Molecular Phylogenetics and Evolution 94 (2016) 410–423

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Molecular data reveal spatial and temporal patterns of diversification and a cryptic new species of lowland *Stenocercus* Duméril & Bibron, 1837 (Squamata: Tropiduridae) ☆

Mauro Teixeira Jr. [a,*], Ivan Prates [b], Carolina Nisa [a], Nathalia Suzan Camarão Silva-Martins [c], Christine Strüssmann [c], Miguel Trefaut Rodrigues [a]

[a] *Laboratório de Herpetologia, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, 05508-090 São Paulo, SP, Brazil*

[b] *Department of Biology, City College and Graduate Center, City University of New York, New York, NY 10031, USA*

[c] *Departamento de Ciências Básicas e Produção Animal, Faculdade de Agronomia, Medicina Veterinária e Zootecnia, Universidade Federal de Mato Grosso, 78060-900 Cuiabá, MT, Brazil*

ARTICLE INFO

Article history:
Received 11 April 2015
Revised 28 July 2015
Accepted 9 September 2015
Available online 30 September 2015

Keywords:
Andes
Climatic niche
Historical biogeography
Iguania
Stenocercini
Taxonomy

ABSTRACT

Phylogenetic studies have uncovered biogeographic patterns and the associated diversification processes of Neotropical wet forest taxa, yet the extensive open and drier biomes have received much less attention. In the *Stenocercus* lizard radiation, restricted sampling and phylogenetic information have limited inferences about the timing, spatial context, and environmental drivers of diversification in the open and dry lowland settings of eastern and southern South America. Based on new DNA sequence data of previously unsampled species, we provide an updated historical biogeographic hypothesis of *Stenocercus*. We infer phylogenetic relationships, estimate divergence times, and track ancestral distributions, asking whether cladogenetic events within the genus correlate to reported shifts in South American landscapes during the past 30 million years, focusing in the open and drier areas. To examine correlations between genetic and ecological divergence, we extracted environmental data from occurrence records and estimated climatic envelopes occupied by lowland taxa. Our results suggest that *Stenocercus* began to diversify around the South American Midwest by the late Oligocene. We recovered two main lowland and two main Andean clades within the genus; within both Andean clades, most cladogenetic events date back to the Miocene, synchronously with the most intense phase of Andean uplift. In the western clade of lowland *Stenocercus*, species ranges and divergence times are consistent with major landscape shifts at the upper Guaporé and Paraguay River basins as a result of Andean orogeny, suggesting vicariant speciation. By contrast, in the ‘horned’ lowland clade, we find evidence that dispersal and ecological differentiation have shaped species divergences and current ranges in the Brazilian Cerrado, Caatinga, Pampas and Atlantic Forest, possibly under a vanishing refuge scenario. Lastly, our phylogenetic results indicate two divergent clades within the formerly recognized taxon *S. sinesaccus*, and further evaluation of morphological data corroborates the existence of a distinct, new species of *Stenocercus*, here described. The new taxon occurs in the Chapada dos Parecis massif in the Brazilian states of Mato Grosso and Rondônia.

1. Introduction

Phylogenetic approaches aiming to uncover historical biogeography patterns and the associated drivers of diversification in Neotropical taxa have focused primarily on species from wet forested environments (Carnaval et al., 2009; Costa, 2003; Cracraft and Prum, 1988; Hall and Harvey, 2002; Ribas et al., 2005, 2007). Unfortunately, this focus on wet environments has often resulted in exclusion of species occurring in open and drier biomes from major discussions about the origin of Neotropical biodiversity (Redford et al., 1990; Sánchez-Azofeifa et al., 2005). As a result, early views of a poor and homogeneous biotic composition across the great dry South American diagonal composed of Chaco, Cerrado, Caatinga and Dry Forest biomes have prevailed (Marris, 2005; Vanzolini, 1988, 1994).

More recently, biotic surveys across previously unsampled areas have provided new material for biodiversity studies in open and dry Neotropical settings, supporting biogeographic and

---

☆ This paper was edited by the Associate Editor J.A. Schulte.

* Corresponding author.

E-mail address: tropidurus@gmail.com (M. Teixeira Jr.).

http://dx.doi.org/10.1016/j.ympev.2015.09.010

phylogenetic approaches (Pennington et al., 2004; Nogueira et al., 2011; Werneck et al., 2012; Guedes et al., 2014). This renewed interest has led to unexpected discovery of biodiversity. A noticeable case is that of *Stenocercus* lizards, for which a number of species occurring in open settings has only recently been described and recorded (Nogueira and Rodrigues, 2006; Ribeiro et al., 2009; Torres-Carvajal, 2005). Currently, *Stenocercus* is one of the most speciose South American lizard genera, with 66 valid taxa (Torres-Carvajal, 2007a; Torres-Carvajal and Mafla-Endara, 2013; Venegas et al., 2013, 2014; Köhler and Lehr, 2015). The genus is particularly diverse along the Andes, from Venezuela in the north to central Argentina in the south, reaching up to 4000 m in elevation (Torres-Carvajal, 2007a). Yet, a number of species are also found in the wet Amazonian lowlands, and in the drier, open settings of southern, central and northeastern Brazil (Nogueira and Rodrigues, 2006; Torres-Carvajal, 2007a).

Stenocercus has been addressed by a number of comprehensive systematic revisions (Cadle, 1991; Fritts, 1974; Torres-Carvajal, 2007a). Recently, the implementation of molecular tools and detailed morphological analyses have shed light onto phylogenetic relationships and geographic patterns of diversification within the genus (Torres-Carvajal, 2000, 2007a, 2009; Torres-Carvajal et al., 2006). Importantly, these studies revealed that Andean species compose two main clades, which likely originated in the Central Andes and subsequently dispersed and diversified throughout the Andes. However, because some non-Andean species were described only recently, the full diversity of lowland *Stenocercus* has not yet been addressed in biogeographic studies (e.g., Torres-Carvajal, 2007b; Torres-Carvajal et al., 2006). These gaps have limited our understanding of the temporal and spatial diversification of *Stenocercus* in the open and drier South American lowlands east to the Andes. These species occur in a range of contrasting environments, such as *S. azureus* (Müller, 1880) in the southern Atlantic Forest and Pampas grasslands, *S. quinarius* Nogueira and Rodrigues, 2006 and *S. squarrosus* Nogueira and Rodrigues, 2006 in Atlantic dry forests, eastern Cerrado savannas and western Caatinga scrublands, *S. caducus* (Cope, 1862) and *S. sinesaccus* Torres-Carvajal, 2005 in western Cerrado savannahs, *S. tricristatus* (Duméril, 1851) in southeastern Cerrado savannahs (Torres-Carvajal, 2007a), *S. dumerilii* (Steindachner, 1867) in eastern Amazonian forest, and *S. fimbriatus* Avila-Pires, 1995 and *S. roseiventris* (Duméril and Bibron, 1837) in western Amazonian forest.

To improve our understanding about diversification processes in open and dry Neotropical biomes, we provide an updated historical biogeographic scenario of *Stenocercus*, focusing on the genus' diversification to the east of the Andes. We generated new DNA sequence data of previously unsampled *Stenocercus* species, including *S. dumerilii*, *S. quinarius*, *S. sinesaccus*, *S. squarrosus*, and *S.* cf. *tricristatus* recently collected in Brazil. By combining these data with existing molecular datasets, we inferred phylogenetic relationships, estimated divergence times, and tracked ancestral distributions, to examine whether cladogenetic events within *Stenocercus* correlate with reported shifts in South American landscapes during the past 30 million years. We also used environmental data to estimate the climatic envelopes currently occupied by lowland *Stenocercus*. We integrated niche and phylogenetic data to test for correlations between genetic and ecological divergence (Graham et al., 2004) and to examine the role of past climatic fluctuations, habitat change and local adaptation in shaping current distribution patterns. Instead of focusing on the better known Andean *Stenocercus*, we emphasize those species from the dry and open lowland settings of South America.

Our new molecular information reveals a highly divergent clade within previously recognized *S. sinesaccus*. As morphological data support that this is a distinct species from the closely related *S. caducus* and *S. sinesaccus*, we formally describe the new taxon herein.

2. Materials and methods

2.1. Molecular analyses

2.1.1. Sampling of molecular data

We generated DNA sequences for 15 specimens: two *Stenocercus caducus*, one *S. doellojuradoi*, four *S. quinarius*, five specimens assigned to *S. sinesaccus*, two *S. squarrosus*, and one *S.* cf. *tricristatus*. We combined our new sequences with GenBank data of several Tropiduridae taxa, including species of *Stenocercus*, *Microlophus*, *Plica*, *Tropidurus*, *Uracentron*, and *Uranoscodon*. Our final dataset comprised 73 samples representing 62 species (Supplementary Table S1).

We extracted total genomic DNA from liver or tail fragments preserved in ethanol using standard protocols. Matching available datasets (Torres-Carvajal, 2007b; Torres-Carvajal et al., 2006), we generated sequences of a long mitochondrial fragment containing the NADH dehydrogenase subunit 1 (ND1) and 2 (ND2) and eight transfer RNAs (tRNA-Ile, tRNA-Gln, tRNA-Met, tRNA-trp, tRNA-Ala, tRNA-Asx, tRNA-Cys, tRNA-Tyr), following Torres-Carvajal et al. (2006). Sequences were edited and aligned using Geneious Pro 6 (Biomatters, Auckland). Models of nucleotide evolution and best-fit partition schemes were determined with Partition Finder v.1.1.1 (Lanfear et al., 2012), implementing PhyML for likelihood estimation (Guindon and Gascuel, 2003) and the Akaike information criterion for model selection (Akaike, 1974).

2.1.2. Inferring phylogenetic relationships

We performed phylogenetic inference under a Bayesian framework using MrBayes 3.2.1 (Ronquist et al., 2012), implementing three independent runs of four Markov chains of 20 million generations each, and sampling every 1000 steps. We partitioned protein-coding genes by codon position as indicated by Partition Finder. Due to the short length of each of the eight tRNAs (~70 base pairs), we treated them as a single partition (631 base pairs total). We assessed convergence and stationarity of model parameters using Tracer 1.5, combined runs in LogCombiner 1.8 (with 25% discarded as burn-in), and summarized a maximum clade credibility tree in TreeAnnotator 1.8 (Drummond et al., 2012). We unlinked parameters of substitution rates and nucleotide frequencies between partitions. The resulting topologies were visualized in FigTree 1.4 (available from http://tree.bio.ed.ac.uk/software/figtree/).

For descriptive purposes, we also estimated Tamura–Nei corrected pairwise genetic distances (Tamura and Nei, 1993) for the mitochondrial DNA fragment of all populations assigned to *Stenocercus sinesaccus* and *S. caducus*, using the APE 3.1 package (Paradis et al., 2004) of the R 3.0.2 platform (R Core Team, 2015).

2.1.3. Divergence time estimation

To estimate divergence times between *Stenocercus* species, as well as between the genus and related Tropiduridae taxa, we performed simultaneous phylogenetic reconstruction and divergence time estimation using BEAST v.1.8 (Drummond et al., 2012). To calibrate the root of Tropiduridae, we set a normally-distributed prior on the node corresponding to the most recent common ancestor of *Stenocercus*, *Uranoscodon* and *Plica* (mean = 49 Mya, standard deviation = 5.1 Mya) following Prates et al. (2015). We rooted our tropidurid tree by implementing a molecular clock strategy, which yields rooted trees in the absence of outgroups through the simultaneous estimation of tree topology and branch lengths (Felsenstein, 2004; Drummond and Rambaut, 2007). Molecular clock-based rooting has been found to be a robust and effective method (Huelsenbeck et al., 2002), especially useful in cases where an outgroup is not available or where deep divergence between the group of interest and its sister leads to extensive substitution saturation (e.g., Ribas et al., 2012; Cohen, 2013). We implemented an uncorrelated lognormal relaxed clock strategy (Drummond et al., 2006) with a uniform prior distribution (interval = 0–1) to the mean rate of the molecular clock (ucld.mean parameter), while implementing default settings for the parameters relative to substitution rates, nucleotide frequencies, and the Yule tree prior. We ran three independent chains of 100 million steps, sampling every 10,000 steps. After assessing stationarity and convergence of model parameters in Tracer, we discarded 25% as burn-in, combined the runs, and summarized results into a maximum clade credibility tree as described in Section 2.1.2.

2.2. Biogeographical analyses

2.2.1. Ancestral area reconstruction

To perform ancestral area reconstructions, we combined the South American ecoregions of Olson et al. (2001) (proposed based on fauna and flora distributions) into 13 geographic units. Due to computational limits on the maximum number of areas implemented in the analyses (see below), we also merged ecoregions sharing the same *Stenocercus* fauna when defining these geographic units. This strategy resulted in the following areas (Supplementary Fig. S1): (1) the semi-arid Caatinga in northeastern Brazil (Caa), (2) Chaco shrublands and the Bolivian savannahs of Beni (Cha), (3) the eastern Cerrado in Brazil (ECe), (4) the western Cerrado in Brazil (WCe), (5) the Atlantic Forest and Pampas grasslands (SAF), (6) northern (NAn), (7) central (CAn), (8) and southern Andes (SAn), (9) western Amazonia, adjacent to the Andean foothills (WAm), (10) eastern Amazonia and the Brazilian Babaçu forests of Maranhão (EAm), and (11) the southern Amazonia (SAm). In analyses including outgroup taxa, we also included (12) a broad northern Amazonian area which included Tepui mountains, Llanos, and Guiana grasslands (NAm), and lastly (13) the Galapagos islands (Gal). To define the distributions of *Stenocercus* taxa, we obtained geographical data from our own collection records and from published references; a complete list is provided in the online Supplementary References S1.

We performed ancestral area reconstruction under a maximum likelihood framework using the BioGeoBEARS package (*Biogeography with Bayesian and Likelihood Evolutionary Analysis in R Scripts*; (Matzke, 2013) in R (R Core Team, 2015). BioGeoBEARS estimates the geographic distribution of ancestral nodes on a time-calibrated phylogeny. It iteratively optimizes a likelihood function incorporating a range of free parameters that describe the rate or the relative weights of several biogeographic events, including range expansion, local extinction, and cladogenesis through vicariance and sympatric speciation. Importantly, BioGeoBEARS allows for comparisons of model fitting across different parameter combinations, using the Akaike information criterion (AIC) and AIC weights (Burnham and Anderson, 2002; Wagenmakers and Farrell, 2004).

We compared six biogeographic models using BioGeoBEARS: (1) the dispersal-extinction-cladogenesis (DEC), originally implemented in Lagrange (Ree et al., 2005); (2) DEC with founder events (DECj); (3) DIVALIKE, a maximum likelihood implementation of the parsimony-based dispersal-vicariance analyses (DIVA) (Ronquist, 1997); (4) DIVALIKE with founder events (DIVALIKEj); (5) BayAreaLIKE, a maximum likelihood implementation of the BayArea model, which incorporates no cladogenetic events (Landis et al., 2013); and (6), BayAreaLIKE with founder events (BayAreaLIKEj). We allowed for a maximum of six areas per node, which corresponds to the highest observed number of areas occupied by a sampled taxon (*Stenocercus caducus*).

To conduct ancestral range inferences, we pruned our resulting dated phylogeny to include only one terminal per species. We initially performed analyses including 20 tropidurid outgroup taxa available in GenBank. However, presumably because outgroup genera (e.g., *Microlophus*, *Plica*, *Tropidurus*) often contain species having broad ranges in South America, and because most species within those genera have not yet been sampled genetically, their inclusion provided little or no information about ancestral ranges within *Stenocercus*. As a result, we also performed ancestral area reconstructions including no outgroups (see Section 3.4.1).

2.2.2. Environmental analyses

To explore climatic space occupancy that underlies the distribution of analyzed *Stenocercus* species, we extracted environmental data from 19 bioclimatic variables (Hijmans et al., 2005) at each geographical record of the lowland *Stenocercus* species sampled in this study, using ArcGIS v. 10.0 (ESRI, 2011) at a 30-s resolution. We included *S. prionotus* and *S. pectinatus*, which are not included in our molecular analyses but are likely closely related to *S. caducus*/*S. sinesaccus* and to *S. doellojuradoi*/*S. azureus*, respectively, as suggested by morphological data (Torres-Carvajal, 2007b). We implemented a principal component analysis (PCA) (Field, 2009) on the environmental variables upon a correlation matrix, using SPSS v.20 (SPSS, 2011). Following best practices for PCA (Field, 2009), we avoided both redundant (e.g. correlation > 0.9) and non-correlated variables ($p > 0.05$) by checking the correlation matrix and their significance levels prior to analyses.

2.3. Morphological analyses

Because we found high genetic divergence between two clades originally assigned to *Stenocercus sinesaccus* (see results in Section 3.1), we evaluate the species' current taxonomic status by carrying out an examination of morphological variation in this and in closely related *S. caducus*. We refer to the lineage that comprises specimens from the vicinities of *S. sinesaccus*' type locality, and which exhibit the species' typical morphology, simply as *S. sinesaccus*; we refer to the second, highly divergent lineage as an "unconfirmed candidate species" (UCS), following Padial et al. (2010).

A list of specimens examined for morphological comparisons is presented in the Supplementary data 4. A detailed description of the statistical procedures performed in our morphological analyses, including tests of data normality and homoscedasticity, is presented in the Supplementary data 5 (Morphological methodology S1).

3. Results

3.1. Molecular analyses

3.1.1. Phylogenetic relationships of Stenocercus

Phylogenetic analyses recovered two main clades within *Stenocercus*: one composed solely of Andean species (A) and another harboring both Andean and lowland taxa (B; Fig. 1). Clade A includes 16 sampled taxa (Fig. 1). Most occur in the central Andes, except for *S. humeralis*, *S. imitator*, and *S. varius*, which are restricted to the northern portion of the cordillera, and for *S. marmoratus*, which is distributed throughout the central and southern Andes and in the adjacent Chaco.

The second main *Stenocercus* clade (B) is composed of lowland (clades 1, 2) and Andean species. Clade 1 was maximally supported (PP = 1) and includes six lowland species exhibiting largely allopatric distributions across a diversity of habitats, from the Andean foothills in Argentina to the northern Atlantic coast in Brazil. This clade was recovered as the sister of *Stenocercus roseiventris* from western Amazonia and northwestern Argentina, although with low support. Within the clade 1, we recovered the 'horned' species

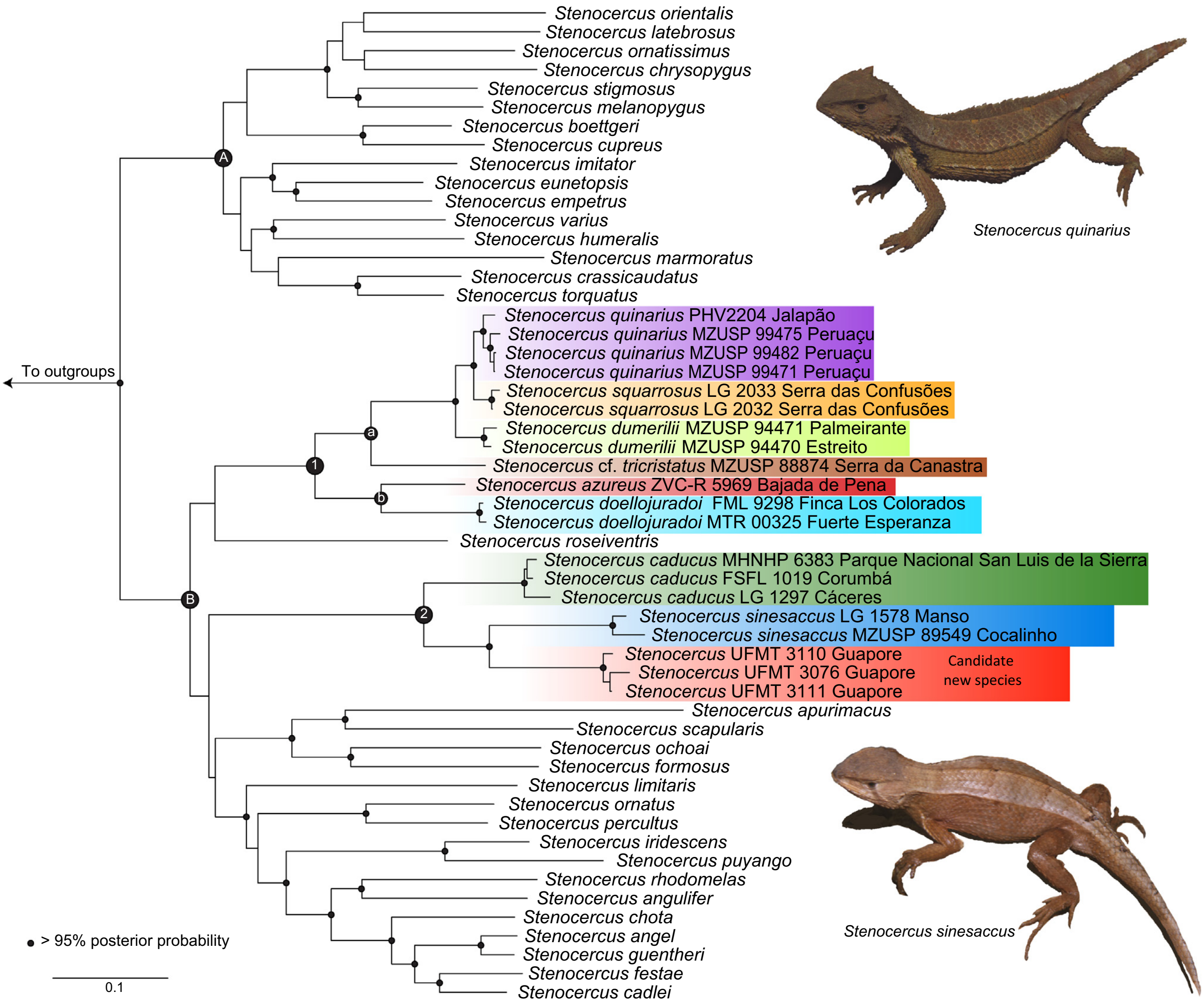

Fig. 1. Phylogram showing the phylogenetic relationship of *Stenocercus* species addressed in the study, recovered through a Bayesian analysis (MrBayes) on the concatenated dataset of mitochondrial genes. Scale bar represents estimated substitution per site. Black circles on nodes represent clades with posterior probability values higher than 95%. Posterior probability values for all nodes are presented in the complete tree provided in the Supplementary Material (Fig. S2).

(clade 1a) *Stenocercus quinarius* and *S. squarrosus* from Atlantic dry forests as sister taxa, closely related to the eastern Amazonian *S. dumerilii*. The most recent common ancestor of these three taxa is sister to *S.* cf. *tricristatus* (Fig. 1), which is restricted to the eastern Cerrado. Altogether, these four species share a common ancestor with the more southern *S. doellojuradoi* and *S. azureus* (clade 1b), a pair of sister species whose distributions span the Chaco and the southern Atlantic Forest including Pampas grasslands, respectively.

Stenocercus clade 2 (the western lowland clade, Fig. 1) is composed of *S. caducus* and of two highly divergent clades assigned to *S. sinesaccus*. We refer to such clades as *S. sinesaccus*, in the western Cerrado, and as an 'unconfirmed candidate species', whose distribution includes both Cerrado and southern Amazonia. We recovered *Stenocercus* Clade 2 as sister to another major Andean clade composed of 16 species, yet this relationship was poorly supported (PP = 0.54). Most species within this clade occur in the northern Andes, although *S. apurimacus*, *S. formosus*, *S. ochoai*, and *S. scapularis* comprise a maximally supported clade restricted to the central portion of the cordillera (Fig. 1).

Corrected pairwise genetic distances between the candidate species and the closely related *S. sinesaccus* ranged between 9.6% and 10.3%. Similarly, the candidate species and *S. caducus* exhibited pairwise genetic distances ranging from 9.6% to 11% (Table 1).

Table 1

Corrected pairwise genetic distances (%) for mtDNA, among species in the clade 2, *S. sinesaccus*, *S. caducus* and the unconfirmed candidate species (UCS).

		1	2	3	4	5	6	7
1	*Stenocercus* UCS UFMT3076	–						
2	*Stenocercus* UCS UFMT3110	0.6	–					
3	*Stenocercus* UCS UFMT3111	0.1	0.4	–				
4	*S. sinesaccus* MZUSP89549	9.6	10.0	9.8	–			
5	*S. sinesaccus* LG1578	10.1	9.8	10.3	2.6	–		
6	*S. caducus* FSFL1019	10.0	9.6	9.8	12.3	10.9	–	
7	*S. caducus* LG1297	11.0	10.7	10.8	12.8	11.1	1.6	–
8	*S. caducus* MHNHP6383	10.2	9.8	10.0	12.3	11.3	0.6	1.6

3.1.2. Divergence times within Stenocercus

Dating analyses suggest that the most recent common ancestor (MRCA) of sampled *Stenocercus* dates back to 27.1 Mya (median value; 95% of the highest posterior density [HPD] = 20–34.4 Mya) (Supplementary Fig. S2). Diversification within *Stenocercus* clade A, which occurs mostly in the central Andes, dates back to approximately the early Miocene, at 18 Mya (95% HPD = 13–23 Mya) (Supplementary Fig. S2). On the other hand, the MRCA of the northern Andean species within clade B dates back to 22 Mya (95% HPD = 16–28 Mya). Nearly all diversification events within these clades date back to the Miocene, between 6.7 and 22 Mya (median values). Exceptions are the younger divergence between *S. festae* and *S. cadlei*, which dates back to the Pliocene (5.2 Mya, 95% HPD = 3.3–7.4 Mya), and that between *S. angel* and *S. guentheri*, dating back to the Pleistocene (2.4 Mya, 95% HPD = 1.4–3.6 Mya). (Supplementary Fig. S2).

The MRCA of *Stenocercus* species in clade 1a dates back the late Miocene at 8.4 Mya (95% HPD = 5.5–11.7 Mya), while the MRCA of *S. dumerilii*, *S. quinarius* and *S. squarrosus* was found to be more recent, dating back to the transition between the Pliocene and Pleistocene, approximately 2.7 Mya (95% HPD = 1.8–3.9 Mya). The latter two taxa diverged during the Pleistocene, around 1.5 Mya (95% HPD = 0.9–2.2 Mya). The MRCA of species in the clade 1b, *S. azureus* and *S. doellojuradoi*, dates back to the late Miocene, around 8.4 Mya (95% HPD = 4.4–10.13 Mya). Both clade 1a and 1b shared a MRCA approximately 12.4 Mya (95% HPD = 8.7–16.7 Mya). In the second lowland clade of *Stenocercus* (clade 2), *S. caducus* and *S. sinesaccus* and our candidate species share a MRCA approximately 11 million years old (95% HPD = 7.6–15 Mya). The MRCA of *S. sinesaccus* and of the candidate species dates back to the late Miocene (7.9 Mya, 95% HPD = 5.2–11 Mya), which is older than the divergences between several recognized *Stenocercus* species (Supplementary Fig. S2).

3.2. Morphological analyses

We examined 87 individuals of *Stenocercus caducus*, 53 of *S. sinesaccus*, and 160 of our candidate species in morphological analyses (Supplementary Examined Specimens S1). Comparisons between species revealed significant differences in several morphological and morphometric variables, as described in detail in the Supplementary data 6 (Morphological Results S1).

3.3. Taxonomic results

3.3.1. A new species of Stenocercus

In the face of deep, old divergences (see Section 3.1.2), and of a large number of significant differences between *Stenocercus sinesaccus* and the proposed candidate species in both quantitative (see Section 3.2) and qualitative variables (see Section 3.3.1.1), and between them and *S. caducus* (Fig. 2), we recognize our candidate species of *Stenocercus* as a 'confirmed candidate species' (Padial et al., 2010). We describe the new taxon in the following sections.

3.3.1.1. Taxon description. **Stenocercus albolineatus sp. nov.**

Fig. 3, Figs. S3, S4, S5A and S6

Stenocercus caducus – Silva et al., 2010
Stenocercus sinesaccus – Nogueira and Rodrigues, 2006 – part; Torres-Carvajal, 2007a – part
Stenocercus sp. – Silva, 2007 – part

Holotype: MZUSP 97964, adult male; Brazil: Mato Grosso: municipality of Vale de São Domingos, UHE Guaporé hydroelectric dam (approximate coordinates 15°07′S, 58°57′W). Collected by the rescue team during lake filling in 2002.

Paratypes: Brazil: Mato Grosso: UHE Guaporé: MZUSP 97956–97963, MZUSP 97965, UFMT 3076–3114, UFMT 3510–3511, UFMT 6277–6280, UFMT 7268; same data as the holotype.

Referred specimens: Brazil: Mato Grosso: Araputanga: INPA 15963–15964, INPA 15968–15969; Cotriguaçu: UFMT 8964; Indiavai: INPA 1562, INPA 15967; PCH Ombreiras: UFMT 2871–2879, UFMT 9537; Juína: PCH Juína: UFMT 5745; Lambari d'Oeste: MZUSP 102986–102987; Quatro Marcos: INPA 15065; Rio Branco: INPA 1966; Sapezal: UFMT 7365–7366, UFMT 7450, UFMT 7462, UFMT 7494–7495; Vale de São Domingos: UFMT 7401, UFMT 7404, UFMT 7406, Vila Bela da Santissima Trindade: Serra da Borda: UFMT 2290. Rondônia: Espigão d'Oeste: MPEG 21937,

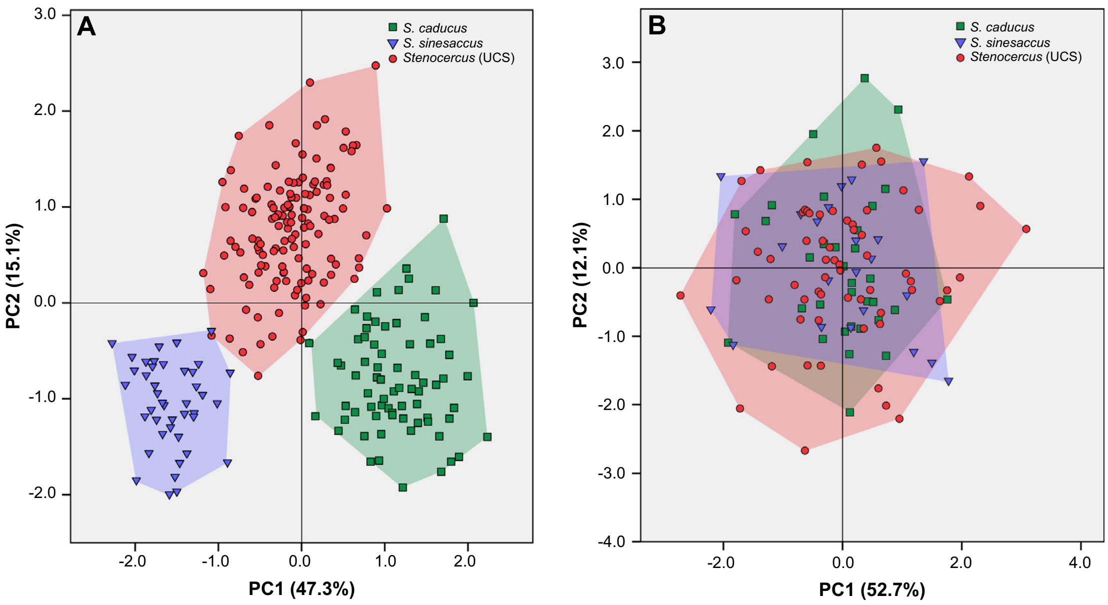

Fig. 2. Ordination diagram of principal component analysis, upon meristic (A) and size-corrected morphometric (B) data of *Stenocercus caducus*, *S. sinesaccus* and the unconfirmed candidate species (UCS).

Fig. 3. Live individual of *Stenocercus albolineatus* **sp. nov.** from Cotriguaçu, Mato Grosso, Brazil (A); lateral views of the heads of *S. albolineatus* **sp. nov.** (B), *S. sinesaccus* (C) and *S. caducus* (D).

MPEG 21487; Pimenta Bueno: CHUNB 18042–18049; Vilhena: CHUNB 11473–11474.

Etymology: The specific epithet *albolineatus* is derived from the Latin words *albus* (=white) and *linea* (=line) and *atus* (=that bears), as all members of the new species present a whitish line on the anterior surface of the forelimbs, characteristic of this species.

Diagnosis: Data from species in comparison are given in parentheses. The new species differs from all other species of *Stenocercus* except *S. caducus*, *S. dumerilii*, *S. prionotus*, *S. quinarius*, *S. sinesaccus*, *S. squarrosus* and *S. tricristatus* by having strongly keeled and mucronate body scales, laterally oriented nostrils, and lacking a postfemoral mite pocket.

It differs from *Stenocercus caducus* and *S. prionotus* by lacking a posthumeral mite pocket (present). It can be distinguished from *S. dumerilii*, *S. tricristatus*, *S. quinarius* and *S. squarrosus* by lacking triangularly enlarged horn-like post-supraciliaries (present). From *S. caducus* it can be further distinguished by the presence of complete dorsolateral crests (incomplete) and higher number of scales along the white line on forelimb, 4–10 (1–5) (Supplementary Fig. S5). From *S. sinesaccus*, the new species differs by having a higher number of vertebral scales, 32–45 (26–34), paravertebrals, 36–53 (32–41), scales around body, 31–41 (27–36), transverse dorsals between dorsolateral crests, 11 in 75% of the individuals (9 in 88% of the individuals), scales along the white line on forelimb, 4–10 (1–5) (Supplementary Fig. S5) and ventrals, 19–27 (16–21). Furthermore, *S. albolineatus* **sp. nov.** lacks a complex pattern of markings over the shoulder (present in *S. caducus*) and a whitish scale on the anterior border of the ear (present in *S. sinesaccus*).

The new species is currently known to be sympatric with *Stenocercus roseiventris*. Besides overall body color and enlarged scales on tail, which produce a spiny shape in *S. roseiventris*, the new species can be distinguished by lower number of vertebral scales 32–45 (50–59), paravertebrals, 36–53 (64–75), scales around body, 31–41 (59–64), gulars, 11–20 (30–35), and transverse dorsals between dorsolateral crests, 9–13 (15–19), as well as higher number of lamellae under the fourth toe, 21–30 (17–20) and caudal scales, 111–136 (49–52).

Characterization: (1) SVL in males 70.2–85.5 mm ($n = 26$); (2) SVL in females 73.3–92.2 mm ($n = 49$); (3) vertebrals 32–45; (4) paravertebrals 35–53; (5) scales around midbody 31–41; (6) gular scales 11–20; (7) transversal dorsals between crests 9–13; (8) ventral scales 19–27; (9) caudal scales 111–134; (10) supraoculars 3–6; (11) internasals 4–7; (12) subdigitals on Finger IV 13–19; (13) subdigitals on Toe IV 21–30; (14) posthumeral mite pocket absent; (15) postfemoral mite pocket absent; (16) parietal eye visible through interparietal cornea; (17) scales on occipitoparietal region large, keeled, juxtaposed; (18) row of enlarged supraoculars occupying most of supraocular region absent; (19) preauricular fringe present; (20) neck folds absent; (21) lateral and dorsal nuchals similar in size; (22) posterior gulars rhomboidal, projected posteriorly, strongly keeled and imbricate, not notched; (23) dorsal body scales larger than laterals; (24) vertebrals larger than adjacent paravertebrals; (25) dorsolateral crest present; (26) ventrals keeled, imbricate; (27) scales on posterior surfaces of thighs keeled, imbricate; (28) inguinal granular pocket absent; (29) inguinal groove absent; (30) tail not compressed laterally in adult males; (31) tail length 68–71% of total length; (32) caudal autotomic segments absent; (33) caudals not spinose; (34) dark patch extensively covering gular region of females absent; (35) dark patch extensively covering gular region of adult males absent; (36) black patch on ventral surface of neck in adult males absent; (37) dark midventral longitudinal mark such as faint line, conspicuous stripe, or extensive patch in adult males absent; (38) dark patches on ventral surface of thighs in adult males absent; (39) white line over forelimb; (40) scales along anterior border of ear homogeneously dark-colored.

Coloration in preservative: In males, background coloration ranges from dark to pale brown; dorsal color, limited at each side by the dorsolateral keel, is always paler than flanks and limbs. Dorsum and flanks with blurred inconspicuous bars, those on dorsum oblique at each side forming a chevron pointing posteriorly. Post-pelvic chevrons darker and with sharper edges than pre-pelvic ones. Tail banded with darker and pale brown; sharp-edged marks along tail are often observed. Forelimbs mostly homogeneous brown, bearing a long whitish longitudinal line on arm; hindlimbs usually with transverse bar on tight and shank (Supplementary Fig. S6A). Venter pale brown, with irregular scattered faded blurred markings.

In females, background coloration ranges from dark to pale and grayish brown; dorsal color, limited at each side by the dorsolateral keel, is sometimes paler than flanks and limbs. Dorsum and flanks mostly with blurred conspicuous bars, sometimes inconspicuous; those on dorsum oblique at each side forming a chevron pointing posteriorly, often with sharp edges. The series of sharp edged chevrons start at the level of forelimbs and extends to the tail. Tail banded with darker and pale brown; sharp-edged marks along tail are often observed. Forelimbs mostly homogeneous brown, bearing a long whitish longitudinal line on arm; hindlimbs usually with transverse bar on tight and shank (Supplementary Fig. S6B). Venter ranging from cream to pale brown, usually with irregular scattered faded blurred dark markings, throat and chin with oblique series of blurred dark bars on each side.

Description of the holotype: (Supplementary Figs. S3 and S4) Adult male, 78.6 mm SVL, 184 mm TL. Head length 0.23 times SVL, 1.4 times as long as wide, 1.7 times as wide as high. Snout bluntly pointed in dorsal view, pointed in profile. Canthal ridge well defined, continuous with supraciliaries. Neck slightly narrower than head and body. Body roughly cylindrical. Limbs slender, forelimbs 0.4 times SVL, hindlimbs 0.7 times. Tibia 0.2 times SVL, and 0.3 times length of hindlimb. Tail roughly rounded in cross-section from base to tip, 2.3 times SVL.

Rostral semicircular, largest width about three times median height, barely visible from above. Three postrostrals, wider than long. Occipitals, parietals, interparietal, and postparietals large, strongly keeled, juxtaposed. Supraorbital semicircle anteriorly distinct and supraocular scales differentiated from surrounding scales. Canthal single, not reaching the postrostrals, bordered anteriorly by an elongate, keeled internasal. Supraciliaries seven, first four overlapping posteriorly, with similar size. The two last smaller, sixth acuminate. Canthals and supraciliaries form a distinct crest that ends in a strongly keeled post-supraciliary. Interparietal moderately enlarged, in the shape of an asymmetric pentagon, parietal eye distinct. Posterior region of head bearing irregular, keeled shields; interparietal and parietals not differentiated.

Nasal lateral, large, undivided; nostril in posterior part of nasal, directed laterally. Loreal region with three vertical rows of slightly keeled scales, first and third double, second triple. One horizontal row of mostly elongate lorilabials. One subocular, about four times as long as high, with a longitudinal keel close to its upper margin. Subocular separated from supralabials by lorilabials. Supralabials four, narrow, anterior one smallest, fourth largest, below center of eye. Temporal region with irregularly polygonal, strongly keeled scales; seven scales in an oblique row from lower posterior border of orbit to above ear opening. Ear opening relatively large, vertically oval, anteriormost part covered by a fringe. Tympanum slightly recessed.

Mental small, not distinctively larger than adjacent infralabials; bordered posteriorly by two bulky, keeled scales and by two (one on each side) elongate and keeled infralabials. Infralabials five, elongate, strongly keeled; first smallest, third one largest, below anterior half of eye. One row of elongated sublabials, with a right median keel. Scales on chin anteriorly relatively small, elongate, subimbricate, posteriorly grading into gulars. Gulars larger than scales on chin and smaller than adjacent ventrals, strongly keeled and mucronate, in irregular longitudinal rows; no gular or lateral folds.

Scales on nape similar to dorsals, anteriormost ones smaller. A vertebral crest of enlarged, prominent and sharply keeled scales extends from nape to first third of tail. A dorsolateral crest of scales extends from above ear opening to anteriormost part of tail. Dorsals phylloid, imbricate. Eleven transverse rows of dorsal scales at midbody, between dorsolateral crests (included). Thirty-nine vertebral scales from occiput to base of tail. Flanks with similar but distinctively smaller scales. Twenty-three rows of ventral scales between anterior level of forelimbs and anterior level of hind limbs. Thirty-three scales around midbody.

Scales on preanal plate in irregular transverse rows, mite pockets absent. Scales on both dorsal and ventral part of tail similar to dorsals, phylloid, flat, keeled, anteriormost ones bearing a short mucron, distal ones smaller. No distinct caudal verticils.

Limbs with phylloid, imbricate, strongly keeled and mucronate scales, smaller than dorsals. The keels form distinct ridges on dorsal, anterior and posterior aspect of limbs. Subdigital lamellae single, tricarinate, 17 under fourth finger and 26 under fourth toe.

Variation: all variables presented some variation (see Supplementary Tables S8 and S9). The transverse dorsal scales (TD), although ranging from 9 to 13, 121 specimens out of the 160 examined presented 11 TD (75%). The number of scales along the whitish line over the forearm (LIN) ranged from 6 to 9 on 131, out of the 160 (81%). Comparatively in *Stenocercus sinesaccus*, also although TD ranges from 8 to 11, 47 out of 53 specimens had 9 TD (88%), and only two individuals presented 11 TD, and in LI, 46 out of the 53 specimens presented 2–4 scales along the white line on arm (86%). In the morphometric variables, there was a strong variation regarding the sexes (Supplementary Table S9).

Distribution: Currently known from localities at the top and surrounding Chapada dos Parecis, from the western portion of Mato Grosso to eastern Rondônia states, Brazil (Fig. 4). This area encompasses a large Mesozoic sandstone plateau, limited by the Guaporé River at its western side and by the Paraguay River at its eastern side (Supplementary Fig. S7).

Natural history: Stenocercus albolineatus **sp. nov.** seems to be more abundant during the rainy season, when adults are commonly found; during the dry season only juveniles were observed, suggesting a seasonal reproduction by the end of the wet and beginning of the dry season (Silva et al., 2010). It is a generalist species in habitat occupancy, occurring over pasturelands, forest edge, and pristine forest; feeds on terrestrial arthropods, with Coleoptera, Hymenoptera (Formicidae) and Isoptera as the most frequent (Silva et al., 2010).

3.4. Biogeography

3.4.1. Historical biogeography of Stenocercus

Of the six historical biogeographic models compared using BioGeoBEARS, the Dispersal-extinction-cladogenesis model with founder events (DECj) demonstrated the best fit for the data as supported by AIC weights (>0.94). Results suggest that the most probable ($p = 0.28$) distribution of the MRCA of all *Stenocercus* was a broad are encompassing the Chaco, central and southern Andes, and western and southern Amazonia simultaneously (Fig. 5).

The resulting model recovered broad ancestral ranges for both lowland clades of *Stenocercus*. The most likely distribution of the MRCA of *S. caducus*, *S. sinesaccus* and *S. albolineatus* **sp. nov.** included the Chaco, central and southern Andes, and western Cerrado ($p = 0.83$). The MRCA of the *S. sinesaccus* and *S. albolineatus* **sp. nov.** was likely distributed in the western Cerrado ($p = 0.54$) or in both western Cerrado and southern Amazonia ($p = 0.44$). In turn, we inferred a broad ancestral distribution for the horned lowland clade of *Stenocercus*, including at least part of the Chaco, central and southern Andes, and western and southern Amazonia ($p = 0.75$). The MRCA of *S. quinarius*, *S. squarrosus*, *S. dumerilii* and *S. tricristatus* likely occurred in the eastern Cerrado ($p = 0.92$); colonization of eastern Amazonia and Caatinga seem to have favored the divergences of *S. dumerilii* and *S. squarrosus*, respectively, from

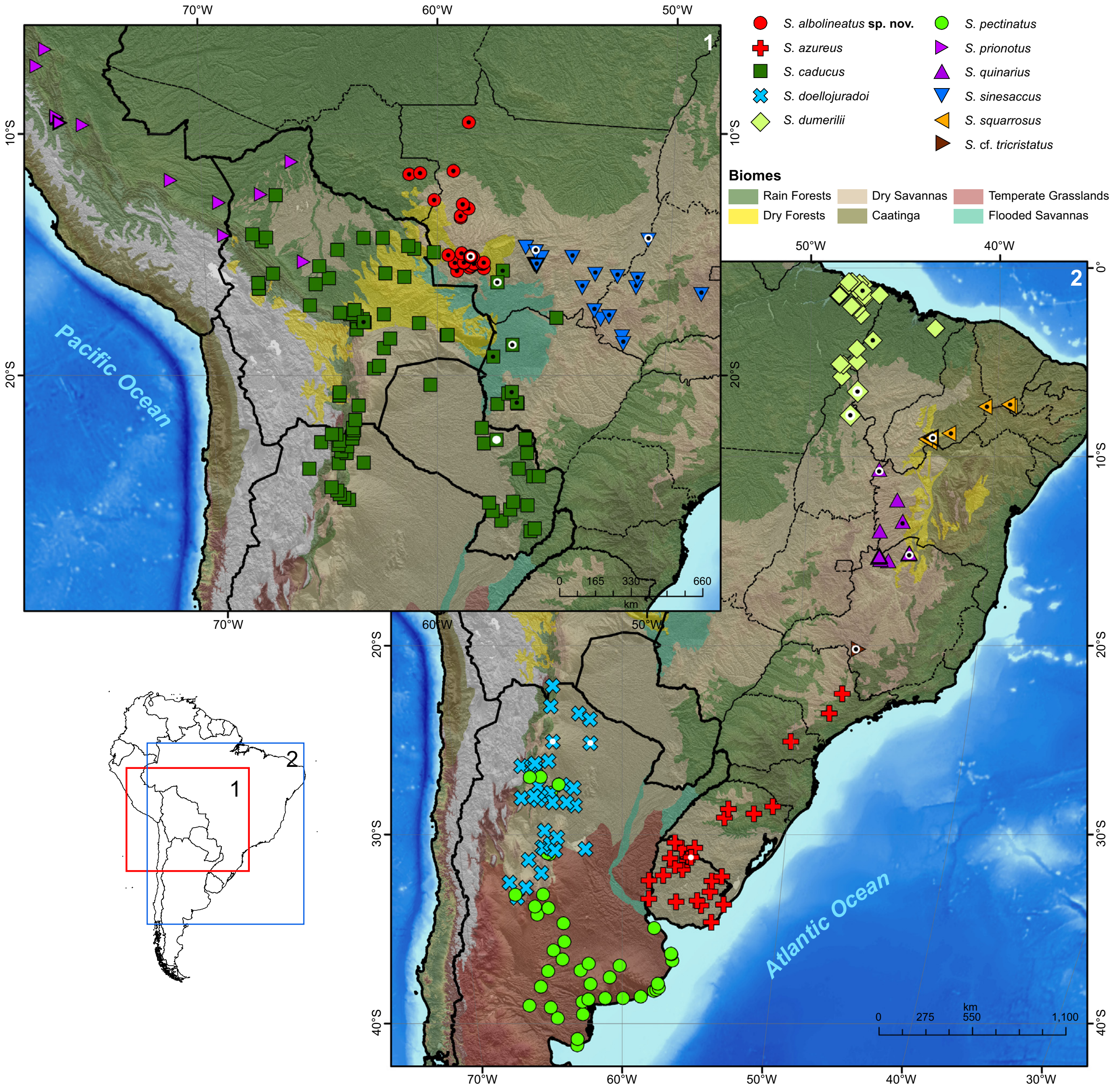

Fig. 4. Map showing the known distribution of *Stenocercus albolineatus* **sp. nov.**, *S. caducus*, *S. prionotus* and *S. sinesaccus* (A), and *S. azureus*, *S. doellojuradoi*, *S. dumerilii*, *S. pectinatus*, *S. quinarius*, *S. squarrosus* and *S.* cf. *tricristatus* (B). Markers with a black central dot represent examined specimens; white central circles indicate molecular samples. Bold-outlined markers represent type localities, when available.

their eastern Cerrado sister lineages. The common ancestor of *S. doellojuradoi* and *S. azureus* probably occurred in the Chaco ($p = 0.61$); subsequent expansion into the southern Atlantic Forest and Pampas seems to correlate to the divergence between these two species. Our analyses suggest that the most likely ancestral distribution of the six aforementioned Brazilian *Stenocercus* species corresponds to the Chaco area. Lastly, we found that the most likely ancestral range for both Andean clades was the central Andes ($p > 0.84$), from which different lineages dispersed into the northern and southern Andes, Chaco, and western Amazonia.

3.4.2. Environmental envelopes

After evaluating communalities, multicolinearity and uncorrelated variables, we retained seven bioclimatic variables for a PCA of environmental data (Supplementary Table S10). The resulting correlation matrix included variables having correlation coefficients ranging from 0.3 to 0.9, most of which significant; communalities were above 0.7.

For clade 1, three components were extracted in a PCA of environmental data (eigenvalues > 1), with 40.6% of the observed variance explained by PC1 and 35.5% by PC2 (Supplementary Table S10; Fig. 6A). PC1 was positively correlated with precipitation on the warmest and driest quarter, annual mean temperature and temperature of the wettest quarter, and negatively correlated with minimum temperature of the coldest month. PC2 was positively correlated with annual precipitation and precipitation of the driest month and negatively correlated with precipitation of the wettest month and mean diurnal temperature range

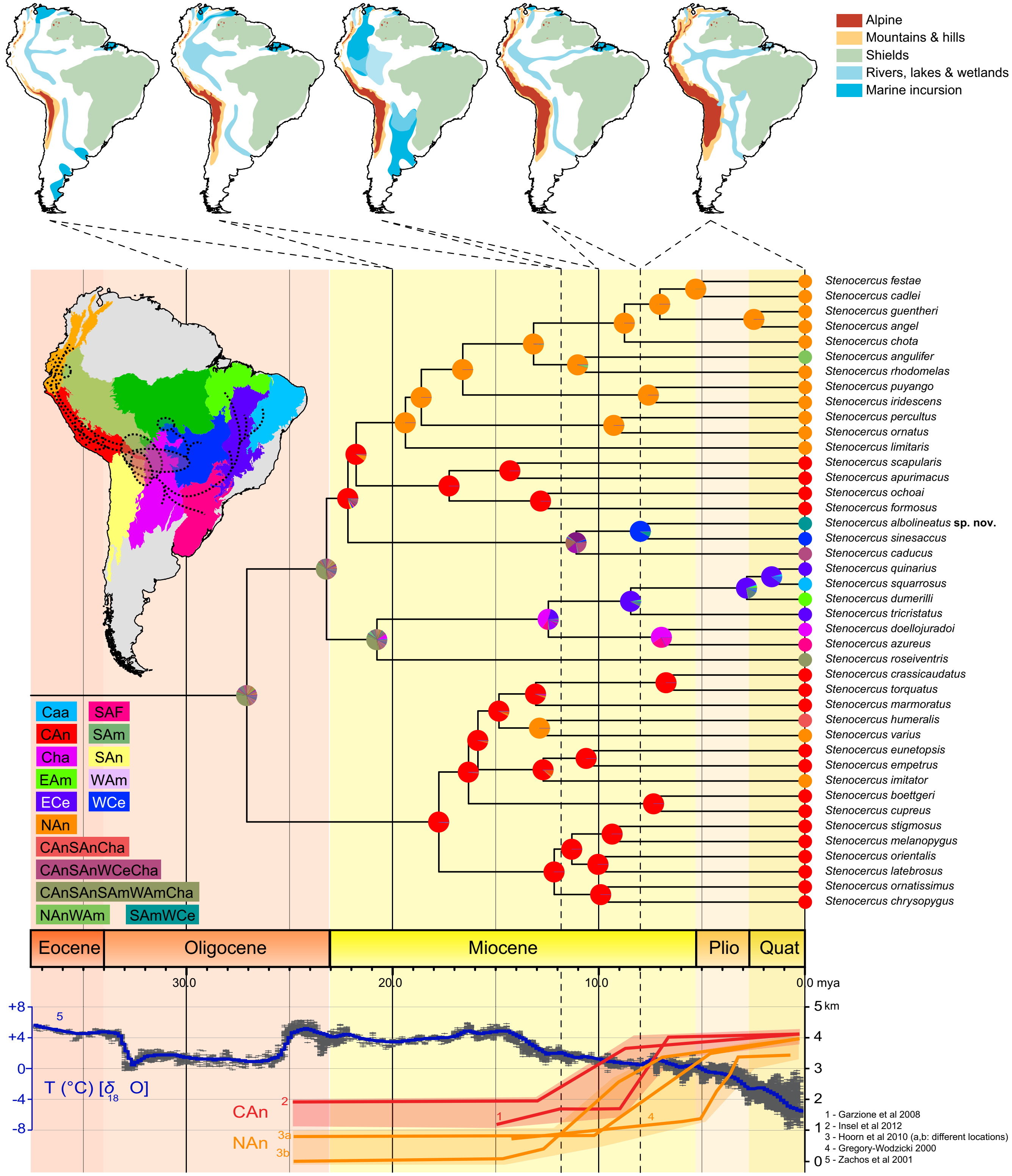

Fig. 5. Biogeographical history of *Stenocercus*; top panel: landscape changes (adapted from Cook et al., 2012; Hoorn et al., 2010; Lundberg et al., 1998); middle panel: ancestral area reconstruction (Caa = Caatinga; CAn = Central Andes; Cha = Chaco; EAm = Eastern Amazonia; ECe = Eastern Cerrado; NAn = Northern Andes; SAF = South Atlantic Forest; SAm = Southern Amazonia; SAn = Southern Andes; WAm = Western Amazonia; WCe = Western Cerrado); lower panel: temperature changes (adapted from Zachos et al., 2001) and Andean uplift (adapted from Garzione et al., 2008; Gregory-Wodzicki, 2000; Hoorn et al., 2010; Insel et al., 2012).

(Supplementary Table S10). Each species occupied distinct regions of the environmental space: *Stenocercus dumerilii* occurs in warmer and wetter areas, *S. squarrosus*, *S. quinarius* and *S. doellojuradoi* in warmer and drier areas, *S. azureus* and *S.* cf. *tricristatus* in cooler and wetter areas, and *S. pectinatus* ranging from warmer and drier to cooler and wetter areas (Fig. 6A).

For the *Stenocercus* clade 2 PCA, three components were extracted, with 46.5% of the observed variance explained by PC1

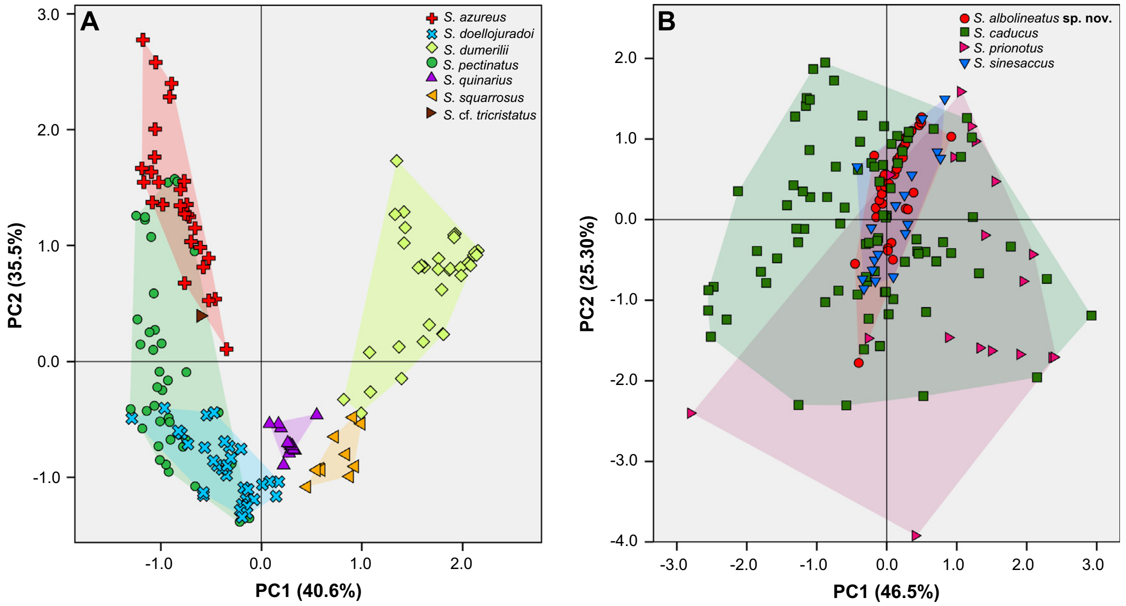

Fig. 6. Ordination diagram of a principal component analysis upon environmental data from each known record of species within clade 1, *Stenocercus azureus*, *S. doellojuradoi*, *S. dumerilii*, *S. prionotus*, *S. quinarius*, *S. squarrosus* and *S.* cf. *tricristatus* (A), and clade 2, *S. albolineatus* **sp. nov.**, *S. caducus*, *S. pectinatus* and *S. sinesaccus* (B).

and 25.3% by PC2 (Supplementary Table S10; Fig. 6B). PC1 was positively correlated with annual precipitation, minimum temperature of the coldest month, precipitation of the wettest month, annual mean temperature and precipitation of the driest month, negatively correlated with mean diurnal temperature range. In turn, PC2 was positively correlated with maximum temperature of the warmest month and annual mean temperature, and negatively correlated with precipitation of the driest month (Supplementary Table S10). Species in clade 2 presented a broad overlap across the environmental space, with *S. caducus* and *S. prionotus* occupying a broad range along both PCs, and with *S. sinesaccus* and *S. albolineatus* **sp. nov.** presenting an intermediate position along PC1 and a broad occurrence along PC2 in both positive and negative directions (Fig. 6B).

4. Discussion

4.1. *Historical biogeography and the timing of Stenocercus diversification*

Our analyses found that the most recent common ancestor (MRCA) of *Stenocercus* dates back to the late Oligocene, and that it exhibited a broad distribution simultaneously including at least part of the Chaco, central and southern Andes, and western and southern Amazonia (Fig. 5; Supplementary Fig. S7). These findings are in partial agreement with a previous ancestral area analysis of this group; Torres-Carvajal (2007b) found that the MRCA of *Stenocercus* occupied the eastern cordillera of the central Andes, an area that is included within our resulting ancestral range. Our finding of a broader ancestral area for *Stenocercus* may be related to a number of factors. First, we defined a larger number of areas, which are not fully equivalent to those implemented previously. This is especially true for taxa occurring in the lowlands to the east of the Andes, such as *S. caducus*, *S. tricristatus*, *S. doellojuradoi*, *S. azureus* and *S. pectinatus*, previously assigned to a broad 'Atlantic lowlands' area (Torres-Carvajal, 2007b). Moreover, we implemented an additional set of ancestral area reconstruction algorithms, obtaining a higher fit to the data for the dispersal-extinction-cladogenesis model (DEC) as compared to the dispersal-vicariance analysis (DIVA) previously explored. Lastly, differences in resulting tree topologies are expected to have affected the outcome of ancestral area analyses.

Previous works (Torres-Carvajal et al., 2006; Torres-Carvajal, 2007b), also found two major clades within *Stenocercus* composed mostly of Andean species, while the species from the dry lowlands were all grouped in a single clade. Those results presented *Stenocercus caducus* as sister to *S. prionotus*, and both to *S. sinesaccus*. This group was inferred to be sister to a group comprising *S. dumerilii* and *S. tricristatus*. Although low supported, this clade had *S. roseiventris* as sister, forming a clade sister to *S. doellojuradoi*, *S. azureus* and *S. pectinatus*. Our results however present those species in two distinct clades (clades 1 and 2; Fig. 1; see following sections). Nonetheless, basal splits in our recovered phylogeny are poorly supported, and thus a different history could be recovered with the inclusion of more genetic markers and taxa.

We found that a biogeographic model incorporating founder event speciation (DECj) had the best fit to our data. Founder event describes a particular case of allopatric speciation in which a small set of individuals, or a single individual, perform a long-distance dispersal and colonization, presenting a random subsample of the genetic pool of the source population, prompting it to subsequent differentiation (Mayr, 1954; MacDonald, 2003; Lomolino et al., 2006; Cox and Moore, 2010; Matzke, 2014). The parameter '*j*' has been shown to be highly predictive in island systems (see Matzke, 2014), in which species often show high dispersal capabilities (e.g., birds or flight invertebrates), or are helped by wind and ocean currents; nonetheless it has not been broadly addressed in intracontinental terrestrial species. Such a model is thus problematic as the major promoter of speciation in continental, terrestrial, sedentary species, as no analogous mechanism to ocean currents is known to affect such species. Dispersal capabilities in *Stenocercus* is unknown for most species, but for some forms in the clade 1 they seem to be strictly sedentary, moving only a few meters per day (Teixeira Jr., 2010). Nevertheless, a scenario of colonization and divergence fits some *Stenocercus* species pairs. For instance, we found that the ancestor of *S. quinarius* (an eastern Cerrado species) and *S. squarrosus* (a Caatinga species) was most likely distributed in the eastern Cerrado, suggesting that colonization of the Caatinga with subsequent interruption of gene flow has favored divergence between *S. quinarius* and *S. squarrosus* (Fig. 5). Similarly, we found that the ancestor of *S. doellojuradoi* (a Chaco species) and *S. azureus* (a Pampas species) was most likely distributed in the Chaco, indicating that range expansion to a new area likely triggered cladogenesis in this case as well. A role for founder event speciation in the diversification of such terrestrial organisms deserves to be examined in additional continental groups.

4.1.1. The clade 1 – the "horned" Stenocercus and related taxa

Our biogeographic analyses recovered the most likely ancestral range of *Stenocercus* lowland clade 1 to the Chaco biome, from which lineages have reached the eastern Cerrado and the area comprising the southern Atlantic Forest and Pampas grasslands (Fig. 5). Subsequently, both the arid Caatinga and eastern Amazonia were likely colonized from eastern Cerrado ancestors (Fig. 5).

This inferred role of dispersal in the diversification of lizards occurring in the dry diagonal contrasts with the traditional view that establishment of vicariant barriers has been the major promoter of population divergence and subsequent speciation in continental South America (Moritz et al., 2000). Allopatric distributions of closely related Neotropical taxa have been widely attributed, for instance, to the formation of rivers, mountain chains, and geologic faults (Nascimento et al., 2013; Ribas et al., 2012; Ribeiro et al., 2013; Smith et al., 2014). Even in the absence of evident barriers, clusters of co-distributed taxa have been interpreted as a result of vicariant speciation in the Cerrado and Caatinga (Guedes et al., 2014; Nogueira et al., 2011). While broadly distributed taxa across the entire dry diagonal are likely exposed to a complex set of geographical features that could promote differentiation (Werneck et al., 2012), it has been challenging to identify landscape features that correlate with the deep genetic breaks observed within the core regions of the Caatinga and Cerrado (Domingos et al., 2014; Gamble et al., 2012; Prado et al., 2012; Santos et al., 2014). As a result, it is still largely unclear what are the mechanistic factors involved with species divergences within the South American dry diagonal.

Our analyses of environmental space occupancy in the *Stenocercus* clade 1 indicate that, following colonization of a new area, ecological differentiation may have favored genetic divergence and speciation even in the absence of pronounced geographic discontinuities. An examination of climatic envelopes reveals nearly complete environmental segregation among most species in this clade (Figs. 4 and 6), suggesting that they are subjected to contrasting regimes of temperature and water availability. In the Cerrado, environmental heterogeneity correlates to spatial turnover of anuran assemblages, suggesting physiological and life history constraints to species' distributions (Valdujo et al., 2013). Strong natural selection favoring locally-adapted phenotypes may promote genetic divergence between populations even in the presence of substantial gene flow, a process referred to as ecological speciation (Nosil, 2012). Our data on the environmental spaces occupied by *Stenocercus* clade 1 support the largely unexplored idea that prominent environmental gradients and ecological differentiation have shaped biodiversity patterns in open and dry Neotropical settings.

However, dispersal and colonization alone are unlikely to have produced the observed distributional patterns in this clade. Although typically found in forested habitats (with the exception of *Stenocercus*. cf. *tricristatus*), species in the horned clade often show broad habitat tolerance, being found in lower abundances at adjacent open areas (Avila-Pires, 1995; Nogueira and Rodrigues, 2006; Teixeira Jr., 2010). These habitats have undergone a turbulent mixing at this portion of the dry diagonal in the last few million years (Ab'Saber, 2000), during climatic fluctuations of high amplitude (Zachos et al., 2001). This local fragmentation and disappearance of habitats coupled with the exhibited environmental tolerances may have facilitated the dispersal and colonization between distinct habitats, as described in the vanishing refugia model (VRM) (Damasceno et al., 2014; Vanzolini and Williams, 1981). This model proposes a situation in which gradual environmental change allows for populations to progressively adapt locally, ultimately triggering divergence (Damasceno et al., 2014; Vanzolini and Williams, 1981). Speciation under the VRM predicts distinct ecologies between closely related parapatric taxa, which contrasts sharply with the common pattern under phylogenetic niche conservatism, in which a species pair is ecologically similar (Crisp and Cook, 2012; Losos, 2008). In the face of geographic and environmental segregation, and of temporal congruence between species divergences and periods of extensive climatic fluctuations and habitat fragmentation in South America (Fig. 5), the VRM may be a candidate mechanistic model for the initial divergence between some lowland *Stenocercus* pairs.

4.1.2. The clade 2 – the western lowland Stenocercus

Contrasting with the horned clade, our results indicate that the three species with available molecular data in the *Stenocercus* lowland clade 2, which presumably includes also *S. prionotus* (see results of Torres-Carvajal, 2007b), may have evolved allopatrically within the western Cerrado and adjacent Amazonia. Marked morphological differentiation and deep genetic divergences pose the question of how these ecologically similar species, which show broad overlap in environmental space occupancy (Fig. 6), have differentiated. Niche conservatism may lead populations to diverge when isolated by intervening unsuitable environmental conditions, as in the case of populations occurring in high elevations separated by lowlands (Wiens and Graham, 2005). It has been shown that closely related species occurring in parapatry and sharing similar ecological requirements may have diverged in allopatry followed by secondary contact (Graham et al., 2004; Wiens and Graham, 2005). In the *Stenocercus* clade 2, contact areas between species ranges broadly coincide with the limits of the upper Guaporé and Paraguay depressions (see definition in Ross, 1985). The Guaporé depression currently separates the Chapada dos Parecis plateau in western Brazil from the pre-Andean highlands to the west, where *S. caducus* is found; the Paraguay depression separates this plateau from the Brazilian shield to the east, where *S. sinesaccus* and some populations of *S. caducus* are found; and the area between (and north to) both depressions is occupied by *S. albolineatus* **sp. nov.** (Supplementary Fig. S6).

Divergence times between these three species are consistent with the timing of reported shifts in this region as a result of Andean orogeny. Lowlands between the Andean foothills and the Brazilian shield underwent large scale landscape transformations between 11.8 and 8 Mya, with shifts in the course and contacts of major rivers, marine incursions coming from both north and south, and the establishment and vanishing of large lacustrine or marine systems (Cook et al., 2012; Hernández et al., 2005; Hoorn, 2006; Lovejoy et al., 2006; Lundberg et al., 1998; Räsänen et al., 1995). Formation of large water bodies seems to have affected the composition of ecological communities at the Paraguay and Guaporé depressions (Cook et al., 2012; Lundberg et al., 1998), with connections between basins promoting faunal exchange (Lundberg et al., 1998; Montoya-Burgos, 2003; Ribeiro et al., 2013). Our results are consistent with the hypothesis that the formation of these water systems may have isolated the ancestor of *Stenocercus. caducus* from its eastern sister, while the later establishment or shifting courses of the Paraguay River could have led to the divergence of *S. sinesaccus* and *S. albolineatus* **sp. nov.**, in the absence of ecological differentiation. Geomorphological change in this region has also been associated with species divergences in other lizard groups (Werneck et al., 2012).

4.1.3. The Andean Stenocercus

The diversification and history of colonization in both Andean clades of *Stenocercus* (clades A and B) have been comprehensively addressed in the literature (Torres-Carvajal, 2007b), yet no information about the timing of diversification was previously available. Our results indicate that these Andean clades are as old as the cordillera itself; the highest areas corresponding to the present-day Andes reached up to 2000 m above the sea level by the onset of Andean *Stenocercus* diversification, at around 27 Mya (Garzione et al., 2008; Insel et al., 2012). On the other hand, while the MRCA of *Stenocercus* likely occupied part of the developing cordillera in the late Oligocene, our dating analysis indicates that most extant Andean lineages originated more recently, between the early and the late Miocene (Fig. 5). During this time, major orogenetic processes took place on both the central and northern Andes, resulting in pronounced uplift of the cordillera (Benjamin et al., 1987; Garzione et al., 2008; Garzione et al., 2006, 2007; Ghosh et al., 2006; Gregory-Wodzicki, 2000). In other animal groups, lineage diversification is also synchronous with Andean uplift (Chaves et al., 2011; Mendoza et al., 2015). Our results support a relationship between the increase in topographic complexity and diversification of the Andean *Stenocercus*. Yet, we also found evidence of cladogenesis associated to independent founder events from a central Andean source into the northern Andes, as well as repeated range expansions from the central to the southern cordillera, Chaco, and western Amazonia, a pattern observed in other groups as well (Mendoza et al., 2015).

5. Concluding remarks

Our results suggest that a complex set of biogeographic processes acted in the diversification of *Stenocercus* lizards, especially in the open and dry lowlands of the dry diagonal of South America. We found that habitat change and fragmentation resulting from past climatic and geographic shifts are consistent with inferred divergence times, current species ranges, and observed ecological differentiation in open and dry lowland settings. South American open biomes, including the Dry Forests, Caatinga, Chaco, and savannas of Brazilian Cerrado are of great interest to the study of Neotropical biogeography due to their unique history of climatic fluctuations, expected to have greatly affected the distribution of biodiversity (Prance, 2006). Our data on *Stenocercus* suggest that major landscape changes may have led to contrasting selective regimes across space. By favoring local adaptation, such variation may have fostered species divergence in the absence of pronounced geographic discontinuities, a hypothesis that deserves further examination in additional groups. The processes outlined herein may have been key in shaping unique faunas within the dry diagonal, such as that of the Chapada dos Parecis, a recognized center of endemism within the Brazilian Cerrado (Nogueira et al., 2011) where the new species, *S. albolineatus* **sp. nov.**, is found.

Acknowledgments

We would like to thank H. Zaher, C. Castro, A. B. de Carvalho (MZUSP), F. Curcio (UFMT), N. Maciel (UFG), G. Colli, Í. Arantes (CHUNB), A. Prudente (MPEG), F. Werneck (INPA), S. Gomides and P. Garcia (UFMG) and R. Avila (URCA) for access to specimens under their care; D. Pavan, F. Curcio, A. Hernando, C. Nogueira, P. Valdujo, H. Zaher, V. Xavier, R. Recoder, A. Camacho and Marco Sena for help in field or tissue samples; M. Sena and S. Geurgas for help at the molecular laboratory; M. Dewynter for providing photos of live animals; S. Pavan for advice on BioGeoBEARS implementation; and M. Strangas and D. Rivera for English review and comments on the manuscript. This study was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2003/10335-8 and 2011/50146-6), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and by the Dimensions of Biodiversity Program [FAPESP (BIOTA, 2013/50297-0), NSF (DOB 1343578), and NASA]. CS acknowledges funding from CNPq research fellowship (process # 309541/2012-3).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.09.010.

References

Ab'Saber, A.N., 2000. Spaces occupied by the expansion of dry climates in South America during the quaternary ice ages. Rev. Inst. Geol. 21, 71–78.

Akaike, H., 1974. New look at statistical-model identification. IEEE Trans. Automat. Control 19, 716–723.

Avila-Pires, T.C.S., 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Meded. 299, 1–706.

Benjamin, M.T., Johnson, N.M., Naeser, C.W., 1987. Recent rapid uplift in the Bolivian Andes – evidence from fission-track dating. Geology 15, 680–683.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Cadle, J.E., 1991. Systematics of lizards of the genus *Stenocercus* (Iguania, Tropiduridae) from Northern Peru – new species and comments on relationships and distribution patterns. Proc. Acad. Nat. Sci. Phila. 143, 1–96.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T., Moritz, C., 2009. Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. Science 323, 785–789.

Chaves, J.A., Weir, J.T., Smith, T.B., 2011. Diversification in *Adelomyia* hummingbirds follows Andean uplift. Mol. Ecol. 20, 4564–4576.

Cook, G.M., Chao, N.L., Beheregaray, L.B., 2012. Marine incursions, cryptic species and ecological diversification in Amazonia: the biogeographic history of the croaker genus *Plagioscion* (Sciaenidae). J. Biogeogr. 2012, 724–738.

Cohen, B.L., 2013. Rerooting the rDNA gene tree reveals phoronids to be 'brachiopods without shells'; dangers of wide taxon samples in metazoan phylogenetics (Phoronida; Brachiopoda). Zool. J. Linn. Soc. 167, 82–92.

Cope, E.D., 1862. Catalogues of the Reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uraguay Rivers, by Capt. Thos. J. Page, U.S.N.; and of those procured by Lieut. N. Michler, U.S. Top. Eng., commander of the expedition conducting the survey of the Atrato River. Proc. Acad. Nat. Sci. Phila. 14, 346–359.

Costa, L.P., 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. J. Biogeogr. 30, 71–86.

Cox, C.B., Moore, P.D., 2010. Biogeography – An Ecological and Evolutionary Approach. John Wiley & Sons, Hoboken, NJ, USA.

Cracraft, J., Prum, R.O., 1988. Patterns and processes of diversification – speciation and historical congruence in some Neotropical birds. Evolution 42, 603–620.

Crisp, M.D., Cook, L.G., 2012. Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? New Phytol. 196, 681–694.

Damasceno, R., Strangas, M.L., Carnaval, A.C., Rodrigues, M.T., Moritz, C., 2014. Revisiting the vanishing refuge model of diversification. Front. Genet. 5, 1–12.

Domingos, F.M.C.B., Bosque, R.J., Cassimiro, J., Colli, G.R., Rodrigues, M.T., Santos, M. G., Beheregaray, L.B., 2014. Out of the deep: cryptic speciation in a Neotropical gecko (Squamata, Phyllodactylidae) revealed by species delimitation methods. Mol. Phylogenet. Evol. 80, 113–124.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4, 699–710.

Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7, 1–8.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.

Duméril, A.M.C., 1851. Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle de Paris. Gide et Baudry/Roret, Paris.

Duméril, A.M.C., Bibron, G., 1837. Erpétologie Générale ou Histoire Naturelle Complete des Reptiles, vol. 4. Encyclopédique Roret, Paris.

ESRI, 2011. ArcGis Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Felsenstein, J., 2004. Inferring Phylogenies. Sinauer Associates, Sunderland.

Field, A., 2009. Discovering Statistics using SPSS. SAGE, Los Angeles, London, New Delhi, Singapore, Washington.

Fritts, T.H., 1974. A multivariate and evolutionary analysis of the Andean iguanid lizards of the genus *Stenocercus*. San Diego Soc. Nat. Hist. Mem. 7, 1–89.

Gamble, T., Colli, G.R., Rodrigues, M.T., Werneck, F.P., Simons, A.M., 2012. Phylogeny and cryptic diversity in geckos (*Phyllopezus*; Phyllodactylidae; Gekkota) from South America's open biomes. Mol. Phylogenet. Evol. 62, 943–953.

Garzione, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P., Mulch, A., 2008. Rise of the Andes. Science 320, 1304–1307.

Garzione, C.N., Molnar, P., Libarkin, J.C., MacFadden, B.J., 2006. Rapid late Miocene rise of the Bolivian Altiplano: evidence for removal of mantle lithosphere. Earth Planet. Sci. Lett. 241, 543–556.

Garzione, C.N., Molnar, P., Libarkin, J.C., MacFadden, B.J., 2007. Reply to comment on "Rapid late Miocene rise of the Bolivian Altiplano: evidence for removal of mantle lithosphere" by Garzione et al. (2006), Earth Planet. Sci. Lett. 241 (2006) 543–556. Earth Planet. Sci. Lett. 259, 630–633.

Ghosh, P., Garzione, C.N., Eiler, J.M., 2006. Rapid uplift of the Altiplano revealed through $^{13}C^{18}O$ bonds in paleosol carbonates. Science 311, 511–515.

Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J., Moritz, C., 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58, 1781–1793.

Gregory-Wodzicki, K.M., 2000. Uplift history of the Central and Northern Andes: a review. Geol. Soc. Am. Bull. 112, 1091–1105.

Guedes, T.B., Sawaya, R.J., Nogueira, C.D., 2014. Biogeography, vicariance and conservation of snakes of the neglected and endangered Caatinga region, north-eastern Brazil. J. Biogeogr. 41, 919–931.

Guindon, S., Gascuel, O., 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Syst. Biol. 52, 696–704.

Hall, J.P.W., Harvey, D.J., 2002. The phylogeography of Amazonia revisited: new evidence from riodinid butterflies. Evolution 56, 1489–1497.

Hernández, R.M., Jordan, T.E., Dalenz Farjat, A., Echavarría, L., Idleman, B.D., Reynolds, J.H., 2005. Age, distribution, tectonics, and eustatic controls of the Paranense and Caribbean marine transgressions in southern Bolivia and Argentina. J. S. Am. Earth Sci. 19, 495–512.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hoorn, C., 2006. Mangrove forests and marine incursions in Neogene Amazonia (lower Apaporis River, Colombia). Palaios 21, 197–209.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, 927–931.

Huelsenbeck, J.P., Bollback, J.P., Levine, A.M., 2002. Inferring the root of a phylogenetic tree. Syst. Biol. 51, 32–43.

Insel, N., Poulsen, C.J., Ehlers, T.A., Sturm, C., 2012. Response of meteoric delta $\delta^{18}O$ to surface uplift – implications for Cenozoic Andean Plateau growth. Earth Planet. Sci. Lett. 317, 262–272.

Köhler, G., Lehr, E., 2015. Two new species of lizards of the genus *Stenocercus* (Iguania, Tropiduridae) from central Peru. Zootaxa 3956, 413–427.

Landis, M.J., Matzke, N.J., Moore, B.R., Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. Syst. Biol. 62, 789–804.

Lanfear, R., Calcott, B., Ho, S.Y.W., Guidon, S., 2012. Partition finder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701.

Lomolino, M.V., Riddle, B.R., Brown, J.H., 2006. Biogeography. Sinauer Associates Inc., Sunderland, MA.

Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol. Lett. 11, 995–1003.

Lovejoy, N.R., Albert, J.S., Crampton, W.G.R., 2006. Miocene marine incursions and marine/freshwater transitions: evidence from Neotropical fishes. J. S. Am. Earth Sci. 21, 5–13.

Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L., Wesselingh, F.P., 1998. The stage for Neotropical fish diversification: a history of tropical South American rivers. In: Malabarba, L.R., Reis, R.E., Yari, R.P., Lucena, Z.M., Lucena, C.A.S. (Eds.), Phylogeny and Classification of Neotropical Fishes. Edipucrs, Porto Alegre, pp. 13–48.

MacDonald, G., 2003. Biogeography – Introduction to Space, Time and Life. Hohn Wiley & Sons, New York, NY.

Marris, E., 2005. The forgotten ecosystem. Nature 437, 944–945.

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Front. Biogeogr. 5, 242–248.

Matzke, N.J., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Syst. Biol. 63, 951–970.

Mayr, E., 1954. Change of genetic environment and evolution. In: Huxley, J., Hardy, A. C., Ford, E.B. (Eds.), Evolution as a Process. Allen & Unwin, London, pp. 157–180.

Mendoza, A.M., Ospina, O.E., Cárdenas-Henao, H., García-R, J.C., 2015. A likelihood inference of historical biogeography in the world's most diverse terrestrial vertebrate genus: diversification of direct-developing frogs (Craugastoridae: *Pristimantis*) across the Neotropics. Mol. Phylogenet. Evol. 85, 50–58.

Montoya-Burgos, J.I., 2003. Historical biogeography of the catfish genus *Hypostomus* (Siluriformes: Loricariidae), with implications on the diversification of Neotropical ichthyofauna. Mol. Ecol. 12, 1855–1867.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: an integrated molecular approach. Annu. Rev. Ecol. Syst. 31, 533–563.

Müller, F., 1880. Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verh. Naturforsch. Ges. Basel 7, 120–165.

Nascimento, F.F., Lazar, A., Menezes, A.N., Durans, A.D., Moreira, J.C., Salazar-Bravo, J., D'Andrea, P.S., Bonvicino, C.R., 2013. The role of historical barriers in the diversification processes in open vegetation formations during the Miocene/Pliocene using an ancient rodent lineage as a model. PLoS One 8, 1–13.

Nogueira, C., Ribeiro, S., Costa, G.C., Colli, G., 2011. Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. J. Biogeogr. 38, 1907–1922.

Nogueira, C., Rodrigues, M.T., 2006. The genus *Stenocercus* (Squamata: Tropiduridae) in extra-Amazonian Brazil, with the description of two new species. S. Am. J. Herpetol. 1, 149–166.

Nosil, P., 2012. Ecological Speciation. Oxford University Press, New York, USA.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burguess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Strand, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T. H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51, 933–938.

Padial, J.M., Miralles, A., De la Riva, I., Vences, M., 2010. The integrative future of taxonomy. Front. Zool. 7, 1–14.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K., Butterworth, C.A., 2004. Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philos. Trans. R. Soc. Lond. B: Biol. Sci. 359, 515–537.

Prado, C.P.A., Haddad, C.F.B., Zamudio, K.R., 2012. Cryptic lineages and Pleistocene population expansion in a Brazilian Cerrado frog. Mol. Ecol. 21, 921–941.

Prance, G.T., 2006. Tropical savannas and seasonally dry forests: an introduction. J. Biogeogr. 33, 385–386.

Prates, I., Rodrigues, M.T., Melo-Sampaio, P.R., Carnaval, A.C., 2015. Phylogenetic relationships of Amazonian anole lizards (*Dactyloa*): taxonomic implications, new insights about phenotypic evolution and the timing of diversification. Mol. Phylogenet. Evol. 82, 258–268.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Räsänen, M.E., Linna, A.M., Santos, J.C.R., Negri, F.R., 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269, 386–390.

Redford, K.H., Taber, A., Simonetti, J.A., 1990. There is more to biodiversity than tropical rainforests. Conserv. Biol. 4, 328–330.

Ree, R.H., Moore, B.R., Webb, C.O., Donoghue, M.J., 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 59, 2299–2311.

Ribas, C.C., Aleixo, A., Nogueira, A.C.R., Miyaki, C.Y., Cracraft, J., 2012. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. Proc. R. Soc. Lond. B: Biol. Sci. 279, 681–689.

Ribas, C.C., Gaban-Lima, R., Miyaki, C.Y., Cracraft, J., 2005. Historical biogeography and diversification within the Neotropical parrot genus *Pionopsitta* (Aves: Psittacidae). J. Biogeogr. 32, 1409–1427.

Ribas, C.C., Moyle, R.G., Miyaki, C.Y., Cracraft, J., 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. Proc. Roy. Soc. B – Biol. Sci. 274, 2399–2408.

Ribeiro, A.C., Jacob, R.M., Silva, R.R.S.R., Lima, F.C.T., Ferreira, D.C., Ferreira, K.M., Mariguela, T.C., Pereira, L.H.G., Oliveira, C., 2013. Distributions and phylogeographic data of rheophilic freshwater fishes provide evidences on the geographic extension of a Central-Brazilian Amazonian palaeoplateau in the area of the present day Pantanal Wetland. Neotrop. Ichthyol. 11, 319–326.

Ribeiro, S.C., Roberto, I.J., Sales, D.L., Almeida, W.O., 2009. Distribution extension of *Stenocercus squarrosus* Nogueira and Rodrigues, 2006 (Reptilia, Squamata, Tropiduridae) in Northeastern Brazil. Biotemas 22, 165–167.

Ronquist, F., 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst. Biol. 46, 195–203.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 31, 1–4.

Ross, J.L.S., 1985. Relevo Brasileiro: Uma Nova Proposta de Classificação. Rev. Dep. Geogr. 4, 25–39.

Sánchez-Azofeifa, G.A., Kalacska, M., Quesada, M., Calvo-Alvarado, J.C., Nassar, J.M., Rodríguez, J.P., 2005. Need for integrated research for sustainable future in tropical dry forest. Conserv. Biol. 19, 285–286.

Santos, M.G., Nogueira, C., Giugliano, L.G., Colli, G.R., 2014. Landscape evolution and phylogeography of *Micrablepharus atticolus* (Squamata, Gymnophthalmidae), an endemic lizard of the Brazilian Cerrado. J. Biogeogr. 41, 1506–1519.

Silva, D.J., Santos-Filho, M., Sanaiotti, M.T., 2010. Aspectos ecológicos de *Stenocercus caducus* (Squamata: Iguanidae) em fragmentos de floresta no sudoeste de Mato Grosso, Brasil. Rev Colomb. Cienc. Anim. 2, 286–302.

Silva, N.S.C., 2007. Caracterização morfométrica de uma população topotípica de *Stenocercus caducus* (Iguana, Tropiduridae) e de material adicional do gênero *Stenocercus* depositado na Coleção Zoológica da UFMT. Departamento de Ciências Básicas e Produção Animal. UFMT, Cuiabá, MT, p. 31.

Smith, B.T., McCormack, J.E., Cuervo, A.M., Hickerson, M.J., Aleixo, A., Cadena, C.D., Perez-Eman, J., Burney, C.W., Xie, X.O., Harvey, M.G., Faircloth, B.C., Glenn, T.C., Derryberry, E.P., Prejean, J., Fields, S., Brumfield, R.T., 2014. The drivers of tropical speciation. Nature 515, 406–409.

SPSS, 2011. IBM SPSS Statistics, Version 20. IBM.

Steindachner, F., 1867. Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zoologie, Reptilien. Kaiserlich-Königliche Hof- und Staatsdruckerei, Wien.

Tamura, K., Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10, 512–526.

Teixeira Jr., M., 2010. Os lagartos do vale do rio Peruaçu, MG, Brasil: Aspectos biogeográficos, história natural e implicações para a conservação. Master Dissertation. Departamento de Zoologia. Universidade de São Paulo, São Paulo, p. 132.

Torres-Carvajal, O., 2000. Ecuadorian Lizards of the Genus *Stenocercus* (Squamata: Tropiduridae). Sci. Pap. Nat. Hist. Mus. Univ. Kans. 2000, pp. 1–38.

Torres-Carvajal, O., 2005. A new species of *Stenocercus* (Squamata, Iguania) from central-western Brazil with a key to Brazilian *Stenocercus*. Phyllomedusa 4, 123–132.

Torres-Carvajal, O., 2007a. A taxonomic revision of South American *Stenocercus* (Squamata: Iguania) lizards. Herpetol. Monogr. 21, 76–178.

Torres-Carvajal, O., 2007b. Phylogeny and biogeography of a large radiation of Andean lizards (Iguania, *Stenocercus*). Zool. Scr. 36, 311–326.

Torres-Carvajal, O., 2009. Sistemática filogenética de las lagartijas del género *Stenocercus* (Squamata: Iguania) de los Andes del norte. Rev. Mex. Biodivers. 80, 727–740.

Torres-Carvajal, O., Mafla-Endara, P., 2013. A new cryptic species of *Stenocercus* (Squamata: Iguanidae) from the Andes of Ecuador. J. Herpetol. 47, 184–190.

Torres-Carvajal, O., Schulte, J.A., Cadle, J.E., 2006. Phylogenetic relationships of South American lizards of the genus *Stenocercus* (Squamata: Iguania): a new approach using a general mixture model for gene sequence data. Mol. Phylogenet. Evol. 39, 171–185.

Valdujo, P.H., Carnaval, A.C.O.Q., Graham, C.H., 2013. Environmental correlates of anuran beta diversity in the Brazilian Cerrado. Ecography 36, 708–717.

Vanzolini, P.E., 1988. Distributional patterns of South American lizards. In: Vanzolini, P.E., Heyer, W. (Eds.), Proceedings of a Workshop on Neotropical Distributional Patterns. Academia Brasileira de Ciências, Rio de Janeiro, pp. 317–342.

Vanzolini, P.E., 1994. Brazilian reptiles in open and closed formations: evolutionary implications. An. Acad. Bras. Cienc. 66, 173–176.

Vanzolini, P.E., Williams, E.E., 1981. The vanishing refuge: a mechanism for ecogeographical speciation. Pap. Avul. Zool. 34, 251–255.

Venegas, P.J., Duran, V., Garcia-Burneo, K., 2013. A new species of arboreal iguanid lizard, genus *Stenocercus* (Squamata: Iguania), from central Peru. Zootaxa 3609, 291–301.

Venegas, P.J., Echevarría, L.Y., Alvarez, S.C., 2014. A new species of spiny-tailed iguanid lizard (Iguania: *Stenocercus*) from northwestern Peru. Zootaxa 3753, 47–58.

Wagenmakers, E.-J., Farrell, S., 2004. AIC model selection using Akaike weights. Psychon. Bull. Rev. 11, 192–196.

Werneck, F.P., Gamble, T., Colli, G., Rodrigues, M.T., Sites Jr., J.W., 2012. Deep diversification and long-term persistence in the South American 'Dry Diagonal': integrating continent-wide phylogeography and distribution modeling of geckos. Evolution, 1–21.

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519–539.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.