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.


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 prefrontal 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 Procellosaurus, 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 superciaries, and three pairs of mentals, which distinguished G. multiscutatus and G. rubricauda from other Gymnophthalmus species (presenting one supraocular, two superciaries, 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 Procellosaurus 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 (cyt b) 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 Microablepharus maximiliani (Reinhardt & Lütken, 1862) as out-groups in the analyses. A fragment of nearly 740 bp of cyt b was amplified by polymerase chain reaction (PCR) using primers CB1 (5'-CCATCCAACATCTCAGCATGATGAAA-3') and CB3 (5'-GGCAAATAGGAARTATCATTC-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'-CATTACTTTTTACTTGGATTGCACA-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 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 (MNHN), 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.
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 comparisons, 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 (\( \pi \)) was 9.6%. The phylogenetic 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, \( U_{1,645} = 20874, P < 0.01 \)) 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).
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).
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; $F_{2,16} = 13.70$, $P < 0.01$), 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)...

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**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.

<table>
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<tr>
<th></th>
<th>CAA</th>
<th>ECE</th>
<th>WCE+CHA</th>
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<tbody>
<tr>
<td></td>
<td>Sex</td>
<td>Average</td>
<td>SD</td>
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<tr>
<td>DOR</td>
<td>F</td>
<td>35.9</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>34.0</td>
<td>0.20</td>
</tr>
<tr>
<td>VEN</td>
<td>F</td>
<td>26.3</td>
<td>0.19</td>
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<tr>
<td></td>
<td>M</td>
<td>23.2</td>
<td>0.21</td>
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<tr>
<td>GUL</td>
<td>F</td>
<td>10.3</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>10.3</td>
<td>0.12</td>
</tr>
<tr>
<td>SAM</td>
<td>F</td>
<td>16.0</td>
<td>0.04</td>
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<tr>
<td></td>
<td>M</td>
<td>16.0</td>
<td>0.05</td>
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<tr>
<td>LFT</td>
<td>F</td>
<td>16.8</td>
<td>0.17</td>
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<tr>
<td></td>
<td>M</td>
<td>17.0</td>
<td>0.17</td>
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<tr>
<td>FPO</td>
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<td>M</td>
<td>11.2</td>
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<td>SCA</td>
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<td>35.0</td>
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<td></td>
<td>M</td>
<td>32.8</td>
<td>1.17</td>
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</tbody>
</table>

$P = 0.017$ indicates significance after Bonferroni correction; CAA, Caatinga; ECE, eastern Cerrado; WCE + CHA, western Cerrado + Chaco.
forelimbs long relative to trunk length, with FAL 60.8 ± 0.03% of TRL in females and 63.3 ± 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 supraciliary, first supraocular, and loreal. Frontal longer than wide, slightly wider anteriorly. Frontoparietals absent. Interparietial 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...
Prefrontals. 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 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 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.

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

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...
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)


**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 ± 0.02% of TRL in females and 57.8 ± 0.02% in males; (5) colour pattern simple, 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...
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)


**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 ± 0.02% of TRL in females and 57.5 ± 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).
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–Withney, $U_{1,132} = 1256.5$, $P < 0.05$). 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. Procellosaurus, 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; Siedchlag et al., 2010), we cannot discard a relationship between environmental variation and color 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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Pedro Nunes kindly examined the holotype of *V. rubricauda*, housed in the British Museum, under the permission of Patrick Campbell. The Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support. G.R.C. thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), CNPq, and Fundação de Apoio à Pesquisa do Distrito Federal (FAPDF) for financial support. F.P.W. thanks CAPES/Fulbright, National Geographic Society, National Science Foundation (DDIG award; DEB-1210346), Society of Systematic Biologists, FAPDF, and Programa Ciências Sem Fronteiras (CNPq/BJT-374307/2012-1) for financial support, Instituto Chico Mendes de Conservação da Biodiversidade for collecting permits (ICMBio: no. 16381-2), and the following researchers: D.O. Mesquita, M. Moura, A. Bocchiglieri, A.F. Mendonça, V.L. Ferreira, C. Strussmann, D.M. Borges-Nojosa, D. Loebman, F.S. Rodrigues, M. Pérsoa, V.H.G.L. Cavalcante. F.P.W. would also like to thank the curators of the following institutions for providing tissue samples for this study: CHUNB, MZUSP, CHUFPB, Coleção Herpetológica da Universidade Federal do Ceará (CHUFC), Laboratório de Zoologia da Universidade Federal do Piauí (LZUFPB), and Coleção Herpetológica da Universidade Federal do Mato Grosso do Sul (UFMS/CH).

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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 3579, 3580, 3582); Várzea da Conceição (CHUFPB 00280, 00283, 00284, 00286, 00288, 00289, 00290, 00292); Viçosa do Ceará (CHUNB 57373).

Paraíba: Arcoverde (FRD 1034); Buíque (MTR 15378); Nascente (FRD 0926, 0979, 0982, 0983); Serra Talhada (CHUFPP 00049, 00796); Trindade (FRD 0990, 1000, 1060). Piauí: Castelo do Piauí (CASTH 0379, 0716), Floriano (MPEG 27630, 27631); Paulistania (FRD442), Rio Grande do Piauí (FRD 0923). Sergipe: Monte Alegre (FSCHFPB 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). Paraguai: 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); Uruçuí (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 (MNJR 17631–17632); Piranhas: UHE Xingó (CHUNB 49907, 49911; MZUSP 78943–78943, 78944–78944, 79142, 79144–79142). Bahia: Barra (MZUSP 75620); Ibiraba (CHUFPP 39063–39070; 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); Caçoeira (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); Itibepe (CHUNB 24224). Oleos: Sítios Novos (MTR 21223); Riachão do Jacuie (MNJR 10530–10531); Santa Maria da Vitória (MTR 17967–17969). Xique-Xique: Capoeiras (FRD 860). Pernambuco: Arcoverde (FRD 1034); Buíque (MTR 15378); Nascente (FRD 0926, 0979, 0982, 0983), Serra Talhada (CHUFPP 00049, 00796); Trindade (FRD 0990, 1000, 1060). Piauí: Castelo do Piauí (CASTH 0379, 0716), Floriano (MPEG 27630, 27631); Paulistania (FRD442), Rio Grande do Piauí (FRD 0923). Sergipe: Monte Alegre (FSCHFPB 00003, 00004, 00032, 00033, 00038, 00045, L121, 132, 137, 139, 153).

*Vanzosaura savanicola* sp. nov. (N = 63, including type series*). BRAZIL. Bahia: 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); Uruçuí (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).


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.