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Source: South American Journal of Herpetology, 8(3):186-197. 2013.

Published By: Brazilian Society of Herpetology

DOI: <http://dx.doi.org/10.2994/SAJHD1200019.1>

URL: <http://www.bioone.org/doi/full/10.2994/SAJHD1200019.1>

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Spatial Variation in Morphometry in *Vanzosaura rubricauda* (Squamata, Gymnophthalmidae) from Open Habitats of South America and its Environmental Correlates

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Abstract. Patterns of geographical variation in morphology provide an empirical framework for testing the effects of ecological and historical factors on species differentiation. Environmental gradients play an important role in intraspecific differentiation through morphological adaptation in locations with distinct selective pressures. *Vanzosaura rubricauda* is a small microteiid lizard that is widespread in the great diagonal of dry biomes of South America, occurring in Cerrado, Caatinga, and Chaco open habitats with contrasting environmental conditions. Using multivariate morphometrics and spatial analysis, we show that *V. rubricauda* presents a structured pattern of geographic variation, with populations of the eastern Cerrado being distinct in morphometry. Geographical variation was observed in size and shape, with a general trend of contrast between trunk length and forelimb length among populations. Ecogeographical models that best explained geographic patterns of variation were aridity and precipitation.

Keywords. Ecogeography; Intraspecific Differentiation; Microteiids; Morphometry; Spatial Analysis.

Resumo. Padrões de variação geográfica na morfologia fornecem uma base empírica para testes dos efeitos de fatores ecológicos e históricos na diferenciação de espécies. Gradientes ambientais desempenham um papel importante para a diferenciação intraespecífica através de adaptações morfológicas em locais com distintas pressões seletivas. *Vanzosaura rubricauda* é um pequeno lagarto microteídeo amplificado ao longo da grande diagonal de biomas secos da América do Sul, ocorrendo no Cerrado, Caatinga e Chaco, em habitats com condições ambientais contrastantes. Com o uso de morfometria multivariada e análises espaciais, mostramos que *V. rubricauda* apresenta um padrão de variação geográfica estruturada, com as populações do leste do Cerrado sendo distintas em morfometria. Variação geográfica foi observada em tamanho e em variáveis de forma, com uma tendência geral de contraste entre comprimento do tronco e tamanho dos membros anteriores entre as populações. Os modelos ecogeográficos que melhor explicam o padrão geográfico de variação foram aridez e precipitação.

INTRODUCTION

The occurrence of geographical variation in morphological traits is ubiquitous in widely distributed organisms (Mayr, 1970). The identification of patterns of morphological variation is a basic step in zoological systematics research, and aids in the discrimination among species or populations (Vanzolini, 1970). Therefore, the variation observed among populations of widespread species provides a fundamental basis for understanding the processes of genetic divergence and natural selection that lead to speciation and adaptation of organisms (Gould and Johnston, 1972; Schneider *et al.*, 1999; Thorpe, 2002; Futuyma, 2009).

Environmental gradients play an important role in geographical differentiation by applying different selective pressures across a species' geographic range, favoring morphological adaptation (Vitt *et al.*, 1997; Schluter, 2001; Kaliontzopoulou *et al.*, 2010; Thorpe *et al.*, 2010). As such, examining the patterns of geographic variation in species that occur throughout regions with heterogeneous

ecological conditions provides an empirical framework for testing the causal effects of historical constraint and ecological opportunities on population differentiation (Brown *et al.*, 1991; Schneider *et al.*, 1999; Thorpe *et al.*, 2004).

A remarkable diversity of squamate reptiles (*i.e.*, lizards, snakes and amphisbaenians) occurs in tropical South America (Greene, 1997; Pianka and Vitt, 2003). Nevertheless, few studies have explored patterns of inter-population morphological variation in lizards of the region. Most studies have focused on species from forests (*e.g.*, Jackson, 1978; Gallagher *et al.*, 1986; Freire, 1998; Miralles and Carranza, 2010; Peloso and Avila-Pires, 2010), with a few examples of species from dry biomes (*e.g.*, Rodrigues, 1987; Vitt *et al.*, 1997; Frost *et al.*, 1998). Because hypotheses for the causes of morphological differentiation in this region are still lacking in empirical support, knowledge about the role of biogeographic processes in driving faunistic patterns is still poorly understood (Zanella, 2011; Werneck, 2011).

Vanzosaura rubricauda (Boulenger, 1902) is a small microteiid lizard (Gymnophthalmidae) that is widespread

in the great diagonal of dry biomes of South America (Vanzolini and Carvalho, 1991). The species belongs to a lineage of small lizards that presents variable degrees of morphological adaptation to fossoriality (*i.e.*, limb reduction, body elongation, loss of eyelids) and is generally restricted to discontinuous sandy-soil habitats (Rodrigues, 1991a, b; Rodrigues *et al.*, 2001; Benozzati and Rodrigues, 2003; Rodrigues and Santos, 2008). *Vanzosaura rubricauda* is a terrestrial, heliophilous, insectivorous, and active-forager lizard, yet it presents cryptic activity (Vitt, 1995; Rodrigues, 2003; Mesquita *et al.*, 2006). The species is usually associated with leaf litter in open to semi-open dry habitats (Vanzolini *et al.*, 1980; Cruz, 1994; Vitt, 1995; Mesquita *et al.*, 2006; Nogueira, 2006; Delfim and Freire, 2007).

Along its distribution, populations of *Vanzosaura rubricauda* occur in environments that present contrasting climatic conditions, defined by different regimes of precipitation and temperature (Cruz, 1994; Vitt, 1995; Mesquita *et al.*, 2006). Moreover, the diagonal of dry biomes in South America has a complex history in which geological events substantially impacted the faunal diversity of the region. Examples of such events include the uplift of the Central Plateau, the presence of marine introgressions in the Paraná/Paraguay basins, erosion of large areas of sandstone plateaus, and paleoclimatic fluctuations that promoted spatial dynamics between forested and open formations (Colli, 2005; Zanella, 2011; Werneck, 2011; Werneck *et al.*, 2012).

Thus, the aims of this study were: 1) to test the presence of geographical variation in morphometric traits among populations of *Vanzosaura rubricauda*; 2) to reveal the spatial pattern of morphometric variation among populations; and 3) to infer which environmental model best explains the pattern of intraspecific morphometric variation observed.

MATERIALS AND METHODS

Samples

We examined the morphological characteristics of 852 *Vanzosaura rubricauda* museum specimens (461 males, 391 females) from 90 localities distributed along the range of the species (Fig. 1). The material examined (Appendix S1) is housed in the following institutions: Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Coleção Herpetológica da Universidade de Brasília (CHUNB), Brasília; Museu de Zoologia Prof. Adão José Cardoso (ZUEC), Campinas; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro; Coleção Herpetológica do Departamento de Botânica, Ecologia e Zoologia da Universidade Federal do Rio Grande do Norte (CHDBEZ), Natal; Coleção Herpetológica da Universidade Federal da

Paraíba (CHUFPB), João Pessoa; Fundación Miguel Lilló (FML), San Miguel de Tucumán; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires; Museo de Historia Natural Noel Kempff Mercado (MNKM), Santa Cruz de la Sierra; Museo Nacional de Historia Natural del Paraguay (MNHNP), Asunción.

Morphological data

We obtained 11 morphometric measurements (precision 0.01 mm) with a digital caliper under stereomicroscope (Fig. 2). SVL: snout–vent length, from border of cloaca to tip of snout; INL: interbrachial–nasal length, from anterior border of central interbrachial scale to tip of snout; TRL: trunk length, between anterior margin of hind limb to posterior margin of forelimb; HH: head height at highest point in longitudinal axis; HW: head width at widest point; HL: head length from anterior margin of tympanic aperture to tip of snout; FEM: femur length, from knee joint to margin of outer scale of anal plate; TIB: tibia length, from knee joint to margin of sole; FTL: hind foot length, from margin of sole to tip of fourth toe, excluding claw; HUM: humeral length, from axilla to elbow joint; FAL: forearm length, from elbow joint to tip of fourth finger, excluding claw. We also measured the tail length (TAL) of specimens that presented unbroken tails ($n = 175$; 24% of samples). The same person performed all measurements; each specimen was measured twice, and the average for each character was used to minimize the effect of measurement error (Yezerinac *et al.*, 1992). Limb measurements (FEM, TIB, FTL, HUM, FAL) and HL were taken on the right side only.

Morphometric data were \log_{10} transformed to meet requirements of normality (Zar, 2010). Juveniles were poorly represented in museum collections, so we excluded individuals shorter than 24.5 mm SVL (outliers). The remaining dataset did not deviate from normality (Lilliefors test; $P > 0.1$) and conformed to homogeneity of variances for all variables (Levene’s test; $P > 0.05$). For shape comparisons, a size-free dataset was obtained through linear regressions of each morphometric measurement on the first principal component of a pooled within-group principle components analysis (PCA), which can be considered a multivariate size vector (Rohlf and Bookstein, 1987). The SVL was highly correlated with PC1 and TRL ($r > 0.90$; $P < 0.01$) and, therefore, was not used in shape analysis.

MORPHOMETRIC ANALYSIS

For among-population analyses, we used a subset ($n = 630$) containing only samples from 16 localities represented by more than five individuals of each gender

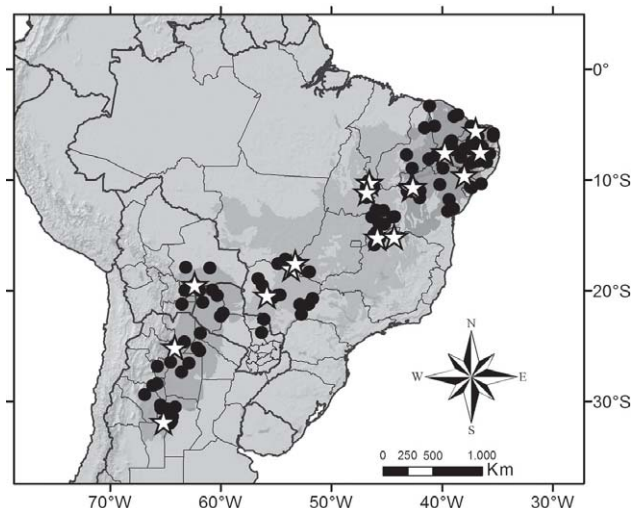


Figure 1. Records of *Vanzosaura rubricauda* in the great diagonal of open formations of South America. Black dots indicate museum and literature records. Stars indicate the samples used in geographical analyses.

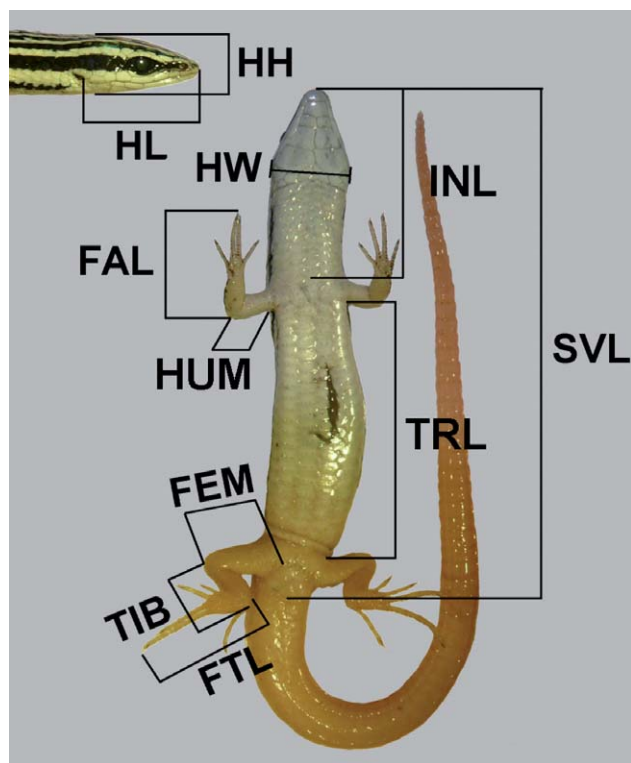


Figure 2. Schematic model of the morphometric measurements taken from specimens of *Vanzosaura rubricauda* for this study. SVL = snout-vent length; TRL = trunk length; INL = interbrachial-nasal length; HH = head height; HW = head width; HL = head length; FEM = femur length; TIB = tibia length; FTL = hind foot length; HUM = humeral length; FAL = forearm length.

(Table 1, Fig. 1). We grouped samples from nearby sites (< 50 km) and used this dataset to test geographic differentiation. We tested for significant differences in size (SVL) between sexes and among populations using two-way analysis of variance (ANOVA) with sex and

population as factors. We tested for differences in shape (size-free dataset) using a two-way multivariate analysis of variance (MANOVA) with sex and population as factors. For size comparisons, we used the largest 50% of individuals of each population as an approximation of the average size of adults, assuming asymptotic growth in the species (Brown *et al.*, 1999). To assess the patterns of geographical variation in shape, we performed a canonical variates analysis (CVA) on the size-free dataset, which seeks the axes that best explain variation among groups (*i.e.*, populations) (Manly, 2004).

Spatial analysis

We used population averages of \log_{10} -transformed SVL and the first canonical function (CV1) of the CVA on the size-free data to represent the geographic variation in size and shape, respectively. To visualize geographical patterns in morphological variation, we interpolated morphological variables in a map using the Kriging method. To test for spatial autocorrelation in population morphometric data (SVL and CV1), we used correlograms based on Moran's I index (Legendre and Legendre, 1998; Perez *et al.*, 2010). The index ranged from 1 (high positive spatial correlation) to -1 (high negative spatial correlation), and was calculated for 10 distance classes in such a way that each group had approximately the same number of samples.

Model selection

For the creation of explanatory environmental models, we used three groups of variables: (A) 48 climatic variables (mean precipitation, average temperatures, minimum and maximum temperatures of each month) and elevation data from the *WorldClim* website (Hijmans *et al.*, 2005); (B) three variables of soil conditions (pH, moisture, and amount of organic carbon) from the *Atlas of the Biosphere* website (Willmott and Matsuura, 2001); and (C) 13 variables of aridity (annual aridity, mean monthly potential evapotranspiration) from the website of the *CGIAR Consortium for Spatial Information* (Trabucco and Zomer, 2009). We subtracted minimum temperatures from maximum temperatures to obtain values of temperature amplitude for each month. Environmental layers have a spatial resolution of 2.5 arc-minutes (5 km × 5 km), except soil layers that have 0.5 degree resolution.

Principal component analysis was used in order to reduce data redundancy of abiotic variables and to diminish the number of parameters in the models. Thus, to summarize the (a) monthly averages of mean temperatures, (b) temperature amplitude, and (c) potential evapotranspiration, we retained one axis of greatest variation

Table 1. List of populations used in morphological comparisons, represented by samples larger than five exemplars of *Vanzosaura rubricauda* for each sex. For some populations, we grouped samples from nearby sites (< 50 km) as listed in the locality column. Geographic information and sample size for each population are provided.

#	Population	Locality	Municipality/ province/ departament	UF	Country	Latitude	Longitude	Morphoclimatic domain	Sample size (females/ males)
1	Cordoba	Bañado de Paja	Cordoba	-	ARG	-31.8553	-65.1764	Chaco	16/18
2	Salta	Joaquín V. Gonzales	Salta	-	ARG	-25.1333	-64.1333	Chaco	21/34
3	Cordillera	Izozog (Cordillera)	Santa Cruz	-	BOL	-19.4815	-62.3583	Chaco	14/18
4	Aquidauana	Aquidauana	Aquidauana	MS	BRA	-20.4633	-55.8172	Cerrado (W)	10/7
5	Taquari	PE Nascentes do Rio Taquari	Alcinópolis	MS	BRA	-17.9914	-53.6292	Cerrado (W)	10/16
6	Araguaia	Faz. Saramandaia	Alto Araguaia	MT	BRA	-17.5100	-53.2600	Cerrado (W)	13/9
		Faz. Granado	Alto Taquari	MT	BRA	-17.7047	-53.2703		
7	Formoso	RPPN Serra das Araras	Chapada Gaúcha	MG	BRA	-15.3000	-45.6167	Cerrado (E)	18/19
		PN Grande Sertão Veredas	Formoso	MG	BRA	-15.2167	-45.8000		
		Fazenda Trijunção	Cocos	BA	BRA	-14.7667	-45.9167		
8	Januária	PN Cavernas do Peruacuú	Januária	MG	BRA	-15.1544	-44.3030	Cerrado (E)	21/17
9	Jalapão	PE do Jalapão	Mateiros	TO	BRA	-10.2628	-46.5656	Cerrado (E)	8/22
		São Félix do Tocantins	São Félix do Tocantins	TO	BRA	-10.1500	-46.6500		
10	Serra Geral	ESEC Serra Geral do Tocantins	Formosa do Rio Preto	BA	BRA	-10.6800	-46.1508	Cerrado (E)	22/28
		ESEC Serra Geral do Tocantins	Almas/Mateiros	TO	BRA	-11.2210	-46.8857		
11	Ibiraba	Ibiraba	Barra	BA	BRA	-10.7833	-42.8167	Caatinga	27/26
		Queimadas				-10.5667	-42.6667		
12	Vacaria	Vacaria	Xique-Xique	BA	BRA	-10.6500	-42.6167	Caatinga	32/36
13	Xingó	UHE Xingó	Piranhas	AL	BRA	-9.6000	-37.9667	Caatinga	12/6
14	Exu	Exu	Exu	PE	BRA	-7.5000	-39.7167	Caatinga	44/71
15	Cariri	ESEX Univ. Fed. da Paraíba	São João do Cariri	PB	BRA	-7.4667	-36.5167	Caatinga	8/8
		Faz. Almas	São José de Cordeiros	PB	BRA	-7.4667	-36.8667		
16	Seridó	ESEC do Seridó	Serra Negra do Norte	RN	BRA	-6.5767	-37.2558	Caatinga	7/11
		FLONA de Assu	Assú	RN	BRA	-5.5667	-36.9333		

(PC1) that accounted for 84.3%, 74.8% and 69.5% of variation respectively. For average precipitation, we retained the first two principal components (52.0% and 35.3% of variation). Due to the high correlation between the soil pH and amount of organic carbon variables ($r = 0.940$; $P < 0.01$), we used only soil pH in the model.

We thus used nine environmental variables to represent abiotic variation along the species range: (1) elevation, (2) mean precipitation 1 (PC1), (3) mean precipitation 2 (PC2), (4) mean temperature, (5) temperature amplitude, (6) soil moisture, (7) soil pH, (8) annual aridity, and (9) potential evapotranspiration 1 (PC1). We obtained the dataset by extracting climatic information from the locality points with morphological data. The fit of the mathematical models that best represent the relationships between abiotic variables and morphology for each of the theoretical environmental models was made through generalized additive models (GAM; Zuur *et al.*, 2009).

We determined five general ecogeographical explanatory models to test the effects of environmental variables on the patterns of morphological variation. This was performed to represent different aspects of environmental heterogeneity observed along the diagonal of open formations of South America, including

(1) elevation gradient (ELEV = elevation), (2) gradient in rainfall (PRECIP = mean precipitation 1 + mean precipitation 2), (3) gradient in temperature (TEMP = mean temperature + temperature amplitude), (4) soil conditions (SOIL = soil moisture + soil pH), and (5) aridity (ARID = annual aridity + potential evapotranspiration 1). We also included one categorical model (BIOME) in which each of the three morphoclimatic domains (*i.e.*, Cerrado, Caatinga, and Chaco) was identified by a distinct letter, a geographical model using coordinates (GEO = latitude + longitude) to test for presence of geographical cline, and a null model representing the absence of environmental effects on morphology (NULL = constant).

To compare which explanatory models were most likely to explain morphological variation, we selected among candidate models based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). AIC is a measure of the models' fit to the data and selects the model that best explains the variation in the data set (Burnham and Anderson, 2002; Mazerolle, 2006). Models with values of AICc (AIC corrected for reduced samples) < 2 are considered to be equally plausible as the best models to explain the observed patterns. Akaike's weights (wAICc) is another useful index for model selection that indicates the relative fit of each explanatory model given a

Table 2. Results of one-way ANOVA on size (log SVL) and shape (residuals) of males and females of *Vanzosaura rubricauda* with populations ($n = 16$, Table 1) as factors. Significance level of 0.003 after Bonferroni correction.

	Males ¹		Females ²	
	F	P	F	P
SIZE				
log SVL	8.11	< 0.001	8.20	< 0.001
SHAPE				
res INL	4.314	< 0.001	3.014	< 0.001
res TRL	55.165	< 0.001	20.748	< 0.001
res HH	14.970	< 0.001	5.048	< 0.001
res HW	20.334	< 0.001	3.420	< 0.001
res HL	13.526	< 0.001	3.110	< 0.001
res FEM	20.115	< 0.001	7.118	< 0.001
res TIB	26.064	< 0.001	6.148	< 0.001
res FTL	30.042	< 0.001	11.390	< 0.001
res HUM	29.451	< 0.001	17.166	< 0.001
res FAL	57.231	< 0.001	20.886	< 0.001

¹df = 15, 334; ²df = 15, 256.

set of competing models (Burnham and Anderson, 2002). To infer the individual contribution of each model in the multi-model inference, we calculated the average Akaike’s weight (Average wAICc).

Analyses were performed using R environment (R Development Core Team, 2011), IBM SPSS Statistics (version 20.0, SPSS Inc., 2011), and SAM 4.0 (Rangel *et al.*, 2010). Extraction of environmental data and interpolation of continuous variables on maps were performed with the program ArcGIS 10.0.

RESULTS

Morphometric variation

Females were significantly larger than males on average ($F_{(1,591)} = 70.05, P < 0.01$). Sexes were also dimorphic in shape (Wilks’ lambda = 0.723, $F_{(15,591)} = 11.26, P < 0.01$) with significant differences in FEM and TRL ($P < 0.05$). Sexual dimorphism interacted with geographical variation for size ($F_{(16,584)} = 1.85, P < 0.05$) and shape (Wilks’ lambda = 0.560, $F_{(16,583)} = 2.16, P < 0.01$). Therefore, we performed subsequent geographical analyses for each sex separately.

Populations of *Vanzosaura rubricauda* differed significantly in SVL (Females: $F_{(15,328)} = 8.20, P < 0.001$; Males: $F_{(15,334)} = 8.11, P < 0.001$), with Chacoan populations being significantly larger than populations from other regional groups in females, and larger than those from Cerrado in males (Tukey HSD *ad hoc* test, $P < 0.01$) (Table 2). Multivariate differences in shape were also significant among populations (females: Wilks’ lambda = 0.20, $F_{15,328} = 20.01, P < 0.001$; males: Wilks’ lambda

Table 3. Results of canonical variate (CV) analysis of size-adjusted data (shape) of males and females *Vanzosaura rubricauda* from the 16 populations listed in Table 1.

Variables	Males		Females	
	CV1	CV2	CV1	CV2
TRL	0.633	0.243	0.341	0.028
FAL	0.659	0.192	0.336	0.019
HUM	0.319	0.582	0.264	0.456
FEM	0.155	0.204	0.105	0.383
TIB	0.424	0.176	0.155	0.080
FTL	0.352	0.460	0.195	0.042
HH	0.234	0.037	0.063	0.362
HL	0.153	0.256	0.075	0.045
HW	0.016	0.667	0.029	0.115
INL	0.013	0.044	0.013	0.064
Eigenvalues	5.936	1.770	9.455	1.165
% of variance	58.8	17.5	77.5	9.5
Cumulative %	-	76.4	-	87.0

= 0.13, $F_{(15,334)} = 33.16, P < 0.001$), and when controlling for size differences, all remaining variables also presented significant variation in males and females ($P < 0.001$) among populations (Table 2).

CVA of size-free morphometric measurements showed that 79.7% of variation among populations in males and 81.0% in females are explained by two canonical functions (Table 3). In both males and females, the first canonical function (CV1) is principally correlated with positive variation in FAL, and negative variation in TRL. The second canonical function is strongly correlated with positive variation in FEM and negative variation in HUM in females, and positive variation in FEM and negative variation in HW in males (Table 3). In both males and females, populations from eastern Cerrado are significantly separated from other regional groups in the morphometric space defined by the first canonical functions for males ($F_{1,337} = 843.30, P < 0.01$) and females ($F_{1,267} = 522.55, P < 0.01$) (Fig. 3).

Spatial analysis

The spatial autocorrelation observed in body size (SVL) in males and females of *Vanzosaura rubricauda* are not pronounced, with Moran’s *I* indices varying from -0.3 to 0.3 (Fig. 4). For shape variation (CV1), both sexes presented a similar pattern, with significant positive autocorrelation in distance categories between 0–250 km and negative autocorrelation observed at the distance category of 870 km and 1120 km (Fig. 4). The spatial patterns of variation in size and form among populations presented in maps of interpolation of CV1 and SVL are regionally complex (Fig. 5). Geographical differentiation in shape among populations within the Cerrado and Caatinga regions can be observed.

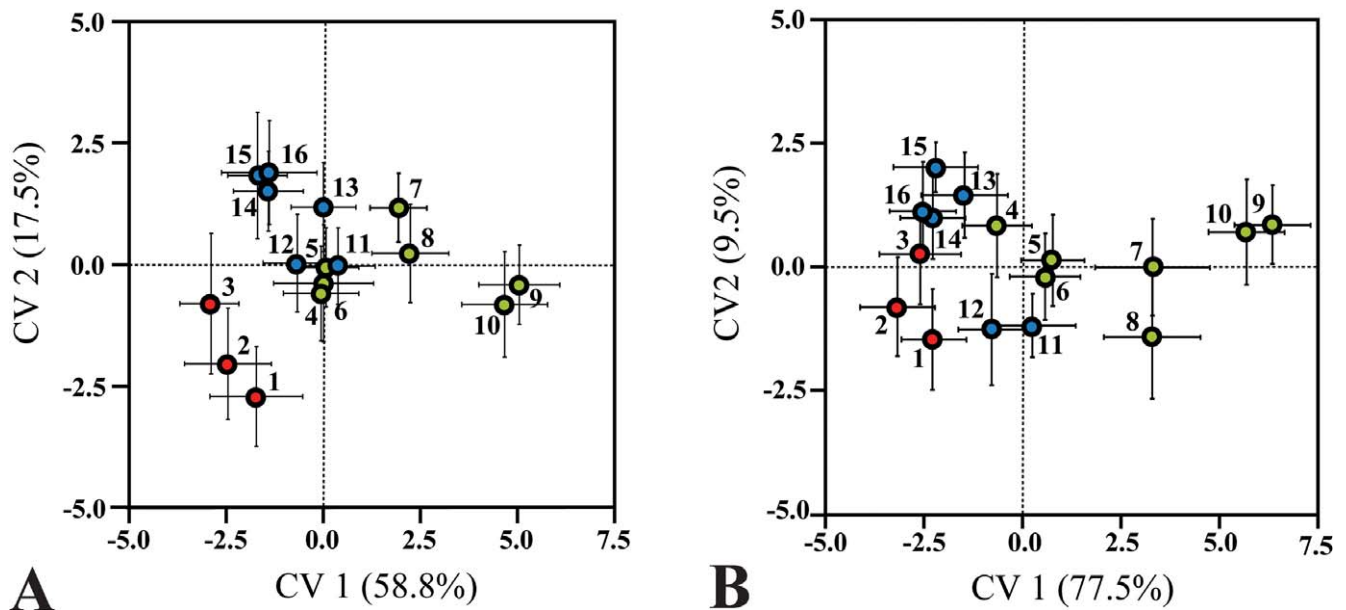


Figure 3. Results of the canonical variates analysis of the size-corrected morphometric data for (A) males and (B) females of *Vanzosaura rubricauda*. The centroids and standard deviations of the canonical coefficients for each population are shown. Symbols correspond to the regions: Chaco (red circles), Cerrado (green circles) and Caatinga (blue circles). Numbers correspond to populations listed in Table 1.

Model selection

The models that best fit the variation in SVL were composites of temperature and precipitation for males and aridity and geography for females (Table 4). Precipitation presented the highest individual contribution to model inference (wAICc = 0.029; average wAICc = 0.103) for males, and aridity (wAICc = 0.069; average wAICc = 0.108) for females (Table 5). The model that best

explained variation in shape (CV1) in males was a composition of precipitation, temperature, and aridity (sum of wAICc = 0.470); and for females a composition of all abiotic models (sum of wAICc = 0.784) (Table 4). Aridity presented the highest individual contribution to model inference based on the Akaike’s weights to males (average wAICc = 0.163) and females (Average wAICc = 0.188) (Table 5).

DISCUSSION

Our results show that a contrast between body elongation and limb length summarizes the overall shape variation in *Vanzosaura rubricauda*, which is in great part explained by geographical variation among populations. This axis of variation reflects a general evolutionary trend observed among species of Gymnophthalmidae (Rodrigues *et al.*, 2005; Wiens *et al.*, 2006; Grizante *et al.*, 2012), but in a subtle degree at the intraspecific level explored in the present study. The evolution of a snake-like form, or the elongation of the body accompanied by limb reduction, is ubiquitous in Squamata and has been referred to as an adaptation to fossoriality or cryptic habits (Wiens *et al.*, 2006). Although *V. rubricauda* is a cryptic species that is rarely seen in activity (Vitt, 1995) and has an elongate body, it presents well-developed limbs. It has been demonstrated that the presence of longer limbs in lizards favors higher performance in superficial locomotion (Losos, 1990; Garland and Losos, 1994; Bauwens *et al.*, 1995; Bergmann and Irschick, 2010) with direct consequences for habitat use (Calsbeek and Irschick,

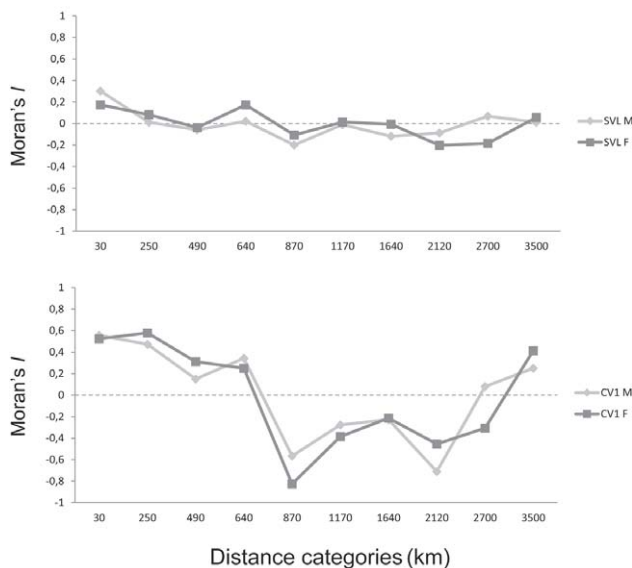


Figure 4. Correlograms based on Moran's I indices for spatial autocorrelation of size (SVL) and shape (CV1) in *Vanzosaura rubricauda*. Lines represent values for males (light grey) and females (dark grey) in each distance category.

2007; Losos, 2009). Thus, the longer limbs in populations from eastern Cerrado might be related to greater terrestrial activity or exposure to predators (Husak and Rouse, 2006), which remains to be tested.

The geographical pattern of morphometric variation observed in *Vanzosaura rubricauda*, although spatially structured, is not clinal (*sensu* Thorpe, 2002), as revealed by the interpolation maps and lower performance of the GEO model. Two important characteristics were revealed: (1) there is a marked heterogeneity in shape morphology among populations within the Cerrado and Caatinga domains; and (2) the most morphologically differentiated populations occur in eastern Cerrado at the core of the species range.

Although our model-based analyses indicate that climatic conditions explain the geographical variation in morphometry of *Vanzosaura rubricauda*, we also found weak support for classical ecogeographical patterns such as “Bergmann’s rule”, or the clinal relationships between size and latitude or temperature (Meiri, 2011). Although different degrees of support have been observed for Bergmann’s rule for reptiles in general (Ashton and Feldmann, 2003; Pincheira-Donoso and Meiri, 2013), the complex association between size and environmental variables observed for *Vanzosaura* might be better interpreted in the context of life history variation (Angilleta Jr. *et al.*, 2004) or might be spatially constrained by phylogeny (Meiri, 2011). The observed

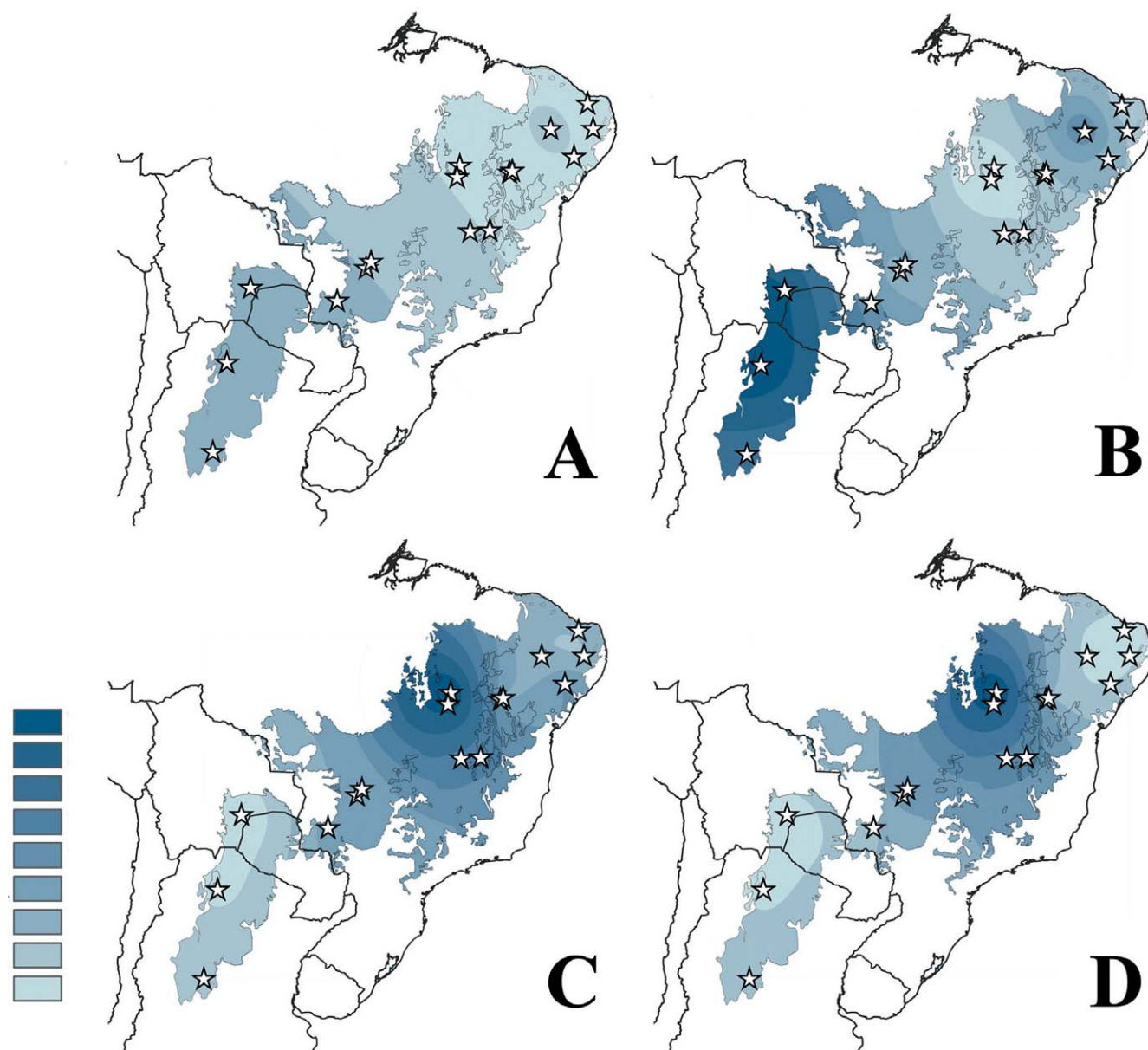


Figure 5. Interpolation of population averages of morphological characters in *Vanzosaura rubricauda*: geographical variation in size (SVL) for males (A) and females (B) and geographical variation in shape (CV1) for males (C) and females (D). Lighter colors indicate lower values and darker colors higher values.

Table 4. AICc, number of parameters (*K*) and Akaike weights (*w*AICc) of the multi-model inference of explanatory effects of seven candidate ecogeographical models and a constant model, on the morphometric variation (size and shape) of *Vanzosaura rubricauda*. SVL = snout vent length; CV1 = first canonical function (refer to text for details).

	Ecogeographical model	K	Males			Females		
			AICc	df	wAICc	AICc	Df	wAICc
SVL	ARID	3	15.2	12.5	0.001	4.0	16.4	0.064
	TEMP	3	13.0	10.7	0.001	29.9	12.1	0.001
	PREC	3	4.4	14.5	0.029	18.6	13.6	0.001
	GEO	3	11.5	15.8	0.001	16.0	14.9	0.001
	ELEV	2	40.6	10.0	0.001	73.1	4.2	0.001
	SOIL	3	16.8	11.8	0.001	12.4	14.2	0.001
	BIOME	2	49.1	4.0	0.001	41.1	4.0	0.001
	PREC*TEMP	5	0.0	14.8	0.255	9.0	15.9	0.005
	ARID*SOIL	5	3.5	21.5	0.044	6.4	16.7	0.019
	ELEV*SOIL	4	8.4	15.2	0.004	12.7	14.8	0.001
	ARID*ELEV	4	8.8	16.9	0.003	7.6	15.0	0.011
	GEO*ARID	5	0.8	17.6	0.174	0.0	13.8	0.461
	GEO*ELEV	4	3.1	18.7	0.055	6.8	22.6	0.015
	GEO*SOIL	5	11.8	12.1	0.001	11.4	11.8	0.002
	PREC*TEMP*SOIL	7	1.6	14.8	0.112	7.3	20.3	0.012
	PREC*TEMP*ARID	7	2.6	14.5	0.070	3.3	20.0	0.088
	PREC*TEMP*GEO	7	1.6	15.4	0.114	3.4	17.6	0.083
	PREC*TEMP*ELEV	6	1.4	17.5	0.124	1.4	18.2	0.233
	PREC*TEMP*ARID*GEO*ELEV*SOIL	12	5.7	23.2	0.015	8.5	23.2	0.007
	NULL	2	87.6	2.0	0.001	75.3	2.0	0.001
CV1	ARID	3	74.4	16.9	0.001	60.3	19.8	0.001
	TEMP	3	146.6	19.9	0.001	264.2	17.3	0.001
	PREC	3	42.7	16.8	0.001	38.5	12.8	0.001
	GEO	3	36.1	14.8	0.001	26.2	19.6	0.001
	ELEV	2	541.4	10.6	0.001	421.8	10.3	0.001
	SOIL	3	38.3	18.0	0.001	38.6	13.1	0.001
	BIOME	2	302.9	4.0	0.001	292.2	4.0	0.001
	PREC*TEMP	5	11.5	28.3	0.001	7.6	29.0	0.018
	ARID*SOIL	5	21.0	18.3	0.001	12.9	24.9	0.001
	ELEV*SOIL	4	24.8	23.4	0.001	22.5	19.8	0.001
	ARID*ELEV	4	4.2	22.5	0.058	16.0	25.1	0.001
	GEO*ARID	5	10.2	26.5	0.003	5.7	26.0	0.046
	GEO*ELEV	4	22.8	22.0	0.001	35.2	20.8	0.001
	GEO*SOIL	5	6.7	19.6	0.016	19.1	17.2	0.001
	PREC*TEMP*SOIL	7	15.4	22.6	0.001	7.7	27.4	0.017
	PREC*TEMP*ARID	7	0.0	19.9	0.470	4.0	27.3	0.108
	PREC*TEMP*GEO	7	7.4	19.9	0.012	7.1	28.8	0.023
	PREC*TEMP*ELEV	6	7.7	25.1	0.010	10.6	28.6	0.004
	PREC*TEMP*ARID*GEO*ELEV*SOIL	12	0.2	20.3	0.429	0.0	24.6	0.784
	NULL	2	601.4	2.0	0.0	497.8	2.0	0.001

importance of aridity and precipitation for morphometric variation could result from morphological similarity between Caatinga and Chacoan populations, which share a semi-arid climate compared to the more mesophilous environmental conditions of the Cerrado (Nimer, 1989). Accordingly, a recent study on morphological variation in Gymnophthalmidae suggested an association between body shape and climate and found that species from arid environments were usually more elongated (Grizante *et al.*, 2012).

The populations of western and eastern Cerrado presented dissimilarity in morphology in accordance with the great geographical gap in *Vanzosaura*'s range. For instance, several phylogenetically distant species of lizards that are distinct in ecology and morphology, such as *Phyllolopezus pollicaris*, *Tropidurus etheridgei*, and *Bachia bresslaui*, also present a similar range disjunction at the central portion of the Cerrado (Vanzolini, 1968; Rodrigues, 1987; Nogueira, 2006; Rodrigues *et al.*, 2008; Teixeira Jr. *et al.*, 2013), which for *P. pollicaris* delimits an ancient genetic

Table 5. Average Akaike's weights (Average wAICc) of each ecogeographical model based on the multi-model inference of explanatory effects of abiotic data on the morphometric variation (size and shape) of *Vanzosaura rubricauda*. n = number of composite models in which a variable was present (see Table 4); SVL = snout-vent length; CV1 = first canonical function (refer to text for details).

Variable*	N	SVL		CV1	
		Males	Females	Males	Females
ARID	6	0.051	0.108	0.163	0.188
TEMP	7	0.099	0.061	0.134	0.159
PREC	7	0.103	0.061	0.134	0.159
GEO	6	0.060	0.095	0.091	0.171
ELEV	6	0.034	0.045	0.085	0.132
SOIL	6	0.029	0.007	0.088	0.134

* ARID = aridity;
TEMP = temperature;
PREC = precipitation;
GEO = geography;
ELEV = elevation;
SOIL = soil conditions.

divergence between populations from the two portions (Gamble *et al.*, 2012; Werneck *et al.*, 2012). In fact, the uplift of the Central Plateau has been regarded as an important geological event for allopatric speciation in the region (Colli, 2005; Zanella, 2011; Werneck, 2011).

Historical factors might have been operative in explaining the pattern of variation. However, morphological resemblance among geographically distant populations, such as Caatinga and Chaco populations inhabiting similar environments, and dissimilarity among geographically proximate populations without a clear physical barrier to gene flow (such as eastern Cerrado populations), suggests that morphological adaptation driven by ecological factors may also be involved (Brown *et al.*, 1991; Schneider *et al.*, 1999; Kaliontzopoulou *et al.*, 2010).

Ecological factors might be particularly important in accounting for morphological variation in *Vanzosaura rubricauda* on a local scale. Habitat structure and soil conditions impose selective pressures on morphological diversification within Gymnophthalmidae (Rodrigues, 1991a; Barros *et al.*, 2011; Grizante *et al.*, 2012). The association of some populations with sandy-soil habitats, irregularly distributed along the species range, was discussed in the literature (Nogueira, 2006; Delfim and Freire, 2007), but its consequences for intraspecific variation remains to be investigated. It is also interesting that the most distinct forms occur in the eastern Cerrado, comprising the *Jalapão-Serra Geral* region, which is an important area of endemism that harbors a rich fauna of lizards, including many exclusive species (Nogueira *et al.*, 2011). The region has a complex geomorphologic history related to the ancient formation and subsequent erosion of sandstone of the *Serra Geral* plateau, thus favoring the presence and diversification of many sand-dwelling species (Rodrigues *et al.*, 2008; Colli *et al.*, 2009).

In our approach, we emphasize the importance of considering variation in a spatial context. We found that the geographical pattern of variation is complex in *Vanzosaura*, and this may be the rule for species in the Tropics in which high diversity, historical constraints, and spatial heterogeneity may interact with climate to drive patterns of differentiation (Schneider *et al.*, 1999; Moritz *et al.*, 2000; Hill and Hill, 2001; Thorpe *et al.*, 2010). We expect that future studies focused on intraspecific variation of widespread species in a spatially explicit framework, should help reveal general patterns of species diversification in the great diagonal of dry biomes of South America and the ecological context of the appearance of morphological novelties.

ACKNOWLEDGMENTS

We thank the following curators of herpetological collections that provided access to specimens examined in this work: Carolina Mello and Hussam Zaher (MZUSP); Marcela Brasil, Mariana Caixeta and Guarino Colli (CHUNB); Luis Felipe Toledo and Paulo Manzani (ZUEC); Roberta Pinto (MNRJ); Eliza Maria Freire (CHD-BEZ); Gustavo Vieira (CHUFPPB); Sônia Kretzschmar and Gustavo Scrocchi (FML); Santiago Nenda, Daiana Ferraro and Julián Faivovich (MACN); Lucindo Gonzales and Ronald Sosa (MNKM); Martha Motte and Pier Cacciali (MNHNP); Karina Atkinson and Helen Pheasey (CHPLT). The Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support (2008/075980 and 2003/103358).

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APPENDIX I

Specimens examined

Vanzosaura rubricauda

ARGENTINA: *Catamarca:* Depto. Valle Viejo: Sumalao (FML 01088). *Córdoba:* Depto. San Alberto: Villa Dolores: Bañado de Paja (MACN 33074–33079, 33241–33257; MZUSP 72599–72601); Depto. Calamuchita: Villa General Belgrano (MACN 7998–7999); Depto. Punilla: Icho Cruz (FML 020481, 020482), Villa Carlos Paz (FML 23386); Depto. Santa María: Villa Serranita (MACN 36275); Depto. Totoral: Sierra de Macha (MACN 12503); Depto. Cruz del Eje: Serrezuela (MACN 12504). *La Rioja:* Depto. Capital: Dique Los Sauces (MACN 25153); Depto. Chilecito: Chilecito (MACN 33499). *Salta:* Depto. Anta: Joaquín Víctor Gonzáles: Finca Pozo Largo (FML 02709, 03124, 03126, 03305–03306 [02], 03307 [17], 03310 [13], 03311 [12], 03312, 03313 [12], 03314 [14], 03316, 03318, 03320–03323, 06108, 06110, 06112 [12], 06113, 06117 [12], 06118 [12], 06122, 06123 [12], 06124 [14], 06125 [13], 06708, 08183, 03315, 03317 [12], 06121); Coronel Olleros: Río Juramento (FML 00450, 00607). *Santiago del Estero:* Dique “Los Quintogas” (MACN 32531); Depto. Alberdi: Campo Gallo (MACN 10099); Depto. Figueroa: Caspi Corral (FML 01086); Depto. Pellegrini: Pampa Pozo (MACN 26645, MACN 30962). **TUCUMÁN:** Depto. Tafí del Valle: Tafí Del Valle (FML 00210).

BOLÍVIA: *Santa Cruz:* Prov. Chiquitos: Monte Abayoi (MNKM 3223); Prov. Cordillera: Cerro Colorado (MNKM 3187, 3189–3190, 3192–3194); Pista de estación Isoso: Parque Nacional ANMI Kaa Iya (MNKM 4023–4030, 4099–4104; 4150–4163, 4183, 4202–4204).

BRAZIL: *Alagoas:* Delmiro Gouveia (CHUNB 49910); Piaçabuçu (MNRJ 17631–17632); Piranhas (CHUNB 49907, 49911); UHE Xingó (MZUSP 78943–78945; 79140–79153). *Bahia:* Barra: Barra (MZUSP 75620), Ibiraba (CHUNB 30963–30970; MZUSP 71865, 71868, 71845, 71850–71852, 71856–71857, 71872–71874, 71881–71882, 71884–71886, 71894–71895, 93468–93471), Queimadas (MZUSP 74970–74974, 75318, 76917–76922, 76924–76926, 77889–77892, 77995–78003); Cachoeira (MZUSP 55819); Central: Jussara: Toca da Esperança (MZUSP 89287); Cocos: Fazenda Triunção (CHUNB 23752, 49175–49178, 49180–49190, 51296–51298); Correntina (MTR 17938); Curaçá (MZUSP 77170); Formosa do Rio Preto: Estação Ecológica Serra Geral do Tocantins (MZUSP 103203–103210); Ibipecta (CHUNB 24224); Gentio do Ouro: Santo Inácio (MTR 11245, 11295, 11391, 71606, 74966–74968, 76240; MTR 20191); Glória (MTR 21222); Riachão do Jacuípe (MNRJ 10530–10531); Santa Maria da Vitória (MTR 17967–17969); São Desidério (MTR 17844, 17853–17855, 17888–17889); Senhor do Bonfim (MZUSP 48685, holótipo); Xique-Xique: Capim Verde (MZUSP 71607–71608), Vacaria (MZUSP 71609–71613, 71615, 71618–71622, 71624–71630, 71632–71633; 71635–71638, 71640–71642, 71644–71647, 71650, 71652, 71658, 71663–71666, 74236–74237, 75476, 76298–76304, 76932–76941, 76943, 76945–76951, 76957–76958, 76960–76962, 76966–76968, 76973, 76975, 76984–77886, 77888, 77986–77994, 71614, 71616–71617, 71621, 71623, 71631, 74233–74235, 77887). *Ceará:* Baturité: Açudinho (MZUSP 2428); Milagres (CHUNB 56529; MNRJ 18498); Várzea da Conceição (CHUFPPB 280, 290, 298); Viçosa do Ceará (CHUNB 57373). *Goiás:* Mineiros: RPPN Nascentes do Araguaia (CHUNB 23752–23753), São Domingos (CHUNB 12848); Serranópolis (CHUNB 12847, 58588–58589, 58591–58592, 58586–58587, 58590, 58593). *Minas Gerais:* Arinos (CHUNB 37302–37304); Chapada Gaúcha: Parque Estadual da Serra das Araras (CHUNB 33994–33996); Formoso (CHUNB 23821), Parque Nacional Grande Sertão Veredas (MZUSP 94144–94178; 95705–94711); Januária: Parque Nacional Cavernas do Peruaçu (MZUSP 99857–99895). *Mato Grosso:* Alto Araguaia (PHVAR 001–020; MZUSP 78875); Alto Taquari (MTR 15564); Itiquira (FLI 004–005, 016, 038–039, 045), UHE Ponte de Pedra (MZUSP 98637). *Mato Grosso do Sul:* Alcinoópolis: Parque Estadual Nascentes do Rio Taquari (CHUNB 27951–27980); Aquidauana (CHUNB 58277, 58572–58578; FML 06897; MZUSP 82326–82331, 98091–98095); Santa Rita do Pardo (MZUSP 89275–89277); Três Lagoas: Usina Termoeletrica Luís Carlos Prestes (ZUEC 3519), Faz. Canaã (MZUSP 14430); UHE Sérgio Mota (MZUSP 87644, 9228592286). *Paraíba:* Cabaceiras (MZUSP 66232); Piancó (MZUSP 5590); São João do Cariri: Estação Experimental da UFPPB (CHUFPPB 395–396, 404, 408, 411, 417–418, 805); São José dos Cordeiros (CHUFPPB 803, CHDBEZ 2035–2039); Serra Branca (MNRJ 19686); Umbuzeiro (MZUSP 4723). *Pernambuco:* Agrestina (21820–21834); Arcoverde (CHUFPPB 282); Buíque: Parque Nacional do Catimbau (ACG 114–115; 121); Exu (MZUSP 45944–45947; 48648–48743, 50152–50166, 57788–57791). Nascente (CHUFPPB 46); Serra Talhada (CHUFPPB 281); Trindade (CHUFPPB 766). *Piauí:* Paulistana (CHUFPPB 300); Rio Grande do Piauí (CHUFPPB 794); São Raimundo Nonato: Serra da Capivara (ZUEC 0872; MZUSP 54841). *Rio Grande do Norte:* Assú: Floresta Nacional de Assú (CHDBEZ 889–900); Macaíba (CHDBEZ 2664–2665); Monte Alegre (CHDBEZ 1003); Mossoró: Campo do Amaro (CHDBEZ 614, 1002); Tenente Laurentino Cruz (CHDBEZ 2957–2959); Serra Negra do Norte: Estação Ecológica do Seridó (CHUNB 30565; CHDBEZ 773–776). *Sergipe:* Areia Branca: 88097–88900); Canindé do São Francisco: UHE Xingó (CHUNB 49908–49909, 49913). *Tocantins:* Almas: Estação Ecológica Serra Geral do Tocantins (MZUSP 103186–103202); Dianópolis (CHUNB 33076, 33090); Mateiros: Parque Estadual do Jalapão (CHUNB 28161, 28163–28174, 28176–28182, 28185–28186, 28188–28189), Estação Ecológica Serra Geral do Tocantins (MZUSP 94119–94143); ZUEC 3022–3025); São Félix do Tocantins (CAB 1723, 1731).

PARAGUAI: *Alto Paraguay:* Parque Nacional Defensores del Chaco (MNHNP 11212); *Amambay:* Parque Nacional Cerro Corá (MNHNP 2835–2836, 8461); *Boquerón:* Ayoreo Yunucujai (MNHNP 10616), Parque Nacional Teniente Encisto (MNHNP 10720); *San Pedro:* Nueva Germánia: Reserva Natural Laguna Blanca (CZPLT H 015, 021, 029, 153, 154).