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Luíza Zuchetto Magnus

VARIAÇÃO GEOGRÁFICA DO TAMANHO E FORMA DO CRÂNIO DE MAMÍFEROS COM AMPLA DISTRIBUIÇÃO NA AMÉRICA DO SUL (MARSUPIALIA, XENARTHRA E GLIRES)

Santa Maria, RS
2018

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Tese apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Doutor em Biodiversidade Animal**.

Orientador: Prof. Dr. Nilton Carlos Cáceres

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Dedico aos meus pais Claudia e Gilberto, e ao meu
namorado e companheiro de vida Luís Ricardo,
pelo apoio incondicional durante essa jornada.

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"How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be, compared with those accumulated by nature during whole geological periods."

Charles Darwin

RESUMO

VARIAÇÃO GEOGRÁFICA DO TAMANHO E FORMA DO CRÂNIO DE MAMÍFEROS COM AMPLA DISTRIBUIÇÃO NA AMÉRICA DO SUL (MARSUPIALIA, XENARTHRA E GLIRES)

AUTOR: Luíza Zuchetto Magnus
ORIENTADOR: Nilton Carlos Cáceres

Os crânios são estruturas morfológicas complexas que apresentam plasticidade fenotípica e adaptações a diferentes funções e processos e estão sob diferentes pressões, como as geográficas ou ambientais. A América do Sul é um continente latitudinalmente amplo, abrangendo uma variedade de biomas e condições climáticas, revelando variações ecomorfológicas em muitas espécies de mamíferos. O principal objetivo deste estudo foi investigar padrões biogeográficos e fatores determinantes relacionados a variações cranianas em espécies e gêneros de mamíferos com ampla distribuição geográfica na América do Sul (Marsupialia, Xenarthra e Glires), com base em dados de tamanho e forma. A partir de fotografias cranianas de 1,017 espécimes na vista ventral em coleções científicas, técnicas de morfometria geométrica foram usadas para entender a variação do crânio nos diferentes grupos. Duas espécies de marsupiais foram estudadas no Capítulo I, *Caluromys philander* e *C. lanatus*, as quais foram semelhantes na forma, demonstrando trajetórias fenotípicas similares. O efeito do tamanho na forma (alometria) foi importante para *C. lanatus*, ajudando biomecanicamente em ambientes ao sul da Amazônia. Ainda, as duas espécies foram estruturadas espacialmente, além de demonstrarem grande influência ambiental (especialmente temperatura), seguindo o inverso a Regra de Bergmann. No Capítulo II, três espécies da superordem Xenarthra (*Bradypus variegatus*, *Tamandua tetradactyla*, e *Dasypus novemcinctus*) apresentaram uma fraca influência alométrica. Entretanto, fatores geográficos (neutros) influenciaram a forma de *B. variegatus* e o tamanho de *T. tetradactyla*, o que poderia ser um reflexo da baixa capacidade de mobilidade e dispersão de ambas as espécies. Mais importante, a influência ambiental (nicho) afetou as três espécies, com destaque para *B. variegatus* (seguindo a regra de Bergmann), e *D. novemcinctus* (espécie altamente móvel, sendo afetada localmente pelo ambiente). O Capítulo III trata da variação da forma dos táxons *Cuniculus paca*, *Hydrochoerus hydrochaeris*, *Nectomys* spp., e *Sylvilagus brasiliensis*. A alometria esteve presente notoriamente para o gênero *Nectomys*, sugerindo uma associação com o dimorfismo sexual encontrado apenas neste gênero. A influência ambiental foi perceptível para as espécies altamente dispersivas e com grande tamanho corporal, como *H. hydrochaeris* e *C. paca*. Essas duas espécies também foram afetadas pelos filtros espaciais (geografia), mas em menor grau, como ocorreu para os outros dois táxons. E por fim, o Capítulo IV abordou mais especificamente o aparato mastigatório (conjunto dos molares e arco zigomático) das espécies dos gêneros *Rhipidomys* e *Nectomys*. A distinção interespecífica dentro de cada gênero foi visível para algumas espécies de *Rhipidomys* (tamanho e forma), enquanto as espécies de *Nectomys* apresentaram fraca disparidade. Em relação às hipóteses biogeográficas, a resposta fenotípica de cada gênero foi divergente, com a forma de *Rhipidomys* relacionada com a produtividade primária, e o tamanho de *Nectomys* relacionado com a precipitação e temperatura. Esses resultados distintos sugerem respostas diferentes de acordo com restrições e atributos ecológicos de cada gênero (especialista e generalista respectivamente). De modo geral, os resultados encontrados neste estudo sugerem que a resposta de cada táxon frente às várias influências sofridas não é necessariamente a mesma, mas depende de suas características e particularidades que induzem a modificações cranianas distintas.

Palavras-chave: Morfometria Geométrica. Regra de Bergmann. Adaptação da forma. Alometria. Variação interespecífica. Ambiente. Ecogeografia.

ABSTRACT

GEOGRAPHICAL VARIATION OF SKULL SIZE AND SHAPE OF MAMMALS WITH WIDE DISTRIBUTION IN SOUTH AMERICA (MARSUPIALIA, XENARTHRA AND GLIRES)

AUTHOR: Luíza Zuchetto Magnus
ADVISOR: Nilton Carlos Cáceres

Skulls are complex morphological structures that exhibit phenotypic plasticity and adaptations to different functions and processes, and are under different pressures, such as the geographical or environmental ones. South America is a latitudinal broad continent, encompassing a variety of biomes and climatic conditions, revealing ecomorphological variations in many mammal species. The main objective of this study was to investigate ecogeographical patterns and determinant factors related to cranial variations in species and genera of mammals with wide geographic distribution in South America (Marsupialia, Xenarthra and Glires), based on size and shape data. From skull photographs of 1.017 specimens in the ventral view in scientific collections, geometric morphometric techniques were used to understand skull variation within the different groups. Two species of marsupials were studied in Chapter I, *Caluromys philander* and *C. lanatus*, which were similar in shape, showing similar phenotypic trajectories. The effect of size on shape (allometry) was important for *C. lanatus*, helping biomechanically in environments southern Amazonia. In addition, the two species were spatially structured, also showing great environmental influence (especially temperature), following the inverse of the Bergmann's rule. In Chapter II, three species of the Xenarthra superorder (*Bradypus variegatus*, *Tamandua tetradactyla*, and *Dasypus novemcinctus*) presented a weak allometric influence. However, geographical (neutral) factors influenced the shape of *B. variegatus* and the size of *T. tetradactyla*, which could be a reflection of the low mobility and dispersion capacity of both species. Importantly, the environmental influence (niche) affected the three species, most notably *B. variegatus* (which follows the Bergmann's rule), and *D. novemcinctus* (highly mobile species, being locally affected by the environment). Chapter III deals with the taxa *Cuniculus paca*, *Hydrochoerus hydrochaeris*, *Nectomys* spp., and *Sylvilagus brasiliensis*. Allometry was present notably for the genus *Nectomys*, suggesting an association with the sexual dimorphism found only in this genus. The environmental influence was noticeable for highly dispersive and large body size species, such as *H. hydrochaeris* and *C. paca*. These two species were also affected by spatial filters (geography), but to a lesser extent, as occurred for the other two taxa. Finally, Chapter IV addressed more specifically the masticatory apparatus (molar series and zygomatic arch) of the species of *Rhipidomys* and *Nectomys* genus. The interspecific distinction within each genus was visible for some species of *Rhipidomys* (size and shape), whereas the species of *Nectomys* presented weak disparity. In relation to the biogeographical hypotheses, the phenotypic response of each genus was divergent, with *Rhipidomys* shape being related to the primary productivity, and the *Nectomys* size related mainly to precipitation and temperature. These distinct results suggest different responses according to constraints and ecological attributes of each genus (specialist and generalist, respectively). In general, the results found in this study suggest that the response of each taxon to the various influences suffered is not necessarily the same, but depends on its characteristics and particularities that induce different cranial modifications.

Keywords: Geometric morphometrics. Bergmann's rule. Shape adaptation. Allometry. Interspecific variation. Environment. Ecogeography.

LISTA DE FIGURAS

ARTIGO I. Comparative ecogeographical variation in skull size and shape of two woolly opossums (genus *Caluromys*)

Fig. 1. Map of South America showing the sampling distribution of *Caluromys* specimens. The sampling localities of different species are shown by different symbols. 34

Fig. 2. Position of 13 landmarks on a skull of *Caluromys philander.* Landmark definitions: 1 = midpoint of central incisors; 2 = labial-most point of canine; 3 = lingual-most point of cusp of the first molar; 4 = labial-most point of cusp of the first molar; 5 = lingual-most point of cusp of the fourth molar; 6 = labial-most point of cusp of the fourth molar; 7 = anterior-most point on curvature of the zygomatic process; 8 = posterolateral tip of palate; 9 = base of the posterior border of the alisphenoid portion of the zygomatic process; 10 = posterolateral-most point on curvature of the zygomatic process; 11 = posterior-most tip of suture between palates; 12 = anterior-most point of foramen magnum; 13 = exterior border of braincase, anterior to the posttympanic process. Scale bar is 1 cm. 35

Fig. 3. Box plot with standardized deviation of centroid size (natural log trans-formed – lnCS) across the two species of *Caluromys*. Black string = median; box = first interquartile; bar = second interquartile..37

Fig. 4. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the species shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. Every species is labeled with minimum convex hull superimposed...38

Fig. 5. Scatter plot obtained by regression of shape onto the size (lnCS) for (A) *Caluromys philander* and (B) *C. lanatus*. Graphical deformation grids are shown for negative and positive extremes of the regression scores computed for each species. 39

Fig. 6. Centroid size (natural log transformed – lnCS) variation relative to latitude. *Caluromys philander* vs. absolute value of latitude (A), and *C. lanatus* vs. absolute value of latitude (B). Symbol size increases with size...40

Fig. 7. Plot of the first pair of Singular Warps for size (lnCS) and shape variation in (A) *Caluromys philander* and (B) *C. lanatus* with temperature (BIO1-11 bioclimatic block) and rainfall (BIO12-19 bioclimatic block). 42

Fig. 8. Plot of the first pair of Singular Warps for size (lnCS) variation in *Caluromys philander* and *C. lanatus* and climate (axis X is block size, axis Y is block climate). 43

Fig. 9. Plot of the first pair of Singular Warps for shape variation in *Caluromys philander* and *C. lanatus* and climate (axis X is block shape, axis Y is block climate). Below there are variable profiles and deformation grids from the most negative to the most positive Singular Warp scores. The numbers in the variable profiles are originated from the 19 variables of WorldClim. In deformation grids, (A) is for *Caluromys philander* and (B) is for *C. lanatus*.....................44

ARTIGO II. The environment is a major driver of shape and size variation in widespread extant xenarthrans

Fig. 1. Map of South America showing the sampling distribution of xenarthran skulls. Sampling localities of different species are shown by different symbols...68

Fig. 2. Position of 13 landmarks on a skull of *Bradypus variegatus*. Landmark definitions: 1 = anterior extremity of the nasal bone; 2 = anteriormost point of the maxilla; 3 = posteriormost

tip of suture between palates; 4 = anteriormost point of foramen magnum; 5 = anteriormost point of the root of the zygomatic arch; 6 = anteriormost point on curvature of the zygomatic arch; 7 = intersection between frontal and palate; 8 = posteriormost point on curvature of the zygomatic arch; 9 = anterolateral extremity of the auditory bulla; 10 = posterior extremity of the auditory bulla; 11 = posterolateral extremity of the auditory bulla; 12 = projection onto the external edge of the zygomatic arch, drawn from the midpoint of landmarks 5-7 at an angle of 90° with the line perpendicular to the line between the landmarks 2-3; 13 = projection onto the external edge of the skull, drawn from the midpoint of landmarks 3-4 at an angle of 90° with the line perpendicular to the landmarks. Scale bar is 1 cm. 69

Fig. 3. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the overall species shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C). 72

Fig. 4. Natural log transformed centroid size (lnCS) variation relative to absolute value of Latitude. *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C). Symbol size increases with specimen size. 74

Fig. 5. Plot of environmental variables and shape scores from the most negative to the most positive Singular Warps (first pair). Below are variable profiles and deformation grids from the most negative to the most positive Singular Warp scores. The numbers in the variable profiles are originated from the 19 variables of WorldClim plus average annual relative humidity (20), net primary productivity (21), and evapotranspiration (22). *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C). 76

Fig. 6. Schematic depiction of proportion (Adj.R^2) of shape and size variance explained by allometry, geography, and environment for each species. Shape: (A) *Bradypus variegatus*; (B) *Tamandua tetradactyla*; and (C) *Dasypus novemcinctus*. Size: (D) *Bradypus variegatus*; (E) *Tamandua tetradactyla*; and (F) *Dasypus novemcinctus*. Values <0 not shown. 77

ARTIGO III. Ecogeography of South-American Rodentia and Lagomorpha (Mammalia, Glires): roles of body size, environment, and geography

Fig. 1. Maps of South America showing the sampling distribution of Rodentia and Lagomorpha skulls. (A) *Cuniculus paca*, (B) *Hydrochoerus hydrochaeris*, (C) *Nectomys* spp., and (D) *Sylvilagus brasiliensis*. 103

Fig. 2. Position of 16 landmarks on a skull of *Sylvilagus brasiliensis*. Landmark definitions: 1 = midpoint of central incisors; 2 = anteriormost midpoint of the incisive foramen; 3 = junction between maxillar-premaxillar suture and lateral margin of incisive foramen; 4 = lateralmost point of maxillar-premaxillar suture; 5 = anteriormost point of the root of zygomatic arch; 6 = anteriormost point of the first molar (molar row); 7 = posteriormost point of the third molar (molar row); 8 = anteriormost point on curvature of the zygomatic arch; 9 = posteriormost midpoint of the zygomatic process; 10 = posterolateralmost point on curvature of the zygomatic process; 11 = posteriormost tip of suture between palates; 12 = anteriormost edge of auditory bulla; 13 = posteriormost edge of auditory bulla; 14 = lateralmost edge of auditory bulla; 15 = medialmost edge of auditory bulla; 16 = anteriormost point of foramen magnum. Scale bar is 1 cm. 104

Fig. 3. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the taxa shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. In (A) deformations are for *Cuniculus paca*, in (B)

for *Hydrochoerus hydrochaeris*, in (C) for *Nectomys*, and in (D) for *Sylvilagus brasiliensis*. 106

Fig. 4. Scatter plot obtained by regression of shape onto the size (lnCS) for (A) *Cuniculus paca*, (B) *Hydrochoerus hydrochaeris*, (C) *Nectomys*, and (D) *Sylvilagus brasiliensis*. Graphical deformation grids are shown for negative and positive extremes of the regression scores computed for each group. 108

Fig. 5. Plot of environmental variables and shape scores from the most negative to the most positive Singular Warps (first pair). Below are deformation grids and variables profile from the most negative to the most positive Singular Warps scores. The numbers in the variables scores are from the 19 variables of WorldClim plus average annual relative humidity (20), net primary productivity (21), and evapotranspiration (22). In (A) deformations are for *Cuniculus paca*, in (B) for *Hydrochoerus hydrochaeris*, in (C) for *Nectomys*, and in (D) for *Sylvilagus brasiliensis*. 109

ARTIGO IV. Morphological and environmental variation in the genus *Rhipidomys* and *Nectomys* (Mammalia: Rodentia): implications from molars and zygomatic arch

Fig. 1. Maps of South America showing the sampling distribution of (a) *Rhipidomys* and (b) *Nectomys*. 136

Fig. 2. Position of landmarks for the molar series (landmarks 1-8) and zygomatic arch (landmarks 9-13) on the ventral view of the skull in *Rhipidomys macrurus*. Landmark definitions: 1 = anteriormost point of the first molar; 2 = posteriormost point of the third molar; 3 = lateral midpoint of the first molar; 4 = medial midpoint of first molar; 5 = lateral anterior point of the second molar; 6 = medial anterior point of the second molar; 7 = lateral anterior point of the third molar; 8 = medial anterior point of the third molar; 9 = anteriormost point on curvature of the zygomatic arch; 10 = posteriormost point on curvature of the zygomatic arch; 11 = lateral projection onto the internal edge of the zygomatic arch, drawn from the midpoint of landmarks 9-10 at an angle of 90◦; 12 = lateral projection onto the internal edge of the zygomatic arch, drawn from a quarter of landmarks 9-10 at an angle of 90◦; 13 = medial projection onto the internal edge of the zygomatic arch, drawn from three quarters of landmarks 9-10 at an angle of 90◦. Scale bar is 1 cm. 137

Fig. 3. Size (natural log transformed centroid size – lnCS) variation in *Rhipidomys* and *Nectomys* species. (a) *Rhipidomys* and (b) *Nectomys*. 139

Fig. 4. Scatter plot of first versus second canonical variate axes (CV1 and CV2) of the *Rhipidomys* skull and percentage of variance explained by the CVs. Graphical deformation shapes are shown for negative and positive extremes scores (solid lines are canonical variate shape and dashed lines are de consensus shape). 140

Fig. 5. Scatter plot of first versus second canonical variate axes (CV1 and CV2) of the *Nectomys* skull and percentage of variance explained by the CVs. Graphical deformation shapes are shown for negative and positive extremes scores (solid lines are canonical variate shape and dashed lines are de consensus shape). 141

Fig. 6. Size (natural log transformed centroid size – lnCS) of genera (species) versus each predictor variable (standardized variables). Mean annual temperature - bio1 (a), annual precipitation - bio12 (b), and net primary productivity – npp (c). The lines represent the trend for each species of genera. Blue circles and lines: *Rhipidomys*, and red circles and lines: *Nectomys*. 143

Fig. 7. Shape (PC1 size-free) of genera (species) versus each predictor variable (standardized variables). Mean annual temperature - bio1 (a), annual precipitation - bio12 (b), and net primary

productivity – npp (c). The lines represent the trend for each species of genera. Blue circles and lines: *Rhipidomys*, and red circles and lines: *Nectomys*. In (d) the graphical deformation shapes are shown for negative and positive extremes scores of each genus (solid lines are canonical variate shape and dashed lines are de consensus shape).. 144

LISTA DE TABELAS

ARTIGO I. Comparative ecogeographical variation in skull size and shape of two woolly opossums (genus *Caluromys*)

Table 1. Skull sample size for *Caluromys philander* and *C. lanatus* included in this study....33

Table 2. Multivariate regressions and multivariate multiple regressions of dependent variables (Y) Size (lnCS) and Shape (relative warps corresponding to 95% of shape variation) with PCNM (principal coordinates of neighbour matrices) predictors (representing geographical space) for South-American *Caluromys*. Significance is highlighted in bold. 39

Table 3. Regressions and multivariate regressions of dependent variables (Y) Size (lnCS) and Shape (relative warps corresponding to 95% of shape variation) with the predictor variable Latitude for South-American *Caluromys*. Significance is highlighted in bold. 40

Table 4. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors (SW1) of Size (lnCS) and Shape comparing to Temperature (BIO1-11 bioclimatic variables), Rainfall (BIO12-19 bioclimatic variables) and Climate overall (BIO1-19 bioclimatic variables) for South-American *Caluromys*. Significance is highlighted in bold. 41

ARTIGO II. The environment is a major driver of shape and size variation in widespread extant xenarthrans

Table 1. Skull sample size for the three species of Xenarthra included in this study. 67

Table 2. Multivariate regressions of dependent variables (Dep.) Shape (relative warps corresponding to 95% of shape variation) and Size with the predictor variable Latitude for South American xenarthran species. Significance (P < 0.05) is highlighted in bold.........................73

Table 3. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors (SW1) of Shape and Size (lnCS) comparing to environmental variables (22) for South American xenarthran species. Significance (P < 0.05) is highlighted in bold...............75

ARTIGO III. Ecogeography of South-American Rodentia and Lagomorpha (Mammalia, Glires): roles of body size, environment, and geography

Table 1. Skull sample size for the four taxa of Rodentia and one of Lagomorpha included in this study. 102

Table 2. Procrustes ANOVA results analysing the skull shape variation in South-American Rodentia and Lagomorpha taxa according to: Size (natural logarithm of centroid size = allometry), Environment (22 environmental variables), Geographical distance (spatial filters) and *Environment (spatial filters as covariates). Significance (P < 0.05) is highlighted in bold. 107

Table 3. Procrustes ANOVA results analysing the skull shape variation in *Nectomys* females and males according to: Size (natural logarithm of centroid size = allometry), Environment (22 environmental variables), Geographical distance (spatial filters) and *Environment (spatial filters as covariates). Significance (P < 0.05) is highlighted in bold....................................108

Table 4. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors comparing shape and environmental variables (n = 22) for South-American Rodentia and Lagomorpha taxa. Significance (P < 0.05) is highlighted in bold...................109

ARTIGO IV. Morphological and environmental variation in the genus *Rhipidomys* and *Nectomys* (Mammalia: Rodentia): implications from molars and zygomatic arch

Table 1. Skull sample size of analysed species of genus *Rhipidomys* Tschudi, 1845 and *Nectomys* Peters, 1861. 135

Table 2. Tukey's test pairwise differences in natural log-transformed centroid size (lnCS) between *Rhipidomys* species. Above diagonal P-values, below diagonal Q-values. Significant values are in bold (P < 0.05). 139

Table 3. Tukey's test pairwise differences in natural log-transformed centroid size between *Nectomys* species. Above diagonal P-values, below diagonal Q-values. Significant values are in bold (P < 0.05). 140

Table 4. Mahalanobis distances for shape between species pairs of *Rhipidomys*. Significant values are in bold (P < 0.05). 140

Table 5. Mahalanobis distances for shape between species pairs of *Nectomys*. Significant values are in bold (P < 0.05). 141

Table 6. Results of the simple linear regressions of environmental variables on Size (lnCS) and Shape (PC1 size-free) of *Rhipidomys* and *Nectomys*. Significance is highlighted in bold (P < 0.05). 142

SUMÁRIO

1 INTRODUÇÃO GERAL 17
2 OBJETIVOS.. 27
3 ARTIGO I. Comparative ecogeographical variation in skull size and shape of two woolly opossums (genus *Caluromys*) 28
- **Abstract.. 29**
- **Introduction.. 30**
- **Materials and methods 33**
  - *Data collection* 33
  - *Statistical analyses* 35
- **Results 37**
  - *Sexual dimorphism* 37
  - *Skull size and shape* 37
  - *Allometry* 38
  - *Geography* 39
  - *Size versus climate* 40
  - *Shape versus climate* 41
  - *Size-free analyses* 44
- **Discussion... 44**
- **Acknowledgements 48**
- **References... 49**
- **Supplementary data... 55**
  - Appendix A. 55
  - Appendix B. 59
  - Appendix C. 61

4 ARTIGO II. The environment is a major driver of shape and size variation in widespread extant xenarthrans 62
- **Abstract.. 63**
- **Introduction.. 64**
- **Material and methods.. 66**
  - *Data collection* 66
  - *Geometric morphometrics*.. 67
  - *Statistical analyses* 69
  - *Sexual dimorphism* 69
  - *Skull allometry* 69
  - *Bergmann's rule* 70
  - *Environment versus skull shape and size* 70
  - *Variation partitioning*... 70
- **Results 71**
  - *Sexual dimorphism* 71
  - *Skull shape* 71
  - *Skull allometry* 73
  - *Bergmann's rule* 73
  - *Environment versus skull shape and size* 74
  - *Variation partitioning*... 75

Discussion **77**
Acknowledgements **80**
References **81**
Supplementary data **86**
Appendix S1. 86
Table S1. 88
Table S2. 95
Table S3. 96
5 ARTIGO III. Ecogeography of South-American Rodentia and Lagomorpha (Mammalia, Glires): roles of body size, environment, and geography **97**
Abstract **98**
Introduction **99**
Materials and methods **102**
Results **105**
Discussion **110**
Acknowledgements **112**
References **113**
Supplementary data **119**
Table A1. 119
Table A2. 129
6 ARTIGO IV. Morphological and environmental variation in the genus *Rhipidomys* and *Nectomys* (Mammalia: Rodentia): implications from molars and zygomatic arch **130**
Abstract **131**
Introduction **132**
Materials and methods **135**
Results **138**
Discussion **144**
Acknowledgements **147**
References **147**
Supplementary material **153**
Appendix A. 153
Appendix B. 162
Appendix C. 163
7 DISCUSSÃO GERAL **164**
8 CONCLUSÕES GERAIS **167**
9 REFERÊNCIAS BIBLIOGRÁFICAS **169**

1 INTRODUÇÃO GERAL

Ecogeografia da América do Sul

O continente da América do Sul acompanhou, juntamente com outros continentes do globo, períodos de grandes mudanças devido a cataclismos que resultaram consequentemente em graves extinções. Pressões desde vulcanismos, terremotos, soerguimentos/rebaixamentos de áreas, separação entre continentes e alterações climáticas contribuíram para moldar cada um dos continentes ao que são hoje (LAVINA e FAUTH, 2011), sendo que algumas dessas mudanças ainda são constantes.

A América do Sul em especial é caracterizada por vários momentos marcantes na sua história geológica. Por milhões de anos se manteve associada a outras massas de terra, primeiramente pela Pangeia (supercontinente do Paleozoico), após pela Gondwana (supercontinente do hemisfério sul do Mesozoico), além de estar posteriormente associado também ao continente da África (LAVINA e FAUTH, 2011). No Eoceno, o clima era extremamente favorável à proliferação de organismos como mamíferos e também formações florestais, já que as temperaturas haviam aumentado (BLOIS e HADLY, 2009). Somente no final do Eoceno, o continente sul-americano se tornou um continente isolado e, durante esse período, imigrantes térios se diferenciaram para linhagens mais variadas e singulares de mamíferos (PASCUAL, 2006). No entanto, no final do Eoceno e início do Oligoceno, devido ao surgimento de ciclos glaciais, regiões sazonais, oscilações climáticas, e o aumento de áreas abertas, espécies de animais associadas à habitats florestais foram reduzidas ou extintas (BLOIS e HADLY, 2009; LAVINA e FAUTH, 2011). Mudanças climáticas e ambientais continuaram principalmente também no período do Mioceno, levando a uma aridificação e um aumento ainda maior de áreas abertas, formando biomas como a Caatinga (SIMON et al., 2009). Foi nesse mesmo período do Mioceno (tardio) que começou a grande troca de fauna entre a América do Sul e Norte chamado Grande Intercâmbio Biótico Americano (GABI, do inglês "Great American Biotic Interchange"), o que ocorreu ao longo de vários anos e em várias fases, principalmente devido à formação do Istmo do Panamá na América Central (CIONE et al., 2015). Esse foi um dos maiores eventos ocorridos no continente, especialmente para o grupo de mamíferos.

Atualmente, a grande diversidade de ambientes e biomas sul-americanos se mostra como resultado de uma complexa interação, desde plantas e animais até forças geológicas (DE VIVO e CARMIGNOTTO, 2004; ORTIZ-JAUREGUIZAR e CLADERA, 2006). A totalidade desse conjunto de transformações que ocorreram no continente fez com que espécies se adaptassem e evoluíssem de maneiras distintas, apresentando morfologias particulares (MILLIEN et al., 2006). Como no exemplo de primatas, onde a variação ambiental foi de grande importância para a adaptação ecomorfológica, evidenciando uma direção de mudanças fenotípicas cranianas através dos biomas sul-americanos (ambientes intensamente florestados para não florestados) (MELORO et al., 2014).

Os biomas da América do Sul são diversos, assim como a classificação fitogeográfica dos mesmos (IBGE, 2012). Por exemplo, OLSON et al. (2001) destacam uma abordagem de todas as ecorregiões terrestres relacionada à conservação da biodiversidade. No entanto, outras abordagens mais detalhadas de biomas em outra escala abordam as características particulares de cada unidade biológica (IBGE, 2012). Como a América do Sul ocupa uma grande faixa da região tropical, florestas tropicais são destaques no continente. Primeiramente, a Amazônia é o bioma com maior extensão na América do Sul (mais de 6 milhões de quilômetros quadrados), cujas bacias da região influenciam padrões de circulação atmosférica ao norte e ao sul do Equador. Sua extensão contempla principalmente o Brasil, mas também outros países como Peru e Bolívia (VEBLEN et al., 2007). A maior parte da Amazônia se encontra na zona tropical úmida com temperaturas constantes (temperaturas anuais médias de 23-27ºC), com amplitude térmica diurna baixa e umidade do ar alta devido a rede de rios largos e forte nebulosidade durante todo o ano (NIMER, 1989; VEBLEN et al., 2007). As chuvas são abundantes, com uma precipitação anual de aproximadamente 2,500 mm (FIGUEROA e NOBRE, 1990). Apesar de algumas oscilações climáticas ocorrerem na Amazônia, elas são bem menos intensas do que em outros biomas, mantendo um ambiente constante e homogêneo, ocorrendo inclusive chuvas nas chamadas "estações secas" (NIMER, 1989).

Outro bioma com uma floresta relativamente densa é a Floresta Atlântica, ocupando 98 mil quilômetros quadrados próxima à costa do Brasil, um tamanho extremamente inferior à sua área original, o que faz dela uma das florestas tropicais mais ameaçadas. A temperatura nesse bioma varia mais do que na Amazônia, com temperaturas anuais médias entre 14 e 21ºC, atingindo um máximo de aproximadamente 35ºC e um mínimo menor que 1ºC. A precipitação é um pouco semelhante à da Amazônia, no entanto a topografia da região (leste-oeste) faz com que seja menos homogênea (VEBLEN et al., 2007). Diversas são as espécies endêmicas desse bioma, as quais infelizmente cada vez mais entram na categoria de ameaçadas de extinção, sendo agravadas por problemas relacionados ao impacto humano, a exemplo do desmatamento (SOS MATA ATLÂNTICA e INPE, 2017; VEBLEN et al., 2007).

Em contraste com os biomas citados, podemos também evidenciar biomas mais secos e sazonais, como o Cerrado e a Caatinga. O primeiro se localiza no Planalto Central Brasileiro, caracterizado por formações abertas, com estrato graminoso característico, demonstrando papel ecológico importante do fogo (CARVALHO e ALMEIDA, 2011). As temperaturas são também mais elevadas, variando entre 20 a 26ºC (NIMER, 1989). O Cerrado ainda possui certa limitação hídrica, com uma precipitação média anual variando entre 300 a 1,200 mm, com aproximadamente 5 a 10 meses secos (VEBLEN et al., 2007). Já a Caatinga está localizada principalmente no nordeste do Brasil, com predomínio de árvores decíduas e xerófitas. Como no Cerrado, as temperaturas também são altas, porém a precipitação é escassa em pelo menos nove meses, tendo somente alguns poucos meses com chuvas torrenciais, podendo causar fortes erosões (CARVALHO e ALMEIDA, 2011; VEBLEN et al., 2007).

Esses são apenas alguns dos biomas que representam a Região Neotropical, tendo como base principalmente a extensão do Brasil, evidenciando ecossistemas distintos. Dentro de abordagens de estudos com escala de distribuições amplas, é possível analisar e avaliar algumas hipóteses ecogeográficas, e entender como os diferentes organismos reagem a mudanças de ambientes.

Diferentes condições ambientais (e.g., temperatura) permitem compreender como ocorre a variação do tamanho corporal em espécies ao longo de um gradiente latitudinal, sendo essa relação com o espaço geográfico conhecida como regra de Bergmann (BERGMANN, 1847). Em climas frios (aumento da latitude e elevação) as espécies ou indivíduos endotérmicos de grande porte apresentam menores proporções superfície/volume do corpo permitindo assim uma melhor retenção de calor (ou menor perda de calor) do que os animais de pequeno porte (BERGMANN, 1847; MEIRI, 2011). Apesar da falta de estudos com animais tropicais, a estimativa é que esse efeito esteja presente como previsto pela generalização ecológica da “regra” para diversos mamíferos (CLAUSS et al., 2013; MEIRI e DAYAN, 2003). Não há um consenso quanto a explicação termal dessa variação, sendo possível que diversos outros fatores ambientais ou um conjunto deles (teoria do nicho – HUTCHINSON (1957)) haja no tamanho corporal ou ainda em outras características morfológicas (MILLIEN et al., 2006).

A variação fenotípica também é possível quanto à disponibilidade de chuvas que, consequentemente, levam muitas vezes o ambiente a uma produtividade primária mais elevada (KNAPP e SMITH, 2001; YOM-TOV e GEFFEN, 2006). Por exemplo, diferentes ambientes possuem diferenças na disponibilidade de recursos: uns com produtividade primária maior, mais ricos em alimentos como frutas (e.g., Amazônia), e outros com produtividade menor, com alimentos mais duros e menos abundantes (e.g., Cerrado), refletindo mudanças em alguns mamíferos no tamanho corporal (ALHAJERI e STEPPAN, 2016; MAESTRI et al., 2016) ou na variação craniana (CÁCERES et al., 2014; RYCHLIK et al., 2006). Ou seja, essa “regra de recursos” pode afetar de muitas maneiras o quanto um animal se desenvolve, aumenta em tamanho ou modifica sua forma, bem como também o seu gasto energético (MCNAB, 2010), o que mostra que efeitos de nicho dependem da história de vida e características de cada grupo estudado.

Na verdade, muitas hipóteses ecogeográficas não são exatamente uma “regra”, já que muito se debate a respeito de cada uma, e diversos organismos respondem diferentemente ou ainda não respondem a mudanças (e.g., ALHAJERI e STEPPAN, 2016; GOHLI e VOJE, 2016). Além do ambiente, o processo de variação pode ser simplesmente estocástico, isto é, um acaso sem haver necessariamente uma significância funcional (teoria neutra – HUBBELL (2001)). O neutralismo ressalta a equivalência ecológica dos organimos e o fato da restrição geográfica estruturar as interações entre eles (e.g. nascimentos, mortes, e principalmente dispersões) (ETIENNE e ALONSO, 2007; HUBBELL, 2006). Essa questão da biodiversidade não ser um caso determinístico repercurte discussões, estas que muitas vezes acabam colocando teorias de nicho e neutras como eventos isolados, confrontando as duas ideias que poderiam ser melhor compreendidas se avaliadas em conjunto (WENNEKES et al., 2012). Na realidade, ambas possuem o seu grau de importância, com perspectivas próprias de um espaço multidimensional e de relações espaciais que cada vez mais se complementam para uma melhor assimilação de padrões biogeográficos (ADLER et al., 2007; MATTHEWS e WHITTAKER, 2014). Por isso, estudos a nível específico, populacional ou ainda superiores são necessários para compreender como os grupos respondem a variações ao longo do espaço e por qual motivo, levando em consideração seus atributos funcionais.

Marsupialia, Xenarthra e Glires

Táxons da Região Neotropical como Marsupialia, Xenarthra e Glires estão na base da árvore filogenética dos mamíferos, tendo como principais separações os Marsupiais de Eutérios a cerca de 168–178 milhões de anos (DOS REIS et al., 2012), e Euarchontoglires de Laurasiatheria no período do Cretáceo a cerca de 85–100 milhões de anos (BININDA-EMONDS et al., 2007; DOS REIS et al., 2012). Na América do Sul, esses grupos possuem representantes com ampla distribuição geográfica ao longo de diversos ambientes, além de apresentarem uma longa história no continente (CIONE et al., 2015). Dentre cada um dos grupos podemos ressaltar características gerais e peculiaridades desses representantes que remontam um pouco esse período histórico e a diversidade do continente sul-americano.

Os marsupiais na América do Sul são representados por uma única família, Didelphidae, a qual possui um total de aproximadamente 100 espécies (JANSA et al., 2014). Endêmicos desse continente em sua quase totalidade, surgiram e se diversificaram tanto morfologicamente quanto taxonomicamente desde o início do Terciário (JANSA et al., 2014; ROSSI et al., 2012). Dentre as espécies basais dessa família podemos destacar espécies do gênero *Caluromys* Allen (1900), sendo *C. philander* (Linnaeus, 1758) e *C. lanatus* (Olfers, 1818) as que apresentam maior alcance dispersivo no continente (GARDNER, 2008), e uma divergência entre elas de aproximadamente 3,5 milhões de anos (JANSA et al., 2014). No entanto, essas duas espécies possuem ocorrências diferentes. *Caluromys philander* ocorre em regiões da Venezuela, Trinidade e Tobago, Guianas, leste da Bolívia, e centro e leste do Brasil. Enquanto que *Caluromys lanatus* ocorre no norte e centro da Colômbia, noroeste e sul da Venezuela, leste do Equador, Peru, e Bolívia, leste e sul do Paraguai, norte da Argentina, e oeste e sul do Brasil (GARDNER, 2008). Conhecidas popularmente como cuíca-lanosa, ambas apresentam também similaridades, como peso corporal mediano (~265-435g), hábito arborícola e noturno, e dieta essencialmente frugívora (PAGLIA et al., 2012).

Caluromys lanatus
(Foto: ©mackloy86 / iNaturalist.org)

Caluromys philander

Xenarthra é outro grupo com uma longa história na América do Sul (origem a ~67 milhões de anos) (EMERLING e SPRINGER, 2015; GIBB et al., 2016). Exibiram extraordinária diversificação no período de isolamento do continente no Terciário, com espécies extremamente grandes, mas que acabaram por se extinguir no período do Quaternário (DELSUC et al., 2004). Atualmente representado por 31 espécies (GARDNER, 2008), as que apresentam maior distribuição no continente sul-americano englobam cada um dos grupos principais que compõe essa superordem (Folivora, Vermilingua e Cingulata). De modo geral, *Bradypus variegatus* Schinz, 1825 (preguiça-comum) ocorre de Nicarágua e Honduras ao sul do Equador, Colômbia, Venezuela, a leste dos Andes em regiões florestadas do Equador, Peru e Bolívia para o norte da Argentina e Brasil (exceto extremo norte da Amazônia – Amapá e

Pará) (GARDNER, 2008; HAYSSEN, 2010). No entanto, a distribuição dessa espécie ainda não é totalmente definida (GARDNER, 2008). Por sua vez, *Tamandua tetradactyla* (Linnaeus, 1758), conhecida popularmente como tamanduá-mirim ou tamanduá-de-colete, ocorre em regiões no leste dos Andes, Equador, Peru, Bolívia e Colômbia, Venezuela, Trinidade e Tobago, Guianas, Paraguai, Uruguai, Brasil e ao norte da Argentina (GARDNER, 2008; HAYSSEN, 2011). Enquanto que a espécie *Dasypus novemcinctus* Linnaeus, 1758 (tatu-galinha) ocorre no oeste dos Andes, da Colômbia até o norte do Peru, e a leste dos Andes na Colômbia, Venezuela, Trinidade e Tobago, Guianas, ao sul do Equador, Brasil, Peru, Bolívia, Paraguai, Uruguai e norte da Argentina. Essa espécie possui maior distribuição entre os xenartros, ocorrendo até os Estados Unidos (GARDNER, 2008; MCBEE e BAKER, 1982). Entre as três espécies citadas, a preguiça é a que possui menor tamanho corporal (~4Kg) e tamanduá o maior (~5Kg), sendo o tatu com tamanho intermediário (~4,5Kg) (MCBEE e BAKER, 1982, PAGLIA et al., 2012). A preguiça possui hábito arborícola, tanto diurno quanto noturno, e se alimenta quase exclusivamente de folhas (HAYSSEN, 2010). O tamanduá apresenta hábito escansorial, com atividade principalmente noturna, possuindo uma dieta especialista em mirmecofagia (formigas e cupins) (HAYSSEN, 2011). Por fim, o tatu é uma espécie semifossorial, com hábito noturno/diurno, sendo considerado generalista, consumindo especialmente insetos (MCBEE e BAKER, 1982).


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Bradypus variegatus

© Thomas Marent / www.ardea.com

Tamandua tetradactyla

© David Hosking / www.flpa-images.co.uk

Dasypus novemcinctus

O grupo dos roedores na região Neotropical também permanece desde um longo período no continente. Os roedores caviomorfos foram os primeiros a habitarem a América do Sul, muito possivelmente no período do Eoceno (~40 milhões de anos), quando chegaram a partir da África navegando em troncos e ilhas de vegetação (ANTOINE et al., 2012). Logo em seguida, irradiaram e diversificaram no continente, ao passo que muitas linhagens persistem até os dias atuais (VIZCAÍNO et al., 2012). A subordem Histricomorpha é composta por integrantes com grande alcance dispersivo, como a espécie *Cuniculus paca* (Linnaeus, 1766) (paca), que se distribui ao sul do México, através da América Central, e nos países da América do Sul: Colômbia, Venezuela, Guianas, Equador, Peru, Bolívia, Paraguai e a maior parte do Brasil, tendo sido introduzido em Cuba e nas Pequenas Antilhas (PATTON et al., 2015). *Hydrochoerus hydrochaeris* (Linnaeus, 1766) (capivara) ocorre ao leste dos Andes, Colômbia, Venezuela, Guianas, Equador, Peru, Brasil, Bolívia, Paraguai, Argentina e Uruguai (PATTON et al., 2015). Essas duas espécies são consideradas de grande porte, sendo a capivara o maior roedor atual, podendo pesar até ~90Kg (MONES e OJASTI, 1986), e *C. paca* ~9Kg (PAGLIA et al., 2012). Ambas espécies também apresentam hábito terrestre com aptidões aquáticas, principalmente a capivara, que é especialista nesse tipo de ambiente (MONES e OJASTI, 1986; PAGLIA et al., 2012). Entretanto, a paca possui hábito noturno e dieta generalista com tendência à frugivoria, enquanto que a capivara possui hábito diurno e é totalmente herbívora (MONES e OJASTI, 1986; PÉREZ, 1992).

Cuniculus paca

Hydrochoerus hydrochaeris

Em contrapartida, outra família de roedores (Cricetidae) chegou à América do Sul a partir de um continente diferente: a América do Norte (VIZCAÍNO et al., 2012). Durante esse primeiro momento, os roedores cricetídeos desceram da América do Norte em direção ao sul, ou por ilhas ou por dispersão transoceânica, ocupando diversos nichos ecológicos a aproximadamente 9–12 milhões de anos (LEITE et al., 2014; PARADA et al., 2013). Assim, foram um componente importante no início do Grande Intercâmbio Biótico Americano, ou seja, da ligação entre os continentes americanos Norte e Sul (CIONE et al., 2015). Entre esses roedores, pode-se atualmente constatar gêneros com dispersão ao longo de toda a América do Sul, pertencentes a subordem Myomorpha, como é o caso de *Rhipidomys* Tschudi, 1845 e *Nectomys* Peters, 1861. A distribuição do complexo de espécies (~24) de ratos arborícolas (*Rhipidomys*) se estende desde o norte da Venezuela, até o noroeste da Argentina, leste do Paraguai, Brasil, leste do Panamá e em certas ilhas costeiras, incluindo Trinidade e Tobago (PATTON et al., 2015). Por sua vez, as espécies (5) de ratos d'água (*Nectomys*) são endêmicos da América do Sul e ocorrem em todos os países (exceto no Chile) e nas ilhas da plataforma continental (PATTON et al., 2015). Os dois gêneros possuem tamanho corporal reduzido (~50-

230g) (PAGLIA et al., 2012). *Rhipidomys*, como o próprio nome popular indica, possui morfologia adaptada para escalar árvores, é também um animal noturno que consome frutas e sementes em sua dieta (EISENBERG e REDFORD, 1999; PAGLIA et al., 2012). Já *Nectomys* possui hábito semiaquático, com atividade noturna e dieta generalista (ERNEST, 1986).

Rhipidomys sp. (Foto: Bonvicino C. R.)

Nectomys sp. (Foto: Bonvicino C. R.)

Por fim, a aproximadamente 0.125 milhões de anos, no período do intercâmbio entre as Américas, coelhos do gênero *Sylvilagus* Gray, 1867 vindos da América do Norte ocuparam a América do Sul (GOIN et al., 2012). A espécie *S. brasiliensis* (Linnaeus, 1758), conhecida popularmente como tapiti, é a principal espécie amplamente distribuída entre os diversos ambientes sul-americanos, desde o sul do México até parte da Argentina, e em quase todo o Brasil (CHAPMAN e CEBALLOS, 1990). O tapiti é um coelho de tamanho mediano, pesando aproximadamente 1Kg, que apresenta hábito terrestre e noturno, com uma dieta herbívora (PAGLIA et al., 2012).

Sylvilagus brasiliensis

Morfometria geométrica: forma e tamanho

Para estudos morfológicos, novas ferramentas se estabelecem para quantificar a variação da forma e tamanho dos organismos. Com o advento da morfometria geométrica, essa ofereceu dados mais informativos e uma maior compreensão dos organismos estudados (BOOKSTEIN, 1991; ROHLF e MARCUS, 1993). Seu surgimento a partir das décadas de 80–90, sendo, portanto, uma ferramenta atual, aprimorou o que antes se obtinha apenas através de organismos que eram submetidos a uma quantificação linear, ou seja, ângulos e medidas diretas

(MONTEIRO e REIS, 1999). A partir da forma do corpo do organismo, medidas lineares eram adquiridas e muitas vezes utilizadas posteriormente em análises multivariadas. Dessa maneira, era frequente a utilização da chamada morfometria tradicional (ROHLF e MARCUS, 1993).

O estabelecimento da morfometria geométrica ao longo do tempo trouxe mais acurácia para as tomadas de medidas morfológicas, incorporando o conhecimento de geometria com as coordenadas cartesianas, nominadas marcos anatômicos (= *landmarks*) (BOOKSTEIN, 1991; ROHLF e MARCUS, 1993). Marcos anatômicos são denominados como pontos os quais são localizados de modo preciso em estruturas, e esses pontos devem ser identificáveis igualmente em todos os espécimes de estudo, devendo possuir correspondência biológica (homologia) (BOOKSTEIN, 1991; MONTEIRO e REIS, 1999). A partir da configuração desses marcos é que se obtém o formato dos organismos (várias variáveis de forma e uma variável de tamanho), possibilitando a comparação por exemplo tanto intraespecífica quanto interespecífica, sejam os táxons proximamente relacionados ou não (BOOKSTEIN, 1991; MONTEIRO e REIS, 1999). Considera também as variações geométricas da forma com base na redução dos efeitos inerentes como a escala, a localização e a posição estrutural ocupada (BOOKSTEIN, 1989).

Hoje já existe uma variedade de programas computacionais para realizar análises geométricas da forma (ADAMS et al., 2013; ZELDITCH et al., 2012). É possível não apenas quantificar a porção de variação do objeto de estudo como antigamente, mas também explorar as consequências que induzem a diferenças da forma e os processos biológicos envolvidos, fatores internos (e.g., alometria) ou externos (e.g., fatores geográficos e ambientais) (ZELDITCH et al., 2004). A constatação da presença do tamanho corporal como um fator intrínseco atuante na variação da forma é essencial e necessária quando se quer entender as influências na mesma, visto que tamanho e forma estão estreitamente ligados ao desenvolvimento (KLINGENBERG, 2010). Essa dependência da forma é chamada de alometria (GAYON, 2000; GOULD, 1966), e pode estar atuante tanto ao longo do período de desenvolvimento de uma espécie (alometria ontogenética), entre linhagens filogenéticas em um determinado estágio de vida (alometria evolutiva), ou ainda na covariação dentro de um estágio ontogenético específico de uma espécie, como espécies adultas (alometria estática) (KLINGENBERG, 1998, 2016). Diferenças alométricas em espécies podem levar a um desempenho divergente, como por exemplo, na aptidão ecológica, refletindo variação na morfologia (e.g., MARROIG, 2007), sendo essa dependência da forma com o tamanho sempre algo relevante a ser considerado além das condições externas.

Assim, a origem das variações da forma e suas causas a partir de metodologias que abordam a diversidade biológica são exploradas com ainda mais precisão (FORNEL E CORDEIRO-ESTRELA). Outro exemplo importante disso é o uso da morfometria geométrica para reconstruir graficamente a forma, visualizá-la e interpretá-la anatomicamente (KLINGENBERG, 2010). A grande maioria dos estudos ainda utiliza dados bidimensionais, mas cada vez mais frequentemente estudos mais robustos com dados tridimensionais aperfeiçoam a visualização dessas mudanças na forma e trazem ainda mais clareza para entender os processos envolvidos (ADAMS et al., 2013; ZELDITCH et al., 2004).

Entre os diversos objetos de estudo da forma, as estruturas cranianas de mamíferos se mostram modelos importantes para a investigação de descritores de forma e tamanho, especialmente a vista ventral, a qual é potencialmente informativa (e.g., inferências de audição, alimentação, olfato, etc.) (CÁCERES et al., 2014; CARDINI e O'HIGGINS, 2004). Isso implica na busca de uma melhor compreensão das espécies de mamíferos mediante variações morfológicas, através do auxílio de técnicas alternativas e mais refinadas, como a morfometria geométrica.

2 OBJETIVOS

Objetivo geral

Definir padrões biogeográficos e fatores determinantes relacionados a variações cranianas em mamíferos dos grupos Marsupialia, Xenarthra e Glires, com ampla distribuição geográfica na América do Sul, com base em dados de forma e tamanho.

Objetivos específicos

Artigo I: Examinar a diferenciação morfométrica dos crânios de dois marsupiais sul-americanos, *Caluromys philander* e *C. lanatus*, analisando variações do crânio (tamanho e forma) de acordo com fatores alométricos, geográficos e climáticos.

Artigo II: Analisar a variação morfométrica craniana de representantes amplamente distribuídos da superordem Xenarthra em toda a América do Sul (*Bradypus variegatus*, *Tamandua tetradactyla*, e *Dasypus novemcinctus*), testando suas alterações ecogeográficas na forma e no tamanho.

Artigo III: Verificar as diferentes influências das variáveis alométricas, ambientais e geográficas na forma craniana de *Cuniculus paca*, *Hydrochoerus hydrochaeris*, *Nectomys* spp., e *Sylvilagus brasiliensis*.

Artigo IV: Investigar variações no tamanho e na forma de *Rhipidomys* e *Nectomys* através de parte do aparato mastigatório (série molar em conjunto com o arco zigomático), avaliando também a influência ambiental (temperatura, precipitação e produtividade primária) nas suas modificações.

3 ARTIGO I. COMPARATIVE ECOGEOGRAPHICAL VARIATION IN SKULL SIZE AND SHAPE OF TWO WOOLLY OPOSSUMS (GENUS *CALUROMYS*)

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Comparative ecogeographical variation in skull size and shape of two woolly opossums (genus *Caluromys*)

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Abstract

Environmental pressures are key mechanisms in the change of size or shape of an organism. In addition to external factors, the pressure of allometry (size-related shape changes) can also be present itself in the way that shape varies even in adulthood. In this study, we used a geometric morphometric approach to analyse skull size and shape variation in South-American Didephidae, genus *Caluromys*, represented by two species, *Caluromys philander* and *C. lanatus*, in relation to allometry, geography and climate. We found significant allometric effects on these species, especially *C. lanatus*. The strong role of geographical space mainly on size of both species and on shape of *C. lanatus* suggests that they are spatially structured, supporting neutral processes, such as drift, in their evolution. Size of both species was related to latitudinal variation, the inverse pattern of Bergmann's rule. Temperature and the set of bioclimatic variables influenced both size and shape of species. The shape of *C. philander* was influenced by bioclimatic variables (e.g. rainfall), while the shape of *C. lanatus* showed such influence (mostly temperature) but just when under the presence of allometry. Our results indicate the importance of allometry and environment in the patterns of skull shape variation in the South-American *Caluromys*, with a concomitant influence of geography. Climatic factors, such as the temperature, have strong influence on cranial changes along populations, with the two species varying similarly in skull size and shape along a climatic gradient. The latitudinal distribution, although mostly parapatric, of these congeneric species in South America should be in part responsible for their similarities in the observed phenotypic variation.

Keywords: Neotropical marsupials. Geometric morphometrics. Geography. Climate. Bergmann's rule. South America.

Introduction

The association between morphology and ecology can provide relevant information on the expression of phenotypic interactions with the environment, showing both directions and patterns of phenotypic evolution (Adams and Collyer, 2009). The trajectory of such relationships can be seen through time (e.g. Siepielski et al., 2009) or along a spatial gradient (e.g. Doebeli and Dieckmann, 2003). Phenotypic characteristics, particularly those related to body shape, highlight similarities and differences according to the environment in which the animal lives, resulting in the selection of determining characteristics, especially in the phenotypic differentiation of taxa (Adams and Collyer, 2009). However, besides verifying that these morphological and environmental interactions do in fact occur, one of the key aims in the study of shape is to determine how the environment acts on these changes (Blois and Hadly, 2009; Polly et al., 2011).

Extant marsupials of the order Didelphimorphia consist only of Didelphidae, the species-richest family of the Neotropical marsupials, with 19 genera and about 100 species. The didelphids originated in South America during the lower Tertiary, with Caluromyinae being one of the most basal groups (Jansa et al., 2014). Within the Caluromyinae subfamily, the genus *Caluromys* Allen (1900) is currently composed of three species: *Caluromys derbianus* (Waterhouse, 1841), *Caluromys lanatus* (Olfers, 1818) and *Caluromys philander* (Linnaeus, 1758). The latter two are distributed throughout South America (*C. philander* in the eastern portion and *C. lanatus* in the western portion), with some regions of sympatry (Costa and Patton, 2006). The distribution of *C. derbianus* is mostly restricted to Central America (Gardner, 2008). *Caluromys* species are forest-dwellers with arboreal habits and mostly frugivorous diets (Gardner, 2008; Paglia et al., 2012).

Differences in general morphology suggest that this group requires further study (Voss et al., 2001). Its morphological variation indicates an average of eight subspecies of *C. derbianus* (Bucher and Hoffmann, 1980; Gardner, 2008), six of *C. lanatus* (Cáceres and

Carmignotto, 2006; Gardner, 2008), and four of *C. philander* (Gardner, 2008). These morphological differences within the genera may be a result of variation in skull shape under the expression of size as an allometric factor, as seen for other species of didelphids (Astúa, 2010; Flores et al., 2003; Sebastião and Marroig, 2013). Allometry mainly affects developmental processes commonly seen during the ontogenetic period, accounting for a strong presence in the form of a final structure in the adult stage of an individual (Klingenberg, 1998). This relationship with size remains strong in didelphids and other marsupial groups so that it may be a conservatism factor in skull development (Flores et al., 2010). In addition, allometry could remain in adults, even taking into account the effect of geographical variation, as recently reported for other widely distributed geographically groups such as capuchin and howler monkeys (Cáceres et al., 2014; Meloro et al., 2014a).

Selective pressures indicated that geographical distance per se also drives changes in the size and shape of the skulls in different orders of mammals (Fornel et al., 2010; Martinez et al., 2013; Meloro et al., 2014a). The geographical space (e.g. at continental scale) can influence size more strongly than shape, since size presents higher plasticity and adaptation (Cardini and Elton, 2009; Cardini et al., 2007). Furthermore, geography has a great importance in relation to stochastic events of the species, such as dispersal limitation and drift (Rosindell et al., 2011). Regarding latitude, mammals generally follow a gradient of increasing body size toward higher latitudes (cold climates), according to the Bergmann's rule (Ashton et al., 2000; Meiri and Dayan, 2003), but this trend seems to occur in the opposite way for some genera of Didelphidae (Damasceno and Astúa, 2016; Fonseca and Astúa, 2015). Although it has not been tested, there is a tendency even for *C. lanatus* to have smaller body sizes at higher latitudes (Fonseca and Astúa, 2015). Therefore, latitude should be more important than longitude in species variation in the tropics due to the strong environmental gradient across latitudes (Davies et al., 2009).

Recently, Fonseca and Astúa (2015) examined the intraspecific geographic variation of the species *C. derbianus* and *C. lanatus* among populations from different localities using skulls and mandibles, dealing with possible taxonomic classifications of their subspecies. Together with geometric morphometric techniques and comparative analyses between populations, the authors found no substantial geographical variation among populations of *C. derbianus* in skull size or shape. However, skull size of *C. lanatus* varies significantly over geographical space, but the shape remains more conserved, with little geographical variation. Thus, based on the geographic variation of these species, both geographic and bioclimatic variables may act on the cranial shape and size of *C. lanatus* (Fonseca and Astúa, 2015) as well as on its closely related species *C. philander* (Costa and Patton, 2006).

Another explanation for morphological differences within the genus can be the effects of environmental variation (Fonseca and Astúa, 2015; López-Fuster et al., 2008). The environment is constantly changing in space and time, and this is especially true due to the climatic changes that occurred during the Quaternary period (Davis et al., 2005). In this context, South-American mammals mainly evolved in isolation during the Tertiary, marked by rare episodes of dispersion and faunal exchange in more recent times (Croft, 2012). Over the time, the basal lineages of didelphids inhabited rainforests and sporadically have diversified to inhabit grasslands and drier environments (Jansa et al., 2014). Consequently, *Caluromys* representatives may be responding adaptively to the climate throughout their geographical range, extending from the equatorial to the subtropical zones (Gardner, 2008).

South America presents a wide variety of biomes, ranging from highly forested environments (Amazon and Atlantic Forest) through an extensive region of seasonally dry and wet environments (Cerrado) to regions with very dry climate (Caatinga and Chaco) (Da Silva and Bates, 2002). On this continent, some ecogeographical studies have focused on skull size and shape variation between mammal species, including the comparison of climatically stable and seasonal regions (e.g. Bubadué et al., 2015; Cáceres et al., 2014; Machado and Hingst-Zaher, 2009) and tests for the presence of the Bergmann's rule (e.g. Martinez et al., 2013; Meloro et al., 2014a). Dealing with these issues may indicate that some species of South-American mammals are influenced by climate change, and this observation may be extended to other mammal groups (e.g. Monteiro et al., 2003). Climate influences skull shape in a way that is adaptive to different environments, wet or dry, revealing that distinct phenotypes are influenced for example by rainfall or temperature (Bubadué et al., 2015; Cardini et al., 2007; Meloro et al., 2014b). Thus, the skull of mammals is a crucial structure for verifying morphological differences between and within taxa along a geographical gradient (López-Fuster et al., 2000; Souto-Lima and Millien, 2014).

Phenotypic variation in mammals is one of the primary responses to changes in climate, and it is essential to understand this interaction in terms of species conservation (Barnosky et al., 2003). The aim of this study is to examine the morphometric differentiation in the skulls of two South-American marsupials, *Caluromys philander* and *C. lanatus*. We analysed the cranial variation in size and shape of *Caluromys* species according to allometric, geographic and climatic factors, verifying the ecogeographical variations of these species. We tested the hypothesis that size and shape of *Caluromys* species are influenced by multiple factors along the continent; in addition, there are slight differences between *C. philander* and *C. lanatus* since they are mostly parapatric on this continent. Subsequently, we predicted that allometry drives at least in part the skull shape. The species follow the converse to Bergmann's rule as suggested in the literature for some didelphid species. Differences in size and shape among populations reflect changes over the different biomes of South America where the two species are distributed, i.e. the different regional climatic conditions linked to hot, humid vs. arid and dry environments found in the continent.

Materials and methods

Data collection

We made skull pictures of 158 adult specimens in ventral view (N = 133, *C. philander*; and N = 25, *C. lanatus*) (Table 1, see also Appendix A in Supplementary material). Additionally, we recorded the geographical coordinates of collection samples for each specimen (Fig. 1). Skull pictures were obtained by applying a standard protocol to avoid possible image deformation. We used a digital camera Nikon CoolPix P530 placed at a fixed distance of 1.5 m using a tripod. We placed the skull with the palate perpendicular to the camera lens, also with a scale bar placed close to the skull for subsequent labeling.

Table 1. Skull sample size for *Caluromys philander* and *C. lanatus* included in this study.

Species	$N_{localities}$	$N_{specimens}$	$N_{females}$	N_{males}	$N_{undetermined}$
Caluromys philander (Linnaeus, 1758)	46	133	74	57	2
Caluromys lanatus (Olfers, 1818)	17	25	15	8	2
Total	63	158	89	65	4

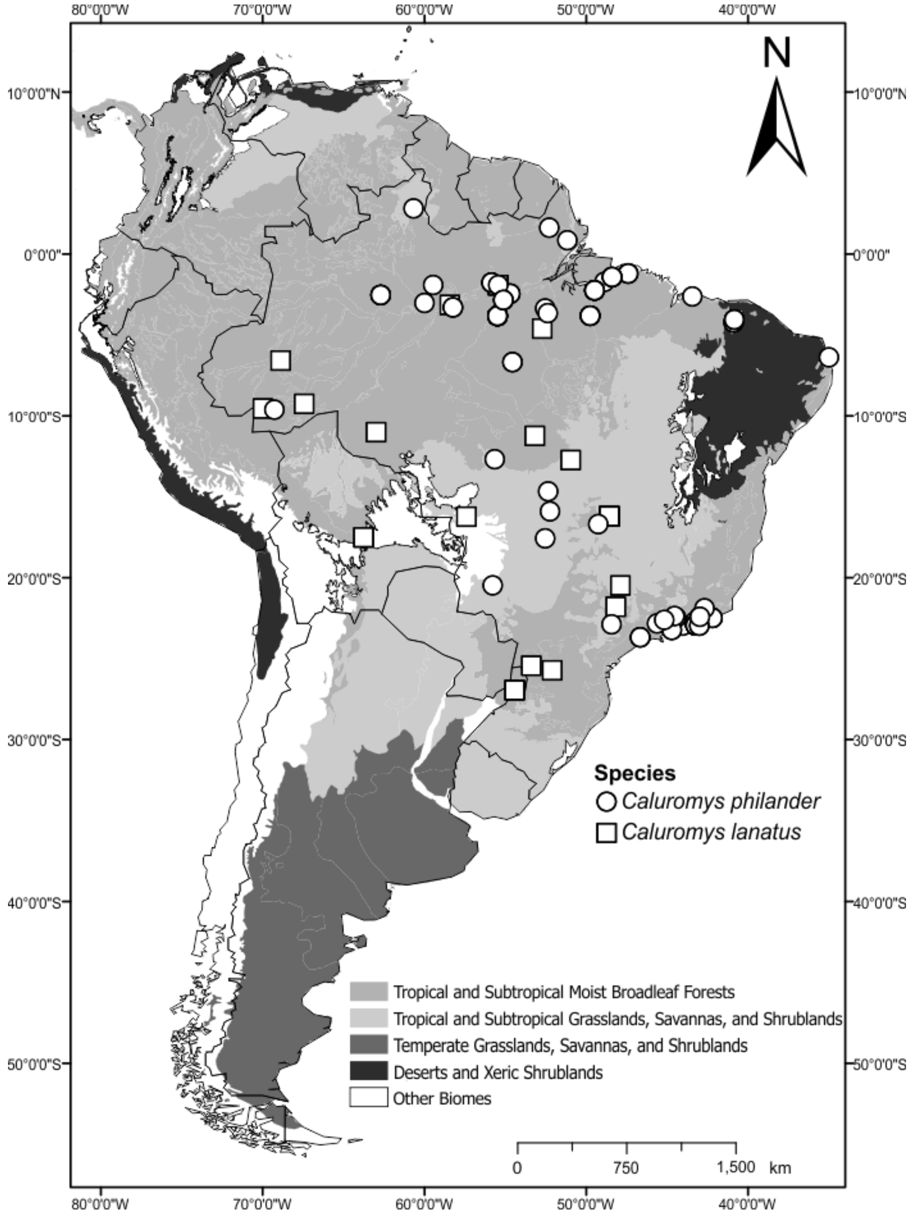

Fig. 1. Map of South America showing the sampling distribution of *Caluromys* specimens. The sampling localities of different species are shown by different symbols.

Thirteen two-dimensional homologous landmarks were digitized (Fig. 2) using the software tpsDig2 v. 2.16 (Rohlf, 2010a), carried out by a single observer (L.Z.M.) in order to avoid inter-observer error. Additionally, to assess the accuracy and repeatability of these landmarks, we randomly landmarked four specimens (two of each species) twice (on different days), obtained inter-landmark distances, and compared the mean error for each specimen. A landmark error smaller than 3% was observed, indicating that our intra-observer error is negligible (Cardini and Tongiorgi, 2003; Meloro, 2011). The landmarks chosen describe the overall skull shape, the braincase, the temporal muscle area (zygomatic arch), the muzzle (palate), and the position and size of the teeth.

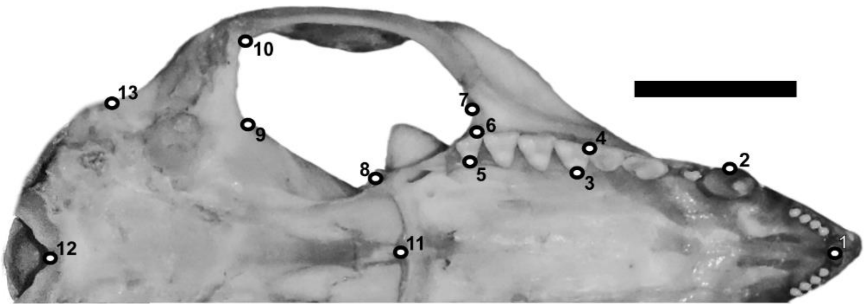

Fig. 2. Position of 13 landmarks on a skull of *Caluromys philander*. Landmark definitions: 1 = midpoint of central incisors; 2 = labial-most point of canine; 3 = lingual-most point of cusp of the first molar; 4 = labial-most point of cusp of the first molar; 5 = lingual-most point of cusp of the fourth molar; 6 = labial-most point of cusp of the fourth molar; 7 = anterior-most point on curvature of the zygomatic process; 8 = posterolateral tip of palate; 9 = base of the posterior border of the alisphenoid portion of the zygomatic process; 10 = posterolateral-most point on curvature of the zygomatic process; 11 = posterior-most tip of suture between palates; 12 = anterior-most point of foramen magnum; 13 = exterior border of braincase, anterior to the posttympanic process. Scale bar is 1 cm.

Statistical analyses

From the Generalized Procustes Analysis (GPA) (Rohlf and Slice, 1990), a reference configuration was obtained (Procrustes coordinates = shape), in accordance to the removal effects of size, orientation and position from original landmark coordinates, using the software tpsRelw v. 1.49 (Rohlf, 2010b). A principal component analysis (PCA) was also performed using the covariance matrix of the Procrustes coordinates obtained by GPA in order to obtain new axes, reducing the dimensionality of the data set and supporting the independence of variables (Klingenberg and Gidaszewski, 2010), using the software tpsRelw. We scaled the configuration of skull size from the centroid size (CS), which is the square root of the sum of squared distances between each landmark and the centroid (Bookstein, 1991). The principal component axes (here called “relative warps” – RW) and the Procrustes coordinates determine the shape, and the centroid size in natural logarithm (lnCS) determines the size.

To test the sexual dimorphism within species we applied a Procrustes ANOVA for size and shape including sex as a factor. Subsequently, we applied these same analyses to test the differences in size and shape between the two species. The presence of allometry (size effect) on the skull shape was tested by multivariate regression analyses with the software MorphoJ 1.05 (Klingenberg, 2011), with size as independent variable and shape variables as dependent ones. After checking the allometric impact on shape, we used MorphoJ software to compare the direction of allometric regression vectors between *C. philander* and *C. lanatus*. This provides a direct test to assess the impact of allometry on shaping *Caluromys* species, observing if phenotypic changes are on the same direction in an allometric gradient. If the observed angles are significantly smaller than 90º ($P < 0.05$), then non-independence occurs between the two vectors. To test the spatial structure and its effect on skull size and shape, we performed a spatial analysis using a method based on principal coordinates of neighbor matrices (PCNM) (Borcard and Legendre, 2002). Then a forward selection with permutation tests was performed. We tested the resulted PCNM variables against size (lnCS) and shape (scores of RW axes that explained at least 95% of variance) dependent variables through multivariate regressions and multivariate multiple regressions respectively.

Additionally, to test the relationship of variable size against latitude (a predictor variable), we applied linear regressions for each species separately. Furthermore, it was performed multivariate regressions with shape variables (scores of RW axes that explained at least 95% of variance) against the latitude. We performed the analyses in R environment 2.8.1 (R Development Core Team, 2013) using routines in the package *geomorph* (Adams and Otárola-Castillo, 2013) for sexual dimorphism and differences between species. Package *vegan* (Oksanen et al., 2015) and *packfor* (Dray et al., 2009) were used for spatial structure analyses. To test the impact of climate on skull size and shape we extracted 19 environmental variables including temperature, rainfall and seasonality data with a resolution of 10' from the WorldClim raster database (Hijmans et al., 2005) for each specimen locality, by using the DIVA-GIS 7.5 software (http://www.diva-gis.org/download).

First, we used the two-block partial least squares (PLS) analysis to test the influence of variable blocks temperature (BIO1-11) and rainfall (BIO12-19) against skull size (lnCS) and shape (Procrustes coordinates). After, we performed an analysis of PLS to test the correlation between size and shape with the block of environmental variables (BIO1-19). PLS extracts vectors from the correlation matrix of each block so that the degree of co-variation between one block and the other is maximised (Rohlf and Corti, 2000). Finally, we compared the angle between PLS shape vectors of these two species to a random distribution. If the two vectors are not independent, it shows that the two species vary their shapes similarly along the same environmental gradient (Klingenberg et al., 2002). For PLS analyses, we used MorphoJ 1.05 (Klingenberg, 2011). TpsPLS v.1.18 (Rohlf, 2006) was used specifically for plotting the relationship between shape and environment. In addition, we also generated “size-free” shape variables as a second approach to control the effect of allometry, with shape variables obtained as the residuals of multivariate allometry. We applied a second PCA on the Procrustes coordinates for latitude and geography analyses. Then, we reanalyzed the regressions (with latitude and PCNM as predictors) and PLS with these new size-free shape variables.

Results

Sexual dimorphism

There is no interaction between species and sex regarding size (F = 0.195, P > 0.05) and shape (F = 0.459; P > 0.05). Thus, since sexual dimorphism is not detected, all subsequent analyses are treated with both sexes and undetermined specimens all together (Fonseca and Astúa, 2015; López-Fuster et al., 2008).

Skull size and shape

Caluromys philander and *C. lanatus* differ in size (F = 64.442, P < 0.001; Fig. 3), with *C. lanatus* being larger. The two species also show significant differences in shape (F = 9.175, P < 0.001).

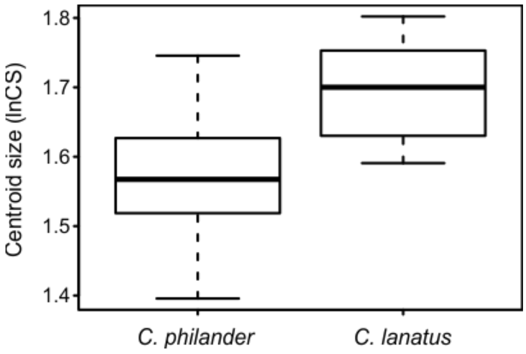

Fig. 3. Box plot with standardized deviation of centroid size (natural log trans-formed – lnCS) across the two species of *Caluromys*. Black string = median; box = first interquartile; bar = second interquartile.

The first 14 relative warps cumulatively explain 95% of total variance. Plotting the first (33.93%) with the second (11.75%) RW, the plot shows little differences between the two species related to skull shape (Fig. 4). For RW1, there is a large overlap between species samples, with negative values being related to a more elongated temporal muscle area, smaller molars, and a slightly elongated and thin muzzle, whereas the opposite is seen at the positive values. The RW2 does not segregate the two species either, with a wide range of morphospace occupied by *C. philander* whereas *C. lanatus* samples are located more in the negative values, describing shape changes related to a narrower and longer skull, a narrower temporal muscle area, and a more elongated and thin muzzle. On the positive scores of RW2, specimens (particularly for *C. philander*) have a thick temporal muscles area, a shorter muzzle, and a wider braincase.

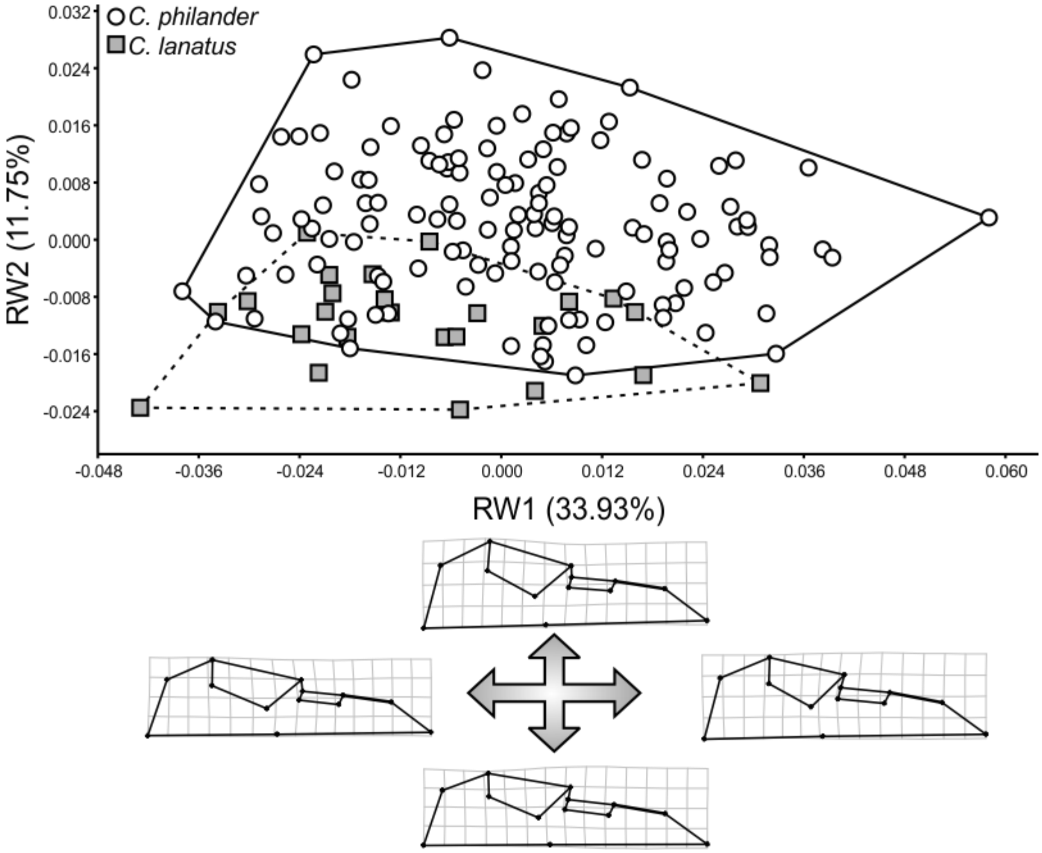

Fig. 4. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the species shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. Every species is labeled with minimum convex hull superimposed.

Allometry

There is a significant impact of allometry on skull shape, explaining 19.40% for *C. philander* and 33.67% for *C. lanatus*. The changes of cranial shape relative to allometry are similar for both species, but more pronounced in *C. lanatus*, both showing a narrow and elongated skull and temporal muscle area toward an increase in size (Fig. 5A and B). When compared the directions of PLS shape vectors due to size gradient, they are significantly distinct of 90º (angle = 30.04º; P < 0.001), indicating similar trajectories between species along the allometric trajectory.

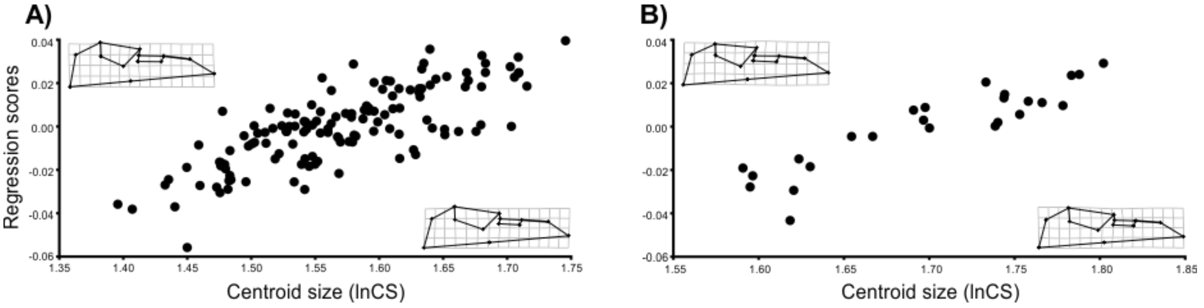

Fig. 5. Scatter plot obtained by regression of shape onto the size (lnCS) for (A) *Caluromys philander* and (B) *C. lanatus*. Graphical deformation grids are shown for negative and positive extremes of the regression scores computed for each species.

Geography

A geographical pattern of influence is found with the PCNM analyses (Table 2). Geography strongly affects the size of *C. philander* and *C. lanatus*, but only the shape of *C. lanatus*.

The influence of latitude on size is significant for *C. philander* and *C. lanatus*, following the converse of Bergmann's rule (Fig. 6A and B; see also Appendix B in Supplementary material for different approaches). That is, size increases in low latitudes for both species. For skull shape, there is no significant impact of latitude for *C. philander* or *C. lanatus*. However, *C. lanatus* shape variation on latitude becomes significant after allometric control (size-free) (Table 3).

Table 2. Multivariate regressions and multivariate multiple regressions of dependent variables (Y) Size (lnCS) and Shape (relative warps corresponding to 95% of shape variation) with PCNM (principal coordinates of neighbour matrices) predictors (representing geographical space) for South-American *Caluromys*. Significance is highlighted in bold.

Species	Y	R^2	adjusted R^2	F-statistic	Df	P value
C. philander	Size	0.17	0.15	9.058	3/129	**<0.001**
	Shape	0.01	-0.01	0.537	3/129	0.658
C. lanatus	Size	0.28	0.25	8.995	1/23	**0.006**
	Shape	0.19	0.16	5.458	1/23	**0.028**
Size-free						
C. philander	Shape	0.03	-0.00	0.955	4/128	0.435
C. lanatus	Shape	0.31	0.28	10.160	23	**0.004**

Forward selection by permutation of residuals under reduced model performed using R package *packfor*. *C. philander*: size (PCNM4, PCNM14, PCNM18), shape (PCNM4, PCNM6, PCNM18), size-free (PCNM4, PCNM6, PCNM16, PCNM17); *C. lanatus*: size (PCNM10), shape (PCNM3), size-free (PCNM6).

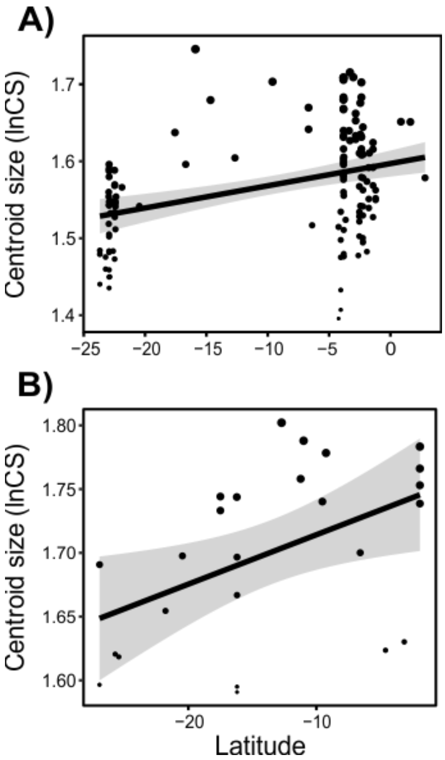

Fig. 6. Centroid size (natural log transformed – lnCS) variation relative to latitude. *Caluromys philander* vs. absolute value of latitude (A), and *C. lanatus* vs. absolute value of latitude (B). Symbol size increases with size.

Table 3. Regressions and multivariate regressions of dependent variables (Y) Size (lnCS) and Shape (relative warps corresponding to 95% of shape variation) with the predictor variable Latitude for South-American *Caluromys*. Significance is highlighted in bold.

Species	Y	R^2	adjusted R^2	F-statistic	Df	P value
C. philander	Size	0.13	0.12	19.140	131	**<0.001**
	Shape	0.01	0.00	1.500	131	0.223
C. lanatus	Size	0.22	0.19	6.680	23	**0.017**
	Shape	0.05	0.01	1.114	23	0.302
Size-free						
C. philander	Shape	0.00	-0.01	0.070	131	0.792
C. lanatus	Shape	0.18	0.15	5.129	23	**0.033**

Size versus climate

Size is covarying with temperature for *C. philander* but mainly for *C. lanatus* (Table 4, Fig. 7A and B). However, rainfall is significant only for *C. philander* (Table 4, Fig. 7A). In general, climate (mainly temperature) influences more the size of *C. lanatus* than the size of *C. philander* (Table 4).

Table 4. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors (SW1) of Size (lnCS) and Shape comparing to Temperature (BIO1-11 bioclimatic variables), Rainfall (BIO12-19 bioclimatic variables) and Climate overall (BIO1-19 bioclimatic variables) for South-American *Caluromys*. Significance is highlighted in bold.

Species	Size			Shape		
	rv (%)	r	P value	rv (%)	r	P value
Temperature						
C. philander	100	0.45	**<0.001**	97	0.59	**<0.001**
C. lanatus	100	0.62	**0.002**	92	0.70	**0.024**
Rainfall						
C. philander	100	0.22	**0.044**	82	0.48	**<0.001**
C. lanatus	100	0.48	0.061	80	0.59	0.178
Climate overall						
C. philander	100	0.41	**<0.001**	92	0.57	**<0.001**
C. lanatus	100	0.62	**0.004**	82	0.69	**0.034**

Size-free	Shape		
Species	rv (%)	r	P value
Temperature			
C. philander	92	0.57	**<0.001**
C. lanatus	93	0.65	0.287
Rainfall			
C. philander	73	0.54	**<0.001**
C. lanatus	59	0.69	0.173
Climate overall			
C. philander	83	0.58	**<0.001**
C. lanatus	71	0.67	0.222

Two-block partial least squares analysis of size vs climate variables extracted a significant pair of axes. The plot shows only small overlap between the two species (*C. philander* on positive SW1 size scores and *C. lanatus* on negative SW1 size scores), but there is no separation from the SW1 climate (Fig. 8).

Shape versus climate

Temperature has a significant covariation with shape mainly for *C. lanatus* than for *C. philander* (Table 4, Fig. 7A and B). Rainfall, on the other hand, only has influence on *C. philander* (Table 4, Fig. 7A). In addition, overall climate influences the shape variation of *C.*

philander and particularly of *C. lanatus* (Table 4, Fig. 9). As shown for size, rainfall appears to be less important than temperature in the association with shape variation in these *Caluromys* species (see also Appendix C in Supplementary material), especially for *C. lanatus*.

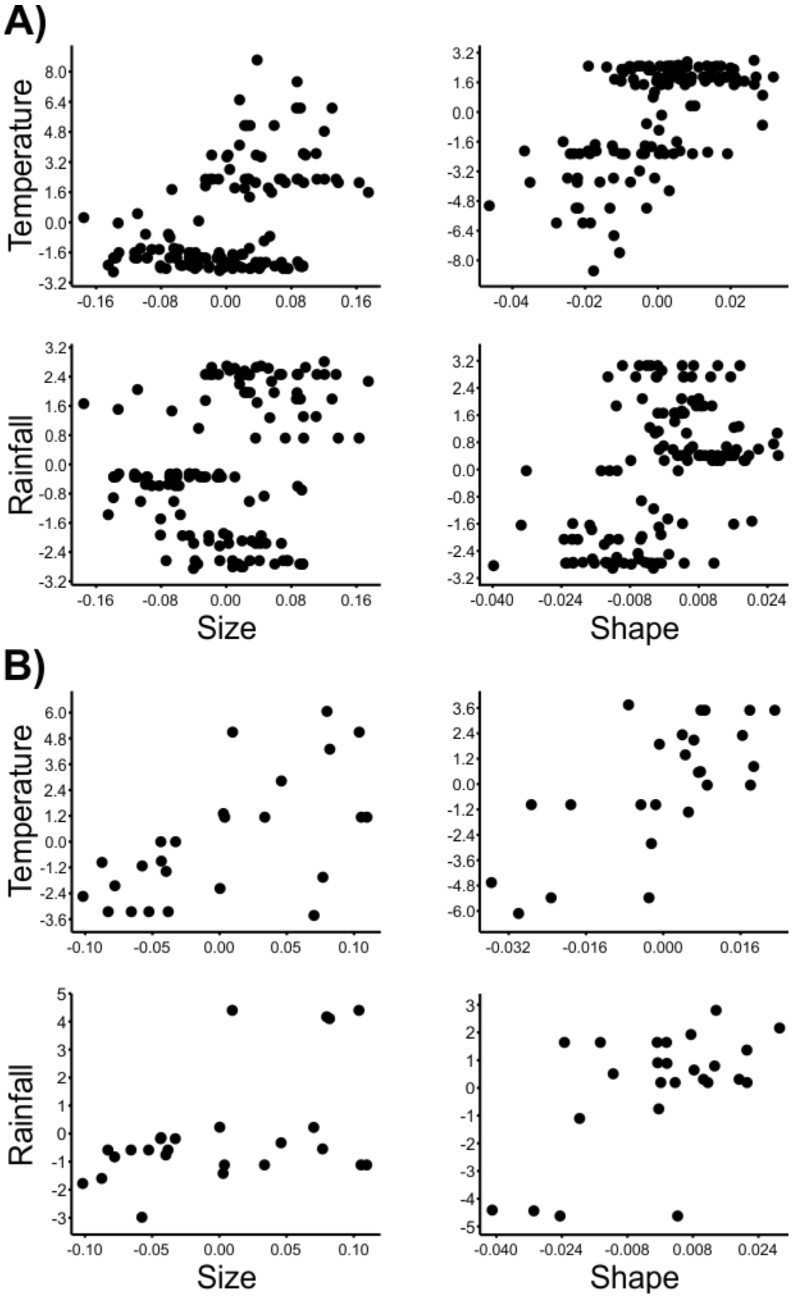

Fig. 7. Plot of the first pair of Singular Warps for size (lnCS) and shape variation in (A) *Caluromys philander* and (B) *C. lanatus* with temperature (BIO1-11 bioclimatic block) and rainfall (BIO12-19 bioclimatic block).

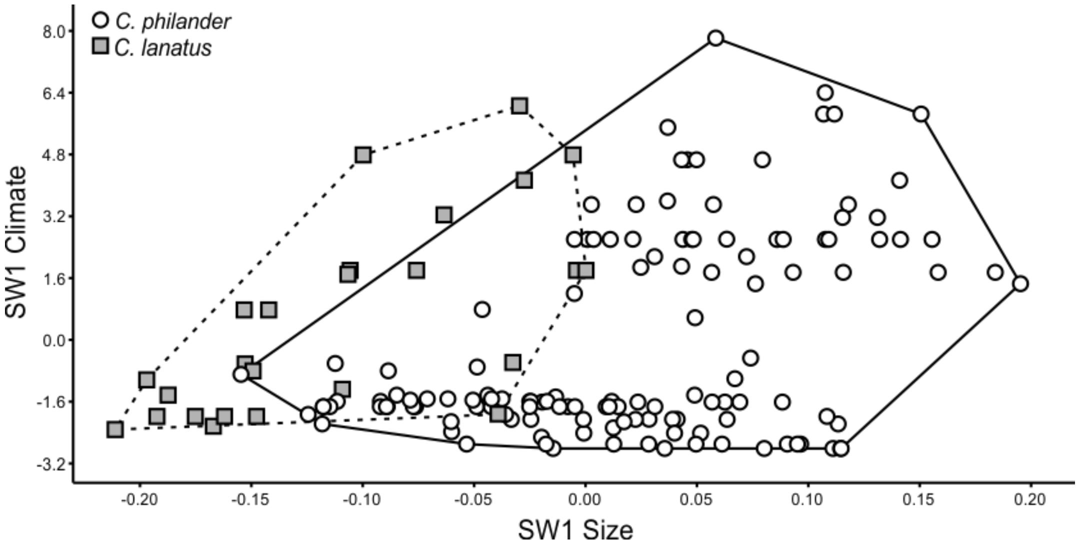

Fig. 8. Plot of the first pair of Singular Warps for size (lnCS) variation in *Caluromys philander* and *C. lanatus* and climate (axis X is block size, axis Y is block climate).

A scatter plot with Singular Warp SW1 shape vs. SW1 climate variables supports little separation among species, but it shows a tendency of the skull shape variation along an environmental gradient, mainly influenced by variables of temperature (Fig. 9, see Appendix C in Supplementary material). Populations of *C. philander* (Fig. 9A) distributed in more arid or seasonal regions (SW1 climate negative scores) exhibit a more compressed skull as a whole, with a wider braincase, and a shorter and thicker temporal muscle area. Conversely, the opposite is seen in *C. philander* of warm and humid environments (SW1 climate positive scores). *Caluromys lanatus* in more arid regions exhibits a compressed skull as a whole, a wider braincase, a shorter and thicker temporal muscle area (similar to *C. philander*), and wider molar areas (only in this species). The species exhibits the opposite cranial traits in warm and humid regions (Fig. 9B).

The angle between the PLS shape vectors of *C. philander* and *C. lanatus* is 54.81°, which is significantly different from a 90° angle (P = 0.004), meaning similar trajectories in the patterns of skull shape covariation between the two species along the South-American biomes.

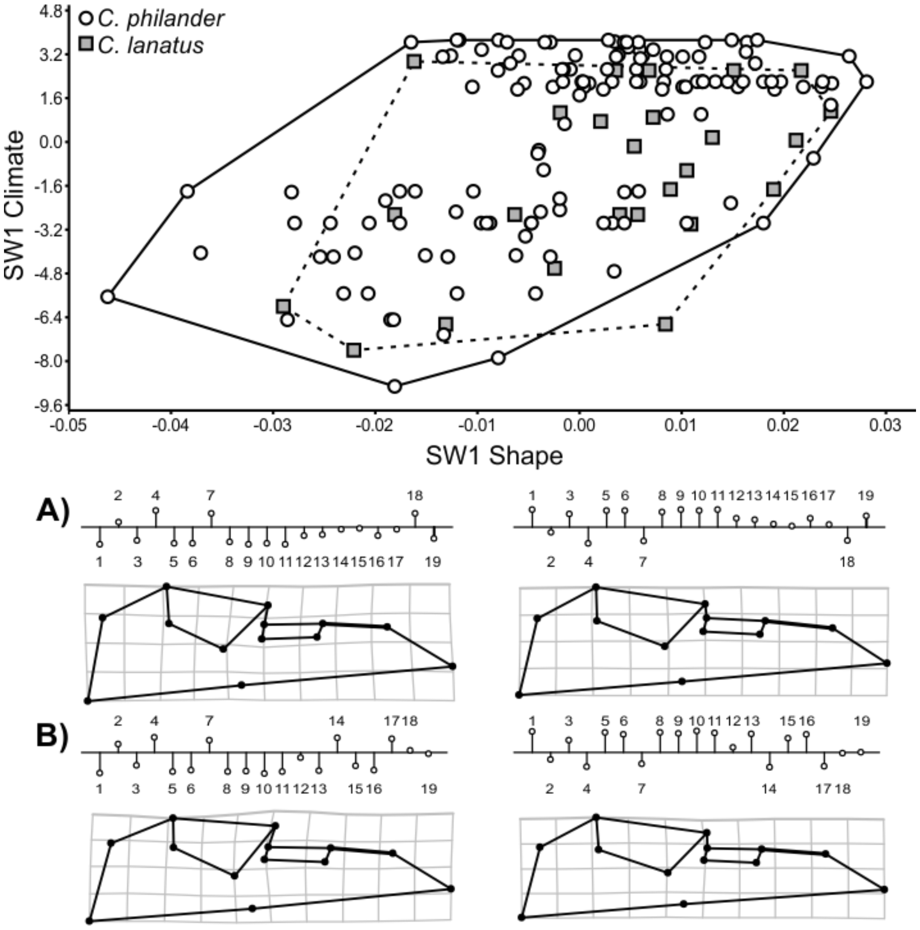

Fig. 9. Plot of the first pair of Singular Warps for shape variation in *Caluromys philander* and *C. lanatus* and climate (axis X is block shape, axis Y is block climate). Below there are variable profiles and deformation grids from the most negative to the most positive Singular Warp scores. The numbers in the variable profiles are originated from the 19 variables of WorldClim. In deformation grids, (A) is for *Caluromys philander* and (B) is for *C. lanatus*.

Size-free analyses

Part of the analyses with non-allometric cranial shape variation shows no difference for *C. philander* results when compared with previous analyses containing size effects. This is true for geography and climate (Tables 2–4). Conversely, response variables of *C. lanatus* have a more pronounced influence of geography (Table 2) and latitude (Table 3), but lose the effect of climate regarding previous analyses (Table 4).

Discussion

Our results show similarities, but also divergences when comparing size and shape variations of the two *Caluromys* species in the South-American continent. In general, the species variation is similar in relation to climate, with both species being plastic when responding to environmental predictors. However, this plasticity is moderated by a large allometric effect on their shape. The analyses at population level suggest that *C. philander* and *C. lanatus* behave differently at fine scale in regard to their phenotypic variation. This species difference in phenotypic variation confirms the high degree of molecular divergence between the two species (11.91% average genetic distances), besides the high intraspecific difference found within populations (1.5% for *C. lanatus* and 4.5% for *C. philander*) (Costa and Patton, 2006).

The separation of the two species by size and shape agrees with other studies based on body measurements (Eisenberg and Redford, 1999; Rossi et al., 2012), but these studies show little differences between the species. Here, we present a more noticeable differentiation in the skull, especially considering the fact that the two species are considered similar in shape (López-Fuster et al., 2008). Phenotypic differences between closely related species such as those of the genus *Caluromys* are often difficult to quantify and, when observed, can be related to external (e.g. environmental components – Caumul and Polly, 2005) or even internal factors (e.g. allometry – Marroig, 2007) acting beyond the phylogenetic heritage. Our results for the two species studied here also corroborate the relatively old divergence time between them (3–4 million years ago; Jansa et al., 2014), leading them to differ more morphologically than if their split was more recent. Besides, the differential distribution of the two species in the eastern and western regions of South America (Costa and Patton, 2006) is also crucial for phenotypic changes since each species experiences different regimes of seasonality. That species (*C. philander*) distributed closer to the Atlantic Ocean has a minor pressure of seasonality (Morellato and Haddad, 2000), being more related with rainfall (see below).

The two species of *Caluromys* showed an important influence of allometry on shape, confirming the prediction of allometry for cranial structures in the genus (Flores et al., 2010). Therefore, allometry had the greatest influence on overall phenotypic variation in each individual species, with both following the same direction in their changes within populations. For *C. lanatus*, allometry explained almost two times the variation in skull shape than that for *C. philander*, corroborating the strong allometric effect in adults of this species and even in the genus. In other words, part of shape modification follows size changes (Klingenberg, 1998; Marroig, 2007; Meloro et al., 2014b), especially for *C. lanatus*. Thus, the species deals with indirect ecomorphological changes, which help *C. lanatus* to better fit with the seasonal environmental requirements south of Amazonia (such as larger temporal muscles and wider molars – see Fig. 5B), as happens to primates living under the same pressures (Cáceres et al., 2014; Meloro et al., 2014a). In addition, most of the results remained the same even with the absence of allometry in the analyses.

Phenotypic changes related to geography indicate a more accurate look at the effect of the geographical distance on such species, in which their dispersal capacity and possible physical barriers to dispersal could be substantial determinants driving particularly the size variation. The two species are thought to be limited to forest areas and, because of that, grasslands and scrublands between the two main forest biomes in South America (Amazon and Atlantic Forest) may impede gene flow between isolated populations (Pardini et al., 2005). Moreover, the presence of distance effects supports the neutral theory of biodiversity (Hubbell, 2001), which comprises adaptation not only related to the environment, but a perspective related to restrictions of dispersion and stochasticity (Hubbell, 2001; Rosindell et al., 2011). So both *Caluromys* species show variations of size, and *C. lanatus* for shape, that are spatially structured, and not only environmentally dependent. Since neutral processes (drift, stochasticity) have the potential for increasing divergences (Maurer and McGill, 2004), the low dispersion capacity of smaller species, primarily arboreal and forest dwellers such as *Caluromys*, makes them subjected to geographical distance per se, with part of phenotypic changes being possibly related to these processes (Rosindell et al., 2011).

Skull variation between the two species related to latitude was important, particularly in terms of size variation. It is notable that latitude here, as a proxy for environmental variation, strongly influences the skull size of species, but contrary to Bergmann's rule, where an increasing latitude relates to a decreasing size. This agrees with independent studies of populations of *Chironectes* Illiger (1811) (Cerqueira and Weber, 2016; Damasceno and Astúa, 2016), *Didelphis* Linnaeus (1758) (J.M. Bubadué, pers. comm.) and even *C. lanatus* (Fonseca and Astúa, 2015), reflecting a tendency for the family Didelphidae to increase body size towards the Amazon. This result could be related to other kind of environmental factors, such as habitat and climate stability (Ashton et al., 2000; Clauss et al., 2013). The amount of food resources can be restricted at higher latitudes, with body size following habitat productivity (McNab, 2010; Meiri et al., 2007), which may be one of the causes for certain organisms to reduce body size in southern latitudes (e.g. Ochocińska and Taylor, 2003). Fruit availability varies seasonally (Terborgh, 1986), and high numbers of fruits tend to coincide with the availability of rain in most tropical regions (Fleming et al., 1987). Thus, since *Caluromys* species are highly dependent on the availability of foods such as fruits and pollen (Julien-Laferrière, 1995), which are not easily available in seasonal regions (Gribel, 1988; Santori et al., 2012), they may be responding to the habitat productivity by becoming larger in more stable and productive regions such as the Amazon.

When taking climate into account, it clearly shows an influence and even a tendency for the species to follow an environmental gradient in size and shape (Table 4, Fig. 9), mainly influenced by temperature variation. This relationship between species and temperature in different regions (warm and constant temperature, with lack of seasonal change, in contrast with more arid areas) suggests that South America presents a high climatic clinal variability, with a strong latitudinal climate gradient from the Amazon to the south (Da Silva and Bates, 2002; Werneck, 2011), and that species follow it (Bubadué et al., 2015; Cáceres et al., 2014; Hendges et al., 2016; Martinez et al., 2013; Meloro et al., 2014a; this study). The influence of climate could be seen in each species separately, such as in *C. philander* and *C. lanatus*. The influence of climate and temperature on shape of *C. lanatus* appears to be even stronger (by considering its smaller sample size) than on *C. philander*, which is in turn more influenced by the rainfall. Nonetheless, the allometric effect overlaps this shape change in relation to the climate, and cannot be explained by it alone (e.g. Meloro et al., 2014a). Thus, changes in *C. lanatus* shape suggest a dependence on the allometry pressure, a phenomenon that may help this species to be more plastic due to the more seasonal environments where it occurs.

In general, these two species occur allopatrically, with *C. lanatus* occurring in the western parts of South America (Costa and Patton, 2006; Gardner, 2008), which are characterised by high seasonality due to continentality. The species tend to be mostly affected by temperature seasonality, since periods of food shortage occur more frequently where environments are more seasonal (Ashton and Feldman, 2003). Moreover, *C. lanatus* can eat hard food items for possible protein supplementation of its highly frugivorous diet (Cáceres, 2005; Lessa and Costa, 2010), a strategy to deal with food shortage in seasonal regions south of Amazonia. This corroborates the fact that this species exhibits large molar areas and stronger temporal muscles, which facilitate mastication of hard foods (e.g. insects – Casella and Cáceres, 2006) in these seasonal regions (see Cáceres et al., 2014; for primates). Otherwise, *C. philander* is also influenced by rainfall, which corroborates its dependence and better chances of obtaining food in rainy environments, which are consequently richer in flesh fruits (Fleming et al., 1987).

Overall, shape changes for both species corroborate the climatic cline, with both species becoming more robust in the skull in the south, showing stronger temporal muscles. The contrary is also true, with Amazonian *Caluromys* having less powerful masticatory muscles, which could be related to the more frequent consumption of fleshy fruits in this highly productive region (see Cáceres et al., 2014; Julien-Laferrière, 1999; Meloro et al., 2014a). Therefore, also regarding the already cited differences, the two species show the same phenotypic trajectory along the environmental gradient, reinforcing the importance of shape changes moulded by the environment (Cardini and Elton, 2009; Meloro et al., 2014a). Nevertheless, the differences found between them can be attributed mostly to allometry, environment, and neutral processes as key drivers of their phenotypic changes along the South-American biomes, as also occurs in other mammalian groups such as peccaries (Hendges et al., 2016).

There is strong evidence that *C. philander* and *C. lanatus*, being mostly allopatric (Costa and Patton, 2006), have important, but subtle, differences that distinguish them regarding size and shape variations. These South-American species are examples that phylogenetically related species can show similar evolutionary trajectories, but are subjected to different geographical effects, climatic conditions, and allometric constraints. Future studies should investigate the impacts of allometry as well as niche and neutral determinants on size and shape variations of other allopatric (or sympatric), close related species. Such studies might reveal patterns not necessarily similar to those we found.

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Supplementary data

Appendix A. List of skull specimens photographed, with data of specie, sex, museum number, latitude and longitude. F = female; M = male; UND = undetermined.
Museums: Museu Nacional (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB), Museu de História Natural Capão da Imbuia (MHNCI), and Coleção de Mamíferos da Universidade Federal de Santa Maria (UFSM).

Species	**Sex**	**Nº Museum**	**Latitude**	**Longitude**
Caluromys_lanatus	UND	MACN_23632	-26.94	-54.43
Caluromys_lanatus	F	MACN_25891	-26.94	-54.43
Caluromys_lanatus	F	MACN_50181	-17.50	-63.77
Caluromys_lanatus	UND	MACN_50188	-17.50	-63.77
Caluromys_lanatus	F	MNRJ_11705	-11.23	-53.18
Caluromys_lanatus	M	MNRJ_1222	-16.22	-57.42
Caluromys_lanatus	M	MNRJ_20963	-16.20	-48.58
Caluromys_lanatus	F	MNRJ_243	-12.72	-50.97
Caluromys_lanatus	F	MNRJ_4599	-16.20	-48.58
Caluromys_lanatus	F	MNRJ_4782	-16.20	-48.58
Caluromys_lanatus	M	MNRJ_4785	-16.20	-48.58
Caluromys_lanatus	F	MPEG_28000	-6.58	-68.90
Caluromys_lanatus	F	MZUSP_27390	-11.00	-63.00
Caluromys_lanatus	F	MZUSP_32103	-9.53	-70.00
Caluromys_lanatus	M	MZUSP_3766	-21.79	-48.18
Caluromys_lanatus	F	MZUSP_4530	-3.14	-58.45
Caluromys_lanatus	F	MZUSP_4531	-1.92	-55.45
Caluromys_lanatus	M	MZUSP_4532	-9.25	-67.45
Caluromys_lanatus	M	MZUSP_4533	-1.92	-55.45
Caluromys_lanatus	M	MZUSP_4534	-1.92	-55.45
Caluromys_lanatus	M	MZUSP_4883	-1.92	-55.45
Caluromys_lanatus	F	MZUSP_8975	-4.60	-52.72
Caluromys_lanatus	F	MHNCI_4206	-25.43	-53.41
Caluromys_lanatus	F	MHNCI_930	-25.72	-52.12
Caluromys_lanatus	F	MHNCI_6470	-20.47	-47.89
Caluromys_philander	F	MNRJ_72297	-22.88	-48.44
Caluromys_philander	F	MACN_242278	-22.96	-44.04
Caluromys_philander	F	MNRJ_10432	-22.70	-43.27
Caluromys_philander	F	MNRJ_10434	-22.93	-43.24
Caluromys_philander	M	MNRJ_10436	-22.93	-43.24
Caluromys_philander	M	MNRJ_10437	-22.93	-43.24
Caluromys_philander	M	MNRJ_10438	-22.93	-43.24
Caluromys_philander	M	MNRJ_10440	-22.93	-43.24
Caluromys_philander	M	MNRJ_10441	-22.93	-43.24
Caluromys_philander	M	MNRJ_10442	-22.93	-43.24

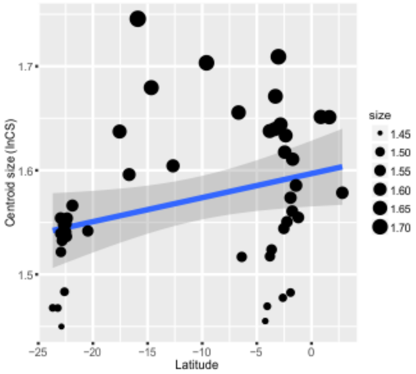
Caluromys_philander	F	MNRJ_10444	-22.93	-43.24
Caluromys_philander	M	MNRJ_10448	-22.93	-43.24
Caluromys_philander	F	MNRJ_10450	-22.93	-43.24
Caluromys_philander	M	MNRJ_11673	-12.67	-55.66
Caluromys_philander	M	MNRJ_1225	-1.72	-48.88
Caluromys_philander	F	MNRJ_1230	-22.42	-42.98
Caluromys_philander	F	MNRJ_1232	-2.24	-49.50
Caluromys_philander	M	MNRJ_16113	-4.05	-40.86
Caluromys_philander	F	MNRJ_16114	-4.23	-40.90
Caluromys_philander	F	MNRJ_16115	-4.23	-40.90
Caluromys_philander	F	MNRJ_16121	-4.05	-40.86
Caluromys_philander	F	MNRJ_16123	-4.05	-40.86
Caluromys_philander	M	MNRJ_16124	-4.05	-40.86
Caluromys_philander	F	MNRJ_16125	-4.05	-40.86
Caluromys_philander	M	MNRJ_18812	-22.93	-43.24
Caluromys_philander	M	MNRJ_20236	1.63	-52.29
Caluromys_philander	F	MNRJ_20588	-3.03	-60.00
Caluromys_philander	M	MNRJ_20773	-2.53	-62.72
Caluromys_philander	M	MNRJ_20776	-2.53	-62.72
Caluromys_philander	M	MNRJ_20778	-2.53	-62.72
Caluromys_philander	F	MNRJ_20782	-2.53	-62.72
Caluromys_philander	F	MNRJ_20783	-2.53	-62.72
Caluromys_philander	F	MNRJ_20784	-2.53	-62.72
Caluromys_philander	M	MNRJ_20964	-1.21	-47.41
Caluromys_philander	M	MNRJ_20965	-1.21	-47.41
Caluromys_philander	F	MNRJ_20966	-1.21	-47.41
Caluromys_philander	M	MNRJ_20968	-22.42	-42.98
Caluromys_philander	F	MNRJ_20969	-22.42	-42.98
Caluromys_philander	F	MNRJ_25785	-22.93	-43.24
Caluromys_philander	M	MNRJ_27828	-22.47	-44.45
Caluromys_philander	F	MNRJ_27829	-22.47	-44.45
Caluromys_philander	M	MNRJ_28997	-22.93	-43.24
Caluromys_philander	F	MNRJ_29084	-1.42	-48.41
Caluromys_philander	M	MNRJ_30421	-22.48	-42.20
Caluromys_philander	F	MNRJ_30439	-22.48	-42.20
Caluromys_philander	F	MNRJ_30460	-22.48	-42.20
Caluromys_philander	F	MNRJ_30462	-22.48	-42.20
Caluromys_philander	M	MNRJ_30562	-6.38	-35.00
Caluromys_philander	M	MNRJ_33432	-22.93	-43.24
Caluromys_philander	M	MNRJ_5591	-21.88	-42.70
Caluromys_philander	F	MNRJ_5970	-2.83	-55.13
Caluromys_philander	M	MNRJ_6100	-23.22	-44.72
Caluromys_philander	M	MNRJ_66232	-22.96	-43.01
Caluromys_philander	F	MNRJ_66233	-22.96	-43.01

Caluromys_philander	M	MNRJ_71032	-14.66	-52.36
Caluromys_philander	UND	MNRJ_77418	-23.22	-44.72
Caluromys_philander	F	MNRJ_7831	-22.42	-42.98
Caluromys_philander	M	MNRJ_80627	-22.37	-44.55
Caluromys_philander	M	MPEG_10150	-2.45	-54.70
Caluromys_philander	M	MPEG_10256	-1.76	-55.86
Caluromys_philander	F	MPEG_10434	-1.76	-55.86
Caluromys_philander	F	MPEG_10524	-1.76	-55.86
Caluromys_philander	F	MPEG_10552	-9.61	-69.29
Caluromys_philander	F	MPEG_1184	0.86	-51.18
Caluromys_philander	M	MPEG_12422	-3.80	-49.77
Caluromys_philander	F	MPEG_12423	-3.80	-49.77
Caluromys_philander	F	MPEG_12424	-3.80	-49.77
Caluromys_philander	F	MPEG_12425	-3.80	-49.77
Caluromys_philander	M	MPEG_12426	-3.80	-49.77
Caluromys_philander	F	MPEG_12582	-3.80	-49.77
Caluromys_philander	F	MPEG_12712	-2.45	-54.70
Caluromys_philander	F	MPEG_15304	-1.42	-48.41
Caluromys_philander	M	MPEG_1926	2.82	-60.68
Caluromys_philander	M	MPEG_20316	-2.36	-55.12
Caluromys_philander	M	MPEG_20317	-2.36	-55.12
Caluromys_philander	M	MPEG_20319	-2.36	-55.12
Caluromys_philander	F	MPEG_20320	-2.36	-55.12
Caluromys_philander	F	MPEG_20321	-2.36	-55.12
Caluromys_philander	F	MPEG_20322	-2.36	-55.12
Caluromys_philander	F	MPEG_20325	-2.36	-55.12
Caluromys_philander	F	MPEG_20326	-2.36	-55.12
Caluromys_philander	F	MPEG_22137	-1.92	-59.47
Caluromys_philander	M	MPEG_2399	-15.90	-52.25
Caluromys_philander	F	MPEG_33933	-2.24	-49.50
Caluromys_philander	F	MPEG_8940	-3.37	-52.55
Caluromys_philander	F	MZUSP_10030	-22.83	-45.63
Caluromys_philander	M	MZUSP_10107	-2.45	-54.70
Caluromys_philander	M	MZUSP_10117	-3.82	-55.49
Caluromys_philander	F	MZUSP_11572	-1.42	-48.41
Caluromys_philander	F	MZUSP_11576	-3.82	-55.49
Caluromys_philander	F	MZUSP_11577	-3.82	-55.49
Caluromys_philander	F	MZUSP_11578	-3.82	-55.49
Caluromys_philander	F	MZUSP_11579	-3.82	-55.49
Caluromys_philander	M	MZUSP_11580	-3.82	-55.49
Caluromys_philander	F	MZUSP_11582	-3.82	-55.49
Caluromys_philander	M	MZUSP_11586	-3.82	-55.49
Caluromys_philander	F	MZUSP_11587	-3.82	-55.49

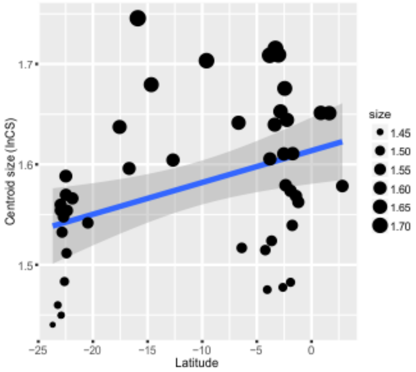
Caluromys_philander	M	MZUSP_11590	-3.82	-55.49
Caluromys_philander	M	MZUSP_11591	-3.82	-55.49
Caluromys_philander	M	MZUSP_11593	-3.82	-55.49
Caluromys_philander	M	MZUSP_11594	-3.82	-55.49
Caluromys_philander	F	MZUSP_11595	-3.82	-55.49
Caluromys_philander	M	MZUSP_11596	-3.82	-55.49
Caluromys_philander	M	MZUSP_11597	-3.82	-55.49
Caluromys_philander	F	MZUSP_11602	-3.82	-55.49
Caluromys_philander	F	MZUSP_11603	-3.82	-55.49
Caluromys_philander	F	MZUSP_11607	-16.69	-49.26
Caluromys_philander	M	MZUSP_11608	-1.42	-48.41
Caluromys_philander	M	MZUSP_11609	-3.82	-55.49
Caluromys_philander	F	MZUSP_11611	-23.69	-46.68
Caluromys_philander	F	MZUSP_11612	-23.69	-46.68
Caluromys_philander	M	MZUSP_11678	-23.69	-46.68
Caluromys_philander	F	MZUSP_122	-22.61	-45.19
Caluromys_philander	F	MZUSP_16398	-2.24	-49.50
Caluromys_philander	UND	MZUSP_19253	-1.42	-48.41
Caluromys_philander	F	MZUSP_21283	-3.65	-52.38
Caluromys_philander	F	MZUSP_3173	-2.62	-43.45
Caluromys_philander	F	MZUSP_4163	-3.30	-58.25
Caluromys_philander	M	MZUSP_4515	-2.24	-49.50
Caluromys_philander	F	MZUSP_4516	-2.24	-49.50
Caluromys_philander	M	MZUSP_4518	-2.24	-49.50
Caluromys_philander	M	MZUSP_4521	-2.83	-55.13
Caluromys_philander	F	MZUSP_4522	-6.67	-54.57
Caluromys_philander	M	MZUSP_4525	-2.24	-49.50
Caluromys_philander	F	MZUSP_4541	-1.92	-55.45
Caluromys_philander	F	MZUSP_4661	-2.24	-49.50
Caluromys_philander	F	MZUSP_4662	-2.24	-49.50
Caluromys_philander	M	MZUSP_4663	-2.83	-55.13
Caluromys_philander	F	MZUSP_4751	-2.83	-55.13
Caluromys_philander	F	MZUSP_4752	-3.30	-58.25
Caluromys_philander	M	MZUSP_4754	-6.67	-54.57
Caluromys_philander	F	UFSM_203	-17.56	-52.55
Caluromys_philander	F	UFSM_234	-20.47	-55.79

Appendix B. Bergmann's rule plots (regressions of dependent variable Size with the predictor variable Latitude) for South-American *Caluromys philander*. We reanalysed the Bergmann's tests to verify the possible influence of trends in the samples due to over collection in certain regions or latitudes. Then five analyses were repeated for *Caluromys philander* with average specimens per locality near 10 km radius (1); randomly choosing one specimen from these locations in a 10 km radius (2); averaging specimens by each grid of one degree (~110 km) (3); randomly selecting one specimen from the specimens within the last grid of one degree (4); and averaging specimens by each grid of 0.25 degree (~27 km) (5). In general, our original result is maintained. Significance is highlighted in bold.

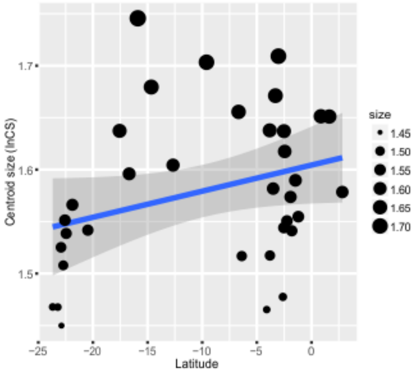
1) Average specimens per locality near 10 km radius.
N = 46; R^2 Adj: 0.069; P = **0.043**



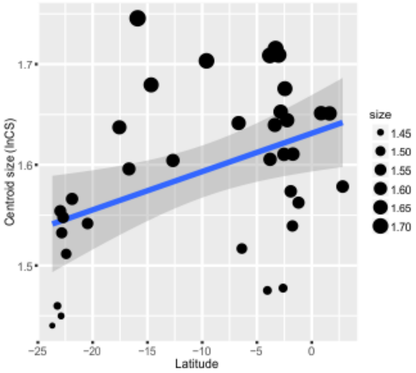
2) Randomly choosing one specimen from these locations in a 10 km radius.
N = 46; R^2 Adj: 0.126; P = **0.009**



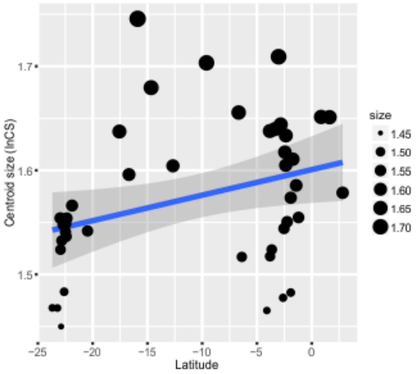
3) Averaging specimens by each grid of one degree (~110 km).
N = 35; R^2 Adj: 0.064; P = 0.077



4) Randomly selecting one specimen from the specimens within the grid of one degree.
N = 35; R^2 Adj: 0.155; P = **0.011**



5) Averaging specimens by each grid of 0.25 degree (~27 km).
N = 43; R^2 Adj: 0.83; P = **0.033**



Appendix C. Loading coefficients on SW1 block variables based on different PLS analyses with Size or Shape as block 1 and climate as block 2 for South-American *Caluromys philander* and *C. lanatus* using 13 landmarks.

	C. philander		*C. lanatus*	
Bioclimatic variables	Size	Shape	Size	Shape
BIO1	**-0.345**	**0.315**	**-0.307**	**0.291**
BIO2	-0.019	-0.062	0.056	-0.125
BIO3	-0.224	**0.253**	-0.136	0.143
BIO4	**0.276**	**-0.275**	**0.266**	**-0.278**
BIO5	**-0.360**	**0.297**	**-0.303**	**0.240**
BIO6	**-0.287**	**0.296**	**-0.267**	**0.267**
BIO7	0.153	-0.220	0.169	-0.221
BIO8	**-0.281**	0.249	**-0.365**	**0.332**
BIO9	**-0.333**	**0.318**	**-0.284**	**0.272**
BIO10	**-0.324**	**0.289**	**-0.287**	**0.257**
BIO11	**-0.340**	**0.317**	**-0.308**	**0.296**
BIO12	-0.176	0.172	-0.099	0.046
BIO13	-0.104	0.138	-0.206	0.195
BIO14	-0.032	0.056	0.225	**-0.265**
BIO15	0.047	0.000	-0.195	**0.256**
BIO16	-0.129	0.159	-0.205	0.193
BIO17	-0.054	0.065	0.217	**-0.270**
BIO18	0.177	**-0.247**	0.018	-0.021
BIO19	-0.111	0.209	0.002	0.006

Variables and values generally higher than the others are in bold. Annual mean temperature (BIO1), mean diurnal temperature range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), maximum and minimum temperature of the warmest and coldest months (BIO5 and BIO6), temperature annual range (BIO7), mean temperature of the wettest, driest, warmest, and coldest quarters (BIO8–11), annual precipitation (BIO12), precipitation of the wettest and driest months (BIO13 and BIO14), precipitation seasonality (BIO15), and precipitation of the wettest, driest, warmest, and coldest quarters (BIO16–19).

4 ARTIGO II. THE ENVIRONMENT IS A MAJOR DRIVER OF SHAPE AND SIZE VARIATION IN WIDESPREAD EXTANT XENARTHRANS

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The environment is a major driver of shape and size variation in widespread extant xenarthrans

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Abstract

Xenarthra is one of the most peculiar mammalian groups to have originated in South America, where most of its evolutionary history has taken place. Xenarthrans have experienced significant climatic changes and also geographical isolation for most of the Cenozoic. Thus, the cranial morphology of xenarthrans may reflect the different pressures that the group is currently undergoing. Our objective is to identify the drivers of phenotypic variation of the skull (both shape and size) in widespread representatives of the superorder Xenarthra throughout South America. We tested the influence of allometry and neutral and niche processes on three extant species, using a geometric morphometric approach: the three-toed sloth *Bradypus variegatus*, the lesser anteater *Tamandua tetradactyla*, and the armadillo *Dasypus novemcinctus*. Our results show that allometry is present, but has a weak effect on shape variation. Geography has a greater impact than allometry in explaining the size variation of *T. tetradactyla* and the shape of *B. variegatus* which is, interestingly, the only studied species that follows Bergmann's rule. Most importantly, the environment drives most of the variation in the shape and size of the three species studied. The responses of *B. variegatus* and *T. tetradactyla* to geographical space are congruent with their low mobility and more limited dispersal. The environment mainly affected *B. variegatus* (e.g., following Bergmann's rule), probably because of its particularly low metabolism, and *D. novemcinctus*, due to its high dispersal capacity.

Keywords: Bergmann's rule; Geometric morphometrics; Geographical distance; South America; Allometry

Introduction

An organism may be subject to different pressures related to biotic or abiotic factors, reflecting its evolutionary history (Agrawal, 2001). These selective pressures affect the phenotype, enabling adaptive evolution (Ghalambor et al., 2007). However, any phenotype change can lead to a cost in maintenance, particularly in traits related to changes in the environment (Chevin et al., 2010). Spatial and environmental factors can influence morphological variation (Millien et al., 2006), molding and expressing how an animal adapts to different local conditions. An example is the complex cranial structure of mammals, which is a source of morphological variation and adaptation. Moreover, many traits of the mammalian skull reflect a large amount of ecological, physiological, and evolutionary information, allowing exploration of the major causes of their diversification (e.g., Cáceres et al., 2014b; Cardini and Polly, 2013).

Xenarthrans are morphologically peculiar mammals that still need detailed studies regarding the causes of their biogeographical variation (Superina and Loughry, 2015). The clade is composed of three main lineages: Folivora (sloths), Vermilingua (anteaters), and Cingulata (armored forms: armadillos, glyptodonts, and pampatheres) (Gardner, 2008). Molecular clock studies suggest that Xenarthra originated in South America at the end of the Mesozoic (approximately 67 Ma, Gibb et al., 2016), and its current distribution ranges from North America (USA) to southern Patagonia (Gardner, 2008). The three most widely distributed extant South American species, which are the focus of this research, are the sloth *Bradypus variegatus* Schinz, 1825 (sloth), the anteater *Tamandua tetradactyla* (Linnaeus, 1758), and, especially, the armadillo *Dasypus novemcinctus* Linnaeus, 1758 which reaches the southeast of USA (Gardner, 2008). Xenarthra are unusual mammals with peculiar adaptations, such as the suspensory arboreal sloths (Nyakatura, 2012), the semifossorial armadillos (McBee and Baker, 1982), and the myrmecophagous anteaters (Hayssen, 2010, 2011).

One of the sources of cranial variation that is still under-explored in xenarthrans is allometry (e.g., Milne et al., 2012). One way to define allometry is through the direct covariation of size and shape (Klingenberg, 1998, 2016). When shape deformation is analyzed, the influence of size as a modulator of shape among individuals of a given age becomes evident

(Klingenberg, 1998). In the case of *B. variegatus*, *T. tetradactyla*, and *D. novemcinctus*, the influence of allometry on skull shape variation is probably not accentuated, as xenarthrans have simple skulls and, even though, showing biomechanical efficiency (Vizcaíno, 2009).

In addition to allometry, skull variation may be partially related to geographical (neutral) processes, usually in species with limited dispersal capacity (Hubbell, 2001; Rosindell et al., 2011). The genera *Tamandua* and *Dasypus* have higher dispersal capacity, higher power shift (Schloss et al., 2012), and occur not only in forest but also in open biomes (Hayssen, 2011; McBee and Baker, 1982). As opposed to sloths, which are largely restricted to rainforests. Moreover, *D. novemcinctus* shows a mobility advantage by having the highest dispersal capacity among all extant xernarthran species, inhabiting a wide variety of biomes (McBee and Baker, 1982), and possibly suffering a low geographical influence related to easily crossing barriers. In the case of *Bradypus*, the geographical influence is thought to be strong (i.e., natural barriers are meaningful for the species), reflecting its low mobility and its close interaction with rainforests (Nyakatura, 2012; Sunquist and Montgomery, 1973) feeding largely on *Cecropia* leaves (Hayssen, 2010). Furthermore, *Bradypus* dispersal has possibly been limited by climatic changes occurring since the end of Pleistocene, limiting the occurrence of sloths to more humid forests (Pujos et al., 2017). Thus, the effects of random genetic drift or gene flow, as fully random processes—not necessarily related to environmental adaptation only (Rosindell et al., 2011)—may be present in *B. variegatus*.

An overview of body size of these xenarthran species reveals the effects that physiological and ecological factors have on its variation, as already seen in other mammals (McNab, 1971). Through time, body size rather than shape is more likely to change (Cardini and Elton, 2009). The tendency of larger body sizes at high latitudes due to its relation to cold climates is known as Bergmann’s rule (Meiri, 2011). This rule is still much debated, and there is no consensus of its overall validity, besides being little explored in xenarthrans (Clauss et al., 2013). According to the latter authors, Cingulata may have an inverse relation to Bergmann's rule, suggesting the possibility that *D. novemcinctus* will increase size at low latitudes (the reverse of Bergmann’s rule). In addition to the heat retention factor with increasing latitude, McNab (2010) reinforces the idea that other factors related to resource availability can also have a major effect on size. Thus, climatic and other environmental factors directly linked to feeding resources may also influence size variation (McNab, 2010), and may potentially modify the skull shape of these three widespread xenarthran species.

Environmental variables, such as temperature, can also influence the behavior of xenarthrans, and this might strongly affect their activity patterns (Chiarello, 1998; Mourão and Medri, 2007). In addition, the environment has acted on these species, which in turn exhibit a progressive biome specialization, explaining their dispersal and diversification over time (Gibb et al., 2016). Consequently, the effect of environment is expected to be higher on *D. novemcinctus* and *T. tetradactyla* (the most dispersive species among the three ones in focus here), promoting a higher local variation of traits, since widespread species are subject to pressures from different environmental conditions and need to be plastic to deal with them (Ghalambor et al., 2007). Hence, the environment is expected to be a fundamental influence on the phenotypic variation of populations, especially for those species with higher dispersal capacities that can easily move to new habitats, experiencing local adaptation (e.g., Chase and Leibold, 2003).

The study of widely distributed species is necessary in order to evaluate the effects of distinct environmental and spatial conditions to which they are subjected (e.g., temperature, rainfall, seasonality, and geographical barriers) (Cáceres et al., 2014b; Magnus et al., 2017; Meloro et al., 2014). South America is a vast continent in which we can investigate the effects of environment and geography on the species phenotypes (Veblen et al., 2007). In this context, our aim is to analyze the cranial morphometric variation of three species of the superorder Xenarthra that are widespread throughout South America, testing for ecogeographical variation in shape and size. We investigate cranial variation in these three xenarthrans, to test whether it is related to environmental (niche) or geographical (neutral) processes, or both. Our hypotheses predict a low allometric influence, but a reasonable effect of geography on shape variation (especially on *B. variegatus*, which has the lowest dispersal capacity among the three focal species). Nevertheless, the environment should affect all three taxa more strongly than other factors, because these species have wide distributions and are often subjected to different local environmental conditions (especially *D. novemcinctus*). This means that the environment, rather than neutral processes, may have a major impact on the cranial variation of these species.

Material and methods

Data collection

We took photographs of skulls (ventral view) of 284 adult specimens belonging to three different species of Xenarthra (n = 86 for *B. variegatus*; n = 96 for *T. tetradactyla;* and n = 102 for *D. novemcinctus*) (Table 1). We used the ventral view because of its flattened surface and landmarks of interest (e.g., for temporal foramen and auditory bulla; Hendges et al., 2016; Meloro et al., 2014; Mikula and Macholán, 2008). We chose these species because they are widely distributed in South America. We identified adult specimens based on criteria such as suture closures and tooth eruption. The data were collected from specimens housed in the main scientific collections of Brazil and Argentina (see Table S1 in Supplementary material).

Table 1. Skull sample size for the three species of Xenarthra included in this study.

Species	$N_{specimens}$	$N_{females}$	N_{males}	$N_{undetermined}$
Bradypus variegatus Schinz, 1825	86	44	42	0
Tamandua tetradactyla (Linnaeus, 1758)	96	64	28	4
Dasypus novemcinctus Linnaeus, 1758	102	53	44	5
Total	284	161	114	9

Skull pictures were taken by applying a standard protocol to avoid possible image deformation due to the lenses, with a Nikon CoolPix P530 digital camera placed at a fixed distance of 1.5 m on a tripod. Each skull was positioned with the palate perpendicular to the camera lens, having a scale bar placed adjacent to the skull for subsequent labeling. Additionally, we recorded the geographic coordinates of collection localities for each specimen (Fig. 1). Most geographic coordinates were obtained using Google Earth (http://earth.google.com.br) through the geographic center of the locality; a small portion of the coordinates were obtained from information available from the museums consulted (e.g., specimen labels, museum catalogues, etc.).

Geometric morphometrics

We defined 13 two-dimensional homologous landmarks (Fig. 2) using the software tpsDig2 v. 2.16 (Rohlf, 2010a). These anatomical landmarks described the overall skull shape, braincase (LM 3, 4, 13), temporal foramen of the zygomatic arch (LM 6–8, 12), auditory bulla (LM 9–11), and muzzle (LM 1, 2, 5). A single observer (L.Z.M.) digitized the landmarks in order to avoid inter-observer error. In addition, we found negligible intra-observer error (<2%; Meloro, 2011) when we randomly landmarked six specimens twice (two of each species on different days), and compared the mean error for each specimen through inter-landmark distances.

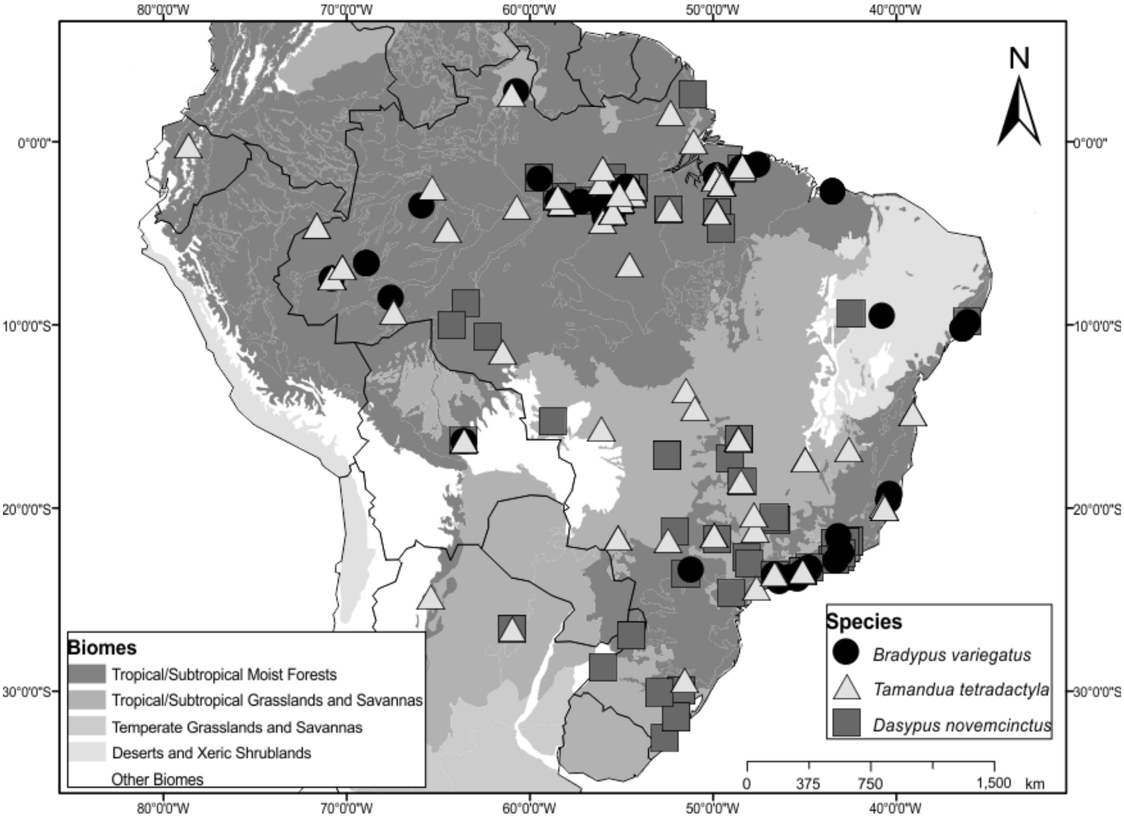

Fig. 1. Map of South America showing the sampling distribution of xenarthran skulls. Sampling localities of different species are shown by different symbols.

For each species, a Generalized Procrustes Analysis (GPA; Rohlf and Slice, 1990) was performed from the landmark coordinate superimposition in order to remove variation resulting from the use of different scales, orientations, and positions. A principal component analysis (PCA) was then conducted based on the covariance matrix of the Procrustes coordinates to obtain new, independent shape axes (Zelditch et al., 2004), and to visualize shape changes (= relative warp, RW). These analyses (GPAs and PCAs) were conducted with the software tpsRelw v. 1.49 (Rohlf, 2010b). We scaled the configuration of skull size from the centroid size (CS), which is the square root of the sum of squared distances between each landmark and the skull centroid (Bookstein, 1991).

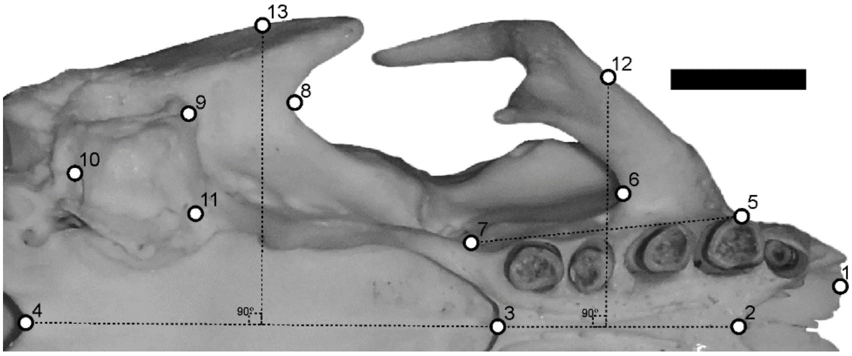

Fig. 2. Position of 13 landmarks on a skull of *Bradypus variegatus*. Landmark definitions: 1 = anterior extremity of the nasal bone; 2 = anteriormost point of the maxilla; 3 = posteriormost tip of suture between palates; 4 = anteriormost point of foramen magnum; 5 = anteriormost point of the root of the zygomatic arch; 6 = anteriormost point on curvature of the zygomatic arch; 7 = intersection between frontal and palate; 8 = posteriormost point on curvature of the zygomatic arch; 9 = anterolateral extremity of the auditory bulla; 10 = posterior extremity of the auditory bulla; 11 = posterolateral extremity of the auditory bulla; 12 = projection onto the external edge of the zygomatic arch, drawn from the midpoint of landmarks 5-7 at an angle of 90◦ with the line perpendicular to the line between the landmarks 2-3; 13 = projection onto the external edge of the skull, drawn from the midpoint of landmarks 3-4 at an angle of 90◦ with the line perpendicular to the landmarks. Scale bar is 1 cm.

Statistical analyses

Sexual dimorphism

We focused on intraspecific analyses rather than on interspecific ones. Each skull was considered as a sample unit.

We used multivariate analysis of variance (MANOVA) and analysis of variance (one-way ANOVA) to test for plausible sexual dimorphism regarding skull shape and size respectively in each species. Scores of relative warp axes that explained at least 95% of shape variance were included as dependent variables in the MANOVA models to avoid possible biases due to the high dimensionality of scores (Meloro and O'Higgins, 2011). Selected axes from a total of 22 relative warp axes were as follows: the first 14 RWs (95.73%) for *B. variegatus*; the first 14 RWs (95.37%) for *D. novemcinctus*; and the first 13 RWs (95.36%) for *T. tetradactyla*.

Skull allometry

For the statistical tests of allometric effects within each species, we used the logarithm of centroid size (= lnCS) as an independent variable and the shape variables as dependent ones. This task was implemented by performing a multivariate regression with the software MorphoJ 1.05 (Klingenberg, 2011).

Bergmann's rule

We conducted two analyses to test for the Bergmann's rule for each of the three species. First, we employed a multivariate regression to test the relationship of shape variables (95% RWs) against latitude, which was used as predictor. We then used a linear regression with the variable size (lnCS) against latitude (i.e. Bergmann's rule in its original form).

Environment versus skull shape and size

From each specimen locality, we extracted values for nineteen bioclimatic variables, including temperature, rainfall, and seasonality data (cf. Magnus et al., 2017), with a resolution of 10' from the WorldClim raster database (Hijmans et al., 2005). In addition, we extracted values for three variables related to local vegetation (average annual relative humidity, evapotranspiration, and net primary productivity), which were obtained from the Atlas of the Biosphere (http://www.sage.wisc.edu/atlas/index.php). We used the software DIVA-GIS 7.5 for these extractions (http://www.divagis.org/download).

To test the impact of the environment on skull shape and size, we used an analysis of two-block partial least squares (PLS) conducted with the software MorphoJ 1.05 (Klingenberg, 2011). One block comprised the 22 environmental variables and the other block comprised the shape or size. In order to represent graphically the relationship of shape and environment, we used the software tpsPLS v. 1.18 (Rohlf, 2006).

Additionally, to obtain the independent spatial structure of the three species, we performed a spatial analysis using a method based on principal coordinates of neighbor matrices (PCNM; Borcard and Legendre, 2002) using the *vegan* package (Oksanen et al., 2015) in the R environment, version 2.8.1 (R Development Core Team, 2015). Then, a forward selection with permutation tests was performed using the R package *packfor* (Dray et al., 2009) to select only the informative spatial filters (significantly correlated with shape and size; Borcard et al., 2011). We included the PCNM variables (spatial filters) that resulted from the application of this method into the subsequent variation partitioning analyses (see Table S2, S3).

Variation partitioning

A variation partitioning by redundancy analysis (Desdevises et al., 2003) was conducted to identify the contribution of each predictor (alone or interrelated) for the shape change in each species. Predictors were allometry (lnCS), geography (spatial filters), and environment (22 environmental variables). They were tested as predictors (X) of the skull shape (Y, described by the 22 shape variables, 2n−4, where n is the number of landmarks) (Rohlf and Slice, 1990) by using multiple multivariate regression models. The variation partitioning analysis was also used to quantify the portion of variance that explains the size variation (response variable) in regard to geography and environment (predictor variables). Variance partitioning was performed using the *vegan* package (Oksanen et al., 2015) in the R environment.

Results

Sexual dimorphism

There is no sexual dimorphism in either size or shape in *B. variegatus* (size: F = 0.255; d.f. = 1; P = 0.615 – shape: Pillai's trace = 0.164; $F_{14, 71}$ = 0.999; P = 0.464), *T. tetradactyla* (size: F = 0.338; d.f. = 1; P = 0.562 – shape: Pillai's trace = 0.164; $F_{13, 78}$ = 1.180; P = 0.310), or *D. novemcinctus* (size: F = 2.164; d.f. = 1; P = 0.145 – shape: Pillai's trace = 0.189; $F_{14, 82}$ = 1.366; P = 0.189). Since no sexual differences were detected, all subsequent analyses were carried out with data for both sexes and undetermined specimens pooled together.

Skull shape

With regard to skull shape variation in *B. variegatus,* RW1 and RW2 correspond to 27.12 and 14.65% of the total variation, respectively (Fig. 3A). For RW1, the negative extreme describes a more elongated skull and zygomatic arch, and a narrower muzzle. For RW2, the negative extreme describes shape changes related to a smaller braincase and auditory bulla, and a shorter muzzle. The opposite trends are seen in the positive extremes.

Relative warps explaining the skull shape variation of *T. tetradactyla* are 29.59% (RW1) and 15.37% (RW2) (Fig. 3B). Specimens in the RW1 negative extreme are characterized by a smaller zygomatic arch and auditory bulla, and a longer and thinner muzzle. For RW2, the negative extreme represents a more elongate braincase. Opposite trends are seen in the positive extremes.

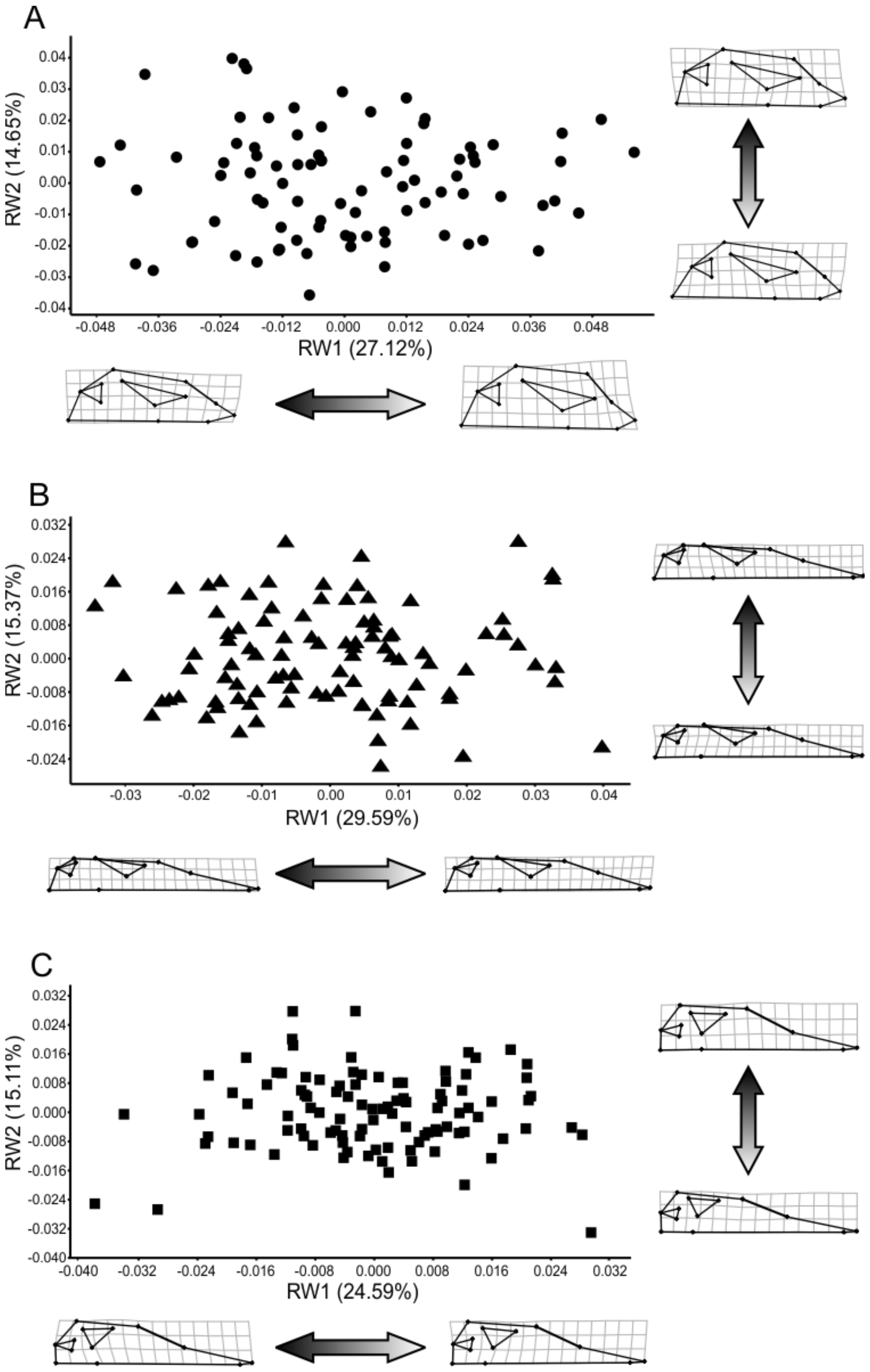

Fig. 3. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the overall species shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C).

Finally, with respect to the skull shape variation of *D. novemcinctus*, RW1 corresponds to 24.59% of the total variation and RW2 to 15.11% (Fig. 3C). RW1 negative extremes represent an elongated skull, a thinner and shorter braincase, and a more posteriorly positioned zygomatic arch. Specimens at the negative extreme of RW2 exhibit a more elongate skull, a smaller zygomatic arch, and a thinner muzzle. Opposite trends are seen in the positive extremes.

Skull allometry

There is a small but significant effect of allometry on the skull shape in all three species, with 3.71% of the total variance being explained for *B. variegatus* ($P = 0.003$), 5.43% for *T. tetradactyla* ($P < 0.001$), and 5.29% for *D. novemcinctus* ($P < 0.001$).

Bergmann's rule

The effect of latitude on skull shape is significant for *B. variegatus* and *D. novemcinctus*, but not for *T. tetradactyla* (Table 2). This result serves as a proxy for the observation that environmental variation plays an important role in cranial morphology (Meloro et al., 2014). With respect to size, we found a significant impact of latitude only for *B. variegatus*, with a pattern of size increase with increasing latitude, consistent with Bergmann's rule (Fig. 4, Table 2; see also Appendix S1 in Supplementary material showing that the result remains consistent even under different approaches).

Table 2. Multivariate regressions of dependent variables (Dep.) Shape (relative warps corresponding to 95% of shape variation) and Size with the predictor variable Latitude for South American xenarthran species. Significance ($P < 0.05$) is highlighted in bold.

Species	Dep.	R^2	adjusted R^2	F-statistic	Df	P value
Bradypus variegatus	Shape	0.07	0.06	6.850	84	**0.010**
	Size	0.19	0.18	19.060	83	**<0.001**
Tamandua tetradactyla	Shape	0.01	−0.00	0.773	94	0.381
	Size	0.00	-0.01	0.000	94	0.982
Dasypus novemcinctus	Shape	0.07	0.06	7.671	100	**0.007**
	Size	0.01	−0.00	0.835	100	0.363

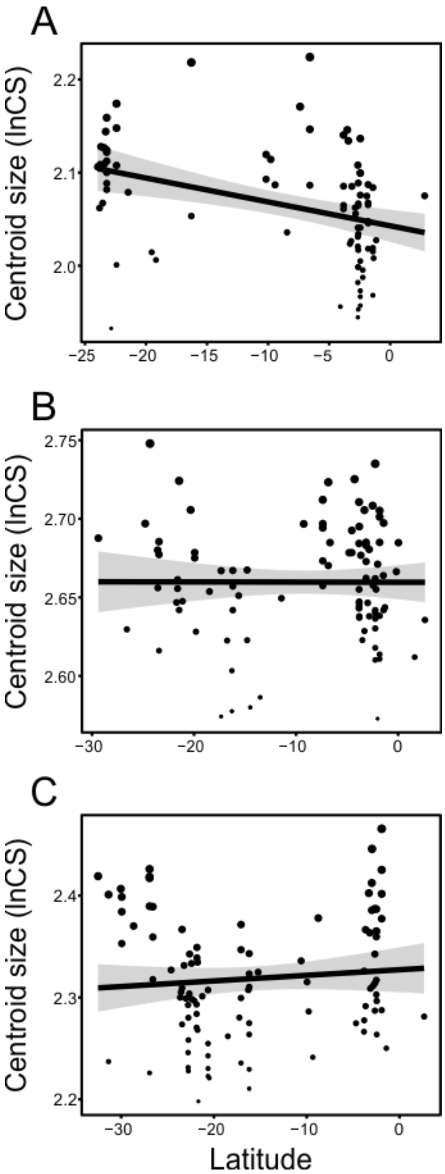

Fig. 4. Natural log transformed centroid size (lnCS) variation relative to absolute value of Latitude. *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C). Symbol size increases with specimen size.

Environment versus skull shape and size

Environmental correlates of shape variation are significant for all three species, especially for *B. variegatus*. The latter species and also body size variations in *D. novemcinctus* are highly influenced by the environment, whereas *T. tetradactyla* shows only a moderate influence of environmental variables (Table 3).

The plot of environmental variables (= singular warp, SW1 Environment) against shape (SW1 Shape) shows a gradient between seasonal and drier environments (negative scores), and warmer and humid environments (positive scores) (Fig. 5). *Bradypus variegatus* individuals from more seasonal regions (SW1 environment negative scores) exhibit a shorter skull and muzzle, with a smaller braincase and auditory bulla (Fig. 5A). *Tamandua tetradactyla* individuals from more seasonal regions exhibit a wider skull and shorter muzzle, with smaller, elongated zygomatic arch and auditory bulla (Fig. 5B). Finally, *D. novemcinctus* individuals found in more seasonal regions exhibit a thinner skull, with a larger zygomatic arch and auditory bulla, and a more elongated and thinner muzzle (Fig. 5C). In all cases, positive scores represent opposite trends in skull shape to those described above for negative scores.

Table 3. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors (SW1) of Shape and Size (lnCS) comparing to environmental variables (22) for South American xenarthran species. Significance ($P < 0.05$) is highlighted in bold.

	Shape			Size		
Species	rv (%)	r	P value	rv (%)	r	P value
Bradypus variegatus	89.690	0.76	**< 0.001**	100	0.43	**< 0.001**
Tamandua tetradactyla	86.150	0.44	**0.007**	100	0.28	**0.045**
Dasypus novemcinctus	59.906	0.51	**< 0.001**	100	0.51	**< 0.001**

Variation partitioning

Through the analysis of variation partitioning, considering shape as a response variable, allometry explains a small but significant proportion of the variance when isolated for the three species (Fig. 6A–C), and also explains only a small proportion of the total variation (see Table S2). Geography, when isolated, is relevant only for *B. variegatus*. Environment (isolated or not) is the best explanation of shape variance for the three species, but mainly as an isolated component for *B. variegatus* (Fig. 6A) and *D. novemcinctus* (Fig. 6C). The interaction between geography and environment is also important for *B. variegatus* and *D. novemcinctus* in terms of explaining shape variance (Fig. 6A, C).

For the analysis considering size as a response variable, geography in isolation shows no significant explanation for any species (Fig. 6D–F) (see Table S3), but it is significant for explaining the total variation seen in *T. tetradactyla* (Fig. 6E). Environment provides a better explanation for variation in size, mainly for *D. novemcinctus* (Fig. 6F) and *B. variegatus* (Fig. 6D). Furthermore, interactions of the geography and environment variables provide the best explanations of variance for *T. tetradactyla* (Fig. 6E) and *B. variegatus* (Fig. 6D).

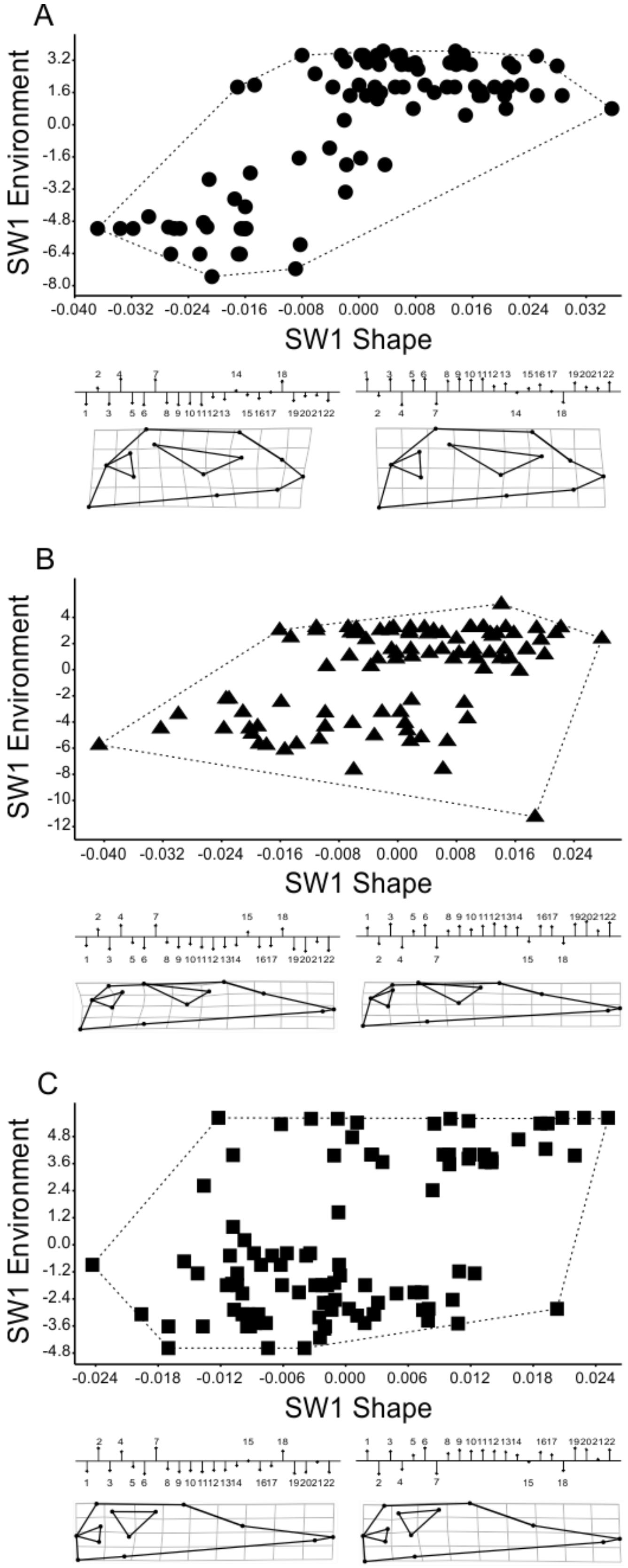

Fig. 5. Plot of environmental variables and shape scores from the most negative to the most positive Singular Warps (first pair). Below are variable profiles and deformation grids from the most negative to the most positive Singular Warp scores. The numbers in the variable profiles are originated from the 19 variables of WorldClim plus average annual relative humidity (20), net primary productivity (21), and evapotranspiration (22). *Bradypus variegatus* (A), *Tamandua tetradactyla* (B), and *Dasypus novemcinctus* (C).

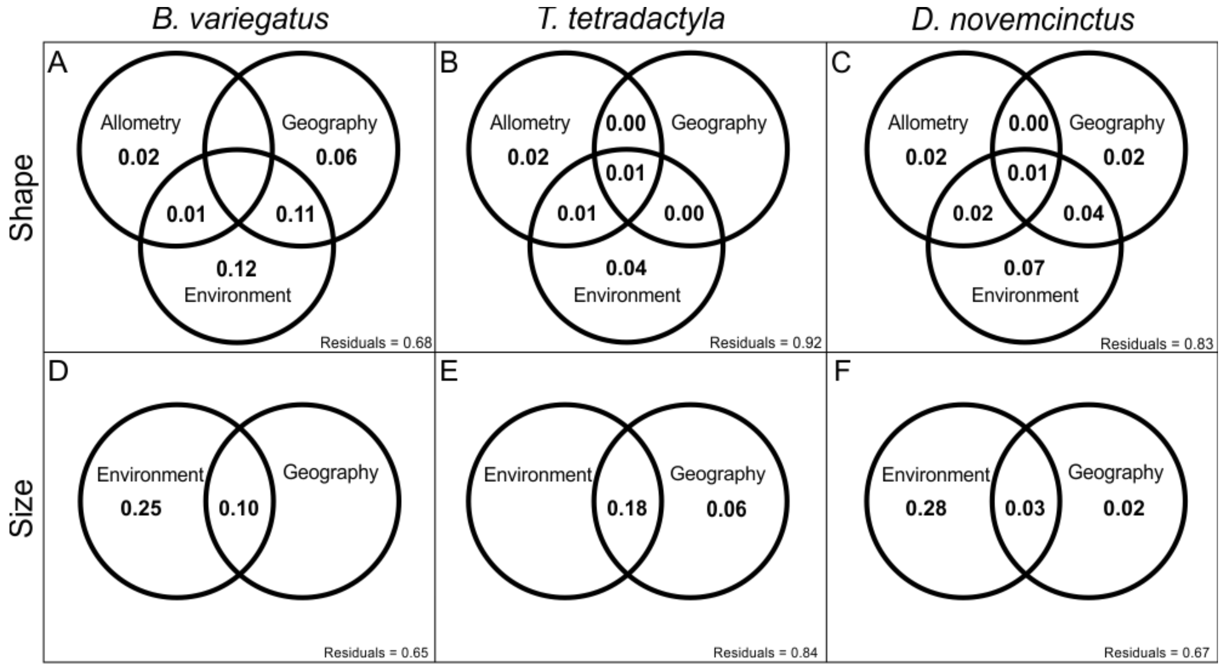

Fig. 6. Schematic depiction of proportion (Adj.R^2) of shape and size variance explained by allometry, geography, and environment for each species. Shape: (A) *Bradypus variegatus*; (B) *Tamandua tetradactyla*; and (C) *Dasypus novemcinctus*. Size: (D) *Bradypus variegatus*; (E) *Tamandua tetradactyla*; and (F) *Dasypus novemcinctus*. Values <0 not shown.

Discussion

Our results suggest that allometry has only a weak effect on the cranial shape variation in adults of the three xenarthran species studied here. However, we confirm the strong influence of geography and environment on shape and size variation in all three species. Geographical distance was relatively important, especially for *B. variegatus* shape and *T. tetradactyla* size variation. Latitudinal variation (Bergmann's effect) was only significant for *B. variegatus*, and indicated an increase in size towards the south, which may be related to constraints related to the unique physiological attributes of this species, such as its low basal metabolism and mobility (McNab, 1988). Moreover, the environment had a moderate influence on shape and size of all three species, but mainly on *B. variegatus* and *D. novemcinctus* size, confirming the higher lability of size compared to shape (Cardini and Elton, 2009).

Regarding allometry, we confirmed the presence of an allometric influence on the shape variation of the three species studied, but, as expected, it was not a major factor, since it explained only a small proportion of shape variation. Allometry is an important source of variation in some species and can lead to a series of morphological changes, even in adults (Cardini and Polly, 2013; Meloro et al., 2014). Therefore, sometimes shape can become size dependent and related to biomechanical performance. For adult individuals, allometry can be an important biomechanical factor related to masticatory morphology (Cardini and Polly, 2013; Hendges et al., 2016). This biomechanical demand is probably present here in the three species, even at low levels, especially because they have a quite unusual dental structure among mammals (e.g., hypselodont or completely toothless as Vermilingua, Vizcaíno, 2009), which suggests little complexity for chewing food, and consequently requires little force for efficient feeding. The other results we found for xenarthrans here highlight that predictors other than allometry (e.g., environment) are more important in explaining their cranial variation.

Geography seems to be important for cranial shape variation in *B. variegatus*, especially as a pure predictor variable. Cranial shape in this species is spatially structured—which means that the variation is geography-dependent—, corroborating the hypothesis that the species most affected by the geographical distance are those with more limited dispersal capabilities (Moraes-Barros et al., 2006). This effect of neutral processes (Hubbell, 2001) suggests that populations of sloths might be more isolated, which may result in genetic drift and reduced gene flow (Hautier et al., 2014; Moraes-Barros et al., 2006). Therefore, the geographical-distance effect on sloth shape may be related to the limited gene flow among populations, which (for example) might have promoted the variation that have led to the recognition of seven subspecies for this species (Gardner, 2008). The effect of geographical distance is also found for *T. tetradactyla* body size variation, also confirming the action of neutral processes, possibly related to a dispersal limitation of such species. *Tamandua tetradactyla* is a food specialist as it feeds mostly on ants and termites (McNab, 1984). Because of its combination of a specialized diet and a relatively large body size in comparison with other current Xenarthran species, its home range area is larger than expected (Hayssen, 2011), which leads the animal to maximize the search for food in sparsely distributed colonial insect nests (Montgomery, 1985). This should make it more dependent on a spatially-structured environment, changing its size according to distance-related effects combined with environment quality (in which interaction is 18%); this reflects an interactive influence of neutral and niche processes (Gravel et al., 2006). On the other hand, the generalist *D. novemcinctus* consumes food that is more available in the environment (McBee and Baker, 1982), and so is not being by distance-related spatial factors in regard to shape and size variations. Moreover, *D. novemcinctus* has the highest dispersal capacity among the three studied species (McBee and Baker, 1982). In fact, despite its South American origin (Gardner, 2008), the range of this species currently extends into the United States (Taulman and Robbins, 2014).

In relation to the environment, there is a clear correlation between size and latitude for sloths, which follows Bergmann's rule. This is supported by the significant explanation ($R^2 = 0.13$, $P < 0.001$) of mean temperature and skull size of *B. variegatus* using the same dataset ($n = 85$). Usually, a large animal is favored in colder environments due to its low surface to volume ratio (McNab, 1971; Meiri, 2011), and this is true for *B. variegatus* especially because of an important feature in xenarthrans: their low basal metabolism (McNab, 1985). Sloths are the species with the lowest basal metabolism of any placental mammals (McNab, 1988), suggesting that they face this problem by increasing size where it is less climatically stable and cold (i.e. southern latitudes in South America having Atlantic forest with mean annual temperatures ranging from 14 to 21ºC, whereas in Amazon forest they range from 23 to 27ºC; Veblen et al., 2007). Sloths supposedly benefit from their fur coverage, which promotes better heat conservation (Scholander and Krog, 1957), but this does not seem to be sufficient, and an increase in size appears to be the solution to preventing excessive heat loss. Moreover, *B. variegatus* cannot thermoregulate and protect themselves in burrows as armadillos and anteaters do (McNab, 1979; Superina and Loughry, 2012), which makes it even more vulnerable to temperature oscillations.

The environment also affects the shape of *B. variegatus*, but also, and to a greater extent, the size of *D. novemcinctus.* As reported for size, the unusual physiological and ecological aspects of *B. variegatus* (Hayssen, 2010; Sunquist and Montgomery, 1973) contribute to its susceptibility to climate variability, with shape variation also following an environmental gradient. *Bradypus variegatus* shape changes show a generally longer skull in warm/humid environments, and the opposite configuration in more seasonal environments (Fig. 5A), a similar pattern found in representatives of other clades like primates (Meloro et al., 2014) and marsupials (Magnus et al., 2017). In the case of the three-toed sloth, its general shape configuration is thought to be adaptive to the climatic cline in South America, following a general biogeographical rule of having slender bodies in warm/wet climates (Millien et al., 2006) and facilitating food intake by having more robust feeding apparatus in more seasonal environments (Cáceres et al., 2014b; Hendges et al., 2016). However, the environment also acts on *D. novemcinctus* size more intensively than on shape. This species is very common, has a wide distribution, and consequently disperses easily through various biomes (McBee and Baker, 1982), experiencing different pressures depending on the local environment (Cáceres et al., 2014a). Corroborating that, *D. novemcinctus* can achieve higher dispersal rates, as its litter size per year is four times higher than those of *B. variegatus* or *T. tetradactyla* (Hayssen, 2010, 2011; McBee and Baker, 1982). Thus, we believe that body size of this armadillo is locally regulated by ecological factors, such as predation and/or productivity (De Azevedo, 2008; Foster et al., 2010). Shape variation of *D. novemcinctus* in more seasonal environments shows a larger zygomatic area (Fig. 5C), which may be related to the acquisition of harder foods in these regions (since it feeds mostly on insects; McBee and Baker, 1982), as the zygomatic area is related to temporalis muscle size. Assuming that clinal variations of shape are partly related to the environment, the relatively large auditory bulla found in the armadillo here might be an adaptation to living in drier environments, as inferred for rodents (e.g., Bueno and Motta-Junior, 2015).

Our study highlights the strength of neutral and niche processes on living representatives of the oldest mammal lineages in South America, helping to clarify the role of important predictors for shape and size variation. The shape and size of species with more limited dispersal are more strongly influenced by geography, while in a one species in particular, the three-toed sloth, size shows a substantial change in relation to the environmental gradient, as a probable response to life history characteristics unique for its clade. On the other hand, the armadillo, which is a more mobile species, is most strongly influenced by environmental factors of the three species studied here, particularly with regard to size variation. As evidenced by the geographical and ecological trends shown here, and previous novel developmental discoveries (Hautier et al., 2016), much is still expected to be revealed about this unique and neglected group of placentals (Superina and Loughry, 2015). Future studies could address other issues such as integration and modularity analyses, testing for example whether some specific modules are correlated with environmental variables more than others.

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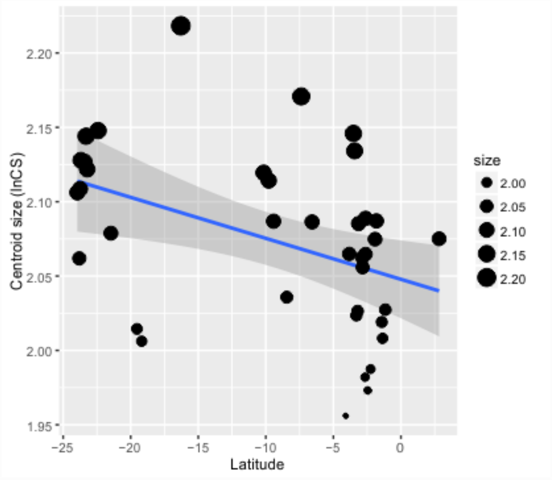
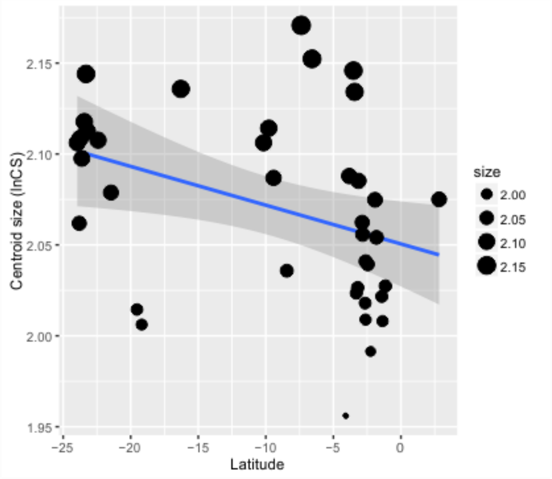
Supplementary data

Appendix S1. Bergmann's rule plots (regressions of dependent variable Size against the predictor variable Latitude) for South American *Bradypus variegatus*. We reanalyzed the Bergmann's tests to verify the possible influence of trends in the samples of extreme latitudes or over-collection in certain latitudinal degrees of the geography. Therefore, four new analyses were made for *B. variegatus* under different perspectives to show how consistent the pattern is: randomly selecting one specimen from the specimens within the grid of 0.25 degree (1); averaging specimens by each grid of 0.25 degree (~27 km) (2); randomly selecting one specimen from the specimens within the grid of one degree (~110 km) (3); and averaging specimens by each grid of one degree (~110 km) (4). From the four tests redone, three remained with the same results as previously reported and one was only marginally significant. Significance is highlighted in bold.

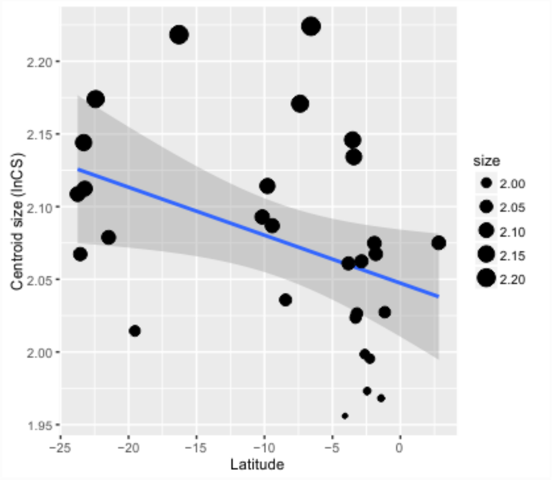
1) Randomly selecting one specimen from the specimens within the grid of 0.25 degree.
n = 38; R^2 Adj: 0.155; P = **0.008**



2) Averaging specimens by each grid of 0.25 degree (~27 km).
n = 38; R^2 Adj: 0.115; P = **0.021**



3) Randomly selecting one specimen from the specimens within the grid of one degree (~110 km).
n = 29; R^2 Adj: 0.128; P = **0.032**



4) Averaging specimens by each grid of one degree (~110 km).
n = 29; R^2 Adj: 0.101; P = 0.052

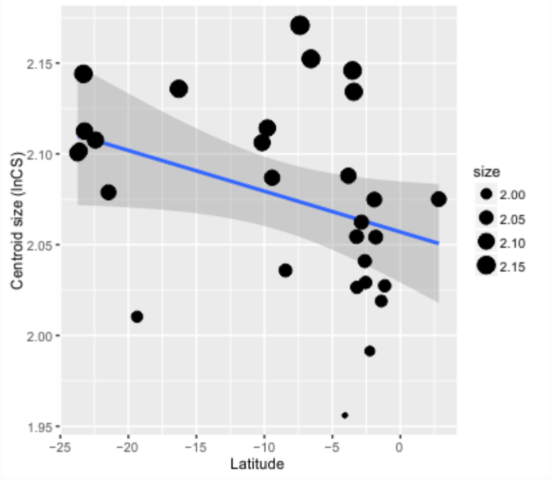


Table S1. List of skull specimens photographed, with data of species, sex, museum number, latitude and longitude. F = female; M = male; UND = undetermined.
Museums: Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB), Museu de Ciências e Tecnologia da PUCRS (MCP), Museu Nacional (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (MZUSP), and Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN).

Species	**Sex**	**Nº Museum**	**Latitude**	**Longitude**
Bradypus_variegatus	F	MACN_271	-3.43	-65.85
Bradypus_variegatus	F	MACN_50119	-16.29	-63.59
Bradypus_variegatus	F	MACN_50120	-16.29	-63.59
Bradypus_variegatus	F	MNRJ_1162	-22.85	-43.26
Bradypus_variegatus	F	MNRJ_2387	-22.42	-42.98
Bradypus_variegatus	M	MNRJ_23888	-21.46	-43.16
Bradypus_variegatus	M	MNRJ_23892	-22.42	-42.98
Bradypus_variegatus	M	MNRJ_23899	-2.45	-54.70
Bradypus_variegatus	M	MNRJ_23900	-2.45	-54.70
Bradypus_variegatus	F	MNRJ_23901	-2.45	-54.70
Bradypus_variegatus	F	MNRJ_23902	-2.45	-54.70
Bradypus_variegatus	M	MNRJ_26929	-1.92	-59.47
Bradypus_variegatus	F	MNRJ_30482	-3.20	-57.23
Bradypus_variegatus	F	MNRJ_5015	-1.81	-49.80
Bradypus_variegatus	F	MNRJ_5019	-1.81	-49.80
Bradypus_variegatus	M	MNRJ_5033	-1.81	-49.80
Bradypus_variegatus	M	MNRJ_5034	-1.81	-49.80
Bradypus_variegatus	F	MNRJ_5037	-1.81	-49.80
Bradypus_variegatus	M	MNRJ_5038	-1.81	-49.80
Bradypus_variegatus	M	MNRJ_5040	-1.81	-49.80
Bradypus_variegatus	M	MNRJ_5648	-23.22	-44.72
Bradypus_variegatus	F	MNRJ_5650	-23.22	-44.72
Bradypus_variegatus	F	MNRJ_6103	-23.22	-44.72
Bradypus_variegatus	M	MNRJ_6702	-23.22	-44.72
Bradypus_variegatus	M	MNRJ_7262	-22.42	-42.98
Bradypus_variegatus	M	MNRJ_7608	-23.22	-44.72
Bradypus_variegatus	F	MNRJ_7609	-23.22	-44.72
Bradypus_variegatus	F	MNRJ_7615	-22.42	-42.98
Bradypus_variegatus	M	MNRJ_8450	-23.22	-44.72
Bradypus_variegatus	M	MPEG_10232	-1.42	-48.41
Bradypus_variegatus	M	MPEG_10233	-1.42	-48.41
Bradypus_variegatus	F	MPEG_10235	-2.45	-54.70
Bradypus_variegatus	F	MPEG_10236	-1.42	-48.41
Bradypus_variegatus	F	MPEG_13266	-2.45	-54.70
Bradypus_variegatus	M	MPEG_13268	-2.45	-54.70
Bradypus_variegatus	M	MPEG_13285	-2.65	-54.95
Bradypus_variegatus	M	MPEG_13286	-2.45	-54.70
Bradypus_variegatus	M	MPEG_20169	-2.65	-54.95

Bradypus_variegatus	F	MPEG_20171	-2.65	-54.95
Bradypus_variegatus	M	MPEG_20172	-2.65	-54.95
Bradypus_variegatus	M	MPEG_20174	-2.65	-54.95
Bradypus_variegatus	M	MPEG_20192	-2.62	-54.70
Bradypus_variegatus	F	MPEG_20193	-2.62	-54.70
Bradypus_variegatus	F	MPEG_20194	-2.65	-54.95
Bradypus_variegatus	F	MPEG_20199	-2.83	-54.37
Bradypus_variegatus	F	MPEG_20203	-2.65	-54.95
Bradypus_variegatus	M	MPEG_2354	-1.15	-47.57
Bradypus_variegatus	F	MPEG_2693	-1.36	-48.24
Bradypus_variegatus	M	MPEG_8533	-2.45	-54.70
Bradypus_variegatus	M	MZUSP_10417	-23.81	-45.40
Bradypus_variegatus	F	MZUSP_10660	-1.42	-48.41
Bradypus_variegatus	M	MZUSP_13497	-3.82	-55.49
Bradypus_variegatus	M	MZUSP_13498	-3.82	-55.49
Bradypus_variegatus	F	MZUSP_13500	2.82	-60.68
Bradypus_variegatus	M	MZUSP_13501	-3.82	-55.49
Bradypus_variegatus	F	MZUSP_13502	-3.82	-55.49
Bradypus_variegatus	F	MZUSP_13505	-8.45	-67.53
Bradypus_variegatus	F	MZUSP_1811	-23.43	-45.08
Bradypus_variegatus	M	MZUSP_1869	-23.43	-45.08
Bradypus_variegatus	F	MZUSP_20003	-3.52	-56.02
Bradypus_variegatus	F	MZUSP_20005	-4.08	-55.88
Bradypus_variegatus	F	MZUSP_2240	-19.18	-40.31
Bradypus_variegatus	M	MZUSP_2420	-19.54	-40.40
Bradypus_variegatus	F	MZUSP_2578	-2.62	-43.45
Bradypus_variegatus	M	MZUSP_2755	-2.62	-43.45
Bradypus_variegatus	F	MZUSP_2892	-2.62	-43.45
Bradypus_variegatus	M	MZUSP_2893	-2.62	-43.45
Bradypus_variegatus	M	MZUSP_2894	-2.62	-43.45
Bradypus_variegatus	M	MZUSP_3534	-23.96	-46.33
Bradypus_variegatus	F	MZUSP_3535	-23.69	-46.56
Bradypus_variegatus	M	MZUSP_4287	-9.43	-40.73
Bradypus_variegatus	M	MZUSP_5300	-3.30	-58.25
Bradypus_variegatus	M	MZUSP_5301	-3.14	-58.45
Bradypus_variegatus	F	MZUSP_5426	-2.87	-55.07
Bradypus_variegatus	M	MZUSP_5428	-7.38	-70.78
Bradypus_variegatus	M	MZUSP_5429	-2.24	-49.50
Bradypus_variegatus	F	MZUSP_5434	-2.24	-49.50
Bradypus_variegatus	F	MZUSP_6639	-23.30	-51.17
Bradypus_variegatus	F	MZUSP_7369	-9.78	-36.10
Bradypus_variegatus	M	MZUSP_7528	-10.17	-36.37
Bradypus_variegatus	M	MZUSP_7529	-10.17	-36.37

Bradypus_variegatus	F	MZUSP_7701	-23.55	-46.63
Bradypus_variegatus	F	MZUSP_783	-6.58	-68.90
Bradypus_variegatus	F	MZUSP_785	-6.58	-68.90
Bradypus_variegatus	F	MZUSP_798	-6.58	-68.90
Bradypus_variegatus	F	MZUSP_8247	-23.75	-45.82
Dasypus_novemcinctus	M	MACN_39458	-26.59	-60.95
Dasypus_novemcinctus	M	MACN_39461	-26.59	-60.95
Dasypus_novemcinctus	M	MACN_39465	-26.59	-60.95
Dasypus_novemcinctus	M	MACN_49350	-26.94	-54.43
Dasypus_novemcinctus	M	MACN_49383	-26.94	-54.43
Dasypus_novemcinctus	F	MACN_49391	-26.94	-54.43
Dasypus_novemcinctus	F	MACN_49397	-26.94	-54.43
Dasypus_novemcinctus	F	MACN_50123	-16.29	-63.59
Dasypus_novemcinctus	F	MACN_5133	-26.94	-54.43
Dasypus_novemcinctus	M	MCN/FZB_2440	-29.94	-51.71
Dasypus_novemcinctus	F	MCN/FZB_2553	-28.66	-56.00
Dasypus_novemcinctus	UND	MCN/FZB_2554	-29.94	-51.71
Dasypus_novemcinctus	UND	MCN/FZB_2788	-29.94	-51.71
Dasypus_novemcinctus	UND	MCN/FZB_986	-32.49	-52.58
Dasypus_novemcinctus	M	MNRJ_10046	-20.64	-46.51
Dasypus_novemcinctus	M	MNRJ_10049	-20.64	-46.51
Dasypus_novemcinctus	F	MNRJ_10050	-20.64	-46.51
Dasypus_novemcinctus	M	MNRJ_10051	-22.12	-43.22
Dasypus_novemcinctus	F	MNRJ_10054	-20.64	-46.51
Dasypus_novemcinctus	F	MNRJ_10056	-20.64	-46.51
Dasypus_novemcinctus	F	MNRJ_10063	-21.87	-43.31
Dasypus_novemcinctus	M	MNRJ_10064	-21.87	-43.31
Dasypus_novemcinctus	F	MNRJ_10070	-22.76	-43.46
Dasypus_novemcinctus	F	MNRJ_10073	-22.76	-43.46
Dasypus_novemcinctus	F	MNRJ_10075	-21.87	-43.31
Dasypus_novemcinctus	M	MNRJ_10077	-20.50	-46.64
Dasypus_novemcinctus	F	MNRJ_10078	-23.55	-51.46
Dasypus_novemcinctus	M	MNRJ_10079	-22.76	-43.46
Dasypus_novemcinctus	M	MNRJ_10092	-23.43	-45.08
Dasypus_novemcinctus	F	MNRJ_10099	-17.26	-49.03
Dasypus_novemcinctus	F	MNRJ_1853	-22.79	-43.31
Dasypus_novemcinctus	M	MNRJ_2192	-21.77	-42.54
Dasypus_novemcinctus	M	MNRJ_24012	-22.66	-43.04
Dasypus_novemcinctus	F	MNRJ_2432	-22.79	-43.31
Dasypus_novemcinctus	M	MNRJ_2433	-22.79	-43.31
Dasypus_novemcinctus	M	MNRJ_24460	-17.08	-52.51
Dasypus_novemcinctus	F	MNRJ_24465	-17.08	-52.51
Dasypus_novemcinctus	F	MNRJ_24468	-17.08	-52.51
Dasypus_novemcinctus	F	MNRJ_24470	-17.08	-52.51

Dasypus_novemcinctus	F	MNRJ_2605	-21.77	-42.54
Dasypus_novemcinctus	M	MNRJ_26917	-1.92	-59.47
Dasypus_novemcinctus	M	MNRJ_26919	-1.92	-59.47
Dasypus_novemcinctus	F	MNRJ_27945	-8.75	-63.45
Dasypus_novemcinctus	F	MNRJ_30484	-3.20	-57.23
Dasypus_novemcinctus	F	MNRJ_30686	2.66	-51.07
Dasypus_novemcinctus	M	MNRJ_30687	-9.78	-36.10
Dasypus_novemcinctus	M	MNRJ_42850	-9.96	-64.23
Dasypus_novemcinctus	F	MNRJ_4669	-16.20	-48.58
Dasypus_novemcinctus	M	MNRJ_4670	-16.20	-48.58
Dasypus_novemcinctus	F	MNRJ_4672	-16.20	-48.58
Dasypus_novemcinctus	M	MNRJ_4673	-16.20	-48.58
Dasypus_novemcinctus	M	MNRJ_4674	-16.20	-48.58
Dasypus_novemcinctus	F	MNRJ_4974	-16.20	-48.58
Dasypus_novemcinctus	F	MNRJ_5010	-16.20	-48.58
Dasypus_novemcinctus	M	MNRJ_5500	-21.83	-42.73
Dasypus_novemcinctus	F	MNRJ_5501	-21.83	-42.73
Dasypus_novemcinctus	M	MNRJ_5789	-3.14	-55.05
Dasypus_novemcinctus	F	MNRJ_5969	-1.92	-55.50
Dasypus_novemcinctus	M	MNRJ_6071	-3.30	-58.25
Dasypus_novemcinctus	M	MNRJ_63451	-9.34	-42.44
Dasypus_novemcinctus	F	MNRJ_69848	-15.24	-58.73
Dasypus_novemcinctus	F	MNRJ_7592	-18.50	-48.38
Dasypus_novemcinctus	F	MNRJ_7600	-22.42	-42.98
Dasypus_novemcinctus	M	MNRJ_7605	-22.42	-42.98
Dasypus_novemcinctus	M	MNRJ_8464	-23.22	-44.72
Dasypus_novemcinctus	UND	MPEG_11881	-3.80	-49.77
Dasypus_novemcinctus	F	MPEG_12330	-3.80	-49.77
Dasypus_novemcinctus	F	MPEG_20152	-2.83	-54.37
Dasypus_novemcinctus	F	MPEG_20153	-2.65	-54.95
Dasypus_novemcinctus	F	MPEG_20154	-2.65	-54.95
Dasypus_novemcinctus	M	MPEG_20155	-2.65	-54.95
Dasypus_novemcinctus	M	MPEG_20156	-2.65	-54.95
Dasypus_novemcinctus	F	MPEG_20196	-4.68	-49.53
Dasypus_novemcinctus	F	MPEG_20531	-10.60	-62.31
Dasypus_novemcinctus	F	MPEG_4669	-2.49	-54.30
Dasypus_novemcinctus	F	MPEG_4671	-2.49	-54.30
Dasypus_novemcinctus	F	MPEG_4672	-2.49	-54.30
Dasypus_novemcinctus	F	MPEG_4673	-2.49	-54.30
Dasypus_novemcinctus	M	MPEG_4677	-2.49	-54.30
Dasypus_novemcinctus	F	MPEG_4679	-2.49	-54.30
Dasypus_novemcinctus	M	MPEG_8527	-2.45	-54.70
Dasypus_novemcinctus	F	MPEG_8528	-2.45	-54.70

Dasypus_novemcinctus	M	MPEG_939	-1.42	-48.41
Dasypus_novemcinctus	M	MZUSP_10431	-22.62	-48.16
Dasypus_novemcinctus	F	MZUSP_13801	-23.02	-48.01
Dasypus_novemcinctus	F	MZUSP_1641	-31.36	-51.98
Dasypus_novemcinctus	F	MZUSP_1642	-31.36	-51.98
Dasypus_novemcinctus	F	MZUSP_19969	-3.82	-55.49
Dasypus_novemcinctus	M	MZUSP_19976	-2.98	-58.48
Dasypus_novemcinctus	M	MZUSP_19977	-2.98	-58.48
Dasypus_novemcinctus	M	MZUSP_19978	-2.96	-58.26
Dasypus_novemcinctus	M	MZUSP_20923	-3.65	-52.38
Dasypus_novemcinctus	F	MZUSP_21301	-3.65	-52.38
Dasypus_novemcinctus	F	MZUSP_23167	-1.92	-59.47
Dasypus_novemcinctus	M	MZUSP_23168	-1.92	-59.47
Dasypus_novemcinctus	M	MZUSP_2711	-23.43	-45.08
Dasypus_novemcinctus	F	MZUSP_27799	-24.62	-48.95
Dasypus_novemcinctus	F	MZUSP_28769	-21.26	-52.04
Dasypus_novemcinctus	M	MZUSP_3244	-23.43	-45.08
Dasypus_novemcinctus	F	MZUSP_6166	-21.67	-49.74
Dasypus_novemcinctus	M	MZUSP_6276	-23.63	-46.62
Dasypus_novemcinctus	UND	MCP_780	-30.03	-52.89
Tamandua_tetradactyla	UND	MACN_108	-24.78	-65.41
Tamandua_tetradactyla	UND	MACN_14896	-26.59	-60.95
Tamandua_tetradactyla	UND	MACN_31168	-0.17	-78.60
Tamandua_tetradactyla	F	MACN_50110	-16.29	-63.59
Tamandua_tetradactyla	F	MACN_50111	-16.29	-63.59
Tamandua_tetradactyla	M	MNRJ_11607	-23.57	-46.54
Tamandua_tetradactyla	M	MNRJ_2341	-3.50	-60.68
Tamandua_tetradactyla	F	MNRJ_24832	-4.80	-64.45
Tamandua_tetradactyla	F	MNRJ_24849	1.63	-52.29
Tamandua_tetradactyla	M	MNRJ_3846	-16.20	-48.58
Tamandua_tetradactyla	M	MNRJ_4536	-1.81	-49.80
Tamandua_tetradactyla	F	MNRJ_5050	-1.81	-49.80
Tamandua_tetradactyla	F	MNRJ_5053	-1.81	-49.80
Tamandua_tetradactyla	F	MNRJ_5054	-16.20	-48.58
Tamandua_tetradactyla	F	MNRJ_5055	-1.81	-49.80
Tamandua_tetradactyla	F	MNRJ_5056	-21.61	-55.17
Tamandua_tetradactyla	F	MNRJ_5058	-1.81	-49.80
Tamandua_tetradactyla	M	MNRJ_5059	-16.20	-48.58
Tamandua_tetradactyla	F	MNRJ_5060	-1.81	-49.80
Tamandua_tetradactyla	M	MNRJ_5061	-21.61	-55.17
Tamandua_tetradactyla	F	MNRJ_5064	-2.01	-49.86
Tamandua_tetradactyla	F	MNRJ_5070	-2.01	-49.86
Tamandua_tetradactyla	F	MNRJ_5510	-3.14	-55.05
Tamandua_tetradactyla	M	MNRJ_5515	-19.82	-40.68

Tamandua_tetradactyla	F	MNRJ_5634	-19.94	-40.60
Tamandua_tetradactyla	F	MNRJ_5638	-3.14	-55.05
Tamandua_tetradactyla	F	MNRJ_5726	-3.14	-55.05
Tamandua_tetradactyla	F	MNRJ_5743	-3.14	-55.05
Tamandua_tetradactyla	F	MNRJ_5883	-19.94	-40.60
Tamandua_tetradactyla	F	MNRJ_73484	-16.76	-42.59
Tamandua_tetradactyla	F	MNRJ_7620	-18.49	-48.44
Tamandua_tetradactyla	F	MNRJ_9677	-14.79	-39.05
Tamandua_tetradactyla	M	MNRJ_9678	-14.79	-39.05
Tamandua_tetradactyla	F	MPEG_10031	-1.42	-48.41
Tamandua_tetradactyla	F	MPEG_12474	-3.80	-49.77
Tamandua_tetradactyla	F	MPEG_12475	-3.80	-49.77
Tamandua_tetradactyla	F	MPEG_12476	-3.80	-49.77
Tamandua_tetradactyla	M	MPEG_12477	-3.80	-49.77
Tamandua_tetradactyla	F	MPEG_13302	-4.27	-55.99
Tamandua_tetradactyla	F	MPEG_1589	-4.54	-71.62
Tamandua_tetradactyla	F	MPEG_20201	-2.83	-54.37
Tamandua_tetradactyla	F	MPEG_2340	-1.42	-48.41
Tamandua_tetradactyla	F	MPEG_38517	-2.16	-56.09
Tamandua_tetradactyla	F	MPEG_4662	-2.49	-54.30
Tamandua_tetradactyla	M	MPEG_4666	-11.44	-61.45
Tamandua_tetradactyla	F	MPEG_6758	0.04	-51.07
Tamandua_tetradactyla	F	MPEG_7088	-4.54	-71.62
Tamandua_tetradactyla	M	MZUSP_10483	-6.84	-70.24
Tamandua_tetradactyla	M	MZUSP_10484	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_10708	-1.45	-56.02
Tamandua_tetradactyla	M	MZUSP_1813	-23.43	-45.08
Tamandua_tetradactyla	M	MZUSP_1861	-23.43	-45.08
Tamandua_tetradactyla	F	MZUSP_1862	-23.43	-45.08
Tamandua_tetradactyla	F	MZUSP_19949	-2.45	-65.34
Tamandua_tetradactyla	M	MZUSP_19951	-3.82	-55.49
Tamandua_tetradactyla	F	MZUSP_19952	-3.82	-55.49
Tamandua_tetradactyla	F	MZUSP_19953	-3.82	-55.49
Tamandua_tetradactyla	F	MZUSP_19960	-3.82	-55.49
Tamandua_tetradactyla	F	MZUSP_19961	-3.82	-55.49
Tamandua_tetradactyla	F	MZUSP_19962	-3.82	-55.49
Tamandua_tetradactyla	M	MZUSP_19964	-21.13	-47.72
Tamandua_tetradactyla	F	MZUSP_19972	-3.82	-55.49
Tamandua_tetradactyla	M	MZUSP_21329	-3.65	-52.38
Tamandua_tetradactyla	F	MZUSP_2837	-21.46	-49.95
Tamandua_tetradactyla	F	MZUSP_2838	-21.46	-49.95
Tamandua_tetradactyla	F	MZUSP_2997	-20.34	-47.79
Tamandua_tetradactyla	F	MZUSP_3065	-17.34	-44.92

Tamandua_tetradactyla	M	MZUSP_3112	-17.34	-44.92
Tamandua_tetradactyla	F	MZUSP_4978	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_4979	-2.24	-49.50
Tamandua_tetradactyla	M	MZUSP_4989	-7.38	-70.78
Tamandua_tetradactyla	F	MZUSP_4991	-9.25	-67.45
Tamandua_tetradactyla	F	MZUSP_4993	-7.38	-70.78
Tamandua_tetradactyla	F	MZUSP_5136	-7.38	-70.78
Tamandua_tetradactyla	F	MZUSP_5137	-3.30	-58.25
Tamandua_tetradactyla	M	MZUSP_5138	-7.38	-70.78
Tamandua_tetradactyla	F	MZUSP_5139	-7.38	-70.78
Tamandua_tetradactyla	M	MZUSP_5234	-2.24	-49.50
Tamandua_tetradactyla	M	MZUSP_5236	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_5238	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_5240	-2.83	-55.13
Tamandua_tetradactyla	F	MZUSP_5439	-3.30	-58.25
Tamandua_tetradactyla	F	MZUSP_5442	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_5443	-6.84	-70.24
Tamandua_tetradactyla	M	MZUSP_5449	-2.24	-49.50
Tamandua_tetradactyla	F	MZUSP_5454	-6.67	-54.57
Tamandua_tetradactyla	M	MZUSP_5455	-2.98	-58.48
Tamandua_tetradactyla	M	MZUSP_5765	-24.32	-47.64
Tamandua_tetradactyla	F	MZUSP_6335	-15.62	-56.08
Tamandua_tetradactyla	F	MZUSP_7037	-13.52	-51.45
Tamandua_tetradactyla	F	MZUSP_7038	-14.49	-50.99
Tamandua_tetradactyla	F	MZUSP_7788	-21.72	-52.42
Tamandua_tetradactyla	M	MZUSP_8471	-23.55	-46.63
Tamandua_tetradactyla	M	MZUSP_8999	-1.29	-48.40
Tamandua_tetradactyla	M	MZUSP_9693	2.63	-60.98
Tamandua_tetradactyla	UND	MCP_661	-29.38	-51.54

Table S2. Variation partitioning results with skull shape representing the dependent variable for *Bradypus variegatus* (n = 86), *Tamandua tetradactyla* (n = 96) and *Dasypus novemcinctus* (n = 102). Allometry, Geography and Environment represent independent variables. P-values test for the significance of F after 1000 permutations. Significance ($P < 0.05$) is highlighted in bold.

Bradypus variegatus	Df	R^2	Adj.R^2	F	P
Allometry	1	0.037	0.026	3.238	**< 0.005**
Geography*	3	0.194	0.164	6.577	**< 0.005**
Environment	21	0.430	0.243	2.301	**< 0.005**
Allometry + Geography	4	0.234	0.196	6.176	**< 0.005**
Allometry + Environment	22	0.452	0.260	2.359	**< 0.005**
Geography + Environment	24	0.495	0.296	2.489	**< 0.005**
All factors	25	0.519	0.319	2.590	**< 0.005**
Allometry “Pure”	1		0.023	3.020	**< 0.005**
Geography Pure”	3		0.058	2.801	**< 0.005**
Environment “Pure”	21		0.123	1.695	**< 0.005**

* PCNM2, PCNM3, PCNM6

Tamandua tetradactyla	Df	R^2	Adj.R^2	F	P
Allometry	1	0.054	0.044	5.400	**< 0.005**
Geography*	1	0.017	0.006	1.618	0.097
Environment	21	0.268	0.061	1.293	**0.026**
Allometry + Geography	2	0.063	0.043	3.154	**< 0.005**
Allometry + Environment	22	0.298	0.086	1.407	**< 0.005**
Geography + Environment	22	0.274	0.056	1.255	**0.024**
All factors	23	0.303	0.081	1.363	**0.007**
Allometry “Pure”	1		0.025	2.984	**0.006**
Geography “Pure”	1		-0.005	0.572	0.781
Environment “Pure”	21		0.037	1.268	0.084

* PCNM6

Dasypus novemcinctus	Df	R^2	Adj.R^2	F	P
Allometry	1	0.053	0.043	5.580	**< 0.005**
Geography*	4	0.106	0.069	2.883	**< 0.005**
Environment	21	0.318	0.139	1.776	**< 0.005**
Allometry + Geography	5	0.145	0.101	3.263	**< 0.005**
Allometry + Environment	22	0.340	0.156	1.847	**< 0.005**
Geography + Environment	25	0.365	0.156	1.745	**< 0.005**
All factors	26	0.384	0.171	1.800	**< 0.005**
Allometry “Pure”	1		0.015	2.380	**0.018**
Geography “Pure”	4		0.015	1.357	0.093
Environment “Pure”	21		0.070	1.386	**0.008**

* PCNM3, PCNM5, PCNM6, PCNM23

Table S3. Variation partitioning results with skull size representing the dependent variable for *Bradypus variegatus* (n = 86), *Tamandua tetradactyla* (n = 96) and *Dasypus novemcinctus* (n = 102). Environment and Geography represent independent variables. P-values test for the significance of F after 1000 permutations. Significance ($P < 0.05$) is highlighted in bold.

Bradypus variegatus	Df	R^2	Adj.R^2	F	P
Geography*	1	0.107	0.097	10.108	**< 0.005**
Environment	21	0.515	0.355	3.231	**< 0.005**
All factors	22	0.517	0.348	3.064	**< 0.005**
Geography "Pure"	1		-0.007	0.294	0.626
Environment "Pure"	21		0.251	2.542	**< 0.005**

* PCNM3

Tamandua tetradactyla	Df	R^2	Adj.R^2	F	P
Geography*	4	0.274	0.242	8.574	**< 0.005**
Environment	21	0.304	0.106	1.537	0.093
All factors	25	0.384	0.163	1.743	**0.033**
Geography "Pure"	4		0.057	2.271	0.081
Environment "Pure"	21		-0.078	0.594	0.909

* PCNM2, PCNM5, PCNM6, PCNM22

Dasypus novemcinctus	Df	R^2	Adj.R^2	F	P
Geography*	2	0.068	0.049	3.591	**0.038**
Environment	21	0.456	0.313	3.193	**< 0.005**
All factors	23	0.484	0.332	3.179	**< 0.005**
Geography "Pure"	2		0.018	2.106	0.121
Environment "Pure"	21		0.283	2.995	**< 0.005**

* PCNM3, PCNM5

5 ARTIGO III. ECOGEOGRAPHY OF SOUTH-AMERICAN RODENTIA AND LAGOMORPHA (MAMMALIA, GLIRES): ROLES OF BODY SIZE, ENVIRONMENT, AND GEOGRAPHY

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Ecogeography of South-American Rodentia and Lagomorpha (Mammalia, Glires): roles of body size, environment, and geography

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Abstract

Groups of species that are widely distributed along an environmental gradient can exhibit adaptations and plasticity, resulting from susceptibility to different pressures. Certain groups of rodents and rabbits that are distributed throughout the Neotropical region are ideal models to evaluate such trait changes. Using geometric morphometric procedures, our objective was to analyse the influences of allometric, environmental, and geographical variables on the skull shape of *Cuniculus paca*, *Hydrochoerus hydrochaeris*, *Nectomys* spp., and *Sylvilagus brasiliensis*. Our results indicate the effect of allometry was particularly evident in *Nectomys*, which should be related, in part, to the sexual dimorphism present in that genus. The environment was a determinant for skull shape for all taxa, but was most prominent in *H. hydrochaeris*. A smaller effect of geographical distance (geography) on skull shape was present in all taxa, but was more relevant for *H. hydrochaeris* and *C. paca*, suggesting a spatially-structured environmental dependence. Overall, our findings highlight the importance of different biological processes acting on smaller-sized and less mobile taxa, compared to larger and more dispersive taxa. Therefore, we can dissociate the neutral and niche processes that relate to the characteristics of each taxon. This includes environmental filtering in more dispersive taxa, which is responsible for changing shape structures in a relevant manner, such as the larger auditory bulla found in more arid and climatically seasonal sites.

Keywords: Allometry – Geometric morphometrics – Hystricomorpha – Myomorpha – Shape adaptation – Neotropical region

Introduction

Cranial morphology is an important research area for detecting variations within or between species (e.g., Hautier et al., 2012) and for elucidating the factors that lead to such divergences (e.g., Menegaz et al., 2010). In vertebrates, the shape and size of the skull can be extremely diverse because of a number of taxonomic changes, such as ecological and developmental changes (Hanken and Hall, 1993). In this way, the mammalian skull consists of a series of elements that demonstrate complex morphological integration and reaction to various processes, resulting in different evolutionary responses between taxonomic groups (Porto et al., 2009; Porto et al., 2013). Thus, the drivers of cranial shape variation are still unclear for several taxa, particularly Neotropical taxa with broad geographical distributions.

Allometry (size-related change of traits) is often present in biological systems (Gould, 1966). Allometry is usually studied in relation to the ontogenetic perspective (Klingenberg, 1998), but can also be inferred at the static level, for instance, within a given age class (e.g., adult samples) (Klingenberg, 1998, 2016). In mammals, size often influences shape variation, suggesting that allometry could be a major engine in mammalian life history (Cardini and Polly, 2013; Marroig, 2007). An allometric influence can also be related to ecological factors. One example concerns rodent feeding ecology, with species consuming similar diets converging to a similar morphology (Wilson, 2013; Wilson and Sánchez-Villagra, 2010). Alternatively, an allometric influence may be present in mammals with widespread habitats throughout different environments, relating to geographical and environmental variations (Bubadué et al., 2015; Magnus et al., 2017; Meloro et al., 2014). Allometry can also generate changes associated with the differences between sexes, increasing sexual dimorphism (Cardini and Elton, 2008). Despite these different perspectives, allometry is not an exclusive factor dictating shape variation (Caumul and Polly, 2005).

Ecogeographical effects on widely distributed species can be related to two basic considerations: the environment and its climatic variation – known as the niche theory Hutchinson (1957) or to space, or geographical distance – known as the neutral theory Hubbell (2001). The niche theory aims to determine the ecological conditions and requirements that a certain species needs to survive in its own habitat (Hutchinson, 1957; Schoener, 2009). For that reason, one environment can contain several organisms exhibiting shape-variations that result from adaptations (or partial adaptations) to that habitat (Hutchinson, 1957). However, shape variations in these organisms will not necessarily change at the same intensity nor the same direction. For example, organisms can suffer environmental pressures, such as a climatic pressure, that could potentially have a strong influence that promotes trait changes (Blois et al., 2013; Yang and Rudolf, 2010). Environmentally related modifications will be mainly emphasized in habitat-generalist species with a high dispersal potential (Hendges et al., 2016; Magnus et al., 2017), according to the selective pressures of different environments. However, organisms can end up living in the same habitat due to merely random factors, e.g., a geographical constraint that can have a greater impact than an environmental influence in a particular habitat (Hubbell, 2001).

Randomness and neutrality between organisms are related to the neutral process perspective (Bell, 2001; Hubbell, 2001). Ecologically similar organisms can remain in the same place due to random variation in births, deaths, and predominantly by a dispersion limitation (Hubbell, 2001; Hubbell, 2006). According to this theory, dispersion has an important function in species with equivalent fitness where similarity increases with the proximity of two localities (Hubbell, 2001), commonly seen in plant communities (e.g., Tuomisto et al., 2003). The stochastic phenomenon related to migration failure is a reflection of the distance to new habitats that hampers migration to these regions (Chave, 2004; Rosindell et al., 2011). This dispersive capacity, when limited, can restrict organisms to a given place or region. As such, their characteristics become moulded as a consequence of the geographical restriction, and not as a result of biotic and abiotic processes (Hubbell, 2001). Nevertheless, there exists the possibility that both niche and neutral processes will influence organismal trait variation conjunctly and not exclusively (Adler et al., 2007).

South America is a geographically large and latitudinally broad continent that encompasses a variety of biomes, each with characteristics ranging from dry and seasonal, to humid and climatically stable ecoregions (Veblen et al., 2007). Widely distributed species in South America, such as monkeys (Meloro et al., 2014), canids (Bubadué et al., 2015; Machado and Hingst-Zaher, 2009), peccaries (Hendges et al., 2016), and marsupials (Magnus et al., 2017), are responsive to climatic clines in the continent, measureable through skull shape variation. Nevertheless, other mammalian groups like rodents and lagomorphs still need to be further analysed regarding the potential for climatic cline variation.

In South America, some taxa of these groups (Glires) inhabit almost all South American biomes. Among rodents, the suborder Hystricomorpha includes *Cuniculus paca* (Linnaeus,

1766) and *Hydrochoerus hydrochaeris* (Linnaeus, 1766) as widely distributed representatives (Patton et al., 2015), whereas Myomorpha has some widespread sigmodontine representatives, mainly the genus *Nectomys* Peters, 1861 (Patton et al., 2015). The order Lagomorpha has only one widespread representative in South America, the rabbit *Sylvilagus brasiliensis* (Linnaeus, 1758) (Chapman and Ceballos, 1990). With regards to all species examined in this study, *Cuniculus paca* is the species with the most expansive spread in the present day, reaching Northeastern Mexico (Rodríguez-Ruíz et al., 2012).

The ecology of the examined species is diverse, with diets ranging from an herbivorous diet (*H. hydrochaeris* and S. *brasiliensis*), an omnivorous diet (*Nectomys*), to a fruit-dependent diet (*C. paca*) (Eisenberg and Redford, 1999; Paglia et al., 2012). With respect to habitat, some species can be very dispersive, such as *C. paca*, but also *H. hydrochaeris* that lives in herds and spreads its population throughout extensive areas (Herrera, 2013; Mones and Ojasti, 1986). Some taxa, especially *S. brasiliensis*, can occupy a wide range of habitats, ranging from pastures to forests (Chapman and Ceballos, 1990); the same is observed for *Nectomys*, despite their dependence on living near watercourses (Ernest, 1986). In terms of body size, *H. hydrochaeris* and *C. paca* are the largest species; *H. hydrochaeris* is the biggest living rodent in the world weighing ~50kg, whereas *C. paca* weighs ~9kg. *Sylvilagus brasiliensis* has an intermediate size of ~1kg, whereas *Nectomys* has the smallest body size, ranging ~100–400g (Eisenberg and Redford, 1999; Paglia et al., 2012). These taxa have not been examined in relation to the degree of sexual shape dimorphism, except for *H. hydrochaeris*, which in principle does not exhibit shape dimorphism (Aeschbach et al., 2016).

Given the potentially broad morphological and ecological variations of such taxa along their extensive distributions in South America, they are ideal models to determine the most influential process that determines their overall variation in shape. Our hypothesis was that an allometric effect would be present in all examined taxa, modifying shape along a geographic gradient (Bubadué et al., 2015; Meloro et al., 2014), or even acting on differences between the sexes in the case of sexual dimorphism (Cardini and Elton, 2008). Our hypothesis also considered that continental environmental heterogeneity would reveal a bigger shape change in taxa considered here generalist, such as those with a larger body size and a higher dispersal capacity throughout several habitats (*H. hydrochaeris* and *C. paca*). Alternatively, smaller-sized taxa (*Nectomys* and *S. brasiliensis*) are expected to change their shape primarily by neutral processes linked to the spatial isolation of populations that are more limited in dispersal capacity. The main emphasis here was to compare the four taxa with respect to niche and neutral ecological theories, and sexual dimorphism of the taxa, as appropriate.

Materials and methods

We collected 430 skull pictures of adult specimens of Glires belonging to four taxa of Rodentia (*C. paca* n = 54; *H. hydrochaeris* n = 45; and *Nectomys* spp. n = 244) and one taxon of Lagomorpha (*S. brasiliensis* n = 87) (Table 1; see also Supplementary material, Table A1). Pictures were taken of the ventral view of the skull (skull with the palate perpendicular to the camera lens, in a horizontal plane), with a digital camera Nikon CoolPix P530 using a similar-adjusted zoom for all photos. The camera was positioned at a fixed distance using a tripod (2 m for *C. paca* and *H. hydrochaeris*, 1.5 m for the other taxa), with a scale bar placed close to the skull. For each specimen, we also recorded the geographic coordinates of the collection point (Fig. 1), mainly obtained using Google Earth (http://earth.google.com.br) through the geographic locality centre. This method has proven effective for museum specimens for which there was no information available regarding geographical coordinates (Magnus et al., 2017). Due to the lack of many species-level classifications of *Nectomys* deposited in museums, species of that genus were identified according to geographic distribution (allopatric) and boundary according to Patton et al., (2015) (Table 1; see also Supplementary material, Table A1).

Table 1. Skull sample size for the four taxa of Rodentia and one of Lagomorpha included in this study.

Family	Species	$N_{specimens}$	$N_{females}$	N_{males}	$N_{undetermined}$
Cuniculidae	*Cuniculus paca* (Linnaeus, 1766)	54	5	45	4
Caviidae	*Hydrochoerus hydrochaeris* (Linnaeus, 1766)	45	14	13	18
Cricetidae	*Nectomys* Peters, 1861	244	99	144	1
	N. rattus Pelzeln, 1883	67	26	40	1
	N. squamipes Brants, 1827	177	104	73	0
Leporidae	*Sylvilagus brasiliensis* (Linnaeus, 1758)	87	53	34	0
Total		430	171	236	23

We digitized 16 two-dimensional homologous landmarks (Fig. 2) using tpsDig2 v. 2.16 software (Rohlf, 2010a), carried out by the same individual (L.Z.M.) to avoid inter-observer error. The landmarks represent the overall skull shape, zygomatic arch (temporal muscle area), auditory bulla, muzzle (palate), and molar series. We also randomly landmarked specimens (two of each taxon twice on different days) and compared the mean error of inter-landmark distance of each specimen to determine the intra-observer error. We found a small error (2.6%) that is considered negligible (Cardini and Tongiorgi, 2003; Meloro, 2011).

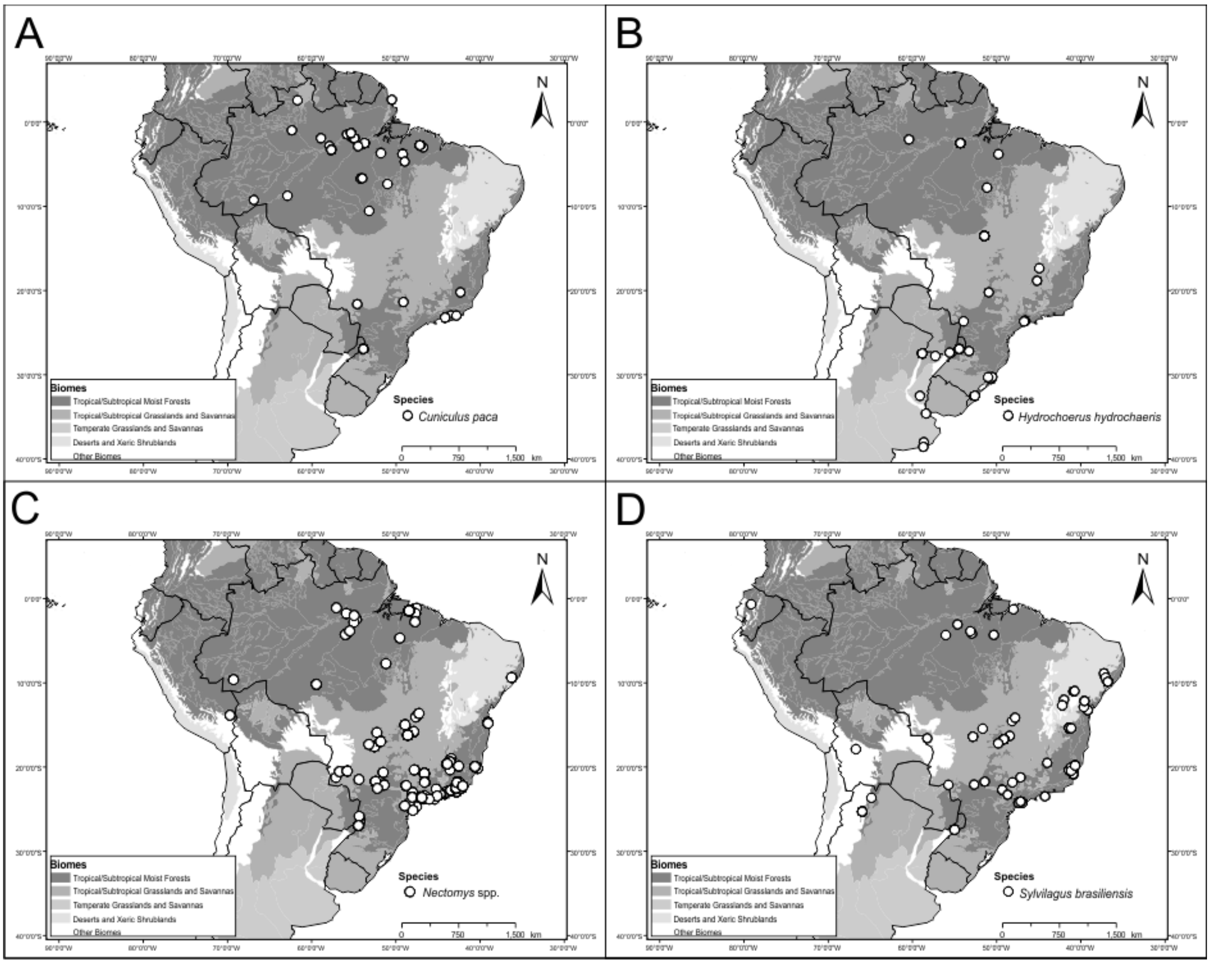

Fig. 1. Maps of South America showing the sampling distribution of Rodentia and Lagomorpha skulls. (A) *Cuniculus paca*, (B) *Hydrochoerus hydrochaeris*, (C) *Nectomys* spp., and (D) *Sylvilagus brasiliensis*.

Geometric morphometric procedures were applied using Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990), to extract shape (Procrustes coordinates) and size data (centroid size, the square root of the sum of squared distances between each landmark and the centroid, according to Bookstein (1991)) from the single generalized superposition of landmark-estimated points (Bookstein, 1991; Rohlf and Slice, 1990). This method removes variation related to scale, orientation, and position from the original landmark coordinates. Additionally, new axes of shape were obtained from a principal component analysis (PCA) using the covariance matrix of the Procrustes coordinates, reducing the dimensionality of the data set and generating independence (corresponding to relative warp analysis, RWA), with tpsRelw v. 1.49 software (Rohlf, 2010b). For the following tests, we focused on intraspecific analyses rather than interspecific ones, considering each skull as a sample unit.

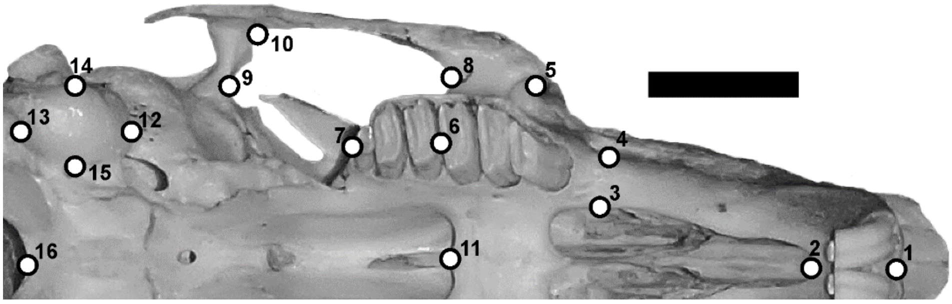

Fig. 2. Position of 16 landmarks on a skull of *Sylvilagus brasiliensis*. Landmark definitions: 1 = midpoint of central incisors; 2 = anteriormost midpoint of the incisive foramen; 3 = junction between maxillar-premaxillar suture and lateral margin of incisive foramen; 4 = lateralmost point of maxillar-premaxillar suture; 5 = anteriormost point of the root of zygomatic arch; 6 = anteriormost point of the first molar (molar row); 7 = posteriormost point of the third molar (molar row); 8 = anteriormost point on curvature of the zygomatic arch; 9 = posteriormost midpoint of the zygomatic process; 10 = posterolateralmost point on curvature of the zygomatic process; 11 = posteriormost tip of suture between palates; 12 = anteriormost edge of auditory bulla; 13 = posteriormost edge of auditory bulla; 14 = lateralmost edge of auditory bulla; 15 = medialmost edge of auditory bulla; 16 = anteriormost point of foramen magnum. Scale bar is 1 cm.

We used a Procrustes ANOVA via 9,999 permutations to test the sexual dimorphism in each taxon (skull shape) in the R environment, version 2.8.1 (R Development Core Team, 2015), using the R package *geomorph* (Adams and Otárola-Castillo, 2013).

To test the relationship of skull shape with respect to the environment, we extracted important variables related to the climate and vegetation (e.g., Hendges et al., 2016; Meloro et al., 2014). For each specimen location, a total of nineteen climatic variables regarding temperature, rainfall, and seasonality were obtained with a resolution of 10’ from the WorldClim raster database (Hijmans et al., 2005) and three other variables related to local vegetation (average annual relative humidity, evapotranspiration, and net primary productivity), obtained from the Atlas of the Biosphere (http://www.sage.wisc.edu/atlas/index.php). We used DIVA-GIS 7.5 software (http://www.divagis.org/) to extract the values for the variables.

Spatial structure and the effect on skull shape were tested with a spatial analysis based on principal coordinates of neighbour matrices (PCNM), which is a principal coordinate analysis of the truncated geographical distance matrix among spatial units (Borcard and Legendre, 2002) using the R *vegan* package (Oksanen et al., 2015). Subsequently, a forward selection was performed with permutation (999) tests using the R package *packfor* (Dray et al., 2009) to select only the explanatory spatial filters (significantly correlated with shape) (Borcard et al., 2011). This procedure selected the spatial filters that were used in subsequent regression analyses. In fact, the spatial filters represent the spatial relationship between our samples (geographical distance), which we consider here to be probably spatially autocorrelated due to the dispersal limitation of taxa (Borcard et al., 2004). That is, some pattern of biological response not directly measured here (Rodrigues et al., 2017).

After, using the R package *geomorph* (9,999 permutations) (Adams and Otárola-Castillo, 2013), we performed separated multivariate regressions with the variables size (natural logarithm of centroid size, lnCS = allometry), environment (22 environmental variables), geographical distance (spatial filters = geography) and *environment (with the spatial filters as additional covariates to account for spatial autocorrelation) as independent variables to explore the influence on shape within each taxon.

Finally, we applied an additional analysis of two-block partial least squares (PLS) with the 22 variables that describe the environment, with MorphoJ 1.05 software (Klingenberg, 2011), to verify the correlation between skull shape and environment for each taxon and view the shape changes. To represent graphical deformation grids, we also used tpsPLS v. 1.18 software (Rohlf, 2006).

Results

We did not find sexual dimorphism in any taxon (*C. paca* F = 1.44, P = 0.122; *H. hydrochaeris* F = 1.08, P = 0.361; *S. brasiliensis* F = 1.49, P = 0.147), with the exception of *Nectomys* (F = 2.77, P = 0.003). Since only *Nectomys* shows sexual dimorphism, we performed the main analyses separating males and females for this taxon. All subsequent analyses were treated with data for both sexes and undetermined specimens pooled together for the other taxa.

Our results show for the skull shape of *C. paca* that RW1 and RW2 correspond to 16.94 and 12.75 % of the total variation, respectively (Fig. 3A). For RW1, a negative extreme describes a larger zygomatic arch, a small auditory bulla, and a thin/elongated muzzle. For RW2, a negative extreme describes shape changes related to a larger skull, an elongated zygomatic arch, and a larger molar series.

For the skull shape variation of *H. hydrochaeris*, RW1 corresponds to 17.88 % and RW2 to 14.66 % of the total variation (Fig. 3B). A RW1 negative extreme describes the relative expansion of the zygomatic arch and muzzle, while specimens at a negative extreme of RW2 exhibit a larger skull and small auditory bulla.

For the skull shape of *Nectomys*, RW1 corresponds to 17.26 % and RW2 to 12.69 % of the total variation (Fig. 3C). RW1 negative extreme describes an elongated skull, and a small/elongated zygomatic arch, auditory bulla, and muzzle. The negative extreme of RW2 exhibits a smaller molar series and auditory bulla.

Finally, the skull shape variation of *S. brasiliensis* corresponds to 29.77 and 14.50 % respectively (Fig. 3D). The RW1 negative extreme describes shape changes related to a larger auditory bulla. For RW2, a negative extreme describes a larger skull, a smaller zygomatic arch, and a relatively larger muzzle. An opposite trend is seen in the positive extreme for all taxa.

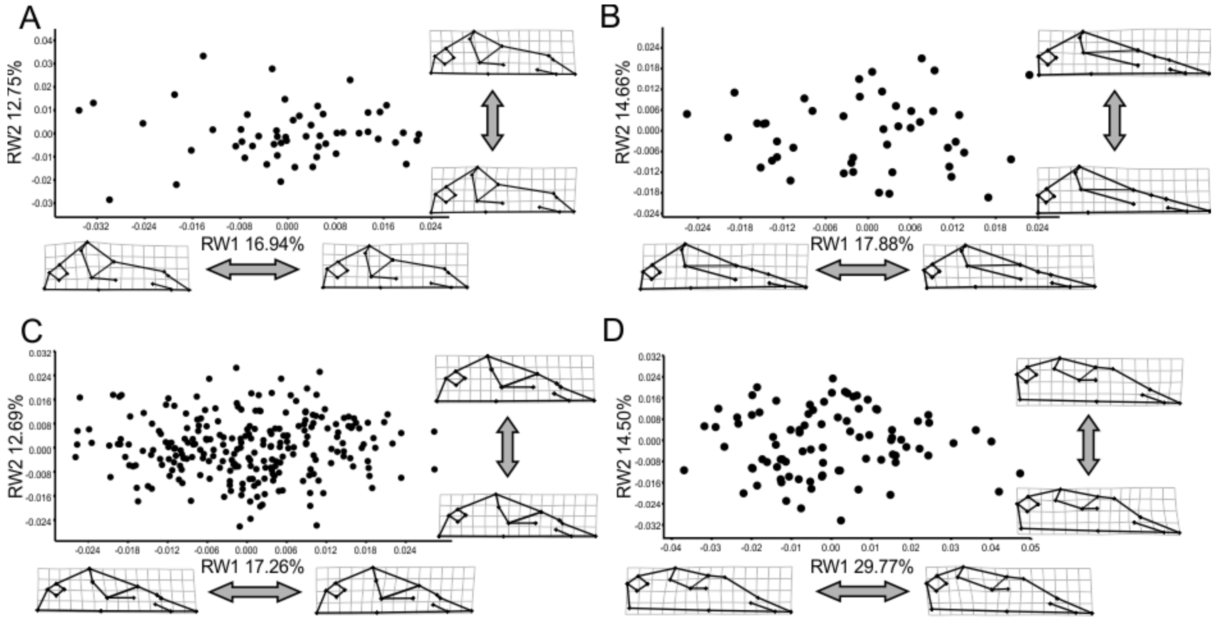

Fig. 3. Scatter plot of the first pair of relative warps (RW1 vs. RW2) showing the taxa shape variation. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of relative warp axes. In (A) deformations are for *Cuniculus paca*, in (B) for *Hydrochoerus hydrochaeris*, in (C) for *Nectomys*, and in (D) for *Sylvilagus brasiliensis*.

With respect to allometry, there was a significant impact of size on skull shape in *Nectomys* and *S. brasiliensis*. However, the impact of allometry on larger species was weaker (*C. paca*) or non-significant (*H. hydrochaeris*) (Table 2). However, the cranial shape deformation related to allometry (lnCS) was quite similar for all taxa (Fig. 4), but more pronounced for *Nectomys* (Fig 4C). We observed variation patterns, especially in relation to skull thinning and a tendency to have a relatively smaller zygomatic arch area, molar series, auditory bulla, and muzzle, when size increased.

The importance of the environment on shape (even considering the spatial effect on the environment) was higher for *H. hydrochaeris* and *C. paca*, moderate for *S. brasiliensis*, and smallest for *Nectomys*. On the other hand, geographical distance was most important for variation of *H. hydrochaeris* shape, followed by *Nectomys* and *C. paca*, and lastly *S. brasiliensis* (Table 2). Considering the two species as covariate in *Nectomys*, the results remained similar (Size: $R^2 = 0.09$, $P < 0.001$; Environment: $R^2 = 0.14$, $P < 0.001$ and Geographical distance: $R^2 = 0.05$, $P < 0.001$), evidencing little influence of taxonomy, which does not compromise the results found for the genus.

Table 2. Procrustes ANOVA results analysing the skull shape variation in South-American Rodentia and Lagomorpha taxa according to: Size (natural logarithm of centroid size = allometry), Environment (22 environmental variables), Geographical distance (spatial filters) and *Environment (spatial filters as covariates). Significance ($P < 0.05$) is highlighted in bold.

		df	SS	MS	R²	F	P-value
C. paca							
	Size	1	0.002	0.002	0.03	1.754	**0.043**
	Environment	21	0.025	0.001	0.46	1.275	**0.017**
	Geog. distance	2	0.004	0.002	0.07	2.019	**0.002**
	*Environment	21	0.023	0.001	0.42	1.206	**0.012**
H. hydrochaeris							
	Size	1	0.001	0.001	0.04	1.681	0.056
	Environment	21	0.019	0.001	0.59	1.557	**< 0.001**
	Geog. distance	2	0.004	0.002	0.11	2.593	**< 0.001**
	*Environment	21	0.016	0.001	0.51	1.309	**0.001**
Nectomys							
	Size	1	0.016	0.016	0.09	24.071	**< 0.001**
	Environment	21	0.029	0.001	0.16	2.009	**< 0.001**
	Geog. distance	6	0.013	0.002	0.07	3.012	**< 0.001**
	*Environment	21	0.021	0.001	0.12	1.520	**< 0.001**
S. brasiliensis							
	Size	1	0.006	0.006	0.07	5.940	**< 0.001**
	Environment	21	0.030	0.001	0.35	1.682	**< 0.001**
	Geography	2	0.005	0.003	0.06	2.732	**0.002**
	*Environment	21	0.027	0.001	0.31	1.485	**0.001**

*indicates significant spatial filtering as a covariate on the model (spatial autocorrelation): *C.paca* (PCNM1, PCNM2); *H. hydrochaeris* (PCNM1, PCNM4); *Nectomys* (PCNM1, PCNM3, PCNM4, PCNM16, PCNM19, PCNM29); *S. brasiliensis* (PCNM1, PCNM2)

In the case of the separation of the *Nectomys* sex, females exhibited a higher effect of environment and geographical distance, while males had a higher allometric effect (Table 3). Nevertheless, comparing both allometric and PLS vectors, males and females followed similar trajectories in both cases, respectively (angle = 20.17°, $P < 0.001$; angle = 50.32°, $P < 0.001$).

The environmental impact on shape through two-block partial least squares was especially strong for *H. hydrochaeris* and C. *paca*, in that order. For the other two taxa the environment was still a significant, but more moderate influence (*S. brasiliensis* and *Nectomys*) (Table 4; see also Supplementary material, Table A2).

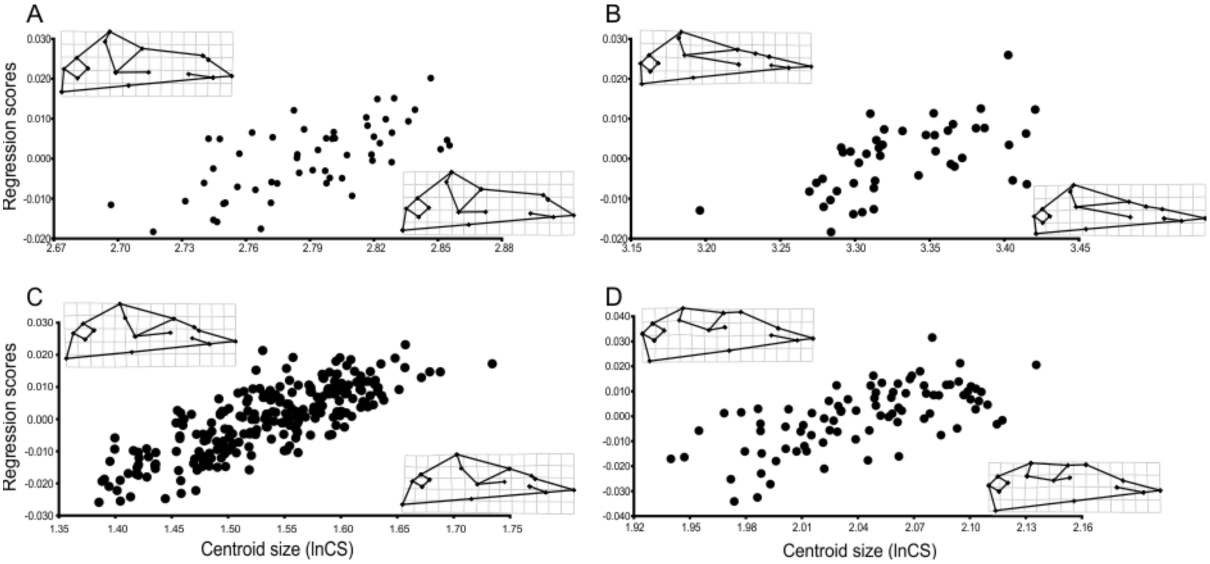

Fig. 4. Scatter plot obtained by regression of shape onto the size (lnCS) for (A) *Cuniculus paca*, (B) *Hydrochoerus hydrochaeris*, (C) *Nectomys*, and (D) *Sylvilagus brasiliensis*. Graphical deformation grids are shown for negative and positive extremes of the regression scores computed for each group.

Table 3. Procrustes ANOVA results analysing the skull shape variation in *Nectomys* females and males according to: Size (natural logarithm of centroid size = allometry), Environment (22 environmental variables), Geographical distance (spatial filters) and *Environment (spatial filters as covariates). Significance ($P < 0.05$) is highlighted in bold.

	df	SS	MS	R^2	F	P-value
Nectomys (females)						
Size	1	0.005	0.005	0.07	7.710	**< 0.001**
Environment	21	0.021	0.001	0.29	1.524	**< 0.001**
Geog. distance	4	0.007	0.002	0.10	2.681	**< 0.001**
*Environment	21	0.017	0.001	0.23	1.223	**0.003**
Nectomys (males)						
Size	1	0.010	0.010	0.10	14.932	**< 0.001**
Environment	21	0.021	0.001	0.20	1.427	**0.001**
Geog. distance	4	0.006	0.002	0.06	2.171	**< 0.001**
*Environment	21	0.018	0.001	0.17	1.273	**0.003**

*indicates spatial filtering as a covariate on the model (spatial autocorrelation):
Nectomys female (PCNM1, PCNM2, PCNM3, PCNM9); *Nectomys male* (PCNM1, PCNM3, PCNM7, PCNM9)

The plot of environmental variables (=singular warp, SW1 Environment) with skull shape scores (SW1 Shape) highlights mainly the samples of two species most affected by the environment (Fig. 5), *H. hydrochaeris* and *C. paca*. In locations that tend to be more arid and seasonal (SW1 environment negative scores), *Cuniculus paca* (Fig. 5A) exhibited an expanded zygomatic arch, a slightly larger auditory bulla and a relative thicker muzzle; *Hydrochoerus* *hydrochaeris* (Fig. 5B) exhibited a thinner skull and zygomatic arch, larger auditory bulla, and a thicker muzzle; *Nectomys* presented a subtle, smaller molar series, and slightly larger auditory bulla (Fig. 5C). Finally, *S. brasiliensis* exhibited a thicker skull, zygomatic arch, and auditory bulla. In all cases, positive scores showed an antagonistic skull shape related to warmer and more humid and stable places (Fig. 5D).

Table 4. Two-block partial least squares (PLS) covariation (rv) and correlation (r) of the first pair of vectors comparing shape and environmental variables (n = 22) for South-American Rodentia and Lagomorpha taxa. Significance ($P < 0.05$) is highlighted in bold.

Species	rv (%)	R	P-value
Cuniculus paca	78.698	0.605	**0.030**
Hydrochoerus hydrochaeris	81.483	0.634	**0.027**
Nectomys	76.930	0.465	**< 0.001**
Sylvilagus brasiliensis	64.470	0.473	**0.009**

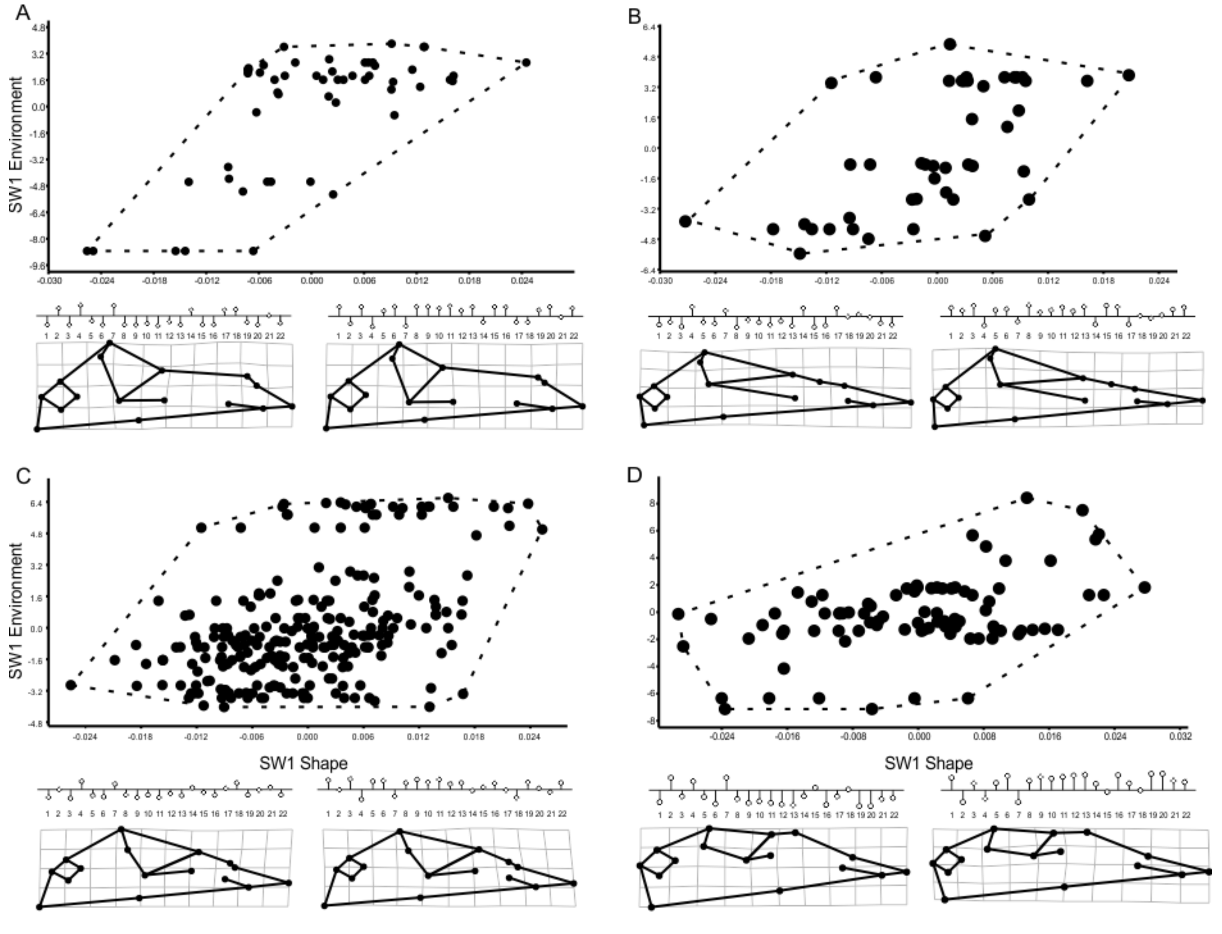

Fig. 5. Plot of environmental variables and shape scores from the most negative to the most positive Singular Warps (first pair). Below are deformation grids and variables profile from the most negative to the most positive Singular Warps scores. The numbers in the variables scores are from the 19 variables of WorldClim plus average annual relative humidity (20), net primary productivity (21), and evapotranspiration (22). In (A) deformations are for *Cuniculus paca*, in (B) for *Hydrochoerus hydrochaeris*, in (C) for *Nectomys*, and in (D) for *Sylvilagus brasiliensis*.

Discussion

The widespread taxa of Rodentia and Lagomorpha in South America show different pressures on shape variation, related to their intrinsic characteristics. An allometric effect was present for almost all taxa, especially in the small-sized *Nectomys*, which should be related to the presence of sexual shape dimorphism in that genus. Similarly, as expected, all taxa had in common the influence of environment to a variable degree, reflecting both intrinsic characteristics and biome heterogeneity along the continent (Veblen et al., 2007). Moreover, the environmental influence was noticeable for highly dispersive species, such as *H. hydrochaeris* and *C. paca*. Both species were also affected by spatial filters, but to a lesser extent, as occurred for the other two taxa.

Moderate allometry was present in most taxa analysed here. In a broad scenario, all groups showed a trend of a general thinning of the skull and a proportional reduction of the zygomatic area and auditory bulla when size increased. This general allometric tendency of skull elongation in larger animals followed the pattern observed in the study by Álvarez et al. (2013), which analysed shape variation in several species of Hystricomorpha. In addition, this allometric pattern has been found in other mammalian groups and confirms a shorter, rounded skull in small-sized species (Cardini et al., 2015; Cardini and Polly, 2013). This suggests a conserved feature from an evolutionary perspective, as generally seen in tetrapods (Emerson and Bramble, 1993). Another relevant finding is that an allometric effect was especially present in the genus *Nectomys*, probably related to the sexual dimorphism, as seen in some primate species (Meloro et al., 2014). There are few studies about *Nectomys* ecology, but the higher environmental effect on the females may be related to intense foraging behaviour, as reported for *N. squamipes* (Lima et al., 2015). While the prominent allometric influence here in males may suggest some fitness related to female search during the breeding season (Lima et al., 2015). In addition, the degree of sexual dimorphism can vary geographically (Bubadué et al., 2016), and, indirectly, the size variation driving shape changes (related or not to dimorphism) can be associated with environmental factors (Caumul and Polly, 2005).

Another important (and indeed the main) predictor of shape change was the environment. Hutchinson (1957) realised that a niche could be described as n-dimensional environment axes, what we can translate here as the set of temperature, rainfall and vegetation variables, related to the shape variation of the taxa analysed (Fig. 5). The main species affected by the environment was *H. hydrochaeris* (capybara), which occupies large territorial areas (Herrera, 2013), with a high dispersal velocity (Iwamura et al., 2014; Schloss et al., 2012).

Although living close to watercourses, the species may also occupy drier environments, such as open savannas and floodplains (Mones and Ojasti, 1986; Moreira et al., 2013), subjected to high seasonality (Mones and Ojasti, 1986) and shape flexibility. For *C. paca*, its high impact of influence from the environment can reflect a sum of three phenomena: high dispersal velocity (Schloss et al., 2012), relatively large body size, and dependence on fruit in the diet (Pérez, 1992) (seasonally food – Fleming et al. (1987)). All these characteristics support the findings of a prominent environmental influence on these species, which was much higher than that on the other two taxa examined here, which are smaller and more dispersal-limited. Thus, such highly mobile species should arrive more easily in every site, being locally shaped according to local environmental conditions (Cáceres et al., 2014; Wearn et al., 2016).

Furthermore, the environment can influence the shape of organisms indirectly through available food resources and therefore, diet (Samuels, 2009). The seasonality of food availability can be important for diet-generalist taxa that also include hard foods (e.g., seeds) in their diet (Pacheco and Peralta, 2011; Pérez, 1992). This can be seen for frugivorous *C. paca*, and even for the herbivorous *S. brasiliensis*, through the larger zygomatic arch area in more arid and seasonal environments (see Fig. 5), and consequently increasing the strength of masticatory processing (Hautier et al., 2012). Another relevant change found is in relation to the auditory bulla. In all taxa, the auditory bulla was enlarged in more arid and seasonal environments than in more humid and stable environments (Fig. 5). Sheets (1989) points out that increasing rodent bulla can lead to increased sound perception, which may benefit a prey against predators (also suggested by Webster and Webster, 1971). Besides avoiding predators, species such as *Nectomys* can also be important predator of insects as well as small fish (Ernest, 1986), with the increasing auditory bulla also favouring the perception of sounds of their prey in seasonal environments. The results found here may further assume the importance of this auditory structure in these arid/open environments, since this same pattern has been found in other species of Rodentia (Álvarez et al., 2013; Bueno and Motta-Junior, 2015; Maestri et al., 2018) and Lagomorpha (Ge et al., 2015) in similar habitat types.

In contrast to environmental pressures, geographical distance was not as important for the small size species, indicating that the environment or even allometry (in the case of *Nectomys*) have a meaningful role in shape variation. *Nectomys* possibly adjusts phenotypically from the ingestion of different food items in its omnivorous diet (Ernest, 1986), consuming food that is more available, following its gradient of distribution and shape change. Similarly, *S. brasiliensis*, as mentioned before, does not only occupy tropical forest areas but also grasslands, which allows flexibility in shape change according to the different local environmental conditions (Chapman and Ceballos, 1990). Thus, reduced body size does not necessarily lead to pressures related to a limited dispersal capacity on these taxa, and it is possible that other additional biotic or abiotic factors not measured here also regulate their shape. Nevertheless, *H. hydrochaeris* and *C. paca* shape also showed a variation by the geographical distance, influenced by the dependence of a minimally spatially structured environment, which suggests, for example, a relation with the fact that both species have territorial behavior (Eisenberg and Redford, 1999; Moreira et al., 2013).

Therefore, widely distributed taxa inhabiting the Neotropical region range across a variety of biomes and are mainly affected by niche processes. On the other hand, geographical distance, that is, neutral processes, is significant and present, but it is not as relevant in explaining shape variation in these taxa. However, we also reinforce that the two theories can work together in explaining shape change, as is the case of capybaras (Table 2). These results add knowledge to the understanding of Rodentia and Lagomorpha biogeography in the continent, and clarify which ecological or biological processes regulate their shape variation when taxa have wide, continental distributions. Future studies should test these ecogeographical predictions in reference to other important response variables, such as body size (e.g., Magnus et al., 2017), as well as taking into account the phylogenetic signal and distribution extent of species (e.g., Álvarez et al., 2013; Maestri et al., 2018).

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Supplementary data

Table A1. List of skull specimens photographed, with data of specie, sex, museum number, latitude and longitude. F = female; M = male; UND = undetermined.
Museums: Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB), Museu Nacional (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), and Coleção de Mamíferos da Universidade Federal de Santa Maria (UFSM).

Species	Sex	Nº Museum	Latitude	Longitude
Cuniculus_paca	UND	MACN_25781	-26.94	-54.43
Cuniculus_paca	F	MACN_49314	-26.94	-54.43
Cuniculus_paca	M	MACN_49379	-26.94	-54.43
Cuniculus_paca	M	MACN_49463	-26.94	-54.43
Cuniculus_paca	UND	MACN_51136	-26.94	-54.43
Cuniculus_paca	M	MNRJ_20416	2.66	-51.07
Cuniculus_paca	F	MNRJ_24278	-10.54	-53.76
Cuniculus_paca	M	MNRJ_26930	-1.92	-59.47
Cuniculus_paca	F	MNRJ_28507	-8.75	-63.45
Cuniculus_paca	M	MNRJ_3881	-22.96	-44.04
Cuniculus_paca	M	MNRJ_4872	-21.61	-55.17
Cuniculus_paca	F	MNRJ_69168	-0.97	-62.93
Cuniculus_paca	M	MNRJ_8283	-22.97	-43.39
Cuniculus_paca	M	MNRJ_8449	-23.22	-44.72
Cuniculus_paca	M	MNRJ_8458	-23.22	-44.72
Cuniculus_paca	M	MNRJ_8461	-23.22	-44.72
Cuniculus_paca	M	MPEG_10429	-1.76	-55.86
Cuniculus_paca	M	MPEG_10518	-1.47	-56.38
Cuniculus_paca	M	MPEG_12403	-3.80	-49.77
Cuniculus_paca	M	MPEG_12500	-3.80	-49.77
Cuniculus_paca	M	MPEG_12506	-3.80	-49.77
Cuniculus_paca	M	MPEG_12508	-3.80	-49.77
Cuniculus_paca	UND	MPEG_1888	-7.35	-51.57
Cuniculus_paca	M	MPEG_20210	-4.68	-49.53
Cuniculus_paca	UND	MPEG_30678	-3.00	-47.35
Cuniculus_paca	M	MPEG_5420	-2.49	-54.30
Cuniculus_paca	M	MPEG_5422	-2.49	-54.30
Cuniculus_paca	M	MPEG_5424	-1.92	-55.50
Cuniculus_paca	M	MPEG_5433	-1.92	-55.50
Cuniculus_paca	M	MPEG_5436	-1.92	-55.50
Cuniculus_paca	M	MPEG_5438	-2.49	-54.30
Cuniculus_paca	M	MPEG_5441	-2.49	-54.30
Cuniculus_paca	M	MPEG_5442	-2.49	-54.30
Cuniculus_paca	M	MPEG_5446	-6.69	-54.74
Cuniculus_paca	M	MPEG_5447	-2.49	-54.30
Cuniculus_paca	M	MZUSP_10480	-3.30	-58.25
Cuniculus_paca	M	MZUSP_10481	-2.85	-58.46

Cuniculus_paca	M	MZUSP_10482	-3.30	-58.25
Cuniculus_paca	M	MZUSP_10487	-3.30	-58.25
Cuniculus_paca	M	MZUSP_21335	-3.65	-52.38
Cuniculus_paca	M	MZUSP_25457	-3.70	-52.35
Cuniculus_paca	M	MZUSP_25462	-1.31	-55.92
Cuniculus_paca	M	MZUSP_25464	-1.31	-55.92
Cuniculus_paca	M	MZUSP_5264	-9.25	-67.45
Cuniculus_paca	M	MZUSP_5265	-6.67	-54.57
Cuniculus_paca	F	MZUSP_5267	-2.87	-55.07
Cuniculus_paca	M	MZUSP_5913	-21.37	-49.68
Cuniculus_paca	M	MZUSP_5939	-20.21	-42.91
Cuniculus_paca	M	MZUSP_9616	-2.75	-47.73
Cuniculus_paca	M	MZUSP_9623	-2.75	-47.73
Cuniculus_paca	M	MZUSP_9624	-2.75	-47.73
Cuniculus_paca	M	MZUSP_9625	-2.75	-47.73
Cuniculus_paca	M	MZUSP_9626	-2.75	-47.73
Cuniculus_paca	M	MZUSP_9683	2.60	-62.26
Hydrochoerus_hydracaeris	M	MACN_14038	-27.47	-58.84
Hydrochoerus_hydracaeris	F	MACN_14039	-27.47	-58.84
Hydrochoerus_hydracaeris	M	MACN_16259	-38.02	-58.65
Hydrochoerus_hydracaeris	UND	MACN_16324	-34.60	-58.38
Hydrochoerus_hydracaeris	UND	MACN_16487	-27.77	-57.28
Hydrochoerus_hydracaeris	UND	MACN_214	-27.37	-55.58
Hydrochoerus_hydracaeris	UND	MACN_22844	-27.47	-58.84
Hydrochoerus_hydracaeris	UND	MACN_24495	-27.47	-58.84
Hydrochoerus_hydracaeris	UND	MACN_25788	-26.94	-54.43
Hydrochoerus_hydracaeris	UND	MACN_2812	-32.52	-59.10
Hydrochoerus_hydracaeris	UND	MACN_38248	-38.56	-58.71
Hydrochoerus_hydracaeris	F	MACN_49302	-26.94	-54.43
Hydrochoerus_hydracaeris	F	MACN_49303	-26.94	-54.43
Hydrochoerus_hydracaeris	UND	MCN_1691	-32.49	-52.58
Hydrochoerus_hydracaeris	F	MCN_1698	-32.49	-52.58
Hydrochoerus_hydracaeris	UND	MCN_1098	-27.19	-53.27
Hydrochoerus_hydracaeris	UND	MCN_1699	-32.49	-52.58
Hydrochoerus_hydracaeris	UND	MCN_2727	-30.52	-50.64
Hydrochoerus_hydracaeris	UND	MCN_2830	-32.49	-52.58
Hydrochoerus_hydracaeris	UND	MCN_3362	-30.26	-50.51
Hydrochoerus_hydracaeris	UND	MCN_3405	-30.28	-51.02
Hydrochoerus_hydracaeris	UND	MNRJ_2653	-18.83	-45.19
Hydrochoerus_hydracaeris	F	MNRJ_6097	-2.06	-60.40
Hydrochoerus_hydracaeris	UND	MPEG_12317	-3.80	-49.77
Hydrochoerus_hydracaeris	UND	MPEG_22209	-32.49	-52.58
Hydrochoerus_hydracaeris	M	MPEG_22817	-7.77	-51.13
Hydrochoerus_hydracaeris	M	MPEG_4614	-2.49	-54.30
Hydrochoerus_hydracaeris	M	MPEG_4615	-2.49	-54.30
Hydrochoerus_hydracaeris	M	MPEG_4618	-2.49	-54.30

Hydrochoerus_hydracaeris	F	MPEG_4620	-2.49	-54.30
Hydrochoerus_hydracaeris	F	MPEG_4622	-2.49	-54.30
Hydrochoerus_hydracaeris	M	MPEG_4624	-2.49	-54.30
Hydrochoerus_hydracaeris	M	MPEG_4627	-2.49	-54.30
Hydrochoerus_hydracaeris	M	MZUSP_25319	-23.66	-53.92
Hydrochoerus_hydracaeris	M	MZUSP_3116	-17.34	-44.92
Hydrochoerus_hydracaeris	F	MZUSP_3279	-23.59	-46.60
Hydrochoerus_hydracaeris	M	MZUSP_679	-23.59	-46.60
Hydrochoerus_hydracaeris	F	MZUSP_6977	-13.52	-51.45
Hydrochoerus_hydracaeris	F	MZUSP_6978	-13.52	-51.45
Hydrochoerus_hydracaeris	F	MZUSP_6979	-13.52	-51.45
Hydrochoerus_hydracaeris	M	MZUSP_6980	-13.52	-51.45
Hydrochoerus_hydracaeris	F	MZUSP_6981	-13.52	-51.45
Hydrochoerus_hydracaeris	F	MZUSP_6982	-13.52	-51.45
Hydrochoerus_hydracaeris	M	MZUSP_7684	-23.68	-46.73
Hydrochoerus_hydracaeris	F	MZUSP_9713	-20.21	-50.93
Nectomys_rattus	F	MNRJ_22839	-15.90	-52.25
Nectomys_rattus	M	MNRJ_4379	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4380	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4384	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4388	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4393	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4395	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4399	-16.20	-48.58
Nectomys_rattus	F	MNRJ_46889	-14.04	-47.62
Nectomys_rattus	M	MNRJ_46930	-13.64	-47.25
Nectomys_rattus	M	MNRJ_46890	-14.04	-47.62
Nectomys_rattus	F	MNRJ_50499	-13.64	-47.25
Nectomys_rattus	M	MPEG_10084	-1.76	-55.86
Nectomys_rattus	F	MPEG_10114	-1.76	-55.86
Nectomys_rattus	F	MPEG_10184	-10.18	-59.45
Nectomys_rattus	M	MPEG_10824	-9.61	-69.29
Nectomys_rattus	F	MPEG_10898	-14.97	-48.92
Nectomys_rattus	F	MPEG_10899	-14.97	-48.92
Nectomys_rattus	F	MPEG_12629	-1.08	-57.05
Nectomys_rattus	M	MPEG_12630	-2.45	-54.70
Nectomys_rattus	M	MPEG_13190	-4.27	-55.99
Nectomys_rattus	M	MPEG_13191	-4.27	-55.99
Nectomys_rattus	M	MPEG_13192	-4.27	-55.99
Nectomys_rattus	M	MPEG_13194	-4.27	-55.99
Nectomys_rattus	M	MPEG_13196	-4.27	-55.99
Nectomys_rattus	M	MPEG_13201	-10.18	-59.45
Nectomys_rattus	M	MPEG_13202	-10.18	-59.45
Nectomys_rattus	M	MPEG_13203	-1.42	-48.41
Nectomys_rattus	F	MPEG_15171	-1.76	-47.68

Nectomys_rattus	F	MPEG_15173	-4.27	-55.99
Nectomys_rattus	M	MPEG_1921	-1.42	-48.41
Nectomys_rattus	M	MPEG_2318	-1.30	-47.99
Nectomys_rattus	M	MPEG_2319	-1.30	-47.99
Nectomys_rattus	M	MPEG_2377	-1.15	-47.57
Nectomys_rattus	M	MPEG_8130	-1.76	-47.68
Nectomys_rattus	F	MPEG_8135	-1.76	-47.68
Nectomys_rattus	M	MPEG_8724	-2.45	-54.70
Nectomys_rattus	M	MPEG_8727	-2.45	-54.70
Nectomys_rattus	M	MPEG_8732	-2.45	-54.70
Nectomys_rattus	M	MPEG_8734	-2.45	-54.70
Nectomys_rattus	M	MPEG_9110	-4.68	-49.53
Nectomys_rattus	F	MZUSP_2006	-13.85	-69.68
Nectomys_rattus	M	MZUSP_21226	-2.75	-47.73
Nectomys_rattus	F	MZUSP_21227	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21229	-1.38	-48.34
Nectomys_rattus	F	MZUSP_21231	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21232	-1.42	-48.41
Nectomys_rattus	F	MZUSP_21233	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21235	-1.47	-48.50
Nectomys_rattus	M	MZUSP_21236	-1.42	-48.41
Nectomys_rattus	M	MZUSP_21237	-7.72	-51.18
Nectomys_rattus	F	MZUSP_21240	-2.79	-54.98
Nectomys_rattus	M	MZUSP_21542	-3.82	-55.49
Nectomys_rattus	M	MZUSP_3676	-2.00	-54.93
Nectomys_rattus	UND	MZUSP_6010	-21.23	-57.13
Nectomys_rattus	F	UFSM_133	-20.47	-55.79
Nectomys_rattus	M	UFSM_189	-17.56	-52.55
Nectomys_rattus	M	UFSM_195	-17.56	-52.55
Nectomys_rattus	M	UFSM_218	-20.47	-55.79
Nectomys_rattus	M	UFSM_27	-20.54	-56.71
Nectomys_rattus	M	UFSM_288	-16.95	-51.81
Nectomys_rattus	F	UFSM_289	-16.95	-51.81
Nectomys_rattus	M	UFSM_290	-16.95	-51.81
Nectomys_rattus	F	UFSM_291	-16.95	-51.81
Nectomys_rattus	M	UFSM_304	-17.32	-53.22
Nectomys_rattus	M	UFSM_51	-21.63	-55.16
Nectomys_rattus	F	UFSM_55	-20.47	-55.79
Nectomys_squamipes	F	MACN_18516	-25.85	-54.35
Nectomys_squamipes	F	MACN_18906	-26.94	-54.43
Nectomys_squamipes	M	MACN_20340	-26.94	-54.43
Nectomys_squamipes	F	MACN_44459	-26.94	-54.43
Nectomys_squamipes	M	MACN_49316	-26.94	-54.43
Nectomys_squamipes	M	MACN_49317	-26.94	-54.43
Nectomys_squamipes	M	MACN_49355	-26.94	-54.43
Nectomys_squamipes	M	MACN_49416	-26.94	-54.43

Nectomys_squamipes	F	MACN_5159	-26.94	-54.43
Nectomys_squamipes	F	MACN_5223	-26.94	-54.43
Nectomys_squamipes	M	MACN_5414	-26.94	-54.43
Nectomys_squamipes	M	MACN_5444	-21.83	-42.73
Nectomys_squamipes	F	MACN_5445	-21.83	-42.73
Nectomys_squamipes	F	MACN_5497	-26.94	-54.43
Nectomys_squamipes	F	MNRJ_11614	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11615	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11616	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11617	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11619	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11622	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11629	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11630	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11631	-20.12	-40.31
Nectomys_squamipes	F	MNRJ_11632	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11633	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_12488	-9.37	-36.24
Nectomys_squamipes	F	MNRJ_13358	-19.00	-43.43
Nectomys_squamipes	M	MNRJ_13360	-19.00	-43.43
Nectomys_squamipes	M	MNRJ_13524	-19.52	-43.75
Nectomys_squamipes	M	MNRJ_13526	-19.52	-43.75
Nectomys_squamipes	F	MNRJ_13531	-19.52	-43.75
Nectomys_squamipes	F	MNRJ_13540	-20.33	-43.56
Nectomys_squamipes	M	MNRJ_2061	-22.42	-42.98
Nectomys_squamipes	M	MNRJ_21225	-15.79	-47.88
Nectomys_squamipes	F	MNRJ_21226	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_21228	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_21231	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_2229	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_24367	-23.18	-44.18
Nectomys_squamipes	M	MNRJ_24368	-23.18	-44.18
Nectomys_squamipes	F	MNRJ_24926	-23.18	-44.18
Nectomys_squamipes	F	MNRJ_24933	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_2555	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_2556	-22.76	-43.46
Nectomys_squamipes	F	MNRJ_2591	-22.76	-43.46
Nectomys_squamipes	F	MNRJ_27830	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_27832	-22.93	-42.82
Nectomys_squamipes	F	MNRJ_28540	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_28545	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_26816	-22.05	-42.68
Nectomys_squamipes	M	MNRJ_28991	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_30417	-22.48	-42.20
Nectomys_squamipes	F	MNRJ_31025	-23.18	-44.18

Nectomys_squamipes	M	MNRJ_31395	-19.37	-43.53
Nectomys_squamipes	F	MNRJ_31397	-19.37	-43.53
Nectomys_squamipes	F	MNRJ_32621	-21.78	-46.57
Nectomys_squamipes	M	MNRJ_32622	-21.78	-46.57
Nectomys_squamipes	F	MNRJ_33797	-22.48	-42.20
Nectomys_squamipes	M	MNRJ_33805	-22.48	-42.20
Nectomys_squamipes	M	MNRJ_33807	-22.24	-42.05
Nectomys_squamipes	F	MNRJ_33808	-22.24	-42.05
Nectomys_squamipes	M	MNRJ_4086	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4087	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4091	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4093	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4094	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4095	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4098	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_5291	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5292	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5298	-23.43	-45.08
Nectomys_squamipes	F	MNRJ_5326	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5333	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5334	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5339	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5341	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5342	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5397	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5405	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5429	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5437	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5439	-23.43	-45.08
Nectomys_squamipes	F	MNRJ_5440	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5444	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5445	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_5446	-21.77	-42.54
Nectomys_squamipes	M	MNRJ_5447	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5660	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5781	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_5816	-22.63	-43.25
Nectomys_squamipes	M	MNRJ_6205	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6276	-23.22	-44.72
Nectomys_squamipes	M	MNRJ_6277	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6278	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6279	-23.22	-44.72
Nectomys_squamipes	M	MNRJ_6280	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6462	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_6463	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_67037	-22.57	-42.90

Nectomys_squamipes	F	MNRJ_67039	-22.57	-42.90
Nectomys_squamipes	M	MNRJ_67044	-22.48	-42.85
Nectomys_squamipes	F	MNRJ_67046	-22.48	-42.85
Nectomys_squamipes	F	MNRJ_7519	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_7525	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_8289	-20.15	-40.28
Nectomys_squamipes	M	MNRJ_8290	-20.15	-40.28
Nectomys_squamipes	M	MNRJ_8675	-14.69	-39.09
Nectomys_squamipes	M	MNRJ_8676	-14.69	-39.09
Nectomys_squamipes	F	MNRJ_8677	-14.79	-39.05
Nectomys_squamipes	F	MNRJ_8681	-14.79	-39.05
Nectomys_squamipes	M	MZUSP_10183	-23.50	-47.62
Nectomys_squamipes	M	MZUSP_10184	-23.50	-47.62
Nectomys_squamipes	F	MZUSP_10185	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_10186	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_10222	-22.12	-51.39
Nectomys_squamipes	M	MZUSP_10223	-22.12	-51.39
Nectomys_squamipes	F	MZUSP_10415	-19.94	-40.60
Nectomys_squamipes	F	MZUSP_10450	-23.55	-46.65
Nectomys_squamipes	F	MZUSP_10615	-24.52	-48.67
Nectomys_squamipes	F	MZUSP_10617	-24.00	-47.54
Nectomys_squamipes	F	MZUSP_10656	-15.79	-47.88
Nectomys_squamipes	F	MZUSP_10773	-23.78	-46.72
Nectomys_squamipes	M	MZUSP_10913	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_11000	-23.59	-48.05
Nectomys_squamipes	F	MZUSP_11066	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_11452	-21.78	-46.57
Nectomys_squamipes	M	MZUSP_13706	-23.02	-48.01
Nectomys_squamipes	M	MZUSP_13793	-23.02	-48.01
Nectomys_squamipes	M	MZUSP_1702	-20.64	-51.51
Nectomys_squamipes	M	MZUSP_1703	-20.64	-51.51
Nectomys_squamipes	M	MZUSP_2083	-23.81	-45.40
Nectomys_squamipes	M	MZUSP_21243	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_21246	-22.19	-48.78
Nectomys_squamipes	F	MZUSP_21530	-23.78	-46.72
Nectomys_squamipes	F	MZUSP_21540	-9.37	-36.24
Nectomys_squamipes	M	MZUSP_21931	-23.59	-48.05
Nectomys_squamipes	F	MZUSP_21942	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_22800	-24.71	-47.56
Nectomys_squamipes	F	MZUSP_24832	-23.52	-47.14
Nectomys_squamipes	M	MZUSP_27315	-24.27	-48.40
Nectomys_squamipes	M	MZUSP_27435	-23.59	-48.05
Nectomys_squamipes	F	MZUSP_2766	-22.24	-42.05
Nectomys_squamipes	M	MZUSP_2767	-22.24	-42.05
Nectomys_squamipes	F	MZUSP_2768	-22.24	-42.05

Nectomys_squamipes	M	MZUSP_27750	-25.13	-47.97
Nectomys_squamipes	M	MZUSP_27751	-25.13	-47.97
Nectomys_squamipes	M	MZUSP_27878	-24.62	-48.95
Nectomys_squamipes	M	MZUSP_28857	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28860	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28862	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28865	-21.72	-52.42
Nectomys_squamipes	F	MZUSP_2957	-20.34	-47.79
Nectomys_squamipes	F	MZUSP_2958	-20.34	-47.79
Nectomys_squamipes	M	MZUSP_3516	-19.88	-42.55
Nectomys_squamipes	M	MZUSP_3517	-19.88	-42.55
Nectomys_squamipes	M	MZUSP_3518	-19.88	-42.55
Nectomys_squamipes	F	MZUSP_541	-23.55	-46.63
Nectomys_squamipes	M	MZUSP_58	-22.61	-45.19
Nectomys_squamipes	M	MZUSP_6217	-19.94	-40.60
Nectomys_squamipes	F	MZUSP_6220	-19.94	-40.60
Nectomys_squamipes	M	MZUSP_6284	-23.43	-45.08
Nectomys_squamipes	M	MZUSP_6374	-23.41	-46.60
Nectomys_squamipes	F	MZUSP_8858	-22.53	-52.17
Nectomys_squamipes	F	MZUSP_9573	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9729	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9730	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9799	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_9800	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_9801	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9873	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9874	-23.81	-46.05
Nectomys_squamipes	M	MZUSP_9876	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9895	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9897	-23.60	-46.92
Nectomys_squamipes	M	UFSM_177	-17.56	-52.55
Nectomys_squamipes	M	UFSM_194	-17.56	-52.55
Nectomys_squamipes	M	UFSM_44	-21.47	-54.38
Sylvilagus_brasiliensis	F	MACN_14157	-26.94	-54.43
Sylvilagus_brasiliensis	M	MACN_14679	-23.14	-64.32
Sylvilagus_brasiliensis	M	MACN_18578	-26.94	-54.43
Sylvilagus_brasiliensis	M	MACN_25815	-26.94	-54.43
Sylvilagus_brasiliensis	F	MACN_30340	-24.78	-65.41
Sylvilagus_brasiliensis	M	MACN_30343	-24.78	-65.41
Sylvilagus_brasiliensis	M	MACN_31165	-0.17	-78.60
Sylvilagus_brasiliensis	M	MACN_36328	-24.78	-65.41
Sylvilagus_brasiliensis	M	MACN_36330	-24.78	-65.41
Sylvilagus_brasiliensis	F	MACN_36740	-24.78	-65.41
Sylvilagus_brasiliensis	F	MACN_49312	-26.94	-54.43
Sylvilagus_brasiliensis	F	MACN_49328	-26.94	-54.43
Sylvilagus_brasiliensis	M	MACN_5129	-26.94	-54.43

Sylvilagus_brasiliensis	F	MACN_5138	-26.94	-54.43
Sylvilagus_brasiliensis	F	MNRJ_10035	-10.51	-40.32
Sylvilagus_brasiliensis	F	MNRJ_10036	-10.51	-40.32
Sylvilagus_brasiliensis	F	MNRJ_13356	-19.00	-43.43
Sylvilagus_brasiliensis	M	MNRJ_1836	-14.94	-51.10
Sylvilagus_brasiliensis	M	MNRJ_1837	-19.27	-40.14
Sylvilagus_brasiliensis	F	MNRJ_1842	-14.04	-47.62
Sylvilagus_brasiliensis	F	MNRJ_22256	-15.79	-47.88
Sylvilagus_brasiliensis	F	MNRJ_24037	-9.37	-36.24
Sylvilagus_brasiliensis	F	MNRJ_24038	-9.37	-36.24
Sylvilagus_brasiliensis	F	MNRJ_24039	-8.88	-36.50
Sylvilagus_brasiliensis	F	MNRJ_24040	-9.37	-36.24
Sylvilagus_brasiliensis	M	MNRJ_24041	-8.88	-36.50
Sylvilagus_brasiliensis	F	MNRJ_24046	-12.74	-38.61
Sylvilagus_brasiliensis	F	MNRJ_24047	-12.74	-38.61
Sylvilagus_brasiliensis	M	MNRJ_24048	-11.66	-39.01
Sylvilagus_brasiliensis	F	MNRJ_24049	-12.35	-39.08
Sylvilagus_brasiliensis	F	MNRJ_24050	-11.50	-41.44
Sylvilagus_brasiliensis	F	MNRJ_24055	-12.17	-41.65
Sylvilagus_brasiliensis	F	MNRJ_24064	-20.12	-40.31
Sylvilagus_brasiliensis	F	MNRJ_24065	-20.33	-40.35
Sylvilagus_brasiliensis	F	MNRJ_24070	-16.20	-48.58
Sylvilagus_brasiliensis	M	MNRJ_24530	-20.72	-46.61
Sylvilagus_brasiliensis	F	MNRJ_24531	-19.88	-40.88
Sylvilagus_brasiliensis	F	MNRJ_28581	-12.17	-41.65
Sylvilagus_brasiliensis	F	MNRJ_28584	-12.35	-39.08
Sylvilagus_brasiliensis	F	MNRJ_28587	-11.66	-39.00
Sylvilagus_brasiliensis	F	MNRJ_28588	-14.86	-40.85
Sylvilagus_brasiliensis	M	MNRJ_28589	-14.86	-40.85
Sylvilagus_brasiliensis	M	MNRJ_28590	-14.86	-40.85
Sylvilagus_brasiliensis	M	MNRJ_28591	-14.88	-40.58
Sylvilagus_brasiliensis	M	MNRJ_34443	-22.97	-43.70
Sylvilagus_brasiliensis	M	MNRJ_34445	-8.36	-36.70
Sylvilagus_brasiliensis	F	MNRJ_34446	-19.55	-40.63
Sylvilagus_brasiliensis	F	MNRJ_3884	-20.33	-40.35
Sylvilagus_brasiliensis	F	MNRJ_43004	-13.64	-47.25
Sylvilagus_brasiliensis	M	MNRJ_43303	-8.88	-36.50
Sylvilagus_brasiliensis	F	MNRJ_4768	-21.61	-55.17
Sylvilagus_brasiliensis	F	MNRJ_4769	-16.20	-48.58
Sylvilagus_brasiliensis	F	MNRJ_4771	-16.20	-48.58
Sylvilagus_brasiliensis	F	MNRJ_4773	-16.20	-48.58
Sylvilagus_brasiliensis	F	MNRJ_4775	-16.20	-48.58
Sylvilagus_brasiliensis	F	MNRJ_4776	-16.20	-48.58
Sylvilagus_brasiliensis	M	MNRJ_5623	-20.33	-40.35
Sylvilagus_brasiliensis	M	MNRJ_5624	-17.37	-66.17

Sylvilagus_brasiliensis	M	MNRJ_5625	-17.37	-66.17
Sylvilagus_brasiliensis	F	MNRJ_5626	-20.33	-40.35
Sylvilagus_brasiliensis	F	MNRJ_5627	-19.94	-40.60
Sylvilagus_brasiliensis	M	MNRJ_6114	-16.08	-57.68
Sylvilagus_brasiliensis	M	MZUSP_10142	-23.72	-46.86
Sylvilagus_brasiliensis	F	MZUSP_10470	-15.90	-52.25
Sylvilagus_brasiliensis	F	MZUSP_21304	-3.65	-52.38
Sylvilagus_brasiliensis	M	MZUSP_2285	-23.74	-46.40
Sylvilagus_brasiliensis	M	MZUSP_26750	-2.55	-54.09
Sylvilagus_brasiliensis	M	MZUSP_26751	-3.82	-55.49
Sylvilagus_brasiliensis	F	MZUSP_26752	-10.46	-40.19
Sylvilagus_brasiliensis	M	MZUSP_26753	-16.69	-49.27
Sylvilagus_brasiliensis	F	MZUSP_26755	-23.70	-46.70
Sylvilagus_brasiliensis	M	MZUSP_26756	-22.19	-48.78
Sylvilagus_brasiliensis	F	MZUSP_26757	-22.19	-48.78
Sylvilagus_brasiliensis	F	MZUSP_26758	-22.19	-48.78
Sylvilagus_brasiliensis	F	MZUSP_28771	-21.58	-52.12
Sylvilagus_brasiliensis	F	MZUSP_2932	-23.59	-46.60
Sylvilagus_brasiliensis	M	MZUSP_32618	-23.72	-46.86
Sylvilagus_brasiliensis	F	MZUSP_3817	-21.23	-50.86
Sylvilagus_brasiliensis	M	MZUSP_6196	-19.32	-40.12
Sylvilagus_brasiliensis	F	MZUSP_6270	-21.32	-47.57
Sylvilagus_brasiliensis	F	MZUSP_7383	-9.37	-36.24
Sylvilagus_brasiliensis	M	MZUSP_797	-23.59	-46.60
Sylvilagus_brasiliensis	M	MZUSP_8214	-22.79	-48.13
Sylvilagus_brasiliensis	M	MPEG_12256	-3.80	-49.77
Sylvilagus_brasiliensis	F	MPEG_1493	-15.90	-52.25
Sylvilagus_brasiliensis	F	MPEG_20175	-3.37	-52.55
Sylvilagus_brasiliensis	F	MPEG_22672	-0.77	-47.45

Table A2. Loading coefficients of environmental variables on the first environmental axis (SW1) obtained from the PLS analyses between shape and the environment. Values higher than the others are highlighted for each species.

Environmental variables	*C. paca*	*H. hydrochaeris*	*Nectomys*	*S. brasiliensis*
BIO1	**0.23**	**0.233**	**0.296**	**0.231**
BIO2	-0.183	-0.043	-0.009	**-0.285**
BIO3	**0.28**	**0.342**	**0.329**	0.089
BIO4	**-0.306**	**-0.372**	**-0.288**	-0.16
BIO5	0.084	0.083	**0.246**	0.129
BIO6	**0.281**	**0.254**	**0.285**	**0.286**
BIO7	**-0.301**	**-0.267**	-0.193	**-0.276**
BIO8	**0.21**	**0.267**	0.181	0.172
BIO9	**0.266**	**0.203**	**0.318**	**0.253**
BIO10	0.142	0.106	**0.218**	**0.234**
BIO11	**0.273**	**0.295**	**0.312**	**0.236**
BIO12	0.129	0.129	0.145	**0.254**
BIO13	**0.265**	**0.255**	0.185	**0.28**
BIO14	-0.154	-0.184	-0.049	0.098
BIO15	**0.205**	**0.251**	0.076	-0.046
BIO16	**0.256**	**0.263**	0.176	**0.273**
BIO17	-0.149	-0.19	-0.037	0.111
BIO18	-0.17	-0.132	**-0.274**	-0.015
BIO19	**0.217**	0.053	**0.213**	**0.269**
Average Annual Relative Humidity	0.147	0.123	0.021	**0.331**
Net Primary Productivity	-0.009	0.048	-0.095	0.131
Evapotranspiration	0.133	0.112	0.193	0.107

6 ARTIGO IV. MORPHOLOGICAL AND ENVIRONMENTAL VARIATION IN THE GENUS *RHIPIDOMYS* AND *NECTOMYS* (MAMMALIA: RODENTIA): IMPLICATIONS FROM MOLARS AND ZYGOMATIC ARCH

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Morphological and environmental variation in the genus *Rhipidomys* and *Nectomys* (Mammalia: Rodentia): implications from molars and zygomatic arch

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Masticatory apparatus variation of *Rhipidomys* and *Nectomys*

Abstract

Rodents of the genus *Rhipidomys* and *Nectomys* are widely distributed throughout South America, and are composed of cryptic species still poorly studied which include their morphological variation. With the use of geometric morphometrics, our aim is to search for the patterns of size and shape variation of the masticatory apparatus (molars and zygomatic arch) of such genera, also investigating which environmental variable (temperature, precipitation or primary productivity) better explains those modifications. As a result, interspecific disparity was more accentuated for both size and shape of *Rhipidomys* than that was for *Nectomys*. Biogeographical trends were divergent for each genus, with *Rhipidomys* shape variation being more related to primary productivity (with expansion of the zygomatic arch in more productive regions) whereas *Nectomys* size variation being negatively related to precipitation and temperature (following the Bergmann's rule). The biogeographical patterns show that each species lineage responds in different ways to environment, like being more plastic on shape than on size, depending on the biological characteristics of each genus.

Keywords: Masticatory apparatus. Interspecific disparity. Geometric morphometrics. Bergmann's rule. Sigmodontinae rodents.

Introduction

The impressive diversity of animals found in different habitats reflects an ecological and evolutionary dynamics in practice (Schoener, 2011). The adaptive capacity mainly of the animals with wide geographical distribution raises several questions of how and why they are in these places, if it is just the result of random event or there is any deterministic mechanism involved (Adler, HilleRisLambers & Levine, 2007). However, the occurrence of certain species in the environment may not be so widespread, because of geographic or environmental factors, with a limitation that would even lead to speciation events (Nosil, 2008).

The distribution of species is closely linked to their dispersal potential, with species of smaller body size being more restricted in dispersal capacity on a larger scale (Jenkins *et al.*, 2007; Schloss, Nuñez & Lawler, 2012). The limiting barriers to dispersal are diverse, such as rivers, forest fragmentation or even mountains like the case of Andean uplift in South America, isolating and leading to the speciation of many species (Kozakiewicz, 1993; Patterson, Solari & Velazco, 2012). Thus, these isolated populations in distinct geographical areas result in allopatric populations, either by moving to new environments or even by isolating themselves due to low mobility (Turelli, Barton & Coyne, 2001). On the other hand, new species may have a good adaptability to new adjacent habitats, even expanding their distribution, leading to phenotypic variability and consequently parapatric populations (Gavrilets, Li & Vose, 2000).

In an extensive and heterogeneous region, species will inevitably experience mainly biotic pressures such as competition and predation (Gannon & Rácz, 2006; Bubadué *et al.*, 2015) and abiotic influences such as humidity, temperature, rainfall, and seasonality (Cardini, Jansson & Elton, 2007; Souto-Lima & Millien, 2014). In response, species may express adaptability or phenotypic plasticity (Ghalambor *et al.*, 2007). The morphological variability along a geographical and environmental gradient commonly increases, and is reflected for example on size and shape variation of the skulls (e.g. Cardini *et al.*, 2007; Cáceres *et al.*, 2014; Magnus, Machado & Cáceres, 2017). Understanding the most important factors in this diversification in a wide geographical range, such as the continent of South America, which covers a set of diverse biomes (Silva & Bates, 2002), can unravel the tropical phenotypic diversity in the light of biogeographic hypotheses.

This variability may come from the concept of the Bergmann's rule, which indicates negative relation of body size to temperature, with strong patterns in lower taxonomic levels (Meiri, 2011). The rule is not unanimous (Clauss *et al.*, 2013), but species would have larger body sizes in cold environments to decrease the surface-to-volume ratio and lose less heat (Meiri, 2011). Size and temperature exposes other indirect debates to understand this association, such as the amount of fat stores, food quality, predation and competition (Ashton, Tracy & de Queiroz, 2000). In addition to size, the shape variation can also be highly influenced by temperature (Monteiro, Duarte & dos Reis, 2003; Martínez *et al.*, 2014; Magnus *et al.*, 2017). A tendency for a broad and compacted shape in colder environments could take place, with a probable intensification in the masticatory apparatus (molars and zygomatic arch), related to a lower availability of food in more seasonal environments and more powerful masticatory muscles and broad teeth (e.g. Cáceres *et al.*, 2014; Magnus *et al.*, 2017).

The precipitation is another climatic variable related to size and shape changes and often correlates with productivity (Maestri *et al.*, 2016). Localities with higher precipitation tend to have greater availability of food, that is, they are more productive (McNab, 2010). This facilitates a better acquisition of food, especially in relation to primary consumers, who will tend to increase in size (Aava, 2001). Shape also varies possibly in a similar sense of the temperature change, especially by changing the masticatory apparatus, making it less robust due to the greater abundance of soft and fleshy food (Anderson, Renaud & Rayfield, 2014; Meloro *et al.*, 2014). In fact, the morphological variation is characterized by the effect of a climatic combination, such as temperature and precipitation, but in general, one of these climatic variables is more prominent in its modification (Yom-Tov & Geffen, 2006). Thus, due to the environmental heterogeneity of South America, it is important to know better which predictors are more important in driving the phenotypic change of genera and species to delimit cline differences and comprehend the inherent processes.

As noted by the studies cited above, one of the most modified parts in relation to the skull is the masticatory apparatus section. The zygomatic arch is one of the regions most stressed during bite processes, precisely because both the temporal and masseter muscles are attach or pass through it and contribute to a more efficient bite force (Cox *et al.*, 2012). Thus, a larger area of the zygomatic arch allows a greater amount of muscles attached to it, increasing its biomechanical efficiency for both gnawing and chewing food, subsequently increasing bite force (Samuels, 2009). Similarly, the masseter muscle also increases the biting force applied on molars and incisors (Greaves, 1991) and, together with the increased molar occlusal surface area, allow a better food processing (Pérez-Barbería & Gordon, 1998; Becerra *et al.*, 2012). In this way, strong selective pressures can act on shape and function of zygomatic arch and teeth, especially linked to dietary habits.

Rodents of the subfamily Sigmodontinae are one of the largest group of South American mammals (Patton, Pardiñas & D'Elía, 2015). Among them, we can highlight some genera with wide distribution throughout the continent, such as *Rhipidomys* Tschudi, 1845 and *Nectomys* Peters, 1861. *Rhipidomys* represents approximately 24 species, typically specialized in inhabiting forests, with a climbing habit, and feeding primarily on fruits and seeds (Paglia *et al.*, 2012; Patton *et al.*, 2015). *Nectomys* in turn represents five species, lives next to watercourses, swims, and has generalist feeding habits (Paglia *et al.*, 2012; Patton *et al.*, 2015; Santori *et al.*, 2016). All species have mainly parapatric/allopatric distributions within each genus, and are associated to the relatively recent origin (Steppan & Schenk, 2017), suggesting they will have remaining phenotypical similarities among them. These genera are still poorly studied, and their interspecific taxonomic classification and diversification need to be better understood, as evidenced especially by *Rhipidomys*, who still requires better taxonomic reviews (Costa *et al.*, 2011).

The aims of our work are to investigate the size and shape variations of *Rhipidomys* and *Nectomys* species through their masticatory apparatus, focusing on both intra- and interspecific morphological differentiation, as the influence of environmental variables per se (temperature, rainfall and primary productivity) on their phenotypic variation. Using geometric morphometric approach, we expect a better explanation in the morphological changes along species within each genus, which must present distinct responses due to different ecological demands (Martínez *et al.*, 2014), possibly with a higher environmental influence under the generalist *Nectomys* due to its ecological plasticity. Specifically, we expect that size within genera will increase in colder environments if it responds more to temperature (Bergmann's rule), or will increase in relation to rainier and more productive regions. On the other hand, in seasonal, less rainy and productive environments, the masticatory apparatus will reveal broader or stronger shape area, which could be seen by enlarged teeth in the occlusal surface area and/or enlarged temporal muscle. In addition, it is expected that size will vary more than shape due to its higher plasticity (Stanley, 1979).

Materials and methods

Data collection

We analysed 377 adult specimens of *Rhipidomys* (N = 131) and *Nectomys* (N = 246) (Table 1, see also Appendix A). We identified the adult specimens by the complete eruption of the third molar. The specimens were obtained from the main scientific collections of Brazil and Argentina (see Table S1 in Supporting Information). Due to the lack of many species-level classifications of the genera deposited in the museums, species of each genus were identified according to geographic distribution and boundary following Patton et al. (2015). The correct assignment of species through shape was successful in 77.57% of the cases for *Nectomys* and 73.71% of the cases for *Rhipidomys* (Discriminant Analysis, PAST program version 3.14 (Hammer, Harper & Ryan, 2001)). We assume that the error in regard to this method is minimum and do not interfere in the overall analyses done subsequently.

Table 1. Skull sample size of analysed species of genus *Rhipidomys* Tschudi, 1845 and *Nectomys* Peters, 1861.

Species	N Specimens	N Females	N Males	N Und.
R. cariri Tribe, 2005	10	4	6	0
R. emiliae (J. A. Allen, 1916)	23	13	10	0
R. itoan Costa, Geise, Pereira and Costa, 2011	20	8	12	0
R. macrurus (Gervais, 1855)	47	21	25	1
R. mastacalis (Lund, 1840)	29	15	14	0
R. nitela Thomas, 1901	2	0	2	0
Total	131	61	69	1
N. apicalis Peters, 1861	2	1	1	0
N. rattus Pelzeln, 1883	67	26	40	1
N. squamipes Brants, 1827	177	73	104	0
Total	246	100	145	1
Total both genera	377	161	214	2

For each specimen we also recorded the geographic coordinates of collection point in the field (Fig. 1), mainly from the geographical centre of the locality obtained using Google Earth (http://earth.google.com.br). Through each locality, we obtained bioclimatic variables of mean annual temperature (bio1), annual precipitation (bio12), and net primary productivity (npp). We used DIVA-GIS 7.5 (http://www.divagis.org/) to extract the variables with a resolution of 10’ from the WorldClim raster database (Hijmans *et al.*, 2005) and through the Atlas of the Biosphere (http://www.sage.wisc.edu/atlas/index.php).

Geometric morphometrics

The skull of the species were photographed in ventral view, with a digital camera Nikon CoolPix P530 positioned at a fixed distance of 1.5 m using a tripod, with a scale bar placed close to the skull. We digitized 13 2D homologous landmarks (Fig. 2) using the software tpsDig2 v. 2.16 (Rohlf, 2010a), which describe the shape of the upper teeth (molar series LM 1-8) and the shape of the temporal muscle area (zygomatic arch LM 9-13). The same individual carried out the landmarks (L.Z.M.) to avoid inter-observer error. We randomly landmarked two specimens of each genus twice on different days and compared the mean error of inter-landmark distance for each specimen to verify the intra-observer error. We found a small error less than one percent, which is negligible (Cardini & Tongiorgi, 2003; Meloro, 2011).

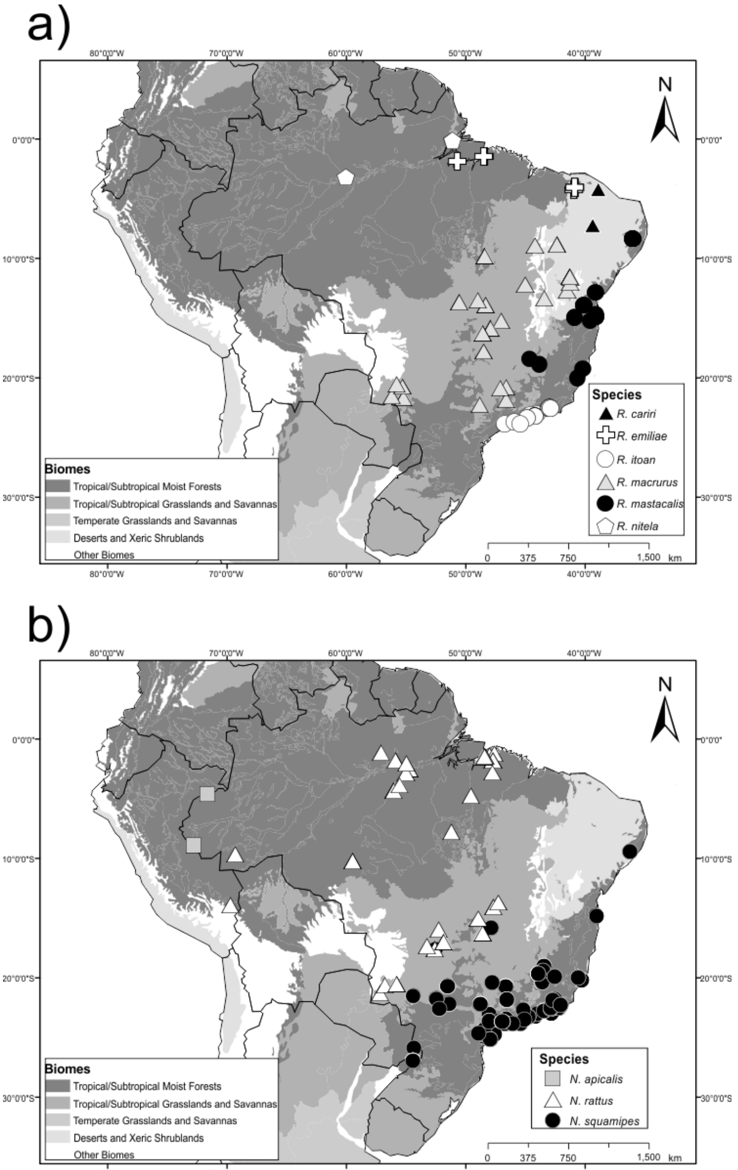

Fig. 1. Maps of South America showing the sampling distribution of (a) *Rhipidomys* and (b) *Nectomys*.

We extract size (centroid size, the square root of the sum of squared distances between each landmark and the centroid – Bookstein (1991)) and shape data (Procrustes coordinates) with superimposed of landmark coordinates using a Generalized Procrustes Analysis (GPA) (Rohlf & Slice, 1990). This procedure removes the variation among landmark configurations unrelated to shape as scale, orientation and position from original landmarks (Rohlf & Slice, 1990; Bookstein, 1991).

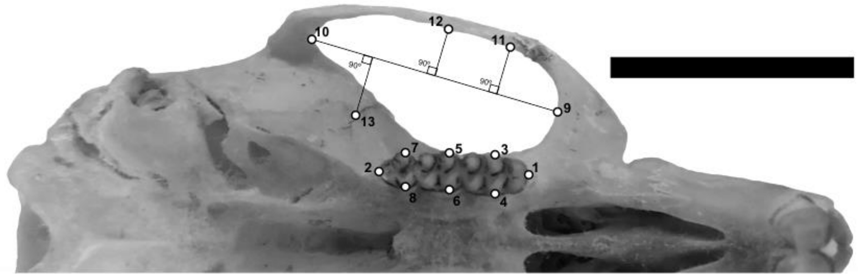

Fig. 2. Position of landmarks for the molar series (landmarks 1-8) and zygomatic arch (landmarks 9-13) on the ventral view of the skull in *Rhipidomys macrurus*. Landmark definitions: 1 = anteriormost point of the first molar; 2 = posteriormost point of the third molar; 3 = lateral midpoint of the first molar; 4 = medial midpoint of first molar; 5 = lateral anterior point of the second molar; 6 = medial anterior point of the second molar; 7 = lateral anterior point of the third molar; 8 = medial anterior point of the third molar; 9 = anteriormost point on curvature of the zygomatic arch; 10 = posteriormost point on curvature of the zygomatic arch; 11 = lateral projection onto the internal edge of the zygomatic arch, drawn from the midpoint of landmarks 9-10 at an angle of 90°; 12 = lateral projection onto the internal edge of the zygomatic arch, drawn from a quarter of landmarks 9-10 at an angle of 90°; 13 = medial projection onto the internal edge of the zygomatic arch, drawn from three quarters of landmarks 9-10 at an angle of 90°. Scale bar is 1 cm.

Statistical analyses

In order to use size as a measure of body size, a Pearson correlation was made between the size of the masticatory apparatus and the size of the skull of each individual (data from the Article 3 in this thesis), resulting in a quite perfect correlation ($r = 0.916$, $P < 0.001$). In addition, a Principal Component Analysis (PCA) using the covariance matrix of the Procrustes coordinates was carried out to determine new independent axes of shape, reducing the dimensionality of the data set (= Relative Warp Analysis, RWA), using the software tpsRelw v. 1.49 (Rohlf, 2010b).

To test the sexual dimorphism in each genus, we used analysis of variance (ANOVA) on size (natural log transformed centroid size – lnCS) and multivariate analysis of variance (MANOVA) on shape, with the factors sex and species. For shape analyses, scores of relative warp axes that explained more than 5% of the total shape variance were included (in this case the first four RWs for each genus) (Zelditch *et al.*, 2004).

We explored size and shape variations of species in each genus through ANOVA and canonical variate analysis (CVA) respectively. For pairwise comparisons among species, we used Tukey's test and Mahalanobis distances. After, we regressed the variable size as independent variable onto shape to explore the influence of allometry (size-related shape changes) within each genus.

To determine the contribution of each environmental factor (annual mean temperature – bio1, annual mean rainfall – bio12, and net primary productivity – npp) to differences in size and shape of the genera, we used linear regression analysis with standardized variables (from each variable, subtract its mean, then divide the result by its standard deviation). No collinearity was found among these variables using Pearson correlation, with $r < 0.3$. In addition, the specific trajectory of each species was searched concerning the main effects of environment on size and shape; if a general trend is strong, most of species will follow, and contribute, to that trend. We used each variable as fixed and random factors (graphical mixed-effect model), including also species nested within genus as an additional random factor. The shape variation was determined by "size-free" shape variables obtained as the residuals of multivariate allometry, and after a second PCA, from which we use the first principal component score that is more explanatory (*Rhipidomys* PC1 size-free = 47.17%; *Nectomys* PC1 size-free = 37.20%). In the case of *Rhipidomys*, here composed of six species, we tested the phylogenetic signal on size and shape data, applying a permutation approach to simulate the null hypothesis of no phylogenetic structure by randomizing tips and node values of the phylogeny (Klingenberg & Gidaszewski, 2010). We used the phylogenetic tree published by Steppan and Schenk (2017) and pruned to include only our sample species (see Appendix B).

For the statistical analyses we used the R environment version 3.3.1 (R Development Core Team, 2016), with the packages *vegan* (Oksanen *et al.*, 2015), *packfor* (Dray, Legendre & Blanchet, 2009), *lme4* (Bates *et al.*, 2015), and the program MorphoJ (Klingenberg, 2011).

Results

The test of sexual dimorphism do not show significant differences between males and females, with no interaction of sex and species in ANOVA for *Rhipidomys* ($F = 0.682$, $P = 0.605$) nor *Nectomys* ($F = 0.170$, $P = 0.844$). The results are also non-significant for sex and species in MANOVA for *Rhipidomys* (Pillai's trace = 0.104; $F_{16,\,476} = 0.792$; $P = 0.696$) nor

Nectomys (Pillai's trace = 0.042; $F_{8,\ 474}$ = 1.269; P = 0.258). Therefore, individuals of undetermined sex were also included in the subsequent analyses.

The size variation shows that *Rhipidomys* species are different according to size (F = 5.706, d.f. = 5, 125, P < 0.001), with *R. nitela*, *R. itoan* (the smallest) and *R. cariri* (the largest) differing more from the others, while *Nectomys* species are more similar, with the three species with almost the same size (F = 0.919, d.f. = 2, 243, P = 0.400) (Fig. 3). For shape, Mahalanobis distances show that the species differing most for *Rhipidomys* are *R. itoan* and *R. nitela* exhibiting the highest values, and *R. mastacalis* and *R. emiliae* that exhibit the lowest values (Table 2). *Nectomys* is particularly significant for shape differences between *N. squamipes* and *N. rattus*, with the lowest values between them (Table 3).

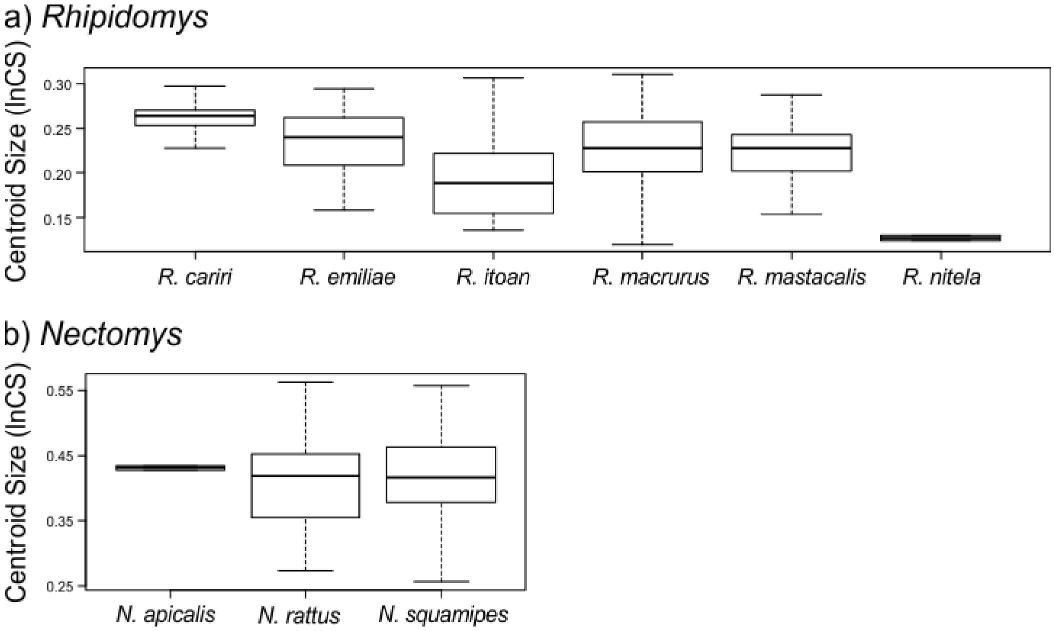

Fig. 3. Size (natural log transformed centroid size – lnCS) variation in *Rhipidomys* and *Nectomys* species. (a) *Rhipidomys* and (b) *Nectomys*.

Table 2. Tukey's test pairwise differences in natural log-transformed centroid size (lnCS) between *Rhipidomys* species. Above diagonal P-values, below diagonal Q-values. Significant values are in bold (P < 0.05).

	R. mastacalis	*R. emiliae*	*R. macrurus*	*R. cariri*	*R. nitela*	*R. itoan*
R. mastacalis	-	0.987	1	0.333	**< 0.001**	0.904
R. emiliae	0.923	-	0.997	0.750	**< 0.001**	0.536
R. macrurus	0.273	0.650	-	0.451	**< 0.001**	0.820
R. cariri	2.850	1.927	2.577	-	**< 0.001**	**0.027**
R. nitela	6.476	7.400	6.750	9.327	-	**0.005**
R. itoan	1.472	2.395	1.745	4.322	5.004	-

Our results show for *Rhipidomys* skull shape that the first and second canonical variate (CV1 and CV2) correspond to 46.35 and 26.08% of the total variation, respectively (Fig. 4). Although CV1 and CV2 show overlap among species, they also show reasonable separation between them (Table 4). CV1 separates *R. itoan* and *R. cariri* in more negative space, with a thinning of the zygomatic arch and expansion of the molar series (mainly the first molar), while in the positive space there are *R. mastacalis*, *R. emiliae* and *R. nitela* with an expansion of the zygomatic arch and reduction of the molar series. CV2 overlap the species even more, with low shape variation along the axis.

Table 3. Tukey's test pairwise differences in natural log-transformed centroid size between *Nectomys* species. Above diagonal P-values, below diagonal Q-values. Significant values are in bold ($P < 0.05$).

	Nectomys squamipes	*Nectomys rattus*	*Nectomys apicalis*
Nectomys squamipes	-	0.946	0.929
Nectomys rattus	0.448	-	0.773
Nectomys apicalis	0.517	0.966	-

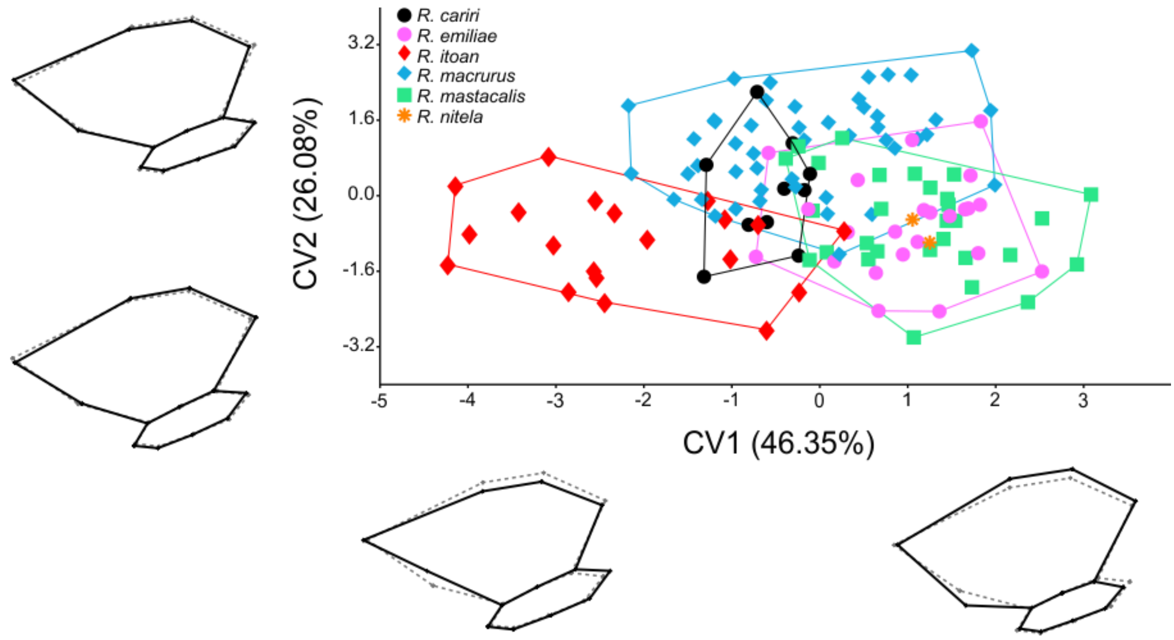

Fig. 4. Scatter plot of first versus second canonical variate axes (CV1 and CV2) of the *Rhipidomys* skull and percentage of variance explained by the CVs. Graphical deformation shapes are shown for negative and positive extremes scores (solid lines are canonical variate shape and dashed lines are de consensus shape).

Table 4. Mahalanobis distances for shape between species pairs of *Rhipidomys*. Significant values are in bold ($P < 0.05$).

	R. cariri	*R. emiliae*	*R. itoan*	*R. macrurus*	*R. mastacalis*
R. emiliae	**2.714**	-	-	-	-
R. itoan	**2.714**	**3.387**	-	-	-
R. macrurus	**2.140**	**2.275**	**2.879**	-	-
R. mastacalis	**2.586**	**1.816**	**3.437**	**2.253**	-
R. nitela	4.309	3.584	**4.776**	4.061	3.707

The skull shape of *Nectomys* show that the CV1 and CV2 correspond to 79.53 and 20.47% of the total variation, respectively (Fig. 5). CV1 shows overlap among the species, but with a moderate separation between *N. squamipes* and *N. rattus* (Table 5). *Nectomys squamipes* tends to be in the most negative values, with expansion of the zygomatic arch and narrow molar series, while the opposite is seen for *N. rattus* at positive values (with a slight enlargement of the first molar). For CV2, *N. apicalis* is in the extreme of positive values, with a thinning of the zygomatic arch but a great expansion of the molar series.

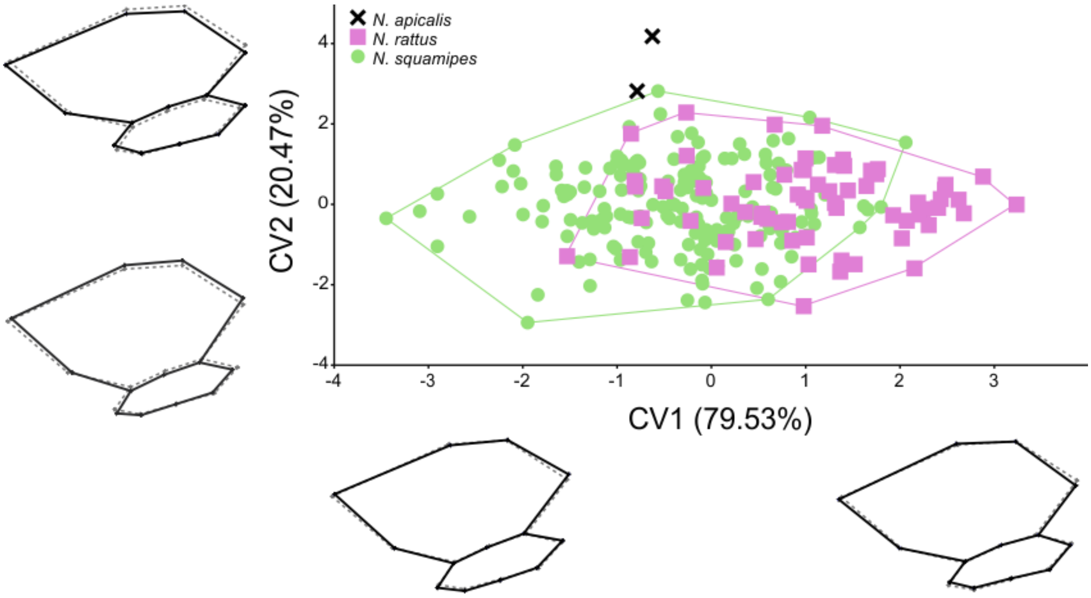

Fig. 5. Scatter plot of first versus second canonical variate axes (CV1 and CV2) of the *Nectomys* skull and percentage of variance explained by the CVs. Graphical deformation shapes are shown for negative and positive extremes scores (solid lines are canonical variate shape and dashed lines are de consensus shape).

Table 5. Mahalanobis distances for shape between species pairs of *Nectomys*. Significant values are in bold ($P < 0.05$).

	Nectomys apicalis	*Nectomys rattus*
Nectomys rattus	3.882	-
Nectomys squamipes	3.562	**1.407**

As a general pattern, the allometry is present in relation to shape variation for both genera. *Nectomys* reflects a relative large amount of allometry (17.57%, $P < 0.001$) and *Rhipidomys* show a minor influence but it is still present (8.57%, $P < 0.001$). Once the relationships between size and shape were confirmed (size-related shape change), the environmental variation analyses with the shape were performed as “size-free”.

The pattern seen for each genus is clearly distinct when related to each potential environmental influence (Table 6). On size, *Rhipidomys* shows no variation with the variables (only slightly with productivity, but not significant) (Fig. 6c), whereas *Nectomys* is more susceptible to size changes mainly through precipitation and secondarily by temperature, decreasing its size in warm and rainy environments (Fig. 6a,b). Primary productivity has influence on *Rhipidomys* shape variation, even stronger than on size variation (Fig. 7c). In productive environments, shape tends to a general expansion of the zygomatic arch, while in less productive environments it presents narrow and elongated zygomatic arch, but with a slightly enlargement of the first molar (Fig. 7d). However, temperature and precipitation have no influence in the genus. On the other hand, *Nectomys* shape responds significantly, despite little, in relation to temperature (Fig. 7a), with narrow and elongated zygomatic arch and molars (with a slightly expansion of the first molar) in warm locations (Fig. 7d). The opposite pattern is seen in cold regions (broad and more compact zygomatic arch and molars). However, the precipitation and primary productivity variables represent non-significant values (Fig. 7b,c). All results remain significant when considering the geographical distance of samples in the models (see Appendix C). The permutation tests support the null hypothesis of the absence of phylogenetic signal on skull size (Tree length = 0.008, P = 0.461) and shape (Tree length = 0.003, P = 0.056) of *Rhipidomys*, and consequently it is not necessary the use of comparative methods (Klingenberg and Gidaszewski, 2010).

Table 6. Results of the simple linear regressions of environmental variables on Size (lnCS) and Shape (PC1 size-free) of *Rhipidomys* and *Nectomys*. Significance is highlighted in bold ($P < 0.05$).

Size	*Rhipidomys*			*Nectomys*		
Variable	R^2	F-statistic	P value	R^2	F-statistic	P value
bio1	0.02	2.175	0.143	0.03	8.314	**0.004**
bio12	0.00	0.385	0.536	0.06	14.250	**<0.001**
npp	0.03	3.879	0.051	0.00	0.781	0.378
Shape	***Rhipidomys***			***Nectomys***		
Variable	R^2	F-statistic	P value	R^2	F-statistic	P value
bio1	0.01	0.802	0.372	0.02	4.578	**0.033**
bio12	0.01	2.362	0.127	0.01	2.920	0.089
npp	0.06	8.792	**0.004**	0.00	0.337	0.562

(bio1) mean annual temperature, (bio12) annual precipitation, and (npp) net primary productivity.

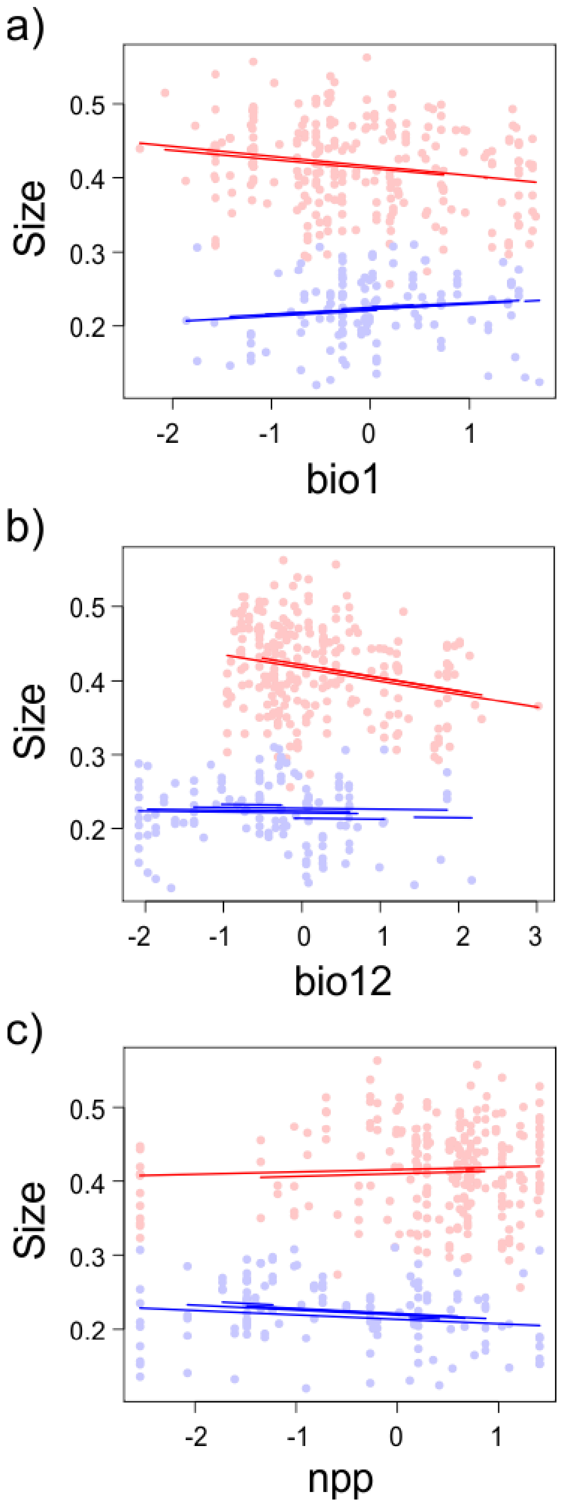

Fig. 6. Size (natural log transformed centroid size – lnCS) of genera (species) versus each predictor variable (standardized variables). Mean annual temperature - bio1 (a), annual precipitation - bio12 (b), and net primary productivity – npp (c). The lines represent the trend for each species of genera. Blue circles and lines: *Rhipidomys*, and red circles and lines: *Nectomys*.

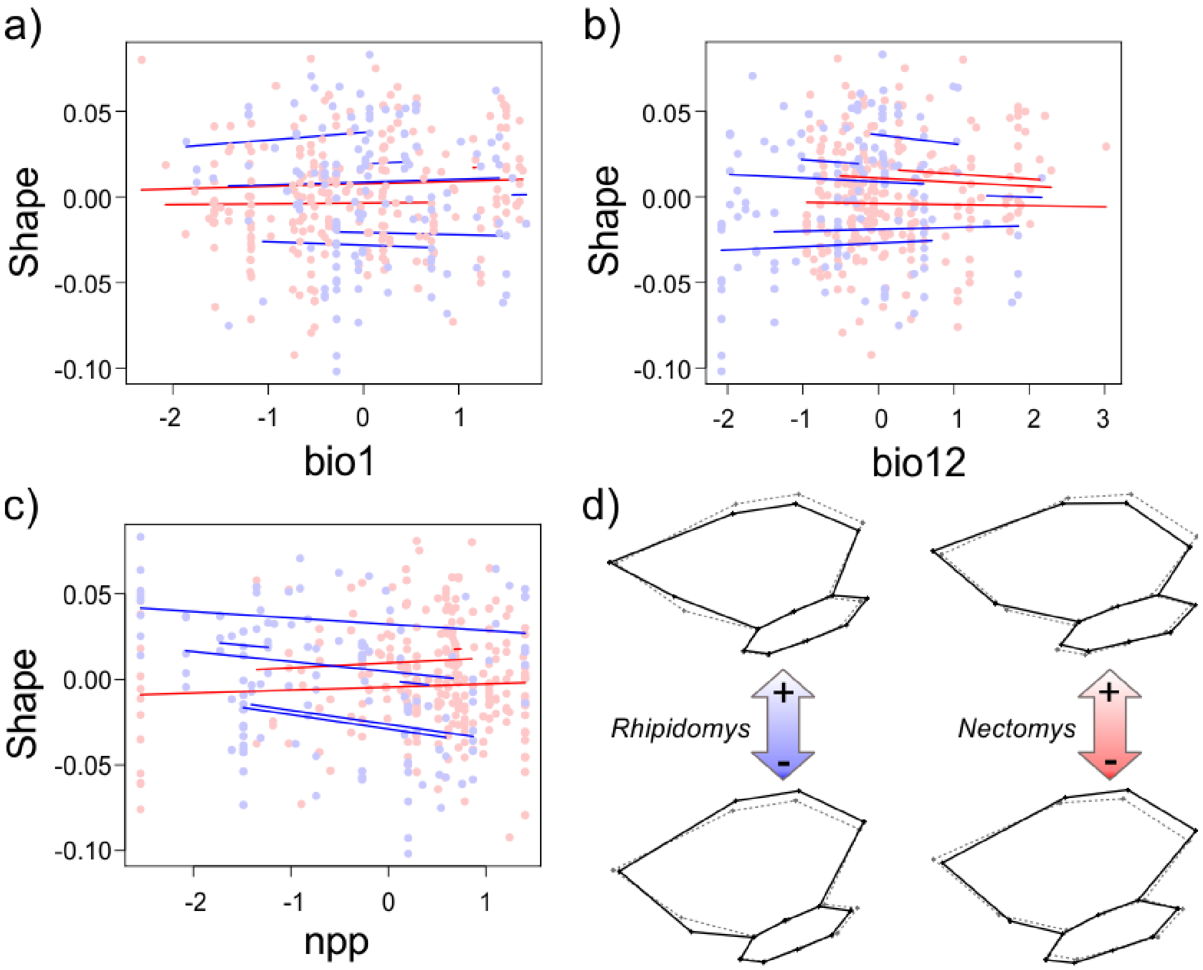

Fig. 7. Shape (PC1 size-free) of genera (species) versus each predictor variable (standardized variables). Mean annual temperature - bio1 (a), annual precipitation - bio12 (b), and net primary productivity – npp (c). The lines represent the trend for each species of genera. Blue circles and lines: *Rhipidomys*, and red circles and lines: *Nectomys*. In (d) the graphical deformation shapes are shown for negative and positive extremes scores of each genus (solid lines are canonical variate shape and dashed lines are de consensus shape).

Discussion

Our overall findings show that the phenotypic variation of species is best recognized through shape for both genera, in addition to size for *Rhipidomys*. However, the masticatory apparatus of *Nectomys* show lower interspecific variation, both for size and shape. Regarding the different environmental variables, the size of *Rhipidomys* does not respond to any variable, but the shape evidences substantial variation driving by the environmental productivity. However, the size of *Nectomys* is more influenced by both precipitation and temperature, and by temperature on shape. In this way, the interspecific variation exists, even subtly, through morphological clines, while the genera show opposite answers in regard to the variables. Remarkably, each genus evidences a clear pattern of variation due to different niche ecological restrictions (Martínez *et al.*, 2014), such as the specialist *Rhipidomys* and the generalist *Nectomys* (Fig. 6, 7).

Rhipidomys species that are closer geographically, such as *R. mastacalis* and *R. emiliae*, corroborate a sharing of similarities in shape and size (cf. Article 3 in this thesis). Similarly, there are the most different in shape and geographically distant species like *R. itoan* and *R. nitela*. Geographical barriers are one of the physical elements that can separate these species, as already demonstrated by the mountain ranges (e.g. Serra da Mantiqueira in the Atlantic Forest) (Costa *et al.*, 2000; Costa *et al.*, 2011). In addition, the fact that these species are forest-dependent (Tribe, 1996) accentuates the dispersal limitation, increasing the differences among them. In the case of *Nectomys*, there is some separation of the three species by shape, but the size of species is similar. Two of the three species sampled for this genus, *N. rattus* and *N. squamipes*, are widely distributed (Patton *et al.*, 2015), leading to the assumption that they are not dispersal limited by barriers, having high dispersion capacity through the landscape (Sexton *et al.*, 2009). Thus, despite the limitation of samples for some species, geographic patterns are found according to their dispersal capacity, but at the same time, environmental pressures are also present and acting on the phenotypic variation of the two rodent genera.

The climbing rats *Rhipidomys* do not show variation related to temperature or precipitation variables, possibly due to the greater niche stability pertinent to their specialist lifestyle, more restricted to forest patches (Patton *et al.*, 2015). In contrast, productivity had a reasonable impact on shape, related to an expansion pattern (especially) of the zygomatic arch toward productive regions, different from expected. Despite that, it is important to notice changes especially related to the first molar. The expansion of the zygomatic arch in less productive and seasonal environments suggests a feeding relationship related to the processing of hard foods that demand more force (Meloro *et al.*, 2014; Souto-Lima & Millien, 2014). For *Rhipidomys*, the overall narrowing of the zygomatic shape in less productive environments could be compensated by the broad area of the first molar. This suggests an increase in biomechanical efficiency of crushing food in these environments, since molars are related to the grinding process (Butler, 1980; Pérez-Barbería & Gordon, 1998) and larger areas are important for animals to consume less nutritious and more abrasive food (Pérez-Barbería & Gordon, 1998; Becerra *et al.*, 2012).

In turn, our findings for *Nectomys* confirm the influence of temperature on size, and consequently show that the species tends to follow the Bergmann's rule. This corroborates that size variation is not the result of interspecific differences since species have similar sizes (see

Fig. 3), but rather a response of a climatic gradient. As expected, *Nectomys* populations probably compensate their energetic balance in colder environments by increasing the size easing body heat retention (Meiri, 2011). This may be aggravated by the general habits of *Nectomys*, which is semiaquatic. Living most part of a life into the water requires an even higher energy cost for thermoregulation because of the higher water conductivity (Scholander *et al.*, 1950; Calder, 1969), being compensated by size increase in higher latitudes. Although the species live always close to streams and watercourses, they occur in both forest and scrubland biomes (Ernest, 1986), which make populations more exposed to the climatic oscillations. Not so evident, the shape of *Nectomys* also changes with temperature, which corroborates a broad shape area in seasonal climates. Therefore, its masticatory apparatus, for the most part the zygomatic arch variation, shows important changes. From the main perspective, increased force (especially of the zygomatic arch) in cold/seasonal climates may be related to a greater food shortage in these places, like arthropods and fruits (Bergallo & Magnusson, 2002). Consequently, it leads to a shape change to a better feeding performance, that is, enlarged and stronger zygomatic arch area (Cox *et al.*, 2012) to access a broader range of food.

Another explanation for the variation of *Nectomys* size is precipitation, with size negatively related to precipitation. The possibility that size decreases in rainy places may be due to inter-competition. In rainy environments, there is a great abundance of resources (McNab, 2010), and consequently equatorial areas such as the Amazon (highly rainy and productive region) present a greater species abundance and richness (Hill & Hill, 2001), which possibly increases the competition/predation in these places for resources (Ashton *et al.*, 2000). Thus, there is a possibility that *Nectomys* are changing its body size due to the character displacement in these environments. However, also this negative link of size and precipitation may be more related to other factors, such as home range. *Nectomys squamipes* home range indicates an increase in more seasonal and dry periods, precisely because of its high dependence on watercourses, and consequently to obtain more food in these periods they end up using larger areas (Lima, Pinho & Fernandez, 2015). The home range usually tends to be associated with a bigger body size, which suggests a relationship of increase size with search of foods, favouring larger animals (Ottaviani *et al.*, 2006). This is also true particularly by energy balance, since bigger animals also expend energy at much lower rates in relation to their body size due to surface/volume ratio (McNab, 1980). Still, studies with platypus (*Ornithorhynchus anatinus* (Shaw, 1799)) indicate the same relationship found here, and would tend to favour larger animals in places with little precipitation to a larger stock of fat/lipids, storing larger quantities to deal with seasonal periods and fasting endurance (Furlan *et al.*, 2011). Thus, this relationship could have the same clue for *Nectomys*.

Costa *et al.* (2011) verified through morphological data that the species of *Rhipidomys* have few discrete characters. Due to the use of techniques such as the geometric morphometrics, it is possible to discriminate particular differences for species separation, as seen for shape here and already shown for other rodent species (Astúa, Bandeira & Geise, 2015). The lack of phylogenetic signal for *Rhipidomys* is unexpected considering the recent time of diversification of the genus (approximately 3 Mya) (Costa, 2003). However, environmental pressures related to different biomes and climatic variations, specifically productivity, suggest a strong action on the shape plasticity of *Rhipidomys*. Besides, temperature and precipitation act more on size variation of the generalist *Nectomys*. In fact, the genera studied respond differently to the environment pressure, on both size (*Nectomys*) and shape (*Rhipidomys*), and future investigations with other species may show similar results regarding morphological and environmental variation.

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Supplementary material

Appendix A. List of skull specimens photographed, with data of species, sex, museum number, latitude and longitude. F = female; M = male; UND = undetermined. *Museums*: Museu Nacional (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), and Coleção de Mamíferos da Universidade Federal de Santa Maria (UFSM).

Species	Sex	Nº Museum	Latitude	Longitude
Rhipidomys_cariri	M	MNRJ_17298	-7.23	-39.38
Rhipidomys_cariri	M	MNRJ_17299	-7.23	-39.38
Rhipidomys_cariri	M	MNRJ_17373	-4.23	-38.92
Rhipidomys_cariri	M	MNRJ_17417	-7.23	-39.38
Rhipidomys_cariri	F	MNRJ_17423	-7.23	-39.38
Rhipidomys_cariri	F	MNRJ_17431	-4.23	-38.92
Rhipidomys_cariri	F	MNRJ_17440	-4.23	-38.92
Rhipidomys_cariri	M	MNRJ_17443	-4.23	-38.92
Rhipidomys_cariri	F	MNRJ_17444	-4.23	-38.92
Rhipidomys_cariri	M	MNRJ_17446	-4.23	-38.92
Rhipidomys_emiliae	M	MNRJ_12394	-4.05	-40.86
Rhipidomys_emiliae	M	MNRJ_12561	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_12564	-4.23	-40.90
Rhipidomys_emiliae	M	MNRJ_12574	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_12587	-4.23	-40.90
Rhipidomys_emiliae	F	MNRJ_17310	-4.23	-40.90
Rhipidomys_emiliae	F	MNRJ_17316	-4.23	-40.90
Rhipidomys_emiliae	M	MNRJ_17407	-4.05	-40.86
Rhipidomys_emiliae	M	MNRJ_17410	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_17411	-4.05	-40.86
Rhipidomys_emiliae	M	MNRJ_17412	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_17415	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_17416	-4.05	-40.86
Rhipidomys_emiliae	F	MNRJ_17425	-4.05	-40.86
Rhipidomys_emiliae	M	MNRJ_17427	-4.23	-40.90
Rhipidomys_emiliae	M	MNRJ_17437	-4.23	-40.90
Rhipidomys_emiliae	M	MNRJ_24195	-1.42	-48.41
Rhipidomys_emiliae	F	MNRJ_68905	-3.99	-40.88
Rhipidomys_emiliae	F	MNRJ_68907	-3.99	-40.88
Rhipidomys_emiliae	F	MNRJ_68908	-3.99	-40.88
Rhipidomys_emiliae	M	MPEG_34001	-1.80	-50.72
Rhipidomys_emiliae	F	MZUSP_10397	-1.42	-48.46
Rhipidomys_emiliae	F	MZUSP_10398	-1.42	-48.46
Rhipidomys_itoan	F	MNRJ_2357	-22.45	-42.98
Rhipidomys_itoan	M	MNRJ_2359	-22.45	-42.98
Rhipidomys_itoan	M	MNRJ_24365	-23.18	-44.18

Rhipidomys_itoan	M	MNRJ_63604	-22.48	-43.00
Rhipidomys_itoan	F	MNRJ_63611	-22.96	-44.04
Rhipidomys_itoan	F	MNRJ_63614	-23.18	-44.18
Rhipidomys_itoan	M	MNRJ_63615	-23.03	-44.58
Rhipidomys_itoan	M	MNRJ_63617	-22.48	-43.00
Rhipidomys_itoan	F	MNRJ_63620	-23.18	-44.18
Rhipidomys_itoan	M	MNRJ_63621	-22.48	-42.85
Rhipidomys_itoan	M	MNRJ_63622	-23.18	-44.18
Rhipidomys_itoan	M	MNRJ_63623	-23.18	-44.18
Rhipidomys_itoan	M	MNRJ_63624	-23.18	-44.18
Rhipidomys_itoan	F	MNRJ_7049	-22.45	-42.98
Rhipidomys_itoan	M	MNRJ_71203	-23.33	-44.83
Rhipidomys_itoan	F	MNRJ_71205	-23.33	-44.83
Rhipidomys_itoan	F	MNRJ_72703	-22.48	-42.85
Rhipidomys_itoan	F	MZUSP_11445	-23.78	-46.72
Rhipidomys_itoan	M	MZUSP_29381	-23.65	-45.90
Rhipidomys_itoan	M	MZUSP_880	-23.81	-45.40
Rhipidomys_macrurus	F	MNRJ_134515	-21.61	-55.17
Rhipidomys_macrurus	M	MNRJ_134517	-21.61	-55.17
Rhipidomys_macrurus	F	MNRJ_21387	-15.79	-47.88
Rhipidomys_macrurus	F	MNRJ_21389	-15.79	-47.88
Rhipidomys_macrurus	F	MNRJ_21392	-15.79	-47.88
Rhipidomys_macrurus	M	MNRJ_21396	-15.79	-47.88
Rhipidomys_macrurus	F	MNRJ_21403	-15.79	-47.88
Rhipidomys_macrurus	M	MNRJ_21972	-15.74	-47.93
Rhipidomys_macrurus	F	MNRJ_22848	-15.18	-47.02
Rhipidomys_macrurus	M	MNRJ_24790	-15.79	-47.88
Rhipidomys_macrurus	M	MNRJ_30014	-20.72	-46.61
Rhipidomys_macrurus	M	MNRJ_30017	-16.20	-48.58
Rhipidomys_macrurus	M	MNRJ_32619	-21.78	-46.57
Rhipidomys_macrurus	M	MNRJ_36358	-13.83	-48.30
Rhipidomys_macrurus	F	MNRJ_36506	-13.83	-48.30
Rhipidomys_macrurus	F	MNRJ_36781	-13.83	-48.30
Rhipidomys_macrurus	M	MNRJ_37350	-13.83	-48.30
Rhipidomys_macrurus	F	MNRJ_37563	-17.75	-48.47
Rhipidomys_macrurus	F	MNRJ_37598	-17.75	-48.47
Rhipidomys_macrurus	M	MNRJ_4142	-13.25	-43.41
Rhipidomys_macrurus	F	MNRJ_4174	-12.15	-45.00
Rhipidomys_macrurus	F	MNRJ_4305	-16.20	-48.58
Rhipidomys_macrurus	M	MNRJ_4335	-16.20	-48.58
Rhipidomys_macrurus	M	MNRJ_63249	-8.81	-42.36
Rhipidomys_macrurus	F	MNRJ_63317	-8.81	-42.36
Rhipidomys_macrurus	M	MNRJ_63327	-8.81	-42.36
Rhipidomys_macrurus	M	MNRJ_67779	-11.59	-41.21

Rhipidomys_macrurus	M	MNRJ_67792	-12.60	-41.46
Rhipidomys_macrurus	M	MNRJ_67875	-12.01	-41.23
Rhipidomys_macrurus	M	MNRJ_69787	-21.47	-56.15
Rhipidomys_macrurus	F	MNRJ_75897	-11.47	-41.23
Rhipidomys_macrurus	F	MNRJ_75902	-11.47	-41.23
Rhipidomys_macrurus	M	MNRJ_75909	-11.47	-41.23
Rhipidomys_macrurus	M	MNRJ_75910	-11.47	-41.23
Rhipidomys_macrurus	F	MNRJ_76732	-9.75	-48.36
Rhipidomys_macrurus	F	MNRJ_76738	-9.75	-48.36
Rhipidomys_macrurus	M	MNRJ_76747	-9.75	-48.36
Rhipidomys_macrurus	M	MNRJ_76757	-9.75	-48.36
Rhipidomys_macrurus	UND	MZUSP_10816	-22.19	-48.78
Rhipidomys_macrurus	M	MZUSP_32642	-8.83	-44.17
Rhipidomys_macrurus	M	MZUSP_3979	-20.78	-47.10
Rhipidomys_macrurus	F	MZUSP_3993	-13.63	-50.49
Rhipidomys_macrurus	F	MZUSP_4005	-13.44	-48.97
Rhipidomys_macrurus	M	MZUSP_4030	-13.63	-50.49
Rhipidomys_macrurus	F	UFSM__156	-20.69	-55.29
Rhipidomys_macrurus	M	UFSM__241	-20.69	-55.29
Rhipidomys_macrurus	F	UFSM__32	-20.47	-55.79
Rhipidomys_mastacalis	M	MNRJ_10862	-14.79	-39.05
Rhipidomys_mastacalis	M	MNRJ_12362	-8.28	-35.97
Rhipidomys_mastacalis	F	MNRJ_12363	-8.28	-35.97
Rhipidomys_mastacalis	M	MNRJ_12373	-8.28	-35.97
Rhipidomys_mastacalis	F	MNRJ_12374	-8.28	-35.97
Rhipidomys_mastacalis	F	MNRJ_12375	-8.28	-35.97
Rhipidomys_mastacalis	M	MNRJ_12393	-8.28	-35.97
Rhipidomys_mastacalis	M	MNRJ_12520	-8.28	-35.97
Rhipidomys_mastacalis	F	MNRJ_17303	-13.86	-40.08
Rhipidomys_mastacalis	F	MNRJ_17305	-13.86	-40.08
Rhipidomys_mastacalis	M	MNRJ_17312	-13.86	-40.08
Rhipidomys_mastacalis	F	MNRJ_17357	-8.28	-35.97
Rhipidomys_mastacalis	M	MNRJ_17362	-8.28	-35.97
Rhipidomys_mastacalis	F	MNRJ_17363	-8.28	-35.97
Rhipidomys_mastacalis	M	MNRJ_17376	-14.86	-40.84
Rhipidomys_mastacalis	M	MNRJ_17447	-14.86	-40.84
Rhipidomys_mastacalis	F	MNRJ_22275	-12.81	-39.09
Rhipidomys_mastacalis	M	MNRJ_22277	-12.81	-39.09
Rhipidomys_mastacalis	M	MNRJ_30020	-14.65	-39.07
Rhipidomys_mastacalis	M	MNRJ_34425	-18.36	-44.62
Rhipidomys_mastacalis	F	MNRJ_34492	-19.17	-40.17
Rhipidomys_mastacalis	M	MNRJ_4212	-18.83	-43.82
Rhipidomys_mastacalis	F	MNRJ_5393	-19.94	-40.60

Rhipidomys_mastacalis	F	MNRJ_9129	-14.79	-39.05
Rhipidomys_mastacalis	M	MNRJ_9280	-14.79	-39.05
Rhipidomys_mastacalis	F	MNRJ_9453	-14.79	-39.05
Rhipidomys_mastacalis	F	MNRJ_9506	-14.79	-39.05
Rhipidomys_mastacalis	F	MNRJ_9657	-14.79	-39.05
Rhipidomys_mastacalis	F	MZUSP_29634	-15.15	-39.52
Rhipidomys_nitela	M	MNRJ_19616	-3.12	-60.02
Rhipidomys_nitela	M	MPEG_43334	-0.04	-51.07
Nectomys_apicalis	F	MPEG_1685	-4.54	-71.62
Nectomys_apicalis	M	MZUSP_21238	-8.83	-72.76
Nectomys_rattus	F	MNRJ_22839	-15.90	-52.25
Nectomys_rattus	M	MNRJ_4379	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4380	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4384	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4388	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4393	-16.20	-48.58
Nectomys_rattus	M	MNRJ_4395	-16.20	-48.58
Nectomys_rattus	F	MNRJ_4399	-16.20	-48.58
Nectomys_rattus	F	MNRJ_46889	-14.04	-47.62
Nectomys_rattus	M	MNRJ_46930	-13.64	-47.25
Nectomys_rattus	M	MNRJ_46890	-14.04	-47.62
Nectomys_rattus	F	MNRJ_50499	-13.64	-47.25
Nectomys_rattus	M	MPEG_10084	-1.76	-55.86
Nectomys_rattus	F	MPEG_10114	-1.76	-55.86
Nectomys_rattus	F	MPEG_10184	-10.18	-59.45
Nectomys_rattus	M	MPEG_10824	-9.61	-69.29
Nectomys_rattus	F	MPEG_10898	-14.97	-48.92
Nectomys_rattus	F	MPEG_10899	-14.97	-48.92
Nectomys_rattus	F	MPEG_12629	-1.08	-57.05
Nectomys_rattus	M	MPEG_12630	-2.45	-54.70
Nectomys_rattus	M	MPEG_13190	-4.27	-55.99
Nectomys_rattus	M	MPEG_13191	-4.27	-55.99
Nectomys_rattus	M	MPEG_13192	-4.27	-55.99
Nectomys_rattus	M	MPEG_13194	-4.27	-55.99
Nectomys_rattus	M	MPEG_13196	-4.27	-55.99
Nectomys_rattus	M	MPEG_13201	-10.18	-59.45
Nectomys_rattus	M	MPEG_13202	-10.18	-59.45
Nectomys_rattus	M	MPEG_13203	-1.42	-48.41
Nectomys_rattus	F	MPEG_15171	-1.76	-47.68
Nectomys_rattus	F	MPEG_15173	-4.27	-55.99
Nectomys_rattus	M	MPEG_1921	-1.42	-48.41
Nectomys_rattus	M	MPEG_2318	-1.30	-47.99
Nectomys_rattus	M	MPEG_2319	-1.30	-47.99
Nectomys_rattus	M	MPEG_2377	-1.15	-47.57

Nectomys_rattus	M	MPEG_8130	-1.76	-47.68
Nectomys_rattus	F	MPEG_8135	-1.76	-47.68
Nectomys_rattus	M	MPEG_8724	-2.45	-54.70
Nectomys_rattus	M	MPEG_8727	-2.45	-54.70
Nectomys_rattus	M	MPEG_8732	-2.45	-54.70
Nectomys_rattus	M	MPEG_8734	-2.45	-54.70
Nectomys_rattus	M	MPEG_9110	-4.68	-49.53
Nectomys_rattus	F	MZUSP_2006	-13.85	-69.68
Nectomys_rattus	M	MZUSP_21226	-2.75	-47.73
Nectomys_rattus	F	MZUSP_21227	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21229	-1.38	-48.34
Nectomys_rattus	F	MZUSP_21231	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21232	-1.42	-48.41
Nectomys_rattus	F	MZUSP_21233	-1.47	-48.50
Nectomys_rattus	F	MZUSP_21235	-1.47	-48.50
Nectomys_rattus	M	MZUSP_21236	-1.42	-48.41
Nectomys_rattus	M	MZUSP_21237	-7.72	-51.18
Nectomys_rattus	F	MZUSP_21240	-2.79	-54.98
Nectomys_rattus	M	MZUSP_21542	-3.82	-55.49
Nectomys_rattus	M	MZUSP_3676	-2.00	-54.93
Nectomys_rattus	UND	MZUSP_6010	-21.23	-57.13
Nectomys_rattus	F	UFSM_133	-20.47	-55.79
Nectomys_rattus	M	UFSM_189	-17.56	-52.55
Nectomys_rattus	M	UFSM_195	-17.56	-52.55
Nectomys_rattus	M	UFSM_218	-20.47	-55.79
Nectomys_rattus	M	UFSM_27	-20.54	-56.71
Nectomys_rattus	M	UFSM_288	-16.95	-51.81
Nectomys_rattus	F	UFSM_289	-16.95	-51.81
Nectomys_rattus	M	UFSM_290	-16.95	-51.81
Nectomys_rattus	F	UFSM_291	-16.95	-51.81
Nectomys_rattus	M	UFSM_304	-17.32	-53.22
Nectomys_rattus	M	UFSM_51	-20.47	-55.79
Nectomys_rattus	F	UFSM_55	-20.47	-55.79
Nectomys_squamipes	F	MACN_18516	-25.85	-54.35
Nectomys_squamipes	F	MACN_18906	-26.94	-54.43
Nectomys_squamipes	M	MACN_20340	-26.94	-54.43
Nectomys_squamipes	F	MACN_44459	-26.94	-54.43
Nectomys_squamipes	M	MACN_49316	-26.94	-54.43
Nectomys_squamipes	M	MACN_49317	-26.94	-54.43
Nectomys_squamipes	M	MACN_49355	-26.94	-54.43
Nectomys_squamipes	M	MACN_49416	-26.94	-54.43
Nectomys_squamipes	F	MACN_5159	-26.94	-54.43
Nectomys_squamipes	F	MACN_5223	-26.94	-54.43

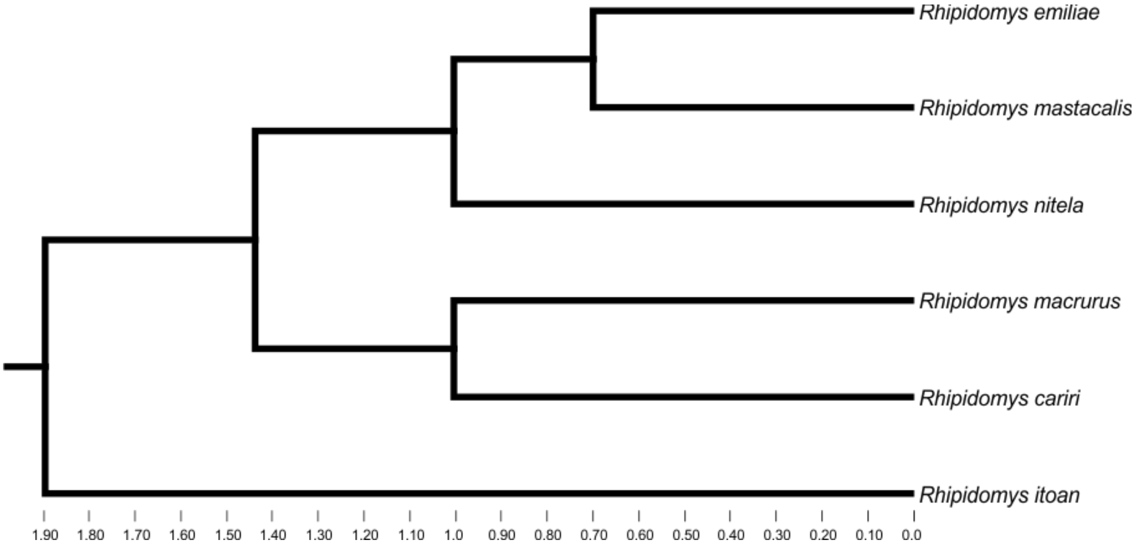
Nectomys_squamipes	M	MACN_5414	-26.94	-54.43
Nectomys_squamipes	M	MACN_5444	-21.83	-42.73
Nectomys_squamipes	F	MACN_5445	-21.83	-42.73
Nectomys_squamipes	F	MACN_5497	-26.94	-54.43
Nectomys_squamipes	F	MNRJ_11614	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11615	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11616	-20.72	-46.61
Nectomys_squamipes	M	MNRJ_11617	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11619	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11622	-20.72	-46.61
Nectomys_squamipes	F	MNRJ_11629	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11630	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11631	-20.12	-40.31
Nectomys_squamipes	F	MNRJ_11632	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_11633	-20.12	-40.31
Nectomys_squamipes	M	MNRJ_12488	-9.37	-36.24
Nectomys_squamipes	F	MNRJ_13358	-19.00	-43.43
Nectomys_squamipes	M	MNRJ_13360	-19.00	-43.43
Nectomys_squamipes	M	MNRJ_13524	-19.52	-43.75
Nectomys_squamipes	M	MNRJ_13526	-19.52	-43.75
Nectomys_squamipes	F	MNRJ_13531	-19.52	-43.75
Nectomys_squamipes	F	MNRJ_13540	-20.33	-43.56
Nectomys_squamipes	M	MNRJ_2061	-22.42	-42.98
Nectomys_squamipes	M	MNRJ_21225	-15.79	-47.88
Nectomys_squamipes	F	MNRJ_21226	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_21228	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_21231	-15.79	-47.88
Nectomys_squamipes	M	MNRJ_2229	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_24367	-23.18	-44.18
Nectomys_squamipes	M	MNRJ_24368	-23.18	-44.18
Nectomys_squamipes	F	MNRJ_24926	-23.18	-44.18
Nectomys_squamipes	F	MNRJ_24933	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_2555	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_2556	-22.76	-43.46
Nectomys_squamipes	F	MNRJ_2591	-22.76	-43.46
Nectomys_squamipes	F	MNRJ_27830	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_27832	-22.93	-42.82
Nectomys_squamipes	F	MNRJ_28540	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_28545	-22.93	-42.82
Nectomys_squamipes	M	MNRJ_26816	-22.05	-42.68
Nectomys_squamipes	M	MNRJ_28991	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_30417	-22.48	-42.20
Nectomys_squamipes	F	MNRJ_31025	-23.18	-44.18
Nectomys_squamipes	M	MNRJ_31395	-19.37	-43.53

Nectomys_squamipes	F	MNRJ_31397	-19.37	-43.53
Nectomys_squamipes	F	MNRJ_32621	-21.78	-46.57
Nectomys_squamipes	M	MNRJ_32622	-21.78	-46.57
Nectomys_squamipes	F	MNRJ_33797	-22.48	-42.20
Nectomys_squamipes	M	MNRJ_33805	-22.48	-42.20
Nectomys_squamipes	M	MNRJ_33807	-22.24	-42.05
Nectomys_squamipes	F	MNRJ_33808	-22.24	-42.05
Nectomys_squamipes	M	MNRJ_4086	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4087	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4091	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4093	-19.63	-43.90
Nectomys_squamipes	M	MNRJ_4094	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4095	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_4098	-19.63	-43.90
Nectomys_squamipes	F	MNRJ_5291	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5292	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5298	-23.43	-45.08
Nectomys_squamipes	F	MNRJ_5326	-23.43	-45.08
Nectomys_squamipes	M	MNRJ_5333	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5334	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5339	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5341	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5342	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5397	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5405	-22.96	-44.04
Nectomys_squamipes	M	MNRJ_5429	-19.94	-40.60
Nectomys_squamipes	F	MNRJ_5437	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5439	-23.43	-45.08
Nectomys_squamipes	F	MNRJ_5440	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5444	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5445	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_5446	-21.77	-42.54
Nectomys_squamipes	M	MNRJ_5447	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_5660	-19.94	-40.60
Nectomys_squamipes	M	MNRJ_5781	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_5816	-22.63	-43.25
Nectomys_squamipes	M	MNRJ_6205	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6276	-23.22	-44.72
Nectomys_squamipes	M	MNRJ_6277	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6278	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6279	-23.22	-44.72
Nectomys_squamipes	M	MNRJ_6280	-23.22	-44.72
Nectomys_squamipes	F	MNRJ_6462	-22.76	-43.46

Nectomys_squamipes	M	MNRJ_6463	-22.76	-43.46
Nectomys_squamipes	M	MNRJ_67037	-22.57	-42.90
Nectomys_squamipes	F	MNRJ_67039	-22.57	-42.90
Nectomys_squamipes	M	MNRJ_67044	-22.48	-42.85
Nectomys_squamipes	F	MNRJ_67046	-22.48	-42.85
Nectomys_squamipes	F	MNRJ_7519	-21.83	-42.73
Nectomys_squamipes	F	MNRJ_7525	-21.83	-42.73
Nectomys_squamipes	M	MNRJ_8289	-20.15	-40.28
Nectomys_squamipes	M	MNRJ_8290	-20.15	-40.28
Nectomys_squamipes	M	MNRJ_8675	-14.69	-39.09
Nectomys_squamipes	M	MNRJ_8676	-14.69	-39.09
Nectomys_squamipes	F	MNRJ_8677	-14.79	-39.05
Nectomys_squamipes	F	MNRJ_8681	-14.79	-39.05
Nectomys_squamipes	M	MZUSP_10183	-23.50	-47.62
Nectomys_squamipes	M	MZUSP_10184	-23.50	-47.62
Nectomys_squamipes	F	MZUSP_10185	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_10186	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_10222	-22.12	-51.39
Nectomys_squamipes	M	MZUSP_10223	-22.12	-51.39
Nectomys_squamipes	F	MZUSP_10415	-19.94	-40.60
Nectomys_squamipes	F	MZUSP_10450	-23.55	-46.65
Nectomys_squamipes	F	MZUSP_10615	-24.52	-48.67
Nectomys_squamipes	F	MZUSP_10617	-24.00	-47.54
Nectomys_squamipes	F	MZUSP_10656	-15.79	-47.88
Nectomys_squamipes	F	MZUSP_10773	-23.78	-46.72
Nectomys_squamipes	M	MZUSP_10913	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_11000	-23.59	-48.05
Nectomys_squamipes	F	MZUSP_11066	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_11452	-21.78	-46.57
Nectomys_squamipes	M	MZUSP_13706	-23.02	-48.01
Nectomys_squamipes	M	MZUSP_13793	-23.02	-48.01
Nectomys_squamipes	M	MZUSP_1702	-20.64	-51.51
Nectomys_squamipes	M	MZUSP_1703	-20.64	-51.51
Nectomys_squamipes	M	MZUSP_2083	-23.81	-45.40
Nectomys_squamipes	M	MZUSP_21243	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_21246	-22.19	-48.78
Nectomys_squamipes	F	MZUSP_21530	-23.78	-46.72
Nectomys_squamipes	F	MZUSP_21540	-9.37	-36.24
Nectomys_squamipes	M	MZUSP_21931	-23.59	-48.05
Nectomys_squamipes	F	MZUSP_21942	-23.59	-48.05
Nectomys_squamipes	M	MZUSP_22800	-24.71	-47.56
Nectomys_squamipes	F	MZUSP_24832	-23.52	-47.14
Nectomys_squamipes	M	MZUSP_27315	-24.27	-48.40
Nectomys_squamipes	M	MZUSP_27435	-23.59	-48.05

Nectomys_squamipes	F	MZUSP_2766	-22.24	-42.05
Nectomys_squamipes	M	MZUSP_2767	-22.24	-42.05
Nectomys_squamipes	F	MZUSP_2768	-22.24	-42.05
Nectomys_squamipes	M	MZUSP_27750	-25.13	-47.97
Nectomys_squamipes	M	MZUSP_27751	-25.13	-47.97
Nectomys_squamipes	M	MZUSP_27878	-24.62	-48.95
Nectomys_squamipes	M	MZUSP_28857	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28860	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28862	-21.72	-52.42
Nectomys_squamipes	M	MZUSP_28865	-21.72	-52.42
Nectomys_squamipes	F	MZUSP_2957	-20.34	-47.79
Nectomys_squamipes	F	MZUSP_2958	-20.34	-47.79
Nectomys_squamipes	M	MZUSP_3516	-19.88	-42.55
Nectomys_squamipes	M	MZUSP_3517	-19.88	-42.55
Nectomys_squamipes	M	MZUSP_3518	-19.88	-42.55
Nectomys_squamipes	F	MZUSP_541	-23.55	-46.63
Nectomys_squamipes	M	MZUSP_58	-22.61	-45.19
Nectomys_squamipes	M	MZUSP_6217	-19.94	-40.60
Nectomys_squamipes	F	MZUSP_6220	-19.94	-40.60
Nectomys_squamipes	M	MZUSP_6284	-23.43	-45.08
Nectomys_squamipes	M	MZUSP_6374	-23.41	-46.60
Nectomys_squamipes	F	MZUSP_8858	-22.53	-52.17
Nectomys_squamipes	F	MZUSP_9573	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9729	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9730	-22.19	-48.78
Nectomys_squamipes	M	MZUSP_9799	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_9800	-23.60	-46.92
Nectomys_squamipes	M	MZUSP_9801	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9873	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9874	-23.81	-46.05
Nectomys_squamipes	M	MZUSP_9876	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9895	-23.60	-46.92
Nectomys_squamipes	F	MZUSP_9897	-23.60	-46.92
Nectomys_squamipes	M	UFSM_177	-17.56	-52.55
Nectomys_squamipes	M	UFSM_194	-17.56	-52.55
Nectomys_squamipes	M	UFSM_44	-21.47	-54.38

Appendix B. Phylogenetic tree of *Rhipidomys* showing only the species used (Steppan and Schenk, 2017). Time is in millions of years (My).



Appendix C. Results of the linear regressions of environmental variables on Size (lnCS) and Shape (PC1 size-free) of *Rhipidomys* and *Nectomys*. We reanalysed the regression models to verify the possible influence of geographical trends. To extract the spatial structure we applied the method based on principal coordinates of neighbor matrices (PCNM) (Borcard and Legendre, 2002). The eigenvalue decomposition of a truncated matrix of geographic distances among samples enable the quantification of spatial patterns over a wide range of scales (Borcard and Legendre, 2002). Then we selected the main explanatory spatial filters (significantly correlated with Size and Shape) (Borcard et al., 2011) using a forward selection with permutation tests. Therefore, we have included these filters in the model to consider a possible spatial autocorrelation. The results are summarized below (significance is highlighted in bold).

Rhipidomys:
Size (PCNM16): bio1 ($\beta = 0.007$, $t = 1.35$, $P = 0.178$); bio12 ($\beta = -0.004$, $t = -1.04$, $P = 0.300$); npp ($\beta = -0.005$, $t = -1.59$, $P = 0.115$).
Shape (PCNM1): bio1 ($\beta = -0.001$, $t = -0.29$, $P = 0.774$); bio12 ($\beta = -0.001$, $t = -0.36$, $P = 0.719$); npp ($\beta = -0.014$, $t = -4.80$, P **< 0.001**).

Nectomys:
Size (PCNM4): bio1 ($\beta = -0.012$, $t = -3.02$, P = **0.003**); bio12 ($\beta = -0.013$, $t = -2.86$, P = **0.005**); npp ($\beta = 0.002$, $t = -0.00$, $P = 0.997$).
Shape (PCNM17): bio1 ($\beta = 0.005$, $t = 2.17$, P = **0.031**); bio12 ($\beta = 0.003$, $t = 1.54$, $P = 0.125$); npp ($\beta = 0.000$, $t = 0.52$, $P = 0.600$).

7 DISCUSSÃO GERAL

A variação fenotípica pode estar associada a diferentes fatores e níveis de importância, como observamos ao longo dos resultados encontrados aqui. Grupos com uma longa história na Região Neotropical são ainda pouco explorados em relação a mudanças ecogeográficas, especialmente utilizando espécies com amplas distribuições. Entretanto, alguns grupos de mamíferos como canídeos sul-americanos já demonstraram mudanças em suas características cranianas, substituindo morfotipos ao longo da variação climática do continente (BUBADUÉ et al., 2015). Da mesma maneira, primatas (CÁCERES et al., 2014; MELORO et al., 2014), taiassuídeos (HENDGES, et al., 2016), roedores (MARTÍNEZ e DI COLA, 2011; MAESTRI et al., 2016), e marsupiais (CERQUEIRA e WEBER, 2016), por exemplo, também variam de acordo com as condições ambientais. Assim, apesar de muitos grupos se modificarem por toda a extensão do continente, nossos resultados corroboram que cada táxon estudado é único, com respostas fenotípicas variáveis.

Quando abordada a alometria do crânio, percebemos para cada táxon a relevância de seus atributos funcionais e a alometria, como a eficiência biomecânica da mastigação (COX et al., 2012; SLATER e VAN VALKENBURGH, 2009). No caso de *C. lanatus*, a espécie apresenta uma maior eficiência para aquisição de alimentos em ambientes sazonais, enquanto que as três espécies de xenartros possuem valores reduzidos por não demandarem muita força biomecânica para se alimentar (retratado pela ausência de esmalte na dentição ou mesmo pela falta de dentes de *T. tetradactyla*) (VIZCAÍNO, 2009). Ainda, a alometria pode ser importante para o dimorfismo sexual, como no caso da forma de *Nectomys*, sugerindo requisitos diferentes de habitat ou nutrição para machos e fêmeas (FAIRBAIRN, 1997). Assim, a alometria nesses mamíferos pode ter evoluído em resposta a diversas pressões seletivas, expandindo algumas aptidões.

Outra explicação para a variação de alguns táxons é devido à distribuição espacial. O espaço geográfico retrata a questão de indivíduos próximos serem mais similares do que os distantes, diminuindo a similaridade ao longo do espaço por uma questão dispersiva, por exemplo, e não exatamente uma variável abiótica refletindo modificação na morfologia (HUBBEL, 2001). Esse fator aleatório é encontrado principalmente em *Caluromys* e *B. variegatus*, os quais possuem em comum hábito arborícola (= dependência de florestas), tamanho corporal pequeno (no caso de *Caluromys*) e dieta frugívora ou folívora, sendo o conjunto dessas características especialistas limitante para uma dispersão eficiente. A baixa mobilidade e capacidade dispersiva destes, portanto, mostra que a teoria neutra é baseada em restrições na dispersão dos indivíduos (ALONSO et al., 2006).

Por outro lado, o ambiente é importante para todos os táxons de algum modo, evidenciando forte influência principalmente em táxons com alta capacidade dispersiva, como *H. hydrochaeris, C. paca* e *D. novemcinctus*, sendo moldados pela pressão dos diferentes biomas e alterações climáticas locais da América do Sul. No caso de *B. variegatus*, sua acentuada modificação com o ambiente possivelmente está ligada aos seus aspectos fisiológicos e ecológicos, como seu extremo baixo metabolismo basal e movimentação restrita (HAYSSEN, 2010). A resposta à regra de Bergmann também é variável entre os mamíferos estudados, indicando respostas relacionadas à disponibilidade de recursos, eficiência energética, ou ainda nenhuma resposta significativa, o que torna improvável indicar um padrão geral abrangendo todos os táxons (MEIRI e DAYAN, 2003). Os pressupostos da teoria do nicho, isto é, o conjunto de condições ambientais locais que regem o modo de vida e características de um organismo (HUTCHINSON, 1957), também são vistos aqui atuando na modificação da forma de estruturas especialmente relacionadas com a alimentação. O aumento da área do arco zigomático, dos molares e focinho mais curto em ambientes mais sazonais estão em concordância com o aumento da força de mordida em outros mamíferos (BUBADUÉ, et al., 2015; CÁCERES et AL., 2014), associando essas modificações aqui com o consumo de alimentos mais rígidos (e.g., insetos, frutas menos carnosas) e pouca disponibilidade de alimentos nesses ambientes. Outra estrutura importante é a bula auditiva, que aumenta em tamanho em ambientes sazonais, principalmente em *D. novemcinctus*, nos roedores, e em *S. brasiliensis*, sugerindo maior percepção do som nesses ambientes (WEBSTER e WEBSTER, 1975), tanto para predação de insetos como para evitar ser predado.

Na abordagem mais detalhada a respeito da diversificação das espécies de *Rhipidomys* e *Nectomys*, o aparato mastigatório se mostra útil para revelar a variação entre algumas espécies de *Rhipidomys*, como a forma de *R. itoan*, descrita como uma nova espécie por COSTA et al. (2011). Dessa maneira, diferenças de tamanho e forma em *Rhipidomys* mostram um esclarecimento sobre a modificação das espécies do gênero, já que este possui pouca variabilidade interespecífica aparente, como destacado pela primeira revisão sistemática de TRIBE (1996). Em contrapartida, o tamanho e a forma do aparato mastigatório em *Nectomys* foram mais homogêneos entre as espécies, manifestando a alta capacidade dispersiva do gênero, não sendo as espécies moldadas pelo isolamento geográfico. Já a reposta oposta entre os dois gêneros em relação à variação ambiental pode ser compreendida através de suas características ecológicas. Sendo *Rhipidomys* mais especialista (em habitat florestal e em dieta frugívora) (PAGLIA et al., 2012), a produtividade primária é a variável que mais influencia sua forma, especialmente a modificação do arco zigomático e do primeiro molar. Enquanto que *Nectomys*, sendo mais generalista (PAGLIA et al., 2012), modifica seu tamanho em reposta a precipitação e temperatura, refletindo plasticidade entre biomas mais sazonais e mais estáveis, além da ligação com a disponibilidade de diferentes recursos alimentares ao longo desses ambientes. Essa variação de *Nectomys* também confirma a tendência do tamanho se modificar ainda mais que a forma (CARDINI e ELTON, 2009), apesar da forma de *Rhipidomys* também se modificar intensamente, mostrando que a alteração maior pelo tamanho não é incontestável, necessitando mais estudos com outros organismos.

Em síntese, conseguimos observar ao longo dos resultados pela abordagem da morfometria geométrica em crânios de diferentes mamíferos que nem todos seguem os mesmos padrões de respostas, e que muitas descobertas e informações relevantes podem surgir para aprimorar o entendimento sobre o que conduz a variação dos organismos.

8 CONCLUSÕES GERAIS

Os resultados obtidos ao longo desta tese sugerem que espécies ou mesmo gêneros com amplas distribuições geográficas, como no caso do continente da América do Sul, sofrem pressões equivalentes, porém respondem de maneiras distintas de acordo com suas histórias de vida e características ecológicas.

No caso das duas espécies de marsupiais proximamente relacionadas – *Caluromys philander* e *C. lanatus* – a separação entre elas é maior pelo tamanho, enquanto é mais sutil pela forma. Ambas apresentam resposta aos efeitos neutros, ou seja, aos efeitos geográficos, mostrando uma estruturação espacial principalmente em relação ao tamanho. Ao mesmo tempo, apresentam respostas similares à influência ambiental, principalmente em relação à temperatura (seguindo também o contrário à regra de Bergmann), com *C. philander* mais influenciado pela precipitação. No entanto, *C. lanatus* apresenta influência na forma apenas sob efeito da alometria, evidenciando mudanças ecomorfológicas relacionadas possivelmente a dieta em ambientes mais sazonais, tornando-se mais plástica nesses ambientes.

As espécies de Xenarthra estudadas mostram semelhanças quanto a resposta alométrica, com pouca presença na variação da forma, sugerindo menor efeito biomecânico na eficiência da mastigação. Padrões geográficos (neutros) são encontrados para as espécies *Bradypus variegatus* (forma) e *Tamandua tetradactyla* (tamanho), indicando restrições espaciais em espécies com dispersões limitadas. Apenas *B. variegatus* segue a regra de Bergmann, uma possível resposta do seu baixo metabolismo e mobilidade, como também evidenciado na influência ambiental encontrada para a espécie. Assim como *B. variegatus*, a resposta à influência ambiental pelo tamanho da espécie *Dasypus novemcinctus* é importante, mas mais relacionada com a sua alta capacidade dispersiva e vagilidade.

A forma dos grupos de Rodentia e Lagomorpha assume variações de acordo com diferentes fatores. A alometria encontrada fortemente presente em *Nectomys* sugere um papel relevante nas diferenças entre machos e fêmeas, referente ao dimorfismo sexual da forma constatado. Fêmeas de *Nectomys* são mais relacionadas ao ambiente, enquanto machos apresentam ainda mais influência alométrica. O ambiente (efeito de nicho) se expressa significativamente para todos os táxons, os quais apresentam modificações em estruturas importantes, como a bula auditiva (maior em locais sazonais). Mas o ambiente influencia ainda mais *Hydrochoerus hydrochaeris* e *Cuniculus paca*, que são espécies de grande porte, plásticas e com alta capacidade dispersiva, do mesmo modo que o conjunto do ambiente e espaço também mostra influência na variação da forma para a espécies num ambiente espacialmente estruturado. A questão da distância geográfica (efeito neutro), apesar do esperado, não tem muito efeito em espécies menores como *Sylvilagus brasiliensis* e *Nectomys*, mostrando que o ambiente ainda predomina na modificação da forma para os dois táxons.

Por fim, algumas espécies de roedores do gênero *Rhipidomys* apresentam diferenças quanto ao tamanho e a forma do aparato mastigatório, segregando-as, refletindo limitação de dispersão. Por outro lado, as espécies de *Nectomys* mostraram maiores sobreposições entre elas, revelando alta mobilidade ao longo dos ambientes, não sendo restritas necessariamente por barreiras. Em relação às variáveis ambientais, os gêneros seguem padrões diferentes, com a forma de *Rhipidomys* mais relacionada com a produtividade primária, enquanto que o tamanho de *Nectomys* variou devido a precipitação e temperatura (seguindo a regra de Bergmann). Portanto, os gêneros respondem diferentemente ao longo do gradiente ambiental, revelando padrões distintos de acordo com suas características.

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