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A New Species of Snail-Eating Snake, *Dipsas* Cope, 1860 (Serpentes: Colubridae: Dipsadinae), from the Atlantic Forest of Brazil

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Abstract. We describe a new species of snail-eating snake from two localities within the Atlantic Forest of the states of Bahia and Minas Gerais, Brazil. The new species differs remarkably from all congeners by its dorsal pattern consisting of sharply bordered triangles resembling the pattern of sympatric pitvipers, more precisely *Bothrops jararaca* and *B. pirajai*. Parameters of external morphology of the new species resemble those of the *Dipsas incerta* species group. Its scalation, body/head shape, and color pattern are most similar to *D. alternans*, a species known to occur 360 km farther south, across the Rio Doce river. The new species differs from *D. alternans* by exhibiting triangular dorsal blotches and a higher number of pileus blotches, by the distribution of ventral spots and morphology of the supratemporal and premaxillae, as well as in hemipenial morphology. We also provide comparisons of the new species with all sympatric and/or parapatric congeners. The finding of a new snake species in the Atlantic rainforest of southern Bahia and adjacent Minas Gerais is particularly surprising as this region is easily accessible and represents a well-sampled area regarding herpetological surveys in the last decades.

Keywords. Color pattern; *Dipsas alternans*; *Dipsas incerta* species group; Hemipenial and skull morphology; Pitviper aposematism.

INTRODUCTION

With nearly 700 species, the family Dipsadidae (sensu Zaher et al., 2009) is the largest group of colubroid snakes in the world (Hedges et al., 2009; Zaher et al., 2009). Within this group, the subfamilies Xenodontinae Bonaparte, 1845 and Dipsadinae Bonaparte, 1838 are particularly diverse, with almost 300 species in South America and more than 10 distinct monophyletic groups (Zaher et al., 2009; Grazziotin et al., 2012). The tribe Dipsadini Bonaparte, 1838, as a subunit of the family Dipsadidae, encompasses the snail-eating genera *Sibon* Fitzinger, 1826 and *Dipsas* Laurenti, 1768, including the former *Sibynomorphus* Fitzinger, 1843, recently synonymized with *Dipsas* (Arteaga et al., 2018).

The genus *Dipsas* contains 41 species distributed from southern Mexico through Central America and into

South America, as far as Argentina, Uruguay, and Paraguay (Uetz et al., 2018). These snakes have small to medium size (rarely longer than 100 cm total length), representing a morphologically unique group specialized for an arboreal, gastropod-eating lifestyle, exhibiting lateral compression of the body, reduction or loss of the mental groove, and inward angling of the maxillary teeth (MacCulloch and Lathrop, 2004). The color pattern is highly polymorphic, but most *Dipsas* species exhibit dark blotches or rings on a light brown to gray ground color.

Peters (1960) provided an extensive revision of the genus, which was followed by more restricted taxonomic studies of several species groups (e.g., Cadle and Myers, 2003; Cadle, 2005; Lima and Prudente, 2009). However, many South American species remain poorly known because of their rarity, and a confusingly large and often species-overlapping variation of color pattern characters

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(Cadle and Myers, 2003; Harvey and Embert, 2008; Barros et al., 2012; Arteaga et al., 2018). Harvey (2008) provided a comprehensive review of South American *Dipsas*, including a diagnosis of the genus based on scalation and hemipenial morphology, as well as a key to South American taxa.

Dipsas species occurring along Brazil's Atlantic Forest have received comparatively less attention. The taxonomic status of some species has been evaluated: *D. neivai* Amaral, 1926 by Porto and Fernandes (1996), which was later synonymized with *D. variegata* Duméril et al., 1854 by Harvey and Embert (2008); *D. alternans* Fischer, 1885 by Passos et al. (2004); *D. albifrons* Sauvage, 1884 by Passos et al. (2005); and the recent description of a new species, *D. sazimai* Fernandes et al., 2010.

In January 2016, KM encountered a fresh road-killed *Dipsas* in Bahia's Atlantic rainforest that could not be clearly referred to any known species from the region. Investigations in Brazilian institutions revealed a second specimen from the Atlantic rainforest of Minas Gerais that was collected in 2004. After comparison with material of other congeners and literature data, we concluded that these two specimens represented a new species that we describe herein.

MATERIALS AND METHODS

Type specimens of the new species are deposited in the collections of Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, state of Rio de Janeiro (holotype); and Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC), Ilhéus, state of Bahia (paratype), both in Brazil. Appendix 1 shows information on all other comparative material. Institutional abbreviations follow Sabaj Pérez (2016). For comparison of color and head scalation characters, we used additional dipsadid snakes from the same region of the new species' localities, as well as data from specimens from more distant locations.

Terminology for cephalic shields follows Peters (1964), whereas ventral and subcaudal counts follow Dowling (1951). We performed all measurements using a dial caliper to the nearest 0.1 mm, except for snout–vent length (SVL) and tail length (TL), which we measured with the aid of a ruler to the nearest 1.0 mm. Unless stated otherwise, we performed measurements and descriptions of paired cephalic scales strictly based on the right side of the head; however, we also refer to some meristic bilateral values in a left/right format. We counted body markings (blotches, spots, and dots) separately on each side of the dorsum, since these markings may be asymmetrical. Herein, the term “blotch” refers to any broad (two or more scales long and wide) dorsal and head markings, whereas the term “spot” refers to smaller (1–2 scales

long and wide) markings on head, dorsum or venter. The term “dot” refers to any marking substantially smaller than a single scale. We determined sex by presence/absence of a hemipenis determined through a ventral incision at the base of the tail. We defined sexual maturity of males through inspection of convoluted and opaque deferent ducts (Shine, 1988, 1994). We examined maxillae and the Harderian gland of the specimens under a stereoscope, through a narrow incision between supralabials and maxillary arch. We followed Cundall and Irish (2008) for skull terminology. We scanned the head of the holotype of the new species and from closely related or sympatric congeners (*Dipsas alternans* MNRJ 19595; *Dipsas indica* Laurenti, 1768 MNRJ 14742; *Dipsas sazimai* MNRJ 15136 [holotype]) at 50 kV and 160 μ A with a high energy microCT Scan at COPPE – Instituto Alberto Cruz Coimbra de Pós-Graduação e Pesquisa de Engenharia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. After acquisition, we produced images of scanned skulls using the FDK algorithm (Feldkamp et al., 1984) and analyzed them with the software CTVOx® version 2.7 (Bruker Corporation, 2014). Terminology for hemipenial descriptions follows Dowling and Savage (1960) and Zaher (1999) with minor adaptations based on Harvey and Embert (2008). We modified the method for preserved hemipenis preparation from Pesantes (1994) in replacing KOH with distilled water according to Passos et al. (2016). Prior to the inflation with petroleum jelly, we placed the organs in an ethyl alcohol (70%) solution with Alizarin red for about 10 min to stain the ornamented calcareous structures according to adaptations from original procedures used by Uzzell (1973). We report elevations as meters above sea level (m a.s.l.).

Dipsas bothropoides sp. nov. (Figs. 1, 2)

Holotype (Fig. 1A–B)

An adult female (MNRJ 26377) collected on 8 November 2004 by Daniel S. Fernandes and Luciana B. Nascimento at “Fazenda Duas Barras” (near 16°25'0.00"S, 40°2'60.00"W, 800 m a.s.l.), a ranch in the district of Talimã, municipality of Santa Maria do Salto, Minas Gerais, Brazil (Fig. 3).

Terra typica

Montane Atlantic rainforest in the Serra do Cariri that occurs along the border between the states of Minas Gerais and Bahia and separates the basins of the Jequitinhonha and Buranhém rivers. The type was found within Fazenda Duas Barras, which includes patches of unprotected Atlantic rainforest and well-preserved secondary



Figure 1. (A) Dorsal and (B) ventral views of the holotype of *Dipsas bothropoides* **sp. nov.** (MNRJ 26377, female, snout–vent length [SVL] 420 mm); and (C) dorsal and (D) ventral views of the paratype of *Dipsas bothropoides* **sp. nov.** (MZUESC 15828, male, SVL 339 mm). Small inset show small section of the mid-body of respective specimens, illustrating the enlarged vertebral scales.

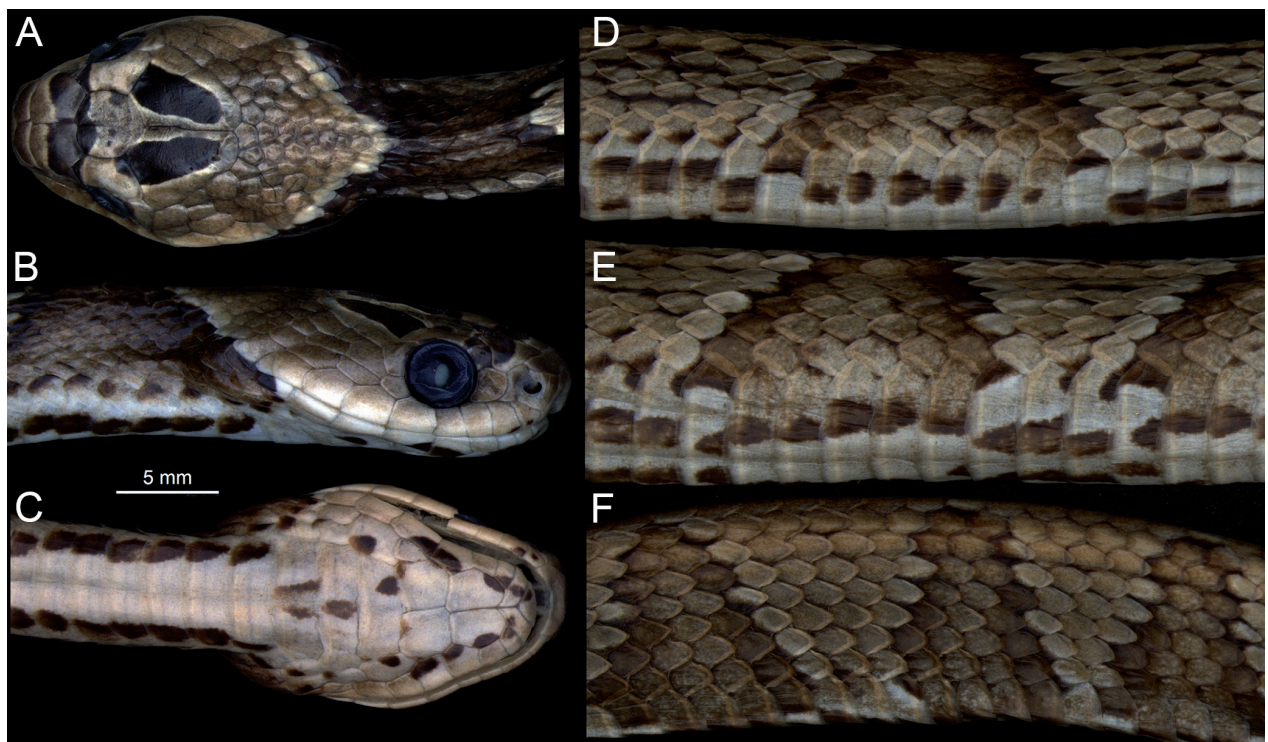


Figure 2. Close views of the holotype of *Dipsas bothropoides* **sp. nov.** (MNRJ 26377, female): left side (A) dorsal, (B) lateral, and (C) ventral views of the head, and right side with lateral views of body on its (D) anterior, (E) medial, and (F) posterior regions.

forests, as well as open pastures associated with cattle breeding (see also Cruz et al., 2007).

Paratype (File S1)

An adult male (MZUESC 15828) found freshly killed on state road BA-001 on 23 January 2016 by Konrad Mebert and Carol Cornélio, 2 km northeast of Cachoeira do Tijupe and 3 km southwest of Txai, Praia (Beach) de Itacarézinho (14°23'43.14"S, 39°2'21.70"W; 53 m a.s.l.), Itacaré, Bahia, Brazil (Figs. 3, 4). We collected no tissue sample from the holotype, but such is available from the paratype at MZUESC.

General diagnosis and variation (Figs. 1, 2, File S1)

The new species is allocated to the genus *Dipsas* by possessing the following derived characters combined from Peters (1960), Cadle (2007), and Arteaga et al. (2018): mental sulcus (groove) absent, shape of chinshields (square or polygonal rather than elongate and

narrow), more than two pairs of chinshields, absence of supralabial noticeably higher than other supralabials and in contact with postocular, and Harderian gland occupying the entire postorbital region.

Dipsas bothropoides **sp. nov.** (holotype and paratype) is distinguished from all currently recognized congeners by the unique combination of the following morphological characters: (1) dorsal scale rows 15/15/15, smooth; (2) one pair of infralabials in contact posterior to mental; (3) infralabials 8–9, 4–6th or only 4th in contact with second pair of chinshields; gulars separating infralabials from prementals and ventrals; (4) supralabials 8–9 (4–5th or 5–6th contacting orbit); (5) nasal partially or fully divided; (6) internasal paired or fused; (7) loreal square usually in contact with orbit, but contact can be obstructed by a tiny interjacent scale; (8) preoculars 1 or 2 present above and/or below loreal, excluding prefrontal from orbit; (9) postoculars two, excluding temporals from orbit; (10) temporals 3/3/3, 2/3/2 or 2/3/3; (11) ventrals 183 in female (holotype), 179 in male (paratype); (12) subcaudals 100 in female (holotype) and 110 in male (paratype);

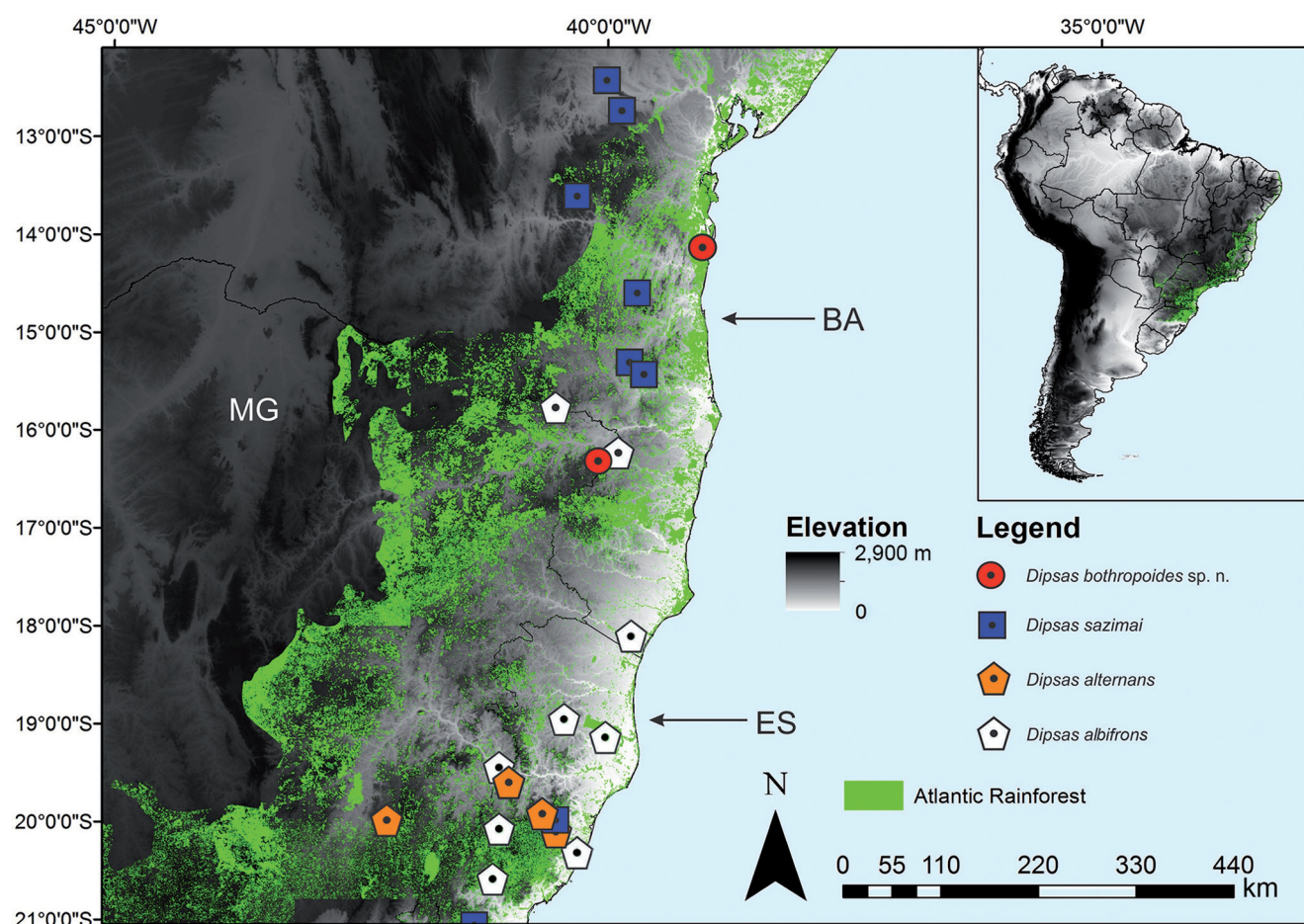


Figure 3. Map showing the two known localities of *Dipsas bothropoides* **sp. nov.** The lower red circle is the holotype, the upper red circle the paratype. Locality records of *D. sazimai* are based on Fernandes et al. (2010), Roberto et al. (2014), Freitas (2015), and unpublished records by Iuri Ribeiro Dias, see Figs. 7C and 8C; *D. alternans* (according to Passos et al., 2004; Nogueira et al., 2019), and *D. albifrons* (Dias et al., 2018 and complementing records from Nogueira et al., 2019). Small inset shows map of South America.

(13) head light brown with 3–7 large, black blotches with light to yellow borders on the pileus, including a preorbital band (holotype) or three blotches instead (paratype), with the paratype exhibiting two additional parallel spots diverging anteriorly along the sutures of parietals-frontal-supraoculars; (14) first dorsal blotch (nuchal collar) 2–5 scales long on the mid-dorsals and 10–14 scales long at paraventral portion; (15) dorsum of body medium brown (paratype before preservation) to light brown (preserved holotype) with well-defined dorsal blotches in the shape of triangles with black (paratype before preservation) to

dark brown borders, becoming lighter towards the center of the blotch, and an additional cream to yellow border on the flanks (both specimens) and venter (paratype), more prominent anteriorly in the male before preservation; (16) number of dorsal blotches 20–26 ($\bar{x}$ = 23; SD = 2.9; n = 4 sides) to vent, arranged in pairs and separated by a light, slightly enlarged row of vertebral scales; (17) mid-level of dorsal blotches 4–7 scales long; (18) number of dorsal blotches on the tail 10–16 ($\bar{x}$ = 13; SD = 2.9; n = 4 sides), dark brown with yellow-cream border, fading increasingly in posterior blotches; (19) venter cream brown anteriorly, becoming variably darker through stippling towards posterior region of body and tail up to exhibit the same coloration as dorsum; (20) maxillary teeth 16–17; (21) pterygoid teeth 16–17; (22) palatine teeth 9/9; (23) hemipenis unilobed with conspicuous capitular arch on asulcate side; (24) capitulum on asulcate face of hemipenis with two lobular longitudinal crests, oriented obliquely and converging medially to tip of organ.

The general body habitus of *Dipsas bothropoides* **sp. nov.** and its elongate head shape, in particular the preorbital-snout area, as well as some features of color pattern resemble members of the *D. incerta* species group (sensu Harvey, 2008; Fernandes et al., 2010). This group currently includes *D. sazimai*, *D. alternans*, *D. incerta* Jan, 1863 (holotype depicted in Jan and Sordelli [1870], reprinted in Passos et al. [2004]), and *D. praeornata* Werner, 1909. The *D. incerta* group is further defined by having a brown dorsal ground color with darker blotches, a mostly immaculate head with few blotches, 15 dorsal scale rows, and loreal in contact with the orbit, all of which are consistent with our specimens. Although Harvey (2008) and Fernandes et al. (2010) stated that the nuchal collar does not reach the rictus in members of the *D. incerta* group, a *D. alternans* specimen depicted in Maia-Carneiro et al. (2012) appears to show a nuchal collar that may reach the rictus, as it does in the new species.

Description of the holotype (Figs. 1A–B, 2)

Adult female, SVL 420 mm, TL 160 mm (38% SVL); head strongly distinct from body, head length 16.2 mm (3.8% SVL), head width 9.9 mm (61.1% head length) at widest point, head height 6.3 mm at tallest point; interocular distance 6.1 mm; snout–orbit distance 4.0 mm (0.65 times interocular distance); nostril–orbit distance 3.1 mm (0.5 times interocular distance); rostral subtriangular, 3.4 mm wide and 1.9 mm high, slightly visible in dorsal view; internasal about twice as wide (2.0 mm) as long (1.1 mm); prefrontal suture sinistral with respect to internasal suture; prefrontals about as long (2.8 mm) as wide (2.6 mm); prefrontals not in contact with orbit; frontal hexagonal, 3.7 mm long and 3.3 mm wide; supraocular 3.7 mm long and 2.2 mm wide; parietal length about 1.70 times (5.8 mm) width (4.1 mm); nasal divided;



Figure 4. Habitat where the paratype of *Dipsas bothropoides* **sp. nov.** was found: (A) general view of the landscape at Atlantic Forest near Itacaré, north of the terra paratypica; (B) Rio do Tijupe near the location of collection; (C) forest habitat near the terra paratypica.

prenasal about as high (1.6 mm) as long (1.5 mm); nostril positioned in the center of prenasal; postnasal twice as high (1.8 mm) as long (0.8 mm); loreal single, rectangular, 1.3 mm long and 1.6 mm high; loreal contacting second and third supralabials ventrally, orbit posteriorly and preocular dorsally; preocular single, as high (1.0 mm) as long (0.9 mm), entering orbit posteriorly; preocular contacting prefrontal anterodorsally and supraocular posterodorsally; eye diameter 3.4 mm; pupil elliptical; postoculars 2/2, upper postocular higher (1.8 mm) and slightly longer (1.2 mm) than lower postocular (1.0 mm high and long); temporals 3+3+3 on both sides of head; anterior two temporals trapezoidal, together 2.2 mm high and long; supralabials 9/9, 3rd, 4th and 5th entering orbit; 6th supralabial tallest (1.7 mm high and 2.0 mm long), 8th supralabial longest (1.3 mm high and 2.5 mm long); mental triangular, about twice as wide (2.2 mm) as long (1.0 mm); infralabials 9/9, first pair in contact with posterior mental, 1st to 4th contacting first chinshields; 4th to 5th on the left and only 4th on the right side contacting second chinshields; first pair of chinshields 2.6 mm long and 1.7 mm wide; second pair 2.5 mm long and 2.0 mm wide; dorsals smooth in 15/15/15 rows; vertebral row 40% broader than adjacent dorsals from anterior region to mid-body, reducing to 20% broader posteriorly; dorsal rows on tail at level of second subcaudal eight on right and seven on left side; three preventrals; three series of gulars between last infralabial and preventrals; ventrals 183; cloacal plate entire; subcaudals 100 plus a terminal spine, longer than the two last subcaudals, conical with acuminate tip; maxillary teeth 16/17; pterygoid teeth 16/17; palatine teeth 9/9; harderian gland 3.1 mm long and 2.8 mm high, occupying the entire postorbital region.

The color pattern of the preserved holotype resembles very much that of the recently collected paratype (see both in Fig. 1), although somewhat faded. Pupil black; dorsal ground color of head light brown; dorsum of head with three large black pileus blotches cream-brown bordered, two parietal blotches elongate, approximately parallel, slightly divergent anteriorly, covering most of parietal scale; left parietal blotch barely extending onto supraocular, right blotch restricted to parietal scale; third pileus black preorbital blotch (transversal band) extending from anterior portion of frontal/supraoculars to middle of prefrontals, reaching preocular laterally; supralabials light brown dorsally, gradually changing to cream along ventral edge; infralabials cream with dark brown spots along suture region with chinshields; chinshields and gulars cream with scattered dark brown spots; gular region cream to white; dorsal ground color of body light brown with 20/21 (left/right) dorsal blotches on the body and 11/10 blotches on the tail; nuchal collar (= first dorsal blotch) butterfly-shaped (12 scales long on paraventral portion and five scales long at mid-dorsals), framed by

light border of one scale width; nuchal collar not contacting parietals, but contacts rictus (= posterior end of mouth opening); all dorsal blotches except anteriormost shaped as dark brown triangles, usually bilaterally paired with some displacements along body axis of paratype, generating bilateral difference of three blotches (File S1); dorsal blotches dark brown, becoming lighter brown (or yellow in the paratype before preservation) towards center with adjacent scales cream (yellow in paratype), producing light margin, pronounced anteriorly. Blotches pointed dorsally, 1–3 scales wide next to mid-dorsals; base of triangles 4–7 scales wide next to ventrals; spaces between blotches longer than blotches mid-laterally; interspaces 1–5 scales long near ventrals, distance between blotches decreasing posteriorly to 2–3 scales at base of tail; interspaces with short, narrow, irregular dark brown scattered streaks, particularly on anterior portion of body; venter of body cream-brown with higher concentration of dots in posterior region, rendering ventral portion of tail almost uniformly brown; each ventral scale with groups of 3–6 lateral, sequentially arranged, squared or triangular dark brown spots forming irregular stripes along the venter; spots often representing ventral edge of dorsal triangular blotches; ventral spots opposite lateral interspaces located more mid-ventrally.

Hemipenial morphology (Fig. 5)

Description based on fully everted and expanded organ of paratype. Organ unilobed, cylindrical, with bulbous shape, larger at hemipenial body; strongly capitate; capitulum completely encircling organ, occupying more than half of hemipenial body on sulcate side and less than half of hemipenial body on asulcate side; capitulum ornamented with numerous calyces, more concentrated on sulcate side; papillate calyces gradually replacing spinulate calyces towards apex of capitulum; asulcate side of hemipenis with medial retraction of capitulum (= capitular arch sensu Harvey and Embert, 2008) and conspicuous lobular crests (sensu Passos et al., 2013); lobular crests formed by high concentration of calyces; each ramus of lobular crest obliquely oriented and converging medially to tip of organ; sulcus spermaticus bifurcated inside capitulum at about midpoint of organ; branches with centrolateral orientation at basal portion of hemipenis, diverging to more centrifugal position and terminating almost at distal region of lobes; distal portion of hemipenial body with large spines (ca. 20 on sulcate side, ca. 30 on asulcate side) arranged in several rows and concentrated on lateral portion of sulcate side and adjacent to capitulum in asulcate side; few spines from base to mid-portion of asulcate side of hemipenis; proximal region with spinules among large spines on both sides, more concentrated at level of capitular sulcus on sulcate side and on basal region of asulcate side.



Figure 5. (A) Sulcate, (B) lateral, and (C) asulcate views of the hemipenis of the paratype (MZUESC 15828) of *Dipsas bothropoides* **sp. nov.**

Comparisons of internal characters

Dipsas bothropoides **sp. nov.** is distinguished from the two related congeners of the *D. incerta* group in the Atlantic Forest, *D. alternans* and *D. sazimai*, by skull features (Fig. 6), such as: supratemporal bone exceeding anterior and posterior portions of supraoccipital dorsally and quadrate ventrally (vs. supratemporal not reaching anterior or posterior level); ascending process of premaxillae projected posteriorly, contacting nasals dorsally (vs. ascending process of premaxillae not approaching nasals dorsally); and anterior portion of premaxillae exceeding level of nasals dorsally (vs. anterior region of premaxillae not reaching the level of nasals dorsally).

The new species differs from all sympatric congeners except *D. sazimai* and *D. variegata* by having a capitular arch on the asulcate side of the hemipenis. *Dipsas bothropoides* **sp. nov.** differs from *D. sazimai* by having the capitulum on the asulcate side of the hemipenis with two longitudinal, obliquely oriented crests converging medially towards the tip of organ (vs. capitulum on the asulcate side of hemipenis lacking crests). *Dipsas bothro-*

poides **sp. nov.** differs from *D. variegata* by having a unilobed hemipenis (vs. moderately bilobed; see Porto and Fernandes, 1996). Finally, the capitular arch in *D. bothropoides* **sp. nov.** is curved proximally towards the sulcus (half-distal convex inclination), which is non-curved and horizontal in *D. alternans*.

To facilitate understanding differences based on external characters for field observations and identifications, we arrange the following comparisons in two sections: (1) comparison with other species of the *D. incerta* group, all apparently allopatric; (2) comparison with other *Dipsas* species that are sympatric with the new species. In both sections, characters of the congeners compared with the new species appear in parentheses if not otherwise noted.

Comparison of external characters within the *Dipsas incerta* group

Dipsas bothropoides **sp. nov.** differs from *D. incerta* (Passos et al., 2004: fig. 4) and *D. praeornata* (Fig. 7D) by its triangular dorsal blotches, dark iris, and 9 infralabi-

als (vs. rhomboid to ovoid dorsal blotches, light iris, and 11–14 infralabials). Furthermore, *D. incerta* and *D. praeornata* have been documented only from several sites within Venezuela and the Guiana region, 2,000–3,000 km from the new species (Jan, 1863; Harvey, 2008; Lotzkat et al., 2008; Natera-Mumaw et al., 2015), and thus can be safely excluded as being conspecific with *D. bothropoides* **sp. nov.** In the latter two publications, *D. praeornata* is

listed and treated as *D. latifrontalis*. However, *D. latifrontalis* belongs to the *Dipsas peruana* group (Arteaga et al., 2018), and until a more detailed analysis clarifies the problem, we assign all *D. latifrontalis* from those two publications to *D. praeornata*, except for the holotype, BMNH 1946.1.20.98.

Dipsas bothropoides **sp. nov.** resembles *D. alternans* in all scalation characters (see Table 1, Figs. 7B, 8D, Passos

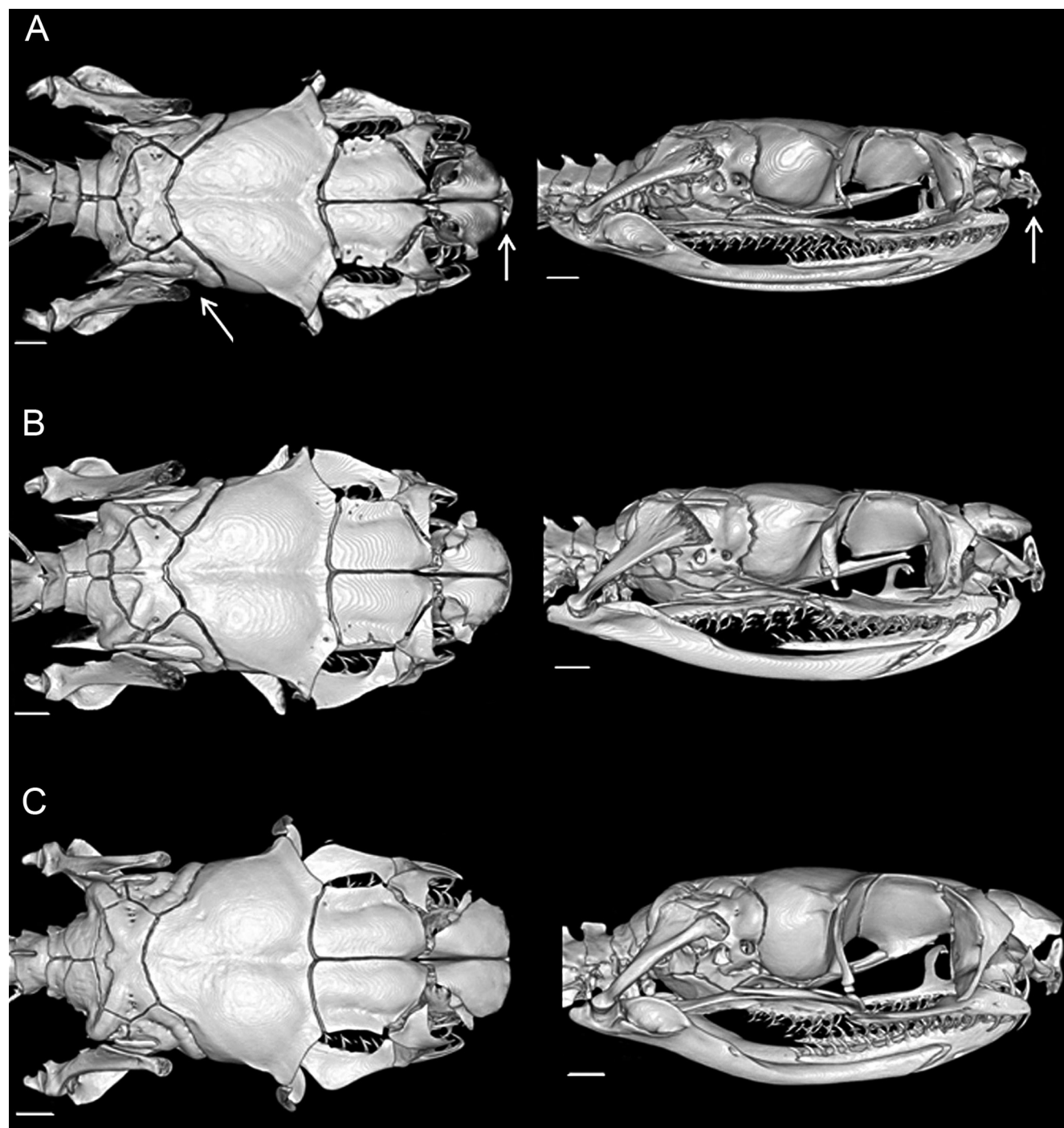


Figure 6. Dorsal and lateral views of the skull of (A) *Dipsas bothropoides* **sp. nov.**, (B) *D. alternans*, and (C) *D. sazimai*. Arrows indicate diagnostic features of the new taxon. Scale bars = 1 mm.

Table 1. Selected external qualitative and quantitative features among *Dipsas bothropoides* **sp. nov.** and other congeners in the *D. incerta* group from the Brazilian Atlantic coastal belt, as well as all sympatric *Dipsadini*. For cephalic scales (e.g., supralabials), only the one or two most frequent values are displayed. For species with a large distribution and potential geographic variations, the representative range for indicated values is given. Character expression displayed on grey-shaded background represents values that clearly differ from *D. bothropoides* **sp. nov.** Data are based on the museum vouchers (Appendix 1) complemented by data from the following literature: Peters (1960), Hoge and Romano (1975), Porto and Fernandes (1996), Harvey and Embert (2008), Lima and Prudente (2009), and Marques et al. (2016). Abbreviations are as follow: fm = former, m = males, f = females, n = number, and SE/NE = southeast/northeast; Brazilian states: AL = Alagoas, BA = Bahia, ES = Espírito Santo, PA = Pará, SC = Santa Catarina.

Character	<i>Dipsas bothropoides</i> sp. nov.	<i>Dipsas alternans</i>	<i>Dipsas sazimai</i>	<i>Dipsas albifrons</i>	<i>Dipsas variegata</i> (fmr. <i>neivai</i>)	<i>Dipsas catesbyi</i>	<i>Dipsas indica</i>	<i>Dipsas newwiedi</i>
Contact prefrontal-orbit	absent	absent	present	absent, rarely present	present (95.7%)	absent	absent	absent, rarely present
Iris color	black	black	black	light or with red vein pattern	light with dark vein pattern	black	light with dark vein pattern	silvery light with granite pattern
Loreal-orbit contact	present (but see text)	present	present	present	present in Bahia specimens	absent	present	absent, present < 20%
Ventrals	183 (f), 179 (m)	174–201 (m+f)	193–202 (f), 187–209 (m)	154–191 (f), 159–187 (m)	173–195 (f; n = 32); 181–200 (m; n = 15), Atl. coast	186–189 (f; n = 2), 186–205; n = 8 SE Bahia	170–185 (f), 182–196 (m); Atlantic Forest BA to PA	167–185 (f; n = 9), 163–190 (m; n = 10) ES to NE Bahia
Subcaudals	100 (f), 110 (m)	78–114 (f), 93–118 (m)	107–116 (f), 107–129 (m)	70–96 (f), 68–97 (m)	66–81 (f; n = 29); 76–90 (m; n = 14), Atl. coast from AL to SC	96–98 (f; n = 2); 102–200 (m; n = 8), entire range	76–110 (f), 83–118 (m), Atl. coast	65–76 (f; n = 5); 67–87 (m; n = 5) ES to NE Bahia
Infralabials (IL)	8–9	9 (34%), 10 (50%)	9 (28%), 10 (50%)	10 (30%), 11 (45%)	11 (32.6%), 12 (52.2)	10–11 (70%)	13 (57%), 12 (18%)	8–9 (90%)
Pairs of IL contact	1 st pair	no data	1 st pair with one of the 2 nd IL pair	1 st to 4 th pairs	1 st and 2 nd pairs Atl. coast from AL to SC	1 st pair, 2 nd pair rarely	1 st and 2 nd (> 90%), 3 rd pair rarely	1 st pair, 2 nd pair rarely
Supralabials	8–9	9 (68%)	8 (28%), 9 (67%)	7 (41%), 8 (52%)	8 (33.3%), 9 (54.8%)	8–9 (85%)	9–10	7 (77%)
IL contact 1 st -pair chinshields	1 st –4 th	1 st –6 th	1 st –5 th or 1 st –6 th (90%)	3 rd –6 th	1 st –5 th Atl. coast from AL to SC	1 st –4 th , 1 st –5 th	2 nd –5 th , 2 nd –6 th	1 st –4 th
Mid-body dorsalia	15	15	15	15	15	13	13	15
Vertebral scale	moderately	moderately	moderately	slight to moderate	moderately	greatly	greatly	moderately

et al. [2004], and details below), but differs from it in the following parameters: color pattern, including black dorsal triangular blotches with light centers and yellow-cream borders fading towards the tail tip (vs. rounded dorsal dark brown blotches that may have a white border); 3–7 large, yellow-bordered pileus blotches on top of head (vs. 2–3 large, yellow-bordered blotches, although some specimens display several small black spots with no light border); groups of tightly arranged square brown ventral spots, increasing posteriorly along lateral margins of ventrals, and alternating with groups of spots closer to mid-venter (vs. fewer and more loosely arranged groups of ventral spots, often triangular and narrower, predominantly along lateral margins of ventrals). Prefrontals not in contact with orbit, as in *D. alternans*, although contact occurs occasionally in the latter species (e.g., *D. alternans* IBSP 22889). However, *D. alternans* is known only from southeastern Brazil, with the nearest records ca. 360 km south at Baixo Guandu (IBSP 9280) and 400 km at Santa Teresa (MNB R704), Espírito Santo (Fig. 3; Peters, 1960; Passos et al., 2004).

From the *Dipsas incerta* group, only *D. sazimai* is known to occur within or near Brazil's northeastern Atlantic coastal belt (Fig. 3) and might be sympatric with *D. bothropoides* **sp. nov.** in mountains up to 100 km from the Atlantic coast of northeastern Brazil (Fernandes et al., 2010; Roberto et al., 2014), but not at the lowland locality of the new species. *Dipsas bothropoides* **sp. nov.** differs from *D. sazimai* in the following characters (Figs. 2, 7A, C, 8A–C): prefrontals not contacting orbit (vs. prefrontals in contact with orbit); gulars separating second pair of chinshields from infralabials (vs. infralabials in direct contact with second pair of chinshields); triangular dark-edged dorsal blotches with light centers slightly shorter than interspaces throughout the body and tail (vs. rounded dorsal dark brown blotches generally wider than interspaces becoming lighter and narrower posteriorly, some with a thin vertical line with an increasing size of interspaces); immaculate interspaces throughout body (vs. posterior interspaces can exhibit a thin vertical line); 3–7 large pileus blotches with yellow borders (vs. variable number of medium to large black blotches without yellow border, although some specimens have several small black spots instead); groups of brown, square ventral spots along lateral margins of ventrals, alternating with similar but smaller groups closer to mid-venter (vs. groups of ventral spots, or spots forming an uninterrupted, continuous line only along lateral margins of ventrals, not alternating with mid-venter brown groups, spots increasing in size posteriorly in some specimens).

Comparison of external characters with sympatric arboreal *Dipsas* species

We compared *D. bothropoides* **sp. nov.** with four sympatric *Dipsas* species (see Argôlo, 2004): (1) *D. cates-*

byi Sentzen, 1796; (2) *D. variegata* (including former *D. neivai*, which represents the Atlantic Forest populations of the widespread *D. variegata*; Harvey and Embert, 2008); (3) *D. indica* sensu lato; and (4) *D. albifrons* (Dias et al., 2018). *Dipsas bothropoides* **sp. nov.** differs from *D. catesbyi* (Figs. 6G, 7H) by: yellow-brown head with a few yellow-bordered black blotches (vs. strongly contrasting black-and-white color pattern on the head with a black-cap extending below the eye); dorsal ground color brown with triangular light centered blotches and a relatively constant blotch/interspace ratio posteriorly (vs. large black-and-white transversal bands anteriorly changing posteriorly to a red-brown body color with oval black bilateral blotches or saddles, blotch/interspace ratio decreasing posteriorly); loreal contacting the orbit, two temporals posterior to postoculars, and vertebral scales only moderately enlarged, 1.4 times larger than adjacent dorsals (vs. loreal not contacting orbit, usually single first large temporal [but see variation among *D. catesbyi* from the Amazon in Lima and Prudente, 2009], and large expanded vertebral scales 2–3 times wider than adjacent dorsal scales); dorsals 15 (vs. 13 in *D. catesbyi*); ventrals 179–183 (vs. 186–201 in Bahia specimens of *D. catesbyi*, in contrast to *D. catesbyi* males from the Amazon with ventrals as few as 160, see Lima and Prudente, 2009).

The new species differs from *Dipsas indica* (Figs. 7I, 8G), *D. variegata* (Figs. 7F, J, 8E), and *D. albifrons* (Figs. 7E, 8F) by: head more elongate (see Peters, 1960 for description of head truncation in these species), particularly preorbital area (vs. a comparatively shorter, but higher snout, and larger eyes resulting in a convex supraocular) and with corresponding different cephalic scale arrangement. For example, *D. bothropoides* **sp. nov.** exhibits predominantly square labials, and only two first infralabials narrow and vertically elongate (vs. anterior 2–5 supralabials and 2–6 infralabials are narrow and tall in *D. indica*, *D. variegata*, and *D. albifrons*); first pair of infralabials contacting each other behind mental scale (vs. 1st and 2nd pair of infralabials contacting each other behind mental scale in *D. variegata*, although this number is variable in *D. indica* and *D. albifrons*); 1st to 4th infralabials in contact with 1st chinshield on each side (vs. usually 2nd to 5th, but less frequently also 6th infralabials in contact with 1st chinshield in *D. indica*, *D. variegata*, and *D. albifrons*); 100–110 subcaudals (vs. 76–93 in *D. variegata* and 70–96 in *D. albifrons*; Passos et al., 2005), although this character overlaps with *D. indica* (Peters, 1960; Hoge and Romano, 1975; Porto, 1993); 15 dorsal scale rows at mid-body (vs. 13 in *D. indica*), while *D. variegata* and *D. albifrons* also exhibit 15 rows; dorsal pattern of strongly black-bordered, straight-sided, upward pointed, light centered triangles with blank and light brown interspaces. The dorsal pattern of *D. indica* comprises subtriangular, trapezoidal to



Figure 7. Snail-eating snake species potentially sympatric with *Dipsas bothropoides* **sp. nov.** or closely related but extralimital, see text: **(A)** paratype of *Dipsas bothropoides* **sp. nov.**, Itacaré, Bahia; **(B)** extralimital *D. alternans* (IBSP 87598) from Núcleo Curucutu, PE Serra, São Paulo; **(C)** *D. sazimai* from Serra da Jiboia, Santa Teresinha, Bahia; **(D)** extralimital *D. praeornata* from Rancho Grande Biological Station, Venezuela; **(E)** *D. albifrons* (MZUESC 14036) from the municipality of Macarani, Bahia, Brazil; **(F)** *D. variegata* from Serra do Condurú State Park, Serra Grande, Bahia; **(G)** *D. catesbyi* from Michelin Ecological Reserve, Igrapiúna, Bahia; **(H)** *D. neuwiedi* from Acuipe, Bahia; **(I)** *D. indica* from Michelin Ecological Reserve, Igrapiúna, Bahia; and **(J)** *D. variegata* female from Vale do Ribeira, São Paulo, Brazil, displaying a few triangular shaped dorsal blotches. Photos by KM except B by Silara Fátima Batista, C and E by Iuri Ribeiro Dias, D by César L. Barrio-Amorós, and J by PP.



Figure 8. Heads of snail-eating snakes species potentially sympatric with *Dipsas bothropoides* **sp. nov.** or closely related but extralimital, see text: **(A)** and **(B)** paratype of *Dipsas bothropoides* **sp. nov.** Itacaré, Bahia; **(C)** *D. sazimai* from Pedra Lascada, Barro Preto, and small inset from Serra da Jiboia, Santa Teresinha, Bahia; **(D)** extralimital *D. alternans* from Serra do Tabuleiro, Santa Catarina; **(E)** *D. variegata* from Serra do Condurú State Park, Serra Grande, Bahia; **(F)** *D. albifrons* (MZUESC 14150), from Guaratinga, Bahia; **(G)** *D. indica* from Michelin Ecological Reserve, Igrapiúna, Bahia; **(H)** *D. catesbyi* from Michelin Ecological Reserve, Igrapiúna, Bahia; **(I)** *D. neuwiedi* from Acupé, Bahia; **(J)** *D. neuwiedi* (dead on road) from Itacaré, Bahia. Photos by KM except C and F by Marcela Sena, inset in C by OME-N D by Thiago Maia Carneiro.

rounded dark gray-brown to light brown filled blotches or saddles, not bordered by thick straight-sided borders, with interspaces being blank or exhibiting a dark spot (small or none in some specimens in southern Bahia) and paraventral white or yellow blotch, while the dorsal patterns of *D. variegata* from southern Bahia and *D. albifrons* are composed of dorsal blotches/saddles vertically stretched rhomboids (more common in *D. variegata* than in *D. albifrons*) or bars (less common in *D. variegata* than in *D. albifrons*) often with a light center (more common in *D. variegata* than in *D. albifrons*) and border zig-zag shaped following the outline of adjacent dorsals, with variable spots in interspaces in *D. variegata*, rarely in *D. albifrons*; morphs of *Dipsas* spp. with straight-sided triangular blotches are rare, but occur in one *D. variegata*, MNRJ 22771, and more often in allopatric populations of *D. variegata* from Venezuela (Lotzkat et al., 2008, Natera-Mumaw et al., 2015); cephalic color pattern of *D. bothropoides* **sp. nov.** yellow to brown with 3–7 large, dark, light-bordered blotches arranged symmetrically on the pileus (vs. in *D. indica*: gray to brown with greater number of dark variably sized, yellow-bordered pileus spots not symmetrically arranged except for two parietal blotches; in *D. albifrons*: unspotted light-colored head with two parallel dark brown blotches extending from parietals onto the neck, occasionally inter-preorbital blotch and brown frontal/parietals; and in *D. variegata*: variable yellow or brown background, no pileus blotches); eye black (vs. lighter in *D. variegata* or *D. albifrons*, and in local *D. indica*, though the latter species contains some darker morphs with dark eyes, but not as black as in *D. bothropoides*); ventral pattern consisting of many small square spots (vs. small dots, speckling, or mottled white becoming darker posteriorly in some *D. indica*, *D. albifrons*, and *D. variegata*). Moreover, regional (southern Bahia) *D. indica* usually possesses a yellow margin (reduced to a few dots or none in some specimens), predominantly along scales contiguous with the eye but also on other cephalic scales, unlike other regional *Dipsas* species. *Dipsas bothropoides* **sp. nov.** has a nuchal blotch < 4 vertebral scales, as in *D. variegata* or *D. albifrons* (but > 4 vertebral scales in *D. indica*), that reaches the rictus, as in most regional *D. indica* from Bahia, also absent in *D. variegata* or *D. albifrons*.

Etymology

The specific epithet represents the Latinized form of “*bothros*” derived from the Greek (βόθρος), referring to the facial pit, and also referring to the genus *Bothrops*, the species-rich terrestrial Neotropical pitvipers. The suffix *-oides* means ‘similar to’ or ‘having the nature of,’ in reference to the great similarity of the dorsal color pattern with many members of the genus *Bothrops*, especially the sympatric *B. jararaca* and *B. pirajai*.

Habitat and climate

Both localities of *Dipsas bothropoides* **sp. nov.** lie within remnants of the once extensive Atlantic Forest ecoregion, a dense ombrophilous rainforest with a uniform canopy ca. 25 m in height and a dense understory (IBGE, 2012), or tropical moist forest following the Holdridge life zones classification (Hartshorn, 1991). However, the two specimens originate from different elevations; the paratype is from near sea level and the holotype is from more inland mountains at 700–1,000 m a.s.l.

The area in a radius of 3 km around the type locality of *Dipsas bothropoides* **sp. nov.** is hilly and covered by a complex combination of submontane tropical rainforest with semi-deciduous seasonal forest that experiences a dry period. Secondary forests and many patches of pasture make up a mosaic of wooded and open disturbed areas. The annual rainfall is at least 1,000–2,000 mm (Landau, 2003) but might be locally higher. The climate is a transition between Köppen Class Af (aseasonal, warm and humid), Class Am (seasonal monsoon), and Class Aw (tropical savanna with a pronounced dry season).

The 3 km around the paratype’s location consists of undulating to rolling hills (10–30% slope), stretching from sea level to ca. 130 m a.s.l. with a straight-line distance of 2.7 km to the Atlantic coast. The vegetation is a mixture of agriculture/pasture, secondary forest at different succession stages (Fig. 4), mixed with patches of recently to old (> 30 years) logged forests. The nearest old growth forest is located 6 km south (Martini et al., 2007). The lowland climate is warm and humid, without a well-defined dry season (Köppen Class Af). Monthly average temperature is 24°C, with July to August being coldest and November to March being warmest. The annual rainfall of 2,400–2,600 mm (Landau, 2003) is well distributed throughout the year, with relative humidity often exceeding 80% (Sá et al., 1982).

DISCUSSION

The discovery and recognition of *Dipsas bothropoides* **sp. nov.** as a new species based on only two specimens found in an apparently well-sampled area qualifies it as a very rare species. Nonetheless, one could also argue that both specimens might represent aberrant individuals of a local—and already known—snail-eating snake. But in this case, we would expect far fewer differences between *D. bothropoides* **sp. nov.** and any of the sympatric arboreal species. Groups of external characters, such as body color tonality, blotch pattern, trunk/tail meristics (segments including ventrals and subcaudals), cephalic scale number, shape and arrangement, hemipenial morphology, and skull osteology, are each coded by separate single or a few main genes (independent loci) and their regulatory

genes, rendering their linked (simultaneous) inheritance among the various genes (respective characters) unlikely (e.g., King, 1993; Bechtel, 1995; Hughes and Kaufman, 2002; Woltering et al., 2009; Lillywhite, 2014). Therefore, one genetic mutation would produce aberrant forms in only one particular group of external characters (i.e., separate mutations for color, blotch type, or scale number), as usually happens in aberrant specimens (for review see Bechtel, 1995).

Such, aberrant morphological forms could result from inbreeding through a small founder population (Gautschi et al., 2002; Mebert, 2011) or through environmental causes (Löwenborg et al., 2010). However, comparisons among the five arboreal *Dipsas* species sympatric with *D. bothropoides* **sp. nov.** revealed differences in at least two groups of external characters (groups = body shapes, scalation, color pattern) simultaneously, as described above in “Comparison of external characters with sympatric *Dipsas* species”.

Within the *Dipsas incerta* group, *D. sazimai* is the only species that shares a similarly elongate head shape and head/body color combination with *D. bothropoides* **sp. nov.** (Fernandes et al., 2010); however, *D. sazimai* exhibits differences in the arrangements of prefrontal and chin scales, nuchal collar extension, cephalic, dorsal, and ventral color pattern, and conspicuous differences in skull and hemipenis morphology that make it extremely unlikely that *D. bothropoides* **sp. nov.** represents an unusual morph of *D. sazimai*. Furthermore, reports of *D. sazimai* in the eastern-central Bahia region are from localities at higher elevations (> 400 m a.s.l.), such as Barro Preto (Figs. 3, 8C) and Camacan (Fernandes et al., 2010), which are, respectively, 68 km and 120 km from the nearest record of *D. bothropoides* **sp. nov.** from the surroundings of the municipality of Itacaré in the coastal lowland and are the shortest known distance between these two species.

With respect to the Mendelian genetic system for morphological characters, it is also unlikely that *Dipsas bothropoides* **sp. nov.** represents a hybrid between two sympatric snail-eating snakes due to the low operational sex ratio (e.g., Mebert et al., 2015; Guiller et al., 2016). This is because the low number of genes involved in morphological characters, their independent inheritance, and asynchronous expression—(1) segmental/scale characters develop early, and (2) color pattern later in the embryogenesis/ontogeny—would produce an F1-hybrid phenotype with scalation traits from only one parental species, while color pattern would be from the other parental species (Chang et al., 2009; Woltering et al., 2009; Murakami et al., 2016). This is unlike the presence of a few characters from both morphological groups, scalation and color pattern, in which *D. bothropoides* **sp. nov.** overlaps with two sympatric *Dipsas* species. Furthermore, neither the triangular dorsal blotches nor the color pat-

tern of head and venter can be generated through crosses between sympatric *Dipsas* species. There is also no evidence of a hybrid zone among sympatric *Dipsas* species that would include deep backcrossing beyond F1-hybridization and their more complex admixed phenotypes (Mebert, 2008, 2010).

The discovery of a new species of snake known from only two localities in the Atlantic Forest of mid-eastern Brazil comes as a great surprise, because this region has been cultivated for centuries, experienced increased seasonal tourism, and has received intense herpetological sampling, revealing a high species richness with 61 snake taxa (e.g., Argôlo, 2004, 2009). While the phenotype of *Dipsas bothropoides* **sp. nov.** generally resembles *D. alternans*, we demonstrated morphological characters allowing their prompt distinction, and *D. alternans* is known only from > 300 km south across the Rio Doce (Passos et al., 2004). While the mid-region of the Atlantic Forest was deemed to be a refuge for the tropical herpetofauna in the Atlantic Forest during the Quaternary climate fluctuations (Carnaval et al., 2009), evidence supports Rio Doce as one of the most determinant biogeographic barriers in that region (Carnaval and Moritz, 2008; Carnaval et al., 2014), promoting species diversification for many taxa (e.g., Menini-Neto et al., 2015), including reptiles (Pellegrino et al., 2005; Marques et al., 2016). Interestingly, a recently described dwarf boa, *Tropidophis grapiuna* Curcio et al., 2012, is also known from only two specimens and shares the same general region as *D. bothropoides* **sp. nov.** Both species represent geographically separated and evolutionarily independent lineages from their putative close relatives south of Rio Doce, *D. alternans* and *T. paucisquamis*, respectively, which have likely become isolated from each other during historic climatic fluctuations in the Pleistocene.

The Brazilian Atlantic Forest is a conservation hotspot (Mittermeier et al., 2004) with a severely threatened permanence and only ca. 7.0–8.5% old growth forest patches of < 100 acres remaining that are disturbed and further fragmented by plantations, pastures, and suburban areas (Ribeiro et al., 2009; SOS Mata Atlântica, 2000). Arboreal snakes, such as the new species *Dipsas bothropoides* **sp. nov.**, are probably at risk of extinction due to perturbation and rapid loss of their habitat (Marques and Sazima, 2004). This species might persist only in low densities. Therefore, and since we currently know *D. bothropoides* **sp. nov.** only from single records at two localities (Fig. 3), we consider this species to be Critically Endangered due to the “B1a,b(iii)” IUCN criteria and the following evaluations: (1) its extent of occurrence is small, composed of only two 10 km² areas that are approximately 250 km apart; (2) together with *Tropidophis grapiuna*, they are the only snake species in the coastal Atlantic Forest and mountains known from only two localities; and (3) it likely suffers severe range contraction and habitat

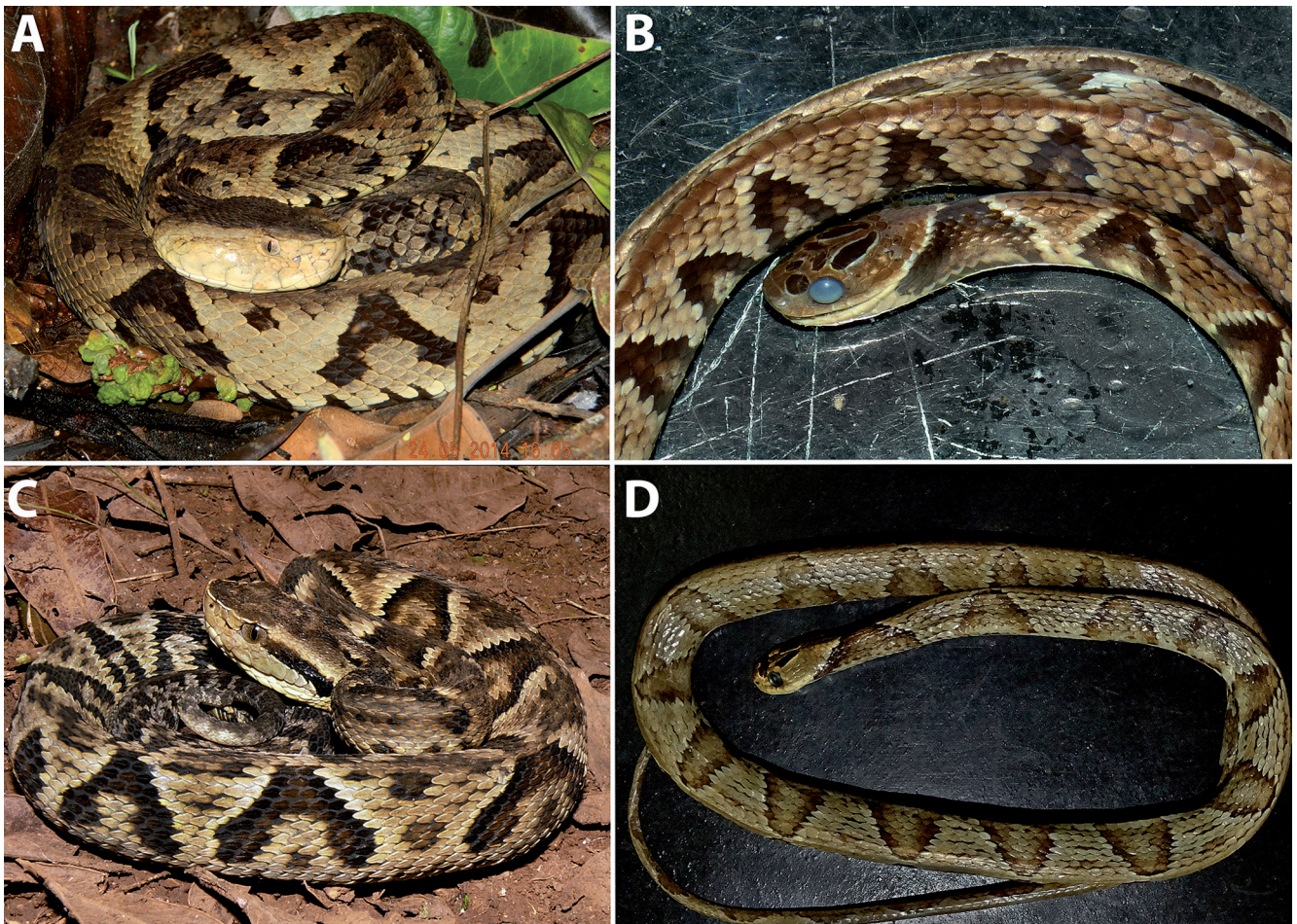


Figure 9. Potential viper mimicry: **(A)** *Bothrops pirajai* from Michelin Ecological Reserve, Igrapiuna, Bahia; **(B)** paratype of the non-venomous *Dipsas bothropoides* **sp. nov.**, exhibiting a similar color pattern with the former venomous pitviper; **(C)** *Bothrops jararaca* from Zortéa, Santa Catarina; and **(D)** holotype of *Dipsas bothropoides* **sp. nov.**, which is sympatric with *B. jararaca*. Photos by KM except A by Caio Vinicius Mendes and D by Roberta Murta-Fonseca.

degradation with a subsequent decline in abundance. Fortunately, a composite of protected areas exists around the montane terra typica (two parks at Alto do Cariri, and Vida Silvestre Mata dos Muriquis Refuge) as well as near the lowland site of the paratype (Serra do Condurú State Park).

Finally, it is remarkable how the dorsal color pattern of *Dipsas bothropoides* **sp. nov.** resembles some specimens of the sympatric *Bothrops pirajai* Amaral, 1923 from the coastal stretch and also *B. jararaca* Wied-Neuwied, 1824 from drier uphill and montane areas. Therefore, we suggest that the new *Dipsas* species might mimic juveniles of sympatric *Bothrops* species (Fig. 9), similar to the suggestion for *D. variegata* with approximative triangular-shaped dorsal blotches (Cadle and Myers, 2003; Lotzk et al., 2008; and Fig. 7J), although those blotches are less contrasting and pointed than in *D. bothropoides* **sp. nov.** We recommend that further studies be undertaken to assist in conservation efforts and determine the phylogenetic relationships of *D. bothropoides* **sp. nov.**

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ONLINE SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

File S1. Description of paratype.

APPENDIX 1

Material examined

Voucher specimens formerly deposited in the Coleção Zoológica Gregório Bondar (CZGB) are now housed at Museu de Zoologia da Universidade Estadual de Santa Cruz, Ilhéus (MZUESC). States are formatted in bold letters, municipalities and other localities in plain letters. Specimens for which prepared hemipenes were examined are indicated with an asterisk. We do not repeat sequential acronyms between brackets, except in the case of type material and when identifying specimens for which we prepared one of the hemipenes.

***Dipsas albifrons* (n = 290):** BRAZIL: Unknown locality (IBSP 17746, lectotype of *Dipsadomorus albifrons*, formerly MNHN 6106); **Espírito Santo:** Afonso Claudio (IBSP 50462*, 50463), Castelo (IBSP 53543), Colatina (IBSP 22872, 34178, IBSP 37490*, 37496, 37521, 45915, 45938), Guandú (IBSP 50015), Santa Teresa (MNRJ 1265), São Gabriel da Palha (IBSP 49194, 49656, 50070, 50658–59, 50661, 51197–98), Vila Velha, Morro do Moreno (MNRJ 11027); **Rio De Janeiro:** Angra dos Reis (IBSP 27608), Cabo Frio (MNRJ 7353), Maricá (MNRJ 7372); **São Paulo:** Apiaí (IBSP 56275), Peruíbe, Ilha da Queimada Grande (IBSP 11486 [holotype of *Dipsas albifrons cavaleiroi*], IBSP 1638 [paratype of *D. a. cavaleiroi*], IBSP 3468 [paratype of *D. a. cavaleiroi*], IBSP 11487 [paratype of *D. a. cavaleiroi*], 11488, IBSP 11489 [paratype of *D. a. cavaleiroi*], IBSP 15808–09, 17151, 17213, 18426–27, 29727, 30088–92, IBSP 30093*, 30094–95, 52670, 55723), Santos, Ilha de Alcatrazes (IBSP 13029, 16972, 62175), São Sebastião, Ilha Bela: (IBSP 60345); **Paraná:** Antonina (IBSP 24952 30236), Itaperuçu (IBSP 37553), Jussara (IBSP 49657*), Mallet (IBSP 18971), Palmeira (IBSP 11363), Paranaguá (IBSP 23025), Ponta Grossa (IBSP 44124); **Santa Catarina:** Unknown locality (IBSP 27574), Bananal (IBSP 6510–12, 6870), Blumenau (IBSP 1639, 20954, 26777–78, 40360, 41411, 55089, IBSP 55718*, 55831, 55901, 55904, 55014, IBSP 55948*, IBSP 56212*, 57557, 67918–19), Campos (IBSP 14584–85), Corupá (IBSP 5077–78, 5546, 5557, 5572, 6227, 6721, 6994–7000, 10331, 11840, 12069, 13225, 13575, 13587, 15610, 15755–7, 15845–46, 17367, 17375, 20953, 22417–31, 22428–31, 22767, 33202, 55902, 56347, 64928, IBSP 64929*, 65015, MNRJ 709–10), Garúva (IBSP 31181), Indaial (IBSP 47325), Jaraguá do Sul (IBSP 1194–97, 1548, 1549–50, 1594–95, 1601, 1639, 4315, 4520, 4525, 4531, 4575–76, 4600, 4609, 4650, 5308, 5816, 5859–60, 5924, 5989, 6056, 6066, 6069, 6098, 6109, 6109-A, 6338, 6370, 6376–78, 6495–97, 6510, 6721, 6869, 6870–73, 6899, 6911–14, 6963–64, 6980–83, 6992–93, 7040, 7064, 7079–81, 7112–16, 7283, 10072, 58679, 58739, 62058–59, 62401), Joinville (IBSP 22888, 22900, 25990, 29312, MNRJ 711–13, 715–16), Massaranduba (IBSP 5188–89, 5211–13, 5269, 5331–33, 5446, 6362, 6366–67, 6959, 6989), Rio Natal (IBSP 576, 13284, 15516), Estação (IBSP 5576, 13284, 15516), Palhoça (MNRJ 20163–65), Pomerode (IBSP 64279), Porto Belo (IBSP 52448), São Bento do Sul (IBSP 4832, MZUSP 9440), Santo Amaro da Imperatriz (MNRJ 20164, 20245), São Francisco do Sul (IBSP 602, 602-A, 6238, 6253–54, 6258, 15471, 16400, 20953, 21099, 27327, 29096, 40469, 55306).

***Dipsas alternans* (n = 79):** BRAZIL: **Espírito Santo:** Baixo Guandu (IBSP 9280); **Minas Gerais:** Caratinga (IBSP 306, holotype of *Sibynomorphus barbouri*); **Rio de Janeiro:** Angra dos Reis, Ilha Grande (MNRJ 8060), Nova Friburgo, Parque Estadual dos Três Picos (MNRJ 20354), Muri, Theodoro de Oliveira (MNRJ 19595), Sitio Sisenlandia Km 66.6 of the RJ-116 highway (MNRJ 17225–26), Petrópolis (IBSP 16699), Rio Claro, Lídice (IBSP 7664), Teresópolis (IBSP 41056), Parque Nacional da Serra dos Órgãos: (IBSP 10412–13, MNRJ 19124, 25493), Volta Redonda: Getúlio Vargas: (IBSP 8944); **São Paulo:** without specific locality (IBSP 2733), Juquitiba (IBSP 64465* neotype of *Leptognathus alternans*), Apiaí (IBSP 9301, 24684), Biritiba Mirim (IBSP 33794), Salesópolis (IBSP 44000), Boraceia Biological Station: (MZUSP 8833), Capão Bonito (IBSP 27897, 32871), Caraguatatuba (IB 29359), Eldorado (IBSP 311640, MNRJ 23001), Guapiara (IBSP 34368, 34373, 34377), Juquiá (IBSP 42613), Leme (IBSP 8603), Mogi das Cruzes (IBSP 4571, 4806), Santo André, Serra de Paranapiacaba (MZUSP 1575), Registro (IBSP 41142), Sete Barras (IBSP 46534), Tapiraí (IBSP 57120); **Paraná:** Curitiba (IBSP 4752, 18051), Antonina (IBSP 24887), Cornélio Procopio (IBSP 9254), Rolândia (IBSP 17766), São João da Graciosa (MZUSP 7339); **Santa Catarina:** Blumenau (IB 5307), Corupá (MZUSP 1574, MZUSP 1576 [holotype of *Sibynomorphus garbei*], IBSP 6973, 8173, 8453, 8849, 8897–98, 9291, 9689), Jaraguá do Sul (IBSP 5513, 6787, 7117, 7191, 7460, 8063, 8818, 9446, 21950–51), Joinville, (IBSP 22823, 22889, 30566, 34162, 46542), Mafra (IBSP 8272), Santo Amaro da Imperatriz, (MNRJ 20249), São Bento do Sul (IBSP 8602), Serra Alta (IBSP 41269), Rio do Campo, (IBSP 49151), **Rio Grande do Sul:** Caxias do Sul (IBSP 15770), Torres (IBSP 11024).

***Dipsas catesbyi* (n = 10):** BRAZIL: **Bahia:** Ilhéus (MZUESC 4650, 4730, 4826, 4876, 4859, 4860, 5646, 5177, 4849, 5791).

***Dipsas indica* (n = 26):** BRAZIL: **Amazonas:** Benjamin Constant (MNRJ 687–88); **Bahia:** Barra do Rocha (MZUESC 1987), Boa Nova (MZUESC 6843), Dario Meira (MZUESC 6023), Firmino Alves (MZUESC 6171), Guaratinga (MZUESC

925), Igrapiúna (MZUESC 3005), Itabela (MZUESC 870), Itacaré, Arco de Pedra Farm (MZUESC 1057), Itagi (MZUESC 2440), Itagibá, Pedra Branca Farm (MNRJ 18548), Itaju do Colônia (MNRJ 14742), Itajuípe (MZUESC 796), Ilhéus, CEPAC Regional Center (MZUESC 1436, 2366), Santa Maria Farm (MZUESC 2681), Nova Ibiá (MZUESC 6808); **Espírito Santo**: Conceição da Barra, Floresta Nacional do Rio Preto (MNRJ 23715), Guarapari, Setiba, Parque Estadual Paulo Cesar Vinha (MNRJ 20050, 22757); **Mato Grosso**: Juína (MNRJ 4512); **Rio De Janeiro**: Rio Claro, Parque Arqueológico e Ambiental de São João Marcos (MNRJ 26653–54), Rio de Janeiro, Jardim Botânico, Dona Castorina road (MNRJ 3996), Grotão (MNRJ 26356).

Dipsas sazimai (n = 8). BRAZIL: **Alagoas**: Murici, Bananeira Farm (MZUESC 8199, paratype); **Bahia**: Camacã, Sítio Maria das Neves (MZUESC 6134, paratype), Serra Bonita, (MZUESC 7848, MZUESC 8466, paratypes), Jequié (MZUESC 7988, paratype), Miguel Calmon, Parque Estadual das Sete Passagens (MZUFBA 1800, paratype); **Espírito Santo**: Mimoso do Sul: Bandarra Farm (IBSP 77835, paratype), Santa Teresa, Santa Lucia Biological Station (MNRJ 19275, paratype); **Rio de Janeiro**: Casimiro de Abreu (MNRJ 15136, holotype); **São Paulo**: Ubatuba (IBSP 69143, paratype).

Dipsas variegata (sensu stricto; n = 3). BRAZIL: **Mato Grosso**: Sinop, Rio Teles Pires (IBSP 56146); **Pará**: Parauapébas (MNRJ 18276); **Rondônia**: Porto Velho (IBSP 56146).

Dipsas variegata (sensu lato, including *D. neivai*; n = 21). BRAZIL: **Alagoas**: Murici (MNRJ 7235*), Quebrangulo (MNRJ 21021); **Bahia**: Buerarema (MZUESC 754), Camacã (MZUESC 1137), Floresta Azul (MZUESC 842–43), Gongogi (MZUESC 771), Ilhéus (MZUESC 832, MNRJ 3995), Itamaraju (MZUESC 1377), Itubera (MZUESC 757), Santa Maria (MZUESC 1020), Teofilândia, Barra Grande Farm: (MNRJ 14722), Trancoso (MNRJ 19626–27, 23575–76), Una (MZUESC 1174); **Espírito Santo**: Conceição da Barra, Floresta Nacional Rio Preto (MNRJ 23713), Jaguaré, Córrego da Abobora (MNRJ 23714); **São Paulo**: Vale do Ribeira (MNRJ 20464, 22771).

Dipsas (former *Sibynomorphus*) neuwiedi (n = 8). BRAZIL: **Bahia**: Boa Nova (MZUESC 1884–85), Barra de Choca (MZUESC 1612), Itamarajú (MZUESC 1695), Ituberá (MZUESC 1613), Jussari (MZUESC 1482, 1492), Ribeirão do Largo (MZUESC 1577).