



Research paper

## Variation of craniodental traits in russet rats *Euryoryzomys russatus* (Wagner, 1848) (Rodentia: Cricetidae: Sigmodontinae) from Eastern Atlantic Forest

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## ABSTRACT

The analyses of geographic variation and the detection of discontinuities among populations of a given taxa is a fundamental step on evolutionary studies. Some recent studies have demonstrated that along the Atlantic Forest of eastern Brazil there are some phylogenetic and phylogeographic discontinuities recovered with molecular markers for several groups of organisms, granting the proposition of biogeographic hypothesis for species diversification in this biome. For instance, a phylogeographic study using cytochrome *b* sequences demonstrated geographic pattern of genetic variation in the oryzomyine rodent *Euryoryzomys russatus*. Considering the widespread occurrence of *E. russatus*, its susceptibility to fragmentation, and the existence of geographic structure in the genetic variation mentioned above, *E. russatus* stands as an interesting species to describe the geographic pattern of craniodental variation. Therefore, we aim to evaluate the morphometric variation patterns coupled with the actual knowledge regarding the evolution of the Atlantic Forest biota, in order to test the hypothesis that the phenotype of *E. russatus* exhibits a structured pattern of variation along the Atlantic Forest similar to that described for the cytochrome *b* gene on continental and coastal islands samples. Our results showed that there is congruence between the gaps here described on morphometric data and the genetic data described in literature. We also detected important variation in size between some insular populations and the continent. Geographic patterns of morphometric variation observed for *E. russatus* were compared to other patterns of diversity for the Atlantic biome, and discussed under historical biogeographic context. We concluded that study of morphometric variation might offer important support to phylogeographic and biogeographic hypothesis based on molecular markers and provide a better scenario on the expression of the phenotypic variation.

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### 1. Introduction

*Euryoryzomys russatus* (Wagner, 1848) is a member of the tribe Oryzomyini, the most diverse assemblage of sigmodontine rodents in the New World (*sensu* Voss and Carleton, 1993; Musser and Carleton, 2005; Weksler, 2006; Weksler and Percequillo, 2011; Patton et al., 2015). The newest concept of *E. russatus* (Weksler and Percequillo, 2011; Percequillo, 2015a) is more restrictive and con-

cise than that of Musser et al. (1998), since the former authors sustain that *Euryoryzomys lamia* (Thomas, 1901) from central Brazil, and *Euryoryzomys legatus* (Thomas, 1925) from northwestern Argentina and southern Bolivia, represent distinct and valid species, based on karyology (Bonvicino et al., 1998; Silva et al., 2000) and phylogenetic relationships (Patton et al., 2000; Weksler, 2003, 2006; Percequillo, 2015a). Hence, the geographic distribution of *E. russatus* is also narrower than previously established: the species is a typical Atlantic Forest inhabitant, being distributed through the eastern Brazil, from the enclaves of moist and semideciduous vegetation (*brejos*) inside the Caatinga, at the northeastern Brazil, to the northern Rio Grande do Sul state; the longitudinal range extends from the Brazilian eastern coast, including some continental islands on São Paulo and Rio de Janeiro states, to the Misiones Province in Argentina, and also eastern Paraguay. The species occupies a wide altitudinal gradient ranging from

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the coastal lowlands through the slopes of mountain ranges and highlands of Southeastern Brazil, Argentina and Paraguay, which commonly reach more than 1000 m high (Prado and Percequillo, 2013; Percequillo, 2015a).

Ecologically, *E. russatus* is uncommon in localities from north-eastern Brazil (Pardini, 2004), but it is an abundant species in southeastern areas (Bergallo, 1994; Pardini and Umetsu, 2006). Moreover, studying populations from localities from the São Paulo highlands, Umetsu and Pardini (2007) and Umetsu et al. (2008) found that fragmentation process affects this species negatively: the decreasing of the size of a forest patch is related to the decreasing of the species' abundance. Apparently, the structure of the forest is not important, but the amount of continuous forest remaining on the landscape. In addition, these authors also suggested that this species exhibits limited ability to disperse throughout non-forested matrices, resulting in isolated populations.

The isolation of populations is one of the processes that lead to structuration of the geographic variation, which is a universal phenomenon in nature and its occurrence has been reported since early zoological systematic studies (Mayr, 1963). Mayr (1963), Gould and Johnston (1972) and, more recently, Perktas (2010) and Zapata and Jiménez (2012) reported several cases of geographic variation and their possible reasons. They express how important are the studies of the variation patterns in search of discontinuities to the taxonomic inferences, and for understanding the origins of the variation and speciation processes (Zapata and Jiménez, 2012). In summary, the analyses of geographic variation and the detection of discontinuities among populations of a given taxa is a fundamental step on evolutionary studies and definition of species limits.

In fact, Miranda et al. (2007) recovered geographic structuration through the distribution of *E. russatus*, by analyzing cytochrome *b* sequences. The authors recovered three clades, one including samples at north of the Rio Paraíba do Sul; another formed by samples between the parallels 23°S and 13°S, south of the Rio Paraíba do Sul; and a third clade of the southernmost samples, which includes the populations occurring in the transitional region between the Pampas grasslands and the Atlantic Forest. However, there is no available evidence concerning the morphological variation of *E. russatus* throughout its distribution (see Musser et al., 1998).

Considering the species widespread occurrence; its susceptibility to fragmentation, either caused by natural (e.g., insular samples from coastal islands) and/or anthropogenic factors (e.g., patches of forest isolated by human activities); and the existence of geographic structure in the genetic variation, *E. russatus* stands as an interesting species to describe the geographic pattern of morphological, more specifically, craniodental variation. Therefore, we aim to evaluate the morphometric variation patterns coupled with the actual knowledge regarding the evolution of the Atlantic Forest biota, in order to test the hypothesis that the phenotype of *E. russatus* will exhibit a structured pattern of variation along the Atlantic Forest, between continental and insular samples, as a consequence of lack of gene flow or other “evolutionary force” (Zapata and Jiménez, 2012).

## 2. Material and methods

### 2.1. Sampling

We sorted 246 adult individuals of *E. russatus* from the following museums and collections: LAMAQ, Laboratório de Mamíferos Aquáticos, Universidade Federal de Santa Catarina, Florianópolis; MHNCI, Museu da História Natural “Capão da Imbuia”, Curitiba; MN, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UFMG, Coleção de Mamíferos, Universidade

Federal de Minas Gerais, Belo Horizonte; AUC, Alexandre Uarth Chirstoff collection; MAM, Meika A. Mustrangi collection, to be deposited at the MZUSP.

The sampled specimens are distributed through 37 localities. Geographic samples were established according to the number of specimens available: few samples are represented by a single locality, while others were obtained by pooling nearby localities in order to constitute a useful sample to permit the statistical analyses (Musser, 1968; Vanzolini, 1970). The geographic samples and their localities are provided in Table 1 (see also Appendix A, for a list of specimens examined). Fig. 1 shows all the localities we surveyed and the distributional range of *E. russatus* based on the recent published information (Prado and Percequillo, 2013; Percequillo, 2015a). The geographical coordinates of surveyed localities of these samples are also listed in Table 1.

### 2.2. Morphometric data

Fourteen craniodental measurements were taken with digital dial calipers to the nearest 0.01 mm (Fig. 2): Total Length (TL); Length of Diastema (LD); Length of Upper Toothrow (LTR); Breadth of the First Upper Molar (BM1); Length of Incisive Foramina (LIF); Breadth of Incisive Foramina (BIF); Breadth of Rostrum (BR); Length of Nasals (NL); Length of Palatal Bridge (LPB); Interorbital Breadth (IOB); Greatest Zygomatic Breadth (ZB); Breadth of Zygomatic Plate (BZP); Condylo-zygomatic Length (CZL); Length of Orbital Fossa (LOF). The definition and homologies of these measurements follow Voss (1988) and Percequillo et al. (2011).

### 2.3. Age and sexual variation

In order to control the variance related to age and growth we employed only ‘adult’ specimens, characterized by fully erupted third molars with moderate enamel wear resulting in a nearly flat crown surface (see Voss, 1991; Musser et al., 1998); adult specimens of *E. russatus* are also characterized by a full-grown dense and soft pelage, that range from orange to reddish or rusty brown dorsal pelage and whitish or grayish-white ventral pelage.

We employed non-parametric Mann-Whitney tests in the continental samples to verify if sexual dimorphism could preclude our analyses of geographic variation (Simpson et al., 2003). All performed tests suggested that sexual variation is insignificant for geographic purposes (see Supplementary material; see also Abreu-Júnior et al., 2012). Therefore, we pooled both sexes together for all subsequent analyses.

### 2.4. Geographic variation

In order to assess the variation, we firstly calculated the descriptive statistics, reporting here the mean values, sample size, standard deviation, minimum and maximum values, for all samples. Subsequently, a principal component analysis (PCA) was conducted using log<sub>10</sub>-transformed original data – excluding the samples of Ilha de Búzios and Ilha Grande, due to their small sample size and occurrence of many missing values – to verify the contribution of the measurements to the total variance. The principal components (PCs) were extracted from the variance-covariance matrix (Jolicœur, 1963; Neff and Marcus, 1980). The scores of principal components were normalized to 1 by dividing each score to the square root of the corresponding eigenvalue. This normalization permits a better comprehension of the contribution of each variable to the variation that its component represents (Neff and Marcus, 1980).

In order to test our previous hypotheses, we assessed the geographic variation throughout two independent, but correlate, approaches. Aside from all continental sample comparison, we also

**Table 1**  
Samples used in the analyses of geographic variation of *E. russatus*, with the localities of each one.

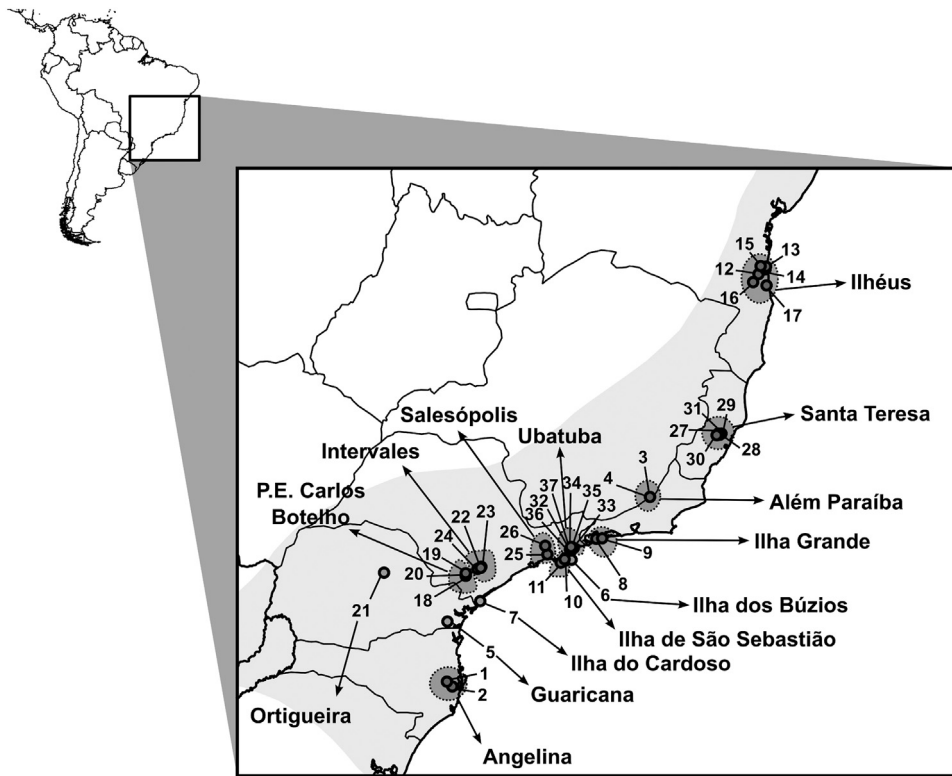
Sample name (sample size)	Acronym	Geographic localities (Coordinates)
Angelina (9)	ANG	1. Angelina, Barragem do Garcia. Not located; here we used the geographic coordinates of Angelina (27°35'S, 48°59'W); 2. Parque Estadual da Serra do Tabuleiro, Caldas da Imperatriz (=Santo Amaro da Imperatriz) (27°44'S, 48°49'W).
Além Paraíba (22)	APB	3. Além Paraíba, Faz. Paraíso. Not located; here we used the geographic coordinates of Além Paraíba (21°51'S, 42°41'W); 4. Além Paraíba, Faz. São Geraldo. Not located; here we used the geographic coordinates of Além Paraíba (21°51'S, 42°41'W).
Guaricana (24)	GUA	5. Guaricana, São José dos Pinhais (25°43'S, 48°58'W).
Ilha de Búzios (7)	IBU	6. Ilha dos Búzios (23°48'S, 45°07'W).
Ilha do Cardoso (8)	ICA	7. Ilha do Cardoso (25°05'S, 47°57'W).
Ilha Grande (4)	IGD	8. Angra dos Reis, Ilha Grande, Praia Vermelha (23°09'S, 44°21'W); 9. Ilha Grande, 1 km Oeste de Abraão (23°08'S, 44°10'W).
Ilha de São Sebastião (8)	ISS	10. Ilha de São Sebastião. Not located; here we used the geographic coordinates of Ilhabela, in Ilha de São Sebastião (23°47'S, 45°20'W); 11. Ilha de São Sebastião, Ilhabela, Fazenda da Toca (23°49'S, 45°54'W).
Ilhéus (29)	ILH	12. Buerarema, Ribeirão da Fortuna. Not located; here we used the geographic coordinates of Buerarema (14°56'S, 39°19'W); 13. Ilhéus, Aritaguá, Urucutuca. Not located; here we used the geographic coordinates of Aritaguá (14°42'S, 39°05'W); 14. Ilhéus, Banco da Vitória, Pirataisque. Not located; here we used the geographic coordinates of Banco da Vitória (14°47'S, 39°06'W); 15. Ilhéus, Rio do Braço, Almada. Not located; here we used the geographic coordinates of Rio do Braço (14°41'S, 39°15'W); 16. Jussari, Serra do Teimoso (15°11'S, 39°29'W); 17. Una, ESCAN. Not located; here we used the geographic coordinates of Una (15°17'S, 39°04'W).
Intervales (18)	INT	18. Faz. Intervales, Carmo (24°18'S, 48°24'W); 19. Faz Intervales, Saibadela (24°13'S, 48°24'W); 20. Faz. Intervales, Sede (24°16'S, 48°24'W).
Ortigueira (10)	ORT	21. Ortigueira (24°12'S, 50°57'W).
P.E. Carlos Botelho (21)	PCB	22. Parque Estadual Carlos Botelho, 840 m (24°03'S, 47°56'W); 23. Parque Estadual Carlos Botelho, São Miguel Arcanjo, 820 m (24°01'S, 47°55'W); 24. Parque Estadual Carlos Botelho, Varginha, 850 m (24°05'S, 48°02'W).
Salesópolis (45)	SAL	25. Boracéia (23°38'S, 45°52'W); 26. Casa Grande (includes Casa Grande, Salesópolis and Casa Grande, Biritiba-Mirim) (23°22'S, 45°56'W).
Santa Teresa (21)	STA	27. Santa Teresa (19°56'S, 40°36'W); 28. Santa Teresa, Est. Biológica de Santa Lúcia, 8.2 km. L de S.T. (19°55'S, 40°31'W); 29. Santa Teresa, Goipapoaçu (Goipaba-açu) (19°53'S, 40°28'W); 30. Santa Teresa, Mata da Caixa d'Água, 1.7 km. W de S. Teresa (19°56'S, 40°37'W); 31. Santa Teresa, Reserva Florestal de Nova Lombardia (19°53'S, 40°34'W).
Ubatuba (20)	UBA	32. Ubatuba (23°26'S, 45°03'W); 33. Ubatuba, Cór. Cachoeira Grande (23°24'S, 45°08'W); 34. Ubatuba, Córrego do Cemitério (23°24'S, 45°07'W); 35. Ubatuba, Cór. Pipoca. Not located; here we used the geographic coordinates of Ubatuba (23°26'S, 45°03'W); 36. Ubatuba, Estação Experimental. Not located; here we used the geographic coordinates of Ubatuba (23°26'S, 45°03'W); 37. Ubatuba, Serra d'Água, Praia Dura (23°29'S, 45°10'W).

compare insular samples to the nearest continental localities and discuss the variation in relation to the processes that led to the isolation of each island from the continent; otherwise eventual size differences would be masked by overall variation.

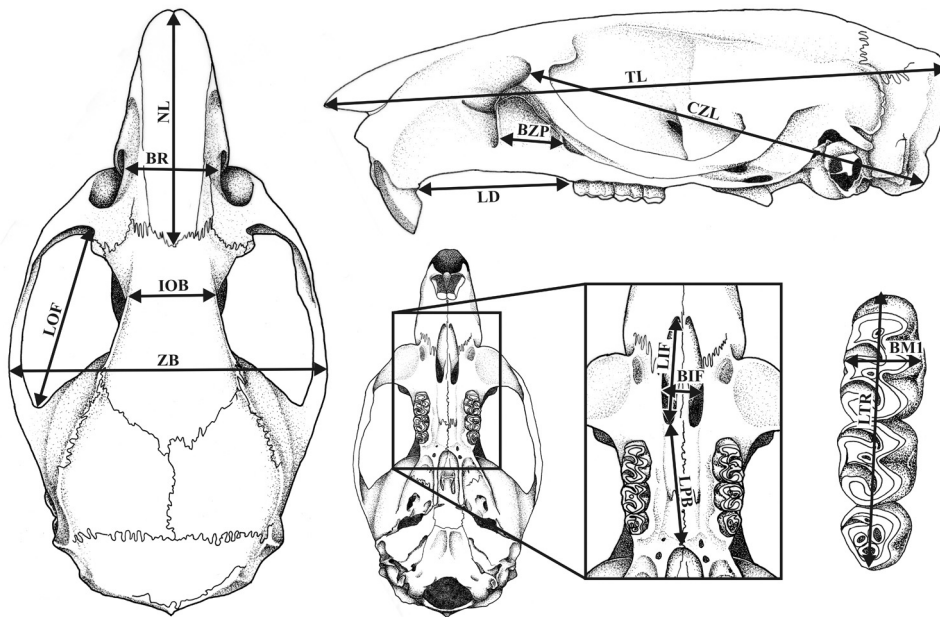
#### 2.4.1. Continental variation

We constructed Dice-Leraas diagrams showing the mean and 95% confidence intervals (Simpson et al., 2003) to visualize geographic patterns of variation among the samples using firstly the original variables and then the first three PCs to view the general variation in the uni- and multivariate space. Discriminant function analyses (DA) also using the transformed data were employed to assess the differences between samples (Strauss 2010). Based on the aforementioned DA, we constructed scatterplot graphics and Dice-Leraas diagrams to graphically evaluate the differences

among different groups. We computed the squared-Mahalanobis distances ( $D^2$ ) using the results from this DA to measure the phenetic similarity between each pair of samples, following Patton et al. (1975) and Voss (1991). To assess the similarity of these samples, we employed a cluster analysis using the UPGMA method (Sneath and Sokal, 1973), based on the  $D^2$ . Mantel's test was employed using the matrices of the  $D^2$  and the minimum geographic distances in order to assess the influence of the distances to their morphometric differences between the pairs of samples (Mantel, 1967; Sokal, 1979; De Queiroz and Good, 1997). For each matrix, all values were divided by the maximum value, in order to eliminate the unit differences of the morphometric and geographic distances. We also verified the correlation between the geographic component and the morphometric variation by performing a PCA with the geographic coordinates in decimal units of each locality from the continental



**Fig. 1.** Map of the collection localities of *Euryoryzomys russatus* in eastern South America. The localities used in the morphometric analyses are indicated following the numbering in Table 1. The samples (localities or groups circled in dark grey) are indicated with arrows. The light gray area in the map represents the distribution of *E. russatus*, according to Percequillo (2015a).



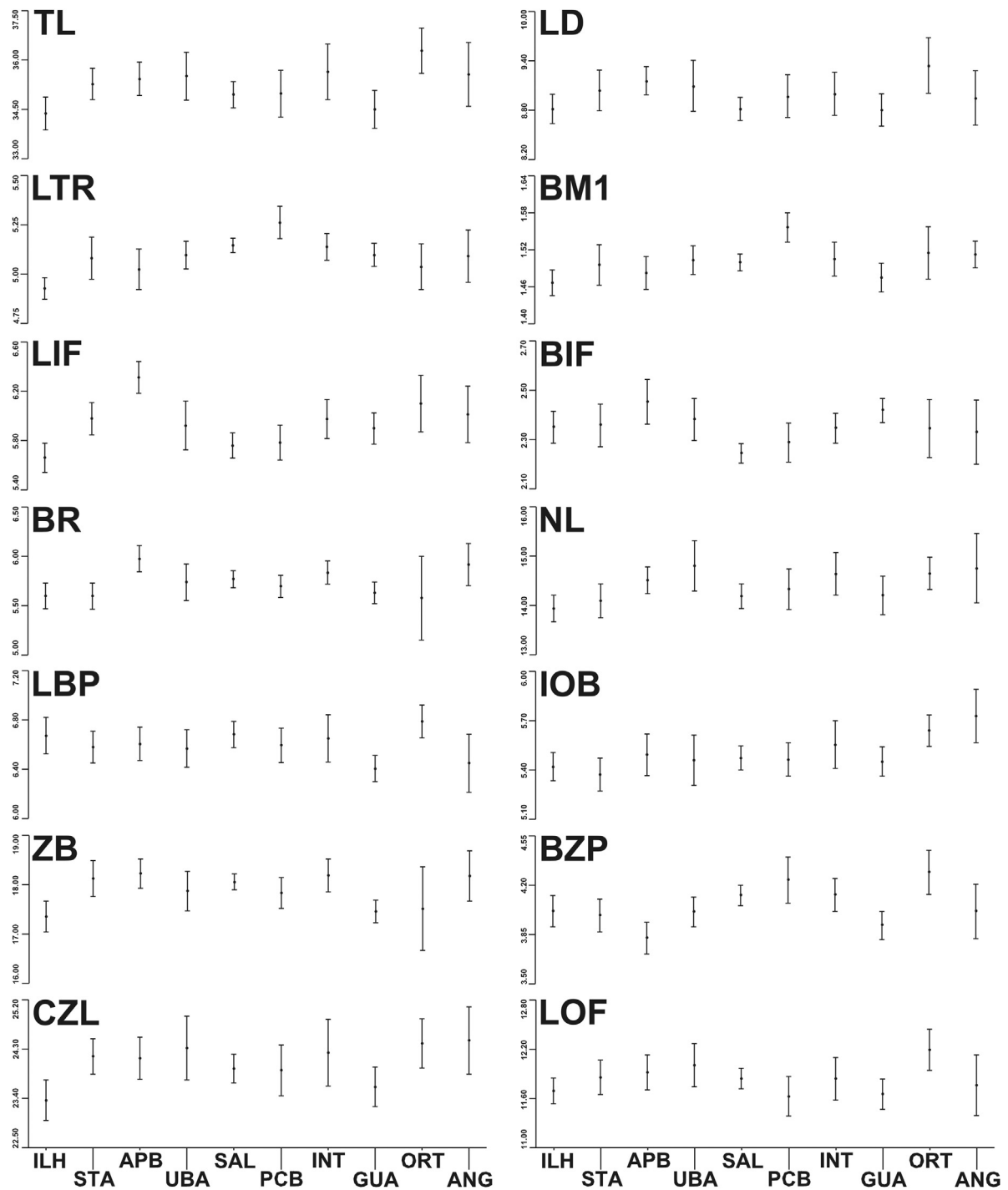
**Fig. 2.** Dorsal, lateral and ventral views of the skull of *E. russatus*, specimen MZUSP 28392, from Ilha do Cardoso, showing the dental and cranial measurements performed in this study. Author: G. S. Libardi.

samples and further using the first component (GEOPC1) to generate a correlation matrix with the log<sub>10</sub>-transformed variables.

#### 2.4.2. Insular variation

The island samples were compared to their continental counterparts, which are the closest continental samples. Ratio diagrams (following Musser et al., 1998; Simpson et al., 2003) were used to

compare graphically multiple measurements among two or more samples; the standard deviations were not considered, to avoid overlapping of bars. We also provide information on the differences between the means of samples for the variables employed on ratio diagrams, performed with non-parametric Mann-Whitney tests. We also employed the Dice-Leeras diagrams and the mul-



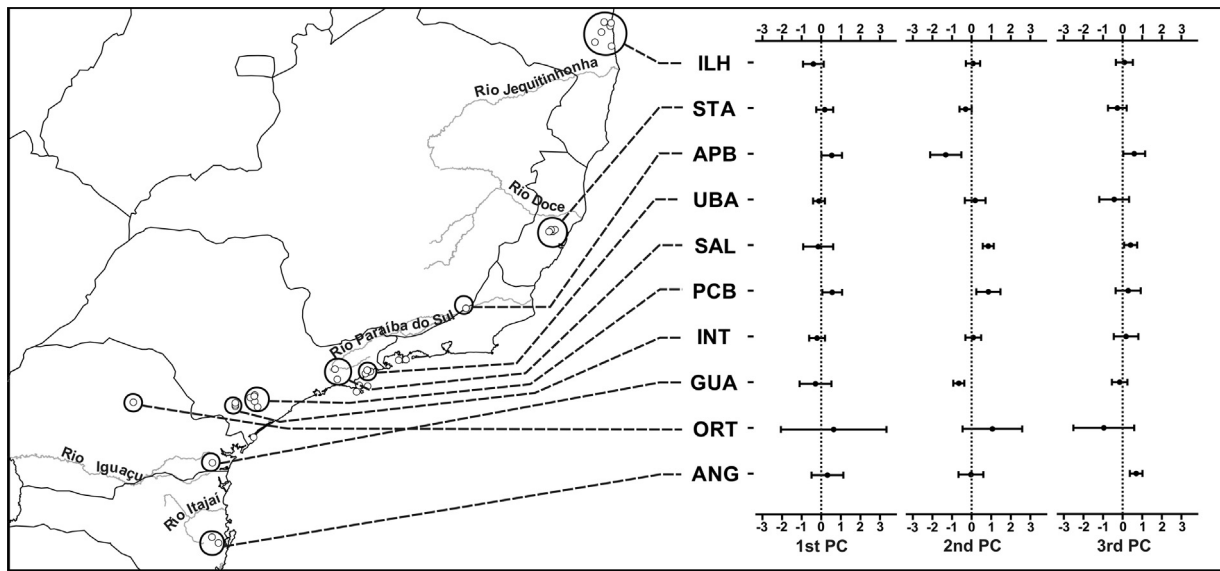
**Fig. 3.** Dice-Leraas diagrams of the original variables for each continental sample, which are organized geographically, from northern (left) to southern samples (right). The black spots represent the means; the bars represent the 95% confidence intervals. Acronyms for samples are explained in [Table 1](#).

tivariate approach also, but excluded the Ilha de Búzios and Ilha Grande from these analyses because of the insufficient sampling.

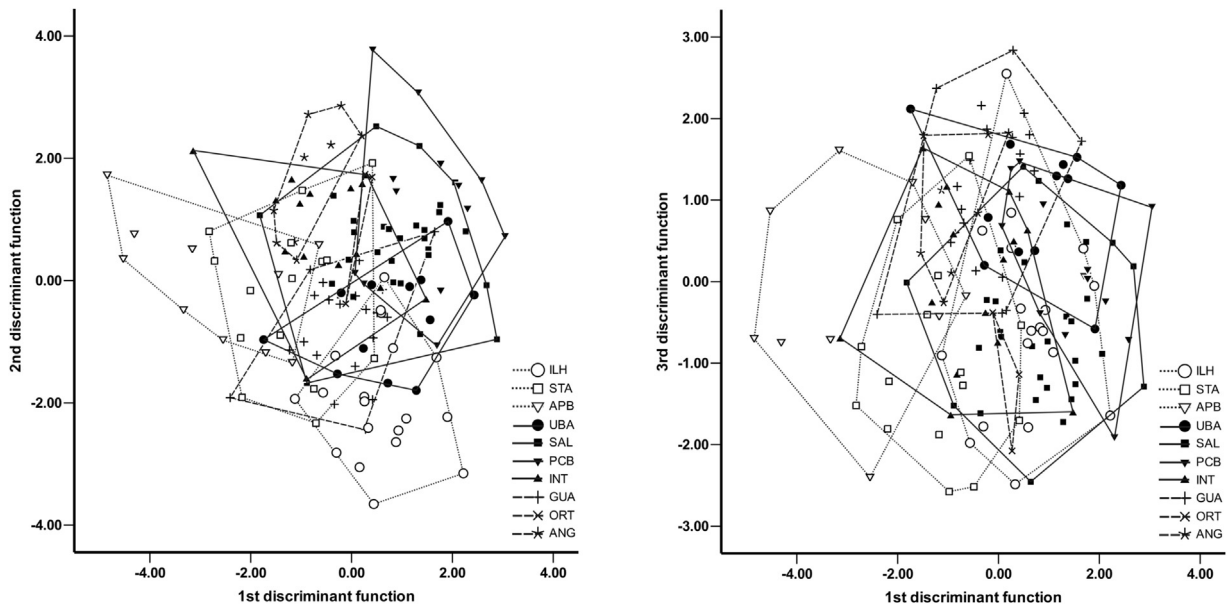
### 3. Results

The descriptive statistics for all geographic samples are shown on the [Appendix B](#). The PCA results based on the data of all samples (excluding Ilha de Búzios and Ilha Grande) show that the first nine principal components concentrate *ca.* 95% of the total variation. The first principal component explains 46.91% of the total variance. After normalizing the scores of the first three principal

components, almost all variables present considerable contribution to the amount of variation on the first principal component ([Table 2](#)), which means this axis is an allometric vector. In the second principal component (14.46% of variance) the incisive foramen variables (LIF and BIF) influence this vector in opposite direction of BZP and LPB. The third principal component, a lesser contributor to the total variance (7.01%), presents some variables related to the general rostral length (LIF, NL and BZP) varying in one side of the axis while general breadth measures (BR and IOB) and LPB vary in the other side.



**Fig. 4.** Distribution of continental samples and the Dice-Leraas diagrams elaborated with the individual scores of three first principal components of the PCA. The black spots represent the mean; the bars represent the 95% confidence intervals. Acronyms for samples are explained in Table 1.



**Fig. 5.** Scatterplot of the individual scores of the first and second (left) and the first and third (right) discriminant functions obtained from the discriminant analysis for the continental samples. The polygons connect external points of each sample. Acronyms for samples are explained in Table 1.

**3.1. Continental variation**

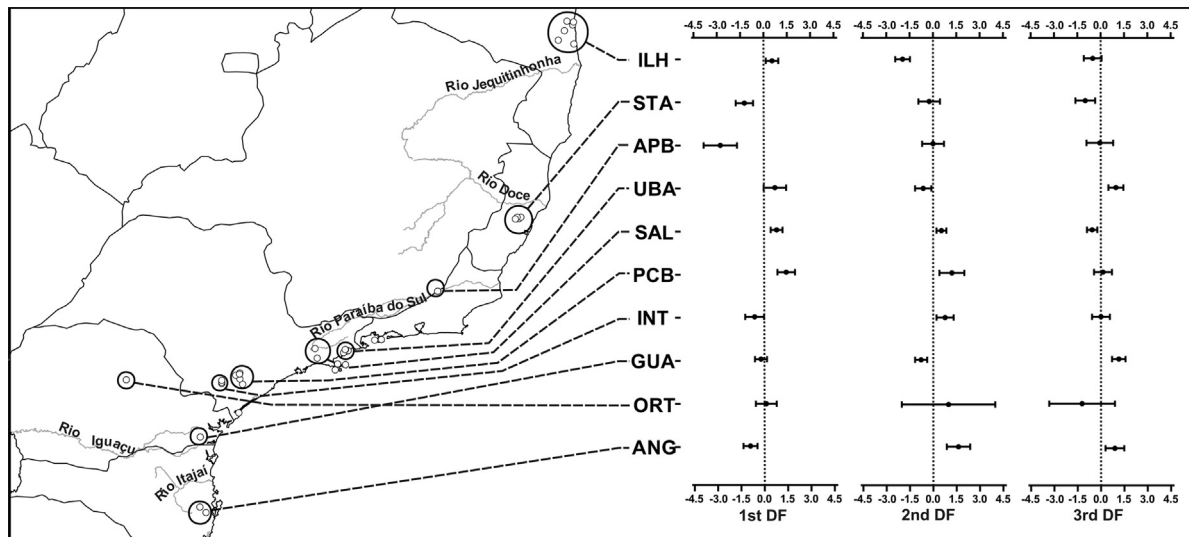
Clinal pattern of variation was found in the northern section of the continental transect (Fig. 3) from Ilhéus to Além Paraíba, in nine of the 14 characters (TL, LD, LIF, BIF, BR, NL, ZB, CZL, and LOF). For some variables, like TL, NL, CZL, and LOF, this trend of clinal variation also reaches the Ubatuba sample; samples increase in size from north to south direction. On the other hand, an inverse clinal pattern is present uniquely in BZP (Fig. 3).

From Ubatuba towards Angelina, the southernmost sample, the variation pattern is different and more complex. The samples mean values generally present a mosaic variation through this section of transect without clear and sharp differences among them, with the exception of the discontinuity between Guaricana and Ortigueira. The Dice-Leraas diagrams show significant differences between both samples for seven (TL, LPB, CZL, LD, IOB, BZP, LOF) of

14 variables, with Ortigueira presenting higher mean values than Guaricana. This pattern is also observed in three other variables (Fig. 3), but with overlapping confidence intervals (LIF, BM1, NL).

A similar pattern of variation can be visualized on the first and second principal components of the PCA realized previously (Fig. 4), showing that both axis of size and form expressed in the univariate space are recoverable at the multivariate one. The first function of the DA shows that the differences among groups are related mostly to the BZP in a positive direction, and to the LIF and ZB in the opposite way. The second function presents higher positive scores for ZB and CZL, while BIF and LOF have the lowest ones (see Table 3 for more details).

The interpopulational differences among samples can be visualized in the scatterplots of the first three discriminant functions (Fig. 5). The individual scores of first discriminant function regarding the three northernmost samples (Ilhéus, Santa Teresa and Além



**Fig. 6.** Distribution of continental samples and the Dice-Leraas diagrams elaborated with the individual scores of the three first discriminant functions of the discriminant analysis over the continental samples. The black spots represent the means; the bars represent the 95% confidence intervals. Acronyms for samples are explained in Table 1.

**Table 2**  
Normalized scores for the three first principal components of the PCA conducted using the data of all samples, excluding Ilha dos Búzios and Ilha Grande. The bold values are the ones presenting more weight in the component.

	1	2	3
TL	<b>0.293</b>	0.087	-0.022
LD	<b>0.372</b>	-0.027	-0.063
LTR	0.072	0.117	0.049
BM1	0.057	0.070	0.125
LIF	<b>0.347</b>	<b>-0.337</b>	<b>-0.241</b>
BIF	<b>0.305</b>	<b>-0.727</b>	-0.004
BR	<b>0.244</b>	-0.127	<b>0.555</b>
NL	<b>0.370</b>	0.107	<b>-0.215</b>
LPB	<b>0.223</b>	<b>0.280</b>	<b>0.318</b>
IOB	0.108	0.077	<b>0.559</b>
ZB	<b>0.237</b>	0.073	0.107
BZP	<b>0.334</b>	<b>0.527</b>	<b>-0.273</b>
CZL	<b>0.282</b>	0.070	0.004
LOF	<b>0.251</b>	0.070	-0.067

Paraíba) are distributed in three clouds of points with some overlap along the left margin of the multivariate space; these three samples are scattered along the second discriminant function, arranged in a pattern recovering the cline observed in univariate analysis. Nearly all-remaining samples present more dispersed distributions, highly

overlapped throughout first and second discriminant function. The graph also reveals that samples from the north of the Rio Paraíba do Sul are scattered on the left portion of the cloud, whereas the southern samples are spread from the middle to the right, with the exception of the Guaricana sample, which is overlapped to all samples.

The Dice-Leraas diagrams (Fig. 6) employing the three first discriminant functions show a clear separation of samples in three groups of variation on first DF (north group, north of Rio Paraíba do Sul, from Ilhéus to Além Paraíba; central group, from Ubatuba to Carlos Botelho; and southern group, from Intervales to Angelina); on the second DF, there is cline from Ilhéus to Angelina, except for the samples of Ubatuba and Guaricana; and, the third DF exhibits with a similar general clinal pattern as to the second DF, although with a break between Ubatuba and Salesópolis, and with Ortigueira apart from the general pattern.

The performed UPGMA cluster analysis (Fig. 7) shows the westernmost sample of Ortigueira is very distant from the others, while Santa Teresa and Além Paraíba samples are more similar among them and separated from all other samples including Ilhéus. Ilhéus is grouped to Guaricana, Ubatuba, Intervales and Salesópolis samples, which present smaller mean values compared to the southern samples of Carlos Botelho and Angelina (Figs. 3 and 4).

**Table 3**  
Functions of the discriminant analysis using only the continental samples. The bold values are the ones presenting more weight in each of the first three canonical functions. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

	1	2	3	4	5	6	7	8	9
TL	-0.482	-0.285	0.122	-0.239	-1.041	1.446	1.479	-2.605	-1.234
LD	0.047	-0.231	0.081	1.680	-0.183	-0.390	-0.828	0.620	-0.129
LTR	0.341	0.279	0.395	0.664	-0.265	-0.603	0.659	0.120	0.087
BM1	0.191	0.313	-0.051	0.361	0.083	0.428	-0.704	-0.123	0.199
LIF	<b>-0.870</b>	0.494	-0.489	-0.094	-0.220	0.627	0.358	0.235	0.554
BIF	-0.161	<b>-0.722</b>	0.245	0.020	-0.054	0.171	0.410	0.023	-0.295
BR	-0.018	0.052	0.332	0.286	0.975	-0.490	0.161	-0.157	0.210
NL	0.321	0.057	<b>0.975</b>	-0.059	0.238	-0.090	-0.516	-0.329	0.591
LPB	-0.024	-0.358	<b>-0.795</b>	-0.107	0.284	0.400	0.194	-0.294	0.102
IOB	0.006	0.284	0.193	-0.390	0.026	0.492	0.149	0.509	0.173
ZB	<b>-0.639</b>	<b>0.735</b>	<b>-0.840</b>	0.018	0.015	-0.278	-0.110	-0.022	0.006
BZP	<b>0.792</b>	0.124	-0.526	-0.001	0.041	0.416	0.382	0.415	0.056
CZL	0.118	<b>0.783</b>	0.249	-1.621	0.497	-1.009	-1.122	1.695	-0.963
LOF	0.468	<b>-0.880</b>	0.124	0.007	-0.257	-0.637	-0.195	-0.001	1.223
Eigenvalue	1.256	1.124	0.588	0.353	0.304	0.223	0.105	0.064	0.031
% of Variance	31.0	27.8	14.5	8.7	7.5	5.5	2.6	1.6	0.8
Wilks' $\lambda$	0.050***	0.113***	0.241***	0.382***	0.517**	0.675**	0.825	0.912	0.970

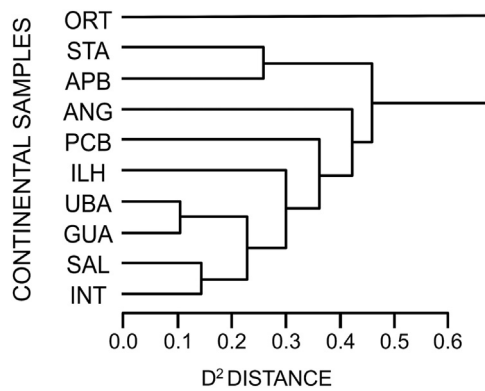


Fig. 7. Dendrogram based on the  $D^2$  Mahalanobis' distances among the continental samples using the UPGMA method. Acronyms for samples are explained in Table 1.

The Mantel's test using all continental samples was not significant ( $p = 0.175$ ), which means the isolation-by-distance model (Wright, 1943) does not explain the phenetic distances (De Queiroz and Good, 1997; Moreira and Oliveira, 2011) for *E. russatus*. However, the correlations between GEOPC1 and the variables showed that almost all measurements are negatively correlated. Furthermore, some of them presented significant correlation (TL, BM1, NL, IOB, BZP, and CZL) (Fig. 8). This result suggests that there is relationship between the variation of some measurements and the distribution of the samples, because the general size of these variables increases as the latitude follows the southern direction.

### 3.2. Insular variation

The insular samples analyzed showed different morphometric patterns when compared to their closest continental samples. The main univariate patterns exhibited by the insular samples in comparison to the closest continent samples are resumed graphically in Dice-Leraas diagrams comparing Ilha de São Sebastião and Ilha do Cardoso (Fig. 9): the confidence intervals of the Ilha de São Sebastião slightly (or do not) overlap the continental samples, while the sample of Ilha do Cardoso presents confidence intervals overlapped to continental samples.

The ratio diagrams clearly show that samples from Ilha de São Sebastião (Fig. 10a) and Ilha de Búzios (Fig. 10b) present higher mean values than near continental samples, Salesópolis and Ubatuba, for most cranial variables (TL, LD, LTR, LIF, BIF, NL, LPB, IOB, BZP, CZL, LOF), except for the breadth of M1 (in both samples) and for the breadth of rostrum (in Ilha de Búzios), but a similar trend is also observed in Ilha de São Sebastião) and zygomatic breadth (in Ilha de Búzios). Mann-Whitney tests indicate that most of these variables were statistically significant, further evidencing differences among samples. These ratio diagrams evidences that skulls from these two islands are proportionately larger than continental samples, except for the ZB.

However, another insular sample, Ilha do Cardoso, shows a variation pattern indistinct from continental samples, Intervaes and Parque Carlos Botelho (Fig. 10c). Ratio diagram evidences only small proportionate differentiation among the three samples, except for breadth of M1 and breadth of rostrum, in which the sample of Parque Carlos Botelho is significantly larger than Ilha do Cardoso and Intervaes; on the contrary, the length of incisive foramina is smaller in both continental samples. Few differences were also observed in the ratio diagram between Ilha Grande and Ubatuba (Fig. 10d). No statistical tests were conducted comparing Ilha Grande sample to Ubatuba, because of small size with several missing values of the former sample.

The results of the DA performed using these two insular samples and the closest continental ones are described in Table 4. The scatterplots (Fig. 11) revealed that the groups are overlapped in the multivariate space, with the Ilha de São Sebastião sample remaining somewhat separated from Ubatuba and Salesópolis, mainly through the combined axis of the first and second discriminant functions, while Ilha do Cardoso sample overlaps the Intervaes and Parque Carlos Botelho samples in any of the three functions. When plotted in Dice-Leraas diagrams, the differences among Ilha de São Sebastião and Ubatuba, and between Ilha de São Sebastião and Salesópolis are better visualized in first (TL, LTR and BM1) and second (TL, LIF, NL, CZL, and LOF) functions, while the sample of Ilha do Cardoso only differs from Parque Carlos Botelho at the first function (Fig. 12).

## 4. Discussion

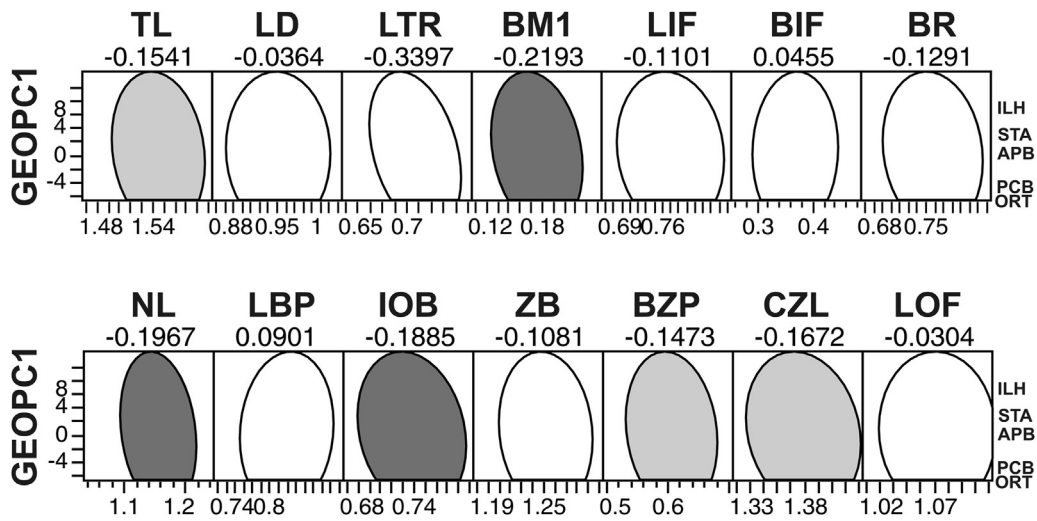
Our results suggest the existence of sharp morphometric discontinuities associated to geography in *E. russatus*: some discontinuities are partially concordant with the pattern of variation described by Miranda et al. (2007) for the molecular marker, with the Rio Paraíba do Sul as a possible area of isolation between populations. Besides, some gaps and patterns are firstly described here for this species, as the variation associated to the latitudinal distribution of samples, as well as the variation associated to samples from some continental islands. Further, we compare the patterns of variation encountered in *E. russatus* to patterns of variation described elsewhere for other groups of continental and insular species.

### 4.1. Continental populations

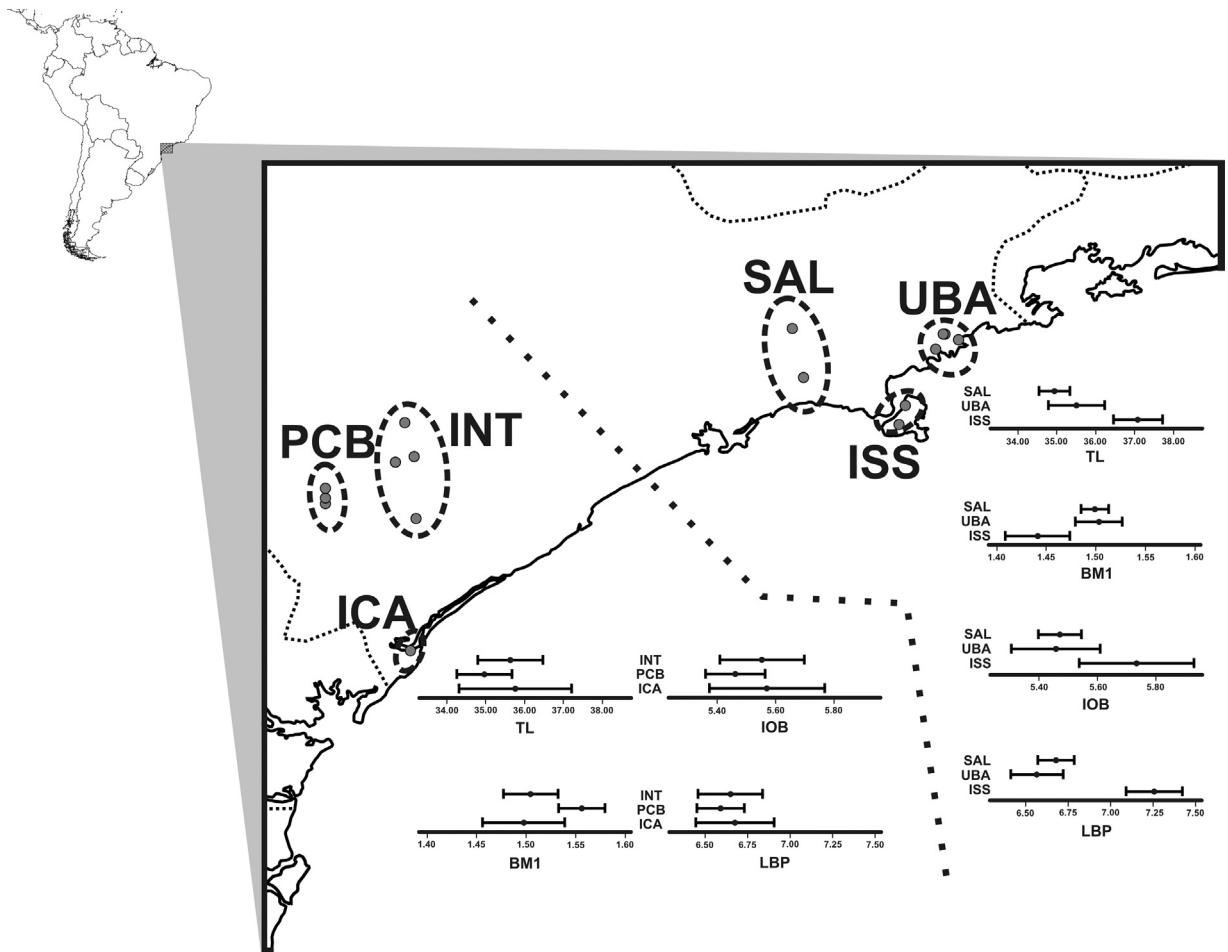
The observed gradual pattern of decrease in size amongst the northern samples (Figs. 3, 4 and 6) is broken somewhere between Além Paraíba and Ubatuba, a region that is coincident with the topology recovered by Miranda et al. (2007). The establishment of a clinal pattern could occur due to many reasons, as the introgression among previously isolated populations or the geographic variation on selective pressures (Futuyma, 2002). This pattern is commonly expressed in continental species and can be understood as a product of the interaction of the selection force and the gene flow (Mayr, 1963).

The geographic distribution of adequate continental samples (i.e., with a minimum size that allow their inclusion on statistical analysis) are uneven through its range, presenting large sampling gaps to the north of the Rio Paraíba do Sul; considering the floristic and physiognomic similarity through this region, the absence of samples is probably a sampling artifact. Artifact or not, Moreira and Oliveira (2011) considered that sampling gaps could mislead the Mantel's tests. In fact, the correlations among measurements and geographic component (Fig. 8) showed that the relationship between geography and continental variation might be more complex. Most of the significant correlations occurred in variables with important contribution on the size axis of the multivariate analysis, while just one of the variables that contributed to the second component did so (see Table 2). We understand that most of the geographic variation is related to general size of skull than to its shape. Besides, according to the ellipses and to the observed negative values of the correlations in Fig. 8, the general size increases with the latitude, as can be viewed in the variables' means (Fig. 3) and in the PC1 (Fig. 4). Furthermore, this clinal variation is not linear from north to south and presents sharp interruptions in the pattern (see Figs. 4 and 6), suggesting that other factors than the just the temperature latitudinal gradient could explain such variation.





**Fig. 8.** Matrix of correlations between the geographic component (GEOPC1) and each variable. The numbers just below the variables names are the correlation values. The ellipses represent the 95% CI of the distribution. White ellipses mean the correlation was not significant; light and dark gray mean it was significant ( $P < 0.05$  and  $P < 0.01$ , respectively). Acronyms for samples are explained in Table 1.

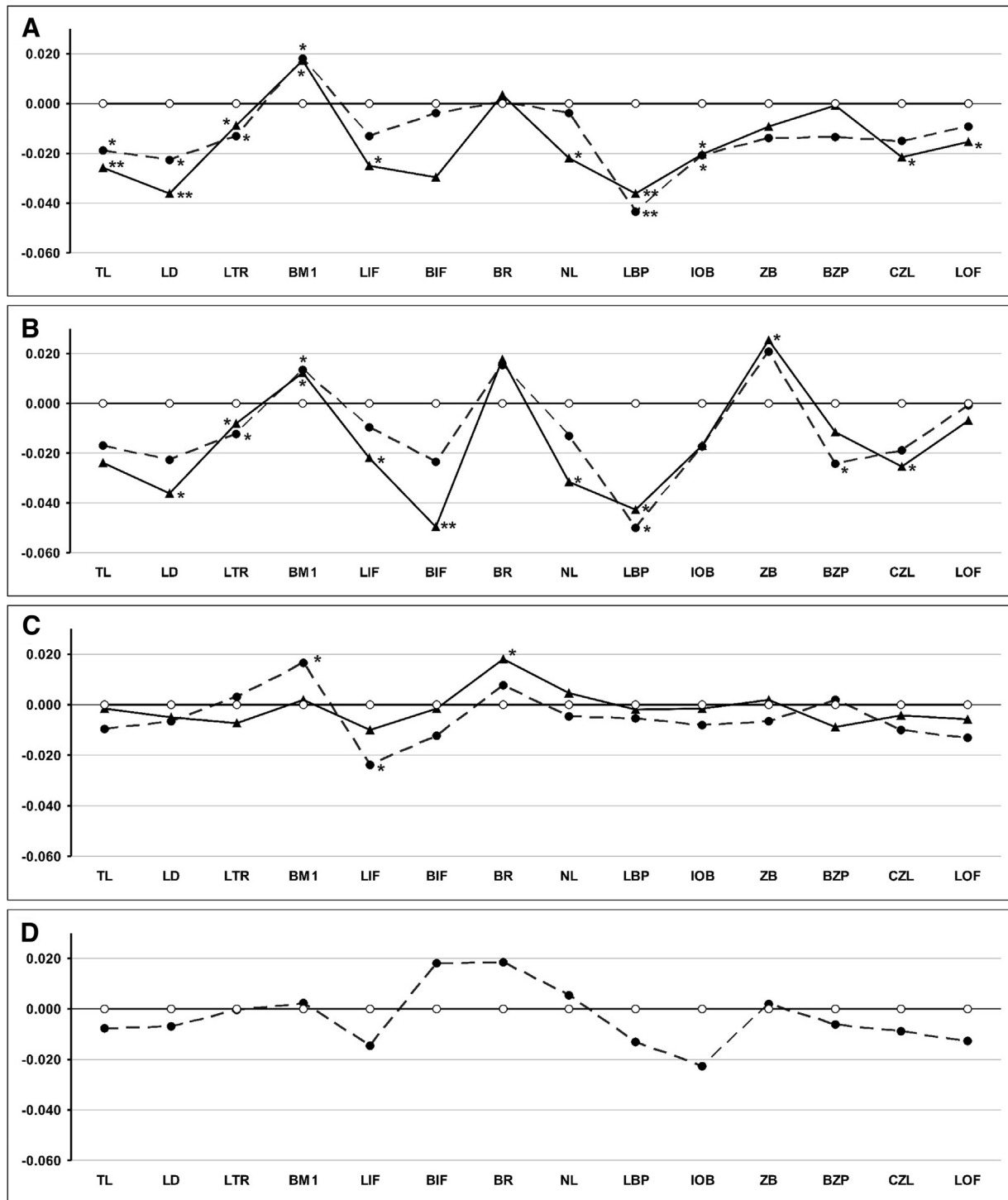


**Fig. 9.** Dice-Leraas diagrams of some of the original cranial measurements (TL, BM1, IOB, LBP) for the insular samples of Ilha de São Sebastião and Ilha do Cardoso samples and their closest continental ones. The black spots represent the means; the bars represent the 95% confidence intervals. Acronyms for samples are explained in Table 1.

It is noteworthy that the gaps that occur between close samples (like the ones between the pairs Guaricana and Ortuera, Além Paraíba and Ubatuba, and Intervalos and Parque Carlos Botelho; Figs. 3, 4, and 6) were recovered in the phenetic dendrogram (Fig. 7). These three pairs of samples, although geographically close, present

enough morphometric distance to remain in separated positions of the dendrogram rather than in nearby positions.

A closer look to this phenetic pattern reveals one striking similarity to the phylogeographic relationships recovered in the study of Miranda et al. (2007). The division between their Northern Atlantic



**Fig. 10.** Ratio diagram showing the mean values for an insular sample, normalized as zero [white circles and continuous line for Ilha de São Sebastião (a), Ilha de Búzios (b), Ilha do Cardoso (c), Ilha Grande (d)], and the mean values for the nearest continental samples [black circles and dashed line for Ubatuba (a, b and d), Intervaes (c); black triangles and continuous line for Salesópolis (a and b); Parque Carlos Botelho (c)]. The “\*\*\*” indicates significant differences between the insular and continental samples, performed with Mann-Whitney tests ( $P < 0.05$ ).

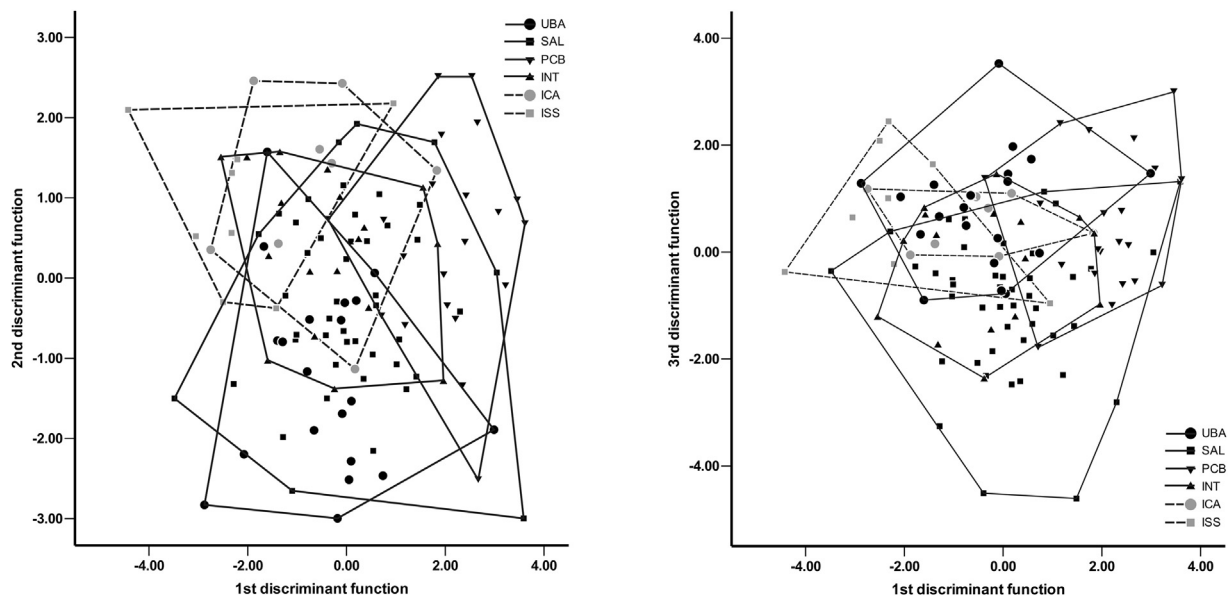
Forest group occurs in the same geographic region to the gap we found between Além Paraíba (north of Rio Paraíba do Sul) and Ubatuba (south of Rio Paraíba do Sul). Unfortunately, [Miranda et al. \(2007\)](#) presents no sampling in the continent from the region just south of Rio Paraíba do Sul to Angelina (their named Florianópolis, locality 17), neither from western regions, as Ortigueira, precluding further comparisons to our results.

Nevertheless, we consider the discontinuities we detected, as the one between Guaricana (which is more similar to samples from northeast São Paulo State) and Ortigueira (our westernmost and more distinctive sample), and the other between Intervaes (more similar to northeast São Paulo State samples) and Parque Carlos Botelho (more similar to Angelina), may be related to the limits between two different populations or lineages, as is the case at Rio Paraíba do Sul valley. Further studies looking these areas should

**Table 4**

Functions of the discriminant analysis using only the UBA, SAL, ISS, PCB, INT e ICA samples. The bold values are the ones presenting more weight in each of the first three canonical functions. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

	1	2	3	4	5
TL	<b>-1.453</b>	<b>1.007</b>	<b>1.682</b>	-1.565	1.095
LD	<b>1.290</b>	0.132	<b>0.946</b>	0.575	0.218
LTR	<b>0.815</b>	0.361	0.496	0.508	-0.012
BM1	0.662	-0.055	0.121	-0.172	0.020
LIF	-0.593	<b>1.084</b>	-0.230	-0.214	-0.687
BIF	-0.120	-0.157	0.429	-0.099	0.075
BR	0.487	-0.263	-0.591	-0.591	0.259
NL	0.319	<b>-0.869</b>	0.427	0.002	0.256
LPB	-0.676	0.146	-0.614	0.300	0.677
IOB	-0.161	0.338	0.160	0.197	-0.164
ZB	0.058	0.667	<b>-0.955</b>	-0.454	-0.247
BZP	0.534	0.525	-0.432	0.525	-0.206
CZL	-0.552	<b>-0.831</b>	<b>-1.068</b>	0.637	-0.633
LOF	0.089	<b>-1.176</b>	-0.222	0.570	-0.517
Eigenvalue	1.546	0.726	0.652	0.259	0.099
% of Variance	47.1	22.1	19.9	7.9	3.0
Wilks' $\lambda$	0.100***	0.254***	0.438**	0.723	0.910



**Fig. 11.** Scatterplot of the individual scores of the first and second (left) and first and third (right) discriminant functions obtained from the discriminant analysis over the insular samples and their closest continental ones. The polygons connect external points of each geographic sample. Acronyms for samples are explained in Table 1.

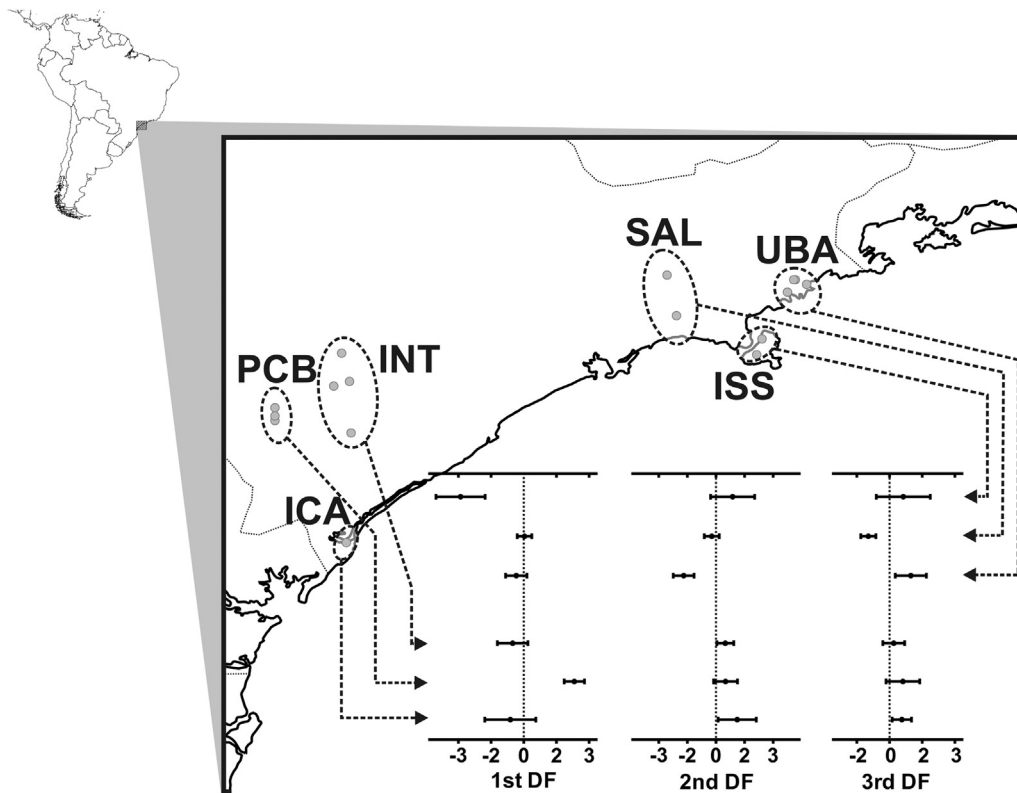
help in testing the consistency of these gaps and their role on the phylogeography of the species.

Which alternative explanations could be established to address this variability? One plausible would be the riverine barrier hypothesis, which recognizes the river systems as natural barriers to the gene flow between populations that could lead to divergence between them and even generate new species if the appropriate time of isolation is given (Wallace, 1852; Ayres and Clutton-Brock, 1992; Patton et al., 2000; Lara et al., 2005). The region of Rio Paraíba do Sul is one of the most investigated barriers to the gene flow or limits to regional faunas of eastern Brazil (Lara et al., 2005; see Costa and Leite, 2012). Recent studies are enhancing the knowledge on the role of this coastal river on Atlantic Forest biogeography. Pellegrino et al. (2005) has noticed genetic divergence between the populations of the lizard *Gymnodactylus darwini* (Gray, 1845) of each margin of Rio Paraíba do Sul. DaSilva and Pinto-da-Rocha (2011) defined many endemism regions for Opiliones species (Arachnida) in Atlantic Forest, and observed that the Paraíba do Sul valley acts as a breaking point between the northern and southern Atlantic Forest faunas. The presence of a river delta associated to the mouth of the Rio Paraíba do Sul during Quater-

nary may account as its role on separating populations along the Atlantic Forest (Suguio, 2010).

Another river also played some role on geographic variation or species diversification on Atlantic Forest small mammal fauna: the Rio São Francisco apparently also represents an area of faunal limits for other species of some oryzomyine rodents, *Cerradomys vivoi* (Percequillo et al., 2008) and *Cerradomys langguthi* (Percequillo et al., 2008) and for *Hylaeamys seunaezi* (Weksler et al., 1999) and *Hylaeamys oniscus* (Thomas, 1904) as well (see Percequillo et al., 2008; Weksler and Percequillo, 2011; Brennand et al., 2013; Percequillo, 2015b).

Besides the riverine barrier hypotheses, climatic changes could have acted to promote the morphometric differentiation of the *E. russatus* populations. As stressed earlier, *E. russatus* is a sensitive species, negatively affected by the fragmentation process in southeastern Atlantic Rainforest, favoring continuous disturbed or undisturbed humid forests rather than small or medium sized undisturbed forests (Umetsu and Pardini, 2007; Umetsu et al., 2008) and presents limited dispersion rate due to small and restrict home ranges (Bergallo and Magnusson, 2004). Several studies reporting the Holocene climatic changes in São Paulo, Minas Gerais,



**Fig. 12.** Distribution of samples and the Dice-Leraas diagrams elaborated with the individual scores of the three first discriminant functions of the discriminant analysis over the insular and their closest continental samples. The black spots represent the means; the bars represent the 95% confidence intervals. Acronyms for samples are explained in Table 1.

and Paraná States point that from 11,000–8,500 years BP the climate was drier than today and the open formations expanded; the present humidity conditions were settled between 5,000–2,000 years BP, and the semideciduous forests and “*cerradão*” (fragments of semideciduous forests inside the savanna-like Cerrado biome) formations returned (Melo et al., 2003; Scheel-Ybert et al., 2003; Pessenda et al., 2004). Considering the sensitiveness of *E. russatus* due to habitat loss and its small home ranges, it is reasonable to predict that climatic changes during the Holocene (and before) could have isolated during thousands of years the populations that are now close one another.

As discussed, there are many hypotheses that had been raised to explain the biogeographic patterns in the Atlantic Forest and could be related to the variation patterns encountered in *E. russatus*, though it is not possible to pinpoint which of them had taken a main role of the process. Lara et al. (2005) argues that, at large scale, as the Atlantic Forest rivers correspond to the breaks between mountain ranges, it is difficult to relate the divergence encountered to the riverine barriers. In fact, the past climatic changes influencing both vegetation changes (Por, 1992; Vivo de and Carmignotto, 2004) and marine transgression events (Suguio and Sallun 2004; Suguio, 2010) have certainly acted together with the distinct orographic patterns of the “mountain systems of Eastern Brazil” (Por, 1992), developing patterns of endemism and genetic divergence of the Atlantic Forest biota, which had been noticed by Müller (1973), Prance (1982) and Amorim and Pires (1996).

Despite the difficulty of assigning the origin of the continental variation patterns of *E. russatus* to specific factors, they find congruence to recent investigations on vertebrate diversification patterns of the Atlantic Forest (for a more detailed and updated review see Costa and Leite, 2012) and partially recover the results of Miranda et al. (2007) on the species phylogeography, with a northern clade

separated from a southern clade by the Rio Paraíba do Sul, and a southernmost clade, formed by samples from Rio Grande do Sul state (a geographic region we did not assess here).

#### 4.2. Island populations

Our results showed that the insular samples from Ilha de São Sebastião and Ilha de Búzios presented important differences in size, when compared to the continental populations. Specimens from both insular samples present larger and more robust skulls, longer incisive foramina and bony palate, and narrower upper molar rows than continental samples (Figs. 10 a,b, 11, and 12). On the other hand, such noticeable differences were not encountered between Ilha do Cardoso and continental populations (Figs. 10 c, 11 and 12). The small sample size of Ilha Grande did not allow more robust comparisons to continental populations.

Interestingly, Ilha de São Sebastião presents an additional case of remarkable variation in size for another rodent species. Ihering (1897) described *Phyllomys thomasi* (Ihering, 1897) as a large form of the genus. In recent taxonomic revisions of the genus, Emmons et al. (2002) and Leite (2003) stated that *P. thomasi* is morphologically close to *Phyllomys nigrispinus* (Wagner, 1842) a continental species, and the main difference between these two taxa is the noticeable larger size of the insular species; poor sampling of *P. thomasi* avoided its inclusion in the molecular phylogeny of the genus and, therefore, any investigation on the evolutionary relationships of these species (Leite, 2003). Such changes in size (in *E. russatus* and *P. thomasi*) agree with the Foster’s Rule, where small mammals would develop increment in overall size in an isolated island population (Foster, 1964; Case, 1978). Remarkably, Ilha de São Sebastião exhibits less diverse mammal and bird faunas than

continental areas and misses the species of the mammalian orders Perissodactyla, Artiodactyla and Lagomorpha (Olmos, 1996).

In the study of Miranda et al. (2007), the sample of Ilha de São Sebastião (their Ilhabela, locality 14) is close related to Angelina (their Florianópolis, locality 17), but the absence of samples from the continent near the island precludes any attempt of comparisons to our study, although both samples present higher mean values for many variables (see Appendix B).

In the case of Ilha do Cardoso, although the island presents many different vegetational formations (São Paulo, 1998) there is no endemism registered of birds and land mammals and its faunal composition is close to the continent (Bernardo, 2004; Galetti et al., 2009). The vespertilionid bat *Lasiurus eburnus* Fazzolari-Corrêa (1994) is endemic to Ilha do Cardoso, but this species is known only from its holotype (Simmons, 2005; Gardner and Handley, 2007), and its endemism should be better studied.

These islands present complete different geological histories. Ilha de São Sebastião and Ilha dos Búzios have 335.93 km<sup>2</sup> and 7.55 km<sup>2</sup> of area, respectively (Ângelo, 1989), and were formed by a deformation of the Serra do Mar shield that begun in Paleocene (ca. 60 million years BP; Almeida and Carneiro, 1998). The continental coast passed by an erosive process since this period, and the geologic formation of the island reduced the effect of this process around its area, generating a depression between the Serra do Mar and the hills of the island (Almeida and Carneiro, 1998; Alves and Gomes, 2001). As a consequence, the channel between the continent and the Ilha de São Sebastião is deeper near the insular coastline: its depth varies from less than 20 m to more than 50 m, and it ranges from 2,000 m to 9,000 m in width to the continent, clearly separated from the coastal sand plains (Ihering, 1897; Kvinge, 1967). Considering studies in southern Brazilian coast (Suguio and Sallun, 2004; Suguio, 2010) we can assume that Ilha de São Sebastião became isolated from the continent as it is today in two moments in the last 32,000 years: in an interval extending from 32,000 to 22,000 years BP, and from about 6,000 years BP until nowadays.

The Ilha do Cardoso is a small island, with 30 km long and 10 km on maximum width, at least 100 m distant from continent (São Paulo, 1998) and has 225 km<sup>2</sup> of area (Ângelo, 1989). Most of the island is a flat coastal sand plain. The island is located in the Cananéia-Iguape Estuarine System, which drains the waters from Rio Ribeira do Iguape. This system is constituted of many small sandy islands separated by several rivers and lagoon channels (Tessler and Souza, 1998), with typical mangrove vegetation. The formation of this system is related to marine regression and transgression events, sediment deposits and lagoon formations since the Pleistocene, 120,000 years ago (see Tessler and Souza, 1998; Suguio 2010).

Ilha Grande is located at Baía de Ilha Grande, Rio de Janeiro state (Gama et al., 2009), and measures 12 km north-south and 28 km east-west, with an area of 193 km<sup>2</sup> (Alho et al., 2002). The origin and geological evolution of Ilha Grande is similar to that described above for Ilha de São Sebastião, including the processes of isolation by the sea transgression (see Gama et al., 2009 for a more detailed revision). As reported for Ilha de São Sebastião (Olmos, 1996), Ilha Grande misses large mammalian orders (for a complete revision of the island fauna see Rocha et al., 2009). Although the mean values of the morphometric variables are similar to those found in the continental samples, the inconsistency of the variation of the Ilha Grande sample obscures any further discussion about its origins and relations between the island and the continent. As occurs in most islands (and throughout the continental samples of *E. russatus* as well) samples size in Ilha Grande is small (n = 4), precluding more detailed comparisons beyond the simple mean, which is far from being a consistent representation of the variation, mainly in small samples (Simpson et al., 2003; Vanzolini, 1993).

The repeated occurrence of contact between populations should diminish the effectiveness of the isolation of the island (Mayr, 1963). Considering the recent history of the islands mentioned in this study, the gene flow between insular and continental populations should had been facilitated by climatic and sea level changes. In the case of Ilha do Cardoso, the contact may had been easier and more frequent, considering the dynamic geomorphologic processes of the region (see Tessler and Souza, 1998). Thus, the morphometric differentiation of Ilha de São Sebastião and Ilha dos Búzios could be due to other processes than solely the isolation by the sea or recent Quaternary events of climatic changes.

A better sampling, along with molecular approaches, could bring valuable information about the relations of insular populations – not only from Ilha Grande, but from every island – and their continental counterparts, in order to enlighten the understanding of how the dynamics of isolation and gene flow work through the different kinds of islands, like the ones of the southeastern Brazilian coast.

## 5. Conclusions

By studying the craniodental morphology of *E. russatus*, we detected geographical structure on variation that is in agreement with phylogeographic studies that dealt with the species, and also with other taxa that present distribution related to the Atlantic Forest of eastern Brazil. Cases of taxa that present congruence on morphological and genetic variation provide very important information that allows us to develop a more integrative perspective on the variation and the level at what it occurs. Moreover, such congruence further indicates that detailed studies on geographic variation of phenotypic traits represent a valuable and sensitive tool to recover historical patterns. Besides, our study shows that morphometric studies offer a view on how the differentiation among populations are expressed on the phenotype, allowing us to construct a better perspective over the variation of the species and to generate stronger hypothesis on the evolutionary and biogeographic process that acted and could still be presently operating through the Atlantic Forest.

## Acknowledgements

First we are grateful for the curators and staff that allowed us to visit the mammalian collections and shared valuable information of the specimens examined. We would like to thank Mario de Vivo, Erika Hingst-Zaher, Gabriel Marroig, and Edson F. Abreu-Junior who kindly read earlier versions of the manuscript and made valuable suggestions to improve our analyses and discussion. We also thank the editor Alexander Kupfer and two other anonymous reviewers for important improvements in the article. Financial support was provided by Programa de Bolsas de Iniciação Científica do Santander (GSL), PIBIC-CNPq (GSL, proc. 100213/2009-0), FAPESP (ARP, proc. 09/16009-1) and CNPq (ARP, proc. 305164/2011-2 and 476249/2008-2), as well as grants from The American Museum of Natural History, The Field Museum, United States National Museum, and Museum of Comparative Zoology.

## Appendix A. – Specimens Examined

**BRAZIL: BAHIA:** Buerarema, Ribeirão da Fortuna: MN 9278, 9397, 9404, 9525; Ilhéus, Aritaguá, Urucutuca: MN 9018, 9093, 9099, 9104, 9119, 9197, 9307, 9514, 9520; Ilhéus, Banco da Vitória, Pirataquise: MN 9017, 9077, 9283; Ilhéus, Rio do Braço, Almada: MN 9273, 9467, 9497, 9572; Jussari, Serra do Teimoso: MZUSP 29597, 29599, 29635, 29690, 29740, 29741, 29743, 29773; Una, ESCAN: UFMG 34. **ESPÍRITO SANTO:** Santa Teresa: MN 32803,

32804, 32805, 32821, 32822; Santa Teresa, Est. Biológica de Santa Lúcia, 8.2 Km. L de S.T.: MN 35891, 35892; Santa Teresa, Goipapoçu (Goipaba-açu): MN 32808, 32811, 32817; Santa Teresa, Mata da Caixa d'Água, 1.7 Km. W de S. Teresa: MN 5484, 32810, 32826, 32827, 35905, 35908; Santa Teresa, Reserva Florestal de Nova Lombardia: MN 32774, 32785, 32794, 32797, 36766. **MINAS GERAIS:** Além Paraíba, Faz. Paraíso: MN 7358, 7470, 11641, 11644, 32731, 32732; Além Paraíba, Faz. São Geraldo: MN 7334, 7420, 7423, 7439, 7489, 32714, 32716, 32721, 32722, 32724, 32725, 32726, 32728, 32729, 32730; MZUSP 20571. **PARANÁ:** Guaricana, São José dos Pinhais: MHNCI 1314, 1324, 1326, 1328, 1332, 1342, 1344, 1356, 1359, 1361, 1395, 1400, 1406, 1408, 1417, 1419, 1420, 1443, 1450, 1455, 1456, 1474, 1477, 1480; Ortigueira: MZUSP 31620, 31629, 31660, 31661, 31662, 31664, 31666, 31667, 31668, 31690. **RIO DE JANEIRO:** Angra dos Reis, Ilha Grande, Praia Vermelha: MN 24373, 24375, 24390; Ilha Grande, 1 km Oeste de Abraão: MN 31033. **SANTA CATARINA:** Angelina, Barragem do Garcia: LABMAQ 640; Parque Estadual da Serra do Tabuleiro, Caldas da Imperatriz: LABMAQ 712, 713, 714, 717, 718, 719, 720, 729. **SÃO PAULO:** Boracéia: MAMustrangi 390, 391, 394, 419, 438, 444, 456; MZUSP 9581, 10169, 10170, 10171, 10422, 10722, 10724, 10818, 10942, 11010, 11013, 11028, 11038, 11161, 20540, 20542, 23937, 23950, 23951, 23955, 23956, 25400, 25676, 27469, 28369; Casa Grande (includes Casa Grande, Salesópolis and Casa Grande, Biritiba-Mirim): MN 32448; MZUSP 10726, 10728, 11431, 21883, 22807, 27413; UFMG 67, 68, 70, 113, 114, 172; Faz. Intervalles, Carmo: MAMustrangi 3, 12, 261, 264, 286, 294, 295, 296, 324, 325; MZUSP 27277; Faz

Intervalles, Saibadela: MZUSP 27279, 27280, 27282, 27284, 27285, 27286; Faz. Intervalles, Sede: MZUSP 27283; Ilha dos Búzios: MZUSP 20546, 20547, 20548, 20549, 20551, 20553, 20557; Ilha do Cardoso: MZUSP 28356, 28373, 28376, 28377, 28384, 28390, 28392, 28393; Ilha de São Sebastião: MZUSP 59, 2091, 2092, 2093, 2147, 3205, 3206; Ilha de São Sebastião, Ilhabela, Fazenda da Toca: MAMustrangi 62; Parque Estadual Carlos Botelho, 840 m: MZUSP 32860, 33345, 33351, 33361, 33362, 33363, 33371, 33374, 33385, 33402, 33413, 33414; Parque Estadual Carlos Botelho, São Miguel Arcanjo, 820 m: MZUSP 33436, 33441, 33443, 33460; Parque Estadual Carlos Botelho, Varginha, 850 m: MZUSP 33447, 33448, 33449, 33450, 33452; Ubatuba: MN 5302; MZUSP 1841, 1842, 1843, 1844, 1894; Ubatuba, Cór. Cachoeira Grande: MN 11639, 32733, 32737; Ubatuba, Córrego do Cemitério: MN 5283, 5368, 32736, 32738; Ubatuba, Cór. Pipoca: MN 32734, 32739; Ubatuba, Estação Experimental: MN 5287, 5481; Ubatuba, Serra d'Água, Praia Dura: MN 24413, 24417, 24441.

## Appendix B. – Descriptive Statistics

See [Tables A1 and A2](#)

## Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jcz.2016.03.005>.

**Table A1**Descriptive statistics of the samples used in the geographic variation analyses, showing the sample size for the variable (upper left), the mean  $\pm$  standard deviation (upper right) and the minimum and maximum values (bottom).

	ILH	STA	APB	UBA	SAL	PCB	INT
TL	28 32.17–36.75 34.38 $\pm$ 1.29	17 34.10–37.22 35.26 $\pm$ 0.93	20 32.99–37.55 35.42 $\pm$ 1.08	20 31.65–37.65 35.51 $\pm$ 1.55	41 30.70–38.08 34.95 $\pm$ 1.26	21 31.57–37.89 34.97 $\pm$ 1.56	16 31.94–37.83 35.64 $\pm$ 1.58
LD	27 8.15–10.16 8.81 $\pm$ 0.45	20 8.18–10.22 9.04 $\pm$ 0.53	20 8.26–9.82 9.16 $\pm$ 0.37	19 7.66–10.06 9.09 $\pm$ 0.64	44 7.84–10.32 8.82 $\pm$ 0.46	20 8.18–10.36 8.97 $\pm$ 0.56	18 7.87–9.78 9.00 $\pm$ 0.53
LTR	26 4.66–5.15 4.93 $\pm$ 0.14	19 4.56–5.44 5.08 $\pm$ 0.22	20 4.63–5.49 5.02 $\pm$ 0.22	19 4.89–5.38 5.10 $\pm$ 0.14	44 4.91–5.46 5.15 $\pm$ 0.12	21 4.90–5.59 5.26 $\pm$ 0.18	17 4.84–5.36 5.14 $\pm$ 0.13
BM1	28 1.37–1.55 1.47 $\pm$ 0.05	21 1.36–1.63 1.50 $\pm$ 0.07	21 1.36–1.56 1.48 $\pm$ 0.06	20 1.39–1.60 1.50 $\pm$ 0.05	43 1.37–1.58 1.50 $\pm$ 0.05	21 1.48–1.67 1.56 $\pm$ 0.05	18 1.43–1.65 1.50 $\pm$ 0.06
LIF	27 5.17–6.25 5.66 $\pm$ 0.30	21 5.29–6.63 5.98 $\pm$ 0.28	22 5.75–6.90 6.31 $\pm$ 0.29	20 5.02–6.61 5.92 $\pm$ 0.42	45 4.96–6.54 5.76 $\pm$ 0.34	21 5.21–6.34 5.78 $\pm$ 0.31	18 5.18–6.46 5.97 $\pm$ 0.32
BIF	28 2.08–2.90 2.35 $\pm$ 0.17	21 1.97–2.77 2.36 $\pm$ 0.19	22 1.89–2.75 2.45 $\pm$ 0.21	19 2.10–2.64 2.38 $\pm$ 0.18	45 1.91–2.57 2.24 $\pm$ 0.13	21 1.98–2.69 2.29 $\pm$ 0.17	18 2.06–2.51 2.34 $\pm$ 0.12
BR	27 5.03–6.44 5.60 $\pm$ 0.33	19 4.90–6.17 5.59 $\pm$ 0.28	22 5.33–6.49 5.97 $\pm$ 0.30	19 5.20–6.45 5.74 $\pm$ 0.38	42 5.17–6.57 5.77 $\pm$ 0.28	16 5.34–6.17 5.69 $\pm$ 0.21	18 5.39–6.20 5.83 $\pm$ 0.24
NL	28 12.57–15.15 13.93 $\pm$ 0.70	19 12.51–15.11 14.09 $\pm$ 0.72	19 13.43–15.39 14.51 $\pm$ 0.56	19 12.98–16.69 14.80 $\pm$ 1.06	41 11.41–16.18 14.18 $\pm$ 0.79	21 12.59–15.64 14.32 $\pm$ 0.90	18 13.12–15.86 14.64 $\pm$ 0.86
LPB	28 5.58–7.35 6.67 $\pm$ 0.38	20 6.13–6.97 6.58 $\pm$ 0.27	22 5.87–7.33 6.60 $\pm$ 0.30	20 5.75–7.12 6.57 $\pm$ 0.33	45 5.76–7.52 6.68 $\pm$ 0.36	20 5.81–7.11 6.59 $\pm$ 0.30	18 6.03–7.30 6.65 $\pm$ 0.38
IOB	29 5.07–6.08 5.42 $\pm$ 0.23	21 5.04–5.71 5.37 $\pm$ 0.22	21 4.99–6.08 5.49 $\pm$ 0.28	20 5.02–6.09 5.46 $\pm$ 0.33	45 4.81–6.07 5.47 $\pm$ 0.25	21 5.06–5.89 5.46 $\pm$ 0.22	18 5.09–6.00 5.55 $\pm$ 0.29
ZB	24 15.74–18.42 17.35 $\pm$ 0.74	19 15.90–19.34 18.12 $\pm$ 0.75	16 17.41–19.20 18.22 $\pm$ 0.55	16 16.75–19.17 17.87 $\pm$ 0.76	37 16.96–19.19 18.05 $\pm$ 0.49	20 16.25–19.06 17.83 $\pm$ 0.66	18 16.90–19.69 18.18 $\pm$ 0.67
BZP	29 3.44–4.71 4.01 $\pm$ 0.30	21 3.33–4.54 3.98 $\pm$ 0.26	22 3.30–4.29 3.82 $\pm$ 0.25	20 3.70–4.56 4.01 $\pm$ 0.22	44 3.48–4.65 4.13 $\pm$ 0.24	20 3.59–4.86 4.23 $\pm$ 0.35	18 3.75–4.47 4.13 $\pm$ 0.23
CZL	27 21.71–25.58 23.36 $\pm$ 0.94	17 23.22–25.39 24.16 $\pm$ 0.64	21 22.45–26.09 24.13 $\pm$ 0.85	18 21.70–25.95 24.31 $\pm$ 1.17	42 21.50–26.20 23.94 $\pm$ 0.84	21 21.65–25.64 23.91 $\pm$ 1.02	16 21.72–26.17 24.23 $\pm$ 1.14
LOF	29 10.81–12.61 11.69 $\pm$ 0.41	21 10.76–12.81 11.86 $\pm$ 0.46	22 11.10–12.82 11.92 $\pm$ 0.48	20 10.72–12.67 12.00 $\pm$ 0.56	44 11.05–12.77 11.84 $\pm$ 0.41	21 10.67–12.45 11.63 $\pm$ 0.53	18 10.89–12.82 11.84 $\pm$ 0.52

**Table A2**Descriptive statistics of the samples used in the geographic variation analyses, showing the sample size for the variable (upper left), the mean  $\pm$  standard deviation (upper right) and the minimum and maximum values (bottom).

	GUA		ORT		ANG		ISS		ICA		IBU		IGD	
TL	22	34.50 $\pm$ 1.31 31.47–36.43	10	36.27 $\pm$ 0.97 35.05–38.16	9	35.56 $\pm$ 1.26 32.94–37.58	6	37.09 $\pm$ 0.60 36.37–37.73	8	35.77 $\pm$ 1.73 32.38–37.48	1	36.93	3	36.14 $\pm$ 1.72 34.56–37.98
LD	24	8.80 $\pm$ 0.47 7.80–9.60	10	9.34 $\pm$ 0.47 8.71–10.12	9	8.95 $\pm$ 0.43 8.36–9.72	8	9.58 $\pm$ 0.27 9.14–9.93	8	9.10 $\pm$ 0.56 8.03–9.77	7	9.58 $\pm$ 0.49 8.98–10.48	4	9.24 $\pm$ 0.35 8.85–9.71
LTR	24	5.10 $\pm$ 0.14 4.66–5.35	10	5.04 $\pm$ 0.16 4.83–5.37	9	5.09 $\pm$ 0.17 4.80–5.29	7	5.25 $\pm$ 0.11 5.11–5.39	8	5.22 $\pm$ 0.13 5.05–5.45	7	5.24 $\pm$ 0.11 5.10–5.45	4	5.10 $\pm$ 0.18 4.88–5.30
BM1	23	1.47 $\pm$ 0.05 1.33–1.61	10	1.52 $\pm$ 0.06 1.44–1.59	9	1.51 $\pm$ 0.03 1.48–1.56	8	1.44 $\pm$ 0.04 1.36–1.48	8	1.50 $\pm$ 0.05 1.45–1.56	7	1.46 $\pm$ 0.05 1.38–1.55	4	1.50 $\pm$ 0.05 1.44–1.55
LIF	24	5.90 $\pm$ 0.30 5.35–6.56	10	6.10 $\pm$ 0.32 5.49–6.63	9	6.01 $\pm$ 0.30 5.65–6.53	8	6.10 $\pm$ 0.27 5.65–6.44	8	6.11 $\pm$ 0.33 5.57–6.67	6	6.06 $\pm$ 0.28 5.63–6.48	4	6.13 $\pm$ 0.39 5.75–6.52
BIF	24	2.42 $\pm$ 0.12 2.22–2.71	10	2.34 $\pm$ 0.16 2.08–2.52	9	2.33 $\pm$ 0.17 2.52–2.73	8	2.40 $\pm$ 0.16 2.17–2.62	8	2.35 $\pm$ 0.18 2.15–2.66	7	2.51 $\pm$ 0.18 2.31–2.87	4	2.28 $\pm$ 0.20 2.05–2.53
BR	24	5.63 $\pm$ 0.26 5.13–6.20	5	5.57 $\pm$ 0.34 5.23–6.10	9	5.91 $\pm$ 0.28 5.67–6.51	7	5.72 $\pm$ 0.17 5.48–5.98	8	5.59 $\pm$ 0.19 5.29–5.86	3	5.54 $\pm$ 0.36 5.17–5.88	4	5.50 $\pm$ 0.34 5.29–6.01
NL	22	14.20 $\pm$ 0.88 12.70–16.05	10	14.65 $\pm$ 0.46 13.90–15.35	9	14.75 $\pm$ 0.92 12.68–15.92	8	14.92 $\pm$ 0.37 14.34–15.36	8	14.48 $\pm$ 1.06 12.14–15.55	6	15.25 $\pm$ 0.66 14.24–16.12	4	14.61 $\pm$ 0.50 14.16–15.19
LPB	24	6.40 $\pm$ 0.25 5.88–6.97	10	6.78 $\pm$ 0.19 6.44–7.03	9	6.45 $\pm$ 0.31 5.93–7.04	8	7.26 $\pm$ 0.20 6.91–7.55	8	6.68 $\pm$ 0.28 6.20–7.03	5	7.37 $\pm$ 0.15 7.16–7.53	4	6.77 $\pm$ 0.19 6.48–6.89
IOB	24	5.45 $\pm$ 0.21 5.06–6.02	10	5.64 $\pm$ 0.13 5.46–5.89	9	5.73 $\pm$ 0.21 5.51–6.16	8	5.73 $\pm$ 0.23 5.36–6.07	8	5.57 $\pm$ 0.24 5.26–5.93	7	5.69 $\pm$ 0.28 5.38–6.00	4	5.76 $\pm$ 0.36 5.39–6.26
ZB	24	17.45 $\pm$ 0.55 16.55–18.52	6	17.51 $\pm$ 0.81 16.81–18.73	9	18.17 $\pm$ 0.67 16.85–19.01	6	18.45 $\pm$ 0.65 17.42–19.11	8	18.10 $\pm$ 0.97 16.48–19.58	3	17.03 $\pm$ 0.72 16.23–17.62	2	17.79 $\pm$ 1.13 16.99–18.59
BZP	24	3.91 $\pm$ 0.24 3.30–4.35	10	4.29 $\pm$ 0.22 4.03–4.73	9	4.01 $\pm$ 0.25 3.58–4.43	8	4.14 $\pm$ 0.33 3.37–4.42	8	4.22 $\pm$ 0.28 3.64–4.52	7	4.24 $\pm$ 0.14 4.03–4.49	4	4.07 $\pm$ 0.27 3.89–4.47
CZL	24	23.61 $\pm$ 0.85 21.48–24.88	10	24.40 $\pm$ 0.62 23.44–25.64	9	24.45 $\pm$ 0.80 22.85–25.79	6	25.16 $\pm$ 0.40 24.58–25.75	8	24.47 $\pm$ 1.26 22.20–25.83	3	25.39 $\pm$ 1.11 24.67–26.67	3	24.82 $\pm$ 1.41 23.35–26.15
LOF	24	11.65 $\pm$ 0.44 10.60–12.34	10	12.19 $\pm$ 0.35 11.73–12.87	9	11.76 $\pm$ 0.48 10.90–12.68	7	12.27 $\pm$ 0.33 11.73–12.69	8	11.99 $\pm$ 0.63 10.79–12.73	7	12.04 $\pm$ 0.44 11.64–12.84	4	12.37 $\pm$ 0.49 11.78–12.87



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