A second new species for the rare dipsadid genus Caaeteboia Zaher et al., 2009 (Serpentes: Dipsadidae) from the Atlantic Forest of northeastern Brazil

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ABSTRACT

Caaeteboia is a rare and elusive monotypic genus of Neotropical snake, being one of the least known dipsadids of the Brazilian Atlantic Forest. Here, we assess the morphological and genetic diversity of this genus, comparing these results with several other genera of Xenodontinae. Our combined results revealed the presence of an unknown species from the northeastern portion of the Atlantic Forest. The new species is distributed throughout the enclaves of coastal open forests mixed with savanna-like habitat, locally known as “Floresta de Tabuleiro”, and submontane ombrophilous forests in the Brazilian states of Paraíba and Pernambuco. This new species is easily distinguished from C. amarali by its lower number of dorsal, ventral, and subcaudal scales, and a remarkable dark lateral stripe from the nostril up to the anterior third of the body. The new species extends the distribution of the genus in approximately 700 kilometers northwards, reinforcing the importance of the conservation of small remnants of Atlantic Forest in northeastern Brazil, which still harbor high levels of endemism and diversity.

Key words: Caaeteboia; Atlantic Forest; Taxonomy; Xenodontinae; New Species.

RESUMO


Palavras-chave: Caaeteboia; Floresta Atlântica; Taxonomia; Xenodontinae; Nova Espécie.

Introduction

Within the highly diverse fauna of snakes distributed in the Brazilian Atlantic Forest, the rare monospecific Caaeteboia Zaher et al., 2009 is one of the poorest known genera of Dipsadidae (Zaher et al., 2009;
Passos et al., 2012, Fig. 1). Since the description of its type species—Liophis amarali Wettstein, 1930—few specimens were deposited in herpetological collections (Passos et al., 2012). Despite the lack of a comprehensive sampling, C. amarali is known to be a small oviparous and predominantly terrestrial snake that forages actively on the terrestrial and arboreal environments looking for frogs and lizards (Marques et al., 2001; Passos et al., 2012). Recently published studies indicated that Caaeteboia amarali represent a unique lineage, through evidence of DNA sequences, as well as cranial and hemipenial morphology (Zaher et al., 2009, 2018, 2019; Grazziotin et al., 2012; Passos et al., 2012). In recent phylogenetic analyses, the genus is recovered as an independent South American Xenodontine lineage with ambiguous affinities with Xenopholis, Saphenophis, and Hydrodynastes (Grazziotin et al., 2012; Zaher et al., 2018, 2019). To indicate this uniqueness, Zaher et al., (2009) erected a monospecific tribe, Caaeteboini, for C. amarali.

Externally, C. amarali is easily distinguished from other Atlantic forest Xenodontine snakes by its light gray head and pale body coloration marked by a “V” shaped dark mark extending backwards from the parietals and forming a vertebral stripe that fades on the anterior portion of the dorsum, and a dark-brown stripe on each side of the head that extends from the nostril to the postocular region, bordering dorsally the light cream supralabials and extending as blotches to the anterior third of the body (Passos et al., 2012). Caaeteboia amarali is known to occur throughout the coastal lowlands of the Brazilian Atlantic Forest, from southern Bahia to southern Santa Catarina states, and the questionable westernmost record of the type-locality, in the state of Minas Gerais (Passos et al., 2012). Two records were recently provided by Passos et al., (2012), from Armação de Búzios, state of Rio de Janeiro, and Sooretama, state of Espírito Santo, filling a persistent gap in the distribution of the genus.

In March 2008, a specimen of Xenodontinae was collected at Cruz do Espírito Santo, state of Paraíba, northeastern Brazil, in a fragment of the Atlantic Forest. Ten years later, in July 2018, another specimen with similar characteristics was collected nearby the previous individual, in the municipality of Pedras de Fogo (Fig. 1), also in state of Paraíba. An additional third specimen was recorded from municipality of Saloá, state of Pernambuco, and was handled and photographed in nature, but not collected. All three exhibit the almost all diagnostic features of the genus Caaeteboia enlisted above. However, these three individuals share characteristics that are easily distinguished from C. amarali, suggesting their recognition as a distinct species. Here we test this hypothesis, employing morphological and genetic data to compare these three individuals with other specimens of Caaeteboia, including the type material of Liophis amarali. The results allowed us to confirm this hypothesis, prompting us to describe a new species for the genus.

**Material and methods**

**Specimens examined and morphological evaluation**

We analyzed 15 specimens of Caaeteboia, including 12 individuals of C. amarali and three of the new species (Appendix 1) deposited in the following Brazilian collections (acronyms given in parenthesis): Instituto Butantan (IBSP), São Paulo; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Paraná; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro; Museu
de Zoologia, Universidade de São Paulo (MZUSP), São Paulo; Coleção Zoológica Gregório Bondar (CZGB), currently belonging to Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC), Itabuna, Bahia. We also included in our analyses the data provided by Passos et al. (2012) from their two additional southeastern Brazilian specimens.

Head measurements were taken with a digital caliper, with precision of 0.01 millimeter (mm). The snout-vent (SVL) and tail (TL) lengths were taken with a flexible ruler to the nearest millimeter. We consider the first ventral scale the anteriormost wider than taller scale that contacts gulars. Sex of individuals was determined by the presence/absence of hemipenes, checked through an incision at the base of the tail. Additional information from other four specimens from Passos et al., (2012) was included.

Hemipenes were prepared using the techniques described by Pesantes (1994) and Zaher & Prudente (2003). Hemipenial terminology follows Dowling & Savage (1960) and Zaher (1999). Specimens from Cruz do Espírito Santo and Pedras de Fogo were collected under permissions number SISBIO 133/06 and 21799-1, respectively.

CT-scanning procedures were conducted on a 300-kV μ-focus X-ray source micro computed tomography GE Phoenix v|tome|x M 300 (General Electric Measurement & Control Solutions, Wunstorf, Germany) at the Laboratório de Microtomografia of the Museu de Zoologia, Universidade de São Paulo. The acquired scan data was processed on a high-end computer HP Z820 workstation with eight-core Intel Xeon E5-2660, 2.20 GHz and 128 GB of memory. Reconstruction of raw data was performed using the system supplied software phoenix datos|x reconstruction v. 2.3.0 (General Electric Measurement & Control Solutions, Wunstorf, Germany). Three-dimensional visualization, segmentation, and analysis of the reconstructed data was performed using VGStudio MAX 2.2.3 64 bit (Volume Graphics GmbH, Heidelberg, Germany).

**DNA sequencing, phylogenetics and divergence assessment**

We sequenced the mitochondrial genes 12S (small subunit ribosomal RNA), 16S (large subunit ribosomal RNA), and cytb (cytochrome b), and the nuclear gene nt3 (Neurotrophin-3) of the holotype of the new species (MZUSP 19559) for which tissue samples were available. We used the molecular dataset available from Zaher et al., (2018), which already included one specimen of *C. amarali* from municipality of Cananéia, state of São Paulo, Brazil (IBSP 72585), and added the representative of the northern population into the alignments by using the “--add” command in the online version of MAFFT v. 7 (Katoh et al., 2017) with default parameters. Genetic divergence between the two individuals of *Caeteboia* was evaluated by taking into account the average divergence among species within the Xenodontinae.

We used RAxML 8.2.3 (Stamatakis, 2014) to analyze our complete matrix, allowing PartitionFinder 2 to only apply GTR+G as the model of molecular evolution without any correction for proportion of invariant sites, as recommended in the RAxML’s manual. We performed the phylogenetic analysis employing Maximum Likelihood (ML) as the optimality criterion, running 1000 pseudoreplications of non-parametric bootstrap (BS) using the rapid bootstrap algorithm implemented in RAxML (-f a). Such approach, besides the bootstrap analysis, performs 200 complete searches for the best-scoring ML tree using each 5th bootstrap tree as a starting tree for the rapid hill-climbing search. Since the overlap among gene fragments was not complete in our dataset, we took the branch length/patristic distance (absolute time vs. mutation rate) among species as a proxy for the genetic distance. We used the package *ape* in the R environment to estimate the patristic distance.

**Results**

Our phylogenetic analysis (see Supplementary Material) recovered a clade containing the two specimens of *Caeteboia* with unambiguous bootstrap support (100%). The analysis of the patristic distances within some genera of Xenodontinae (Fig. 2) indicate that mean value of interspecific distance among all genera is 0.091 (standard deviation of 0.045). The genus *Xenopholis* Peters, 1869 presents the highest interspecific distance mean (0.263), while the insular genus *Borikenophis* Hedges & Vidal in Hedges, Couloux & Vidal, 2009 presents the lowest interspecific distance mean (0.006). The genetic distance (estimated by the patristic distance) between the two specimens of *Caeteboia* is 0.098.

Considering our phylogenetic tree in combination with the estimated patristic distances and the analysis of morphological evidences (see below), we hypothesize that the specimens of genus *Caeteboia*...
from the northeastern region of Brazil represent an undescribed species, that we formally described herein.

**Caaeteboia gaeli** sp. nov.  
urn:lsid:zoobank.org:act: urn:lsid:zoobank.org:pub:BFB360F0-28BA-48A1-A0D2-BDA-4C658585B (Figs. 3, 4A–B, and 5)


**Holotype**  
MZUSP 19559, an adult male from Mata do Açude Cafundó, Companhia São João, municipality of Cruz do Espírito Santo, state of Paraíba, Brazil (07°10’57”S, 35°05’33”W), collected by Gindomar G. Santana on 1 March 2008 (field number: GGS 784). Right hemipenis prepared and deposited in the Hemipenial Collection of the Museu de Zoologia da Universidade de São Paulo (Fig. 6).

**Paratype**  
CHUFPB 24395, an adult female from a forested fragment in the municipality of Pedras de Fogo, state of Paraíba, Brazil (07°25’28”S, 34°57’38.3”W), 27 km southwest from the type locality (Fig. 7), collected by Pedro R. A. Albuquerque in July 2018.

**Etymology**  
The specific name honours Gael Hingst Zaher. GGM,
FEB, GAPF, GGS, FGRF and FGG dedicate this species to the beloved son of the senior author, who sadly left us prematurely in March, 2020.

**Diagnosis**

*Caaeteboia gaeli* sp. nov. is diagnosed by a slender and small body; rounded pupil; eight supralabials (fourth and fifth contacting the orbit); nine infralabials (first to fourth contacting chinshields); loreal absent (fused with prefrontals); a preocular single and wide; two postoculars; temporals 2+2/1+2, or 2+1/2+1; dorsals 15/15/15; at least 158 ventrals, 92–106 paired subcaudals; anal plate divided; continuous dark-brown lateral stripe, bordered in black, extending from nasal, to the anterior portion of body, on rows of dorsals three and four, starting to fade after the 10–15th ventrals, weakening towards the end of body; posterior to parietals, “V” shaped dark-mark, extending backwards and forming a weak vertebral stripe fading posteriorly; hemipenial lobes almost completely covered with calyces and naked area restricted to the small and poorly marked lobular crotch, on the asulcate side; medial edges of lobes poorly demarcated and bordered with spines; lobular crest poorly developed, bearing small spines on its edge (Fig. 6A).

**Description of holotype**

Adult male, with a total length (TTL) of 389 mm, snout-vent length (SVL) 252 mm; tail length (TL) 137 mm (54% of SVL), head length (HL) 11.45 mm (4.5% of SVL), head width 6 mm (52% of HL), and head height 3.04 mm. Measurements corresponds to the right side of head. Interorbital distance 5.05 mm; rostro-orbital distance 3.77 mm; naso-orbital distance 2.54 mm. Head distinct from the neck, flattened in lateral view, and rounded in dorsal view. In lateral view, canthus rostralis is distinct, as well from dorsal view.

Rostral sub-triangular, twice as long as high, 1.94 mm wide, 0.99 mm high, visible from above; internasal contacting nasal, 0.91 mm long, 1.03 mm wide; prefrontal 1.18 mm long, 1.68 mm wide; frontal sub-pentagonal, 3.2 mm long, 1.48 mm wide;
Figure 4. Coloration pattern of lateral stripes of specimens of Caaeteboia gaeti sp. nov. (A–B), and C. amarali (C–H), arranged geographically from northeast to southern Brazil. A: MZUSP 19559 (Holotype), Cruz do Espírito Santo, Paraíba; B: specimen not collected, Saloá, Pernambuco; C: CZGB 2371, Uruçuca, Bahia; D: IBSP 46140, Miracatu, São Paulo; E: IBSP 72585, Cananéia, São Paulo; F: IBSP 73202, Jacupiranga, São Paulo; G: IBSP 9907, Alexandra, Paranaguá, Paraná; and H: MNRJ R 1818, Santa Luzia, Tubarão, Santa Catarina. Scale bar: 5 mm.
supraocular sub-rectangular, 2.96 mm long, 1.47 mm wide; parietal 4.06 mm long, 2.71 mm wide; nasal divided; pre-nasal contacting internasal, prefrontal, and the 1st supralabial, 0.51 mm wide, 0.64 mm high; post-nasal 0.63 mm wide, 0.69 mm high, contacting prefrontal and first and second supralabials; loreal fused with prefrontal, contacting 2nd and 3rd supralabials; preocular 0.62 mm long, 1.17 mm high; eye diameter 1.83 mm; pupil round, postoculars 2/2, upper postocular 0.61 mm long, 1.29 mm high; lower postocular reduced, 0.55 mm long, 0.36 mm high; temporals 1+1+2/1+2 on right and left sides, respectively; upper anterior temporal 0.89 mm long, 0.48 mm width; lower anterior temporal 1.44 long, 0.78 mm width. Supralabials 8/8 (fourth–fifth contacting the orbit), seventh and eighth higher than others; symphysal triangular, 0.85 mm long, 1.33 mm wide; infralabials 9/9, with the first to fourth contacting the first pair, and fourth–fifth contacting the second pair of chinshields; anterior chinshield 2.63 mm long, 0.94 mm wide; posterior chinshield 3.52 mm long, 1.19 mm wide; four gular scale rows, 15/15/15 smooth dorsal scale rows; one preventral, 158 ventrals; anal plate divided; 106 paired subcaudals; caudal spine long and acuminate.

**Coloration**

Ground color of body light brown, with dark marks scattered on top of the head and a poorly defined brownish vertebral stripe on the anterior portion of the body that fades posteriorly (Figs. 3, 4A–B, and 5). Well-defined dark-brown lateral stripe, bordering supralabials dorsally and extending posteriorly, on the lateral side of the dorsum, on rows three and four. Ventrally, head and body immaculate whitish-cream, with a small dark spot on each edge of ventrals.

**Hemipenis**

Hemipenis fully everted and almost maximally expanded. Organ bilobed, semicapitate; semicylindric; centrolateral sulcus spermaticus bifurcating on distal half of the body, ending on the apex of each lobe; capitulum about half of the size of the body, ornamented by papillate calyces uniformly distributed on sulcated surface and larger and irregular on asulcated side; small naked area restricted to the poorly marked lobular crotch on asulcated side; medial region of lobes poorly demarcated and bordered with spines; lobular crest poorly developed bearing small spines on its edge; hemipelvis body and base covered by medium-sized spines, slightly larger on asulcated side; a series of enlarged or hook-like spines on laterals and two on the proximal region of the asulcated side of the body; base with two hook-like spines on the asulcated surface and one on the sulcated (Fig. 6A).

**Remarks on the Paratype**

An adult female (CHUFPB 24395; Fig. 6A); with 411 mm TTL, 279 mm SVL, 132 mm TL (47% of SVL), and 12.33 mm HL (4.4% of SVL). Loreal fused with prefrontals, contacting second and third supralabials; one large preocular; postoculars 2/2; supralabials 8/8 (4–5th contacting the orbit); 9/9 infralabials (first–fourth contacting chinshields) temporals 2+1/2+1, on right and left sides, respectively; 15/15/15 smooth dorsal scales; 158 ventrals; anal plate divided; 92 paired subcaudals. Coloration is very similar to the holotype.

**Comparisons**

*Caaeteboia gaeli* differs from *C. amarali* by the following combination of characters (values of *C.
A second new species of genus *Caaeteboia* \( \text{amarali} \) between parenthesis; Table 1): 15/15/15 smooth dorsal scales (vs. 17/17/15 or 17/17/17); 158 ventrals (vs. 165–184); 92–106 paired subcaudals (vs. 112–124); well-defined dark lateral stripe (Fig. 4) extending posteriorly along the lateral sides of the body on rows three and four (vs. ill-defined dark ocular stripe, separate or poorly connected to the first of nearly ten dark blotches that occupies fourth, fifth and sixth rows; dark stripe absent on the body); hemipenial lobes (Fig. 6) almost completely covered with calyces and naked area restricted to the small and poorly marked lobular crotch on the asulcate side (vs. lobes covered with calyces on sulcate, asulcate and lateral sides, large naked area on the medial surface of lobes and large lobular crotch); medial edges of lobes poorly delimited and bordered with spines (vs. medial edges of lobes strongly delimited and bordered with spines); lobular crest poorly developed bearing small spines on its edge (vs. lobular crest strongly developed bearing enlarged spines on its edge); shorter proximal head of the quadrate and longer supratemporal with a free-ending posterior extremity projecting beyond the braincase (vs. wider proximal head of the quadrate and shorter supratemporal that does not project posteriorly in a free-ending extremity) (Fig. 7); contact between the maxilla and ectopterygoid reaching the level of the post-frontal (sensu Zaher and Scanferla, 2012) in lateral view (vs. maxilla-ectopterygoid contact does not reach the level of the postfrontal); longer angular, three times longer than high (vs. angular twice longer than high); pituitary vein foramen lying between the sphenoid and parietal (vs. pituitary vein clasped by the parietal, sphenoid and prootic).

**Remarks**

The specimen from Saloá, Pernambuco (Fig. 5B), although not collected, only handled and photographed in nature, exhibit characteristics that compelled us to consider it as a putative member of this new species. This individual shares with specimens of the genus *Caaeteboia* eight supralabials, with the fourth and fifth entering the orbit, loreal absent (fused with prefrontal), one preocular, two postoculars and 15 dorsals with no reduction. The dorsal coloration is very similar to the one described for both holotype and paratype of *C. gaeli*. It presents a continuous dark ocular stripe and does not exhibit dark lateral blotches on the anterior portion of the body as observed in specimens of *C. amarali* (Fig. 4) but instead a dark stripe.

**Table 1.** Selected characters of meristics and measurements of species of *Caaeteboia gaeli* sp. nov. and *C. amarali*.

<table>
<thead>
<tr>
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<th><em>Caaeteboia gaeli</em> sp. nov.</th>
<th><em>Caaeteboia amarali</em></th>
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<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
</tr>
<tr>
<td>SVL (mm)</td>
<td>252</td>
<td>279</td>
</tr>
<tr>
<td>TL (mm)</td>
<td>137</td>
<td>132</td>
</tr>
<tr>
<td>HL (mm)</td>
<td>11.45</td>
<td>12.33</td>
</tr>
<tr>
<td>Ventrals</td>
<td>158</td>
<td>158</td>
</tr>
<tr>
<td>Subcaudals</td>
<td>106</td>
<td>92</td>
</tr>
<tr>
<td>Dorsals</td>
<td>15/15/15 (n = 2)</td>
<td></td>
</tr>
</tbody>
</table>
The close geographic proximity between this sample and those from Paraíba also suggest that all individuals are co-specific.

**Distribution**

The distribution of the new species is currently known for three localities, two of them in Floresta de Tabuleiro (Tabuleiro Forest), and one in the submontane ombrophilous Atlantic Forest. The holotype was collected in Mata do Açude Cafundó, Companhia São João, municipality of Cruz do Espírito Santo (Fig. 8A–D), while the paratype was found in a preserved area in the surroundings of the municipality of Pedras de Fogo, ca. 5 km westwards from Alhandra and 11 km northeast from Caaporã. The specimen from Saloá, Pernambuco, extends the distribution of the species of approximately 270 km southwestwards from the type-locality. This speci-
men was observed in a small Atlantic Forest enclave within the Borborema Plateau (Fig. 8E–G), at an altitude above 700 m and 160 km from the coast towards the interior.

**Habitat and Natural History**

The predominant vegetational type where the holotype and paratype were captured is known as “Floresta de Tabuleiro” (Fig. 8). It consists of natural enclaves amidst the ombrophilous forest, characterized by an open-canopy forest with sandy soil, herbaceous vegetation and ground bromeliads, forming savanna-like patches along the low areas of the Northeastern Coast of the Atlantic Forest (between 20 and 100 m.a.s.l.) (Barbosa 2008). The photographed specimen from Saloá (Fig. 5B) occurs in a typical vegetation of submontane forest. The holotype was found within one of the mounted pitfall traps at 10:00 h, while the paratype was captured in activity on the forest floor at 10:15 h. The specimen from Saloá was found inside of a ground bromeliad during the day.

**Discussion**

With the description of a second species, the diagnosis of *Caaeteboia* is slightly modified to include the variation observed here. Now, the genus is defined by the presence of eight supralabials, with the fourth and fifth entering the orbit; loreal scale absent (fused with prefrontal); a large and unique preocular, two postoculars; dorsals smooth, in rows of 17/17/15, 17/17/17 or 15/15/15; 158–184 ventrals; anal plate divided; 92–125 subcaudals; a dark lateral stripe that can be well or ill-defined, extending on the lateral of body, on rows three and four, or only connected to the first lateral blotch, not forming a continuous stripe.

Variation on the dark lateral blotches may be observed among *C. amarali*. It can be occasionally fused to form a dark brown stripe anteriorly, a condition observed in the holotype. According to Passos et al., (2012: figs 5, 7), the holotype presents ill-defined blotches, not as high as those observed on the other specimens, restricted only to fourth and fifth rows. Another specimen of *C. amarali* (CZGB 2371) from the municipality of Uruçuca, Bahia, has also a similar condition. This is not the case observed in *C. gaeli*, which has a unique well-defined stripe from nostril to laterals of anterior portion of the body (Fig. 4). All remaining specimens of *C. amarali* exhibited lateral blotches, at least on the anterior portion of the body, on fourth, fifth and sixth rows.

The geographic distribution of *C. gaeli* extends the range of the genus to the northeastern coastal Atlantic Forest, in the states of Paraíba and Pernambuco (Fig. 1). Therefore, *Caaeteboia* occurs along the Brazilian coastal areas of Atlantic Forest, from southern Santa Catarina (municipality of Tubarão) to northeastern Paraíba state (municipality of Cruz do Espírito Santo), with its westernmost record in Belo Horizonte, state of Minas Gerais (type-locality of *C. amarali*; Bérnils et al., 2004; Passos et al., 2012).

The new species presents an allopatric distribution with *C. amarali*, with the nearest records of both species being actually distant from each other by approximately 700 kilometers (from the northern record of *C. amarali* at Uruçuca, Bahia to the southernmost putative record of *C. gaeli* at Saloá, Pernambuco). This distributional gap may be due to the rarity of both species, with very low densities throughout their natural range.

Although the description of this species increases the diversity and the knowledge of *Caaeteboia,*
it is still considered as a rare dipsadid genus with a broad distribution in one of the most impacted Brazilian biomes (Ribeiro et al., 2009). Finally, this new species reinforces the importance of conservation measures towards the small remnants of Atlantic Forest of Northeastern Brazil, which still harbors an impressive diversity and endemism, but remain largely unprotected (see MMA maps of the Conservation Units in Brazil, http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs/mapas) (Silva and Casteleto 2005; Tabarelli et al., 2005).

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G. Montingelli et al. — A second new species of genus Caeteteboia


Appendix 1
List of specimens examined

Specimens from literature (Passos et al., 2012)

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