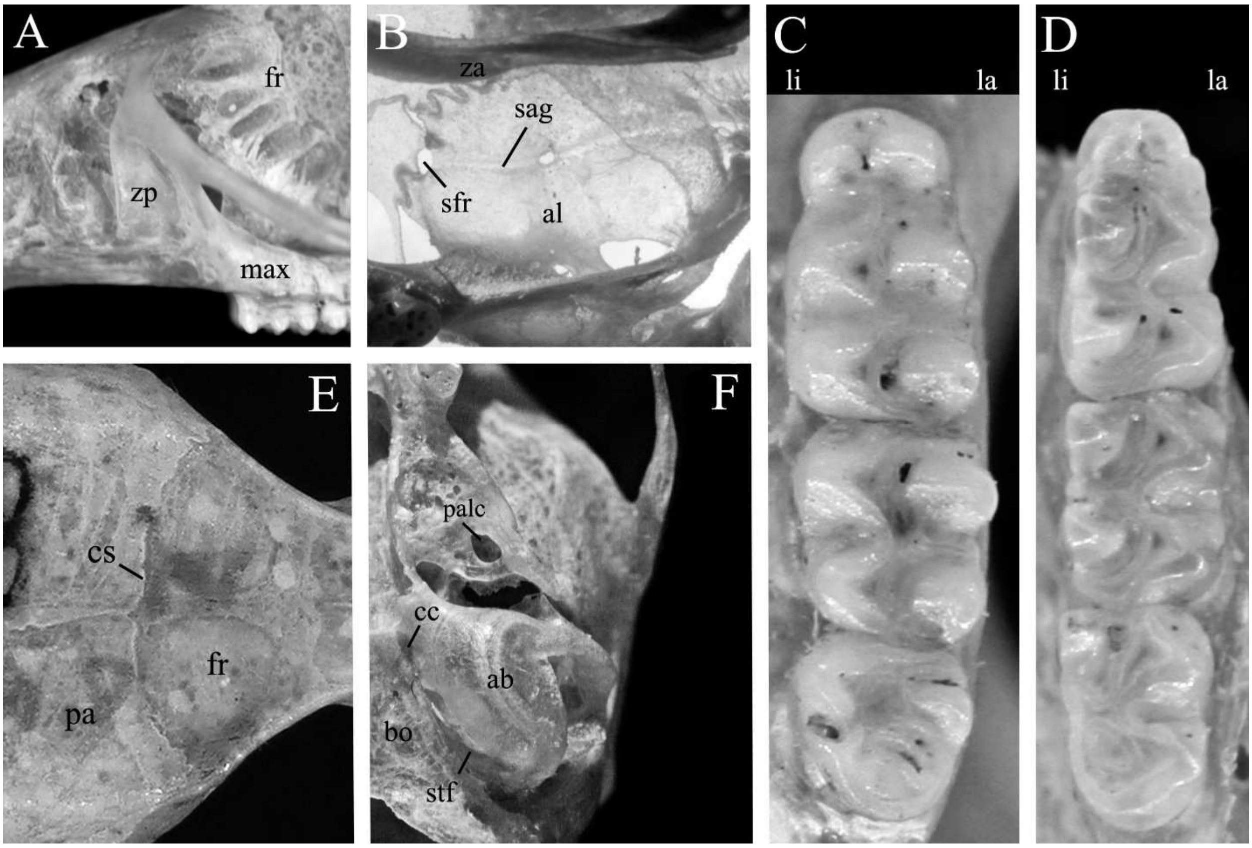

FIG. 7.—Selected cranial details of *Juliomys* sp.1 based on the holotype MCNU 868. A) lateral view of zygomatic region; B) squamosal-alisphenoid region, C) upper molar row, D) mandible molar row, E) dorsal view of interorbital region, and F) left optic capsule and palatal region. ab, auditory bulla; al, alisphenoid; bo, basiocipital; cc, carotid canal; cs, coronal suture; fr. frontal bone; li, lingual; la, labial; max, maxillary; pa, parietal bone; palc, posterior opening of the alisphenoid canal; sag, squamosal-alisphenoid groove; sfr, sphenofrontal foramen; stf, stapedial foramen; za, zygomatic arch; zp, zygomatic plate. Figures not scaled. Photos by Paulo S. Tomasi.

Phallus is short and presents barrel-shaped glans penis with a convex back. Well-developed ventral and dorsal groove confluent to the distal crater. Glans surface covered by small and short spines. Distal baculum tri-partite has a prominent medial bacular mound and smaller lateral bacular mounds.

Comparisons.—*J. ximenezi* is similar in size with *Oligoryzomys flavescens*, but can be distinguished from this species by both external and skull morphology: *J. ximenezi* (Fig. 5) presents an orangish dorsal color, orange nose, brighter ventral color, bigger hind feet, and longer tail. In the skull of *J. ximenezi* (Figs. 5–7), the interorbital region is wider, the zygomatic notch is shallower, the anterior margin of the mesopterygoid fossa reaches M3, and the dentary condyloid process is more developed. M1 presents a more developed anteromedian flexus, anteroloph, and mesoloph.

When we compared *J. ximenezi* with the other taxa of its group of species, is distinguished by the following features: U-shaped coronal suture (Fig. 7e), karyotype 2n = 32, FN = 48 (Paresque et al. 2009), and substantial molecular distance (24 autapomorphies in 800-bp of the Cyt*b* gene) from the other species of the genus (Table 4 and Supporting Information S2; Fig. 2). It is distinguishable from *J. pictipes* also by the cream-white ventral pelage (Fig. 5), and certain skull features namely the presence of a squamosal-alisphenoid groove (carotid arterial supply Type 1, Voss 1988; Fig. 7b), projection of zygomatic plate (Fig. 7a), shallower zygomatic notch, smaller posterolateral palatine pits, smaller rostral height, and ectolophid/ectostylid of m1-m2 conspicuous (Fig. 7d); and also for the rostral height (RH) and bullar width (BW) (Table 1). *Juliomys ximenezi* is distinguishable from *J. rimofrons* by such external features as whiter ventral pelage, lighter dorsal and hindfeet pelage (dark-orange in *J. rimofrons*), orangish nose tip (Fig. 5), and skull features such as absence interfrontal fontanella (Fig. 7e) and smaller posterolateral palatine pits, smaller rostral height, and ectolophid/ectostylid of m1-m2 conspicuous (Fig. 7d). *J. ximenezi* and *J. ossitenuis* morphologically similar species, both externally and cranially. The first is distinguishable from *J. ossitenuis* by skull features such as broader interorbital region and orthogonal zygomatic plate in relation to the molar series in lateral view (Table 1 and 2; Fig. 6).

Natural history.—*J. ximenezi* seems to be endemic to the Mixed Ombrophilous Forest (Brazilian Araucaria Forest), Atlantic Forest domain, where it is associated with forest understory and forest canopy. The 4 specimens collected were captured in the canopy of a natural 26-ha patch of Araucaria forest. There is no available information on its diet, but its arboreal habits and morphology suggest a frugivore-omnivore diet.

DISCUSSION

Taxomomy and comparison.—Since the original description of *Juliomys* (González 2000), the genus has increased to 5 valid species (4 extant), including the one here recognized in this study. Recently, González et al. (2015) provided some substantial information about the taxa, including a compilation of data and a key to the genus. However, species diagnosis is still challenging. We analyzed a substantial sample and covered all characters listed in the literature (González 2000; Oliveira and Bonvicino 2002; Costa et al. 2007; Pardiñas et al. 2008; Pavan and Leite 2011; González et al. 2015). From there, we found a range of intraspecific variation in the following characters as interfrontal fontanella, mid-ventral dark line in tail, lateral extensions of parietals, and posterolateral palatine pits. *J. pictipes* is more clearly differentiated from the other species because of its bigger size and some anatomical traits, such as the cephalic circulation pattern (Pattern 2 according to Voss 1988) that it is unique in the genus. The large number of *J. pictipes* specimens deposited in scientific collections allows comparison and facilitate identification. We bring up a new character, the coronal suture shape (Table 2). This character was consistent in diagnosing, but hardly achieved, for the new species sample. Even finding some anatomical differences between taxa, we interpret *J. ximenezi* as a cryptic species, not easily recognized by morphological features (Bickford et al. 2006; Ceballos and Ehrlich 2009), but some morphological (and also genetic) traits bear its diagnosis. Perhaps an increase of sample would clarify this issue, allowing a better evaluation of character variation (see Carleton and Musser 1989).

Additional material that can fill some geographical gaps and increase sample size for some species not well represented yet, will be crucial to improve the state-of-the-art of its taxonomy.

This is the 1st study of *Juliomys* in which morphometric data is analyzed in a multivariate approach. Although the morphometric data revealed only partial separation among taxa in a multidimensional space (Supporting Information S1; Fig. 1), all the specimens analyzed can be confidently identified based on karyology and/or molecular markers. The inclusion of 3 of the 4 holotypes of *Juliomys* species in the analysis make these results even more solid. The multivariate analysis is important in order to understand how the species are spatially distributed in a multivariate space, contributing to the diagnosis. This informative approach has been extensively used to other sigmodontine (e.g., Carleton and Musser 1993; D’Elía et al. 2015).

Our results fully support the recognition of the new *Juliomys* species. Karyotype, molecular analyses, and even some cranial features distinguished *J. ximenezi* from the other congeneric species. The karyotype 2n = 32, FN = 48 is unique in *Juliomys*, differing both in diploid number and fundamental number. Considering the relevant morphological similarity presented within *J. ximenezi* and the remaining species (excepting *J. pictipes*) cytogenetic and molecular identification are key to the taxon definition.

Molecular and phylogenetic relationships.—The definition of the new species based on Backer and Bradley's (2006) Genetic Species Concept was strongly sustained. Our analyses are supported by genetic distance and nucleotide substitutions, as well as by the Cyt*b* gene phylogeny (Tables 3 and Supporting Information S2). The intraspecific distances ranged from 0% to 1.3%, and interspecific distances ranged from 11.1% to 19.7% (Table 3). Baker and Bradley (2006) considered for Sigmodontinae Cyt*b* gene average distances of 6.8% to 8.1%. According to those authors, genetic distances between taxa above 10% should be satisfactory to propose a new taxon, as values lower than 2% should only indicate intraspecific variation. Our results are solidly congruent to this interspecific delimitation characterizing *J. ximenezi* as an evolutionarily independent species of the genus *Juliomys*.

Four genetically defined haplogroups are clearly formed within the genus *Juliomys*, each one composed by individuals belonging to a unique species (Fig. 2). These distinct clades were strongly reinforced by well-supported nodes, Bayesian inference (≥ 0.98), and bootstrap support values (≥ 84%) from Maximum Likelihood. Moreover, our results are in agreement with Costa et al. (2007), where *J. ossitenuis* is a basal clade from the remaining branches. Despite being closely related molecularly to *J. rimofrons* (Table 3), *J. ximenezi* is morphological more similar to *J. ossitenuis* (Table 2). Morphological and molecular similarities in this genus show incongruences. Phylogenetic reconstructions of Sigmodontinae have been based uniquely on *J. pictipes* (Weksler 2003; D'Elía 2003; Martínez et al. 2012; Parada et al. 2013; Salazar-Bravo et al. 2013). Therefore, the phylogenetic positioning of the genus within the subfamily still requires additional molecular and systematic studies (see Lessa et al. 2014), including morphometric and molecular matrices.

Biogeography.—Pavan and Leite (2011) discussed a “historical biogeographic gap or a collecting artifact” for *Juliomys* in the austral portion of the Atlantic Forest biome. Based on our new data, records of the genus are spread to the southernmost portion of Brazil. This research is the first to delimit species occurrences for *Juliomys* species in Southern Brazil, which constitutes the southernmost limit to the genus (Fig. 4). In addition, we have identified specimens from São Francisco de Paula (29°29′78″S, 50°12′43″W) as *J. ossitenuis*. These results extend ca. 525 km southward the species distribution, which now reaches latitude 30º S. Also, with the identification of one specimen from Dois Irmãos (29°56′00″ S, 51°10′0″ W) as *J. pictipes*, the species distribution extends 200 km southward. According to our data, *J. ossitenuis* and *J. pictipes* has the wider distribution extension, whereas *J. ximenezi* the most restricted distribution.

The 3 species, *J. ximenezi*, *J. pictipes*, and *J. ossitenuis*, occur in sympatry in the southernmost distribution of the genus (Fig. 4). The linear distance between these collection sites of *J. ximenezi* and *J. ossitenuis* is about 37 km in a continuous forest landscape of the Mixed Ombrophilous Forest. Based on this information, we can infer that these species occur in sympatry and probably syntopy. In São Paulo (Brazil), syntopy for *J. ossitenuis* and *J. pictipes* have already been reported (Pavan and Leite 2011). Differential use of microhabitat (Jorgensen 2004) or distinct feeding habits (Schoener 1974) might enable the coexistence of these morphologically similar arboreal species, but this is an open question that needs to be assessed.

Conservation.—According to our findings, *J. ximenezi* is the only species of Sigmodontinae endemic to the Rio Grande do Sul (Brazil). As currently known, this species is based on only 4 specimens collected in 1 region, inside the Parque Nacional de Aparados da Serra, a federal conservation unit in the Brazilian Araucaria Forest. This habitat has been severely reduced in the last 100 years, and is currently restricted to about 4% of its original area of 200,000 km^2 (Lima and Capobianco 1997; Backes 1999; Guerra et al. 2002). The Brazilian Araucaria Forest has a small fraction of unconnected conservation units (about 1%; Rambaldi and Oliveira 2003). Nevertheless, even conservation areas are not free from threat due to poor protection and maintenance. In the Parque Nacional de Aparados da Serra for example, cattle trampling occurs in the grassland matrix and inside forests, favoring habitat degradation. Even with a high extinction ratio among mammals, rodent studies have historically lacked interest and resource allocation, reflecting the low priority of conservation efforts (Brito 2004).

Finally, the description of a new taxon endemic to a Neotropical biome (Atlantic Forest) reflects the lack of knowledge on small mammals richness in a hotspot; the necessity of long term collecting effort of specimens and the importance of scientific collections in order to reveal biodiversity; and the need of integration of molecular and morphological analyses to correctly identify cryptic species. The conservation status of *J. ximenezi* must be evaluated considering its limited distribution and environmental characteristics.

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SUPPORTING INFORMATION

Supporting information S1.—Coeficients of the first 3 components of principal component analysis, eigenvalues, and percentage of variance explained.

Variables	PC 1	PC 2	PC 3
NL	0.604	-0.050	-0.455
RL	0.833	-0.075	-0.280
RB	0.729	-0.074	-0.138
IOB	0.203	-0.195	-0.065
ZB	0.829	0.105	0.039
BCB	-0.195	-0.062	0.028
BIT	0.879	-0.081	0.083
DL	0.849	0.175	0.091
IFL	0.323	0.573	0.050
IFB	0.177	0.620	0.442
M1B	0.302	0.103	0.264
PB1	0.291	0.644	0.324
PB3	0.578	0.063	0.421
PBL	0.752	-0.069	-0.245
PL	0.948	0.040	-0.140
TFL	0.785	-0.107	0.347

MFB	0.680	-0.151	0.414
ONL	0.917	0.041	-0.103
CIL	0.899	0.219	-0.057
PPL	0.917	-0.020	-0.129
BW	-0.161	0.900	-0.016
BL	-0.104	0.826	-0.130
RH	0.781	-0.166	0.099
SH	0.420	0.231	-0.154
ZPL	0.735	0.208	-0.513
MRC	0.271	0.099	0.000
MMR	0.021	0.190	-0.084
GLM	0.889	-0.003	0.006
DR	0.716	0.149	-0.032
Eigenvalue	0.011	0.005	0.002
% variance explained	49.830	16.650	7.450

Supporting information S2.—Matrix of molecular autapomorphies (in bold) of *Juliomys* sp. and its synapomorphies in comparion with other analysed *Juliomys* species.

	Nucleotide position	Codon position	State in *Juliomys* sp.	Character CI	State in *J. rimofrons*	State in *J. pictipes*	State in *J. ossitenuis*
1	**21**	**3**	**A**	0.50	**C**	**C**	**T/C**
2	51	3	T	1.00	T	T	C
3	57	3	T	0.50	T	T	C
4	66	3	T	1.00	T	T	C
5	99	3	T	0.50	C	T	C
6	**106**	**1**	**T**	1.00	**C**	**C**	**C**
7	**114**	**3**	**T**	0.66	**C**	**C**	**C**
8	138	3	T	0.50	T	T	C
9	**144**	**3**	**T**	0.50	**C**	**C**	**C**
10	**145**	**1**	**T**	0.50	**C**	**C**	**C**
11	**151**	**1**	**T**	1.00	**C**	**C**	**C**
12	**156**	**3**	**A**	1.00	**T**	**T**	**T**
13	162	3	T	0.50	T	C	T/C
14	178	1	A	1.00	A	A	A/T
15	**189**	**3**	**C**	0.50	**T**	**T**	**T**
16	195	3	A	1.00	A	A	C
17	201	3	C	0.33	T	T	C
18	222	3	C	1.00	C	T	T
19	225	3	T	0.50	T	T	C
20	237	3	C	1.00	C	T	T
21	**249**	**3**	**T**	0.50	**C**	**C**	**C**
22	**252**	**3**	**T**	1.00	**C**	**C**	**C**

23	255	3	T	0.50	C	T	C
24	258	3	A	1.00	A	G	A
25	273	3	C	0.50	T	C	T
26	**276**	**3**	**T**	1.00	**C**	**C**	**C**
27	279	3	C	0.50	C	T	T/C
28	280	1	C	0.33	T	T	C
29	**282**	**3**	**G**	1.00	**A**	**A**	**A**
30	285	3	C	0.33	C	T	T/C
31	288	3	T	0.50	T	C	T/C
32	291	3	C	0.33	T	T	C
33	**303**	**3**	**C**	1.00	**T**	**T**	**T**
34	306	3	C	0.50	C	T	C
35	**315**	**3**	**T**	1.00	**C**	**C**	**C**
36	318	3	C	1.00	C	A	C
37	321	3	T	0.33	T	T	C
38	**325**	**1**	**T**	1.00	**C**	**C**	**C**
39	327	3	A	1.00	A	C	A
40	345	3	C	0.50	C	T	C
41	349	1	A	1.00	A	A	G
42	351	3	T	0.50	C	T	T/C
43	354	3	T	1.00	T	C	C
44	357	3	A	1.00	A	C	T
45	**358**	**1**	**T**	0.50	**C**	**C**	**C**
46	**364**	**1**	**G**	1.00	**A**	**A**	**A**
47	369	3	T	0.25	T	T/C	C
48	384	3	C	0.50	T	T	C
49	387	3	A	0.50	A	G	A

50	**390**	**3**	**C**	0.50	**T**	**T**	**T**
51	393	3	T	1.00	T	C	C
52	397	1	T	0.33	T	T/C	C
53	**411**	**3**	**G**	1.00	**A**	**A**	**A**
54	438	3	T	1.00	T	C	C
55	**447**	**3**	**T**	1.00	**C**	**C**	**C**
56	456	3	A	0.50	A	T	A
57	457	1	A	1.00	A	A	G
58	462	3	T	0.66	C	C	T
59	**468**	**3**	**T**	0.50	**C**	**C**	**C**
60	474	3	T	0.50	T	C	T
61	477	3	C	0.50	C	C	T
62	478	1	T	0.50	T	C	T
63	486	3	A	1.00	A	A	G
64	489	3	A	1.00	A	G	A
65	492	3	C	0.50	C	C	T
66	**501**	**3**	**A**	1.00	**C**	**C**	**C**
67	513	3	C	0.50	T	T	C
68	516	3	A	1.00	A	G	A
69	519	3	C	0.66	T	T	C
70	522	3	A	1.00	A	C	A
71	543	3	C	0.50	C	T	C
72	546	3	C	0.50	T	C	T
73	549	3	T	0.33	C	C	T
74	555	3	A	1.00	A	C	A
75	558	3	A	0.50	A	A	T/A
76	561	3	C	0.50	T	C	C

77	564	3	C	0.50	T	T	C
78	**567**	**3**	**C**	0.50	**T**	**T**	**T**
79	570	3	C	0.50	T	T	T/C
80	**574**	**1**	**T**	0.50	**C**	**C**	**C**
81	580	1	T	0.50	C	T	C
82	612	3	A	0.50	A	C	A
83	615	3	A	0.50	A	A	T
84	621	3	C	1.00	C	T	C
85	627	3	A	0.50	A	A	C/A
86	630	3	C	0.50	C	C	A
87	642	3	C	1.00	C	T	T
88	657	3	A	1.00	A	T	A
89	672	3	T	0.50	C	T	C
90	678	3	T	1.00	T	C	T
91	684	3	C	0.50	T	C	T
92	685	1	C	1.00	C	C	T
93	688	1	C	0.50	T	T	T
94	696	3	C	0.33	C	T	T/C
95	697	1	A	1.00	A	A	G
96	703	1	A	1.00	A	A	T

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APPENDIX I

Specimens.—Gazetteer of collecting localities and specimens examined. All localities listed are from the voucher specimens analyzed or reported in the literature (Cherem et al. 2004, 2005; Oliveira et al. 2005; Pardiñas et al. 2008; De la Sancha et al. 2009; Paresque et al. 2009; Melo et al. 2011; Pavan and Leite 2011; Aguieiras et al. 2013; Fonseca et al. 2013; Grazzini et al. 2015). Countries and States are listed from north to south, followed by specific localities, latitude and longitude (south and west, respectively, in negative decimal degrees), and elevation in meters, when available. Sex and age class, when available, follows the museum acronyms). Numbers in bold correspond to numbered localities on the map (Fig. 4). Specimens underlined compose the sample used on morphometric analyses. Specimens followed by * compose the map (Fig. 4) but were not examined in this study.

Juliomys sp.1.—BRAZIL: *Rio Grande do Sul*: Cambará do Sul: **1.** Parque Nacional de Aparados da Serra, -29.16 -50.10, 900 m (type locality, <u>MCNU 464</u> ♂A, <u>MCNU 868</u> ♂A, <u>MCNU 689</u> ♂A, <u>MCNU 870</u> ♂A).

Juliomys ossitenuis.—BRAZIL: *Espírito Santo*: Castelo: **2.** Parque Estadual do Forno Grande, -20.52 -41.00, 1200-2039 m (MBML 2607 ♀A); Dores do Rio Preto: **3.** Casa

Queimada; Parque Nacional do Caparaó, -20.46 -41.81, 2079 m (MBML 2784 ♂A); Macieira: **4.** Parque Nacional do Caparaó, -20.48 -41.83, 1788 m (MBML 2783 ♂A). *Minas Gerais*: Fervedouro: **5.** Fazenda Neblina, Parque Estadual da Serra do Brigadeiro, 20 km W Fervedouro, -20.72 -42.48, 1300 m (type locality, MN 69752 ♀A, MN 69753 ♀A, UFMG 3174 ♂A, MZUFV 608, MZUFV 627, MZUFV 679, MZUFV 683); Passa Quatro: **6.** Fazenda do Itaguaré, 16 km SW Passa Quatro, -22.47 -45.08, 1500 m (UFMG 3173 ♀A). *Rio de Janeiro*: Teresópolis: **7.** Parque Nacional da Serra dos Órgãos, Abrigo Paquequer -22.27 -42.59, 1200 m (MN 81077 ♀A, MN 81078 ♂A); **8.** Parque Nacional da Serra dos Órgãos, Rancho Frio, -22.27 -43.00, 1200 m (MN 81079 ♀J, MN 81080 ♂A, MN 81081 ♂A, MN 81082 ♂A, MN 81083 ♀A, MN 81080 ♀J, MN 81085 ♂J, MN 81086 ♂A, MN 81087 ♂A, MN 81080 ♂A, MN 81088 ♀A, MN 81089 ♂A, MN 81090 ♂J, MN 81091 ♂J, MN 81092 ♀A). *São Paulo*: Bananal: **9.** Estação Ecológica do Bananal, -22.80 -44.37, 1119-1164 m (MZUSP uncatalogued EEB 536, EEB 537, EEB 596, EEB 602); Cotia: **10.** Sítio Até Que Enfim, Caucaia do Alto, -23.68 -47.03, 900 m (MZUSP 33170 ♀A, MZUSP 33171 ♂A); **11.** Quilombo, Reserva Florestal do Morro Grande, Caucaia do Alto, -23.76 -47.00, 800-1000 m (MZUSP 32648); **12.** Grilos, Reserva Florestal do Morro Grande, Caucaia do Alto, -23.78 -47.01, 800-1000 m (MZUSP 32650); Piedade: **13.** Cristo, -23.85 -47.47, 800-1000 m (MZUSP uncatalogued AB 473); **14.** Fragmento Eme, -23.88 -47.48, 800-1000 m (MZUSP uncatalogued AB 258); Tapiraí: **15.** Fragmento Antenor, -23.92 -47.45, 800- 1000 m (MZUSP uncatalogued AB 196); **16.** Janzinho, -23.97 -47.51, 800-1000 m (MZUSP uncatalogued AB 469); Ribeirão Grande: **17.** Mulheres, -24.05 -48.37, 800-1000 m (MZUSP uncatalogued AB 350, AB 357); **18.** Museros -24.22 -48.40, 800-1000 m (MZUSP uncatalogued AB 395); **19.**

Mina Limeira, -24.17 -48.33, 800-1000 m (MZUSP 32276 A). *Paraná*: Piraí do Sul: **20.** FLONA Piraí do Sul, -24.56 -49.95 (MHNCI 6478). *Santa Catarina*: Dr. Pedrinho: **21.** Rebio Sassafrás, -26.71 -49.66, 900 m (CZFURB 18593 ♂A). *Rio Grande do Sul*: São Francisco de Paula: **22.** Centro de Pesquisas e Conservação da Natureza Pró-Mata, -29.49 -50.21, 900 m (MCNU 1461 ♂A, MCNU 1977 ♂A).

Juliomys pictipes.—BRAZIL: *Espírito Santo*: Cariacica: **23.** Reserva Biológica Duas Bocas, Alto Alegre, -20.28 -40.51, 550 m (UFES 556 ♂J, UFES 557 ♀A). *Minas Gerais*: Santa Bárbara: **24.** Estação de Pesquisa e Desenvolvimento Ambiental de Peti, -19.9 -43.37, 630-806 m (UFMG 3161 ♂A, UFMG 3162 ♀, UFMG 3163 ♂A, UFMG 3164 ♂A); **25.** Reserva Particular do Patrimônio Natural do Caraça, 25 km SW Santa Bárbara, -20.08 -43.5, 1300 m (MN 69764, UFMG 3159 ♀A, UFMG 3160 ♀A). Itabira: **26.** No specific locality provided, -19.38 -43.15 (MCN-M 2195 ♀A, MCN-M 2439 ♀A). *Rio de Janeiro*: Teresópolis: **27.** Parque Nacional da Serra dos Órgãos, Abrigo 4, -22.27 -43.01, 2130 m (MN 81094 ♂A); **28.** Parque Nacional da Serra dos Órgãos, Rancho Frio, -22.27 -43.00, 1200 m (MN 81097 ♀A); Cachoeiras de Macacu: **29.** Estação Ecológica de Paraíso, -22.31 -42.51, 87 m (MN 79853 ♂A); Guapimirim: **30.** Garrafão, -22.29 -43.00, 700 m (MN 81095 ♂A, MN 81096 ♂A); **31.** Fazenda Boa Fé, -22.43 -42.98, 902 m (MN 62182); Angra dos Reis: **32.** Mata do Mamede, -23 -44.32 (MN 69765 ♀A). *São Paulo*: São Luís do Paraitinga: **33.** Fragmento G4, -23.22 -45.31, 900 m (ZUEC-MAM 2399); Piedade: **34.** No specific locality provided, -23.72 -47.41, 800-1000 m (MZUSP 31113); Mogi das Cruzes: **35.** Parque Natural Municipal da Serra do Itapety, -23.47 -46.15, 807-1141 m (MN uncatalogued 61 ♀A); Cotia: **36.** Reserva Florestal do Morro Grande, Caucaia do Alto -23.68 -46.96, 800-1000 m

(MZUSP 32263, MZUSP 32264, MZUSP 32265, MZUSP 32266, MZUSP 32649 A); Sorocaba: **37.** Floresta Nacional de Ipanema, 20 km NW -23.44 -47.63, 701 m (MVZ 197563, MVZ 197564, MVZ 197565, UFMG 3165 ♂A, UFMG 3166 ♂J, UFMG 3167 ♂A, UFMG 3168 ♂A, UFMG 3169 ♂J, UFMG 3170 ♀A UFMG 3171 ♂A UFMG 3172 ♂A); São Bernardo do Campo: **38.** Riacho Grande, -23.80 -46.58, 777 m (MZUSP 30710, MZUSP 30724, MZUSP 30747, MZUSP 30779); Buri: **39.** No specific locality provided, -23.81 -48.70, 666 m (MZUSP 31025); Ribeirão Grande: **40.** Mulheres, -24.05 -48.37, 800-1000 m (MZUSP uncatalogued AB 348, AB 388, AB 410); **41.** Museros, -24.22 -48.40, 800- 1000 m (MZUSP uncatalogued AB 402, AB 562); **42.** Fragmento Citadini, -24.06 -48.39, 800-1000 m (MZUSP uncatalogued AB 78); **43.** Fragmento Divisa, -24.06 -48.37, 800-1000 m (MZUSP uncatalogued AB 75); **44.** Três Quedas, -24.22 -48.37, 800-1000 m (MZUSP uncatalogued AB 571); **45.** Paraguai, -24.23 -48.39, 800-1000 m (MZUSP uncatalogued AB 559, AB 591); Capão Bonito: **46.** Fazenda Sakamoto, Campinho, -24.18 -48.24, 800-1000 m (MZUSP uncatalogued AB 110, AB 113, AB 115, AB 141, AB 143, AB 145); **47.** Fazenda Intervales, -24.33 -48.42, 700 m (MN 60570, MN 60571, MN 69766, MVZ 182079). *Paraná*: Telêmaco Borba: **48.** Fazenda Monte Alegre, -24.2 -50.55, 885 m (MN 68336 ♀, MN 68347 ♀J). Morretes: **49.** No specific locality provided, -25.26 -48.55 (DZUP 393 A, DZUP 394 A, DZUP 395 A, DZUP 498 A, DZUP 499 A, DZUP 502 A). *Santa Catarina*: Indaial: **50.** Parque Nacional da Serra do Itajaí, Vale do Espingarda, -26.56 -49.11, 600 m (CZFURB 9423 ♀A); **51.** Parque Nacional da Serra do Itajaí, Mono, -26.57 -49.4 (CZFURB 5372, CZFURB 9622 ♂A, CZFURB 9623 ♂A, CZFURB 9624 ♂A, CZFURB 9625 ♂A, CZFURB 9667 ♂A, CZFURB 9669 ♀A, CZFURB 9834 ♂A, CZFURB 9837 ♂A, CZFURB 9922 ♀A); Blumenau: **52.** Terceira Vargem, -27.3 -49.5, 300 m (CZFURB 9770 ♂A, CZFURB 9775 ♀A, CZFURB 12243 ♀A). Santo

Amaro da Imperatriz: **53.** Parque Estadual da Serra do Tabuleiro, -27.74 -48.81, 400-500 m (UFSC 652 ♂A, UFSC 862 ♂A, UFSC 853 ♂A, UFSC 864 ♂A, UFSC 670). *Rio Grande Do Sul*: Dois Irmãos: **54.** No specific locality provided, -29.56 -51.10 (MCNU 4307 ♀A). Derrubadas: **55.** Parque Estadual do Turvo, -27.20 -53.88, 100-400 m (no voucher number provided). ARGENTINA: *Misiones*: Cainguas: **56.** Reserva Privada de Usos Múltiples de la Universidad Nacional de La Plata “Valle del Arroyo Cuña Pirú”, -27.08 -54.95, 200 m (MLP 1.I.03.24*); Iguazú: **57.** Parque Nacional Iguazú, Sendero Macuco, -25.68 -54.43, 200 m (CIES-M 23*); Montecarlo: **58.** Puerto Caraguatay -26.62 -54.76, 192 m (type locality, FMNH 26814*); **59.** Parque Provincial “Ernesto Che Guevara” Arroyo de Salamanca -26.61 -54.78, 147 m (CNP 895*). PARAGUAY: Alto Paraná: Hernandarias: **60.** Refugio Biológico Limoy, North of Rio Limoy, -24.80 -54.45, 270 m (CZ 014*).

Juliomys rimofrons.—BRAZIL: *Minas Gerais*: Itamonte: **61.** Brejo da Lapa, -22.21 -44.44, 2000 m (type locality; MN 46703 ♂A, MN 61646 ♂A, MN 61647 ♀A). *Rio de Janeiro*: Paraty: **62.** Parque Nacional da Serra da Bocaina, -23.83 -44.68 (MN 77793 ♂A). *São Paulo*: São José do Barreiro: **63.** Parque Nacional Serra da Bocaina, -22.50 -44.41, 1700 m (MN 76263 A); Capão Bonito: **64.** Parque Estadual Intervales, -24.16 -48.18, 800 m (MN 60571 ♂).

Oligoryzomys flavescens.—BRAZIL: *Rio Grande do Sul*: MCNU 1632 and MCNU 1611.

Specimens.—List of Sigmodontinae specimens from which Cytb sequence data was used for phylogenetic analyses. * Holotype; ** Paratype.

Taxon	Specimen number	GenBank number	Sequence lenght (bp)	Locality	Source
Juliomys ximenezi	MCNU 464**	KT749862	801	Brazil: Rio Grande do Sul	Present study
Juliomys ximenezi	MCNU 868*	KT749863	801	Brazil: Rio Grande do Sul	Present study
Juliomys ximenezi	MCNU 869**	KT749864	801	Brazil: Rio Grande do Sul	Present study
Juliomys pictipes	UFMG 3160	EF127515	441	Brazil: Minas Gerais	Costa et al. 2007
Juliomys pictipes	UFMG 3168	EF127513	801	Brazil: São Paulo	Costa et al. 2007
Juliomys pictipes	UFMG 3171	EF127514	801	Brazil: São Paulo	Costa et al. 2007
Juliomys pictipes	MLP 1.I.03.24	EU157764	801	Argentina: Misiones	Pardiñas et al. 2008
Juliomys pictipes	MVZ 141	AF108688	1144	Brazil: São Paulo	Smith and Patton 1999
Juliomys pictipes	TK145073	FJ026733	801	Paraguay: Alto Parana	de la Sancha et al. 2009
Juliomys ossitenuis	AB 187	EF127521	565	*Not provided by authors*	Costa et al. 2007
Juliomys ossitenuis	AB 196	EF127519	801	Brazil: São Paulo	Costa et al. 2007
Juliomys ossitenuis	AB 258	EF127520	720	Brazil: São Paulo	Costa et al. 2007
Juliomys ossitenuis	MZUSP 33170	EF127518	801	Brazil: São Paulo	Costa et al. 2007

Juliomys ossitenuis	UFMG 3173**	EF127516	792	Brazil: Minas Gerais	Costa et al. 2007
Juliomys ossitenuis	MN 69752*	EF127517	792	Brazil: Minas Gerais	Costa et al. 2007
Juliomys ossitenuis	MBML 2783	EF127522	721	Brazil: Espírito Santo	Costa et al. 2007
Juliomys ossitenuis	MVZ 40	AF108689	1144	Brazil: São Paulo	Smith and Patton 1999
Juliomys ossitenuis	MCNU 1461	KT749865	801	Brazil: Rio Grande do Sul	Present study
Juliomys ossitenuis	MCNU 1977	KT749866	801	Brazil: Rio Grande do Sul	Present study
Juliomys rimofrons	MN 61647*	AY029477	711	Brazil: Minas Gerais	Oliveira and Bonvicino 2002
Juliomys rimofrons	MN 46703**	AY029476	720	Brazil: Minas Gerais	Oliveira and Bonvicino 2002
Oligoryzomys microtis	BYU 19014	AY439000	1143	Bolivia: Santa Cruz	Carroll et al. 2005
Rhagomys rufescens	MN 66056	AY206770	825	Brazil: Minas Gerais	Percequillo et al. 2004

6. CAPÍTULO II

PREDICTIVE DISTRIBUTION OF THE MICE *JULIOMYS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) BASED ON THE MORPHOMETRICS AND TAXONOMIC REVIEW OF SPECIMENS

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Predictive distribution of the mice *Juliomys* (Rodentia, Cricetidae, Sigmodontinae) based on the morphometrics and taxonomic review of specimens

Paulo S. Tomasi[1], Alexandre U. Christoff[2], Rafael G. Moura[3], Sérgio L. Althoff[4], Larissa R. Oliveira[1]

1. Laboratory of Mammalian Ecology, University of Vale do Rio dos Sinos - UNISINOS, 950 Unisinos av., São Leopoldo

2. Departament of Biology, Natural Science Museum, University Luterana do Brasil - ULBRA, 8001 Farroupilha av., Canoas, Rio Grande do Sul, Brazil, Rio Grande do Sul, Brazil

3. Laboratory of Fish Ecology, University of Vale do Rio dos Sinos - UNISINOS, 950 Unisinos av., São Leopoldo, Rio Grande do Sul, Brazil

4. Departament of Natural Science, Fundação Universidade Regional de Blumenau - FURB, 140 Antônio da Veiga st., Blumenau, Santa Catarina, Brasil

Corresponding author: Paulo S. Tomasi (paulo.tomasi@gmail.com; +555193523157)

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Abstract

1. Museums and scientific collections are crucial for the information of the species distribution data. However, some drawbacks could exist in collections mainly due to taxonomic identification errors of species and unclear, biased, or vague sampling locations. Therefore, species distribution analyses may include collecting artifacts rather than the real and precise collection information.

2. To generate the potential geographic distribution for the species of *Juliomys* we studied specimens deposited in the 14 museum collections. We analysed the specimens' anatomy and used morphometric analysis to correctly identify the species. Subsequently we completed their locality database based on the sampling coordinates from each mice. After, we conduct the modelling analyses of the spatial distribution of the four species.

3. We identified 190 specimens (7 *Juliomys*. sp 1, 6 *J. rimofrons*, 136 *J. pictipes*, and 46 *J. ossitenuis*) from 217 mice from the total sample based on the anatomical and morphometric results. The generated potential distribution models for the four species of the genus was consistent with previous distribution and ecological information, which suggested that all species were highly linked to the forest formations of the Atlantic Forest biome.

4. Many factors and events may have modelled the species distribution on the Neotropics. The associated fauna to forest environments, as this biome, are also sensible to the historical changes. Habitat fragmentation and defaunation there is collapsing the ecological processes, which is a huge conservation concern.

Key words Atlantic Forest, MaxEnt, morphological analysis, geographical limits, tree mice

Introduction

Rodents are widespread mammals, where the Sigmodontinae specimens are a Neotropical branch. Some of its taxa are insufficiently known, as is the genus *Juliomys* González 2000. Three living species are considered valid for the genus: *J. pictipes* Osgood 1933, *J. rimofrons* Oliveira & Bonvicino 2002, and *J. ossitenuis* Costa, Pavan, Leite & Fagundes 2007. Recently, Christoff et al. (under review, chapter 1) proposed a new species based in Paresque et al. (2009) information. Considering the recent knowledge about its species (descriptions increasing since González 2000), errors or imprecise identifications of specimens from museums and scientific collections could be a common situation.

Museums and scientific collections are crucial for the biological information on taxa. However, their use has some drawbacks and limitations, mainly due to taxonomic identification errors and unclear or vague sampling locations of their specimens (Graham et al. 2004, Newbold 2010). These major issues added to collecting bias can disrupt the usage of museum collection data, and are especially negative for spatial modelling approaches (Graham et al. 2004, Sastre & Lobo 2009). The ideal recognition of the specimens' species must be based on the integrative analysis with methods combining information of karyology, molecular markers, anatomy, traditional and geometric morphometrics (Backer & Bradley 2006, Semedo et al. 2015, Christoff et al. under review, chapter 1). However, not all of this information is always available. Some methods could only support morphological characterization, such as the traditional morphometric analyses, which are faster and easier to implement. In fact, the morphometric analysis has proven to be a useful tool to differ characteristics in small mammals (e.g. Christoff et al. 2000, Özkurt et al. 2007, Breno et al. 2011).

Consequently, the information from geographic distribution data is vastly based on this taxonomic outcome.

Species geographical distribution is a basic data of the organisms and is essential information on conservation terms. However, the distribution limits of many small mammals (and many other taxa) are still poorly understood. In the Neotropics, some Rodent species, such as the species of the genus *Juliomys*, have little information about its ecology and distribution. Recently some studies as Costa et al. (2007), Pavan & Leite (2011), and González et al. (2015) bring some significant overall information for the genus. However, geographical distribution information to the group of species is poorly known, due to the scarce data of properly identified specimens. The locality records of *Juliomys* are restricted from southeast to southern Brazil, northeastern Argentina, and extreme eastern Paraguay (Pavan & Leite 2011). The species of the genus are not abundant in small mammals communities, they bear essentially arboreal habit, and they seem related to the forest interior (Graipel et al. 2006, Püttker et al. 2006, Cadermatori et al. 2008, Passamani & Fernandez 2011). These factors coupled with few collected specimens restrict plentiful data and reinforce the need to collect more information on the biology and natural history of these taxa. Moreover, the tag of the specimen deposited could present some inadequate data, since much of the museum exemplars end up without a proper species identification. In this sense, a clear morphological characterization of the species is imperative to stablish the species of each specimen present in a scientific collection. Besides, usually new records are often relate to distribution extension (Pardiñas et al. 2008, De la Sancha et al. 2009, Fonseca et al. 2013, Cerboncini et al. 2014). In this sense, considering the amount of undetermined *Juliomys* sp. present in scientific collections, the limits of distribution and inhabited environments to each species of the genus are unanswered questions.

Small mammals sampling in the Neotropics are often incomplete and biased (Graham et al. 2004, Moura et al. 2008). Therefore, species distribution analysis may reflect collecting artefacts rather than the real scenario (Newbold 2010; Guillera-Arroita et al. 2015). The form to extrapolate deficient data and estimate the probable geographical occurrence of a species shall be throughout the analysis of the species distribution models (Elith et al. 2006; Newbold 2010). Recent studies using geographic information systems have developed good predictive models of species distributions using small samples sizes (see Pearson et al. 2007). These models assume the niche theory, which adopts that the distribution of species is determined in great part by environmental variables, and so approximations for these variables can be estimated, using the unimodal curve (Austin 2007). In this sense, this study aims to generate the potential geographic distribution for the extant four species of *Juliomys*, based location data gathered on an extensive museum collections review and morphometric and taxonomic analyses.

Material and Methods

Sample

We analysed all *Juliomys* specimens mentioned in the literature, in the database *SpeciesLink* (http://splink.cria.org.br/), and deposited in 14 Brazilian museums and scientific collections. Specimens were deposited in the following institutions: Universidade Federal da Paraíba (UFPB), João Pessoa; Universidade Federal do Espírito Santo (UFES), Vitória; Museu de Biologia Prof. Mello Leitão (MBML), Santa Tereza; Mammal collection of Universidade Federal de Minas Gerais (UFMG), Belo Horizonte; Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M), Belo Horizonte; Museu Nacional da Universidade Federal do Rio de

Janeiro (MN), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Mammal collection of the Universidade Federal do Paraná (DZUP), Curitiba; Zoological collection of the Universidade Regional de Blumenau (CZFURB), Blumenau; Laboratório de Mamíferos Aquáticos of Universidade Federal de Santa Catarina (LAMAQ-UFSC), Florianópolis; Museu de Ciências Naturais, Universidade Luterana do Brasil (MCNU), Canoas – (including specimens that are still not deposited under the acronym AC); Mammal collection of Universidade Federal de Santa Maria (UFSM), Santa Maria; Mammal collection of Universidade Regional Integrada do Alto Uruguai e das Missões (URI), Erechim. Additional material from Mammal collection of Escola Superior de Agricultura Luiz de Queiroz da Universidade de São Paulo (ESALQ-USP), Piracicaba/SP were also analysed, but these specimens were still not deposited and are under the acronym EBM or EEB (Appendix I).

We analysed all specimens identified as *Juliomys*, and also specimens which may have had a mistaken identification, such as *Oligoryzomys* spp. and *Rhagomys* spp., due to their similar morphology. In order to identify at the species level each *Juliomys* specimen, we visually compared the anatomical traits and skull measurements (see Christoff et al., under review, chapter 1) described in the four current species of the genus. Besides, we collected a tissue sample for DNA analysis from each specimen whenever it was possible. The total sample consisted of 217 *Juliomys* spp. specimens (Table 1; Appendix I). The sample was composed by *Juliomys* sp.1 (*n* = 4) (a new species under description by Christoff et al., under review, see chapter 1), *J. ossitenuis* (*n* = 9), *J. rimofrons* (*n* = 4), *J. pictipes*, (*n* = 24), and *Juliomys* sp. (*n* = 176).

Anatomic and morphometric analyses

In order to identify at the species level the remaining 176 *Juliomys* sp. of the 217 museum specimens, we used the diagnostic traits suggested by González (2000), Oliveira & Bonvicino (2002), Costa et al. (2007), Pavan & Leite (2011), González (2015) as well as the diagnosis and morphometric characters proposed by Christoff et al. (under review, chapter 1). Anatomical characters were imperative to the species diagnosis, especially the carotid arterial supply to differentiation of *J. pictipes* from the other species. Based on the diagnostic traits cited above we first analysed and identified 41 specimens as a group that holds reliable markers (RM) for each species of *Juliomys* (*e.g.* type series, karyology and/or molecular markers; details in Appendix I). These RM mice were used to evaluate the morphometric diagnosis of the four species (see Christoff et al. under review). In this sense, only adult specimens were included in the analyses and in each specimen (total sample, n = 217), we took 29 cranial linear measurements (Fig. 1; Tribe 1996), using a digital calliper (the nearest 0.01 mm). We used only those 41 RM specimens in a principal component analysis (PCA) over the variance-covariance matrix of the logarithms of all measurements to explore multivariate differences among taxa (Neff & Marcus, 1980). We then performed a discriminant function analysis (DFA) with the stepwise method, which maximized the differences between the groups found in the PCA, reducing the differences within groups and an optimization of the differences between the groups in terms of variables (Strauss 2010). Thae DFA builds a predictive model for group membership maximally separating groups (species) based on produced constants and the best linear measurements as discriminant variables in these equations. The discriminant analysis thus generate a centroid for each taxon and discriminant equations useful to post exploratory classification. Since the exploratory PCA was able to identify *a priori* groups of *Juliomys,* using only the 41 RMs specimens, the second step included the analysis of canonical variables using of the 29 measurements from the 176 *Juliomys* sp. remaining. This analysis generated two discriminant equations by discriminant function analysis (DFA) (Formula 1 and Formula 2), plotted as X and Y axes in the exploratory analyses with the discriminant centroids first given to the four species. Attempting to classify the non-identified specimens we based the diagnosis on the anatomical characters as mentioned above and the position of each specimen and its proximity of centroids, in order to determine to which species group each specimen belongs. Afterwards, we performed a further DFA analysis to check the assignment reliability of the species groups. All morphometric analyses were conducted in the program SPSS 17.0.

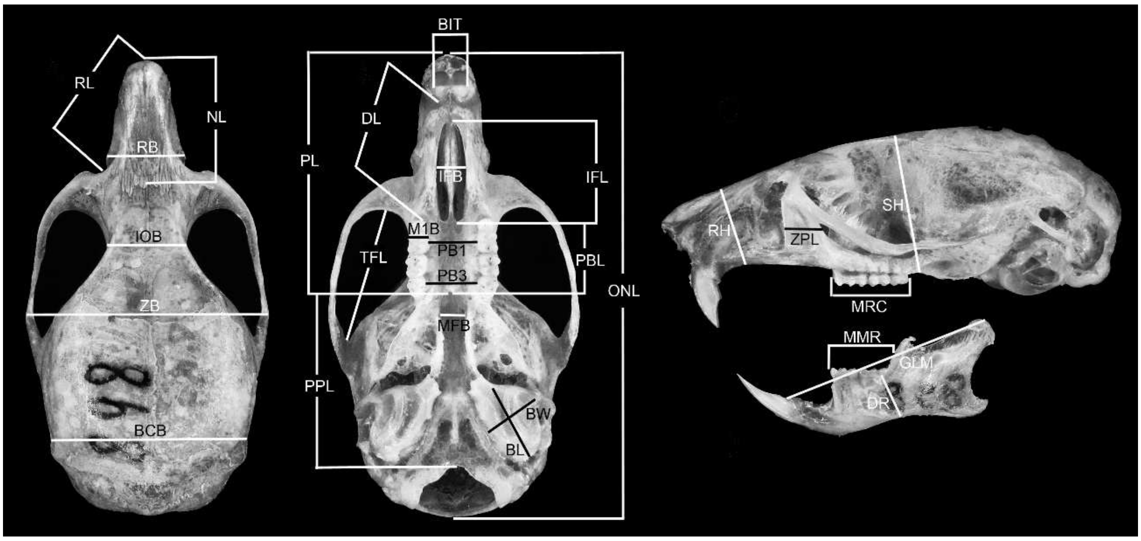

Fig. 1. Cranial linear measurements used in this study: ONL, occipto-nasal length; PL, palatal length; PPL, post-palatal length; MRC, molar row–crown length; M1B, first molar breadth; PBL, palatal bridge length; TFL, temporal fossa length; DL, diastema length; IFL, incisive foramen length; IFB, incisive foramen breadth; PB1, palatal breadth at first molar; PB3, palatal breadth at third molar; MFB, mesopterygoid fossa breadth; BIT, breadth across incisor tips; BW, bullar width; BL, bullar length, BCB,

braincase breadth; SH, skull height; RH, rostral height, RB, rostral breadth; RL, rostral length, NL, nasal length; ZPL, zygomatic plate length; CIL, interorbital breadth; IOB, interorbital breadth; ZB, zygomatic breadth; GLM, greatest length of mandible; MMR, mandibular molar row–alveolar length; DR, depth of ramus.

Geographic distribution modelling

After the taxonomic revision and reclassification of the *Juliomys* sp. specimens, the geographic coordinates of the locality from each reclassified specimen were found based on the museum label and registry book. We conducted the modelling analyses of the spatial distribution of the *Juliomys* species using the algorithm of Maximum Entropy Modeling of Species Geographic Distributions - MaxEnt 3.3.3 (Phillips et al., 2006, 2008). These models use logistic regression algorithms and niche concept to produce distribution models (maps) that allow the evaluation of the relationship between the species and environmental occupation (Austin 2007, Elith et al. 2011). These tools combine numerical occurrence of the species (or abundance) with the environmental estimates (Elith & Leathwick, 2009). We used 30% of the total set of records for testing the models and 70% for training. The data were sampled using bootstrap routine of 10 random partitions with replacement (Pearson, 2007), the runs were configured in random seed, convergence threshold of 1E-5 with 50 iterations and 10,000 background hidden points. To verify the models accuracy, we evaluated the Area Under Curve (AUC) values for the Receiver Operating Characteristic (ROC) curves of each species model.

In the model, the occurrence locations of the specimens added to the environmental data (layers) produce maps of potential distribution of the studied species. We used the Jacknife method in order to stablish the variables importance. In this analysis we used 21 variables as layers (Elith et al. 2011, Hof et al. 2012) from the databases GlobCover (http://due.esrin.esa.int/page_globcover.php) and Bioclim (http://worldclim.org/bioclim) as follows: altitude (alt) landscape cover (geocover), annual mean temperature (bio1), mean diurnal temperature range (bio2), isothermality (bio3), temperature seasonality (bio4), max temperature of warmest week (bio5), min temperature of coldest week (bio6), temperature annual range (bio7), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11), annual precipitation (bio12), precipitation of wettest week (bio13), precipitation of driest week (bio14), precipitation seasonality (bio15), precipitation of wettest quarter (bio16), precipitation of driest quarter (bio17), precipitation of warmest quarter (bio18), precipitation of coldest quarter (bio19). All variables were analysed using a fine spatial resolution (~1 km).

Results

Anatomic and morphometric analyses

The final reclassified sample was composed by 7 *Juliomys* sp.1, 46 *J. ossitenuis*, 6 *J. rimofrons*, and 136 *J. pictipes* resulting in 195 specimens analysed (Appendix I). The unidentified specimens represented 22 mice which were not reclassified due to age, broken structures, and/or inconclusive species after the overall analysis.

In the PCA for the 41 RM specimens, the first three components explained over 73.93% of the total variance (Table 1). The variables most related to PC 1 were PL, ONL and CIL, those most related to PC 2 were PB1, BL and IFL, and to PC 3 were NL, PB3 and IFB. Monospecific groups were formed in the exploratory PCA (Fig. 2), with a partial overlap among *Juliomys* species. *Juliomys* sp. 1 was morphologically more different and separated to the others over the PC 1 and PC 2 axes.

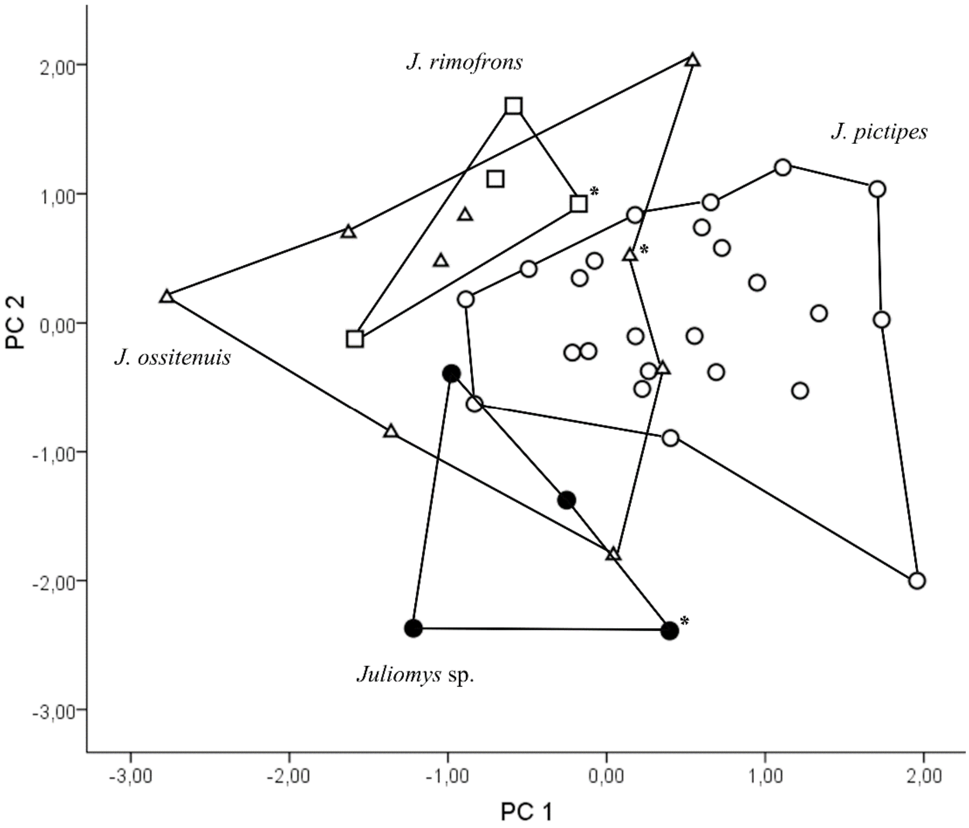

Fig. 2. Scores of the specimens of *Juliomys* in the first two axes (PC 1 and PC 2) of the principal component analysis (PCA). Symbols: □ = *Juliomys* sp.1 ; Δ = *J. ossitenuis*; + = *J. rimofrons*; o = *J. pictipes*.

Table 1. Measurement contributions to each axis of the Principal Component Analysis. ONL, occipto-nasal length; PL, palatal length; PPL, post-palatal length; MRC, molar row–crown length; M1B, first molar breadth; PBL, palatal bridge length; TFL, temporal fossa length; DL, diastema length; IFL, incisive foramen length; IFB, incisive foramen breadth; PB1, palatal breadth at first molar; PB3, palatal breadth at third molar; MFB, mesopterygoid fossa breadth; BIT, breadth across incisor tips; BW, bullar width; BL,

bullar length, BCB, braincase breadth; SH, skull height; RH, rostral height, RB, rostral breadth; RL, rostral length, NL, nasal length; ZPL, zygomatic plate length; CIL, interorbital breadth; IOB, interorbital breadth; ZB, zygomatic breadth; GLM, greatest length of mandible; MMR, mandibular molar row–alveolar length; DR, depth of ramus.

Variables	**PC 1**	**PC 2**	**PC 3**
NL	0.604	-0.050	-0.455
RL	0.833	-0.075	-0.280
RB	0.729	-0.074	-0.138
IOB	0.203	-0.195	-0.065
ZB	0.829	0.105	0.039
BCB	-0.195	-0.062	0.028
BIT	0.879	-0.081	0.083
DL	0.849	0.175	0.091
IFL	0.323	0.573	0.050
IFB	0.177	0.620	0.442
M1B	0.302	0.103	0.264
PB1	0.291	0.644	0.324
PB3	0.578	0.063	0.421
PBL	0.752	-0.069	-0.245
PL	0.948	0.040	-0.140
TFL	0.785	-0.107	0.347
MFB	0.680	-0.151	0.414
ONL	0.917	0.041	-0.103
CIL	0.899	0.219	-0.057
PPL	0.917	-0.020	-0.129
BW	-0.161	0.900	-0.016
BL	-0.104	0.826	-0.130
RH	0.781	-0.166	0.099
SH	0.42	0.231	-0.154
ZPL	0.735	0.208	-0.513
MRC	0.271	0.099	0.000
MMR	0.021	0.190	-0.084
GLM	0.889	-0.003	0.006
DR	0.716	0.149	-0.032
Eigenvalue	0.011	0.005	0.002
% variance explained	49.83	16.65	7.45

Discriminant function analysis of the 41 RM specimens correctly classified 97.6% of the specimens along the first and second axes (Fig. 3, Table 2). For the species *Juliomys* sp.1, *J. pictipes* and *J. ossitenuis* the classification resulted in 100% of specimens correctly classified *the a priori* groups defined based on the diagnostic traits. For the species *J. rimofrons*, 75% specimens (3 of 4) were correctly classified based on the reclassification groups through the discriminant analysis.

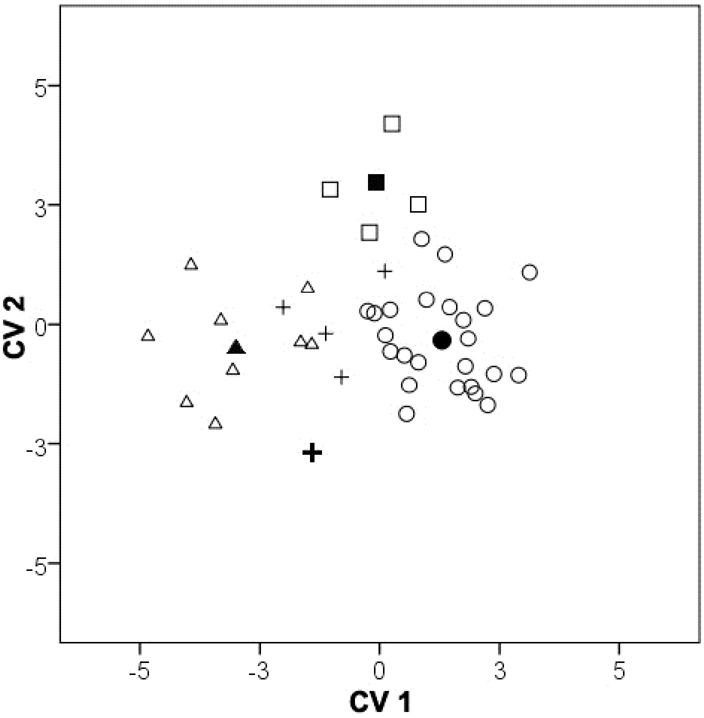

Fig. 3. Axes projection of canonical discriminant analysis for 29 skull measurements in *Juliomys*. Black symbols are centroids; □ = *Juliomys* sp.1; Δ = *J. ossitenuis*; + = *J. rimofrons*; o = *J. pictipes*. CV 1: canonical variant 1; CV 2: canonical variant 2.

Table 2. Measurement contributions to each axis to the Discriminant Analysis. ONL, occipto-nasal length; PL, palatal length; PPL, post-palatal length; MRC, molar row–crown length; M1B, first molar breadth; PBL, palatal bridge length; TFL, temporal

fossa length; DL, diastema length; IFL, incisive foramen length; IFB, incisive foramen breadth; PB1, palatal breadth at first molar; PB3, palatal breadth at third molar; MFB, mesopterygoid fossa breadth; BIT, breadth across incisor tips; BW, bullar width; BL, bullar length, BCB, braincase breadth; SH, skull height; RH, rostral height, RB, rostral breadth; RL, rostral length, NL, nasal length; ZPL, zygomatic plate length; (CIL), interorbital breadth; IOB, interorbital breadth; ZB, zygomatic breadth; GLM, greatest length of mandible; MMR, mandibular molar row–alveolar length; DR, depth of ramus.

Variable	Canonical variates	
	First	Second
GLM	-0.3350	-0.2388
PPL	-0.3150	-0.0719
ONL	-0.3070	0.1436
RB	-0.3040	-0.1858
PBL	-0.3000	-0.1073
ZB	-0.2640	-0.0650
ZPL	-0.2260	0.2195
NL	-0.2110	0.0389
RL	-0.2100	0.0387
RH	-0.2060	0.0246
DR	-0.4460	0.5170
MRC	-0.0060	0.2460
BCB	0.2052	0.2330
BW	0.1542	0.2030
IOB	0.1025	-0.2030
IFB	0.0320	0.1650
SH	-0.1094	0.1550
MFB	-0.0607	0.1110
TFL	-0.3470	0.0718
MMR	0.0763	0.1791
PB1	0.1879	0.1806
DL	-0.1739	-0.1124
BIT	-0.2280	-0.0546
PB3	0.0264	0.0360
M1B	-0.0774	0.2044
PL	-0.1899	0.0089
CIL	-0.1452	-0.0137
IFL	-0.1006	0.1323
BL	0.0899	0.0913

Canonical correlation	0.8800	0.7300
Eigeinvalue	3.5800	1.1600
% Variance	63.3000	20.5000

The five measures chosen by stepwise method in an attempt to classify the four species are IOB, PB1, PB3, MFB, DR. The discriminant equations obtained are:

F1 Escores: -28.897 + 5.035(**IOB**) – 6.638(**PB1**) + 5.096(**PB3**) – 4.482(**MFB**) + 6.083(**DR**), and

F2 Escores: -10.139 + 4.525(**IOB**) + 3.433(**PB1**) + 1.341(**PB3**) – 7.933(**MFB**) – 2.104(**DR**).

The second round of discriminant function analysis correctly classified at the species level 92.7% of the 176 specimens previously only identified as *Juliomys* sp. (see Fig 4).

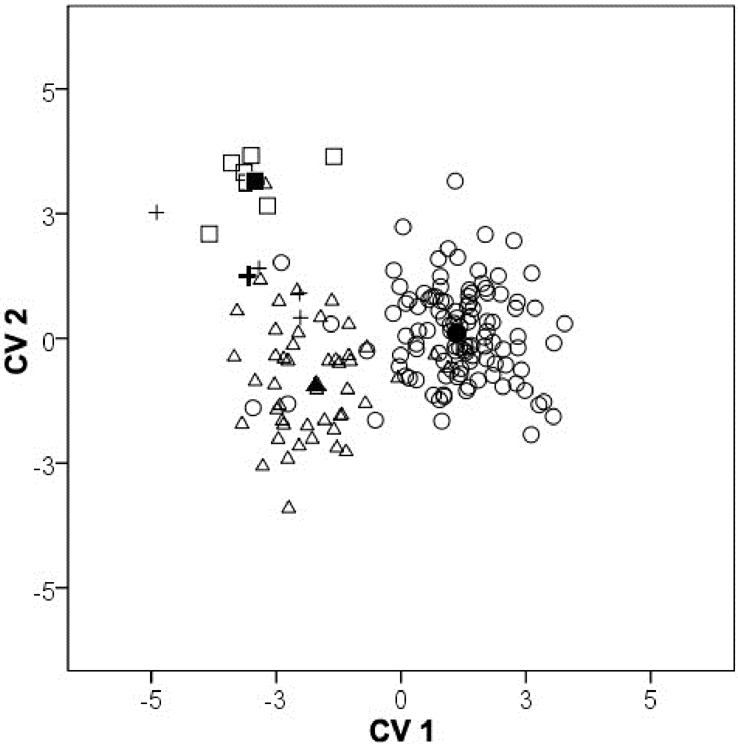

Fig. 4. Discriminant function analysis plot, with the projection of specimens using the F1 and F2 discriminant equations. Symbols: centroids are in bold; □ = *Juliomys* sp.1; Δ = *J. ossitenuis*; + = *J. rimofrons*; o = *J. pictipes*. CV 1: canonical variant 1; CV 2: canonical variant 2.

Geographic distribution modelling

The maps (Figs. 5-9) show the predicted distributions, where the “warmer” colours indicates higher probability of occurrence along South America. MaxEnt models generated satisfactory (> 0.9) AUC results for the genus as a whole and the four species. The average ROC curve for the genus *Juliomys* was AUC = 0.989, for *J. pictipes* (AUC = 0.968), *J. ossitenuis* (AUC = 0.978), *J. rimofrons* (AUC = 0.985), *Juliomys* sp.1 (AUC = 0.999). For the genus as a whole, the principal environmental variables contributions were precipitation of warmest quarter (bio18; 25.9%), temperature seasonality (bio4; 21.5%), max temperature of warmest week (bio5; 14.4%), mean temperature of driest quarter (bio9; 9.8%). The leading environmental variables contributions are different to each species, as follows (Fig. 9): *J. pictipes* – temperature seasonality (bio4), max temperature of warmest week (bio5), mean temperature of driest quarter (bio9), precipitation of warmest quarter (bio18); *J. ossitenuis* – altitute (alt), temperature seasonality (bio4), and precipitation of warmest quarter (bio18); *J. rimofrons* – mean temperature of driest quarter (bio9), precipitation of warmest quarter (bio18), precipitation of coldest quarter (bio19); *Juliomys* sp.1 – altitude (alt), annual mean temperature (bio1), isothermality (bio3), and precipitation seasonality (bio15).

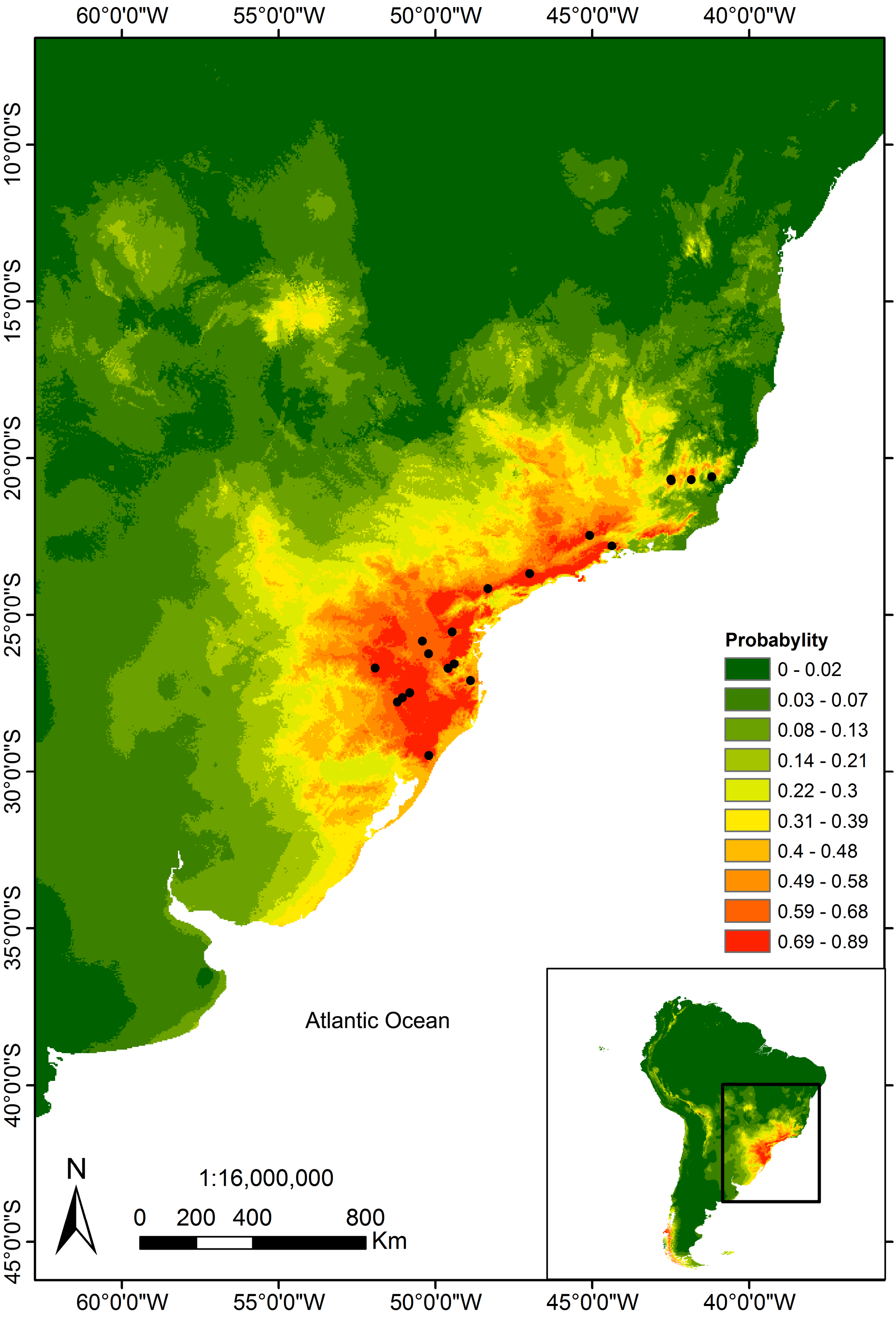

Fig. 5. Prediction model of species distribution for *J. ossitenuis*, AUC = 0.978. Black dots are localities of occurrence.

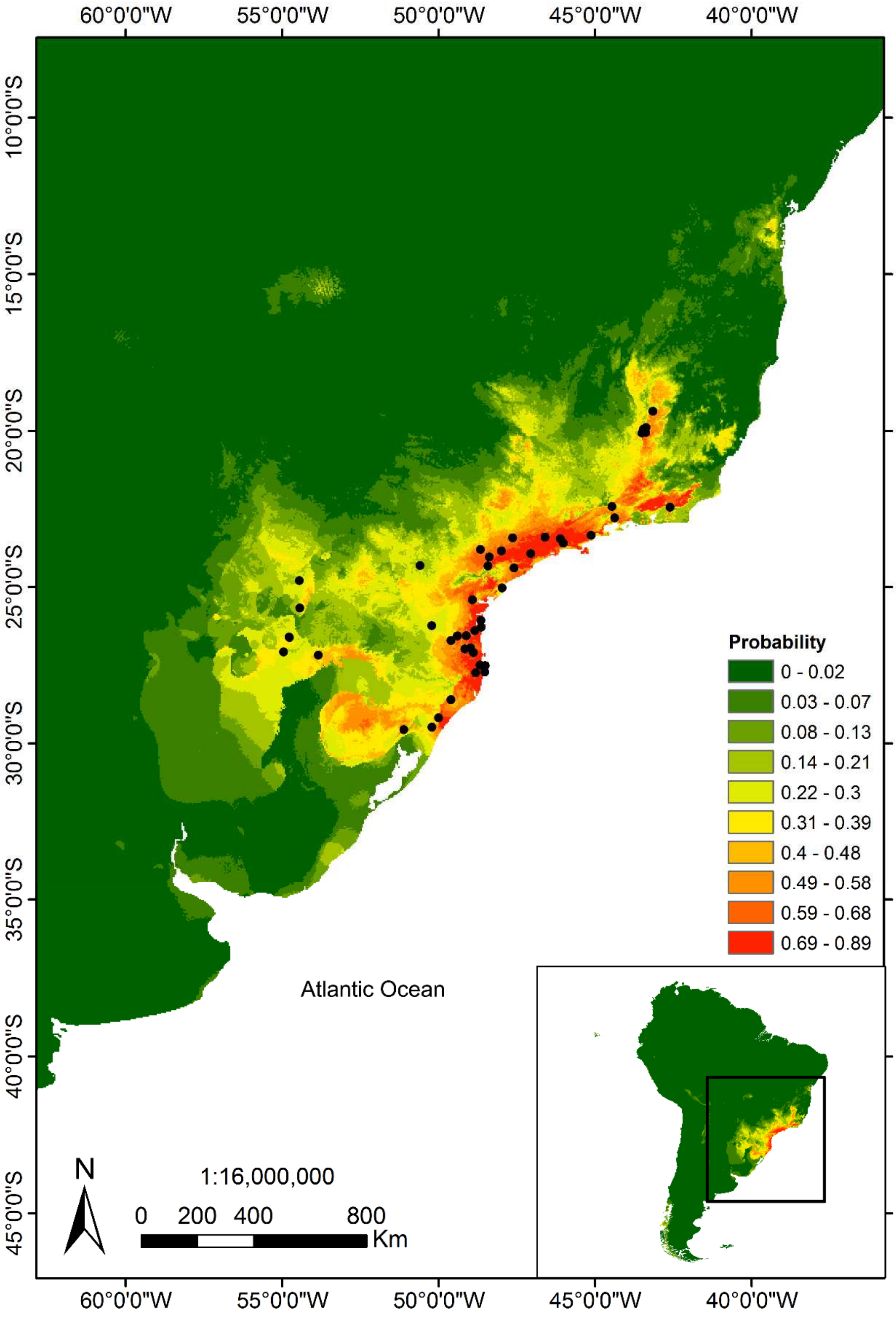

Fig. 6. Prediction model of species distribution for *J. pictipes*, AUC = 0.968. Black dots are localities of occurrence.

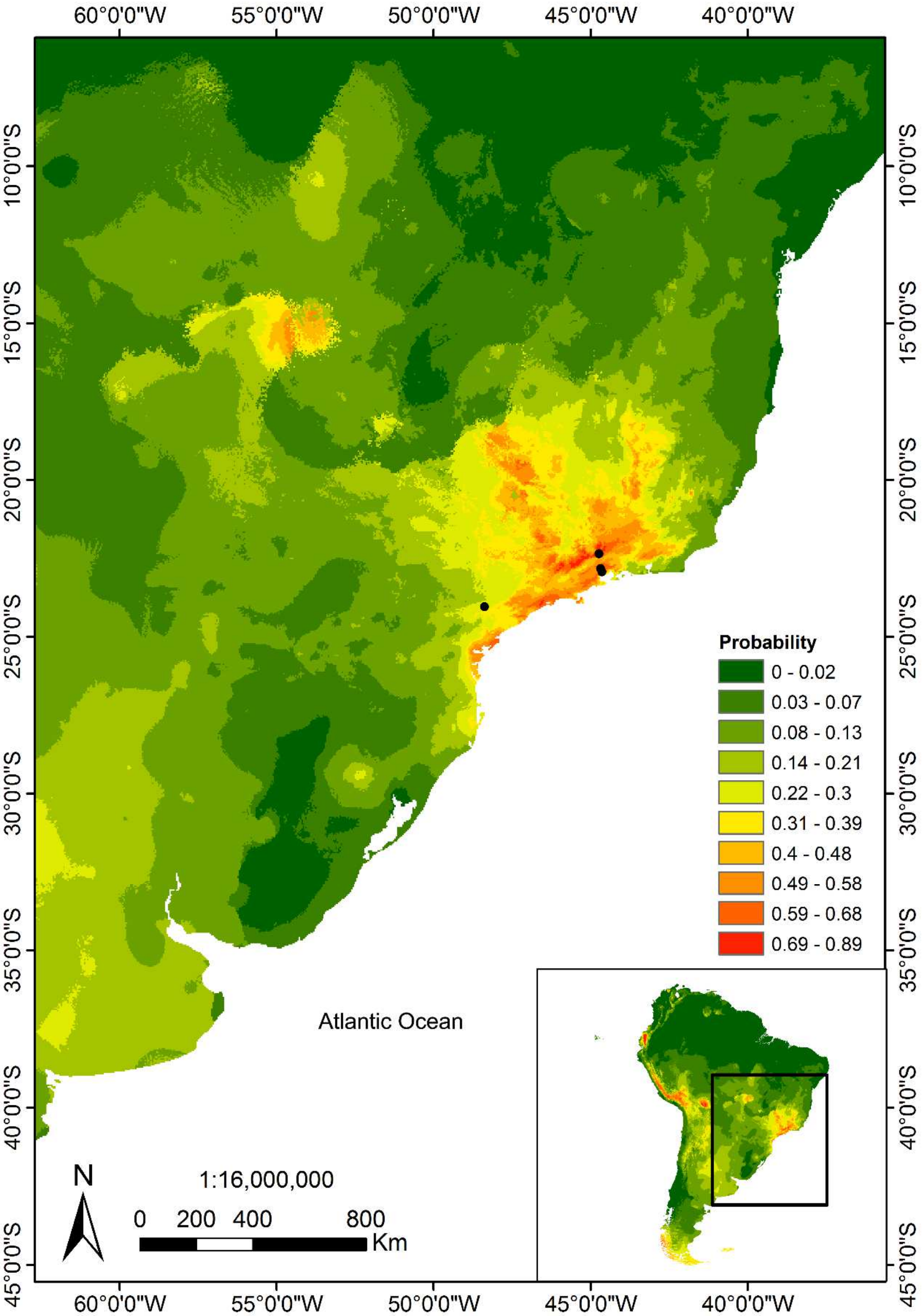

Fig. 7. Prediction model of species distribution for *J. rimofrons*, AUC = 0.985. Black dots are localities of occurrence.

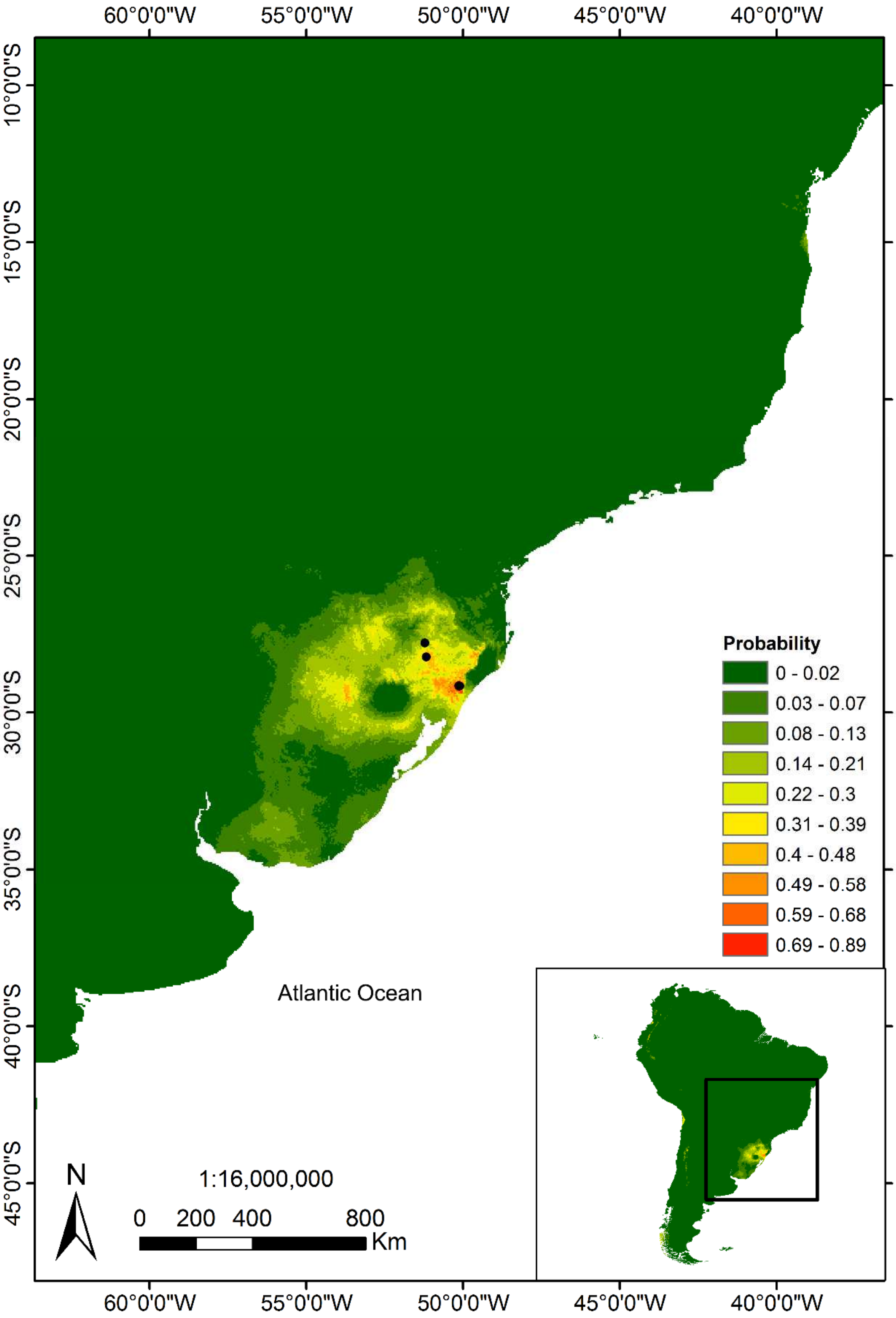

Fig. 8. Prediction model of species distribution for *Juliomys* sp.1, AUC = 0.999. Black dots are localities of occurrence.

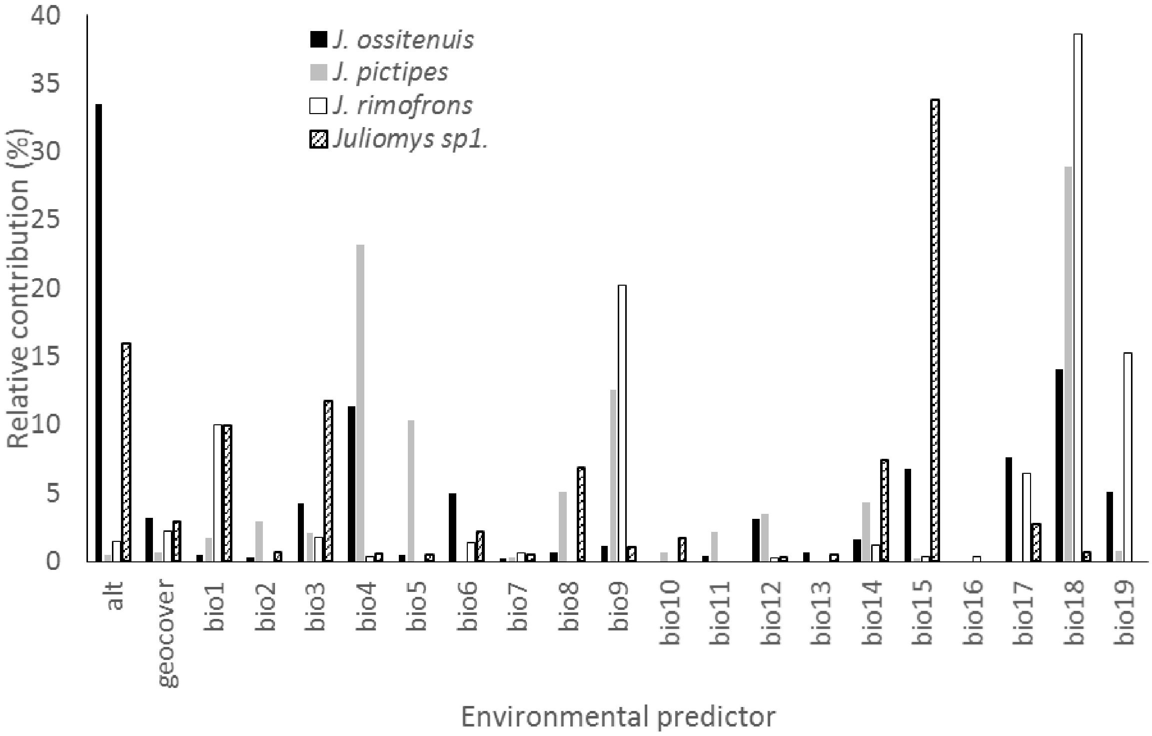

Fig. 9. Environmental variable contribution for the species models. altitude (alt), landscape cover (geocover), annual mean temperature (bio1), mean diurnal temperature range (bio2), isothermality (bio3), temperature seasonality (bio4), max temperature of warmest week (bio5), min temperature of coldest week (bio6), temperature annual range (bio7), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11), annual precipitation (bio12), precipitation of wettest week (bio13), precipitation of driest week (bio14), precipitation seasonality (bio15), precipitation of wettest quarter (bio16), precipitation of driest quarter (bio17), precipitation of warmest quarter (bio18), precipitation of coldest quarter (bio19).

Discussion

The use of morphometric analyses associated with the discriminant function analysis can be a very important a tool for the classification of specimens, mainly if it is carefully used in reduced sample size with relevant diagnostic characters (Kovarovic et al. 2011, Straus 2010). Based on this methodology we were able to identify most of the specimens of the total sample of *Juliomys* deposited in scientific collections and improved the models of the geographic distribution for four species of this genus and stablish more realistic distribution limits. The quantitative predictive methods of distribution of species are an important apparatus for understanding niche held species and their conservation (Peterson & Robins 2003, Anderson & Martínez-Meyer 2004, Kumar & Stohlgren 2009). It can also be a useful tool for protected areas delimitation and species habitat preferences (Sánchez-Cordero 2005). Our final sample was built from an extensive sampling and identification effort. The compilation of a variety of markers provides good support to taxonomic identification. The four living species of *Juliomys* share most of the characteristics, both external and cranial. The carotid arterial supply proved to be an important diagnostic character for *J. pictipes* (Costa et al. 2007). The species *Juliomys* sp.1, *J. ossitenuis* and *J. rimofrons* share the basal carotid arterial supply Type I (Voss 1988). Differently, *J. pictipes* presents the Type II (Voss 1988) differing from Type I mainly in the absence of supraorbital branch of the stapedial artery. Some individuals (*n* = 6) presented some confounding marking on alisphenoid, but with the analysis of the bullae region was possible to ensure the diagnosis.

The generated potential distribution models for *Juliomys* is consistent with previous distribution information and ecological information (Pavan and Leite 2011, González et al. 2015), which suggested that the four species were highly linked to the forest formations of the Atlantic Forest biome. The estimated total range for *J. pictipes* is 437,830.88 km² and for *J. rimofrons* 296.44 km², both linked to forest habitats (Amori et al. 2013), while the predictive models (Figs. 7-8) present a broader scenario. The species *J. rimofrons* (Fig. 7) shows the wider predicted distribution. However, with the area with high probability of occurrence (> 0.49%) confined to southeastern of Brazil (see González 2015). The predicted distribution of *J. pictipes* (Fig. 6) indicates a consistent link to the coastal Atlantic Forest formation, but southern with an extension to the west, congruent to Atlantic Forest domain. The predicted distribution of *J. ossitenuis* (Fig. 5) indicates a vast area of occupation from the higher eastern portion of South America to the countryside. It also suggests a disjunction in the distribution at the eastern slope of the Andes and the southernmost of the continent. As we expected, the predicted distribution of *Juliomys* sp.1 indicates a restricted area in the Araucarian Forest formation in southern Brazil (Fig. 8). The authors Pavan & Leite (2011) discussed a distribution gap at the Araucaria Forest that we have carried out.

In general, the distribution of the *Juliomys* species is linked to factors that shape the forested areas of the Atlantic Forest biome, such as altitude and summer rain (Fig. 9). But the distribution of the different species appears to be distinct. For *J. ossitenuis*, altitude appears to be an important factor for its distribution (Fig. 5 and 9). We observed that predictors related to altitude and the summer rainy season tended to have the largest effects to this species. The original information of Costa et al. (2007) described the taxon as related to semi-deciduous forests above 800 meters of altitude. New records (Aguieiras et al. 2013, Grazzini G et al. 2015, Christoff et al. submitted. chapter 1) at southern localities resemble this information. We also identified as *J. ossitenuis* the specimen UFSM 446 (Appendix I) unidentified by Lima et al. 2010 that Pavan & Leite 2011 comments. On the other hand, *J. pictipes* is more related to coastal lowlands (Cherem 2005, Cerboncini et al. 2014; Fig. 6). This is probably the most abundant species in the genus, but it is rare in high altitudes. The species *J. rimofrons* and *Juliomys* sp.1 presented the most restricted predicted geographical distributions (Figs. 8 and 9). Very little is known about *J. rimofrons* habitat preferences. The species appears to be restricted to a high-altitude northern portion of the Atlantic Forest (Pavan & Leite 2011, Fonseca et al. 2013). Some environmentally fitted areas appear as predicted disjunction of the distribution areas, near to the northwest Andeans slopes. The species *Juliomys* sp.1 have also few recognized specimens and its distribution is, apparently, even more restricted (Fig. 8), it is related to small areas in the Araucaria Forest, southern Brazil (Christoff et al. under review, chapter 1).

The association between species occurrence and environmental variable is crucial in modelling but is not a direct outcome. The factors that determine the geographical distribution of the species are summarized by Hirzel & Lay (2008): local environment, interspecific interactions, and accessibility. Climatic variables, especially temperature, are key factors to species' distribution, where the response of fauna is partly indirect through its correlation with vegetation (Guisan & Zimmermann 2000, Hirzel & Lay 2008). Also, the identification of a scale to explain the presence of a species is not consensual (see Jorgensen 2004, Turner 2005). The floristic formations, shaped mainly by climate and its containing resources may be the key to colonization and immigration of forest-related small mammals. As the Atlantic Forest presents several modifications throughout its distribution (SOS Mata Atlântica 2013), species may follow these patterns. Furthermore, distribution modelling do not account interactions as competitive exclusion, and the ability of species to disperse (Guillera-Arroita et al. 2015). The occurrence of more than one species of *Juliomys* in nearby areas has been related, but sympatry or syntopy were shortly discussed (Pavan and Leite 2011, Grazzini G et al. 2015). Many of these factors, besides environmental ones, may be related to species distribution. The areas of absences in the distribution may be due to simply a lack of sampling or low detectability of the species (Lobo et al., 2007). Due to its smaller ratio of occurrence, rare or geographically restricted species (as *Juliomys*) are usually better predicted in models that use pseudo-absences (Lobo et al. 2007). Ecological processes can not be neglected, the biology and evolutionary history of species must be observed.

Historically, many factors and events may have modelled the species distribution on the Neotropics, as the fauna associated to forest environments as the Atlantic Forest (Carnaval & Moritz 2008, Martins 2011, Rocha et al 2015). In this sense, the results also suggest a potential area for *J. pictipes*, *J. ossitenuis*, and *J. rimofrons* settlement in regions close to the Andes. Some phylogenetic reconstructions based on molecular markers as IRBP and Cytochrome *b* (see D'Elía 2003, Parada et al. 2013) suggested many times *Juliomys* as closely related to a number of Andean Sigmodontinae taxa as *Irenomys* and *Neotomys* (D'Elía 2003, Martínez et al. 2012, Parada et al. 2013). However, the *Juliomys* four extant species are indigenous to the Atlantic Forest (González 2015). Nevertheless, evolutionary process, speciation, and distribution of Sigmodontinae in the Neotropics are a long term discussion (e.g. Herskovitz 1955, Reig 1984, Reig 1987, Prado and Percequillo 2013, Prado et al. 2015, Leite et al. 2016). An alternative approach to estimate the incomplete data of distribution and to understand the genetic diversity partitioning within and between species is the spatial modelling compared to the phylogeographic patterns (Hugall et al., 2002). The search for species evolutionary information, distribution, and ecology is essential to conservation especially in high diverse habitats.

Habitat fragmentation and defaunation in Atlantic Forest is a concern, collapsing the ecological processes. This biome is a biodiversity hotspot, holding more than 261 mammal species where 73 are endemic (Myers 2000). Many of the species are under threat of extinction, including *Juliomys*. The conservation status in IUCN (Bonvicino and Geise 2008) lists *J. rimofrons* as “Vulnerable”: “Because it is known only from three isolated populations, and although these relictual populations are all protected there is increasing threat of effects of isolation and small populations due to its rarity. Its total area of occupancy is less than 300 km², further research is necessary on this species. […] This is a very rare species [...]”. The species *J. pictipes* appears in IUCN as “Least Concern”. In Paraguay, SEAM (2015) does not list any species of genus *Juliomys* as endangered. In Argentina (Ojeda et al. 2012) lists *J. pictipes* as “Vulnerable”: “Little-known species, with four record localities for the province of Misiones. Described in 1933, its presence in Misiones Province was return to documenting nearly eight decades later. Assuming a fragmented distribution and apparent restriction to primary forest, a precautionary approach is assumed”. In the Brazilian list of threatened species (MMA 2014) *Juliomys* is not listed in any category. The regional lists of threatened species of Rio Grande do Sul Estate (SEMA 2014), Santa Catarina Estate (CONSEMA/SC 2011), Paraná (Tossulino et al., 2006), Rio de Janeiro Estate (SEA 2000), Espírito Santo Estate (SEAMA 2005), and Minas Gerais Estate (COPAM 2010) did not list any species of genus *Juliomys* as endangered. The threatened species list of São Paulo Estate (Bressan et al. 2009) classify *J. pictipes* as “Least Concern” and *J. ossitenuis* as “Data deficient”.

As rodents may be important actors in forest sustenance (Galetti et al. 2015), both flora and fauna are threatened due to anthropization. Extensive museum collection reviews, deep anatomical and morphometric analyses provide solid taxonomic information to species diagnosis and its correct use in conservation. Mainly due to the new species *Juliomys* sp.1 (Christoff et al. under review, chapter 1), which occurs in a very restrict area, is endemic to a threatened habitat in a Neotropical biome, reflects the lack of knowledge on small mammals richness in a hotspot and the importance of scientific collections in order to reveal biodiversity. The predictive distribution modeling is a valuable tool to reveal the “hidden” diversity in habitats like these and to guide inherent conservation and management actions (Newbold 2010).

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Appendix 1.

Gazetteer of collecting localities and specimens examined. All localities listed are from the voucher specimens analyzed. Localities are listed from north to south, followed by specific locations, latitude and longitude (south and west, respectively, in negative decimal degrees), and elevation in meters, when available. Sex and age class, when available, follows the museum acronyms). Specimens underlined compose the sample RM (individuals with reliable markers).

***Juliomys ossitenuis*.** *Espírito Santo*: Castelo: **1.** Parque Estadual do Forno Grande, -20.52 -41.00, 1200-2039 m (MBML 2607 ♀A); Dores do Rio Preto: **2.** Casa Queimada; Parque Nacional do Caparaó, -20.46 -41.81, 2079 m (MBML 2784 ♂A); Macieira: **3.** Parque Nacional do Caparaó, -20.48 -41.83, 1788 m (MBML 2783 ♂A). *Minas Gerais*: Fervedouro: **4.** Fazenda Neblina, Parque Estadual da Serra do Brigadeiro, 20 km W Fervedouro, -20.72 -42.48, 1300 m (type locality, MN 69752 ♀A, MN69753 ♀A, UFMG 3174 ♂A, MZUFV 627); Passa Quatro: **5.** Fazenda do Itaguaré, 16 km SW Passa Quatro, -22.47 -45.08, 1500 m (UFMG 3173 ♀A). *São Paulo*: Bananal: **6.** Estação Ecológica do Bananal, -22.80 -44.37, 1119-1164 m (ESALQ-USP 33736 ♂A, ESALQ-USP 33738 ♀A, ESALQ-USP 33739 ♀A, ESALQ-USP 33747♂A, ESALQ-USP EEB 1010 ♀A, ESALQ-USP EEB 802 ♂A, ESALQ-USP EEB 848 ♀A, ESALQ-USP EEB 333 ♂A, ESALQ-USP EEB 837 ♀A, ESALQ-USP EEB 057 ♂A, ESALQ-USP EEB 143 ♂A, ESALQ-USP EEB 247 ♂A, ESALQ-USP EEB 015 ♀A, ESALQ-USP EEB 077 ♀A, ESALQ-USP EEB 204 ♀A, ESALQ-USP EEB 124 ♂A, ESALQ-USP EEB 034 ♀A, ESALQ-USP EEB 184 ♀A, ESALQ-USP EEB 244 ♂A, ESALQ-USP EEB 812 ♂A); Cotia: **7.** Sítio Até Que Enfim, Caucaia do Alto, -23.68 -47.03, 900 m (MZUSP 33170 ♀A, MZUSP 33171 ♂A); **8.** Mina Limeira, -24.17 -48.33, 800-1000 m (MZUSP 32276 A). *Paraná*: São Mateus do Sul: **9.** Petrobrás, -25.84 -50.41 (UFSC 4812 ♂A); Piraquara: **10.** Mananciais da Serra, -25.44 -49.02 (UFSM 483 ♂A); **11.** Araucária, -25.41, -48.91 (DZUP 536 A, DZUP 538 A). *Santa Catarina*: Três Barras: **12.** FLONA, -26.24 -50.21, 800 m (UFSC 950 ♂A); **13.** Passoa Maia, PCH Passos Maia, -26.71 -51.9, 1000 m (UFSC 5010 ♂A); Dr. Pedrinho: **14.** Rebio Estadual Sassafrás, -26.42 -49.35, 1000 m (CZFURB 18593 ♂A). *Rio Grande do Sul*: São Francisco de Paula: **15.** Centro de Pesquisas e Conservação da Natureza Pró-Mata, -29.21 -50.14, 900 m (MCNU 1461 ♂A, MCNU 1977 ♂A, MCNU 2988 ♂A, MCNU 3276 ♀A); Pinhal da Serra: **16.** Barra Grande, -27.78 -51.19 (MCNU AC 1388 A, MCNU AC 1389 A); Santa Maria: **17.** Morro do Elefante, -29.40 -53.43 (UFSM 446).

Juliomys pictipes. *Espírito Santo*: Cariacica: **18.** Reserva Biológica Duas Bocas, Alto Alegre, -20.28 -40.51, 550 m (UFES 556 ♂J, UFES 557 ♀A, UFES 2267 ♂A). *Minas Gerais*: Santa Bárbara: **19.** Estação de Pesquisa e Desenvolvimento Ambiental de Peti, -19.9 -43.37, 630-806 m (UFMG 3161 ♂A, UFMG 3162 ♀, UFMG 3163 ♂A, UFMG 3164 ♂A); **20.** Caraça: Reserva Particular do Patrimônio Natural do Caraça, 25 km SW Santa Bárbara, -20.08 -43.5, 1300 m (MN 69764, UFMG 3159 ♀A, UFMG 3160 ♀A); Itabira: **21.** No specific locality provided -19.38 -43.15 (MCN-M 2195 ♀A, MCN-M 2439 ♀A, MCN-M 2929 ♀J, MCN-M 2989 A); Catas Altas: **22.** No specific locality provided -20.14 -49.95 (MCN-M 2199 ♂A, MCN-M 2933 ♀, MCN-M 3022 ♂A). *Rio de Janeiro*: Cachoeiras de Macacu: **23.** Estação Ecológica de Paraíso, -22.31 -42.51, 87 m (MN 79853 ♂A); Angra dos Reis: **24.** Mata do Mamede, -23 -44.32 (MN 69765 ♀A). *São Paulo*: Bananal: **25.** Estação Ecológica do Bananal, -22.80 -44.37, 1119-1164 m (MZUSP-ESLAQ 036 ♀A, MZUSP-ESLAQ 885 ♂A, MZUSP-ESLAQ JRP 25 A);

São Luís do Paraitinga: **26.** Fragmento G4, -23.22 -45.31, 900 m (UFES 2268 ♂A, UFES 2432 ♂A, UFES 2432 ♂A); Sorocaba: **27.** Floresta Nacional de Ipanema, 20 km NW -23.44 -47.63, 701 m (UFMG 3165 ♂A, UFMG 3166 ♂J, UFMG 3167 ♂A, UFMG 3168 ♂A, UFMG 3169 ♂J, UFMG 3170 ♀A UFMG 3171 ♂A UFMG 3172 ♂A); Mogi das Cruzes: **28.** Parque Natural Municipal da Serra do Itapety, -23.47 -46.15, 807-1141 m (MN uncatalogued 61 ♀A); **29.** Serra da Cantareira -23.39 -46.57 (MZUSP UNIBAN 162 A, MZUSP UNIBAN 410 A, MZUSP UNIBAN 593 A, MZUSP UNIBAN 596 A, MZUSP UNIBAN 620 A, MZUSP UNIBAN 673 A, MZUSP UNIBAN 678 A, MZUSP UNIBAN 693 A, MZUSP UNIBAN 758 A. **30.** Biritiba -23.62 -46.02 (MZUSP UNIBAN 2091 A). Cotia: **31.** Reserva Florestal do Morro Grande, Caucaia do Alto -23.68 -46.96, 800-1000 m (MZUSP 32649 A); Buri: **32.** No specific locality provided, -23.81 -48.70, 666 m (MZUSP 33132 ♂); **33.** Fazenda Intervales, -24.33 -48.42, 700 m (MN 60570, MZUSP 29393 ♀A); Sete Barras: **34.** Parque Estadual Carlos Botelho, -24.4 -47.59, 700 m (MZUSP 32818 A, MZUSP 32189 A, MZUSP 32824 ♂A, MZUSP 32825 ♀A, MZUSP 32826 ♀A, MZUSP 32827 ♂A, MZUSP 32828 ♀A, MZUSP 32855 ♂A); Juquitiba: **35.** No specific locality provided, -23.55 -47.98 (MZUSP 33103 ♂J); Cananéia: **36.** -25.02 -47.96 (UFES 2269 ♂A). *Paraná*: Foz do Iguaçu: Parque Nacional Iguaçu -25.62 -54.41 (UFSM 515 ♂A, UFSM 517 A, UFSM 518 A). Telêmaco Borba: **37.** Fazenda Monte Alegre, -24.2 -50.55, 885 m (MN 68347 ♀J); **38.** Morretes -25.54, -49.46 (DZUP 393 A, DZUP 394 A, DZUP 395 A, DZUP 498 A, DZUP 499 A, DZUP 502 A). *Santa Catarina*: Santo Amaro da Imperatriz: **39.** Parque Estadual da Serra do Tabuleiro, -27.74 -48.81, 400-500 m (UFSC 652 ♂A, UFSC 862 ♂A, UFSC 863 ♂A, UFSC 864 ♂A, UFSC 670 A, UFSC 4461 ♀A); Itapoá: **40.** Reserva Volta Velha, -26.07 -48.64, 20 m (UFSC 2960 ♀A, UFSC 2961 ♀A, UFSC 2962 ♂A, UFSC 2963 ♂J, UFSC 2964 ♂A, UFSC 2965 ♀A,

UFSC 2966 ♀A, UFSC 3228 ♂A, UFSC 3229 ♀A, UFSC 3230 ♀A, UFSC 3253 ♀A, UFSC 3254 ♀A, UFSC 3255 ♀A, UFSC 4484 A, UFSC 4484 A); Indaial: **41.** Parque Nacional da Serra do Itajaí, Vale do Espingarda, -26.56 -49.11, 600 m (CZFURB 5372, CZFURB 9423 ♀A); **42.** Parque Nacional da Serra do Itajaí, Mono, -26.57 -49.4 (CZFURB 9622 ♂A, CZFURB 9623 ♂A, CZFURB 9624 ♂A, CZFURB 9625 ♂A, CZFURB 9632 ♀A, CZFURB 9667 ♂A, CZFURB 9669 ♀A, CZFURB 9757 ♀A, CZFURB 9834 ♂A, CZFURB 9835 ♂A, CZFURB 9837 ♂A, CZFURB 9922 ♀A, CZFURB 9966 ♂A, CZFURB 12037 ♂A, CZFURB 12590 A, CZFURB 12603 ♂A, CZFURB 12587 ♂A, CZFURB 15091 ♂A); Gaspar: **92.** RPPN Figueira Branca, -26.99 -49.00 (CZFURB 9765 A). Blumenau: **43.** Terceira Vargem, -27.3 -49.5, 300 m (CZFURB 9706 A, CZFURB 9770 ♂A, CZFURB 9771 ♂A, CZFURB 9775 ♀A, CZFURB 12243 A); Biguaçú: **94.** No specific locality provided, -27.49 -48.67 (CZFURB 20661 ♂A); Dr. Pedrinho: **21.** Rebio Estadual Sassafrás, -26.42 -49.35, 1000 m (CZFURB 18597 ♂A, CZFURB 18599 ♂A, CZFURB 18674 ♀A). Siderópolis: **44.** Barragem Rio São Bento, -28.60 -49.60, 300 m (UFSC 4962 ♀A, UFSC 5253 A, UFSC 5254 A, UFSC 5255 A, UFSC 5256 A); Três Barras: **45.** Pardo, -26.24 -50.21, 800 m (UFSC 3711 ♂A); Abdon Batista: **46.** Hydroeletric Plant Garibaldi, -27.62 -50.99 (CZFURB 20504 ♂A). São Francisco do Sul: **47.** Rocio Grande, -26.29 -48.64, 20 m (UFSC 3124 ♀A); Florianópolis: **48.** Ilha de Santa Catarina, Ratones, -27.52 -48.50, 250 m (UFSC 3454 ♂A , UFSC 3455 ♂A); **49.** Ilha de Santa Catarina, Lagoa do Peri, -27.72 -48.53, 10 m (UFSC 905 ♂A); Praia Grande: **50.** SC450, -29. 18 -49.99, 600 m (UFSC 4932 ♂A); Brusque: **51.** Nova Brasília, -27.10 -48.88, 100 m (UFSC 4669 ♂A, UFSC 5259 ♂A); Joinville: **52.** Salvador, -26.40 -48.84, 30 m (UFSC 4486 ♂A). *Rio Grande Do Sul*: Derrubadas: **53.** Parque Estadual do Turvo, -27.20 -53.88, 100-400 m

(UFSM 598 ♀A); Dois Irmãos: **54.** No specific locality provided, -29.56 -51.10 (MCNU 4307 ♀A).

***Juliomys rimofrons*.** *Minas Gerais*: Itamonte: **55.** Brejo da Lapa, -22.21 -44.44, 2000 m (type locality; MN 46703 ♂A, MN 61646 ♂A, MN 61647 ♀A). *Rio de Janeiro*: Paraty: **56.** Parque Nacional da Serra da Bocaina, -23.12 -44.49 (MN 77793 ♂A). *São Paulo*: São José do Barreiro: **57.** Parque Nacional Serra da Bocaina, -22.50 -44.41, 1700 m (MN 76263 A); Capão Bonito: **58.** Parque Estadual Intervales, -24.16 -48.18, 800 m (MN 60571 ♂).

***Juliomys* sp.1.** *Rio Grande do Sul*: Cambará do Sul: **59.** Parque Nacional dos Aparados da Serra, -29.16 -50.10, 900 m (MCNU 464 ♂A, MCNU 868 ♂A, MCNU 689 ♂A, MCNU 870 ♂, MCNU 3304 ♀A); Muitos Capões: **60.** Estação Ecológica Aracuri-Esmeralda, -29.22 -51.16 (MCNU 2100 ♂A); Pinhal da Serra: **61.** Hydroeletric plant Barra Grande, -27.78 -51.19 (AC 1387 A).

***Juliomys* sp.** *Espírito Santo*: Jetibá: **62.** -20.03 -40.74 (AC 932 ♀A); Castelo: **63.** -20.60 -41.21 (UFES 1475 ♂). *Rio de Janeiro*: **64.** Fazenda Boa Fé, -22.43 -42.98, 902 m (MN 62182); Resende: **65.** Visconde de Mauá, -22.40 -44.52 (MN 71882 ♀A). *Minas Gerais*: Fervedouro: **66.** Fazenda Neblina, Parque Estadual da Serra do Brigadeiro, 20 km W Fervedouro, -20.72 -42.48, 1300 m (type locality, MN MZUFV 679 ♂A, MN MZUFV 683, MN MZUFB 608 ♂). *Paraná*: Telêmaco Borba: **67.** -24.32 -50.59 (68336 ♀A). *Santa Catarina*: Indaial: **68.** Parque Nacional da Serra do Itajaí, Vale do

Espingarda, -26.56 -49.11, 600 m (CZFURB 9735); Vargem: **69.** UHE São Roque -27.49 -50.81 (UFSC 5075 ♀A); Blumenau: **70.** Terceira Vargem, -27.3 -49.5, 300 m (CZFURB 9191 ♂A). *Rio Grande do Sul*: Pinhal da Serra: **71.** Hydroeletric plant Barra Grande, -27.78 -51.19 (AC 1387 A); Derrubadas: **72.** Parque Estadual do Turvo, -27.20 -53.88, 100-400 m (UFSM 599 ♀J); **73.** Floresta Nacional de São Francisco de Paula, -29.42 -50.39 (MCNU 712 A); São Francisco de Paula: **74.** Centro de Pesquisas e Conservação da Natureza Pró-Mata, -29.21 -50.14, 900 m (MCNU 3303 ♀A, MCNU 3305 ♀A). *Unknown locality* (MCN-M 1471, MCN-M 2161, MCN-M 2842, URI 727).

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7. CAPÍTULO III

MONOPHYLETIC EVIDENCE FOR THE GENUS *JULIOMYS* (RODENTIA, CRICETIDAE, SIGMODONTINAE)

Em preparação para submissão ao periódico *Mammal Research* – Mammal Research Institute, Polish Academy of Sciences, editora Springer.

Monophyletic evidence for the genus *Juliomys* (Rodentia, Cricetidae, Sigmodontinae)

Paulo S. Tomasi[1], Alexandre U. Christoff[2], Vitor H. Valiati[3], Mário J. Müller[3], Larissa R. Oliveira[1]

1. Laboratory of Mammalian Ecology, University of Vale do Rio dos Sinos - UNISINOS, Av. Unisinos 950, São Leopoldo, Rio Grande do Sul, Brazil

2. Departament of Biology, Natural Science Museum, University Luterana do Brasil - ULBRA, Av. Farroupilha 8001, Canoas, Rio Grande do Sul, Brazil

3. Laboratory of Molecular Biology, University of Vale do Rio dos Sinos - UNISINOS, Av. Unisinos 950, São

Leopoldo, Rio Grande do Sul, Brazil

Corresponding author: Paulo S. Tomasi (paulo.tomasi@gmail.com; +555193523157)

Abstract

The sigmodontine genus *Juliomys* has been recently stablished, and currently there are three recognized living species, and a fourth under description. The phylogenetic position of the genus in the Sigmodontinae tribes is uncertain, figuring as *insertae sedis*. Likewise, the monophyly of its group of species (extant composition) was never evaluated. We assembled a significant molecular data set based with 104 cytochrome *b* sequences of 800-bp covering a lrge number of sigmodontine species. Both Maximum Likelihood and Bayesian analyses strongly supported as monophyletic *Juliomys* clade (*PP* = 1; bootstrap = 100%), including the fourth species under descriptin of *Juliomys* and the three remaining ones. *J. pictipes* presents a different cranial circulation, which is a deep anatomical differentiation, the analysis support a strong relation between the taxon inside the genus. Despite the morphological differences, the group of species apparently forms a single set of taxa.Many efforts have been done to solve the *insertae sedis* issue. In our analysis the sister clade of *Juliomys* is *Rhagomys rufescens*, but weakly supported. The major clade that includes the *Juliomys* species is composed by *Rhagomys*, and *Neomicroxus*, but also is weekly supported. Phylogenetic approaches are essential taxonomic tools that shall guide correct ecological interpretations. A robust taxon sampling, several intrageneric species, employing several molecular markers, must highly improve the accuracy of the inferences on the phylogenetic relationships. This may guide the for coming analysis aiming to understand of the position of *Juliomys* in Sigmodontinae.

Key words Monophyly, cytochrome *b*, tree mice, molecular phylogeny

Introduction

Sigmodontinae is the richest clade of the Cricetidae whitin Rodentia (Musser and Carleton 2005). The Sigmodontinae contain 85 genera and more than 400 species (D'Elía and Pardiñas 2015). This rodents are widely distributed throughout the Neotropical region and occupy a variety of habitats, including forest, grasslands, high mountains, and deserts (Carleton and Musser 1989; Vieira and Monteiro-Filho 2003; Belmar-Lucero et al. 2009). The early studies of this group dates back since more than two centuries, but its diversity and organization are still being discovered (see Weksler et al. 2006; D'Elía et al. 2006, 2007, 2015; Percequillo et al. 2008; Percequillo et al. 2011; Hanson et al. 2015). After all, there are gaps especially in systematics and ecology of many of its members (Brito 2004; Lessa et al. 2014).

The sigmodontine *Juliomys* has been stablished by González (2000), which located *J. pictipes* (Osgood, 1933) originally described as *Wilfredomys* in the new genus. Currently, there are three recognized living species of *Juliomys*: *J. pictipes* (Osgood, 1933), *J. rimofrons* (Oliveira and Bonvicino, 2002) and *J. ossitenuis* (Costa, Pavan, Leite and Fagundes, 2007); and one extinct *J. anoblepas* (Pardiñas and Teta 2011). Recently, a new karyotype (2n = 32, NA = 48) was described by Paresque et al. (2009), suggesting a fourth species that is currently under study and formal description (Christoff et al. under review, see chapter 1). Species of *Juliomys* are small arboreal mice, restricted to the forest formations of Atlantic Forest in Brazil, Argentina and Paraguay (Pavan and Leite 2011; González et al. 2015). In a previous study, Costa et al. (2007) presented a comparative diagnostic table among three species using descriptive external and cranial morphology. Even so, species identification in field can be troublesome, due to the similarity in skull and external morphology within genus and species of *Rhagomys*, *Wilfredomys*, and *Oligoryzomys* (Pavan and Leite 2011). In a general way, *Juliomys'* external morphology is characterized by orangish overall coloration of dorsum, a clear division between the dorsum and ventral portion (always brighter), manus and pes yellowish; tail longer than body, very hairy with a brush at distal portion. The skull presents short rostrum, incisive foramen reaching M1, mesopterigoid fossa penetrating through M3 posterior edges, and absence of supra or postorbitals. An overall characterization of the genus has been recently presented by González et al. (2015). Considering the morphological variation among the *Juliomys* species, there is a lack of information in relation to recognize the genus as monophyletic or polyphyletic. Moreover, some species diagnostic characters may be baffling (Christoff et al. under review). As De Queiroz (2007) stated "diagnosability and monophyly are fundamental for systematists". In such cases, the study of molecular markers is a valuable tool to infer evolutionary hypothesis for the phylogenetic relationships among species (Freeland 2005).

Furthermore, the phylogenetic position of *Juliomys* within Sigmodontinae is still uncertain. Smith and Patton (1999) discussed *Wilfredomys pictipes* (currently considered as belonging to the genus *Juliomys*) under Thomasomyini. However, their results placed this taxon distantly and independently of that group, suggesting that it should be considered another unique lineage. Different authors have since provided other phylogenetic hypothesis based on different approaches, which continuously have changed the position of *Juliomys*. The genus has been recovered as sister group of *Irenomys* (interphotoreceptor retinoid binding protein – IRBP; Weksler 2003) or *Reithrodon* (Cyt *b* and IRBP; D'Elía 2003), and distantly of Thomasomyini. More recently, Martínez et al. (Cyt *b* and IRBP; 2012) considered this genus as *incertae sedis*, as D'Elía (2003), but closely related to an Andean clade that included *Irenomys*, *Euneomys*, and *Neotomys*. Parada et al. (Cyt *b* and IRBP; 2013) similarly recovered an

Andean clade comprising 7 genera – *Andinomys*, *Chinchillula*, *Euneomys*, *Irenomys*, *Juliomys*, *Neotomys*, and *Punomys* –, but in their investigation *Juliomys* and *Chinchillula* emerged as a sister group. The phylogenetic position of *Juliomys* continues to oscillate around Phyllotini genera, as shown by Salazar-Bravo et al. (Cyt *b* and IRBP; 2013). Nevertheless, these authors presented analyses in the same article that place this genus as a sister group of *Wiedomys*, which has a geographic distribution in semiarid habitats of east central Southern America. These investigations indicate that *Juliomys* could be closely related to a number of Andean sigmodontine, although its three extant species are indigenous to the Atlantic Forest. All phylogenetic studies that reconstructed the Sigmodontinae affinities invariably had only specimens of *J. pictipes* representing the entire genus (e.g. D'Elía 2003; Weksler 2003; Martínez; Salazar-Bravo et al. 2013; Carrizo and Catalano 2015). The compilation of D'Elía (2015) discuss it and still treats the *Juliomys* position as an open case. In this sense, the monophyly of the genus *Juliomys* (living species composition) was never evaluated, in order to understand the relationships of its species it will be essential to covering its real diversity in any analysis.

The intrageneric information is basic to major systematics, biological, and ecological inferences. For instance, Amorim (2007) stated: “Previous organismal phylogenies, or at least hypotheses of monophyly of given taxa, should be taken as the basis for the study of distribution patterns”. In this sense, systematics needs: “research projects focused on monophyletic taxa; collections that are broadly; […] support for monography and revisional taxonomy, and continued refinement of theories, methods, and computer algorithms that are focused on phylogenetic patterns” (Wheeler 1995). Our study investigate a huge Sigmodontinae sample (66 genera and 94 species), using a molecular maker cytochrome *b* (cyt *b*) widely used in phylogenetic approaches of this group (Lessa et al. 2014). Therefore, our aim is to test the monophyletic hypothesis of *Juliomys*, utilizing sequences from all taxa described for the genus.

Methods

We analyzed a molecular data set (Appendix I) that included mitochondrial DNA cyt *b* sequences from 94 Sigmodontinae taxa as ingroup, including sequences from 5 *Juliomys pictipes*, 7 *J. ossitenuis*, 1 *J. rimofrons* and 1 *Juliomys* sp.1, and 5 Cricetidae species from other subfamilies as outgroup (available from GenBank - http://ncbi.nlm.nih.gov/genbank).

The phylogenetic reconstructions used the partial sequences of *cyt b* gene from a data set consisted of 104 Operational Taxonomic Units (OTUs) covering 94 Sigmodontinae species and 5 other Cricetidae (Appendix I). We aligned the sequences using the multiple alignment tool ClustalW and edited in MEGA 6 program (Thompson *et al*. 1994). We analyzed the levels of saturation using the software DAMBE (Xia et al. 2003, Xia and Lemey 2009) (Fig. 1). To support the position homology hypothesis, we manually inspected both the amino acids and nucleotide alignments. A final alignment of the 104 sequences was generated containing 1144 sites. We employed jModelTest to choose the nucleotide substitution model using Maximum Likelihood (ML) Akaike information criterion (AIC). The model with the best likelihood value by AIC was general time-reversible (GTR) model with proportion of invariant sites (I) and distributed rates among sites (Γ). We performed the Bayesian phylogenetic inference (BI) using BEAST 2 package (Bouckaert *et al.* 2014). BEAUti software generated the XML input file with the following settings: model of nucleotide substitution GTR + I + Γ4 (I = 0.387, Γ = count range category 4, gamma shape = 0.441) with empirical bases frequencies, clock-relaxed Log Normal model, Yule model, Markov chain Monte Carlo

(MCMC) length 20 million generations with Log every 1,000 steps. We performed four independent runs in BEAST 2 package, with the convergence of MCMC verified in Tracer v1.6 with 10 % of the first generations discarded as burn-in (Rambaut and Drummond 2007). The effective sample sizes (ESS) after all the parameter estimates was above 200. We summarized the remaining trees in the TreeAnnotator software with burn-in percentage of 30%, posterior probability limit of 0.5, target tree type maximum clade credibility and node heights mean. The ML phylogenetic tree was generated using the program RAxML (version 7.0.4, CIPRES webserver (Miller et al. 2010), and graphically displayed using Mega 6. Finally, we edited the trees in the Figtree 1.4.2 software. A final consensus tree is presented, with posterior probability and bootstrap support values.

Results and Discussion

As indicative of normal mtDNA protein coding genes, we found no traces of pseudo genes, numts or stop codons. Additionally, the saturation test presented no substantial positive results (Iss = 0.712, Iss.c = 0.757, *P* = 0.040; Fig.1). Both cyt *b* matrix analysis, ML and Bayesian, strongly supported a monophyletic *Juliomys* group (*PP* = 1; bootstrap = 100%) including the 4 lineages (Fig. 2). The internal formation of the group forged 4 clades, corresponding to the following topological organization: (*J. ossitenuis* (*J. pictipes* (*J. rimofrons*, *Juliomys* sp.1))). The basal divergent clade inside the genus is *J. ossitenuis* (*PP* = 1; bootstrap = 100). Another topology branch shows the species *J. rimofrons* as sister clade of *Juliomys* sp.1, the most genetically related species.

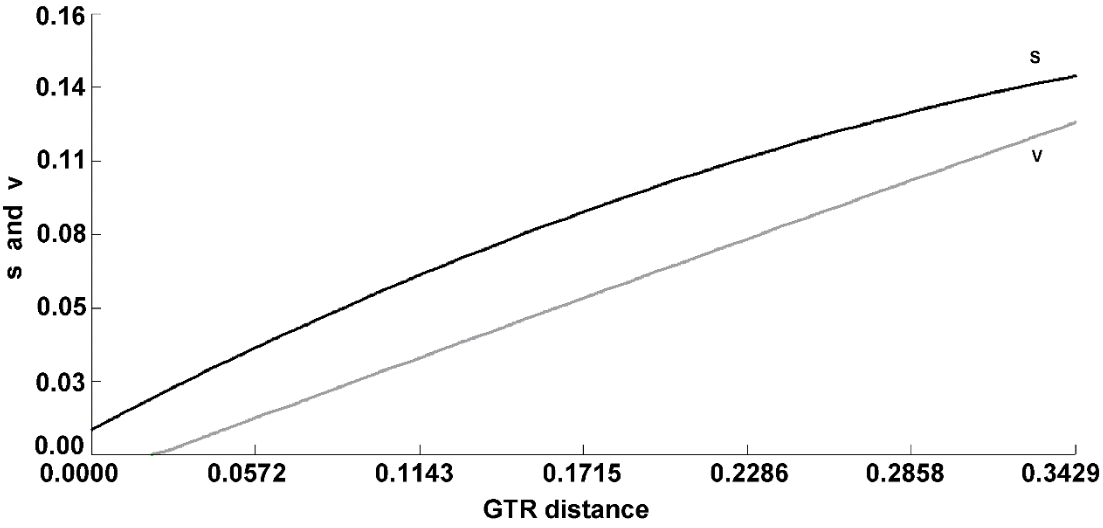

Fig.1. Saturation plot showing the transition (s) and transversion (v) rates plotted against the GTR distances.

The species of *Juliomys* sp.1 and *J. rimofrons* are highly different in terms of numbers of chromosomes and fundamental numbers (*Juliomys* sp.1 2n = 32, FN = 48 and *J. rimofrons* 2n = 20, FN = 34), and also morphologically (both external morphology and skull anatomy). Meanwhile, they are considered allopatric with their known geographically limits very distant from each other (Costa et al. 2007; Paresque et al. 2009; Christoff et al. under review). However, they are sister clades in the present molecular cyt *b* reconstruction as in Christoff et al. (under review), although *Juliomys* sp.1 is morphologically much more related to *J. ossitenuis*. Our analyses also corroborated the results found by Costa et al. (2007), which also suggested that *J. ossitenuis* (2n=20, FN = 36) as a basal clade in their slight phylogenetic reconstruction using cyt *b* analyses. On the other hand, *J. pictipes* emerged as an intermediate clade and, curiously, it presents a different cranial circulation pattern (distinctive carotid circulation) (see Costa et al. 2007; Christoff et al. under review). Even with such anatomical discrepancy, the analysis support a strong relation (*PP* = 1; bootstrap = 100) between the taxon inside the genus.

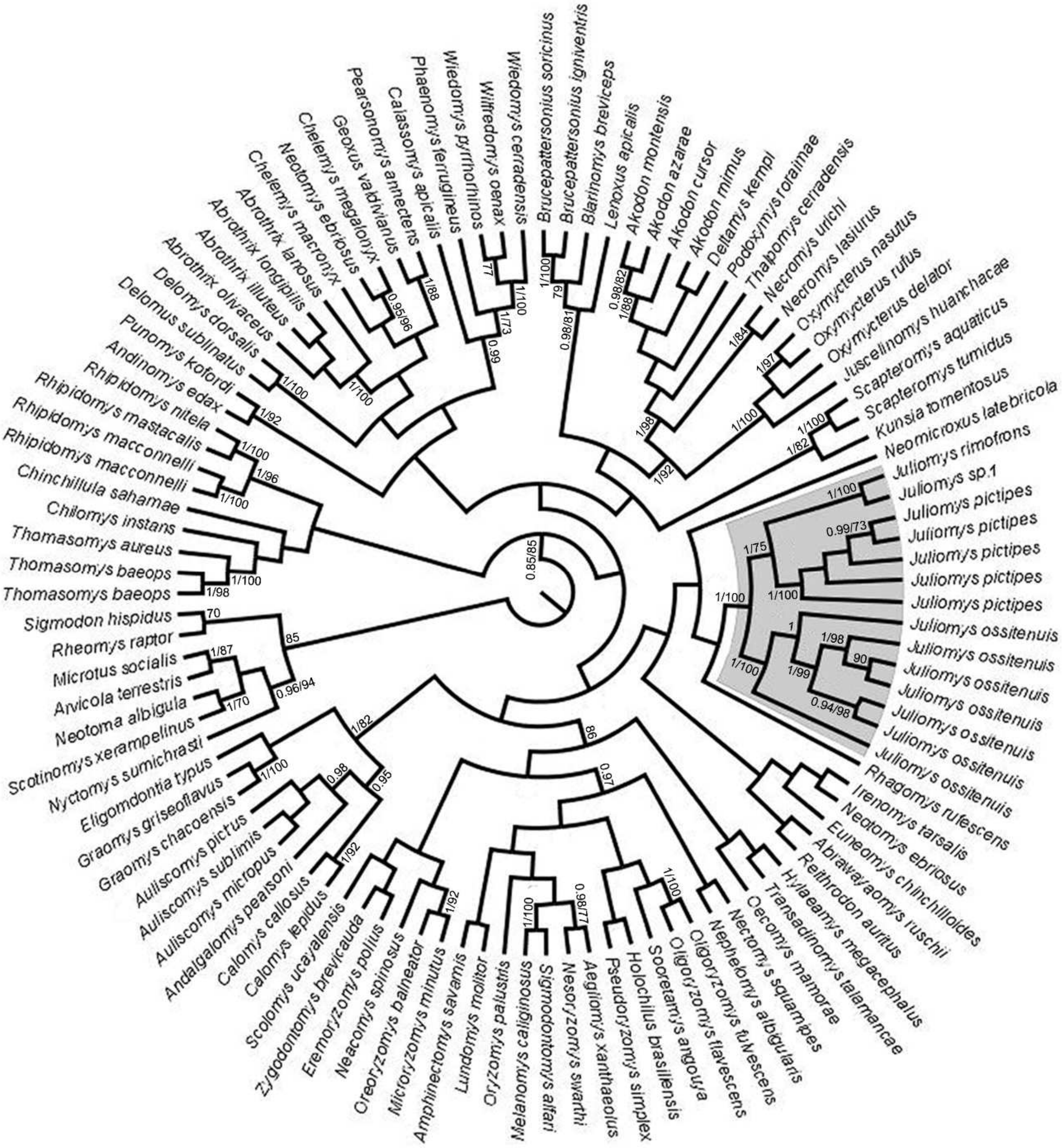

Fig. 2 Phylogenetic relationships among Sigmodontinae species based in cyt *b* gene recovered with BI (>0.95 support values indicated) and ML (>70% support values indicated) methodologies. *Juliomys* group is highlighted in grey. Final branches are species units.

It could be expected that *J. pictipes* should agree with the morphology, especially because of the type of cranial circulation, and stand even in a paraphyletic clade. As shared apomorphies are evidences of unique common ancestry (monophyly), such a profound variation may indicate different ancestors (Amorim 2002). The species *Juliomys* sp.1, *J. ossitenuis*, and *J. rimofrons* share the basal carotid arterial supply Type I (Voss 1988). On the other hand, *J. pictipes* presents the Type II (Voss 1988), differing from Type I mainly in the absence of the supraorbital branch of the stapedial artery. In dorsal view, the bullae region also diverge, where *J. pictipes* presents smaller carotid canal, smaller stapedial foramen, larger posterior opening of the alisphenoid canal, and the sphenofrontal foramen is absent (Fig. 3) (see Bugge 1970; Costa et al. 2007; Christoff et al. under review, chapter 1). D’Elía (2015) provides a valuable morphological key to the genera of Sigmodontinae *insertae sedis*, but the author makes a mistake when presenting to *Juliomys* “carotid circulation pattern Type II or III (*sensu* Voss 1988)”. The cariotidic circulation system vary in other sigmodontine genus (polimorphic character), as the Oryzomini *Oecomys* and *Zygmodontomys* (Weksler 2006). In these examples, *Z. cherriei* presents the pattern I and *Z. brevicauda* presents the pattern III. For *Oecomys*, the species *O. bicolor*, *O. catherinae*, and *O. trinitatis* presents the pattern I, while *O. conocolor* and *O. mamorae* presents the pattern III. Contrawise in Phyllotini we, apparently, found no polimorphy in this character (Steppan 1995). Several anatomical traits have also been used to the classification of Sigmodontinae, separating major groups. For example, the zygomatic plate, bony palate, suspensory process of the squamosal bone, and dental morphology (e.g. Weksler 2006; D’Elía and Pardiñas 2015). An emended morphological diagnosis for *Juliomys* is provided by Pavan and Leite (2011) and a review by González et al. (2015).

Morphological traits shall be useful on many systematics approaches. “Phylogenetic analyses strongly suggest that several morphological state characters have evolved more than once within the sigmodontine radiation, while others may be symplesiomorphies” (D’Elía and Pardiñas 2015). In relation to the discussion on the carotid circulation patter, it can be a case of homoplasy.

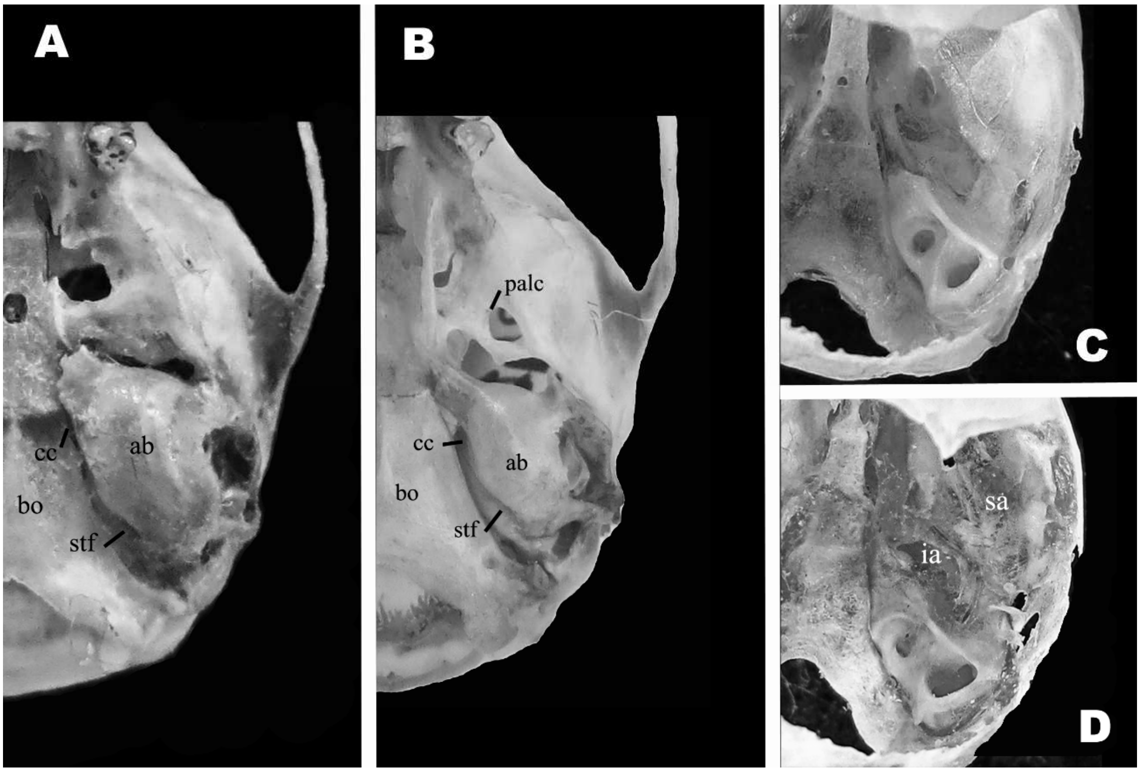

Fig. 3. Illustrative details of *Juliomys ossitenuis* DZUP 536 (A, D) and *J. pictipes* DZUP 394 (B, C), in ventral view (A-B) and inside braincase (C-D). ab, auditory bulla; bo, basiocipital; cc, carotid canal; ia, infraorbital branch of stapedial arthery; palc, posterior opening of the alisphenoid canal; sa, supraorbital branch of stapedial arthery; stf, stapedial foramen. Figures not scaled. Photos by Paulo S. Tomasi. Pictures not scaled.

Sampling improvement is one of the most effective instruments to increase phylogenetic reconstructions accuracy (Heath et al. 2008). We provided a vast matrix covering 66 of the 85 sigmodontine genera. Even so, the inclusion of additional taxa was not enough to provide a good support for a tribal clade containing *Juliomys* (Fig. 2). Additional molecular markers may improve the resolution, but neither novel reconstructions utilizing concatenated matrix achieved (e.g. Carrizo and Catalano 2015). In our analysis, the major clade that includes the *Juliomys* species, *Rhagomys rufensis*, and *Neomicroxus latebricola* also presents a week support (*PP* < 0.7; bootstrap < 75%). The sister clade of *Juliomys* is *Rhagomys rufescens*, but also weakly supported (*PP* < 0.7; bootstrap < 75%). The most likely affinities is found by Ventura et al. 2013 in a Bayesian analyses of cyt *b*, where *Juliomys*, *Neomicroxus* and *Rhagomys* are related in a clade. In our tree a major sister clade related to this clade contained: *Irenomys*, *Neotomys*, *Euneomys*, *Abrawayaomys*, and *Reithrodon*, again weakly supported (*PP* < 0.7; bootstrap < 75%). In Parada et al. (2012) Clade A (cyt *b* and IRBP genes) the taxa most related to *Juliomys* was *Chinchillula*, *Irenomys*, *Neotomys*, and *Euneomys* but weakly supported. Many efforts have been done to solve the *insertae sedis* issue in Sigmodontinae systematics (see Pardiñas et al. 2014; D'Elía 2015) but for now there is no consensus.

The phylogenetic approach is an essential taxonomic tool that shall guide correct ecological interpretations (Santos and Amorim 2007). A robust taxon sampling, as we did, using most sigmodontine genus, highly improve the accuracy of inferences on the phylogenetic relationships and reduce bias (Heat et al. 2008). As a remark, this study is a step forward into the understanding of the position of *Juliomys* in Sigmodontinae. Using only *J. pictipes* studies successively failed to place the genus inside a tribe, even emplying several molecular markers (Salazar-Bravo et al. 2013; Carrizo and Catalano

2015; Pardiñas et al. 2015a; Pardinãs et al. 2015b). Future studies using more than just one species and additional (mitochondrial and nuclear) genes, ideally concatenated with morphological data (Will and Rubinoff 2004), perhaps shall accurately stablish its relations. In turn, as punctuated by D’Elía (2000; 2015), it is possible that *incertae sedis* genera such as *Juliomys* “truly constitute unique members of deep sigmodontine lineages (and, as such, that their uncertain position is not due to the amount or quality of the data analyzed to date)”.

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APPENDIX I. List of specimens from which cyt *b* sequence data used for phylogenetic analyses. * Specimens that compose the outgroup.

Taxon	GenBank number	Voucher-specimen number	Source
Abrawayaomys ruschii	JX949189	MN 67557	Ventura et al. 2013
Abrothrix illuteus	KJ614623	JPJ 1479	Cañón et al. 2014
Abrothrix lanosus	EU683433	PNG 458	Feijoo et al. 2010
Abrothrix longipilis	EU579470	MVZ 154494	Hanson 2008
Abrothrix olivaceus	AY341036	LCM 1884	Palma et al. 2005
Aegialomys xanthaeolus	EU340015	TK 134912	Hanson and Bradley 2009
Akodon azarae	AY702964	GD 327	Pardiñas et al. 2005
Akodon cursor	KF815391	MN 78918	Vilela et al. 2014
Akodon mimus	M35710	MVZ 171512	Smith and Patton 1993
Akodon montensis	AY273905	UMMZ 174969	D'Elía 2003
Andalgalomys pearsoni	AF159285	MSB 55245	Anderson and Yates 2000
Amphinectomys savamis	EU579480	MVZ 70045	Weksler 2003
Andinomys edax	AF159284	MSB 67192	Anderson and Yates 2000
*Arvicola terrestris**	AY332708	P 20	Pfunder et al. 2004
Auliscomys micropus	GU553922	NK 129308	Salazar-Bravo et al. 2013
Auliscomys pictus	U03545	MVZ 172700	Smith and Patton 1999
Auliscomys sublimis	JQ434421	MSB 75260	Salazar-Bravo et al. 2013
Brucepattersonius igniventris	AF108667	MVZ 183250	Smith and Patton 1999
Brucepattersonius soricinus	AY277486	MVZ 183036	D'Elía 2003
Blarinomys breviceps	AF108668	UFMG-MAS 17	Smith and Patton 1999
Calomys callosus	DQ447282	LBCE 5682	Almeida et al. 2007
Calomys lepidus	EU579473	MVZ 171562	Hanson 2008
Calassomys apicalis	JQ434425	DG 176	Salazar-Bravo et al. 2013
Chelemys macronyx	U03533	MVZ 155800	Smith and Patton 1999
Chelemys megalonyx	DQ309559	NK 109208	Rodríguez-Serrano et al. 2008
Chilomys instans	AF108679	JLP 16693	Smith and Patton 1999
Chinchillula sahamae	JQ434422	MSB 75154	Salazar-Bravo et al. 2013
Delomys dorsalis	KF815440	MN 78909	Vilela et al. 2014
Delomys sublineatus	AF108687	MVZ 183075	Smith and Patton 1999
Deltamys kempi	AY195860	UP 42	D'Elía et al. 2003
Eligmodontia typus	AY277445	MVZ 182681	Smith and Patton 1999
Eremoryzomys polius	EU579483	FMNH 129243	Hanson 2008
Euneomys chinchilloides	AY275115	UPLB 018	D'Elía 2003
Geoxus valdivianus	GVU03531	MVZ 154601	Smith and Patton 1999
Graomys griseoflavus	AY275117	UP 278	D'Elía 2003
Graomys chacoensis	KC699943	MONH 1	Martínez et al. 2012
Holochilus brasiliensis	EU579495	GD 081	Hanson 2008
Hylaeamys megacephalus	EU579499	MHNLS8061	Hanson 2008
Irenomys tarsalis	U03534	MVZ 155839	Smith and Patton 1999
Juliomys ossitenuis	EF127521	AB 187	Costa et al. 2007

Juliomys ossitenuis	EF127519	AB 196	Costa et al. 2007
Juliomys ossitenuis	EF127517	MN 69752	Costa et al. 2007
Juliomys ossitenuis	EF127522	MBML 2783	Costa et al. 2007
Juliomys ossitenuis	AF108689	MVZ 40	Smith and Patton 1999
Juliomys ossitenuis	KT749865	MCNU 1461	*submitted*
Juliomys ossitenuis	KT749866	MCNU 1977	*submitted*
Juliomys pictipes	EF127513	UFMG 3168	Costa et al. 2007
Juliomys pictipes	EF127514	UFMG 3171	Costa et al. 2007
Juliomys pictipes	EU157764	MLP 1.I.03.24	Pardiñas et al. 2008
Juliomys pictipes	AF108688	MVZ 141	Smith and Patton 1999
Juliomys pictipes	FJ026733	TK 145073	De la Sancha et al. 2009
Juliomys rimofrons	AY029477	MN 61647	Oliveira and Bonvicino 2002
Juliomys sp.1	KT749863	MCNU 868	*submitted*
Juscelinomys huanchacae	AF133667	LHE 1403	Emmons 1999
Kunsia tomentosus	AY275120	LHE 1619	D’Elía 2003
Lenoxus apicalis	U03541	MVZ 171512	Smith and Patton 1999
Lundomys molitor	JQ966236	MCNU1804	Machado el at. 2014
Melanomys caliginosus	EU665204	RMT 4658	Hanson 2008
Microryzomys minutus	AF108698	MVZ 173975	Smith and Patton 1999
*Microtus socialis**	AY513830	*not provided*	Jaarola et al. 2004
Neacomys spinosus	EU579504	MVZ 155014	Hanson 2008
Nectomys squamipes	EU 074634	TK 63841	Hanson 2008
Necromys lasiurus	U03528	UMMZ134431	Smith and Patton 1999
Necromys urichi	AY 273919	AMNH 257287	D’Elía 2003
Neomicroxus latebricola	KF437365	QCAZ4160	Alvarado-Serrano and D’Elía 2013
*Neotoma albigula**	AF108704	MVZ147667	Smith and Patton 1999
Neotomys ebriosus	HM061604	CML7680	Martínez et al. 2012
Nephelomys albigularis	EU579505	AMNH 268125	Hanson 2008
Nesoryzomys swarthi	EU340014	ASNHC 10003	Henson and Bradley 2009
*Nyctomys sumichrasti**	AY195801	TK 101875	Bradley et al. 2004
Oecomys mamorae	EU579509	JLP 16961	Hanson 2008
Oligoryzomys flavescens	DQ826015	MN 37749	Miranda et al. 2009
Oligoryzomys fulvescens	DQ227457	TK 138080	Milazzo et al. 2006
Oreoryzomys balneator	EU579510	AMNH 268144	Hanson 2008
Oryzomys palustris	DQ185382	TK 91240	Milazzo et al. 2006
Oxymycterus delator	AY275125	UMMZ 175101	D’Elía 2003
Oxymycterus nasutus	AF175286	MVZ 182701	Hoffman et al. 2002
Oxymycterus rufus	AY275126	UPAC 004	D’Elía 2003
Pearsonomys annectens	AF108672	IEE 5462	Smith and Patton 1999
Phaenomys ferrugineus	KM065876	MZUFV 3400	Pardiñas et al. 2014
Podoxymys roraimae	KM816651	PK3335	Leite et al. 2015
Pseudoryzomys simplex	EU579517	GD 065	Hanson 2008
Punomys kofordi	JQ434426	VPT 1890	Salazar-Bravo et al. 2013
Reithrodon auritus	AY275129	UP 500	D’Elía 2003
Rhagomys rufescens	AY206770	MN 66056	Percequillo et al. 2004
Rheomys raptor	KJ921706	KU 159017	Leite et al. 2014
Rhipidomys macconnelli	AY275130	MVZ 160082	D'Elía 2003

Rhipidomys macconnelli	AF108681	MBUCV 14063	Smith and Patton 1999
Rhipidomys mastacalis	HM594644	UFMG 2930	Costa et al. 2011
Rhipidomys nitela	AF108682	MZUSP 21316	Smith and Patton 1999
Scapteromys aquaticus	AY275131	UP BAL509	D’Elía 2003
Scapteromys tumidus	AY275133	MVZ 183269	D’Elía 2003
Scolomys ucayalensis	EU579518	AMNH 272721	Hanson 2008
*Scotinomys xerampelinus**	AF108706	UMMZ 3408	Smith and Patton 1999
Sigmodon hispidus	AF188198	TK 83608	Peppers et al. 2002
Sigmodontomys alfari	EU074635	USNM 449895	Hanson 2008
Sooretamys angouya	EU579512	TK 61763	Hanson 2008
Thomasomys aureus	U03540	MVZ 170076	Smith and Patton 1999
Thomasomys baeops	KR818878	TEL 2791	Lee et al. 2015
Thomasomys baeops	DQ914654	MSB 70704	Salazar-Bravo and Yates 2007
Thalpomys cerradensis	AY273915	MZUSP 30400	D’Elía 2003
Transandinomys talamancae	EU579514	TK 135289	Hanson 2008
Wiedomys pyrrhorhinos	AY275134	MVZ 197567	D’Elía 2003
Wiedomys cerradensis	KC456171	CRB 1839	Bezerra et al. 2013
Wilfredomys oenax	KJ663726	UFSM 619	Machado et al. 2015
Zygodontomys brevicauda	EU579519	TTU 76306	Hanson 2008

8. EPÍLOGO

Os resultados deste estudo expandem o conhecimento acerca dos Sigmodontinae, bem como ressalta a importância das coleções científicas para a sistemática e taxonomia e modelagem de distribuição das espécies. As contribuições do trabalho para os *Juliomys* abrangem a compilação de caracteres morfológicos diagnósticos, bem como a análise morfométrica e filogenética do gênero. Dos 217 espécimes encontrados nas coleções, 81% não apresentavam informação sobre marcadores genéticos ou morfológicos confiáveis ou estavam erroneamente identificados. Fomos capazes de identificar 85% desta amostra, com apenas 15% dos espécimes permanecendo ainda sem identificação precisa (indivíduos sem crânio, fragmentados e/ou muito jovens). De acordo com Blaxter (2004) "os animais vertebrados podem ter mais de 10% dos taxa ainda não descritos". Novas abordagens sobre a taxonomia se fazem necessárias (GODFRAY, 2002). “A incorporação de métodos experimentais e quantitativos para análise de caracteres junto às descrições morfológicas pode também tornar menos parcial a taxonomia tradicionalmente usada, além de evitar julgamentos *a priori* na circunscrição dos táxons” (Barros 2015). A abordagem morfológica em estudos taxonômicos é fundamental, bem como o desenvolvimento de investigações na linha da genética. A análise sistemática molecular deve acompanhar a sistemática tradicional, complementando-se (BLAXTER, 2004).

Coleções de Museu ou coleções científicas são fontes essenciais de informações sobre a biodiversidade e história natural associada a ela (WHEELER 1995; GRAHAM et al. 2004, NEWBOLD 2010). A totalidade da amostra deste estudo foi encontrado neste tipo de fonte. Neste estudo foram enfrentados alguns empecilhos correntes relacionados à coleta de dados, desde a não-disponibilização da totalidade da amostra pela curadoria, material depositado incompleto (sem crânio, sem pele, sem amostra de tecido, etc.), material sem identificação (localidade, coletor, etc.), e a não-informatização dos livros de tombo. Tais fatos remetem principalmente à falta de investimentos nas coleções, formação de profissionais capacitados para atuarem nelas, bem como melhor preparo dos pesquisadores que ali depositam material biológico. Da amostra de *Juliomys* examinada (n = 217) 74 encontravam-se catalogados como *Juliomys* sp., ou seja, mais de um terço do total estudado não possuía a definição da espécie. Neste sentido, ficou evidente a dificuldade de identificação destes táxons e a falta de revisão. A carência de profissionais taxonomistas é um problema real, mesmo para a mastofauna. "Os taxonomistas trabalham um conjunto de caracteres morfológicos complexos sobre os quais se baseiam as suas conclusões" (WILL; RUBINOFF, 2004). A falta de especificidade ou identificação incorreta resulta em modelos não confiáveis. Desta forma, muitos estudos em todos os níveis da biologia, especialmente ecologia e conservação, podem estar equivocados usando informações erradas (BARROS, 2015). Só com uma identificação precisa dos taxa pode produzir resultados consensuais e fundamentais sobre uma espécie, como a sua área de distribuição.

Corroborando os estudos de Paresque et al. (2009), descrevemos uma nova espécie para o gênero, o qual encontra-se em revisão em um conceituado periódico científico da mastozoologia, aguardando a etapa final de revisão para publicação. Utilizamos métodos de análise morfológica, morfométrica e molecular para a definição do novo táxon. Com a proximidade o reconhecimento oficial do novo táxon, o gênero *Juliomys* abarcará quatro espécies viventes, todas elas com distribuição dentro do domínio do bioma Mata Atlântica. As evidências de monofiletismo de *Juliomys* é também instrumento importante em futuras inferências sobre este grupo. Zachos et al. (2013) argumentam que a descrição de um novo táxon, bem como suas relações de parentesco, devem ser perfeitamente embasadas. Tais assertos tem consequências importantes, como por exemplo ações conservacionistas, as quais são fundamentadas pelo uso destas informações.

A modelagem de distribuição das espécies demonstrou alta correlação entre as espécies e o bioma Mata Atlântica. O conhecimento da distribuição geográfica das espécies é de grande importância no âmbito conservacionista. Santos e Amorim (2007) sugerem que estudos em biogeografia devem ser embasados filogeneticamente, bem como clados monofilético devem basear abordagens de distribuição. A distribuição das espécies de *Juliomys* apresentou certa heterogeneidade e influência de fatores como a altitude por exemplo. A modelagem de distribuição pode servir como ponto de partida para novas inferências biogeográficas destes taxa.

Acerca da espécie extinta*, J. anoblepas* Pardiña e Teta, 2011, tivemos acesso às informações do espécime (fotos, medidas e descrição; gentilmente cedidas pelo prof. Alexandre Percequillo – ESALQ-USP). O material constitui-se de crânio fragmentado de um indivíduo, provindo do depósito de Lagoa Santa, Minas Gerais, Brasil. O fragmento contempla a porção rostral do crânio, abrangendo a porção prato zigomático, e as séries molares superiores. A região posterior do crânio, que inclui a bula timpânica, fossa parapterigóide e mesoptetigóide, forames associados, bem como ossos dorsais e ventrais (bular e do alisfenóide), não estão presentes, o que impede a compreensão do padrão de circulação cefálido, por exemplo (dificultando inferências na diagnose da espécie.). Suplementarmente aos estudos apresentados dantes, fizemos algumas inferências sobre este material. Utilizando a amostra e metodologia apresentadas no Capítulo II, avaliamos um conjunto variáveis (medidas cranianas) morfométricas tomadas sobre o fragmento disponível de *J. anoblepas* e processamos análises multivariadas (PCA, DFA; medidas aquelas que puderam ser tomadas devido à fragmentação do crânio). A anatomia craniana e os resultados das análises morfométricas sugerem que o indivíduo pertença à espécie *Juliomys pictipes*. Tais resultados nos instigam a nos aprofundarmos nesta questão, utilizando em estudos futuros análises mais robustas. Análises de DNA antigo, por exemplo, tem sido utilizado com sucesso (ex. HO; PHILLIPS, 2009) e podem auxiliar investigações futuras sobre o espécime analisado por Pardiñas e Teta (2011). Tal linha de estudo deve ademais auxiliar na problemática das inferências filogenéticas e definição da posição de *Juliomys* em Sigmodontinae, agregando-se também marcadores moleculares complementares.

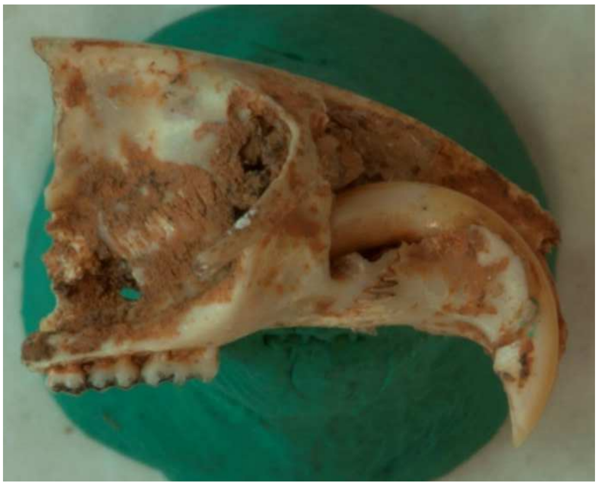

Fig. 2. *Juliomys anoblepas*. Foto: A. Percequillo.

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