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Taxonomic revision of the *Jita* snakes (Lamprophiidae: *Boaedon*) from São Tomé and Príncipe (Gulf of Guinea), with the description of a new species

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ABSTRACT

The taxonomic status of the São Tomé and Príncipe islands 'Cobras Jitas', genus *Boaedon*, has been a subject of confusion. Historically, these island populations have been referred to as part of either the *Boaedon fuliginosus* species complex or *Boaedon capensis* species complex, two of the most taxonomically challenging groups of African snakes, or considered a distinct taxonomic entity, *B. bedriagae*. Here we review the São Tomé and Príncipe populations through a combination of morphological and molecular data. Our results suggest that each island population represents a unique species. After a thorough review of the taxonomic and nomenclatural history of the group, we revalidate *B. bedriagae*, restricting the application of this name to the São Tomé population by the designation of a lectotype. We also describe the Príncipe population as a new species, *Boaedon mendesi* sp. nov. This description has implications to our understanding of the diversity and phylogeographic patterns of the Gulf of Guinea Oceanic Islands.

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Introduction

In just over a decade, several new vertebrate taxa have been described from the small island nation of São Tomé and Príncipe in the Gulf of Guinea. These include the following new species: a shrew, *Crocidura fingui* (Ceríaco et al. 2015); a gecko, *Hemidactylus principensis* (Miller et al. 2012); four species of skinks, *Trachylepis adamastor*, *T. principensis*, *T. thomensis* and *Panaspis thomensis* (Ceríaco 2015; Ceríaco et al. 2016; Soares et al. 2018, respectively); a cobra, *Naja peroescobari* (Ceríaco et al. 2017); a puddle frog;

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This article is registered in ZooBank under: urn:lsid:zoobank.org:pub:13E287C7-E644-4899-95B9-AF5B66931E89
This species is registered in ZooBank under: *Boaedon mendesi*: urn:lsid:zoobank.org:act:0936727A-A15F-4967-936E-645A0EF97DCE

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Phrynobatrachus leveleve (Uyeda et al. 2007); and a reed frog, *Hyperolius drewesi* (Bell 2016). These earlier works have considerably expanded our understanding of the diversity, endemicity and biogeographic patterns of the herpetofauna of these two islands. Five species of amphibians are currently known on São Tomé Island and three species are present on Príncipe (Ceríaco et al. 2018). All of these amphibians are endemic to their respective island. São Tomé Island hosts a total of 12 species of terrestrial reptiles, of which six are island endemics, three are shared endemics with Príncipe Island, and the remaining three also occur elsewhere in the continent (Ceríaco et al. 2018, 2020). A total of 14 species, including confirmed species and species groups with taxonomic and nomenclatural uncertainties, have been recorded for Príncipe Island. Of these taxa, eight are island endemics, three are shared endemics with São Tomé Island, and the remaining three also occur on the continent (Ceríaco et al. 2018, 2020).

Among the endemic reptiles of these islands, the African House Snakes of the genus *Boaedon* Duméril, Bibron and Duméril, 1854, locally known as 'Cobras Jitas' [= Jita snakes], are probably some of the most well-known species in the country. Unlike the famous 'Cobra-Preta', *Naja peroescobari*, the 'Jitas' are usually appreciated by locals and recognised as harmless to humans. Despite this general appreciation, these snakes are still poorly studied, and their taxonomic allocation remains problematic. These island *Boaedon* have one of the most complex and problematic taxonomic and nomenclatural histories of all São Tomé and Príncipe reptiles. Indeed, *Boaedon* ranks amongst one of the most taxonomically challenging genera of African snakes (Greenbaum et al. 2015; Hallermann et al. 2020).

The taxonomic allocation of the São Tomé and Príncipe 'Jitas' has been a matter of discussion and different interpretations by the authors who have recently dealt with them. Historically the São Tomé and Príncipe Jitas have had an uncertain taxonomic allocation and given a varied number of nomina (see below). Boulenger (1906) was the first to recognise the São Tomé and Príncipe Jitas as a different species, *Boaedon bedriagae*. Subsequently, various authors had different interpretations, both on the validity of the taxon and its affinities. Angel (1920) and Roux-Estève and Guibé (1965) followed Boulenger's (1906) interpretation and considered *bedriagae* a valid species. Bogert (1940) considered that *bedriagae* was a subspecies of *B. lineatus*, a decision followed by Manaças (1958) and Capocaccia (1961a, 1961b). Roux-Estève and Guibé (1964), Manaças (1973), Schätti and Loumont (1992), Chippaux (1999) and Hofer (2002), considered it as a subspecies of *Boaedon* (or *Lamprophis*) *fuliginosus*. Chippaux (2006) considered *bedriagae* to be a synonym of *Boaedon fuliginosus*, while Wallach et al. (2014) considered *bedriagae* to be a synonym of *Boaedon lineatus*. Ceríaco et al. (2018) referred to the species as *B. bedriagae*, noting that the Príncipe Jitas were in the process of being described as a new species. Chippaux and Jackson (2019) considered it as a subspecies of *B. fuliginosus*.

One of the main issues regarding the taxonomic identity of the São Tomé and Príncipe Jitas has roots in the contentious taxonomic and nomenclatural history of the remaining species of the genus, especially *B. fuliginosus* and *B. lineatus*, the two taxa typically associated with this population. The taxonomy and nomenclature of *B. fuliginosus* and *B. lineatus* has been a matter of debate for decades. Roux-Estève and Guibé (1964, 1965) presented an initial approach to the understanding of these two taxa.

Boaedon fuliginosus was described by Heinrich Boie (in Friedrich Boie 1827) as *Lycodon fuliginosus*. The original description states that the type locality of the species was Java, which, as noted by Hallermann et al. (2020), represents an error. According to Brogersma

in Roux-Estève and Guibé (1965), the type specimen has been lost. However, meristic scale data and colouration unambiguously identify Boie's *B. fuliginosus* as what most modern authors recognise as the African Brown House Snake, *Boaedon fuliginosus*. It is probable that the specimen was collected en route from Java to Europe. At the time the typical voyages from the Dutch East Indies would have stopped at the Cape of Good Hope (present-day Cape Town) and possibly in West Africa at one of the ports of the 'Dutch Gold Coast', such as Elmina (present-day Ghana). Modern authors (Chippaux 2006; Trape and Mané 2006; Greenbaum et al. 2015; Trape and Mediannikov 2016; Chippaux and Jackson 2019; Hallermann et al. 2020), tend to agree that although *B. fuliginisous* is still a very problematic taxon, it corresponds to the dark-coloured Brown House Snake from Western Africa.

Boaedon lineatus was described by Duméril, Bibron and Duméril (1854) under the French name *Boedon* Quatre-raises [= four lines] based on two specimens collected in 'Cote-D'or', present-day Ghana. Later, Duméril (1861) established *Boaedon quadrilineatum*, *quadrilineatum* literally meaning 'four lines,' as an independent species and also mentions that Günther (1858) considered *Boaedon capense* [= *capensis*] and *Boaedon lineatus* as synonyms. *B. fuliginosus* and *B. lineatus* have sometimes been synonymised (Loveridge 1957; FitzSimons 1962; Roux-Estève and Guibé 1964; Broadley 1983), and much like *B. fuliginosus, B. lineatus* has a complex taxonomic and nomenclatural history, with several names currently placed under its synonymy (Wallach et al. 2014; Uetz et al. 2020). Modern authors (Chippaux 2006; Trape and Mané 2006; Greenbaum et al. 2015; Trape and Mediannikov 2016; Chippaux and Jackson 2019) tend to agree that *B. lineatus* is represented by the Striped House Snake from Western Africa described as uniformly grey to reddish brown coloured, with two stripes on the side of head and two preoculars.

Recent authors tend to agree that both *B. fuliginosus* and *B. lineatus* represent species complexes that need to be readdressed (Kelly et al. 2011; Wallach et al. 2014; Hallermann et al. 2020), but so far this much needed taxonomic revision is still due. Given the considerable number of names coined as subspecies of either *fuliginosus* or *lineatus*, the number of names currently considered as synonyms of these two species and the imprecise data about the type locality of the nominotypical forms, this revision may prove to be one of the most challenging taxonomic works of present-day African herpetology. These species complexes have been the subject of recent studies (Greenbaum et al. 2015; Trape and Mediannikov 2016; Hallermann et al. 2020) that have contributed to our understanding of the diversity of the genus, but have not yet dealt with the root of the question, namely the identity of *B. fuliginosus*, *B. lineatus* or even *B. capensis*.

This paper focuses on the São Tomé and Príncipe *Boaedon* populations. As part of an ongoing revision of the herpetofauna of the islands, this paper presents a taxonomic and nomenclatural review of the Jitas, including the description of a new species. We also provide a taxonomic and nomenclatural review of the problematic *Boaedon nigrum* Fischer, 1856.

Materials and methods

Material examined

For mensural and meristic comparisons, we examined specimens of *Boaedon* from São Tomé and Príncipe. The specimens are deposited in the following institutions:

Muséum national d'Histoire naturelle (MNHN), Paris (France); Instituto de Investigação Científica Tropical (IICT), Lisbon (Portugal); Museu Nacional de História Natural e da Ciência (MUHNAC; formerly Museu Bocage - MB), Lisbon (Portugal); Center of Natural History, Universität Hamburg, Zoologisches Museum (ZMH), Hamburg (Germany); Museo Civico di Storia Naturale 'Giacomo Doria' (MSNG), Genoa (Italy); University of Michigan Museum of Zoology (UMMZ), Ann Arbor, MI (USA); California Academy of Sciences (CAS), San Francisco, CA (USA); and Zoologisches Forschungsmuseum Alexander König (ZFMK), Bonn (Germany). For a complete list of the specimens examined see the respective taxonomic accounts below. Locality geographic coordinates are reported in the form of decimal degrees and use the WGS-84 map datum. Older (non-GPS) records were georeferenced using the GEOLocate web application (https://www.geo-locate.org). All elevations are reported as meters above sea level.

Molecular methods

DNA was extracted from 21 *Boaedon* tissue (Table 1) using a Qiagen DNeasy extraction kit and protocol. We independently amplified two gene fragments (i.e. one mitochondrial [Cytochrome *b* (cyt *b*)], one nuclear [oocyte maturation factor mos (c-mos)]) using Invitrogen Taq master mix by ThermoFisher Scientific (Waltham, MA, USA) with two primer pairs: L14910 + H16064 (cyt *b*) and S77 + S78 (c-mos) from Eurofins Scientific (Louisville, KY, USA). Cyt *b* was amplified in 10 µl PCRs, with an initial denaturing temperature of 94 °C for 3 minutes (min), followed by 40 cycles of denaturation at 94 °C for 30 seconds (s), annealing at 55°C for 30 s**,** and extension at 72°C for 90 s. C-mos was amplified in 10 µl PCRs, with an initial denaturing temperature of 96°C for 1 min, followed by 50 cycles of denaturation at 96°C for 10 s, annealing at 50°C for 30 s**,** and extension at 60°C for 4 min (Slowinski and Lawson 2005). PCR amplicons were visualised with 1% agarose gel with SYBRsafe gel stain and products were purified using

Table 1. Sequences and localities of individuals of *Boaedon* used generated in this study.

Species	Catalog number	cyt *b*	c-mos	Locality description
Boaedon bedriagae	CAS218728	MW228125	MW228146	São Tomé Island
Boaedon bedriagae	CAS218844	MW228126	MW228147	São Tomé Island
Boaedon bedriagae	CAS218962	MW228127	–	São Tomé Island
Boaedon bedriagae	CAS219030	MW228128	–	São Tomé Island
Boaedon bedriagae	CAS219323	MW228129	MW228148	São Tomé Island
Boaedon bedriagae	CAS219005	MW228130	–	São Tomé Island
Boaedon bedriagae	CAS219318	MW228131	MW228149	São Tomé Island
B. capensis b	CAS168909	MW228132	–	East Usambara Mtns, Tanzania
B. capensis b	CAS168920	MW228133	–	East Usambara Mtns, Tanzania
B. fuliginiosus a	CAS201729	MW228134	–	Byumba, Uganda
B. fuliginiosus a	CAS201740	MW228135	–	Byumba, Uganda
B. mendesi sp. nov.	CAS233410	MW228136	MW228150	Príncipe Island
B. mendesi sp. nov.	CAS238883	MW228137	–	Príncipe Island
B. mendesi sp. nov.	CAS238885	MW228138	MW228151	Príncipe Island
B. mendesi sp. nov.	CAS238900	MW228139	MW228152	Príncipe Island
B. mendesi sp. nov.	CAS238884	MW228140	MW228153	Príncipe Island
B. mendesi sp. nov.	CAS238895	MW228141	MW228154	Príncipe Island
B. mendesi sp. nov.	CAS238899	MW228142	MW228155	Príncipe Island
B. radfordi	CAS201634	MW228143	–	Bwindi, Uganda
B. radfordi	CAS201635	MW228144	–	Bwindi, Uganda
B. sp. 1	MVZ249808	MW228145	MW228156	Nkwanta, Volta region, Ghana

ExoSAP-IT or gel excision. Sequencing was performed in both forward and reverse directions using the PCR primers on an Applied Biosystens ABI3130xl Genetic Analyzer at the California Academy of Sciences' Center for Comparative Genomics, and sequence chromatographs were edited using Geneious 5.5. No internal stop codons were found and gaps in alignments were treated as missing data. Novel sequences from this study were deposited in GenBank (MW228125 - MW228156). These sequences were combined with those from other Lamprophiidae utilised in Greenbaum et al. (2015) (see Appendix).

Phylogenetic analyses

To determine the evolutionary history and distinction of *Boaedon* from the islands of São Tomé and Príncipe, we conducted Bayesian mixed-model analyses performed in MrBayes v.3.0b4 (Ronquist and Huelsenbeck 2003) using models selected based on Akaike information criterion (AIC) conducted in MrModeltest 2.2 (Nylander 2004) run in PAUP*v4.0b10 (Swofford 2002). Two simultaneous runs were conducted (three heated and one cold chain with the default Markov chain Monte Carlo settings), for a total of 6×10^6 generations per run, sampling trees and parameters every 100 generations and the first 1.5×10^6 generations from each run were discarded as burn-in. Trees were rooted with outgroup taxa *Amblyodipsas dimidiata*, *Bothrolycus ater*, *Bothrophthalmus lineatus*, *Gonionotophis brussauxi*, and *Lycophidion capense* included in Greenbaum et al. (2015).

Finally, we computed pairwise comparisons of the cyt *b* gene fragment as a measure of estimated genetic distances within and between species of *Boaedon* using MEGA X (Kumar et al. 2018; Table 2). These analyses were conducted using the Maximum Composite Likelihood model (Tamura et al. 2004) and involved 76 informative nucleotide sites including all three codon positions. All ambiguous positions of the final 1 116 bp dataset were removed for each sequence pair (pairwise deletion option).

Morphological methods

Specimens were measured with a flexible measuring tape for snout–vent length (SVL) and tail length (TL) to a precision of one millimetre, and all other measurements were recorded with a digital calliper or an ocular micrometer to a precision of a tenth of a millimetre. Lepidosis was observed with the help of a stereomicroscope. Scale nomenclature, scales counts and measurements used in the descriptions follow Greenbaum et al. (2015) and Hallermann et al. (2020). The following characters were measured: snout-vent length (SVL), from the tip of the snout to the anterior edge of the cloaca; tail length (TL), from the posterior edge of the cloaca to the tip of the tail. For type material we also measured the head length (HL), from the tip of snout to just behind the angle of the jaw; interocular distance and eye diameter. The following scale counts were made: number of dorsal scale rows at midbody (MSR); number of ventral scales (V), from the first scale broader than long to the cloacal plate (we used the traditional method of ventral scale count to make our work comparable to Greenbaum et al. (2015) and Hallermann et al. (2020)); number of subcaudal scales

Table 2. Pairwise sequence divergences within (diagonal in italics) and among (below diagonal) all *Boaedon* species as defined in this study. Sequences used were only from the cyt *b* gene fragment and values are rounded to the nearest hundredth place. Values for *B. mendesi* sp. nov. are in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1– *B. bedriagae*	*0.01*															
2 - *B. capensis* a	0.13	*n/c*														
3 - *B. capensis* b	0.13	0.10	*0.06*													
4 - *B. capensis* c	0.09	0.11	0.11	*n/c*												
5 - *B. fradei*	0.12	0.13	0.12	0.11	*0.01*											
6 - *B. fulginosus* a	0.11	0.13	0.12	0.13	0.11	*0.01*										
7 - *B. fulginosus* b	0.13	0.13	0.13	0.13	0.11	0.09	*0.03*									
8 - *B. lineatus*	0.12	0.13	0.12	0.12	0.14	0.11	0.11	*n/c*								
9 - *B. mentalis*	0.13	0.14	0.15	0.13	0.14	0.13	0.12	0.13	*0.00*							
10 - *B. olivaceus*	0.12	0.12	0.12	0.12	0.12	0.09	0.10	0.10	0.11	*0.01*						
11 - *B. radfordi*	0.11	0.12	0.11	0.12	0.11	0.09	0.07	0.11	0.11	0.10	*0.01*					
12 - *B.* sp. 1	0.18	0.18	0.18	0.18	0.17	0.18	0.17	0.16	0.18	0.17	0.16	*n/c*				
13 - *B.* sp. 2	0.10	0.12	0.12	0.12	0.10	0.08	0.06	0.11	0.11	0.09	0.06	0.16	*n/c*			
14 - *B. upembae*	0.16	0.17	0.17	0.16	0.15	0.17	0.17	0.18	0.17	0.17	0.16	0.16	0.16	*0.00*		
15 - *B. virgatus*	0.18	0.19	0.19	0.18	0.19	0.18	0.18	0.19	0.18	0.19	0.18	0.14	0.17	0.17	*n/c*	
16 - *B. mendesi* sp. nov.	**0.06**	**0.13**	**0.18**	**0.13**	**0.13**	**0.12**	**0.13**	**0.12**	**0.14**	**0.12**	**0.12**	**0.17**	**0.11**	**0.18**	**0.18**	***0.00***

(SC); number of supralabials; number of infralabials; number of preoculars; number of postoculars; number of supralabials touching the eye orbit; the ratio of V and Sc (V/SC) was also recorded. The length and height of the loreal scale (LOR), as well as its ratio (LOR-L/H) were recorded. Snout length is described in relation to the length of the parietal shield (PAR): the PAR is either equal to the distance between the frontal and the rostral scale or longer. Finally, colouration pattern was reported in preserved specimens. A slash (/) represents characters from the right and left sides of the body, always in that order.

Information on morphological characters of species and/or type material that could not be examined, as well as supplemental data for all Central and West African *Boaedon* was obtained from the relevant literature (e.g. Greenbaum et al. 2015; Chippaux 2006; Trape and Mané 2006; Trape and Mediannikov 2016; Chippaux and Jackson 2019; Hallermann et al. 2020). There has been a long history of confusion regarding the identity of some of *Boaedon* taxa, and the allocation of certain names to synonymy. This is especially true for *Boaedon fuliginosus* and *B. lineatus*. For these reasons, we provide comparisons between the two São Tomé and Príncipe *Boaedon* populations and all West and Central African congeners. From a taxonomy and nomenclature perspective, *B. fuliginosus* is still one of the most challenging groups within *Boedon*. Our interpretation of '*fuliginosus*' includes only West African *B. fuliginosus* (from Morocco in the north to Angola in the south), which comprise a genetic unit, following Hallermann et al. (2020). Morphologically similar *fuliginosus*-like species from East and Central Africa are excluded from comparison. This is in accordance with the most updated and informed interpretations of what 'true' *fuliginosus* really is (Greenbaum et al. 2015; Trape and Mediannikov 2016; Chippaux and Jackson 2019). The same comparisons apply to *B. lineatus*. *B. capensis* was not considered for these comparisons, as it is an extralimital species.

Results

Phylogenetic analysis

We conducted a Bayesian phylogenetic analysis using mtDNA (cyt *b*, 1 116 bp) alone and a second analysis that combined cyt *b* and a nuclear (c-mos, 579 bp) gene fragment. MrModeltest 2.2 selected the following partitioned nucleotide substitution models for our dataset: cyt *b* codon 1 (GTR+ Γ), codon 2 (HKY + I+Γ), codon 3 (GTR + I+Γ); c-mos codon 1 (HKY), codon 2 (GTR+ Γ), codon 3 (HKY).

The phylogenies generated from these data and partitions produced nearly identical topologies, though less support in the combined analysis (Figure 1), with comparable relationships as found in recent studies (e.g. Kelly et al. 2011; Greenbaum et al. 2015). Similar to these studies we found strong support for a basal split within *Boaedon* between a clade of *B. upembae* and *B. virgatus* and the remaining *Boaedon*, though our analyses add a potential new species, *B.* sp. 1, that is sister to *B. virgatus*. Furthermore, we concurred support for a split of *B. mentalis* from the remaining *Boaedon*. Similar to previous studies, the majority of interspecies relationships in this clade of *Boaedon* were not supported. One consistency, however, was support for the paraphyly of *B. capensis* and *B. fulginosus*, even after recognizing

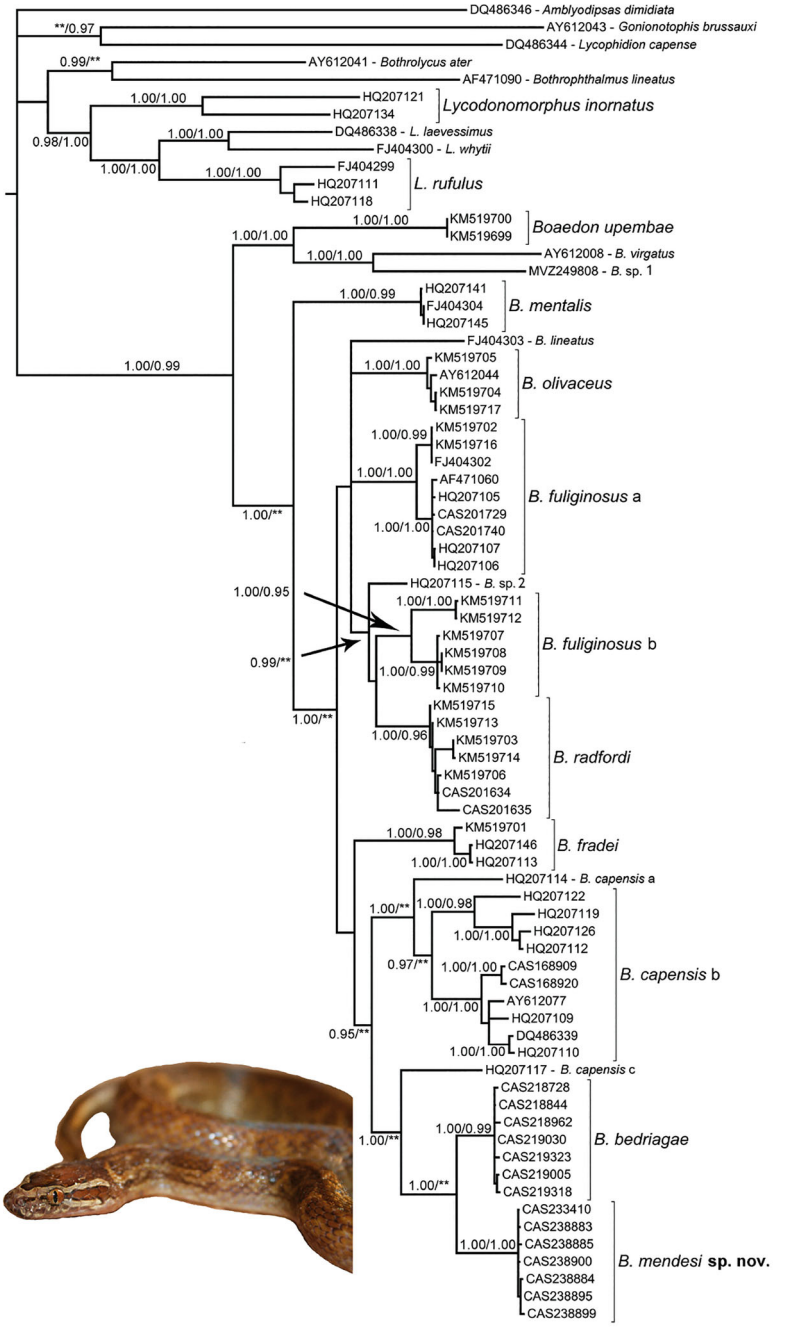

Figure 1. Bayesian 50% majority-rule consensus phylogram of *Boaedon* inferred from a partitioned dataset of the cyt b gene fragment. Posterior probability nodal support values of 0.95 and above are displayed and considered highly supported, while values <0.95 are not displayed or represented by **. Support values on the left result from the cyt b phylogeny, while values on the right are derived from a separate Bayesian phylogeny utilizing a combined mtDNA (cyt b) and nuclear (c-mos) gene fragment dataset (total of 1 695 bp). Species names follow those given in Table 1 and Appendix. Photograph of *Boaedon mendesi* sp. nov. from Príncipe by LMPC.

Table 3. Comparison between *B. bedriagae* and *B. mendesi* sp. nov.

	Boaedon bedriagae ($n = 37$)	*Boaedon mendesi* sp. nov. ($n = 20$)
Maximum SVL (cm)	107	122
Maximum TL (cm)	24.5	22
Midbody scale rows	25–31	24–29
Ventral scales	210–247	206–242
Subcaudal scales	65–95	61–81
Subcaudals rows	Double	Double
Preoculars	1	1 (rarely 2)
Postoculars	2	2
Supralabials touching the eye	Usually 3rd, 4th and 5th, sometimes only 4th and 5th	Usually 3rd, 4th and 5th, rarely 4th, 5th and 6th
Cloacal plate	Entire	Entire
Head stripes	Present, broad	Present, broad
Colouration (dorsum)	Dark brown, with parallel mediodorsal and dorsolateral bands running from the neck to the tail	Dark brown, with a series of dorsolateral cream blotches running from the neck to the midbody
Colouration (ventral)	Cream, heavily speckled with dark markings	Whitish, without markings

some clades as distinct taxa (e.g. *B. fradei*, *B. radfordi*). More specifically, our cyt *b* phylogeny found strong support for a clade consisting of *B.* sp. 2, *B. fuliginosus* b, and *B. radfordi* along with a sister relationship between two distinct island species of *Boaedon* from Príncipe and São Tomé islands that are together sister to the *B. capensis* c lineage found within a clade that includes sister taxa *B. capensis* a and *B. capensis* b.

Our phylogenetic analyses found strong support that all our 16 designated species of *Boaedon* belong to their own unique clade. Sequence divergences of cyt *b* among these taxa ranged from 6 to 19%, while divergences within species ranged between 0.0 and 6% (Table 2). The sequence divergence within the island species from São Tomé (i.e. *B. bedriagae*) was 0.532%, while the population from Príncipe was 0.394%. These species are further supported by a 6% divergence, compared to the next nearest divergence of 9% by *B. bedriagae* and *B. capensis* c. Based on these results we recognise the population from Príncipe as being a distinct species from *B. bedriagae* and other *Boaedon* under the General Lineage Concept of species (de Queiroz 1998) and therefore distinguish it morphologically below.

Morphological analysis

Results of our morphological analyses are shown in Table 3. The populations of São Tomé and Príncipe islands are very similar to each other, without major morphological or meristic characters differences, although they can unambiguously be diagnosed against each other by their colouration patterns (see diagnoses below). As noted by Trape and Mediannikov (2016), colouration pattern is one of the most reliable and useful characters for the genus. Both islands populations can also be distinguished from the continental forms based on a combination of characters (see taxonomic accounts below). Based on these differences and the results of our molecular analyses, we recognise these clades as new or revalidated species, respectively.

Systematics

Boaedon bedriagae Boulenger, 1906

(Figures 2 to 5)
Boaedon quadrilineatus: Jan and Sordelli (1870: Plate II)
Boodon quadrilineatum: Bocage (1879: 87; 1887: 200)
Boodon capensis: Greeff (1884: 48)
Boodon capense: Bocage (1886: 69; 1889: 34); Vieira (1886: 237)
Boodon lineatus [part]: Bedriaga (1892: 904; 1893: 439); Bocage (1905: 93); Henriques (1917: 81, 143); Themido (1941: 6).
Boodon bedriagae [part]: Boulenger (1906: 211).
Boodon bedriagae: Angel (1920: 199)
Boaedon lineatus bedriagae: Bogert (1940: 6)
Boaedon lineatus bedriagai [part]: Manaças (1958: 188); Capocaccia (1961a: 63; 1961b: 288)
Boaedon fuliginosus bedriagae [part]: Roux-Estéve and Guibé (1964: 770); Chippaux and Jackson (2019: 192)
Boaedon bedriagae [part]: Roux-Estéve and Guibé (1965: 400); Ceríaco et al. (2018: 103)
Boaedon fuliginosus bedriagai [part]: Manaças (1973: 225)
Lamprophis fuliginosus bedriagae [part]: Schätti and Loumont (1992: 30); Nill (1993: 72); Hofer (2002: 89)
Lamprophis fuliginosus [part]: Chippaux (2006: 65)
Boaedon lineatus [part]: Wallach et al. (2014: 96)

The first available records referring to the species were published by Jan and Sordelli (1870), who provide an illustration of a São Tomé specimen collected by the German medical surgeon Carl Weiss (dates of birth and death unknown) (Figure 2). The specimen depicted was identified as *Boaedon quadrilineatum* and is still present in the collections of the ZMH (R01256; Figure 3). Subsequently, several authors provided additional records from São Tomé island. Bocage (1879) notes a specimen of *Boaedon quadrilineatum* collected by Custodio de Borja, a navy officer and General Secretary of the Government of São Tomé e Príncipe. Interestingly, Bocage (1879) mentions that the local name was already 'Dgita'. The German naturalist Richard Greeff (1828–1892) who explored the Gulf of Guinea islands between 1879 and 1880, published records of '*Boodon capensis*'

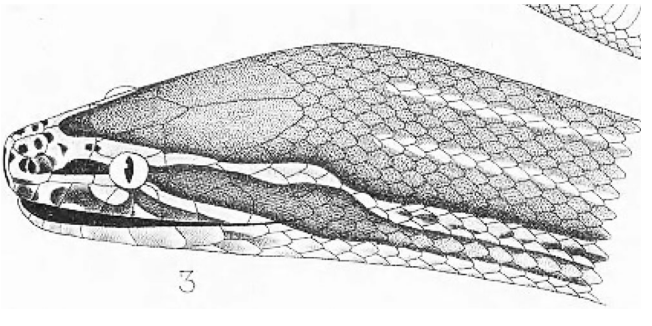

Figure 2. Head of *Boaedon bedriagae* identified as *Boaedon quadrilineatus* by Jan and Sordelli (1870). Adapted from Jan and Sordelli (1870).

Figure 3. Specimen of *Boaedon bedriagae* (ZMH R01256) depicted in Jan and Sordelli (1870).

from São Tomé (Greef 1884). Some of Greef's original specimens are still extant in the collections of ZMH and ZMB.

From May to September 1885, Adolfo F Moller (1842–1920), chief gardener of the Coimbra Botanical Garden, collected plants and animals in São Tomé for the collections of the University of Coimbra. A preliminary list of the material collected by Moller, including a list of herpetological material identified by Bocage, was published by Vieira (1886). In this list, Vieira (1886) cites the presence of '*Boodon capense*, Dum. & Bibr.'. These specimens remained in Portugal in the collections of the Zoological Museum of the University of Coimbra (currently Museu da Ciência da Universidade de Coimbra (MCUC)), Portugal (Themido 1940). Notably, the specimens were not located in a recent visit to the MCUC (LMPC pers. obs.). However, some specimens collected by Moller were sent to the Russian naturalist Jacques von Bedriaga (1854–1906), who published a review of São Tomé herpetofauna based on the specimens from Moller (Bedriaga 1892, 1893). In this review, Bedriaga referred to the presence of '*Boodon lineatus* D.B.' and provided a detailed description of the specimens at hand (Bedriaga 1892, 1893). To date, it is unclear what happened to these specimens. According to the available biographies of Bedriaga (Böhme 1996; Bischoff and Böhme 2001), the Russian herpetologist never visited Portugal. Bedriaga moved to Nice, France in 1881 and later moved to Florence, Italy, where he died in 1906, never returning to Russia (Böhme 1996; Bischoff and Böhme 2001). It is probable that these specimens were sent to Nice, but their whereabouts are currently unknown.

The Portuguese explorer Francisco Newton (1864–1909), hired by the Natural History Museum of Lisbon for the zoological exploration of the Gulf of Guinea, collected and sent several specimens of reptiles from São Tomé Island. Based on these

records Bocage (1886, 1889, 1905) published several records of São Tomé Jitas, either identifying them as *Boaedon capense* (Bocage 1886, 1889) or *B. lineatus* (Bocage 1905). Some years after Newton, the Italian naturalist Leonardo Fea (1852–1903) explored the islands in the Gulf of Guinea between 1899 and 1900 and collected specimens for the natural history museum of Genoa, Italy. Based on five specimens from São Tomé Island (Vista Alegre and Ribeira Palma) and three specimens from Príncipe Island collected by Fea, Boulenger (1906) described '*Boodon bedriagae,*' a new species named in honor of Jacques von Bedriaga. According to Boulenger (1906), the main characters that differentiate *B. bedriagae* from *B. lineatus* were 1) 'the third upper labial constantly entering the eye (only very exceptionally in *B. lineatus*)' and 2) 'the markings of the head' (Boulenger 1906). The type series of *B. bedriagae* is currently extant in the collection of the Museo Civico di Storia Naturale 'Giacomo Doria', in Genoa, Italy (Capocaccia 1961a, 1961b). Angel (1920) presented a subsequent record of the newly described *B. bedriagae* and was the only author until very recently to consider the taxon as a full species.

Bogert (1940) examined a single specimen from São Tomé collected by the Portuguese naturalist José Correia (1881–1954) and he noted that São Tomé [and Príncipe] island Jitas were not sufficiently distinct to be regarded as full species and that they were instead a subspecies of *Boaedon lineatus*. According to Bogert (1940), the distinctive character presented by Boulenger (1906) to distinguish *B. bedriagae* from *B. lineatus*, the contact between labials and the eye, is 'exceedingly variable in the typical form [*lineatus*], and thus can have no diagnostic significance in separating *bedriagae*', but he argued that scale counts, size and colouration warrant diagnostic differences between the two forms. Bogert (1940) also emphasised the considerably larger size of the São Tomé forms compared to those from the continent. Manaças (1958), following the taxonomic interpretation of Bogert (1940), reported three specimens from the island. Cappocacia (1961a) reviewed the type series of *Boodon bedriagae* and other specimens not studied by Boulenger (1906) present in the Genoa museum, noting that São Tomé island population had characters that allowed differentiation from Príncipe island population. Namely, the number of 'longitudinal series of dorsal scales' was lower in specimens from Príncipe than those from São Tomé. Due to the small amount of comparative material at her disposal, Cappocacia (1961a) did not propose any taxonomic change. In a review of the *Boaedon* genus, Roux-Estéve and Guibé (1964) considered *B. bedriagae* a subspecies of *B. fuliginosus*, much like the authors considered *B. lineatus* a synonym of *B. fuliginosus*. These authors refuted Boulenger's (1906) diagnostic characters, noting the main characters that differentiated *bedriagae* from the nominotypic form were a higher number of subcaudal scales in both male and female *bedriagae* and a colouration pattern more closely resembling *B. quadrilineatus* than *B. fuliginosus*. Without further explanations Roux-Estéve and Guibé (1965) considered *B. bedriagae* a full species.

Subsequent authors provided more records of the São Tomé's Jita and revisionary works have presented different interpretations on the taxonomic identity. Manaças (1973) presented the taxon as *Boaedon fuliginosus bedriagae;* Schätti and Loumont (1992) and Nill (1993) as *Lamprophis fuliginosus bedriagae*. Chippaux (2006) considered them a synonym of *B. fuliginosus*. Wallach et al. (2014) synonymised the taxon to *B. lineatus lineatus*. Ceríaco et al. (2018) considered it a full species, while Chippaux and Jackson (2019) considered it a subspecies of *B. fuliginosus*. In the past decade, the species has been collected by teams of the California Academy of Sciences (CAS; Figure 4) and the Museu Nacional de História Natural e da Ciência (MUHNAC; Figure 5) (this paper).

Figure 4. Live photo of *Boaedon bedriagae*. Photo by Andrew Stanbridge.

According to our results, São Tomé and Príncipe islands populations are not conspecific. Since *B. bedriagae* was described based on specimens from both São Tomé and Príncipe, the type series is currently composed by homonyms. Therefore, following Article 74.1 from the International Code of Zoological Nomenclature (ICZN 1999), it is mandatory to designate a lectotype to *B. bedriagae* from the available syntypes. For

Figure 5. Specimen of *Boaedon bedriagae* (MUHNAC/MB03–978) from São Tomé Island.

this, we chose specimen MSNG/CE 30987b, from Vista Alegre, São Tomé island, part of the original type series, as a lectotype of *B. bedriagae*.

Lectotype — MSNG/CE 30987b, an adult from Vista Alegre [0.318941°, 6.676295°, 336 m], Mé-Zochi district, São Tomé Island, collected by Leonardo Fea on 1900.

Additional material — **SÃO TOMÉ ISLAND: Água Grande region:** MUHNAC/MB03-000727, São Marçal [0.32487°, 6.73906°, 9 m] collected by Manuel Sacramento and Afonso A Junior on 7 July 1984; MUHNAC/MB03-000978, São Tomé [0.333333°, 6.733333°, 9 m] collected by an unknown collector on 7 November 1984. **Cantagalo region:** IICT/R 51/1954, Água Izé [0.218168°, 6.725793°, 26 m] collected by Fernando Frade on 9 December 1954; MUHNAC/MB03-00719, 00721, Água Izé [0.217896°, 6.725°, 38 m] collected by Ruben Soares, Teresa Pité and Artur Serrano on 14 and 18 June 1984, respectively; CAS 218844-218847, Caxueira, along Água Péte Péte, [0.298°, 6.73036°, 49 m] collected by Robert C Drewes, Ricka E Stoelting and Jens V Vindum on 5 April 2001; CAS 258789, Roça Água Izé, shade plantation along road to Bernardo Faro [0.227529°, 6.726019°, 33 m] collected by Rayna C Bell, Maria A Jerónimo, Andrew B Stanbridge and Luis Mendes on 39 Setember 2015. **Caué region:** IICT/R 8/1954, Roça Porto Alegre [0.033333°, 6.533333°, 16 m] collected by Fernando Frade on 11 October 1954; IICT/R 2-1967, Angra Toldo [0.15770°, 6.67070°, 19 m] collected by an unknown collector on 1 June 1967; CAS 219311, Cruzeiro [0.288278°, 6.681194°, 303 m] collected by Ricka E Stoelting on 5 May 2001; CAS 258812, inland from Praia Micondo [0.173444°, 6.67625°, 72 m] collected by Rayna C Bell, Maria A Jerónimo and Andrew B Stanbridge on 30 September 2015; UMMZ 187961-187966, Pousada, area 850 m [0.231722°, 6.597921°, 749 m] collected by Ronald A Nussbaum and Michael E Pfrender on 4 and 7 June 1988; UMMZ 187969-187970, Colónia Açoreana 60 m [0.183333°, 6.683333°, 125 m] collected by Ronald A Nussbaum and Michael E Pfrender on 10 June 1988. **Lembá region:** IICT/R STP12, Ponta-Figo [0.339465°, 6.54286°, 151 m] collected by an unknown collector on 24 May 1958; CAS 259001 Contador Valley, road to aqueduct/reservoir system past Ponta Figo [0.316417°, 6.550278°, 639 m] collected by Rayna C Bell, Maria A Jerónimo and Andrew B Stanbridge on 13 October 2015. **Lobata region:** IICT/R 17/1967, Roça Boa Entrada [0.35°, 6.666667°, 180 m] collected by an unknown collector in 20 August 1967; MUHNAC/MB03-000724, Guadalupe [0.379342°, 6.638327°, 14 m] collected by Ruben Soares, Teresa Pité and Artur Serrano on 4 July 1984; CAS 219030, Rio do Ouro below Agustinho Neto [0.365472°, 6.644917°, 160 m] collected by Robert C Drewes, Ricka E Stoelting and Jens V Vindum on 13 April 2001; CAS 218962, base of Muquinqui [0.381194°, 6.648778°, 137 m] on 11 April 2001; CAS 218728, coast road S of Lagoa Azul [0.408083°, 6.58675°, 0 m] on 30 March 2001; CAS 258724, Obo National Park, Monte Carmo Roca, outside of Malanza village, EMOLVE plantation (Agripalma) [0.105194°, 6.602583°, 79 m] collected by Rayna C Bell, Lauren A Scheinberg, Andrew B Stanbridge and Ricardo F de Lima. **Mé-Zóchi region:** IICT/R 4/1966, 18/1967, 21/1967, Roça Potó-Correia [0.29685°, 6.680288°, 291 m] collected by an unknown collector on 20 and 23 August 1967; MUHNAC/MB03-000720, 000722, Nova Moca [0.283333°, 6.633333°, 771 m] collected by Ruben Soares, Teresa Pité and Artur Serrano on 15 June 1984; MUHNAC/MB03-000725, Monte Café [0.299976°, 6.640108°, 694 m] collected by Ruben Soares, Teresa Pité and Artur Serrano on 24 June 1984; MB03-000726, Potó Correia a 7 km da Madalena [0.29685°, 6.680288°, 291 m]

collected by Ruben Soares, Teresa Pité and Artur Serrano on 20 June 1984; MUHNAC/MB03-000978 (Figure 5), Jardim Botânico Bom Sucesso [0.27427°, 6.58581°, 1 209 m] collected by Luis MP Ceríaco and Mariana P Marques on 15 February 2015; CAS 219005, Java [0.261083°, 6.650889°, 588 m] collected by Robert C Drewes, Ricka E Stoelting and Jens J Vindum on 11 April 2001; CAS 219277, Bom Sucesso [0.288861°, 6.612417°, 1 155 m] collected by Robert C Drewes and Ricka E Stoelting on 26 April 2001; CAS 219318, road from Bom Sucesso to radio tower [0.275778°, 6.610417°, 1 234 m] collected by Ricka E Stoelting on 5 May 2011; CAS 219322, W of radio antenna above Bom Sucesso [0.275556°, 6.605194°, 1 324 m] collected by Ricka E Stoelting on 6 May 2011; CAS 219323, Bom Sucesso [0.288667°, 6.612444°, 1 151 m] collected by Ricka E Stoelting on 7 May 2011; CAS 252830, forest between Bom Successo and Lagoa Amelia [0.284811°, 6.602397°, 1 312 m] collected by M Jirku on 31 October 2011; CAS 258725, 258726 Roça Bombaim [0.245861°, 6.632278°, 462 m] collected by Rayna C Bell, Lauren A Scheinberg, Maria A Jerónimo and Andrew B Stanbridge on 23 September 2015; CAS 258858 ca 0.9 km E of Madalena, along ES4 [0.327028°, 6.673222°, 232 m] collected by Rayna C Bell, Lauren A Scheinberg, Maria A Jerónimo and Andrew B Stanbridge on 2 October 2015; CAS 258969, Bom Sucesso [0.2875°, 6.611639°, 1 147 m] collected by Rayna C Bell, Lauren A Scheinberg, Maria A Jerónimo, Andrew B Stanbridge, Robert C Drewes and KB Lim on 12 October 2015; ZFMK 82964 Sao Nicolao [0.27972°, 6.62556°, 968 m] collected by Daniel Hofer on October 2003. **Unknown locality:** IICT/R 3/1966, São Tomé Island collected by unknown collector on 20 August 1966; IICT/R 19/1967, São Tomé Island, collected by unknown collector on 24 August 1967; IICT/R STP13, São Tomé Island, collected by unknown collector on 7 November 1984; MNHN 1920.10-14, Sans localité precise (= without precise locality), 13 February 1920; ZMH R01256 (Figure 3), without precise locality (St. Thomas), collected by Carl Weiss in 1858.

Diagnosis — *Boaedon bedriagae* (Figures 2 to 5) can be distinguished from all of its Central and West African congeners by the following combination of characters: dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail; two broad, cream-coloured, dark brown-bordered bands running on the side of the head; the upper band starting on the nasals and extending above the eye to the posterior part of the head, the lower band usually starting on the posterior lower part of the eye and extending to the corner of the mouth; venter cream-coloured speckled with dark brown markings; the 3rd, 4th and 5th supralabials contacting the eye, one preocular; 25 to 31 midbody scales rows, 210 to 247 ventral scales and 65 to 95 subcaudals, and a maximum snout–vent length of 107 cm.

It can be distinguished from *B. fuliginosus* by its higher number of ventral and subcaudal scales (210 to 247 and 65 to 95, respectively, in *B. bedriagae* versus 194 to 229 and 46 to 71 in W-African *B. fuliginosus* fide Hallermann et al. (2020), by having three supralabials touching the eye (versus only two in *B. fuliginosus* fide Hallermann et al. 2020), by having two broad cream, dark-bordered bands running on the side of the head (versus two thin white lines in *B. fuliginosus*), and by having dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail (versus a homogeneous dark brown colouration in *B. fuliginosus*); it can be distinguished from *B. lineatus* by dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail (versus a uniformly grey to reddish brown colouration in *B. lineatus*) and by having only one preocular (versus usually

two in *B. lineatus*); it can be distinguished from *B. olivaceus*, *B. poensis* and *B. radfordi* by having the subcaudals divided (versus single in B. *olivaceus*, *B. poensis* and *B. radfordi*); it can be distinguished from *B. virgatus* by having two broad cream, dark-bordered bands running on the side of the head (versus two thin white lines in *B. virgatus*), by a higher number of midbody scales rows (25 to 31 in *B. bedriagae* versus 23 to 25 in *B. virgatus*), and a higher number of ventral and subcaudal scales (210 to 247 and 65 to 95, respectively, in *B. bedriagae* versus 186 to 223 and 42 to 64 in *B. virgatus*); it can be distinguished from *B. upembae* by having more ventral scales (210 to 247 in *B. bedriagae* versus 175 to 197 in *B. upembae*), and a higher number of midbody scale rows (25 to 31 in *B. bedriagae* versus 21 to 23 in *B. upembae*). It can be distinguished from *B. perisilvestris* by the 3rd, 4th and 5th supralabial in contact with the eye (versus usually the 4th and 5th in *B. perisilvestris*), by having two broad cream, dark-bordered bands running on the side of the head (versus no lines in *B. perisilvestris*), and by having dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail (versus a homogeneous dark brown colouration in *B. perisilvestris*); it can be distinguished from *B. paralineatus* by the 3rd, 4th and 5th supralabial in contact with the eye (versus only the 4th and 5th in *B. paralineatus*), by its lower number of midbody scale rows (25 to 31 in *B. bedriagae* versus 31 to 35 in *B. paralineatus*); it can be distinguished from *B. subflavus* by the 3rd, 4th and 5th supralabial in contact with the eye (versus only the 4th and 5th in *B. subflavus*); having two broad, cream-coloured and dark-bordered bands running on the side of the head (versus only one line in *B. subflavus*), and by having dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail (versus a homogeneous yellow to light brown colouration in *B. subflavus*); it can be distinguished from *B. longilineatus* by having a higher number of subcaudals (65 to 95 versus 42 to 63 in *B. longilineatus*) and by having two broad coloured and dark-bordered bands running on the side of the head (versus only one, continuous from the snout to the tail, in *B. longilineatus*); it can be distinguished from *B. littoralis* by having dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail (versus homogeneous light brown colouration in *B. littoralis*).

Distribution — The species is endemic to São Tomé island and Rolas islet, Gulf of Guinea. The species has been recorded from the northern, central and south-eastern areas of the island (Figure 6), and is likely distributed throughout.

Habitat and natural history notes — Not much is known about the natural history of this species. Manaças (1973) noted that one female collected in July 1967 had 13 eggs, each around 26 mm high by 12 mm wide. Another female, collected in August 1967, had a total of five eggs, the largest measuring around 63 mm high by 14 mm wide and the smallest measuring 28 mm high by 12.5 mm wide. The species is commonly found in forested areas, but also in slightly disturbed habitats. Nill (1993) noted that in human settlements the species could rely on *Hemidactylus mabouia* and *Panaspis thomensis* as prey items. The same author found juveniles hunting *Hyperolius* and *Phrynobatrachus* at night.

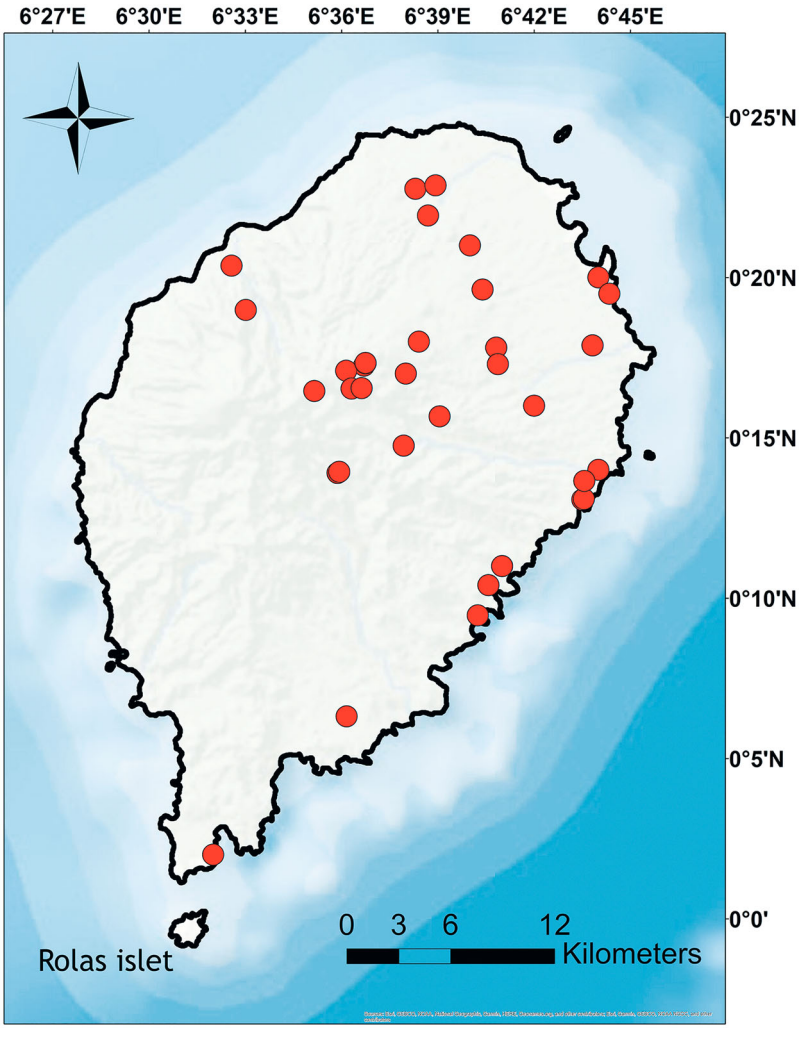

Figure 6. Confirmed records of *Boaedon bedriagae* in São Tomé Island.

Boaedon mendesi sp. nov.

(Figures 7 to 8)
Boodon geometricum ?: Bocage (1887: 199)
Boodon lineatus [part]: Bocage (1903: 54); Henriques (1917: 81)
Boodon bedriagae [part]: Boulenger (1906: 211)
Boaedon lineatus bedriagai Boulenger (Capocaccia 1961a: 63; 1961b: 288; Manaças 1958: 188)
Boaedon fuliginosus bedriagae [part]: Roux-Estéve and Guibé (1964: 770); Chippaux and Jackson (2019: 192)
Boaedon bedriagae [part]: Roux-Estéve and Guibé (1965: 400); Ceríaco et al. (2018: 103)
Boaedon fuliginosus bedriagai: Manaças (1973: 225)
Lamprophis fuliginosus: Chippaux (2006: 65)

Figure 7. Live photo of the holotype of *Boaedon mendesi* sp. nov. (MUHNAC/MB03–977).

Figure 8. Holotype of *Boaedon mendesi* sp. nov. (MUHNAC/MB03–977).

Boaedon lineatus [part]: Wallach et al. (2014: 96).

Fewer historical records of the Príncipe Jita exist compared to the São Tomé Jita. Bocage (1887) provided the first record of the taxon from Príncipe island based on a specimen collected by Francisco Newton and Bocage identified it as a putative *Boodon geometricum*. Subsequently, Bocage (1903) cited additional specimens from Príncipe, this time identifying them as *Boodon lineatus*, and noting the local common name 'Cobra Cabussam'. As noted in the account of *Boaedon bedriagae*, Boulenger (1906) used three specimens from Príncipe island as part of the syntypes of *Boodon bedriagae*. The taxonomic identity of the Príncipe population faced the same uncertainties as *B. bedriagae*, since at the time they were considered the same taxonomic entity. Different authors have argued that the Príncipe population is either a subspecies of *B. fuliginosus* (Roux-Estéve and Guibé 1964; Manaças 1973; Hofer 2002; Chippaux and Jackson 2019), a subspecies of *B. lineatus* (Manaças 1958; Capocaccia 1961a, 1961b;), a valid species (Roux-Estéve and Guibé 1965), a synonym *B. fuliginosus* (Chippaux 2006) or a synonym of *B. lineatus* (Wallach et al. 2014). Capocaccia (1961a) was the first to denote some morphological differences between the São Tomé and Príncipe populations, although she refrained from making any taxonomic decision, due to the small number of individuals at her disposal. Ceríaco et al. (2018) noted that the Príncipe population was different from the one from São Tomé and referenced a description elsewhere (this paper). According to our molecular and morphological results, the Príncipe population is not conspecific with *B. bedriagae* from São Tomé. As there are no available names to the Príncipe population, we describe it here as a new species, *Boaedon mendesi* sp. nov.

Holotype — MUHNAC/MB03-977 (Figures 7 to 8), an adult male collected in the vicinities of Santo Cristo (1.63633°, 7.42690°, 80 m), Príncipe Island, Republic of São Tomé e Príncipe, collected by Luis MP Ceríaco, Mariana P Marques, and Pedro NP Ceríaco on 10 February 2015.

Paratypes — All specimens from the Island of Príncipe, Republic of São Tomé e Príncipe. Three specimens: CAS 233410, Príncipe Island [1.659306°, 7.395389°, 178 m] collected by Robert C Drewes, Joseph Uyeda and Jens V Vindum on 11 May 2006; IICT/R 52-56/1957, Principe Island, collected by Décio Passos on March 1955; MB03-001027, road to Porto Real [1.62617°, 7.41344°, 38 m] collected by Luis MP Ceríaco, Mariana P Marques, Ana C Sousa and Ostilino C Rocha on 17 February 2016.

Additional material. CAS 238883, on road near Ponta do Sol [1.654889°, 7.381278°, 200 m] collected by Robert C Drewes on 29 April 2008; CAS 238884, near Ponta do Sol [1.655889°, 7.380944°, 200 m] collected by Robert C Drewes on 29 April 2008; CAS 238885, 238895, Bom Bom, East slope [1.698833°, 7.403667°, 53 m] collected by Robert C Drewes on 29 April and 2 May 2008, respectively; CAS 238899, 238900, Bom Bom [1.698167°, 7.402667°, 58 m] collected by Robert C Drewes on 3 May 2008; CAS 251572, base of João Dias Filho, João Dias Pai [1.600917°, 7.374278°, 215 m] collected by Robert C Drewes on 27 May 2012; CAS 261030, trail from Pico Mesa camp to Baia das Agulhas [1.588181°, 7.357781°, 293 m] Rayna C Bell, Lauren A Esposito, Felipe Spina, and Ostilino C Rocha on 5 December 2016; IICT/R 26-1954, Roça Sundy [1.668775°, 7.383353°, 169 m] collected by Fernando Frade on 17 November 1954; IICT/R 113, 114-1956, Roça Sundy [1.668775°, 7.383353°, 169 m]

collected by João Tendeiro on 17 November 1954; IICT/R 8/1967, Roça Sundy [1.668775°, 7.383353°, 169 m] collected by an unknown collector on 4 July 1967; IICT/R 63-1955, Principe Airport [1.662259°, 7.41235°, 180 m] collected by Décio Passos on 6 September 1955; IICT/R 109/1955, Santo António [1.636944°, 7.419444°, 12 m] collected by João Tendeiro on 28 November 1955; MB03-000977, trail to Santo Cristo [1.63427°, 7.42802°, 134 m] collected by Luis MP Ceríaco, Mariana P Marques, Pedro NP Ceríaco and Ostilino C Rocha on 10 February 2015; UMMZ 187968, Ribeira Bacharel [1.614117°, 7.401889°, 19 m] collected by Ronald A Nussbaum and Michael E Pfrender on 26 June 1988. **Unknown locality:** IICT/R 58-59/1955, Principe Island, collected by Décio Passos on April 1955.

Diagnosis — *Boaedon mendesi* sp. nov. (Figures 7 to 8) can be distinguished from all of its Central and West African congeners by the following combination of characters: brown to dark brown colouration with a series of parallel dark brown blotches extending from neck to about midbody; two broad, cream-coloured, dark brown-bordered bands running on the side of the head; the upper band starting on the nasals and extending above the eye to the posterior part of the head, the lower band usually starting on the posterior lower part of the eye and extending to the corner of the mouth; whitish to cream venter colouration without markings; the 3rd, 4th and 5th (but sometimes the 4th, 5th and 6th) supralabials contacting the eye, one preocular; 24 to 29 midbody scales rows, 206 to 242 ventral scales and 61 to 81 subcaudals, and a maximum snout–vent length of 122 cm.

The newly described species can be distinguished from *B. bedriagae* by its brown to dark brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus dark brown colouration with parallel mediodorsal and lateral bands running from the neck to the tail in *B. bedriagae*) and a whitish venter (versus cream, heavily speckled with dark markings in *B. bedriagae*). It can be distinguished from *B. fuliginosus* by its higher number of ventral and subcaudal scales (206 to 242 and 61 to 81, respectively, in *B. mendesi* sp. nov. versus 194 to 229 and 46 to 71 in West African *B. fuliginosus* fide Hallermann et al. (2020), by having three supralabials touching the eye (versus only two in *B. fuliginosus*), by having two broad cream-coloured, dark-bordered bands running on the side of the head (versus two thin white lines in *B. fuliginosus*), and by having brown to dark brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus homogeneous dark brown colouration in *B. fuliginosus*). *B. mendesi* sp. nov. can be distinguished from *B. lineatus* by its brown to dark brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus a uniformly grey to reddish brown colouration in *B. lineatus*) and by having only one preocular (versus usually two in *B. lineatus*). *B. mendesi* sp. nov. can be distinguished from *B. olivaceus*, *B. poensis* and *B. radfordi* by having the subcaudals divided (versus single in *B. olivaceus*, *B. poensis* and *B. radfordi*). *B. mendesi* sp. nov. can be distinguished from *B. virgatus* by having two broad cream-coloured, dark-bordered bands running on the side of the head (versus two thin white lines in *B. virgatus*), and a higher number of ventral and subcaudal scales (206 to 242 and 61 to 81, respectively, in *B. mendesi* sp. nov. versus 186 to 223 and 42 to 64 in *B. virgatus*). It can be distinguished from *B. upembae* by having more ventral scales (206 to 242 in *B. mendesi* sp. nov. versus 175 to 197 in *B. upembae*), and a higher number of midbody scale rows (24 to 29 in *B. mendesi* sp. nov. versus 21 to 23 in *B. upembae*). It can be distinguished from *B. perisilvestris* by the 3rd, 4th and 5th

supralabial in contact with the eye (versus usually the 4th and 5th in *B. perisilvestris*), by having two broad cream-coloured, dark-bordered bands running on the side of the head (versus no lines in *B. perisilvestris*), and by having brown to dark-brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus homogeneous dark brown colouration in *B. perisilvestris*). It can be distinguished from *B. paralineatus* by the 3rd, 4th and 5th supralabial in contact with the eye (versus only the 4th and 5th in *B. paralineatus*) and by its lower number of midbody scale rows (24 to 29 in *B. mendesi* sp. nov. versus 31 to 35 in *B. paralineatus*). It can be distinguished from *B. subflavus* by the 3rd, 4th and 5th supralabial in contact with the eye (versus only the 4th and 5th in *B. subflavus*), having two broad cream-coloured, dark-bordered bands running on the side of the head (versus only one line in *B. subflavus*), and by having brown to dark brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus homogeneous yellow to light brown colouration in *B. subflavus*). It can be distinguished from *B. longilineatus* by having a higher number of subcaudals (61 to 81 in *B. mendesi* sp. nov. versus 42 to 63 in *B. longilineatus*) and by having two broad cream-coloured, dark-bordered bands running on the side of the head (versus a single, continuous line from the snout to the tail, in *B. longilineatus*). It can be distinguished from *B. littoralis* by having brown to dark brown colouration with a series of parallel dark blotches extending from the neck to about midbody (versus homogeneous light brown colouration in *B. littoralis*).

Description of holotype — Adult male (Figures 7 to 8), 68.5 cm SVL; head subtriangular, slightly distinct from the neck, HL 3.5% of SVL (2.43 cm); pupil elliptical, eye diameter 0.37 cm; loreal rectangular, almost twice as long (0.27 cm) as high (0.16 cm); body cylindrical; tail moderately short (21.6% of SVL). Supralabials 8/8, 3rd, 4th and 5th on both sides touching the eye; infralabials 9/9, first on each side in contact behind mental, first three on both sides in contact with anterior chin shields and 4th on both sides in contact with posterior chin shields; one preocular on both sides not touching frontal; 2 postoculars, the lower one in contact with 5th and 6th supralabials (both sides of head); temporals 1 + 2+3 on both sides; two internasals; nasal divided; frontal longer than wide; dorsal scales smooth, 22 MSR one head-length posterior to

Table 4: Morphometric and meristic data on *Boaedon mendesi* sp. nov. types series. Measurements are in cm. All abbreviations follow the Materials and methods

	MUHNAC/MB03-977 Holotype	MUHNAC/MB03-1027 Paratype	IICT 52-1955 Paratype	CAS 233410 Paratype
Sex	Male	Unsexed	Unsexed	Female
SVL	69.5	47	122	46.4
Tail length	15	10.2	19	88
SVL/TL				
MDSR	26	27	27	26
Ventral scales (V)	212	208	232	232
Subcaudals (SC)	69	68	62	66
V/SC				
Subralabials (entering eye)	3rd, 4th, 5th	4th, 5th, 6th	3rd, 4th, 5th	3rd, 4th, 5th
Loreal length	2.7	2.6	3.5	2.4
Loreal height	1.6	1.1	1.8	1.0
Loreal L/H ratio				
Preocular	1	1	1	1
Postocular	2	2	2	2

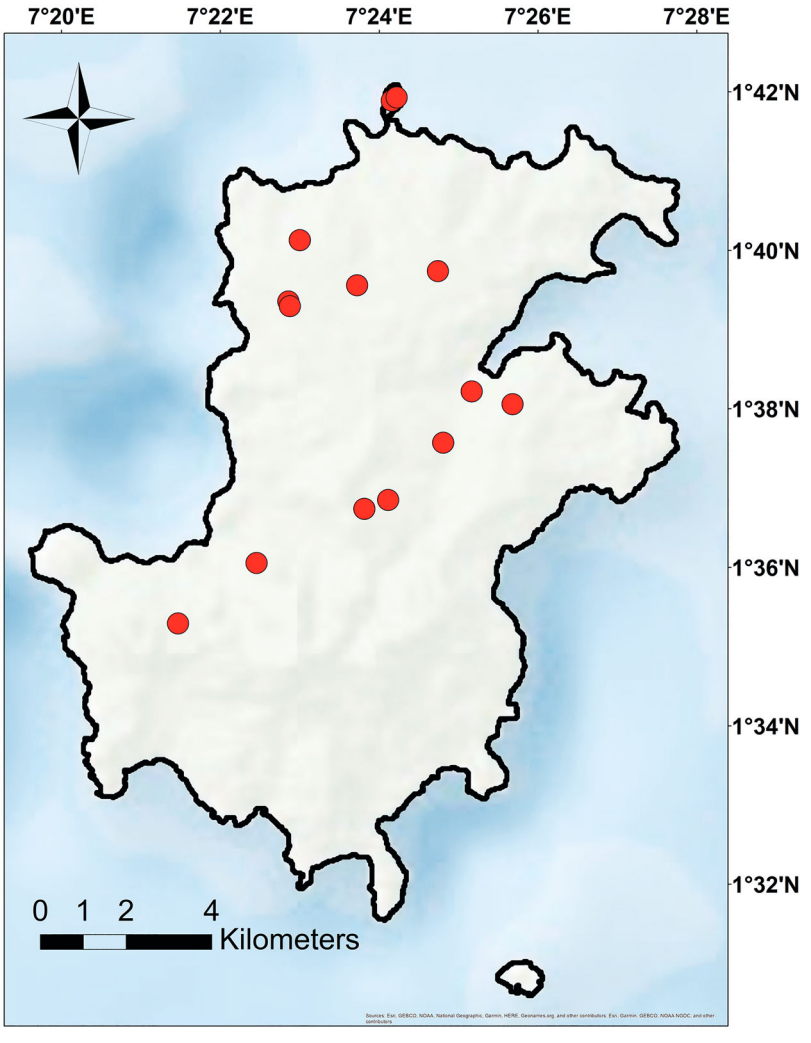

Figure 9. Confirmed records of *Boaedon mendesi* sp. nov. in Príncipe Island.

jaw rictus, 26 MSR at midbody; ventrals 212; cloacal plate entire; 69 subcaudals, all paired.

Colouration of holotype in life — The colouration is brown with a series of parallel dark blotches extending from the neck to about midbody (Figure 7). Two broad cream-coloured, dark-bordered bands running on the side of the head; the upper band starting on the nasals and extending above the eye to the posterior part of the head, the lower band starting on the posterior lower part of the eye and extending to the corner of the mouth (Figure 7). Venter whitish. Colouration in preservative present as described above, but blotches are less evident (Figure 8).

Variation — Variation in measurements and scalation of the paratypes of *B. mendesi* sp. nov. is presented in Table 4. All paratypes agree entirely with the holotype, with the exception

Figure 10. Live photo of the holotype of *Boaedon mendesi* sp. nov. (MUHNAC/MB03–977), basking in a tree during daytime. Photo by Luis MP Ceríaco.

of MUHNAC/MB03-1027, in which the 4th, 5th and 6th supralabials are in contact with the eye.

Distribution — The species is endemic to Príncipe Island, Gulf of Guinea. Currently the species has only been recorded from the northern, central and southwestern areas of the island (Figure 9), although it is most likely widely distributed.

Habitat and natural history notes — Not much is known about the natural history of this species. The holotype was found basking in a tree during day (Figure 10) in an abandoned coffee and cocoa plantation (Figure 11). The species is commonly found in more forested areas, but also in slightly disturbed habitats.

Etymology — The specific epithet is a patronym in the masculine genitive singular named after the Portuguese entomologist Luís Fernando Marques Mendes (Lisbon, 1946 –), former director of the Centro de Zoologia of the former Instituto de Investigação Científica Tropical (Lisbon), from 1998 to 2014, and who has dedicated part of his career to the study of the biodiversity of São Tomé and Príncipe.

Figure 11. Type locality of *Boaedon mendesi* sp. nov. in the vicinities of Santo Cristo, Príncipe Island. Photo by Pedro NP Ceríaco.

The identity of *Boodon nigrum* Fischer, 1856

The first herpetological specimens from São Tomé and Príncipe known to have reached European collections were those collected by the German medical surgeon Carl Weiss and then deposited in the collections of the Hamburg museum. Weiss sailed on the ship 'Adolph' to São Tomé on 20 August 1847, and in September, he continued to the Gold Coast with H Bartsch. He then returned to São Tomé, via Príncipe where he served as a doctor. He then sent specimens from São Tomé to Hamburg in December 1847, 28 February 1848 and on 7 January 1849 (Weidner 1993). As an example of the importance of Weiss collections, eight bird species from São Tomé, including the endemic São Tomé Weaver, *Ploceus sanctithomae* (Hartlaub, 1848) and the Príncipe Golden Weaver, *Ploceus princeps* (Bonaparte 1851), were described based on the material collected by Weiss.

In addition to the specimen studied and published by Jan and Sordelli (1870; Figures 2 to 3), Fischer (1856) described another snake species, *Boodon nigrum*, based on two other specimens from 'St. Thomé (West-Afrika)' collected in 1847 by Weiss. A figure of one of the syntypes accompanied the original description (Figure 12). However, Fischer's description was neglected by the subsequent authors who studied and published on the São Tomé Jitas. Recently Hallermann (2006) rediscovered one of the remaining syntypes and identified the specimen as a *B. virgatus*. This interpretation was followed by Wallach et al. (2014), who considered *nigrum* as a junior synonym of *virgatus*. Our analysis of the extant syntype of *B. nigrum* (ZMH R08378; Figure 13) confirms the identity proposed by Hallermann (2006). The specimen has 22 midbody scale rows, a head with two thin, whitish lines on both sides, and homogeneous brownish body colouration without any

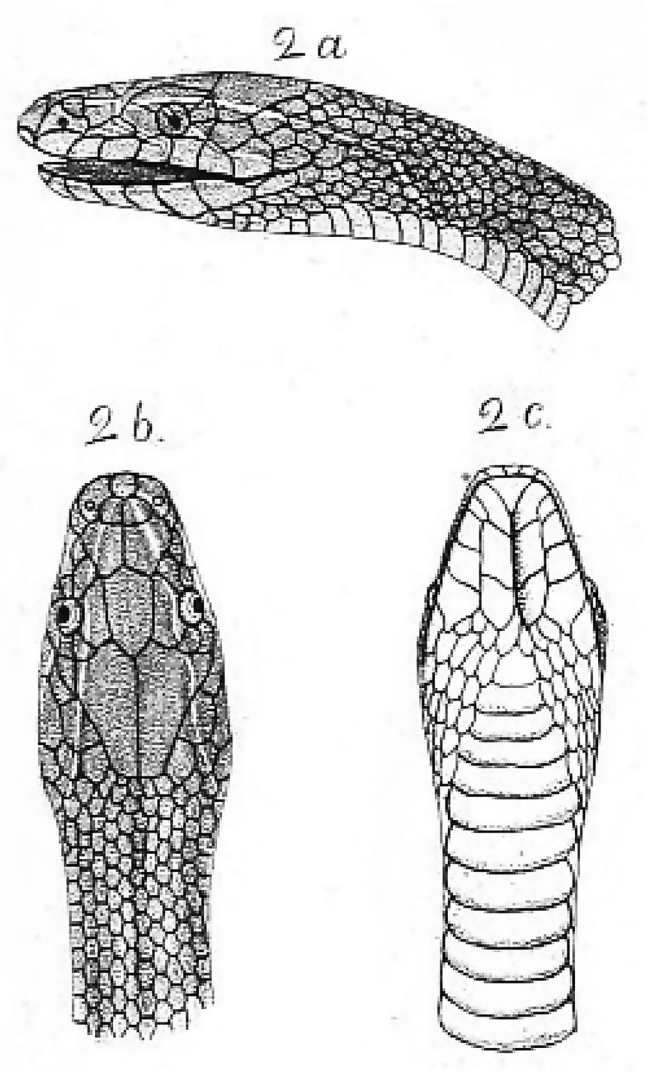

Figure 12. Illustration of one the syntypes of *Boaedon nigrum* by Fischer (1856). Adapted from Fischer (1856).

stripes, typical of *B. virgatus* (see *B. bedriagae* taxonomic account above). *Boaedon virgatus* occurs in continental West Africa, from Guinea to the Republic of the Congo (Wallach et al. 2014; Chippaux and Jackson 2019); it is not known to occur in the Gulf of Guinea Islands. The locality data confusion may be the result of mislabelling and it is likely that Weiss may have unintentionally mixed Gold Coast specimens with those from São Tomé. This scenario is consistent with other similar mistakes recently documented from specimens collected by Weiss and Fischer (Ceríaco et al. 2018). Therefore, we agree with the decisions of Hallermann (2006) and Wallach et al. (2014) and consider *B. nigrum* a junior synonym of *B. virgatus*, which is therefore unavailable to be applied to the São Tomé Island population of Jita.

Figure 13. Syntype of *Boaedon nigrum* (ZMH R08378).

Discussion

Our results support the recognition of Jitas from the São Tomé and Príncipe islands as two distinct species, *Boaedon bedriagae*, endemic to São Tomé island and Rolas islet, and *Boaedon mendesi* sp. nov. endemic to Príncipe island. In the light of the recent reviews of the herpetofauna of these islands, this result is not surprising. Species long considered to be conspecific among the two islands have been shown to represent distinct taxa, sometimes closely related (Jesus et al. 2006; Miller et al. 2012; Bell et al. 2015; Bell 2016; Soares et al. 2018), but in other cases not even being the respective sister species pairs (Uyeda et al. 2007; Ceríaco et al. 2015, 2016). Using an integrative approach, combining molecular and morphological data and a thorough revision of the nomenclatural history of the genus in São Tomé and Príncipe, we contribute to a better understanding of the diversity and endemicity rates of these islands. With the recognition of *Boaedon bedriagae* as a valid species and *Boaedon mendesi* sp. nov. as a new endemic species from Príncipe island, our current understanding of the herpetofauna of São Tomé and Príncipe increase the percentage of island endemics. Currently 13 reptile species are known to occur in Príncipe island: two are introduced (*Hemidactylus longicephalus* and *H. mabouia*, see Ceríaco *et al.* 2020); one is shared with the continent (*Trachylepis affinis*, see Ceríaco et al. 2016); two species are shared with São Tomé, but endemic to the country (*Letheobia feae* and *L. newtoni*, see Ceríaco *et al.* 2018); and eight are island endemics (*Afrotypholps elegans*, *Boaedon mendesi* sp. nov., *Feylinia polylepis*, *Hapsidophrys principis*, *Hemidactylus principensis*, *Lygodactylus delicatus*, *Panaspis africana*, and *Trachylepis adamastor*, see Ceríaco et al. 2018, unpubl. data). For São Tomé island, 11 species are currently recorded: two are introduced (*Hemidactylus longicephalus* and *H. mabouia*, see Ceríaco et al. 2020); one is shared with the continent (*Pelusios castaneus*, see Fritz et al. 2010); two species are shared with Príncipe, but

endemic to the country (*Letheobia feae* and *L. newtoni*, see Ceríaco et al. 2018); and seven are island endemics (*Boaedon bedriagae*, *Hemidactylus greeffii*, *Lygodactylus thomensis*, *Panaspis thomensis*, *Philothamnus thomensis*, *Trachylepis thomensis*, and *Naja peroescobari*, see Ceríaco et al. 2018). These numbers are impressive, especially when taking into account the small area of Príncipe and São Tomé Island (136 and 855 km^2, respectively).

Boaedon mendesi sp. nov. represents the 10th species of the genus described in the past five years (Greenbaum et al. 2015; Trape and Mediannikov 2016; Hallermann et al. 2020). Despite the obvious taxonomic and nomenclatural challenges presented by the group, our knowledge on the genus is currently in a state of flux, with several other species being described from across Africa (JH pers. obs.). Although the most recent descriptions are all based on both morphological and molecular data, our current understanding of several taxa is still deficient. Further studies are required to test the phylogeographic affinities of all known species of the genus, as well as to stabilise the problematic taxonomy of *B. fuliginosus* and *B. lineatus*.

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