



Geographic variation and systematic review of the lizard genus *Vanzosaura* (Squamata, Gymnophthalmidae), with the description of a new species

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Vanzosaura rubricauda (Boulenger, 1902) is a small-bodied gymnophthalmid lizard widespread in dry biomes of South America. Throughout its distribution, *V. rubricauda* populations experience contrasting environmental conditions, and a marked disjunction occurs in the central portion of the Cerrado biome. Previous studies indicate that *V. rubricauda* may be a species complex, and here we used mitochondrial DNA data and external morphology to test for population differentiation and its systematic implications for the genus. We found three geographically cohesive groups recovered as well resolved, and strongly supported mitochondrial DNA (mtDNA) haploclades that are differentiated with respect to morphometry, meristics, and colour pattern. In light of the observed differences, we propose a new taxonomic rearrangement of the genus, where we: (1) restrict *V. rubricauda* to Chaco and western Cerrado regions; (2) resurrect *Vanzosaura multiscutata* (Amaral, 1933) **comb. nov.** for Caatinga populations; and (3) describe *Vanzosaura savanicola* **sp. nov.** for the eastern Cerrado region of Brazil. The new species is diagnosed from its congeners by having longer limbs and tail, fewer smooth subcaudals, and genetic distances ranging from 5 to 13%. The new species, along with other recent discoveries, highlights the Jalapão-Serra Geral region as one of the most important areas of endemism for Cerrado squamates.

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ADDITIONAL KEYWORDS: Caatinga – Chaco – Cerrado – diversity – endemism – microteiid lizards – phylogeny – *Vanzosaura savanicola* **sp. nov.**

INTRODUCTION

The lizard genus *Vanzosaura* Rodrigues, 1991 is widespread along the diagonal of dry biomes in South America (Rodrigues, 1991; Vanzolini & Carvalho,

1991). It is readily diagnosed from other genera of Gymnophthalmidae by the absence of frontoparietals and movable eyelids, presence of prefrontals, dorsals smooth, cycloid, and imbricate, presence of an external ear, limbs well developed with four digits on the forelimbs, and sixteen scales around midbody.

The genus is currently considered monotypic and represented by *Vanzosaura rubricauda* (Boulenger,

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1902), a small-bodied terrestrial species that is heliophilous, insectivorous, and an active forager, but with cryptic habits (Vitt, 1995; Rodrigues, 2003; Mesquita *et al.*, 2006). The species is usually found associated with leaf litter and sandy soils in open to semi-open dry habitats, with populations occurring in contrasting environmental conditions along the Chaco, Cerrado, and Caatinga biomes (Vanzolini, Ramos-Costa & Vitt, 1980; Cruz, 1994; Vitt, 1995; Mesquita *et al.*, 2006; Nogueira, 2006; Delfim & Freire, 2007; Recoder, Ribeiro & Rodrigues, 2013).

TAXONOMIC HISTORY

The type species was described as *Gymnophthalmus rubricauda* by Boulenger (1902) based on a single specimen from Cruz del Eje, province of Córdoba, in the Dry Chaco of Argentina. The author considered the new species distinct from other known *Gymnophthalmus* 'in having the nasal shield divided and scales in even numbers' (Boulenger, 1902: 24). The new species was also characterized by having 16 scales around midbody, and prefrontals separated by the contact between the frontal and the internasal. Amaral (1933: 73) described *Gymnophthalmus multiscutatus* based on an individual from 'Villa Nova', municipality of Senhor do Bonfim, state of Bahia, in the Caatinga of north-eastern Brazil. His diagnosis was based on comparisons with *Gymnophthalmus lineatus* Linnaeus, 1758, and thus he was apparently unaware of Boulenger's *G. rubricauda*. The author mentions the presence of 15 scales around midbody and prefrontals in contact medially as diagnostic characters of the new species. Nevertheless, Amaral (1934, 1935) obtained two specimens of *G. multiscutatus* from the state of Paraíba, north-eastern Brazil, both with 16 scales around midbody, and he noticed the separation between the prefrontals in one exemplar, which by consequence superimposed the diagnoses of *G. multiscutatus* and *G. rubricauda*. Stuart (1939) reviewed the species of *Gymnophthalmus*, but unaware of Amaral's considerations, recognized both species as valid, diagnosed by the absence (*G. rubricauda*) or presence (*G. multiscutatus*) of contact between the prefrontals. Gallardo (1951) examined specimens of *G. rubricauda* from Argentina, provided new localities for the distribution of the species, and commented on an individual from El Sauce (province of Córdoba) that had prefrontals in contact, remarking for the first time that the condition was similar between this species and *G. multiscutatus*.

While describing *Procellosaurinus*, Rodrigues (1991) noticed that populations of *Gymnophthalmus* from the South American dry diagonal shared morphological characters with this new genus, such as the presence of

two supraoculars, three superciliaries, and three pairs of mentals, which distinguished *G. multiscutatus* and *G. rubricauda* from other *Gymnophthalmus* species (presenting one supraocular, two superciliaries, and two pairs of mentals). The author then redefined *Gymnophthalmus* and proposed the genus *Vanzosaura* for populations occurring from north-eastern South America south to the Argentinian Dry Chaco, differing from *Procellosaurinus* by the absence of frontoparietals and hemipenial morphology. With a lack of evidence, and considering that characters discussed in the literature (i.e. contact of prefrontals, number of scales around midbody) were not sufficient to diagnose *G. multiscutatus* from *G. rubricauda*, Rodrigues (1991) considered *G. multiscutatus* as a junior synonym of *V. rubricauda* (Boulenger, 1902).

At the time, *V. rubricauda* was known from the Chaco and Caatinga, and just marginally in the western Cerrado, in the Brazilian state of Mato Grosso do Sul (Vanzolini & Carvalho, 1991). Nevertheless, new populations were subsequently recorded at several locations within the Cerrado, including the eastern portion of the biome (Vitt *et al.*, 2005; Werneck & Colli, 2006; Recoder & Nogueira, 2007; Teixeira Jr., 2010; Recoder *et al.*, 2011). It also became apparent that the large disjunction in the middle of its range was probably not a sampling artifact, given that the species was never recorded at sites in the Central Brazilian Plateau, despite intensive sampling efforts there (Pavan, 2001; Colli, Bastos & Araújo, 2002; Nogueira, Valdujo & França, 2005; Silva Jr. *et al.*, 2005).

Vanzolini *et al.* (1980) mentioned that Caatinga populations of *V. rubricauda* (*G. multiscutatus* at the time) presented variation in colour pattern. Delfim & Freire (2007) observed local polymorphism in colour pattern in populations from the northern portion of the Caatinga, and observed variation in the number of longitudinal stripes, including intermediate states, between the 'simple' (absence of stripes) and 'complex' (presence of 12 longitudinal stripes) patterns discussed by Vanzolini *et al.* (1980). Recently, Recoder *et al.* (2013) observed geographical variation in morphometry among populations of *V. rubricauda*, and showed that populations from the eastern Cerrado were well differentiated from others in having shorter trunks and longer forelimbs.

Because of this remarkable intraspecific morphological variation and disjunct distribution, it seemed necessary to reevaluate the taxonomic status of *V. rubricauda*. Herein, we provide a systematic review of the genus *Vanzosaura* based on a range-wide data set, including morphology (quantitative and qualitative) and mitochondrial DNA. We thus propose a new taxonomic arrangement for the genus, and discuss intraspecific variation.

MATERIAL AND METHODS

MOLECULAR DATA

We obtained partial mitochondrial DNA (mtDNA) sequences from cytochrome *b* (*cytb*) and NADH dehydrogenase subunit 4 (*ND4*) genes to infer phylogenetic relationships within *Vanzosaura*, and to check for concordance between morphological and phylogeographic patterns. Our sampling included 186 individuals (some samples failed to amplify for *ND4*) from 40 localities (Appendix 1). We used two individuals of *Micrablepharus maximiliani* (Reinhardt & Lütken, 1862) as out-groups in the analyses. A fragment of nearly 740 bp of *cytb* was amplified by polymerase chain reaction (PCR) using primers CB1 (5'-CCATCCAACATCTCAGCATGATGAAA-3') and CB3 (5'-GGCAAATAGGAARTATCATTTC-3'), described by Kocher *et al.* (1989), and a fragment of nearly 870 bp of *ND4* using the primers ND4F (5'-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3') and Leu (5'-CATTACTTTTACTTGGATTTCACCA-3') from Arévalo, Davis & Sites (1994). For details regarding laboratory procedures and protocols for DNA extraction, PCR amplification, and sequencing, see Werneck *et al.* (2012a).

PHYLOGENETIC ANALYSES

We estimated mtDNA variation (nucleotide and haplotype diversity) using DNAsp 5 (Rozas *et al.*, 2003), and performed maximum likelihood (ML) analyses on the concatenated mtDNA data set (1612 bp in total) with RAxML 7.0.0 (Stamatakis, 2006) to characterize phylogeographic structure. We implemented the analyses with the GTR + Gamma model, as only GTR-based models are included in RAxML, 200 independent ML searches, and 1000 non-parametric bootstrap replicates to assess nodal support (Felsenstein, 1985). We calculated net

among-group distances between major haploclades within *Vanzosaura* with MEGA 5.05 (Tamura *et al.*, 2011), using uncorrected and Tamura–Nei corrected distances (Tamura & Nei, 1993), and 500 bootstrap replicates to estimate standard errors.

MORPHOLOGICAL CHARACTERS

For the morphology data set we examined a total of 845 specimens (458 males and 387 females) from 95 localities. The material examined (Appendix 2) is housed in the following institutions: Coleção Herpetológica do Departamento de Botânica, Ecologia e Zoologia da Universidade Federal do Rio Grande do Norte (CHDBEZ), Natal, Brazil; Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB), João Pessoa, Brazil; Coleção Herpetológica da Universidade de Brasília (CHUNB), Brasília, Brazil; Fundación Miguel Lillo (FML), San Miguel de Tucumán, Brazil; Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, Brazil; Museo Nacional de Historia Natural del Paraguay (MNHNP), San Lorenzo, Brazil; Museo de Historia Natural Noel Kempff Mercado (MNKM), Santa Cruz de la Sierra, Brazil; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu de Zoologia Prof. Adão José Cardoso (ZUEC), Campinas, Brazil.

We recorded seven scale counts: DOR, dorsal scales between posterior margin of hindlimbs and interparietal; FPO, total number of femoral pores in males; GUL, gulars, between posterior pair of mentals and median interbrachial; LFT, lamellae under fourth toe; SAM, scales around midbody; SCA, number of smooth (non-keeled) subcaudals in a longitudinal line; and VEN, ventral scales between anal plate and median interbrachial. We also recorded the presence of contact or separation between prefrontals (Fig. 1).

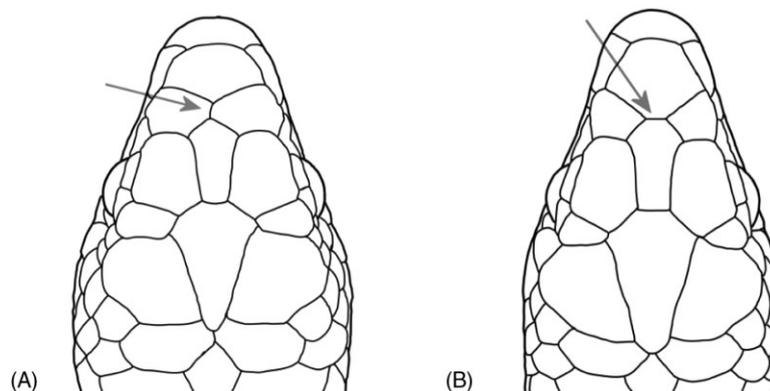


Figure 1. Dorsal view of the head of *Vanzosaura* spp., with arrows indicating the presence (A) or absence (B) of contact between the prefrontals.

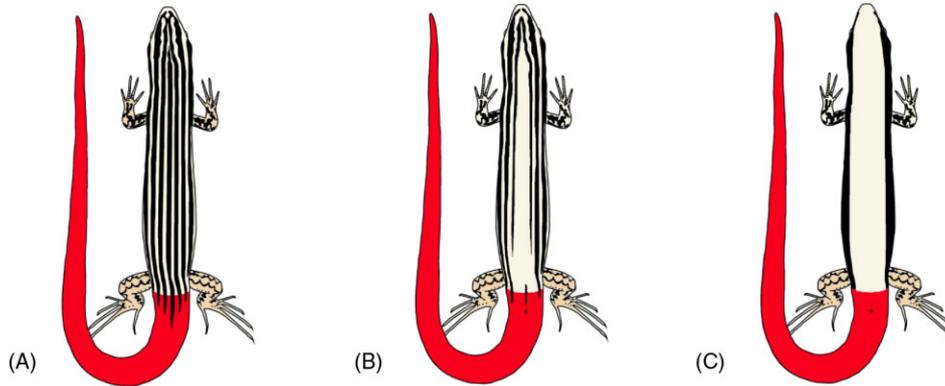


Figure 2. Colour patterns recognized in *Vanzosaura* spp.: complex (A); intermediate (B); and simple (C). See text for details.

We defined three colour patterns based on the number and position of white dorsal longitudinal stripes (Fig. 2): complex, with between 8 and twelve continuous white stripes on the dorsal surface; simple, defined by the absence of stripes, or presence of only a pair of dorsolateral stripes; and intermediate, with between four and eight dorsal stripes. In the complex pattern, lateral stripes may be lacking and mid-dorsal stripes are present, whereas in the intermediate pattern, dorsal and lateral stripes may be lacking and mid-dorsal stripes are absent. We also recorded 12 morphometric measurements with a digital caliper under a stereomicroscope (to the nearest 0.01 mm), following the description given in Recoder *et al.* (2013): FAL, forearm length; FEM, femur length; FTL, hind foot length; HH, head height; HL, head length; HUM, humerus length; HW, head width; INL, interbrachial–nasal length; SVL, snout–vent length; TAL, tail length (not regenerated); TIB, tibia length; TRL, trunk length between limbs.

STATISTICAL ANALYSES

We log-transformed morphometric data to meet the requirements of normality (Zar, 2010). As juveniles were weakly represented in samples, we excluded individuals with $SVL < 24.5$ mm (outliers, $N = 41$). The remaining data set did not deviate from normality (Lilliefors test; $P > 0.1$), and conformed to homogeneity of variances among geographical groups for all variables (Levene's test; $P > 0.05$). We excluded tail length from multivariate analyses because a large proportion of individuals examined (about 80%) had regenerated or broken tails. Because *V. rubricauda* is sexually dimorphic in at least one population (Vitt, 1982), we tested for within-population morphometric dimorphism with a one-way ANOVA, and analysed the sexes separately in subsequent analysis. As meristic data were not normally distributed, we used non-parametric statistics. For geographic compari-

sons, we used the haploclades recovered by the mtDNA phylogeny as groups (see Results). To test for group differences in shape we performed a one-way MANOVA. A discriminant analysis was performed and a classification matrix estimated, to assess the degree of morphometric differentiation among these groups. Statistical analyses were performed in R (R Development Core Team, 2011) and SPSS 20.0.

RESULTS

DNA POLYMORPHISM, GENETIC DISTANCES, AND PHYLOGEOGRAPHIC STRUCTURE

From the 186 *Vanzosaura* mtDNA samples analysed (both genes combined), we resolved 154 unique haplotypes (haplotype diversity, $H_d = 0.994$), and nucleotide diversity (π) was 9.6%. The phylogeographic structure recovered three well-resolved and strongly supported haploclades that are reciprocally monophyletic, which is consistent with the geographic samples from the caatinga biome (CAA), eastern Cerrado (ECE), and western Cerrado and Chaco (WCE + CHA), respectively (Fig. 3). Corrected mtDNA distances between the three major mtDNA groups varied from 5.5% (between ECE and WCE + CHA) to 13.1% (between CAA and WCE + CHA; and CAA and ECE; Table 1). The phylogenetic trees, including the complete data set and all unique haplotypes, are available as online supporting information (Figures S1–S2).

MORPHOLOGICAL VARIATION

The scale counts were significantly different between sexes, with females presenting more DOR (Mann–Whitney, $U_{1,645} = 20\,874$, $P < 0.01$) and VEN ($U_{1,630} = 8976$, $P < 0.01$). All scale counts varied significantly across geographic regions for both sexes (Kruskal–Wallis test, $P < 0.01$), except for the number of scales around midbody (SAM) and gulars (GUL)

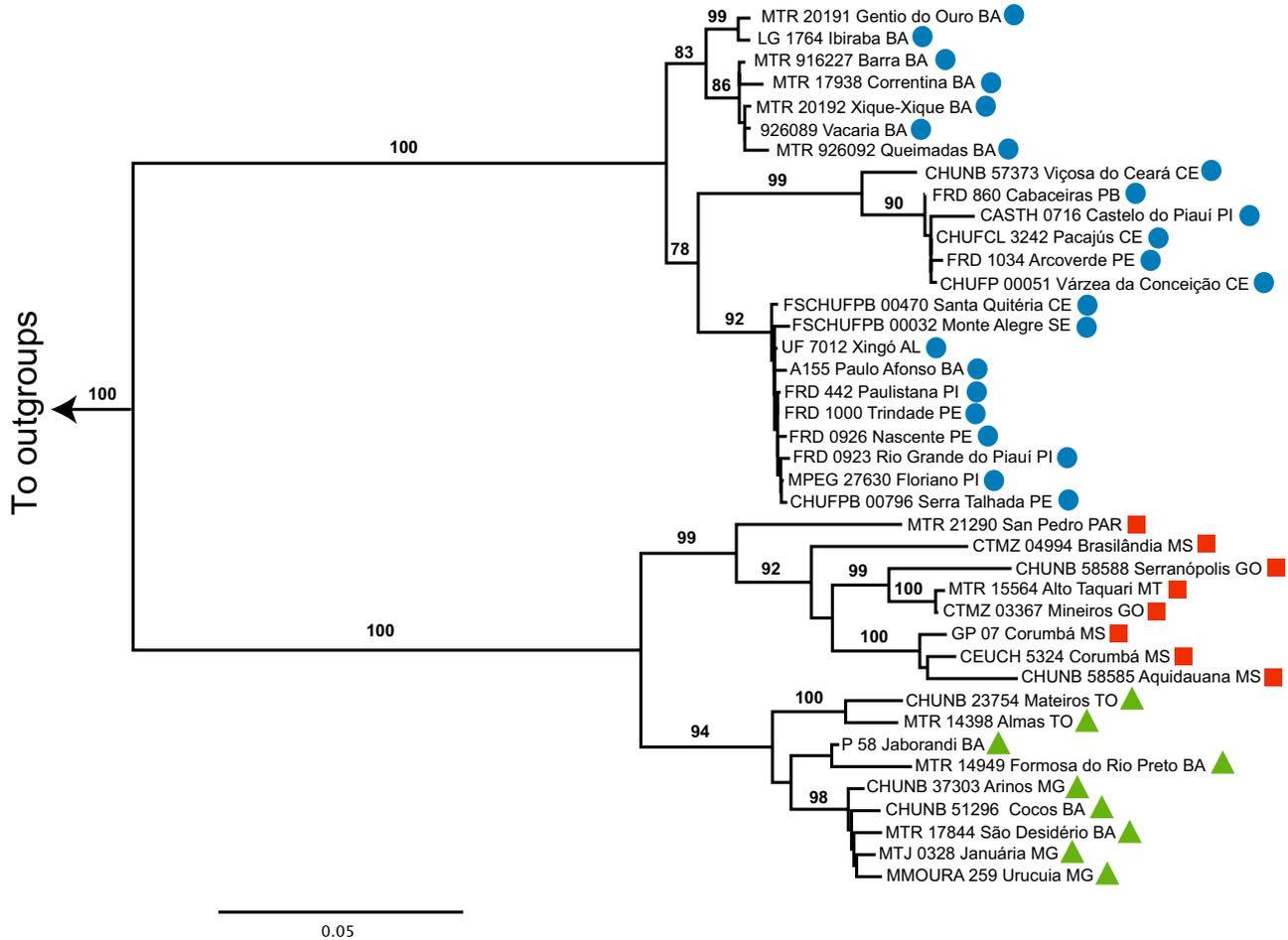


Figure 3. *Vanzosaura* concatenated mitochondrial maximum-likelihood genealogy based on one individual per locality ($N = 40$). Trees based on the complete data set ($N = 186$) and on unique haplotypes ($N = 154$) are presented in Figures S1–S2. Terminal names show the voucher numbers followed by a short code for the locality (for full details, see Appendix 1). Nodes with bootstrap nodal support values ≥ 75 are depicted in the tree. Colours and symbols represent the geographical groups and the species limits proposed here: circles, *Vanzosaura multiscutata* comb. nov. from Caatinga (CAA); squares, *Vanzosaura rubricauda* from Chaco and western Cerrado (CHA + WCE); triangles, *Vanzosaura savanicola* sp. nov. from the Eastern Cerrado (ECE).

Table 1. Net among-group mtDNA distances between major clades of *Vanzosaura*

	CAA	WCE + CHA	ECE
CAA	–	0.131 (0.011)	0.132 (0.011)
WCE + CHA	0.111 (0.998)	–	0.055 (0.005)
ECE	0.112 (0.008)	0.049 (0.004)	–

Values below the diagonal are uncorrected p-distances and respective standard errors, whereas values above the diagonal are Tamura–Nei corrected p-distances and respective standard errors, calculated using 500 bootstrap replicates; CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.

(Table 2). The number of smooth subcaudals (SCA) in the ECE was significantly smaller than in other populations, whereas the number of femoral pores (FPO) was significantly lower in CAA populations (Fig. 4).

The counts of dorsals (DOR) and ventrals (VEN) were also lower in the ECE (Fig. 4). The condition of contact between the prefrontal scales was polymorphic in *Vanzosaura* ($\chi^2 = 259.7$, $P < 0.01$; Fig. 5).

Table 2. Results of the nonparametric Kruskal–Wallis test for comparison among geographic groups for seven scale counts, as represented by the average and the standard deviation values of each count, and the significance level (*P*) of the geographic variation

	Sex	CAA		ECE		WCE+CHA		<i>P</i>
		Average	SD	Average	SD	Average	SD	
DOR	F	35.9	0.20	34.4	0.24	36.4	1.33	< 0.01
	M	34.0	0.20	32.8	0.17	34.6	1.18	< 0.01
VEN	F	26.3	0.19	24.7	0.24	26.4	1.36	< 0.01
	M	23.2	0.21	22.1	0.16	23.3	1.29	< 0.01
GUL	F	10.3	0.16	10.5	0.10	10.5	0.80	0.023
	M	10.3	0.12	10.6	0.10	10.5	0.72	0.019
SAM	F	16.0	0.04	16.0	0	16.0	0	0.165
	M	16.0	0.05	16.0	0	16.0	0	0.202
LFT	F	16.8	0.17	15.7	0.12	16.4	0.91	< 0.01
	M	17.0	0.17	16.0	0.13	16.5	0.68	< 0.01
FPO	F	–	–	–	–	–	–	–
	M	11.2	0.21	13.7	0.13	13.6	0.95	< 0.01
SCA	F	35.0	1.15	16.8	0.76	37.1	4.21	< 0.01
	M	32.8	1.17	13.8	0.56	33.4	3.14	< 0.01

P = 0.017 indicates significance after Bonferroni correction; CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.

Populations from the CAA had, on average, a higher frequency of contact between prefrontal scales (81.1%), whereas the frequency of separation between the scales was on average higher in the ECE (66.4%) and the WCE + CHA (88.7%) groups (Fig. 5).

The colour patterns of *V. rubricauda* showed variation at the local level, especially within the CAA group. In general, the ‘complex’ pattern prevails, and is the only pattern observed in 13 out of the 19 samples examined (Fig. 6). The colour pattern ‘simple’ was observed in three populations of the CAA group (eight samples) and in a single population of the CHA group.

Geographical groups differed significantly in morphometry for both males (MANOVA, Wilk’s $\lambda = 0.257$, $F_{9,392} = 42.22$, $P < 0.01$) and females (Wilk’s $\lambda = 0.331$, $F_{9,322} = 25.73$, $P < 0.01$). The first discriminant function, which accounted for 83.1% of total variation in females and 72.6% in males, was highly and positively correlated with variation in FAL and HUM, and negatively in TRL, thus representing a contrast between trunk elongation and forelimb size for both sexes (Fig. 7; Table 3). The classification matrix (Table 4) based on absolute and cross-validated data indicated that populations from ECE are well differentiated from other groups, with about 90% of the individuals correctly classified. The WCE + CHA and CAA presented a lower percentage of correct classification of the individuals (59–77 and 70–81%, respectively).

The relative tail length varied significantly among groups (ANCOVA; $F_{2,164} = 13.70$; $P < 0.01$), with ECE

populations having longer tails relative to body size in comparison with other regional groups (Tukey’s honestly significant difference test; $P < 0.05$).

The differences observed here in morphometry, colour pattern, and scale counts, allied with a large genetic distance estimated among haploclades, supports a new taxonomic rearrangement, and the recognition of a new species of *Vanzosaura*.

TAXONOMIC ACCOUNTS

Vanzosaura savanicola sp. nov. (Figs 8, 9)

Holotype: MZUSP 103202 (field number MTR 14754) from Estação Ecológica Serra Geral do Tocantins (11°14′51.3″S, 46°55′05.1″W; 590 m a.s.l.; datum WGS84), municipality of Almas, state of Tocantins, Brazil (Fig. 10); collected on 4 February 2008 by M.T. Rodrigues, R.S. Recoder, M. Teixeira Jr, A. Camacho, T. Mott, P.H. Valdujo, J.M. Ghellere, P. Nunes, and C. Nogueira.

Paratypes: MZUSP 103186–103201 (field numbers MTR 14244, 14257, 14304, 14398, 14565, 14624, 14664–14665, 14675, 14740, 14226, 14405, 14567, 14729, 14732, 14735); all from the same locality as the holotype (11°06′–11°18′S; 46°45′–46°56′W), collected between 26 January and 4 February 2008, by the same collectors as for the holotype.

Diagnosis: *Vanzosaura savanicola* sp. nov. is characterized by: (1) 6–21 smooth subcaudals; (2) 12–16 femoral pores in males; (3) snout acute in profile; (4)

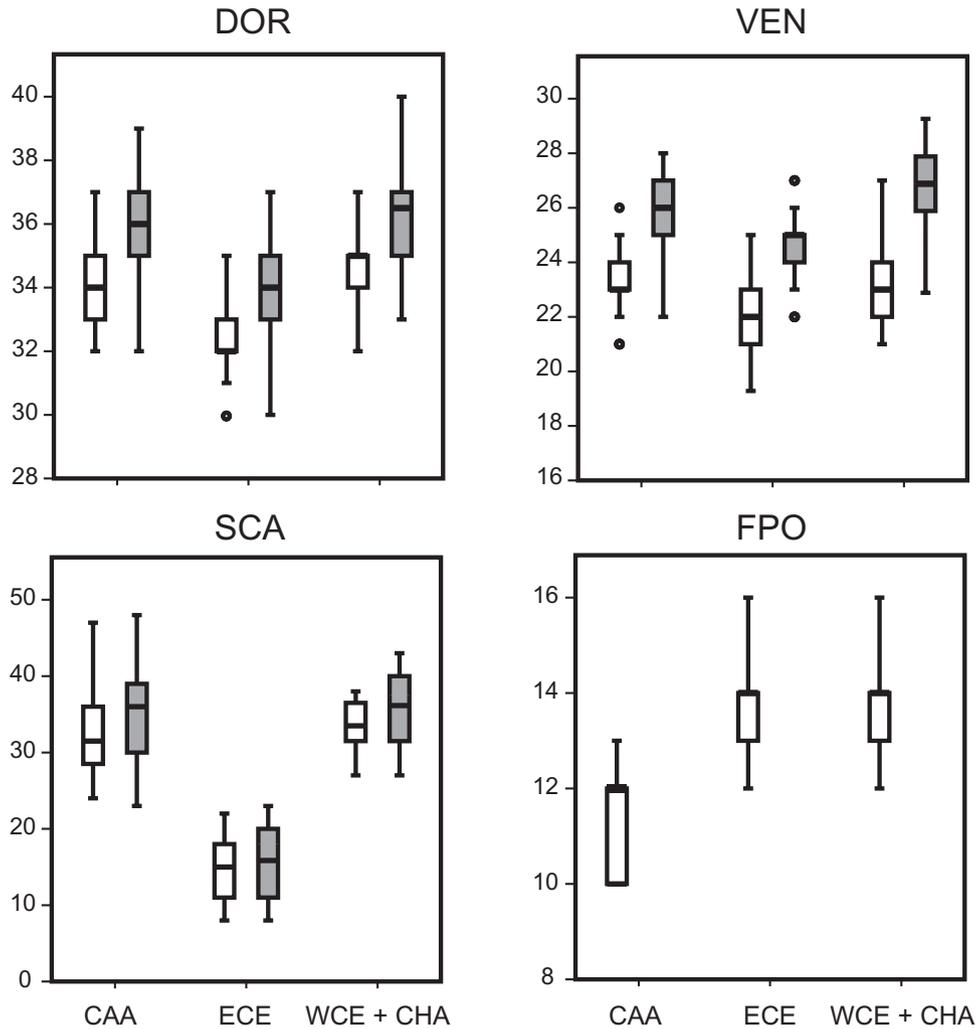


Figure 4. Regional variation in the scale counts of *Vanzosaura* populations: DOR, number of dorsal scales; VEN, number of ventral scales, SCA, number of smooth subcaudals; and FPO, number of femoral pores. White bars represent males; grey bars represent females; CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.

forelimbs long relative to trunk length, with FAL $60.8 \pm 0.03\%$ of TRL in females and $63.3 \pm 0.02\%$ in males; (5) colour pattern 'complex', with eight to ten whitish dorsal stripes that become irregular or discontinuous on the head; (6) inner and outer ventral row of scales nearly subequal in width; (7) prefrontal scales usually separated (66%); (8) small size for the genus, with largest male attaining 34.5 mm SVL and largest female attaining 35.6 mm SVL; (9) proportionally long tails, with an average size of complete tails (not regenerated) in relation to body size (TAL/SVL) of 1.74 ± 0.19 .

Description of the holotype (Fig. 9): An adult male, with 34.2 mm SVL. Body cylindrical, elongate. Limbs well developed. Rostral high, highly visible from above; wide contact with internasal, nasals, and first

supralabial. Internasal (frontonasal) unique, hexagonal, in wide contact with nasals, and a narrow contact with frontal. Two prefrontals, slightly longer than wide; not contacting each other, in contact with internasal, nasal, frontal, first superciliary, first supraocular, and loreal. Frontal longer than wide, slightly wider anteriorly. Frontoparietals absent. Interparietal large, longer than wide; much wider anteriorly; posterior end with round border, transposing the posterior margin of parietals. Two large symmetrical parietals, extending to temporal region; similar in size to interparietal. Two supraoculars, first much larger than second. Three superciliaries, first slightly longer.

Nasal single, divided ventrally and half divided dorsally, elongate, subrectangular, with nostril central. Loreal small, quadrangular, in contact with

prefrontal. Frenocular small and pentagonal, smaller than loreal. Seven supralabials, fourth under the eye, longer and narrow; fifth higher. One long subocular between frenocular and postocular, very narrow below

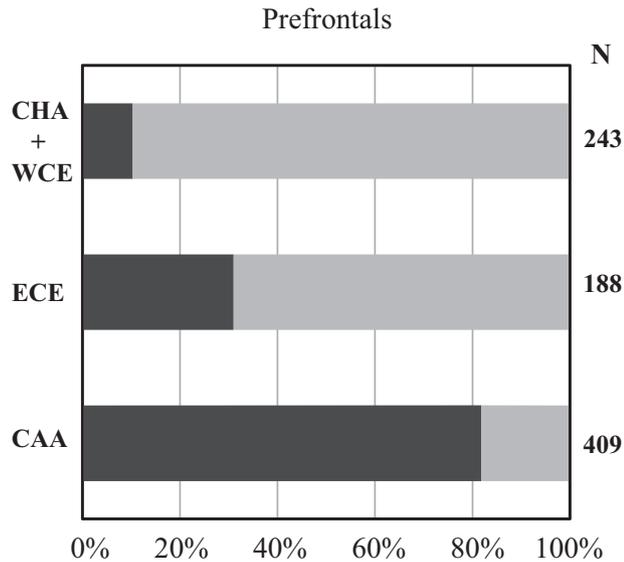


Figure 5. Frequencies of contact (dark grey) and separation (light grey) between the prefrontal scales in the populations from three regional groups of *Vanzosaura*: CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.

the eye. Temporals large, smooth, rounded, and imbricate. External ear present, reduced, partially covered by scales. Movable eyelids absent.

Symphyseal large, wider than long, followed by a larger post-symphyseal and three pairs of mentals. Mentals laterally in contact with infralabials, and contacting each other medially in an asymmetrical suture, first pair smaller and almost quadrangular, posterior pair larger and almost pentagonal. Seven infralabials, fourth and fifth in contact with posterior mental. Presence of a groove, anteriorly arched, between ear openings separated from mentals by a row of scales, or two in the lateral side. Gulars smaller anteriorly, rounded, increasing in size posteriorly until the interbrachials.

Dorsals smooth, cycloid, and imbricate, forming oblique rows; 16 rows around midbody; a pair of mid-dorsal rows narrower than adjacent ones. Seven interbrachials, central largest, conical, and pointed posteriorly. Ventrals large, smooth, subhexagonal, and subequal in size, in four longitudinal rows. Anal plate with four large scales: one anterior, one posterior, and two larger laterals. Tail long, cylindrical, caudals rounded, imbricate, smooth on dorsal surfaces, smooth anteriorly, and becoming keeled distally on ventral surfaces. Eight smooth subcaudals in a longitudinal line; only regenerated portion of tail with keeled scales. Seven femoral pores on each side. Scales covered by numerous irregularly distributed sensorial pits.

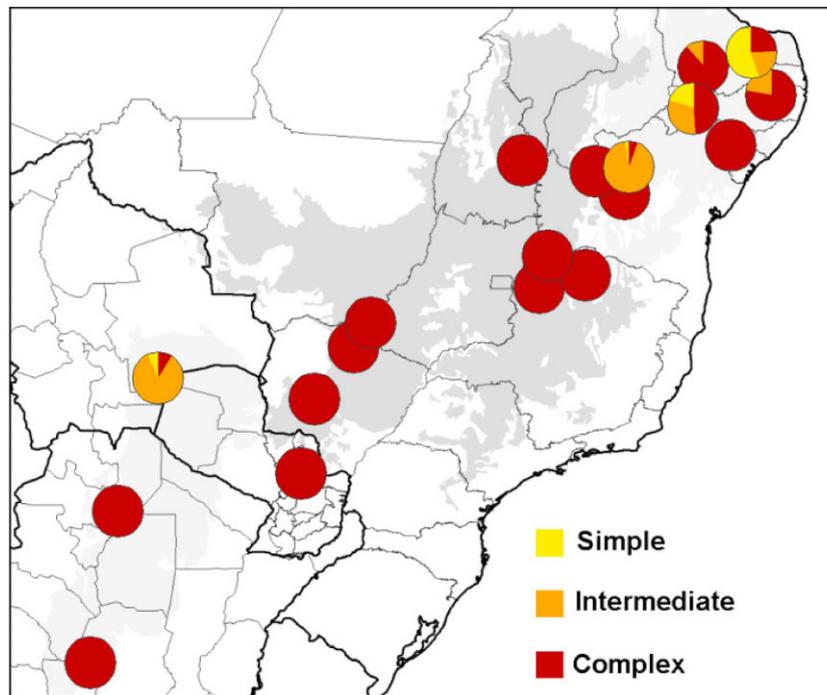


Figure 6. Frequencies of colour patterns observed in different populations of *Vanzosaura* spp. ($N > 10$ individuals) across the distribution of the genus.

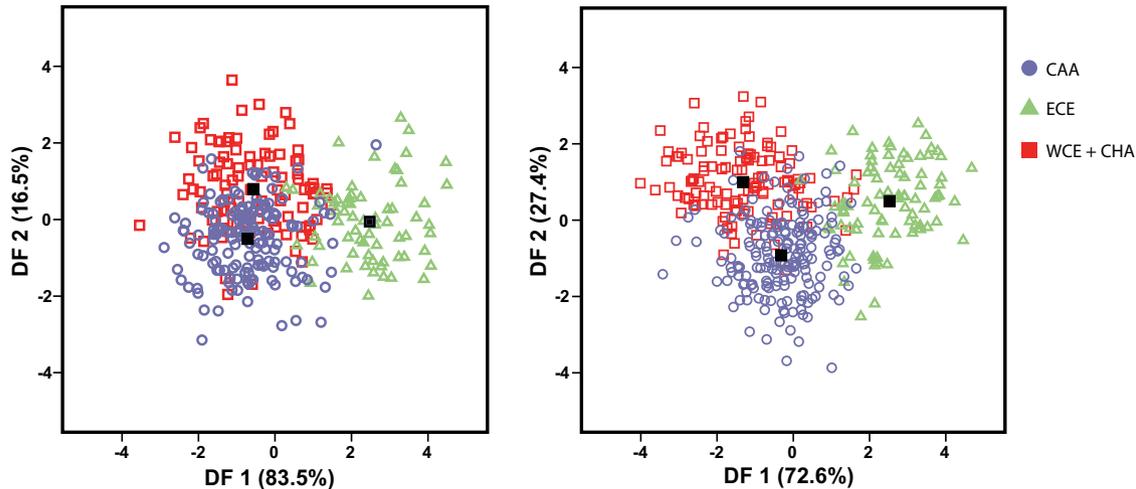


Figure 7. Results of a discriminant analysis on the log-transformed morphometric variables for females (left) and males (right) of *Vanzosaura*. The centroids of each geographical group are shown (solid black squares). Symbols correspond to the regions: □, western Cerrado + Chaco (WCE + CHA); △, eastern Cerrado (ECE); ○, Caatinga, (CAA).

Table 3. Results of discriminant analysis on log-transformed morphometric data for males and females of *Vanzosaura*

Characters	Males		Females	
	DF1	DF2	DF1	DF2
TRL	-0.284	0.010	-0.347	0.499
FAL	0.490	0.307	0.392	0.553
HUM	0.270	0.351	0.375	0.379
TIB	0.264	0.155	0.213	0.433
FTL	0.110	0.416	0.192	0.629
FEM	0.088	0.084	0.032	0.387
HW	0.200	-0.169	0.187	0.511
HL	0.185	-0.205	0.145	0.348
HH	-0.051	-0.165	-0.001	0.482
INL	0.121	-0.238	0.037	0.175
Eigenvalues	1.75	0.50	1.55	0.30
% variance	72.6	27.4	83.5	16.5
Cumulative %	72.6	100	83.5	100

DF1, discriminant function 1; DF2, discriminant function 2.

Dorsal surfaces of forelimbs with large scales, wider than long, smaller ventrally; palm with small conical granules; four fingers, inner finger absent externally. Dorsal surfaces of hindlimbs with large scales; thigh with smaller scales ventrally; soles with small conical granules; five toes. Seventeen single lamellae under fourth toe.

Background coloration dark gray, with ten longitudinal white stripes on dorsal surface that become discontinuous on the head. Ventral surfaces cream,

gular and mental region with discrete small dark blotches. Limbs reddish with dark blotches on dorsal surfaces of arms. Tail bright red; dorsal stripes extending only to proximal quarter of tail length.

Measurements of holotype (in mm): SVL 34.2; INL 12.3; TRL 16.6; HH 2.8; HW 4.3; HL 7.0; FEM 4.8; TIB 3.8; FTL 6.5; HUM 3.2; HAL 6.6; TAL 12.9 + 34.4.

Variation: The new species is sexually dimorphic, with females larger than males (ANOVA, $F_{1,158} = 4.14$, $P < 0.05$), and having larger TRL (ANCOVA, $F_{1,158} = 18.37$, $P < 0.01$), whereas males are significantly larger than females in FEM, TIB, FAL, HW, and HL ($P < 0.01$). Populations from the Jalapão region in the state of Tocantins and from the adjacent Serra Geral Plateau in north-western Bahia are very similar in overall morphology, with minimal variation. Nevertheless, samples from the southern portion of the Serra Geral plateau (border of states of Bahia and Minas Gerais) are more variable, sharing some characteristics with *V. multiscutata* comb. nov. (e.g. contact between prefrontals and high number of smooth subcaudals). When the two portions of the distribution of *V. savanicola* sp. nov. are considered separately, significant variation is observed in the condition of separation between prefrontals (99% in northern populations; 45% in the southern) and the number of smooth subcaudals (6–13 in north; 11–23 in south). In a few individuals (not quantified) the subocular is divided or fused with the preocular, but generally only on one side.

Table 4. Classification matrix based on the results of the discriminant analysis on log-transformed morphometric data for males and females of *Vanzosaura*

Classification matrix			Predicted group membership		
			CHA + WCE	ECE	CAA
Original	% males	CHA+WCE	76.9	8.3	14.8
		ECE	8.2	90.4	1.4
		CAA	15.4	3.3	81.3
	% females	CHA+WCE	63.2	5.7	31.1
		ECE	6.3	92.1	1.6
		CAA	24.0	4.0	72.0
Cross-validated (jackknife)	% males	CHA+WCE	73.1	10.2	16.7
		ECE	9.6	87.7	2.7
		CAA	16.3	4.1	79.7
	% females	CHA+WCE	59.4	7.5	33.0
		ECE	7.9	88.9	3.2
		CAA	24.0	6.0	70.0

Percentages of individuals correctly classified in each group are highlighted in bold; CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.



Figure 8. *Vanzosaura savanicola* sp. nov. in life, MZUSP 103197 (field number MTR 14675), paratype. A female individual with 28.2 mm snout–vent length (SVL) from Estação Ecológica Serra Geral do Tocantins, municipality of Almas, Tocantins state, Central Brazil.

Comparisons: *Vanzosaura savanicola* sp. nov. is readily diagnosed from *V. multiscutata* comb. nov. and *V. rubricauda* by having eight to 22 smooth subcaudals (more than 25 subcaudals in *V. multiscutata* comb. nov. and *V. rubricauda*), snout acute in profile (snout rounded in profile), and forelimbs long in proportion to body length, with FAL 60.7% of TRL in females and 63.6% in males (forelimbs shorter, FAL on average 54.8% of TRL in females and 57.8% in males in *V. multiscutata* comb. nov.; 54.8% of TRL in females and 57.5% in males in *V. rubricauda*).

Vanzosaura savanicola sp. nov. can also be distinguished from *V. multiscutata* comb. nov. and *V. rubricauda* by its smaller size, with the largest male attaining 34.5 mm in SVL and the largest female attaining 35.6 mm in SVL (37.6 and 38.0 mm, respectively, in *V. multiscutata* comb. nov.; 36.0 and 41.5 mm, respectively, in *V. rubricauda*), and by having proportionally longer tails, with a mean TAL/SVL of 1.74 (mean TAL/SVL of 1.65 and 1.53 in *V. multiscutata* comb. nov. and *V. rubricauda*, respectively). Furthermore, *V. savanicola* sp. nov. can be distinguished from *V. multiscutata* comb. nov. by presenting 12–16 femoral pores in males (10–13; Table 2), prefrontals usually separate, 66% (prefrontals usually in contact, 81%), ventral row of scales nearly subequal in width (inner row of ventral scales narrower than outer), and complex colour pattern (colour pattern complex, single, or intermediate; Fig. 11). Strongly supported mtDNA haploclades and corrected distances of up to 13% distinguish *V. savanicola* sp. nov. from *V. multiscutata* comb. nov., and up to 5% distinguish *V. savanicola* sp. nov. from *V. rubricauda*.

Etymology: The specific epithet makes reference to the distribution of the new species in savannah habitats, the predominant type of vegetation in the Cerrado region of central South America.

Distribution and natural history: *Vanzosaura savanicola* sp. nov. is endemic to the north-eastern

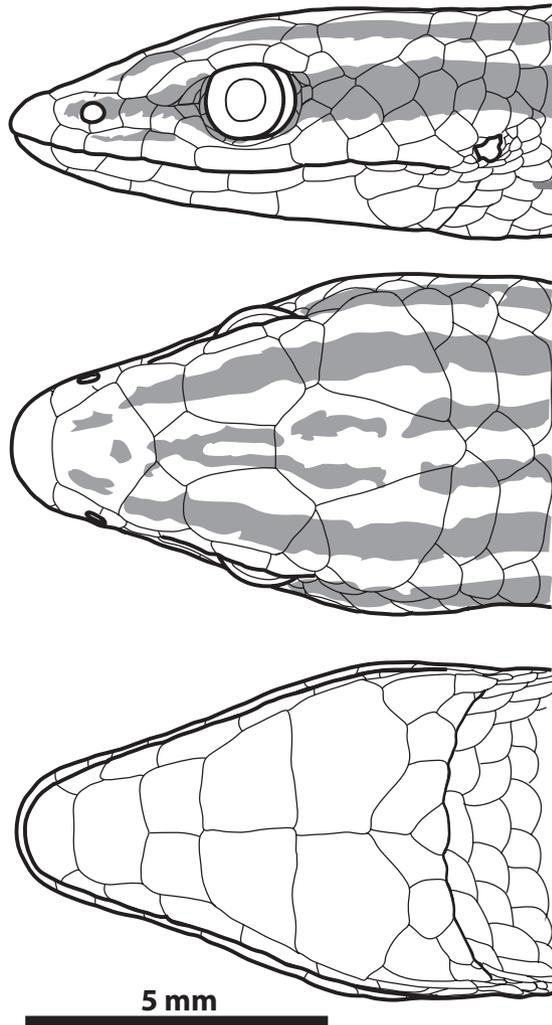


Figure 9. Lateral, dorsal, and ventral views of the head of the holotype of *Vanzosaura savanicola* sp. nov. (MZUSP 103202).

portion of the Brazilian Cerrado (Fig. 10). The species is locally abundant, usually representing one of the most common species in lizard assemblages throughout its range (Recoder & Nogueira, 2007; Vitt *et al.*, 2007; Recoder *et al.*, 2011). The species occurs in open habitats such as grasslands and savannas, and is active at the hottest hours of sunny days (Mesquita *et al.*, 2006; Recoder & Nogueira, 2007; Recoder *et al.*, 2011). It is most commonly found within the leaf litter or herbaceous layer in sandy soil microhabitats (Vitt *et al.*, 2007; Teixeira Jr., 2010), and feeds upon a variety of small-sized arthropods, with spiders representing the most frequent type of prey (Mesquita *et al.*, 2006; Teixeira Jr., 2010). Reproduction is seasonal in one population studied, with the presence of pregnant females and males with nuptial coloration (i.e. the development of a reddish coloration in the

gular and cloacal regions) in the rainy season, and with females producing multiple clutches of two eggs (Teixeira Jr., 2010).

Vanzosaura multiscutata (Amaral, 1933)

comb. nov. (Figs 12, 13)

Gymnophthalmus multiscutatus: Amaral, 1933, p. 23, figs 51–55.

Vanzosaura rubricauda: Rodrigues, 1991, p. 340.

Holotype: MZUSP 40079, adult male from the municipality of Senhor do Bonfim, (10°27'S; 40°11'W), state of Bahia, Brazil (Fig. 10), collected by E. Garbe on 1908.

Diagnosis: *Vanzosaura multiscutata* comb. nov. is characterized by: (1) 25–47 smooth subcaudals; (2) 10–13 femoral pores in males; (3) snout round in profile; (4) forelimbs proportionally short in relation to trunk length, with FAL $54.8 \pm 0.02\%$ of TRL in females and $57.8 \pm 0.02\%$ in males; (5) colour pattern single, complex, or intermediate, when complex, dorsal stripes merge in one continuous stripe on the snout; (6) inner row of ventral scales narrower than outer; (7) prefrontal scales usually in contact (81%); (8) medium size for the genus, with largest male attaining an SVL of 37.6 mm, and largest female attaining an SVL of 38.0 mm; (9) proportionally short tails for the genus, with an average rate of complete tails (not regenerated) in relation to body size (TAL/SVL) of 1.65 ± 0.10 .

Measurements of holotype (in mm): SVL 33.4; INL 11.0; TRL 19.1; HH 3.3; HW 4.3; HL 6.4; FEM 4.4; TIB 3.5; FTL 5.5; HUM 2.7; FAL 5.2.

Variation: *Vanzosaura multiscutata* comb. nov. is sexually dimorphic (Vitt, 1982), with females slightly larger than males (ANOVA, $F_{1,336} = 8.39$, $P < 0.05$). Females have a larger TRL (ANCOVA, $F_{1,336} = 141.95$, $P < 0.01$), whereas males have significantly larger head dimensions (HH, HW, and HL) and longer limbs (FEM, TIB, HUM, and FAL) (ANCOVA, $P < 0.01$). Some populations of *V. multiscutata* comb. nov. are highly polymorphic in colour pattern (Delfim & Freire, 2007), especially at the Cariri/Seridó region of Caatinga (the states of Rio Grande do Norte, Paraíba, and Pernambuco), and at the right bank of the São Francisco River (Xique-Xique, state of Bahia). In most localities, however, the 'complex' pattern is the only one present (Fig. 5).

Distribution and natural history: *Vanzosaura multiscutata* comb. nov. is widely distributed in the Caatinga of north-eastern Brazil, at low to moderate elevations (Fig. 10). A single population was found

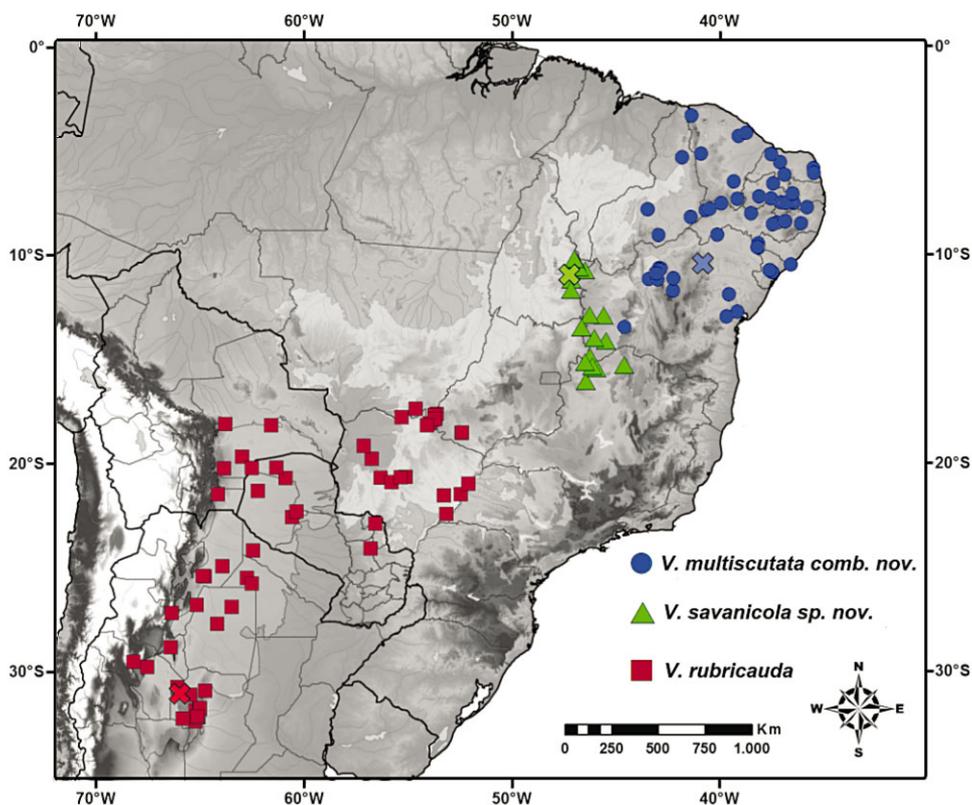


Figure 10. Distribution of *Vanzosaura* species along the diagonal of dry biomes of South America: *Vanzosaura multiscutata* comb. nov. (circles); *Vanzosaura savanicola* sp. nov. (triangles); and *Vanzosaura rubricauda* (squares). Type localities are represented by crosses.

within the eastern Cerrado, in a dry forest habitat in the municipality of Santa Maria da Vitória, state of Bahia, representing a potential contact zone. The species is found in open habitats, and occupies a variety of microhabitats over sandy or rocky soils (Vanzolini *et al.*, 1980; Vitt, 1995; Delfim & Freire, 2007). The species is cryptic in its activity patterns, and feeds upon a variety of small-sized arthropods such as spiders, roaches, and termites (Moraes, 1993; Vitt, 1995). Reproduction is continuous for both males and females in the two populations studied in Caatinga, with year-round oviposition, and females produce multiple clutches of two eggs (Vitt, 1982; Moraes, 1993).

Vanzosaura rubricauda (Boulenger, 1902)

Gymnophthalmus rubricauda: Boulenger, 1902, p. 24.

Vanzosaura rubricauda: Rodrigues, 1991, p. 340.

Holotype: BMNH 1946.8.2, from the municipality of Cruz del Eje, province of Córdoba, Argentina.

Diagnosis: *Vanzosaura rubricauda* is characterized by: (1) 27–43 smooth subcaudals; (2) 12–16 femoral

pores in males; (3) snout round in profile; (4) forelimbs proportionally short in relation to trunk length, with $FAL\ 54.8 \pm 0.02\%$ of TRL in females and $57.5 \pm 0.02\%$ in males; (5) colour pattern variable, ranging from no stripes to 12 whitish dorsal stripes, which become irregular or discontinuous on the head; (6) inner ventral row of scales slightly narrower or subequal in relation to the external scales; (7) prefrontal scales usually separated (89%); (8) medium to large size for the genus, with the largest male attaining an SVL of 36.0 mm and the largest female attaining an SVL of 41.5 mm; (9) proportionally short tails for the genus, with an average rate of complete tails (not regenerated) in relation to body size (TAL/SVL) of 1.51 ± 0.14 .

Variation: As noted for the other species, the sexes are dimorphic in size, with females having a larger SVL (ANOVA; $F_{1,221} = 52.06$, $P < 0.01$) and a larger TRL (ANCOVA, $F_{1,228} = 40.80$, $P < 0.01$), whereas males have longer FEM ($F_{1,228} = 85.21$, $P < 0.01$) and HW ($F_{1,228} = 33.80$, $P < 0.01$). Populations from the western Cerrado of Brazil and Paraguay are distinct from Chaco populations in having smaller body sizes



Figure 11. Colour pattern variation in live specimens of *Vanzosaura*. Individuals of *Vanzosaura savanicola* *sp. nov.* from A, Mateiros, Tocantins (C. Nogueira) and B, Januária, Minas Gerais (M. Teixeira Jr.); *Vanzosaura multiscutata* *comb. nov.* from C, Senhor do Bonfim, Bahia (R. Recoder), D, Correntina, Bahia (M.A. Freitas), E, Santo Inácio, Bahia (M.T. Rodrigues), and F, Vacaria, Bahia (M.T. Rodrigues); *Vanzosaura rubricauda* from G, Laguna Blanca, Paraguai (J. Miller) and H, Mineiros, Goiás, Brazil (C. Nogueira).



Figure 12. Holotype of *Vanzosaura multiscutata* (Amaral, 1933) **comb. nov.**, MZUSP 40079, adult male from municipality of Senhor do Bonfim, Bahia, Brazil.



Figure 13. *Vanzosaura multiscutata* (Amaral, 1933) **comb. nov.**, in life, field number MTR 24601, topotype. Adult female with a snout-vent length (SVL) of 35.6 mm from the municipality of Senhor do Bonfim, Bahia, Brazil.

(ANOVA; females, $F_{1,98} = 17.63$, $P < 0.01$; males, $F_{1,120} = 27.50$, $P < 0.01$), proportionally longer tails (ANCOVA; $F_{1,54} = 9.27$, $P < 0.01$), and fewer ventrals (Mann-Whitney, $U_{1,132} = 1256.5$, $P < 0.05$). Nevertheless, morphological differences are subtle, and individuals from both regions cannot be readily distinguished based on the meristic data used in this study. The Chaco populations are also locally variable, with some individuals having contact between the prefrontals (19%), a condition that is not observed in the western Cerrado populations (Fig. 4), and presenting polymorphism in colour pattern in a population from the province of Santa Cruz, Bolivia, a condition that is only observed in populations of *V. multiscutata* **comb. nov.** from the Caatinga (Fig. 5).

Distribution and natural history: *Vanzosaura rubricauda* occurs along the Dry Chaco region of Argentina, Paraguay, and Bolivia, and in the Cerrado region of eastern Paraguay and western Brazil in the states of Mato Grosso, Mato Grosso do Sul, and Goiás (Fig. 10). In the province of Salta, in the Chaco region of Argentina, annual activity and reproduction is highly seasonal, with individuals being found in the hottest months (Cruz, 1994). The species is found in open formations, and in the Cerrado region it is found almost exclusively in savannah and grassland in regions with sandy soils (Nogueira, 2006; Valdujo *et al.*, 2009).

Remarks: The holotype of *V. rubricauda* is currently in bad condition (P. Nunes, pers. comm.). Nevertheless, it preserves characters that are still useful to recognize the species. A well-preserved specimen from Cruz del Eje (MACN 12504), close to the type locality, is housed in the Museo Nacional de Ciencias Naturales 'Bernardino Rivadavia' in Buenos Aires, Argentina.

DISCUSSION

As expected, based on the wide distribution that encompasses strongly contrasting environmental conditions and the large gap in the range, significant variation in morphology and phylogenetic structure was observed among *Vanzosaura* populations. It became clear that a taxonomic re-evaluation was necessary for the genus, a task that could only be accomplished under a quantitative framework to address the increased availability of study material in the last few decades, especially from the Cerrado biome. We hypothesize boundaries for three geographical groups, leaving some interesting intraspecific variation to be further explored when denser molecular, ecological, and fine-scale morphological sampling become available.

For example, although populations from the Chaco and western portion of the Cerrado are geographically separated by the Paraguay River and adjacent wetlands (Fig. 10), and present differences in morphometry (i.e. Chacoan individuals are on average larger, more elongate, and have shorter tails), samples from both regions cannot be diagnosed based on scale counts or coloration. Furthermore, the paucity of Chacoan individuals in our phylogenetic sampling precludes us from assessing with stronger confidence whether populations from the Chaco (CHA) and the western portion of the Cerrado (WCE) are differentiated at the genetic level. A congruent evolutionary pattern in three major phylogenetic groups, consistent with the CAA, ECE, and CHA+WCE geographical groups, was recently

reported for the gecko *Phyllopezus pollicaris* (Spix, 1825) species complex, which is co-distributed with *Vanzosaura* across the ‘dry diagonal’ (Werneck, 2011; Werneck *et al.*, 2012a). Despite the fact that in the study of Werneck *et al.* (2012a) the CAA and ECE populations were more closely related than the ECE and CHA+WCE populations, as reported here for *Vanzosaura*, the CHA and WCE populations were genetically clustered and assigned to a single candidate species. An explicit comparative phylogeographic study is currently in progress to address whether these patterns show spatial and temporal congruence, and their major biogeographical implications (F.P. Werneck, unpubl. data).

Also interesting is the geographical variation observed within the new species described here, *V. savanicola* sp. nov. The type series and nearby populations from the Jalapão region are readily diagnosed from *V. multiscutata* comb. nov. and *V. rubricauda* in morphometry (i.e. smaller body size, shorter trunks, larger limbs, and longer tails), scalation (i.e. fewer dorsals, ventrals, and subcaudals), and coloration (i.e. some individuals presenting a complex pattern of eight wide whitish stripes, from the loss of two pairs of lateral stripes). Nevertheless, the southern populations of *V. savanicola* sp. nov., although also diagnosable based on scalation, present intermediate conditions in most morphological characters when compared with *V. multiscutata* comb. nov. For instance, the complex pattern of coloration is more similar (presence of ten narrow whitish stripes), a larger proportion of contact between prefrontals is present, the number of subcaudals is slightly larger, and the contrast between forelimb and trunk lengths is less accentuated. More samples are needed from the central portion of the Serra Geral plateau in western Bahia to assess if the geographic variation observed is clinal or categorical.

The ‘simple’ pattern of coloration (i.e. absence or presence of a single pair of stripes), although prevalent in species of other closely related gymnophthalmid genera (e.g. *Procellosaurinus*, *Psilophthalmus*, and *Gymnophthalmus*) is rare in *Vanzosaura*. In fact, the ‘complex’ pattern is unique to *Vanzosaura* when compared with these closely related genera (forming the clade Gymnophthalminae). The observed variation in colour pattern among populations of *Vanzosaura* spp. is not congruent with the observed variation in other morphological characters. This fact suggests that historical factors alone cannot explain the geographical pattern. For example, although several populations of *V. multiscutata* comb. nov. show local polymorphism in coloration, a single population of *V. rubricauda* (Izozog) also showed this pattern. The ‘complex’ pattern is prevalent in the Cerrado biome for both *V. rubricauda* and *V. savanicola* sp. nov.

Delfim & Freire (2007) suggested an association between the ‘simple’ pattern of coloration and sandy soils on a sample from the northern Caatinga region. Although this relationship is not evident in the Cerrado and the dunes of the São Francisco River, with the latter a geologically and historically complex region at the Caatinga (Rodrigues, 1996; Passoni, Benozzati & Rodrigues, 2008; Siedschlag *et al.*, 2010), we cannot discard a relationship between environmental variation and colour pattern. In fact, other populations in which polymorphism was observed (i.e. Izozog in the Bolivian Chaco, and Exu and Catimbau in the Caatingas) are also characterized by sandy soil areas (Gonzales, 1998; Rodrigues & Santos, 2008), but this assertion needs further investigation.

The description of another new species from the Serra Geral plateau adds to the already high number of endemic squamate species known in this region (Colli *et al.*, 2003; Rodrigues *et al.*, 2008; Colli *et al.*, 2009; Ribeiro, Castro-Mello & Nogueira, 2009; Pinto & Curcio, 2011; Ribeiro *et al.*, 2011; Teixeira Jr. *et al.*, 2013), thereby increasing its value as an important area of endemism, historical stability, and species richness across the Brazilian Cerrado (Nogueira *et al.*, 2011; Werneck *et al.*, 2012b).

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APPENDIX 1

GENETIC SAMPLING

Vanzosaura multiscutata comb. nov. ($N = 73$). BRAZIL. Alagoas: Xingó (UF 7012, 7011). Bahia: Barra (MTR 916227); Correntina (MTR 17938); Gentio do Ouro (MTR 20191); Ibiraba (LG 1764, 1766, MTR 3579, 3580, 3582); Paulo Afonso (A155); Queimadas (MTR 907954, 907983, 907992, 926092, 926117, 926138); Santa Maria da Vitória (MTR 17967–17969); Vacaria (MTR 3478, 3479, 3480, 3482, 926089, 926091, VZ15059); Xique-Xique (MTR 20192, 20193, 20194, 20195, 20196, 20197, 20198). Ceará: Pacajús (CHUFC L3242); Santa Quitéria (FSCHUFPB 00470, 00471, 00541, 00923, 00928, 00963, 00982); Várzea da Conceição (CHUFPB 00051); Viçosa do Ceará (CHUNB 57373). Paraíba: Cabaceiras (FRD 860). Pernambuco: Arcoverde (FRD 1034); Buíque (MTR 15378); Nascente (FRD 0926, 0979, 0982, 0983), Serra Talhada (CHUFPB 00049, 00796); Trindade (FRD 0990, 1000, 1060). Piauí: Castelo do Piauí (CASTH 0379, 0716), Floriano (MPEG 27630, 27631); Paulistana (FRD442), Rio Grande do Piauí (FRD 0923). Sergipe: Monte Alegre (FSCHUFPB 00003, 00004, 00032, 00033, 00038, 00045, L121, 132, 137, 139, 153).

Vanzosaura rubricauda ($N = 50$). BRAZIL. Mato Grosso: Alto Araguaia (LG 0846), Alto Taquari (MTR 15564, 15569, 15573). Mato Grosso do Sul: Aquidauana (CHUNB 58277, 58572–58585, 58603); Brasilândia (CTMZ 004994); Corumbá (CEUCH 5324, 5326, 5328, GP 01–07); Goiás: Mineiros (CTMZ 03367); Serranópolis (CHUNB 58586–58602). Paraguay: Departamento San Pedro (MTR 21290).

Vanzosaura savanicola sp. nov. ($N = 63$, including type series*). BRAZIL. Bahia: Cocos (CHUNB 51296–51302, 51306, 51309, 51310); Formosa do Rio Preto (MTR 14949; PHV 2138 2174); Jaborandi (P 1, 2, 3, 58, 59, 60; CHUNB 51121); São Desidério (17844, 17853–17855, 17889). Minas Gerais: Arinos (CHUNB 37303); Januária (MTJ 007, 008, 051, 052, 0226, 0328, 0342, 0435); Urucuaia (MMOURA 259). Tocantins: Almas (MTR 14244*, 14257*, 14304*, 14398*, 14405*, 14565*, 14599, 14732*); Mateiros (CHUNB 23754, 28163, 28164, 28168, 28171, 28172, 28174, 28177, 28179, 28181, 28185, 28186, 28197, 41230, 41233, 41236–41238; CTMZ 03274, 03323).

APPENDIX 2

SPECIMENS EXAMINED

Vanzosaura multiscutata comb. nov. ($N = 408$). BRAZIL. Alagoas: Delmiro Gouveia (CHUNB 49910); Piaçabuçu (MNRJ 17631–17632); Piranhas: UHE Xingó (CHUNB 49907, 49911; MZUSP 78943–78943, 78944–78944, 79142, 79144–79142). Bahia: Barra (MZUSP 75620), Ibiraba (CHUNB 30963–30970; MZUSP 71865, 71868, 71845, 71850–71852 71856–71857, 71872–71874, 71881–71882, 71884–71886, 71894–71895, 93468–93471), Queimadas (MZUSP 74970–74974, 75318, 76917–76922, 76924–76926, 77889–77892, 77995–78003); Cachoeira (MZUSP 55819). Central: Jussara, Toca da Esperança (MZUSP 89287); Correntina (MTR 17938); Curaçá (MZUSP 77170); Gentio do Ouro: Santo Inácio (MTR 11245, 11295 11391, 71606, 74966–74968, 76240; MTR 20191); Glória (MTR 21222); Ibipecta (CHUNB 24224). Óleos: Sitios Novos (MTR 21223); Riachão do Jacuibe (MNRJ 10530–10531); Santa Maria da Vitória (MTR 17967–17969). Xique-Xique: Capim Verde (MZUSP 71607–71608), Vacaria (MZUSP 71609–71613, 71615, 71618–71622, 71624–71630, 71632–71633; 71635–71638, 71640–71642, 71644–71647, 71650, 71652, 71658, 71663–71666, 74236–74237, 75476, 76298–76304, 76932–76941, 76943, 76945–76951, 76957–76958, 76960–76962, 76966–76968, 76973, 76975, 76984, 77886–77888, 77986–77994, 71614, 71616–71617, 71621, 71623, 71631, 74233–74235, 77887). Ceará: Baturité, Açudinho (MZUSP 2428), Milagres (CHUNB 56529; MNRJ 18498), Várzea da Conceição (CHUFPB 00280, 00290, 00298), Viçosa do Ceará (CHUNB 57373). Paraíba: Cabaceiras (MZUSP 71605). São João do Cariri: Estação Ecológica São João do Cariri (CHUFPB 00395–00396, 00402, 00404, 00408, 00411, 00417–00418, 00805). São José dos Cordeiros: Reserva Particular do Patrimônio Natural Fazenda Almas (CHBEZ 2035–2039; CHUFPB 00803). Serra Branca: Bairro dos Pereiras (MNRJ 19686); Umbuzeiro (MZUSP 4723). Pernambuco: Agrestina

(MZUSP 21820, 21822–21824, 21827–21834); Arcoverde (CHUFPB 00282). Catimbau: Parque Nacional de Catimbau (ACG 114–115, 121); Exu (MZUSP 45944–45947, 48648–48743, 50152–50166); Nascente (CHUFPB 00046, 00301); Serra Talhada (CHUFPB 00281); Trindade (CHUFPB 00766). Piauí: Paulistana (CHUFPB 00300); Rio Grande do Piauí (CHUFPB 00794). São Raimundo Nonato: Parque Nacional da Serra da Capivara (ZUEC 0872; MZUSP 54841). Rio Grande do Norte: Açú, Floresta Nacional de Açú (CHBEZ 885–900); Macaíba (CHBEZ 2664–2665); Monte Alegre (CHBEZ 1009). Mossoró: Campo Amaro (CHBEZ 614). Serra Negra do Norte: Estação Ecológica do Seridó (CHBEZ 773–776; CHUNB 30565), Tenente Laurentino Cruz (CHBEZ 2957–2959). Sergipe: Areia Branca (MZUSP 88097–88100). Canindé do São Francisco: UHE Xingó (CHUNB 49908–49909, 49913).

Vanzosaura rubricauda ($N = 244$). ARGENTINA. Catamarca: Depto Valle Viejo, Sumalao (FML 01088). Córdoba: Depto San Alberto, Villa Dolores, Bañado de Paja (MACN 33074–33079, 33241–33257; MZUSP 72599–72601); Depto Calamuchita, Villa General Belgrano (MACN 7998–7999); Depto Punilla, Icho Cruz (FML 02048-1, 02048-2), Villa Carlos Paz (FML 23386); Depto Santa Maria, Villa Seranita (MACN 36275); Depto Totoral, Sierra de Macha (MACN 12503); Depto Cruz del Eje, Serrezuela (MACN 12504). La Rioja: Depto Capital, Dique Los Sauces (MACN 25153); Depto Chilecito, Chilecito (MACN 33499). Salta: Depto Anta, Joaquín Víctor Gonzáles, Finca Pozo Largo [FML 02709, 03124, 03126, 03305–03306 (0–2), 03307 (1–7), 03310 (1–3), 03311 (1–2), 03312, 03313 (1–2), 03314 (1–4), 03316, 03318, 03320–03323, 06108, 06110, 06112 (1–2), 06113, 06117 (1–2), 06118 (1–2), 06122, 06123 (1–2), 06124 (1–4), 06125 (1–3), 06708, 08183, 03315, 03317 (1–2), 06121]; Coronel Olleros, Rio Juramento (FML 00450, 00607). Santiago del Estero: Dique 'Los Quintogas' (MACN 32531); Depto Alberdi, Campo Gallo (MACN 10099); Depto Figueroa, Caspi Corral (FML 01086); Depto Pellegrini, Pampa Pozo (MACN 26645, MACN 30962). Tucumán: Depto Tafi del Valle, Tafi del Valle (FML 00210). BOLÍVIA. Santa Cruz: Prov. Cordillera, Parque Nacional y Area Natural de Manejo Integrado Kaa-Iya del Gran Chaco (MNKR 4023–4030), Pista de Estación Izozog (MNKR 4099–4104, 4150–4163, 4202–4204), puesto militar (MNKR 2764); Prov. Andrés Babiñez, Santa Cruz de la Sierra, Parque Regional Lomas de Arena (MNKR 599); Prov. Chiquitos, Monte Obayoi (MNKR 3223). BRAZIL. Goiás: Mineiros, Reserva

Particular do Patrimônio Natural Nascentes do Araguaia (CHUNB 23752–23753), Serranópolis (CHUNB 12847, 58586–58593). Mato Grosso: Alto Araguaia (MZUSP 78875; PHVAR 001–004, 007–009; 011–013, 015–025); Alto Taquari (MTR 15564); Itiquira (FLI 004–005, 016, 038–039, 045), UHE Ponte de Pedra (MZUSP 98637). Mato Grosso do Sul: Alcínópolis, Parque Estadual Nascentes do Rio Taquari (CHUNB 27951–27980); Aquidauana (CHUNB 58277, 58572–58578; FML 06897; MZUSP 82326–2331, 98091–98095); Batayporã, UHE Engenheiro Sérgio Motta (Porto Primavera) (MZUSP 87644, 92285–92286); Santa Rita do Pardo (MZUSP 89275–89276); Três Lagoas, Usina Termoeletrica Luís Carlos Prestes (ZUEC 3519). PARAGUAY. Alto Paraguay: Mayor Pablo Lagerenza, Parque Nacional Defensores del Chaco (MNHNP 11212). Amambay: Pedro Juan Caballero, Parque Nacional Cerro Corá (MNHNP 2835–2836, 8461). Boquerón: General Eugenio A. Garay, Parque Nacional Teniente Agripino Enciso (MNHNP 10616); Mariscal José Félix Estigarribia, Ayoreo Tunucujai (MNHNP 10720). San Pedro: Nueva Germania, Reserva Natural Laguna Blanca (CZPLT-H 015, 021, 029, 153–154).

Vanzosaura savanicola sp. nov. ($N = 194$, including type series*). BRAZIL. Bahia: Cocos, Fazenda Trijunção (CHUNB 23752, 49175–49178, 49180–49190, 51296–51298); Formosa do Rio Preto, Estação Ecológica Serra Geral do Tocantins (MTR 14912, 14942, 14949, 14967; PHV 2138, 2173–2174, 2200); São Desidério (MTR 17844, 17853–17855, 17888–17889). Goiás: São Domingos (CHUNB 12848). Minas Gerais: Arinos (CHUNB 37302–37304); Chapada Gaúcha: Parque Estadual da Serra das Araras (CHUNB 33994–33996); Formoso (CHUNB 23821), Parque Nacional Grande Sertão Veredas (MZUSP 94144–94145, 94148, 94150–94151, 94154–94155, 94158–94160, 94162–94171, 94173–94174, 94176–94178, 94705–94711); Januária, Parque Nacional Cavernas do Peruaçu (MZUSP 99857–99895). Tocantins: Almas, Estação Ecológica Serra Geral do Tocantins *(MTR 14226, 14244, 14257, 14304, 14398, 14405, 14565, 14567, 14624, 14664, 14665, 14675, 14729, 14732, 14735, 14740, 14754); Dianópolis (CHUNB 33076, 33090); Mateiros, Estação Ecológica Serra Geral do Tocantins (MZUSP 94119–94143), Parque Estadual do Jalapão (CHUNB 28161, 28163–28174, 28176–28182, 28185–28186, 28188–28189; ZUEC 3022–3025); São Félix do Tocantins (CAB 1723, 1731).

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1. *Vanzosaura* concatenated mitochondrial maximum likelihood genealogy based on (a) the complete dataset ($n = 186$). Terminal names show the voucher numbers followed by a short code for the locality (for full information see Appendix 1). Colours represent the geographical groups and the species limits here proposed: blue = *V. multiscutata* comb. nov. from Caatinga, CAA; red = *V. rubricauda* from Chaco, CHA and western Cerrado, WCE; green = *V. savanicola* sp. nov. from eastern Cerrado, ECE.

Figure S2. *Vanzosaura* concatenated mitochondrial maximum likelihood genealogy based on unique haplotypes ($n = 154$). Terminal names show the voucher numbers followed by a short code for the locality (for full information see Appendix 1). Colours represent the geographical groups and the species limits here proposed: blue = *V. multiscutata* comb. nov. from Caatinga, CAA; red = *V. rubricauda* from Chaco, CHA and western Cerrado, WCE; green = *V. savanicola* sp. nov. from eastern Cerrado, ECE.