

A review of the Angolan House snakes, genus *Boaedon* Duméril, Bibron and Duméril (1854) (Serpentes: Lamprophiidae), with description of three new species in the *Boaedon fuliginosus* (Boie, 1827) species complex

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ABSTRACT

An integrative taxonomic review of the genus *Boaedon* in Angola is provided. A molecular phylogeny, based on 99 genetic samples for which the mitochondrial markers 16S rRNA have been sequenced, reveals 23 monophyletic species-level groups in Africa and indicates the presence of nine species in Angola. Based on both phylogenetic and morphological data, we revalidate and designate a neotype for *B. angolensis*, describe three new species for Angola (e.g. *B. bocagei* sp. nov., *B. branchi* sp. nov., and *B. fradei* sp. nov.), revalidate *B. variegatus* from its synonymy with *B. lineatus* and designate a lectotype for this taxon, and identify *B. lineatus* var. *lineolatus* as a junior synonym of *B. variegatus*. The taxonomic status of the recently described *B. parolineatus* from Central Africa is discussed with respect

to the more inclusive *B. lineatus* group. Moreover, we report on a new country record for Angola, namely *B. mentalis*, which we elevate here to full species and discuss the taxonomic status of this species in southern Africa. Finally, we provide an identification key and updated distribution maps for all *Boaedon* species occurring in Angola, including the Cabinda enclave.

KEYWORDS:

Angola, endemism, new country record, new species Squamata taxonomy

Introduction

The African House snakes, *Boaedon* Duméril, Bibron and Duméril, 1854 represent one of the most common and conspicuous groups of lamprophiid snakes on the African continent. Thirteen species, distributed throughout Africa, the Seychelles and Yemen, are currently recognised (Wallach et al. 2014; Hallermann 2017; Uetz et al. 2019). The group has experienced a confusing taxonomic history and nomenclatural changes. The genus *Boaedon* was erected in the mid-nineteenth century by Duméril et al. (1854) and was widely used by most authors for a lengthy period (e.g. Boulenger 1893). However, in the late 20th century most of the species of *Boaedon* were moved to the genus *Lamprophis* Fitzinger, 1843 (Broadley 1983; Lawson 1993; Broadley et al. 2003; Largen and Spawls 2010). This classification stood until a recent molecular phylogenetic study of the family Lamprophiidae was published by Kelly et al. (2011), who recovered the genus *Lamprophis* as polyphyletic, leading to the resurrection of *Boaedon*.

Within *Boaedon* there are several problematic species complexes (Kelly et al. 2011). The most challenging is probably the *Boaedon lineatus-fuliginosus* species complex. Previous attempts to resolve the phylogenetic relationships within this complex, based on morphological data (Roux-Estève and Guibé 1964, 1965; Thorpe and McCarthy 1978; Hughes 1997) were unable to provide a satisfactory solution to the remaining taxonomic problems. Different molecular studies indicate the existence within the group of several morphologically indistinguishable lineages that may represent undescribed cryptic species (Kelly et al. 2011; Greenbaum et al. 2015). Wallach et al. (2014) assigned *B. arabicus* Corkill and Cochrane, 1966, *B. capensis* Duméril, Bibron and Duméril, 1854, *B. fuliginosus* (Boie, 1827), *B. lineatus* Duméril, Bibron and Duméril, 1854, and *B. maculatus* Parker, 1932 to the *B. lineatus-fuliginosus* species complex, and the five recently described species by Trape and Mediannikov (2016) were also regarded by those authors as members of this complex. All these latter species (e.g. *B. littoralis*, *B. longlineatus*, *B. parolineatus*, *B. perisilvestris* and *B. subflavus*) are morphologically very similar and all have relatively prominent light lateral head stripes and a whitish venter, both common features of the *B. lineatus-fuliginosus* species complex.

Angola has always been a country of interest to biologists because of its rich, but poorly documented biodiversity, but was largely inaccessible to researchers, as a result of almost three decades of violent civil war. Since the end of the war in 2002, several field surveys have been conducted in the country, which have led to new species inventories of poorly explored regions, and has led to the discovery of taxa previously unrecorded from the country (Ernst et al. 2014, 2015, 2020; Ceriaco et al. 2014a, 2016a, 2016b, 2018a; Branch and

Conradie 2015; Conradie et al. 2016; Baptista et al. 2019a; Butler et al. 2019), the description of new species (Conradie et al. 2012a, 2012b, 2013; Stanley et al. 2016; Ceriaco et al. 2018b, 2020a, 2020b; Branch et al. 2019a; Marques et al. 2019a, 2019b), and the study of rare and data-deficient species (e.g. Oliveira et al. 2016; Branch et al. 2017a, 2019b; Heinicke et al. 2017; Agarwal et al. 2017; Gonçalves et al. 2019; Vaz Pinto et al. 2019). Other works related to the study of the Angolan herpetofauna include the revision of historical collections (Ceriaco et al. 2014b) and the publication of an atlas on the diversity and distribution of the amphibians and reptiles of the country (Marques et al. 2018) and subsequent abridged syntheses of its overall diversity (Branch 2018; Baptista et al. 2019b; Branch et al. 2019c). Ongoing field surveys and several taxonomical reviews are under way, which will yield further additions to the knowledge of the herpetofauna of the country.

Reflecting the taxonomic and nomenclatural confusion associated with *Boaedon*, several names have been used to refer to Angolan populations of House snakes (classified either as *Boaedon*, *Lamprophis* or even *Holuropholis* Duméril, 1853), namely *B. lineatus*, *B. quadrilineatum* Duméril, Bibron and Duméril, 1854, *B. lineatus* var. *angolensis* Bocage, 1895, *B. fuliginosus*, *B. variegatum* (Bocage, 1867) and *B. olivaceus* (Duméril, 1856). For a detailed review of the chresonymy of Angolan *Boaedon* see Marques et al. (2018). In an attempt to summarise the current knowledge on the genus for Angola, Marques et al. (2018) documented the presence of four species of *Boaedon* in the country namely, *B. fuliginosus*, *B. olivaceus*, *B. angolensis* and *B. variegatus*. The latter two taxa were both described by the Portuguese naturalist José Vicente Barbosa du Bocage (1823–1907) in the nineteenth century from Angola (Bocage 1867a, 1867b, 1895). Various authors have questioned the validity of these taxa and considered them as synonyms of either *B. lineatus* (Ferreira 1897, 1904; Monard 1937; Wallach et al. 2014) or *B. fuliginosus* (Loveridge 1957). This problem was exacerbated, as a result of the loss of the Bocage's type material during a fire in the Museu Bocage, Lisbon, in 1978.

As part of an ongoing review of the genus *Boaedon*, we combined the morphological examination of specimens housed in different natural history collections and mitochondrial DNA analysis of representatives of the extant lineages. The recent collection of fresh material from Angola allowed us to address the true diversity of the genus in the country for the first time. Our results suggest that the currently recognised species diversity is underestimated, and that besides the four taxa listed by Marques et al. (2018), Branch (2018) and Branch et al. (2019c), the country hosts at least five other species, including a new endemic species from the coastal lowlands of north-western Angola (Luanda and Bengo Provinces) and two endemic to near-endemic species from the south-eastern regions of the country (Cuando Cubango and Moxico Provinces), all of which we describe here. We also provide a taxonomic and nomenclatural review of the problematic *Alopecion variegatum* Bocage, 1867, *Boaedon lineatus* var. *angolensis* Bocage, 1895, and *B. mentalis* Günther, 1888. Finally, we provide a species identification key and updated distribution maps for the Angolan representatives of the genus *Boaedon*.

Materials and methods

Material examined

For mensural and meristic comparisons, we examined specimens of the *Boaedon lineatus-fuliginosus* species complex from several locations across its distribution in Africa and Yemen. The specimens are deposited in the following institutions: Muséum national d'Histoire naturelle (MNHN), Paris (France); Laboratoire de Biogéographie et Écologie des Vertébrés de l'École Pratique des Hautes Etudes (BEV), Montpellier (France); Museu Nacional de História Natural e da Ciência (MUHNAC; formerly Museu Bocage - MB), Lisbon (Portugal); Museu de História Natural e da Ciência da Universidade do Porto (MHNCUP), Porto (Portugal); Center of Natural History, Universität Hamburg, Zoologisches Museum (ZMH), Hamburg (Germany); Staatliches Museum für Naturkunde Stuttgart (SMNS), Stuttgart, (Germany); Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn (Germany); Zoologische Staatssammlung München (ZSM), München (Germany). Museum für Naturkunde (ZMB), Berlin (Germany); Museum für Tierkunde Dresden (MTD), Dresden (Germany); California Academy of Sciences (CAS), San Francisco (USA); Museum of Comparative Zoology, Harvard University (MCZ); Cambridge (USA); Museu Regional do Dundo (MD), Dundo (Angola); Port Elizabeth Museum (PEM), Port Elizabeth (South Africa). For a complete list of the specimens examined and tissue samples used see Supplementary material and the respective taxonomic accounts below. Geographic coordinates of localities are reported in the form of decimal degrees and use the WGS-84 map datum. Older (non-GPS) records are mostly derived from Marques et al. (2018) and have been georeferenced using the GEOLocate web application (<https://www.geo-locate.org>). All elevations are reported as meters above sea level.

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 a Carl Zeiss DRC 475003-9902 or Nikon SMZ1270 stereomicroscope. Scale nomenclature, scales counts and measurements used in the descriptions follow Greenbaum et al. (2015). The following characters were measured: snout-vent length (SVL), from the tip of the snout to the anterior edge of 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 the just behind the angle of the jaw; interocular distance (measured as the distance between the anterior corners of orbits) 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, instead of the revised method documented by Dowling 1951); number of subcaudal scales (SC); number of supralabials; number of infralabials; number of preoculars; number of postoculars; number of supralabials touching the eye; the ratio of V and SC (V/SC) was also recorded. The length and height of the loreal scale, as well as its ratio 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.

Phylogenetic methods

Muscle and liver tissues of the specimens collected for the phylogenetic analyses were extracted from fresh frozen material preserved in 95–99% ethanol. We also used a cotton swab to take genetic samples from the buccal mucosa of live snakes not collected. Recent studies on other relatively young African reptile radiations have shown that even a single fast evolving marker like the 16S rRNA gene has enough resolving power to confidently identify the different species within a specific genus, if the fast-evolving, indel-rich loop regions can be unambiguously aligned (Branch et al. 2017b; Ceriaco et al. 2017). Therefore, for our phylogenetic analyses we combined newly sequenced mitochondrial 16S data from specimens of different *Boaedon* species and populations all over Africa and complemented these with previously published and available 16S sequences from GenBank. Genomic DNA was isolated from alcohol-preserved muscle/liver tissue samples or from oral mucosa. Total genomic DNA was extracted following a slightly modified version of the protocol of Sokolov (2000) as detailed in Scheel and Hausdorf (2012), as well as using the E.Z.N.A. Tissue DNA Kit (VWR/Omega bio-tek) following the manufacturers protocol. A portion of the mitochondrial genome (16S rRNA gene) was PCR amplified and sequenced following the methods described in Schmitz et al. (2005). All sequences have been deposited in GenBank (Supplementary material).

DNA sequences were aligned using the original chromatograph data in the program BioEdit (Hall 1999), using ClustalX (Thompson et al. 1997) and the resulting alignment was manually edited. We unambiguously aligned 523 bp of the 16S rRNA gene including some fast-evolving, indel-rich loop regions. Bayesian Inference (MrBayes v.3.26; Ronquist et al. 2012) and Maximum Likelihood (RAxML v.7.0.4; Stamatakis et al. 2006) using the rapid hill climbing algorithm and the GTR + G model of nucleotide substitution following Stamatakis et al. (2006) were implemented to assess phylogenetic relationships. The best-fit model of sequence evolution for the Bayesian analysis was the TIM2 + I + G model with values of I = 0.7350 and G = 0.9340, selected using jModeltest v.2.1.7 (Darriba et al. 2012) using the Bayesian information criterion (BIC).

Bootstrap analyses (BS) with 1 000 pseudoreplicates in the ML analysis were used to evaluate relative branch support in the ML analysis. We regarded tree topologies with bootstrap values of 70% or greater as supported (Huelsenbeck and Hillis 1993). Bayesian analyses were run for 10 million generations using four chains, sampling every 1 000 generations, with the first 25% of trees discarded as burn-in. Stationarity, convergence and mixing of the parameters (ESS values) for the Bayes runs were checked in Tracer 1.7.1 (Rambaut et al. 2018). Clades with posterior probabilities (PP) ≥ 0.95 were considered strongly supported. In total, sequences from 99 *Boaedon* specimens were included in the phylogenetic analyses (Supplementary material) to corroborate our morphological analyses. *Pseudoxyrhopus ambreensis* and *Lamprophis aurora* (ZMH R11340) were chosen as outgroups. Pairwise comparisons of uncorrected sequence divergences (p-distance) were computed in MEGA X (Kumar et al. 2018; Table 1).

Table 1. Percentage uncorrected pairwise distances (16S, averages) between different taxa. Numbers in bold represent divergence within each taxon.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	21
1 <i>Boaedon angolensis</i>	0.004																					
2 <i>B. bocagei</i> sp. nov.	0.036	0.000																				
3 <i>B. olivaceus</i>	0.018	0.027	0.003																			
4 <i>B. sp. Clade_3</i>	0.019	0.032	0.014	0.007																		
5 <i>B. perisilvestris</i>	0.018	0.028	0.014	0.015	0.003																	
6 <i>B. radfordi</i>	0.016	0.029	0.009	0.012	0.012	-																
7 <i>B. subflavus</i>	0.022	0.034	0.019	0.021	0.020	0.012	0.000															
8 <i>B. fuliginosus</i>	0.016	0.034	0.017	0.017	0.015	0.012	0.016	0.000														
9 <i>B. sp. Ethiopia_Clade</i>	0.013	0.028	0.011	0.011	0.011	0.010	0.014	0.006	0.000													
10 <i>B. variegatus</i>	0.034	0.048	0.033	0.033	0.031	0.031	0.036	0.027	0.026	0.012												
11 <i>B. capensis</i> Clade_A	0.034	0.039	0.032	0.035	0.030	0.032	0.031	0.033	0.026	0.046	0.000											
12 <i>B. capensis</i> Clade_B	0.032	0.044	0.031	0.032	0.031	0.025	0.028	0.026	0.023	0.045	0.018	0.000										
13 <i>B. capensis</i> Clade_C	0.023	0.037	0.023	0.024	0.024	0.021	0.026	0.022	0.017	0.038	0.018	0.017	0.004									
14 <i>B. mentalis</i> Southern_Clade	0.038	0.048	0.035	0.038	0.031	0.035	0.034	0.035	0.029	0.045	0.026	0.039	0.034	0.000								
15 <i>B. mentalis</i> Northern_Clade	0.037	0.051	0.036	0.038	0.035	0.034	0.039	0.036	0.029	0.051	0.033	0.040	0.031	0.020	0.005							
16 <i>B. fradei</i> sp. nov.	0.031	0.044	0.035	0.032	0.027	0.032	0.036	0.032	0.027	0.044	0.032	0.041	0.025	0.045	0.041	0.002						
17 <i>B. geometricus</i>	0.055	0.059	0.051	0.054	0.051	0.044	0.048	0.049	0.047	0.052	0.050	0.052	0.051	0.052	0.060	0.049	-					
18 <i>B. longilineatus</i>	0.068	0.071	0.067	0.072	0.061	0.063	0.063	0.063	0.063	0.062	0.068	0.065	0.065	0.061	0.070	0.064	0.044	0.000				
19 <i>B. lineatus</i>	0.053	0.066	0.055	0.056	0.050	0.048	0.051	0.048	0.048	0.052	0.048	0.048	0.047	0.045	0.049	0.051	0.058	0.064	0.017			
20 <i>B. paralineatus</i>	0.057	0.066	0.059	0.060	0.055	0.052	0.050	0.050	0.052	0.059	0.057	0.054	0.052	0.050	0.054	0.060	0.066	0.069	0.019	0.000		
21 <i>B. branchi</i> sp. nov.	0.020	0.035	0.021	0.022	0.020	0.018	0.023	0.021	0.014	0.032	0.025	0.025	0.018	0.036	0.035	0.026	0.044	0.064	0.046	0.053	0.000	

Results

Phylogenetic analyses

For the genetic dataset we compiled sequences from 13 currently recognised *Boaedon* species, as well as from at least five additional potential cryptic taxa. Stationarity and good mixing was confirmed for the Bayes runs by high ESS values that were well above the 200 threshold for all parameters. Both the Bayesian and the Maximum Likelihood analyses agreed fully in the topology of the recovered phylogram (Figure 1), differing only in the degree of support recovered for individual nodes. Although there was only rather low support for the basal nodes of the tree, both analytical methods fully corroborated our morphological results by confirming nearly all previously recognised *Boaedon* species as monophyletic lineages, as well as clearly identifying our three newly described Angolan species to be different from all other described *Boaedon* species in our dataset (Figure 1). Almost all of these species-level clades are strongly supported (PP ≥ 0.95 and/or ML ≥ 70) in at least one of the two phylogenetic approaches, with only the *B. capensis* species complex (PP: 0.84; see discussion below) receiving lower support. For all of these mostly well-supported clades, consistently high interspecific and lower intraspecific genetic distances were evident (Table 1), indicating prolonged reproductive isolation of the different lineages. The only exception to this is the *Boaedon lineatus-paralineatus* species complex, where the intraspecific distances within *B. lineatus* reach a comparatively higher divergence of 1.7%. Although this is on the lower end of all interspecific differences, it still seems to reach a level that can be observed between some closely related species pairs (e.g. *B. perisilvestris/B. radfordi*). This can be explained by the fact that the four *B. lineatus* vouchers included in the analysis are clearly non-monophyletic with respect to *B. paraleineatus* (Figure 1). Follow-up studies are needed to determine if *B. lineatus* and *B. paraleineatus* may in fact be conspecific or if *B. lineatus* comprises a species complex.

Five potentially undescribed cryptic species were identified as monophyletic lineages: one species from north-western Angola (described herein), two species from south-eastern Angola (described herein), one species from the Addis Ababa region of Ethiopia (to be described elsewhere), and an eastern-central African clade from Uganda to Tanzania (to be described elsewhere). Additionally, we found well-supported phylogenetic substructure in three currently recognised *Boaedon* species (*B. capensis*, *B. mentalis*, *B. lineatus*) in our analyses, indicating possible additional cryptic species within those complexes. Our analyses revealed that although monophyletic, *B. capensis* is made up of at least three species-level clades (A, B, C), which correspond to two eastern/southern African lineages (clade A: Kenya, South Africa, Namibia and clade C: Tanzania, South Africa) and a uniquely southern African group (clade B; Figure 1). The resulting genetic distances between these three clades are comparable to those between previously recognised *Boaedon* species and therefore should be evaluated as putatively distinct species (Table 1). A similar genetic split can be found within *B. mentalis*, with the split clearly separating the South African populations from the populations of southern Angola and northern Namibia. The third group with clearly recognisable substructure is represented by samples of the West African species *B. lineatus* and *B. paraleineatus*. Additionally, our phylogenetic results confirm the placement of *Lamprophis geometricus* in the genus *Boaedon* as predicted by Kelly et al. (2015) and tentatively followed by Wallach et al. (2014).

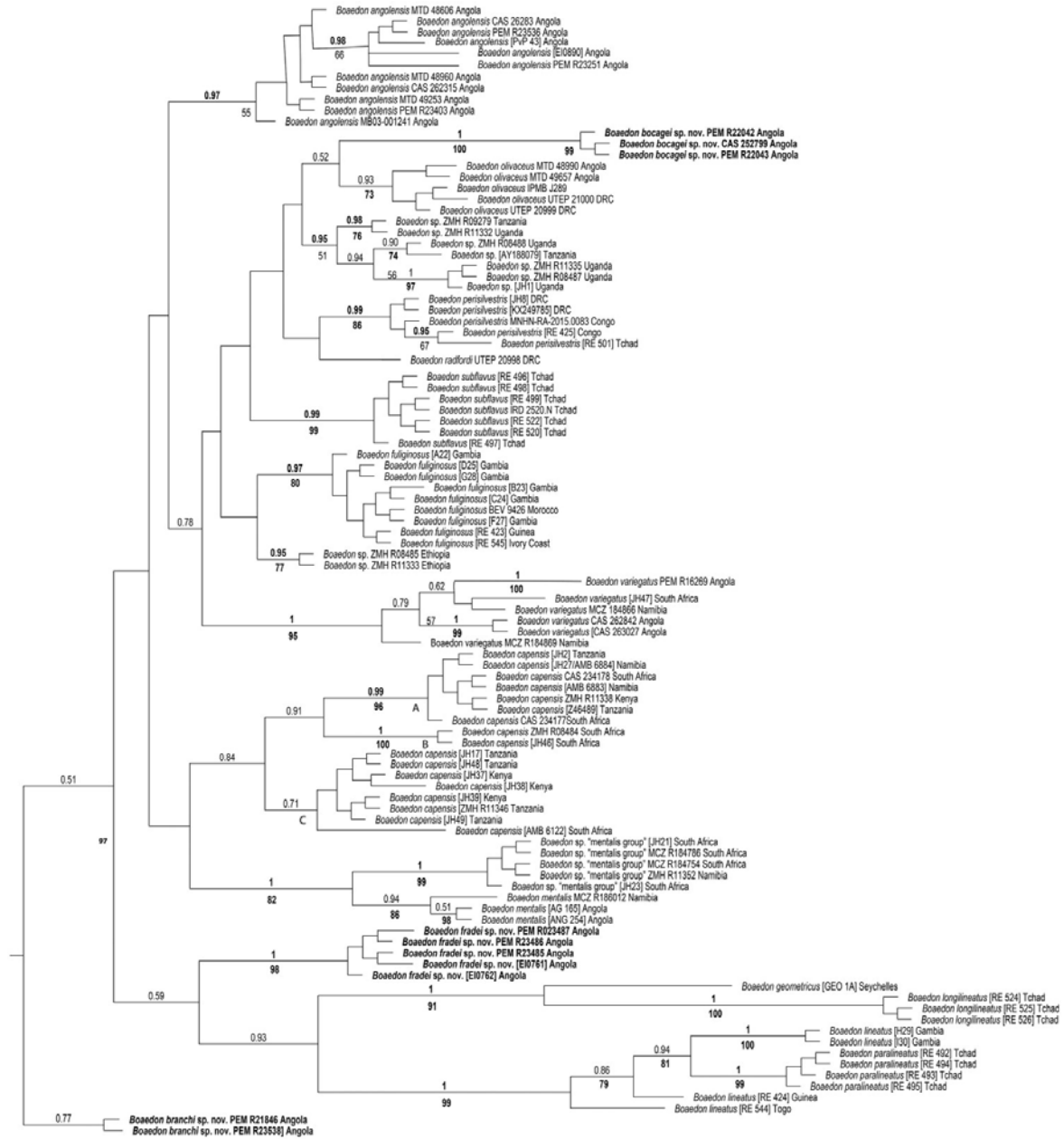


Figure 1. Phylogenetic tree (Bayes/ML) based on the mitochondrial 16S dataset. Numbers at nodes are support values for Bayesian posterior probabilities (above nodes) and ML bootstraps (below node); values below PP <0.5 and ML <50 are not shown. High support values (PP ≥ 0.95 and ML ≥ 70) are marked in bold. Outgroup taxa used are not shown.

Morphological analysis

Results of our morphological analyses are shown in Table 2. Males and females of the newly described species from Angola and the revalidated species differ by a combination of characters from all other congeners (see diagnoses below). Based on these differences and the

Table 2. Comparison between the different species of *Boaedon* occurring in Angola. Measurements in mm.

	<i>Boaedon fuliginosus</i> (n = 5)	<i>Boaedon virgatus</i> (n = 3)	<i>Boaedon olivaceus</i> (n = 2, 1 with incomplete body)	<i>Boaedon mentalis</i> (n = 3)	<i>Boaedon variegatus</i> (n = 8)	<i>Boaedon angolensis</i> (n = 12)	<i>Boaedon bocagei</i> sp. nov. (n = 8)	<i>Boaedon branchi</i> sp. nov. (n = 2)	<i>Boaedon fradei</i> sp. nov. (n = 9)
Maximum SVL (\bar{x}/\pm)	550/705	383/292	395/-	255/330	445 /825	610/882	306/451	508/-	608/738
Maximum TL (\bar{x}/\pm)	132/133	108/64	73/-	46/51	106/140	158/134	47/71	125/-	143/135
MSR	25-31	23-25	25	25-27	27-30	25-28	25-27	29	25-29
Ventral scales (\bar{x}/\pm)	195/247	197/195-199	187-196/198-216	202/204-214	218-220/224-240	198-204/215-224	208-211/221-229	197-210/-	193-219/211-221
Subcaudal scales (\bar{x}/\pm)	64-71/51-58	68/63-65	45/-	57/40-52	66/54-60	58-72/50-62	66/48-53	64-67/-	63-69/50-52
Subcaudals rows	Double	Double	Single	Double	Double	Double	Double	Double	Double
Preoculars	1-2	1-2	1	1	1	1-2	1-2	1-2	1-2
Postoculars	2	2	2	2	2	1-2	2	2	1-2
Supralabials touching the eye	2	2	2-3	3	3	2	3	2	2
Ratio of loreal length to height	>2	<2	<2	<2	<2	>2	<2	>2	≤2
The second chin shields are completely separated from each other by the anterior chin shields	No	No	No	Yes	No	No	No	No	No
Snout length	long	short	short	short	short	short	short	short	short
Cloacal plate	entire	entire	entire	entire	entire	entire	entire	entire	entire
Head stripes	present	faded	absent	present	present	present	present, dark bordered	present	present
Colouration (dorsum)	blackish or dark brown	faded brown	blackish	light brown	brown with yellow looping markings lowest dorsal scale row pigmented	grey-brown to olive-brown	brown to olive	yellowish to yellowish-olive lower 2-3 dorsal scales rows being immaculate white	dark-brown to olive lower 2-3 dorsal scales rows pigmented
Colouration (ventral)	whitish	broad central greyish or yellowish stripe	creamy with dark flecks	whitish	whitish	whitish	whitish	creamy	whitish with scattered yellow scales

results of our phylogenetic analyses, we recognise these clades as new or revalidated species, respectively (Figure 1, Table 1).

Systematics

Below we provide systematic accounts for all *Boaedon* species occurring in Angola, including the Cabinda enclave. We restrict the chresonymies to names referring specifically to Angolan material.

Boaedon fuliginosus (Boie, 1827)

(Figures 2–3A).

Boodon lineatus [?] (Bocage 1895: 78)

Boaedon lineatus lineatus [part] (Laurent 1964: 93; Thys van den Audenaerde 1966: 32)

Boaedon fuliginosus [part] (Wallach et al. 2014: 95; Marques et al. 2018: 329; Branch et al. 2019c: 323)

Boaedon capensis-fuliginosus-lineatus complex [part] (Branch 2018: 57).

Boaedon fuliginosus was described by Heinrich Boie (in Friedrich Boie 1827) as *Lycodon fuliginosus*. The original description states ‘H. Boie Erp. de Java ist das Vaterland bekannt’ [‘H. Boie Erp. de Java is the fatherland known’ (translation by the authors)]. Erp. de Java is Boie’s famous, but never published, *Erpétologie de Java*. This seems a typographic error for ‘unbekannt’, i.e. based on Boie’s *Erpétologie de Java*; the native country is unknown. According to Brongersma in Roux-Estève and Guibé (1965), the type, which was formerly in the collections of the Rijksmuseum van Natuurlijke Historie, currently Naturalis Biodiversity Center (RMNH) in Leiden, Netherlands, is no longer extant. 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*, although there were no white head stripes noted in the original description, as is occasionally the case in this species. 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 (today modern Cape Town) and possibly in West Africa at one of the ports of the ‘Dutch Gold Coast’, such as Elmina (today in modern Ghana).

Formerly considered to be distributed in many parts of Africa (Hughes 1997) our results restrict this species to western Africa, from Morocco to northern Angola. On this basis it is likely that the type was collected somewhere on the ‘Dutch Gold Coast’. As noted in the following accounts the name *B. fuliginosus* has been applied to several different taxa in Angola and Marques et al. (2018) mapped many of these taxa under the ‘*Boaedon fuliginosus* complex’. This solution was also adopted by Branch (2018) and Branch et al. (2019c). The review of many of the original specimens and published data, in combination with our current understanding of the diagnostic characters and species boundaries of the genus in Angola, allows us to confidently restrict the distribution of *B. fuliginosus* in Angola to the extreme northeast of the country. The only Angolan specimens that we positively identified as

belonging to *B. fuliginosus* are those referred by Laurent (1964) and Thys van den Audenaerde (1966) from the Alto Chicapa, Dundo, Luachimo and Muita regions in Lunda Norte Province. These specimens are still extant in the collections of Museu Regional do Dundo (MD 191, 219, 262, 2019, 2021, 2031, 2166, 5013, 5193, 5259, 5261, 5279, 5451, 5803, 5835, 5881, 7062). Specimens from the Cabinda enclave cited by Bocage (1895) might represent this species, but their destruction during the fire that engulfed the Museu Bocage prevents confirmation. All other specimens from eastern, central and coastal regions are representatives of other Angolan taxa (see subsequent accounts).

Nevertheless, a detailed revision of the taxonomic and nomenclatural status of *B. fuliginosus* (with the potential designation of a neotype) is crucial to put to rest all doubts and ambiguities surrounding the identity of true *B. fuliginosus*.

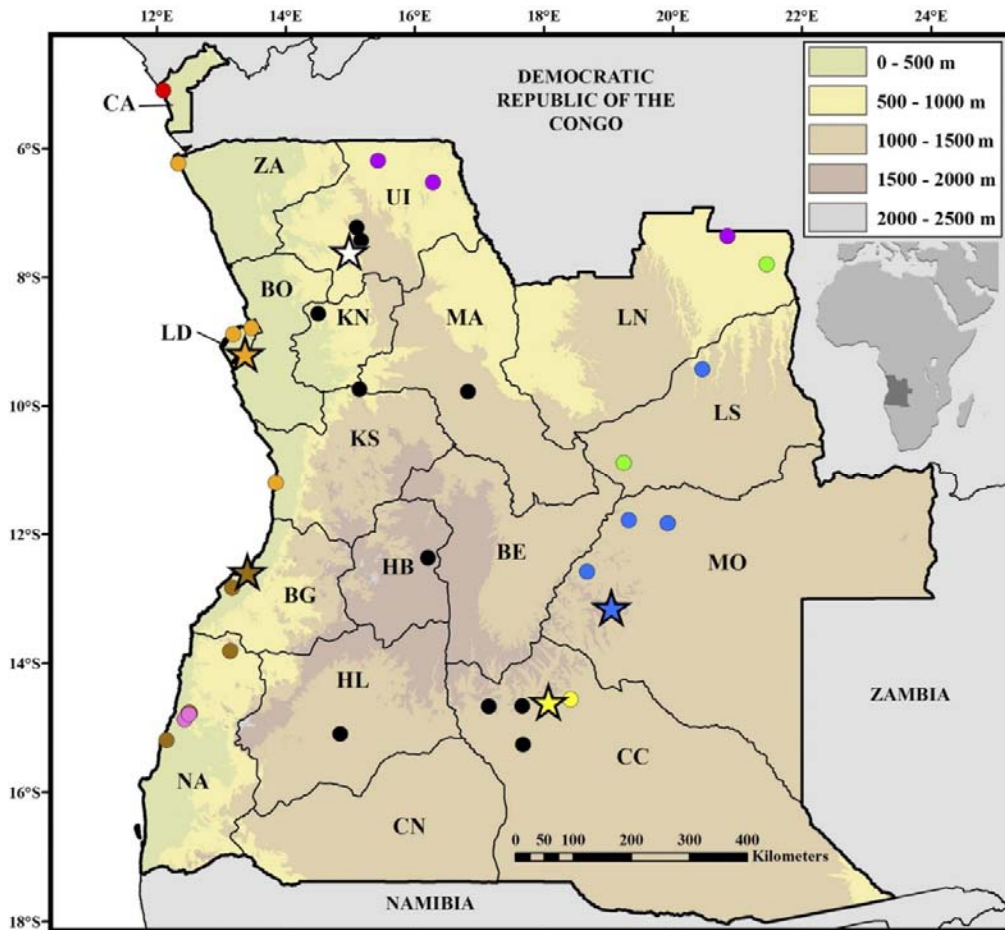


Figure 2. Confirmed records of *Boaedon* species in Angola. Orange dots: *Boaedon bocagei* sp. nov.; Orange star: *Boaedon bocagei* sp. nov. Type Locality; Blue dots: *Boaedon fradei* sp. nov.; Blue star: *Boaedon fradei* sp. nov. Type Locality; Yellow dots: *Boaedon branchi* sp. nov.; Yellow star: *Boaedon branchi* sp. nov. Type Locality; Purple dots: *Boaedon olivaceus*; Red dots: *Boaedon virgatus*; Green dots: *Boaedon fuliginosus*; Pink dots: *Boaedon mentalis*; Brown dots: *Boaedon variegatum*; Brown star: *Boaedon variegatum* Type Locality; Black dots: *Boaedon angolensis*; White star: *Boaedon angolensis* Neotype Locality. Provinces acronyms: CA – Cabinda; ZA – Zaire; UI – Uíge; LD – Luanda; BO – Bengo; Kwanza Norte; KS – Kwanza Sul; HB – Huambo; BG – Benguela; HL – Huíla; NA – Namibe; CN – Cunene; CC – Cuando Cubango; MO – Moxico; BE – Bié; MA – Malanje; LN – Lunda Norte; LS – Lunda Sul.

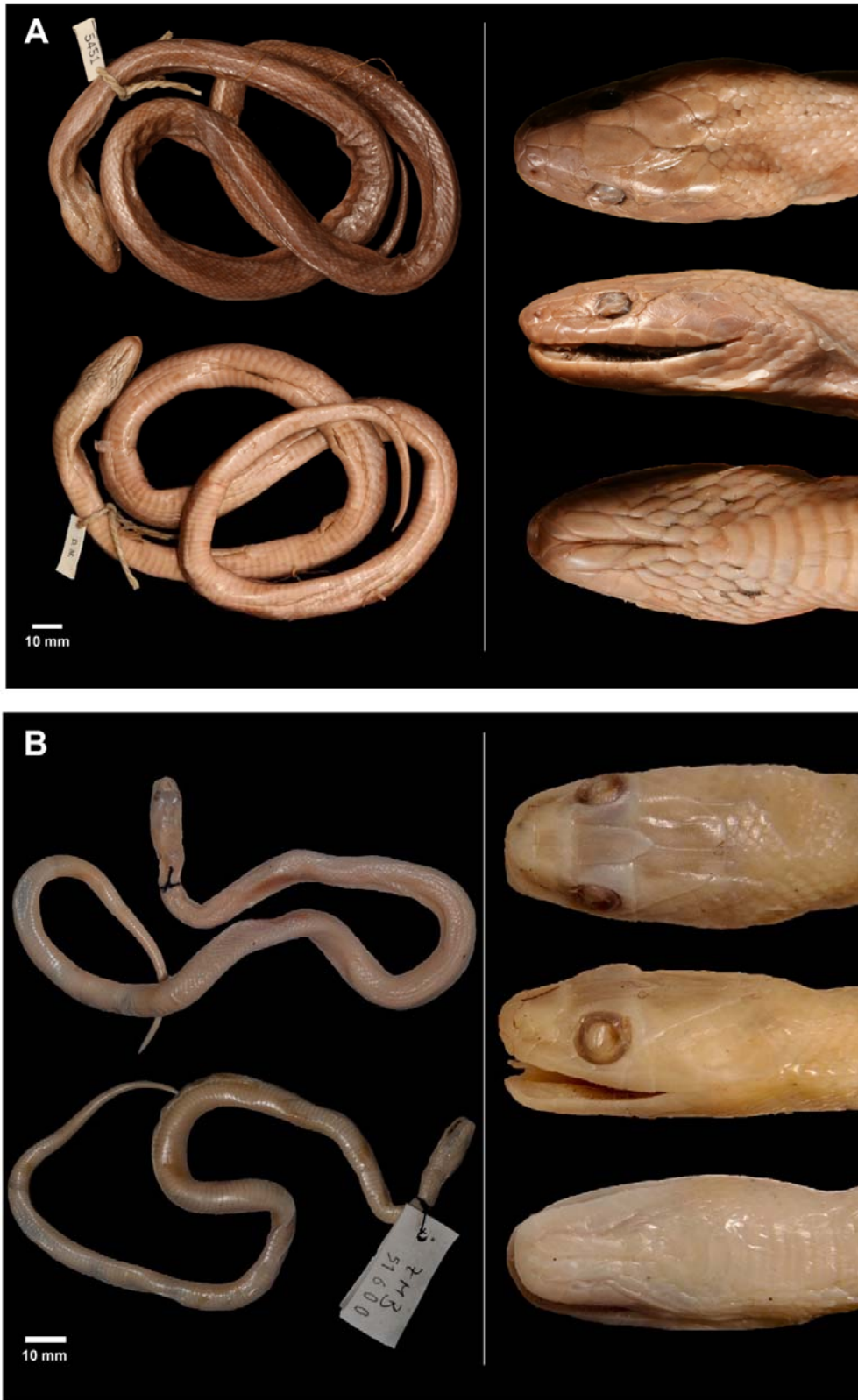


Figure 3. A: Specimen of *Boaedon fuliginosus* (MD 5451) from Dundo, Lunda Norte Province, north-eastern Angola. B: Specimen of *Boaedon virgatus* (ZMB 51600) from Chinchoxo, Cabinda Province, north-western Angola.

Diagnosis: *Boaedon fuliginosus* (Figure 3A) can be distinguished from nearly all Angolan congeners by the following combination of characters: 1) a blackish-brown ground colour, 2) frequently with two thin white stripes on the side of the head, 3) a parietal length equal to distance from frontal to rostral (versus parietal length longer than distance from frontal to rostral in all remaining Angolan *Boaedon*, with the exception of *B. virgatus*, *B. mentalis sensu lato* and *B. olivaceus*) and 4) the ratio of loreal length to height is greater than two (versus less than two). It can be distinguished from *B. virgatus* by having 27–29 MSR (versus 25 or fewer in *B. virgatus*) and by its whitish venter (pigmented laterally in *B. virgatus*); from *B. mentalis sensu lato* by its black-brown body colouration (versus light brown in *B. mentalis sensu lato*) and two supralabials touching the eye (versus 3 in *B. mentalis sensu lato*); and from *B. olivaceus* by having a double row of subcaudals (single row in *B. olivaceus*). It can be distinguished from *B. capensis* by the loreal length to height ratio being greater than 2 (less than 2 in *B. capensis*) and by its black-brown body colouration (versus red or light brown in *B. capensis*). It can be distinguished from *B. upembae* (data fide Greenbaum et al. 2015) by its higher number of ventral scales (198–220 in *B. fuliginosus* versus 175–197 in *B. upembae*) and higher number of MSR (25–31 in *B. fuliginosus* versus 21–23 in *B. upembae*). It can be distinguished from *B. radfordi* by having a double row of subcaudals (single row in *B. radfordi*).

Material examined: Lunda Sul Province: MD 5451 from Alto Chicapa [−10.88333°, 19.23333°, 1 346 m], collected by unnamed local collectors in July 1954. Lunda Norte Province: MD 191, 219, 262, 2019, 2021, 2031, 5013, 5193, 5259, 5261, 5279, 5803, 5835, 5881, 7062 from Dundo [−7.35971°, 20.84098°, 663 m], collected by Barros Machado et al. in the 1950s and 1960s; MD 2166 from Muita, Luembe [−7.80000°, 21.45000°, 731 m], collected by M Petchkowsky in October 1948.

Distribution: Currently the only confirmed records in Angola are limited to the northern regions of the country, namely in north-eastern Provinces of Lunda Norte and Lunda Sul, and potentially Cabinda Province (Figure 2).

Habitat and natural history notes: Nothing is known about the natural history of this species in Angola. The predominant habitat in the region is a combination of Southern Congolian Forest-Savannah mosaics and sparse Angola Miombo woodlands (Grandvaux-Barbosa 1970; Marques et al. 2018)

Boaedon virgatus (Hallowell, 1854)

(Figures 2–3B).

Boodon geometricus [part] Peters 1877: 615)

Boaedon virgatus (Branch et al. 2019c: 296)

This west/central African form, occurring from Guinea to the western parts of the Democratic Republic of the Congo (DRC) (Wallach et al. 2014; Chippaux and Jackson 2019) had never been reported from Angola prior to Branch et al. (2019c), who pre-emptively referred to the results of the present study. The species is characterised by its lower ventral scale counts (< 198) in males, MSR of usually lower 25, and a venter with a central broad greyish or yellowish stripe with the lateral edges being darker. We found three specimens in the collections of the ZMB (ZMB 51599–51601; Figure 3B) from Chinchoxo, Cabinda Province,

Angola, received from the ‘Africanischen Gesellschaft’ (Peters 1877) as *Boodon geometricus* with no collector or collection date stated. *Boaedon geometricus* (Schlegel, 1837), however, is applicable to a species endemic to the Seychelles. Peters’ (1877) usage seems to correspond to *Boodon ventralis* Günther, 1888 syn. *B. virgatus* (Hallowell, 1854). Detailed measurements and scale counts of the specimens are presented in Table 2. Besides these specimens, no other records of this species are known from Angola.

Material examined: Cabinda Province: ZMB 51599–51601 (Figure 3b) from Chinchoxo (approx. -5.10000° , 12.20000° , 16 m), received from the ‘Afrikanischen Gesellschaft’ (Peters 1877).



Figure 4. A: Specimen of *Boaedon olivaceus* (MD 2021) from Dundo, Lunda Norte Province, north-eastern Angola. B: Live photo of the *Boaedon olivaceus* specimen MTD 49657 from Maquela do Zombo, Uíge Province, north-western Angola. Photo by Raffael Ernst.

Diagnosis: *Boaedon virgatus* (Figure 3B) can be distinguished from all Angolan congeners by often having fewer than 25 MSR (versus 25 or more in all other Angolan congeners) and distinct ventral pigmentation with a broad central greyish or yellowish stripe with the lateral edges being darker (versus non-pigmented in all other Angolan congeners). It can be distinguished from *B. upembae* by usually having more ventral scales (195–207 in *B. virgatus* versus 175–197 in *B. upembae*).

Distribution: Known only from Cabinda Province, but may potentially occur in other areas of north-western Angola, such as Zaire and/or Uíge Provinces (Figure 2). Widely distributed in western and central Africa (east to DRC and north to Guinea).

Habitat and natural history notes: The specimens known from Angola were collected in the coastal town of Chinchoxo, which is dominated by a Western Congolian Forest-Savannah mosaic (Grandvaux-Barbosa 1970; Marques et al. 2018).

Boaedon olivaceus (Duméril, 1856)

(Figures 2, 4A, 4B).

Holuropholis olivaceus (Peters 1877: 615)

Boodon olivaceus (Bocage 1895: 81)

Boaedon olivaceus (Boulenger 1915: 202; Laurent 1954: 43; Loveridge 1957: 251; Frade 1963: 252; Thys van den Audenaerde 1966: 32; Wallach et al. 2014: 97; Marques et al. 2018: 330; Branch 2018: 56; Branch et al. 2019c: 301, 307, 323).

Boaedon radfordi [?] (Branch et al. 2019c: 296).

The species has previously been reported from the Cabinda Province by Peters (1877) and from Dundo, Lunda Norte Province, in north-western Angola by Laurent (1954) and Thys van den Audenaerde (1966). Until now, these have been the only records of the species for the country. These specimens are still extant in the collections of Museu Regional do Dundo (MD 2021; Figure 4A). Branch (2018) noted that the material from north-eastern Angola needs revision, because of the possibility of being confused with the recently described *Boaedon radfordi*, from the Albertine Rift. However, the ventral scale counts, a diagnostic character that separates *B. olivaceus* from *B. radfordi*, according to Greenbaum et al. (2015), provided by Laurent (1954) falls within the range of *B. olivaceus*, alleviating the concerns raised by Branch (2018). This western African species is characterised by having single subcaudal scale rows, ventral scale counts lower than 200 (in males), MSR of 25 and two supralabials touching the eye. Specimens MTD 49657 (Figure 4B from Bairro Quivelu and MTD 48990 from Kihuamba represent new records of this species from Uíge Province. The specimens were found in a heavily anthropogenically disturbed mixed forest savannah mosaic near the DRC border.

Material examined: Uíge Province: MTD 49657 (Figure 4B) an adult male from Bairro Quivelu, near the town of Béu in Maquela do Zombo municipality (−6.19320°, 15.42820°, 796 m), collected by Raffael Ernst on 27 September 2018; MTD 48990 (hind part of body missing) from Kihuamba (−6.52655°, 16.2833°, 725 m), collected by Raffael Ernst on 27

September 2018. Lunda Norte Province: MD 2021 (Figure 4A) an adult male from Dundo [−7.35971°, 20.84098°, 663 m], collected by an unknown collector in October 1948.

Diagnosis: *Boaedon olivaceus* (Figures 4A, 4B) can be distinguished from all Angolan congeners by having single subcaudal scale rows (versus double subcaudal scale rows in all other Angolan *Boaedon*). It can be distinguished from the morphologically similar *B. radfordi* by usually having three supralabial scales touching the eye (versus two in *B. radfordi*). Generally, *B. olivaceus* have fewer ventral scales than *B. radfordi* although there is some overlap for females (males: 187–196 in *B. olivaceus* versus 200–221 in *B. radfordi*; females: 198–216 in *B. olivaceus* versus 212–226 in *B. radfordi*).

Distribution: Known only from Uíge and Lunda Norte Provinces, but may potentially also occur in surrounding Provinces like Malanje, Zaire and Cabinda, northern Angola (Figure 2). Otherwise, broadly distributed in central and west Africa (Chippaux and Jackson 2019).

Habitat and natural history notes: The predominant habitat in Lunda Norte region is a combination of Southern Congolian Forest-Savannah mosaics and sparse Angola Miombo woodlands (Grandvaux-Barbosa 1970; Marques et al. 2018)

Boaedon mentalis (Günther, 1888)

(Figures 2–5A).

Boaedon mentalis (Branch et al. 2019c: 296)

Boaedon mentalis was originally described by Günther (1888), based on one specimen from ‘Damara Land’. The type locality seems to be in error. The specimen was part of a commercially purchased collection with the locality ‘Damaraland’, although none of the taxa represented in this collection actually occur in the region (Bauer pers. obs.). Therefore, the origin and terra typica of the type specimen is questionable. Loveridge (1957) and Fitzsimons (1962, 1966) referred to *B. mentalis* as a subspecies of *B. fuliginosus*, a decision that was then followed by subsequent authors, including Buys and Buys (1983) and Chippaux (2006). Broadley (1983) noted that the chin shield separation was not a reliable character and considered that there was no compelling reason to retain *B. mentalis* as a valid taxonomic entity and, therefore, considered it as a junior synonym of *B. fuliginosus* as then construed. Wallach et al. (2014) considered *B. mentalis* as a synonym of *B. capensis*. Vidal et al. (2008), in their molecular phylogeny of the Lamprophiidae, recovered *B. mentalis* as the sister of the clade comprising *B. fuliginosus*, *B. lineatus*, *B. olivaceus* and *B. capensis*, supporting the revalidation of the taxon as a full species. This revalidation is also supported by our phylogenetic and morphological results, which place it as a separate lineage to the majority of the central and southern African members of the genus (Figure 1). Morphologically, the nomenclotypical specimen has the second chin shields (posterior maxillary scale) completely separated from each other anteriorly. This character varies in examined material referred to the *B. mentalis sensu lato* clade (Table 3). All examined specimens have three supralabials touching the eye. This combination of characters diagnoses two closely related species comprising the *Boaedon mentalis sensu lato* clade (Table 3). We therefore here formally elevate *B. mentalis* to full species status. Because of the doubtful type locality of *B. mentalis*, it is currently not possible to allocate the type specimen with certainty to one of the two lineages within this more inclusive clade.

Table 3. Morphometric (in mm) and meristic character comparison of *Boaedon mentalis* and *Boaedon variegatus* available material, X: present, –: absent or missing data.

Examined material	BMNH 1946.1.219 Holotype	PEM R21606	MCZ R186012	ZMB 6469 Lectotype	BMNH 1867.7.23.23 Paralectotype	CAS 262842	CAS 263027	PEM R16269	PEM R241489	MCZ R184869	ZMH R02354
Taxon	<i>Boaedon mentalis</i>	<i>Boaedon mentalis</i>	<i>Boaedon mentalis</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>	<i>Boaedon variegatus</i>
Sex	Female	Male	Female	Female	Female	Female	Female	Female	Male	Male subadult	Female
SVL	330	255	196	305	255	825	540	376	445	247	305
Tail length	51	46	25	47	42	140	70	48	106	Tip missing	50
SVL/TL	6.4	5.5	7.8	6.5	6.1	5.9	7.7	7.8	4.2	–	6.1
MSR	25	27	25	29	29	27	30	29	29	29	27
Ventral scales (V)	214	202	204	238	240	230	232	238	218	220	224
Subcaudals (SC)	52	57	40	55	60	60	56	50	66	39+	54
V/SC	4.1	3.5	5.1	4.3	–	3.8	4.1	–	3.3	–	4.1
Sublabials (entering eye)	8 (3–5)	8 (3–5)	8 (3–5)	8	8 (2–4)	9	8	8 (3–5)	8 (3–5)	9 (3–5)	8
Infralabials (touch 1st chin shields)	9 (1–4)	9 (1–4)	9 (1–4)	9	9/10	10	9	9 (1–4)	9 (1–4)	9/10	9
Loreal length	2.1	3.0	1.1	2.2	2.07	–	–	2.3	3.1	1.3	2.3
Loreal height	0.8	1.3	0.7	1	0.9	–	–	1.2	1.1	1.1	1.0
Loreal L/H ratio	2.1	0.9	1.8	2.2	2.3	2.6*	1.6*		2.8	1.2	2.3
Preocular	1	1	1	1	1	1	1	1	1	1	1
Postocular	2	2	2	2	2	2	2	2	2	2	2
Supralabials touching eye	3	3	3	3	3	3	3	3	3	3	3
Parietal length longer than distance from frontal to rostral	X	X	X	X	X	X	X	X	X	X	X
2nd chin shields separated	X	X	–	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Loreal touches eye	n/a	n/a	n/a	X	one point	X	X	–	X	–	X

Our phylogenetic results suggest the presence of a northern and a southern clade within *B. mentalis sensu lato* (PP: 0.94), with species-level phylogenetic distance between them. The northern clade is present in central Namibe Province, south-western Angola, as well as in the Kunene Region of north-western Namibia. One Angolan specimen (PEM R21606), as well as a specimen from northern Namibia (MCZ R186012), serves as morphological and genetic vouchers for this clade (Table 3, Supplementary material). These specimens agree morphologically with the holotype of *B. mentalis*. Specimen PEM R21606 from Namibe Province has the second chin shields separated (see Figure 5A), but in MCZ R186012 from north-western Namibia, the second chin shields are in good contact. Data from Angolan representatives of the northern clade are limited to PEM R21606 and a road killed specimen from which only a tissue sample was collected (specimen not collected). In Namibia there are several specimens that may potentially represent this clade. A thorough study of available Namibian material and new field surveys in southern Angola are needed to refine additional taxonomic details, as well as to clarify the geographic distribution of the northern clade. The southern clade of *B. mentalis sensu lato* has not been found in Angola, but we recorded several voucher specimens from northern, central and southern Namibia and South Africa (Supplementary material). Although we tentatively consider the northern clade as *B. mentalis sensu stricto*, a detailed taxonomic and nomenclatural revision of the group (including the formal allocation of the type specimen to one of the clades), is needed to fully resolve the status of the *mentalis sensu lato* group.

Material examined: Namibe Province: PEM R21606 (Figure 5A) an adult male from 70 km W (24 km N) on new tar road to Lucira from Lubango-Namibe road (-14.86908° , 12.42806° , 413 m), collected by William R Branch, Johan Marais, Pedro Vaz Pinto and James Titus-McQuillan on 8 December 2012. Namibia: MCZ R186012 a subadult female from 60.6 km N of Kamanjab (-19.66833° , 14.33278° , 1 161 m), Kunene Region, Namibia, collected by Aaron M Bauer, Johan Marais, Ross A Sadlier and Stuart V Nielsen on 12 August 2007.

Additional non-vouchered material: Tissue sample (AG_165) from an adult female from 1.1 km N junction of Farm Mucungo and main road (-14.79528° , 12.49500° , 341 m), Namibe Province, Angola, collected by William R Branch, Pedro Vaz Pinto and João Simões Almeida on 7 November 2015.

Diagnosis: *Boaedon mentalis sensu stricto* (northern clade; Figure 5A, Table 3) can be distinguished from most of its southern African congeners by its light brown ground colour, with two white stripes on the sides of head, three supralabials touching the eye, 202–214 ventral scales and frequently the second chin shields are completely separated from each other by the anterior chin shields. Within Angolan *Boaedon* species, *B. mentalis sensu stricto* differs from *B. fuliginosus* by having a shorter snout (i.e. the length of the parietal is longer than the distance between frontal and rostral versus parietal length equal to the distance between the frontal and rostral in *B. fuliginosus*), and its light brown dorsal colouration (versus blackish-brown in *B. fuliginosus*).

It differs from *B. variegatus*, which also has three supralabials touching the eye, by fewer ventral scales (202–214 versus 218–240 in *B. variegatus*) and its dorsum is light brown in colouration (versus darker brown with white (yellow in life) loops on the body in *B. variegatus*). It differs from *B. angolensis*, and *B. fradei* sp. nov., by having three supralabials touching the eye (versus two) and fewer ventral scales in females 204–214 versus 215–224 (*B. angolensis*) and 211–221 (*B. fradei* sp. nov.). It differs from *B. bocagei* sp. nov., by having fewer ventral scales in females 204–214 (versus 216–229 in *B. bocagei* sp. nov.). It

differs from *B. virgatus* by having 25–27 MSR (versus 25 or fewer), 202–214 ventral scales (versus fewer than 200) and a uniform whitish venter (versus pigmented laterally). It can be distinguished from *B. olivaceus* by having a double row of subcaudals (versus a single row).

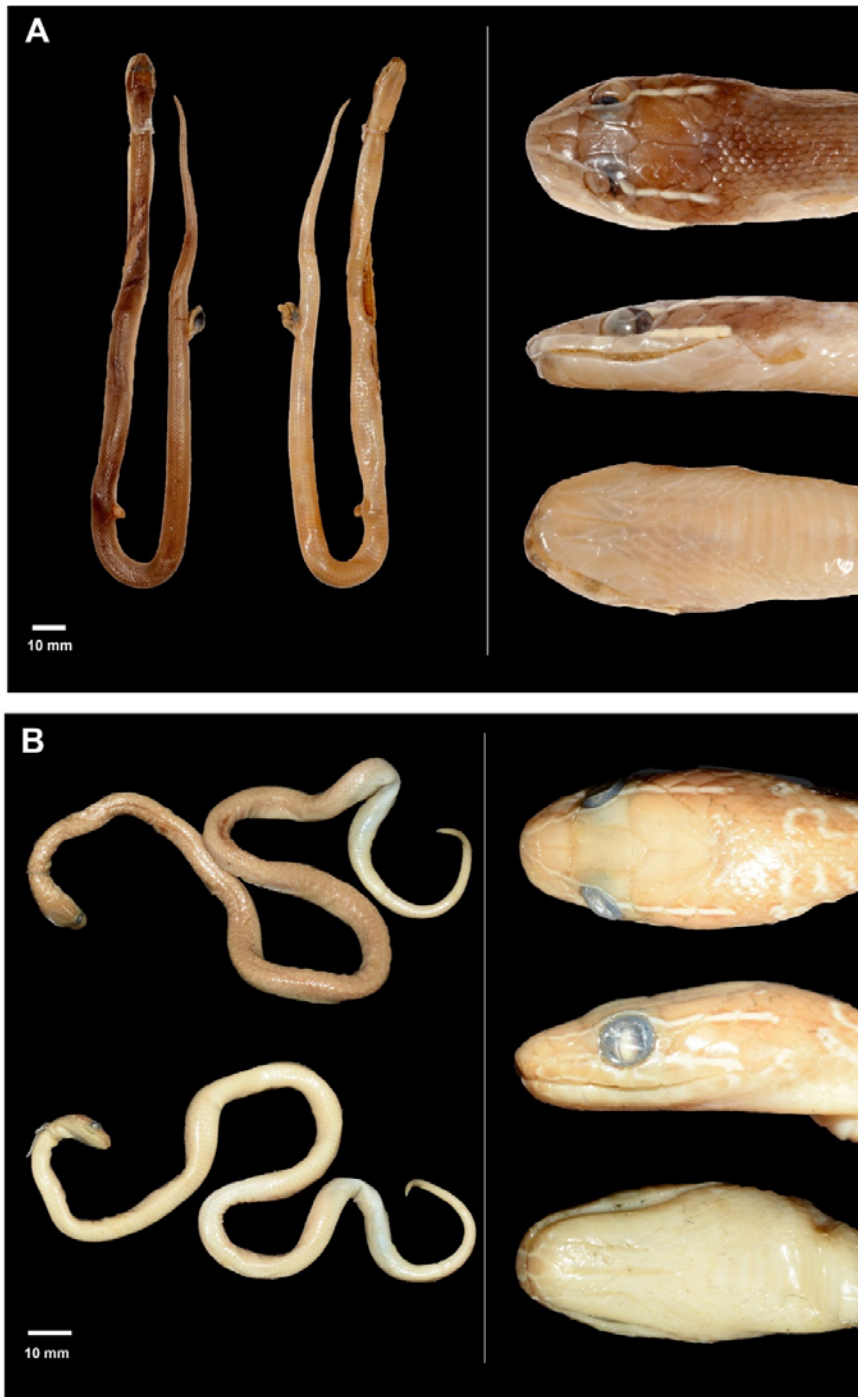


Figure 5. A: Specimen of *Boaedon mentalis* (PEM R21606) collected on road to Lucira from Lubango-Namibe road, Namibe Province, southwestern Angola. B: Paralectotype of *Alopecion variegatum* (BMNH 1867.7.23.23) from Benguela, Benguela Province, southwestern Angola. Photo by Patrick D Campbell.

For other species occurring in the region, it can be distinguished from *B. littoralis* by a lower number of ventral scales in females (204–214 versus 223–234) and the presence of three supralabials (versus two) touching the eye; from *B. subflavus* by having 25–27 MSR (versus 29) and a light brown body colouration (versus yellowish in *B. subflavus*); from *B. perisilvestris* by having a light brown colouration with head stripes (versus uniform brown); from *B. parolineatus* by having fewer ventral scales in females (204–214 versus 239–250), 25–27 MSR (versus more than 31), longitudinal light stripes on head only (versus stripes on head and body in *B. parolineatus*); from *B. longilineatus* by lacking body stripes (versus a broad upper head and body stripe reaching at least the first quarter of the body); from *B. upembae* by having more ventral scales (202–214 versus 175–197); and finally, from *B. radfordi* by having a double row of subcaudals (versus a single row).

Distribution: Known only from Namibe Province, south-western Angola (Figure 2). *B. mentalis sensu stricto* seems to be restricted to northern Namibia and southern Angola, whereas *B. mentalis sensu lato* occurs in Namibia and the Northern Cape Province of South Africa.

Habitat and natural history notes: It is only known from mosaics of steppe and savannah dominated by Mopane trees and sandy soils (Grandvaux-Barbosa 1970).

***Boaedon variegatus* (Bocage, 1867)**

(Figures 2, 5B, 6A, 6B).

Alopecion variegatum (Bocage 1867a: 227; 1867b: 230)

Boodon lineatus (Boulenger 1893: 332; Monard 1937: 113)

Boodon lineatus var. *lineolata* (Bocage: 1895: 80)

Boaedon fuliginosus fuliginosus (Loveridge 1957: 251)

Boaedon capensis-fuliginosus-lineatus complex [part] (Branch 2018: 57)

Boaedon variegatus (Marques et al. 2018: 328)

In two subsequent papers in the same issue of the *Jornal de Sciencias Mathematicas, Phisicas and Naturaes*, *Alopecion variegatum* was introduced as a new species from south-western Angola (Bocage 1867a, 1867b). In the first paper (Bocage 1867a) written in Portuguese, the author coined the *nomen*, noting that it was a new species of the genus *Alopecion*, and noted that illustrations of the new taxon would be provided. He did not, however, provide any description of the taxon, stating that the description would follow in a subsequent paper. In the following paper (Bocage 1867b), this time written in French, Bocage gave a detailed morphological description of the species and provided arguments in favour of his decision on placing the newly described species within the genus *Alopecion*. The two papers had, however, one incongruence related to the type locality and type material used for the description. In the first paper Bocage (1867a) noted that he had ‘one adult and three juveniles, from Benguella [= Benguela] and Dombe [= Dombe Grande] ‘ collected by José de Anchieta and a ‘young specimen from Novo Redondo [= Sumbe] ‘ collected by J.A. Botelho, whereas in the second paper, the one actually containing the full description, Bocage

(1867b) only mentioned three specimens from ‘Benguella’ collected by Anchieta and another specimen from ‘Novo Redondo’ collected by Botelho. Given that the first appearance of the *nomen* (Bocage 1867a) did not provide a description, it can be considered a *nomen nudum*, therefore only the second appearance of the *nomen* (Bocage 1867b) is valid and the type series is restricted to the specimens from ‘Benguella’ and ‘Novo Redondo’, whereas the specimen from ‘Dombe’ is excluded from the type series. Two syntypes, both from ‘Benguella’ still exist in the collections of the ZMB (ZMB 6469, a poorly preserved subadult specimen, partly dried) and the NHMUK (BMNH 1867.7.23.23; Figure 5B), to which they were exchanged by Bocage as duplicate specimens. The remaining two type specimens presumably were lost in the Museu Bocage fire.

In his major review of Angolan herpetology, where Bocage (1895) reviewed his former taxonomic decisions regarding the group, he recognised only *B. lineatus* and *B. olivaceus* as occurring in Angola. Under the account of *Boodon* [*sic*] *lineatus*, Bocage (1895) provided a detailed updated description of the taxon he formerly considered as *Alopecion variegatum*. Following the personal opinion of Albert Günther, Bocage (1895) reconsidered the generic allocation of those specimens and placed them within the genus *Boaedon*, as a variety of *B. lineatus*, which he renamed as *lineolata*. In this nominal taxon he included specimens from Loanda [= Luanda] collected by Toulson and ‘Novo Redondo’ collected by Botelho (the same specimen he included among the types of *A. variegatum*) and from ‘Benguella’ [= Benguela], ‘Catumbella’ [= Catumbela], ‘Dombe’ [= Dombe Grande], and ‘Capangombe,’ all collected by Anchieta, with those specimens from ‘Benguella’ and ‘Dombe’ being the same he cited earlier (Bocage 1867a, 1867b). Bocage should have renamed the taxon because he was not only changing the genus of the taxon, but also regarding it as a variety of *B. lineatus*. Bocage’s action does not conform to the current Code (ICZN 1999), under which *Boodon lineatus* var. *lineolata* Bocage, 1895 is a junior synonym of *Alopecion variegatum* Bocage, 1867. However, the type material of *B. lineatus* var. *lineolata*, although it includes the type material of *A. variegatum*, is not exactly the same, leaving the possibility that some of its syntypes may not belong to the same taxonomic entity. The problem is exacerbated by the fact that the type material of *B. lineatus* var. *lineolata* was also lost in the 1978 fire, but especially because of the fact that one of the species we are currently describing (see *B. bocagei* sp. nov. account) shares the same locality (= Luanda) as one of the syntypes of *B. lineatus* var. *lineolata*. In order to address this potential nomenclatural issue, and given the fact that Bocage intended *B. lineatus* var. *lineolata* to apply to the same entity as *A. variegatum*, we nominate ZMB 6469, one of the surviving syntypes, as the lectotype of *A. variegatum*, which in turn serves as the lectotype of *B. lineatus* var. *lineolata*. By default, the other surviving syntype, BMNH 1867.7.23.23 (Figure 5B) becomes a paralectotype for both nominal taxa. This action is needed to stabilise the nomenclature of the group in the region by definitively rendering *B. lineatus* var. *lineolata* an objective junior synonym of *A. variegatum*.

Lectotype: ZMB 6469, a partly dehydrated subadult from Benguela (−12.57833°, 13.40722°, 11 m), Benguela Province, Angola, most probably collected by José de Anchieta in 1866. The specimen was donated by the Zoological Section of the National Museum of Lisbon to the ZMB in 1869 (Bocage 1869).

Paralectotype: BMNH 1867.7.23.23 (Figure 5B), a subadult in good condition, although somewhat faded, from Benguela (−12.57833°, 13.40722°, 11 m), Benguela Province, Angola, most probably collected by José de Anchieta in 1866. The specimen was donated by the Zoological Section of the National Museum of Lisbon to the NHMUK (BMNH) in 1867.



Figure 6. A: Specimen of *Boaedon variegatus* (CAS 262842) from Chimalavera, Benguela Province, south-western Angola. B: Live photo of the *Boaedon variegatus* specimen CAS 262842 from Chimalavera, Benguela Province, south-western Angola. Photo by Luis MP Ceriaco.

Additional Material: Angola: Benguela Province: CAS 262842 (Figures 6A, 6B), an adult male from the vicinity of the main camp of Chimalavera Nature Reserve (−12.83377°, 13.16991°, 1 198 m), collected by Luis MP Ceriaco, Aaron M. Bauer and David C. Blackburn on 11 December 2015. Namibe Province: CAS 263027 from N'Donlondolo (−13.81045°, 13.13608°, 707 m), collected by Luis MP Ceriaco, Ishan Agarwal and Suzana Bandeira on 21 November 2016; CAS number pending; field no. LMPC 1026) from Fazenda Mucungo (−14.77665°, 12.491127°, 312 m), collected by Luis MP Ceriaco, Mariana P. Marques and Joyce M. Janota on 18 February 2019; PEM R16269, an adult female from 2 km N junction of Fazenda Mucungo and main road (−14.77556°, 12.50944°, 368 m), collected by William R Branch, Pedro Vaz Pinto and João Simões Almeida on 7 November 2015; PEM R24148, a subadult male from the main road near Farm Mucungo (−14.76194°, 12.50361°, 362 m), collected by William R Branch, Pedro Vaz Pinto and João Simões on 7 November 2015; MHNC-UP/REP 572, a juvenile from Moçâmedes vicinities (−15.20032°, 12.138298°, 21 m), collected by Álvaro Baptista (Varito) on 18 July 2019. Namibia: MCZ R184869, a juvenile male from Farm Varianto (−19.3794°, 17.74083°, 1 602 m), Oshikoto Region, Namibia, collected by Aaron M Bauer; ZMH R02354 a subadult female from Namibia with no specific locality.

Diagnosis: *Boaedon variegatus* (Figures 5B–6A, 6B) can be distinguished from most southern African congeners by having three supralabials in contact with the eye, a single preocular contacting the frontal and body colouration with a reticulate network of white lines like loops on a brown background, at least in adults. The loreal is frequently in contact with the eye at a single point.

Within Angolan *Boaedon* species, *B. variegatus* differs from *B. fuliginosus* by having a shorter snout (i.e. the length of the parietals is longer than the distance between frontal and rostral versus parietal length equal to the distance between frontal and rostral) and the loreal length to height ratio is less than 2 (versus greater than 2). *Boaedon variegatus* differs from *B. bocagei* sp. nov., which also has three supralabials touching the eye, by having more ventral scales when compared within sexes (218–220/224–240 versus 208–211/216–229 in *B. bocagei* sp. nov.). *Boaedon variegatus* differs from *B. angolensis* and *B. fradei* sp. nov., by having three supralabials in contact with the eye (versus two) and more ventral scales in females (224–240 versus 215–224 in *B. angolensis*, 211–221 in *B. fradei* sp. nov.). It can be distinguished from *B. mentalis sensu stricto* by having 218–240 ventral scales (versus 202–214), by its darker brown colouration with white loops on the body (versus light brown colouration), and by having the second chin shields in contact with one another (versus often completely separated from each other by the anterior chin shields). *Boaedon variegatus* can be distinguished from *B. virgatus* by having 27–30 MSR (versus 25 or less), 218–240 ventral scales (versus fewer than 200) and a uniform whitish venter (versus laterally pigmented venter). It can be distinguished from *B. olivaceus* by having a double row of subcaudals (versus a single row).

Boaedon variegatus can be distinguished from other species occurring in the region by the following combination of characters: from *B. littoralis* by having three supralabials touching the eye (versus two), preocular touching frontal (versus separate from frontal), and by having the lowest dorsal scale row pigmented (versus white); from *B. subflavus* by having 27–30 MSR (versus more than 29) and a brown body colouration (versus yellowish); from *B. perisilvestris* by its yellowish or white loops on the side of body (versus uniform brown body colouration); from *B. parolineatus* by having fewer ventral scales in females (224–240 versus 239–250), 27–30 MSR (versus more than 31), longitudinal light stripes on head only (versus

longitudinal light stripes on head and body); from *B. longilineatus* by lacking stripes on the body (versus having broad upper head and body stripes reaching at least the first quarter of the body in *B. longilineatus*); from *B. upembae* by having more ventral scales (males: 218–220 versus 175–180; females: 224–240 versus 189–197), and 27–30 MSR (versus 21–23 MSR); and finally, it can be distinguished from *B. radfordi* by having a double row of subcaudals (versus a single row).

Description of lectotype: ZMB 6469, a subadult female, 305 mm SVL; head subtriangular, slightly distinct from the neck, HL 5% of SVL (15 mm); interocular distance 3.5 mm, pupil elliptical, eye diameter 2.8 mm; loreal rectangular, 2.2 times longer (2.2 mm) than high (1.0 mm), touching eye; body cylindrical; tail short (15.4% of SVL). Supralabials 8/8, 3rd, 4th and 5th touching the eye on both sides; 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, touching frontal; 2 postoculars, in contact with 5th and 6th supralabial (on both sides of head); temporals 1 + 2 + 3 on both sides; two internasals; nasal divided; frontal longer (3.5 mm) than wide (2.5 mm); dorsal scales smooth, 23 scale rows one head-length posterior to jaw rictus, 29 MSR, 21 scale rows one head length anterior to vent; ventral scales 237; cloacal plate entire; 55 subcaudals in a double row.

Variation: See Table 3 for summary of measurements. The loreal contacts the eye in 4 out of 6 specimens at least at one point or on one side of head. Lateral side of body with white loops on brown ground colour at least on the first third of body in most adult and subadult specimens examined. Two specimens from Namibia (MCZ R184869 and ZMH R02354) lack these typical markings. Data from the lost type material from the Museu Bocage: 29 MSR, 233–237 V, 55–59 SC, largest individual 771 mm SVL and 120 mm TL (Bocage 1867b).

Distribution: Known from the coastal region of Namibe and Benguela Provinces of Angola (Figure 2). Known localities include: Novo Redondo, Benguela, Catumbela, Capangombe (fide Bocage 1985), Chimalavera Nature Reserve, N'Donlondolo, Fazenda Mucungo and Moçâmedes (this study). *Boaedon variegatus* occurs in adjoining Namibia, as shown by the voucher (No. 34, MCZ R184869) from Farm Varianto, Namibia, and some vouchers ostensibly from KwaZulu-Natal, South Africa clustering in the same clade as *B. variegatus* (see Figure 1).

Habitat and natural history notes: The species can be found in xeric, semi-desert habitats, either moving in open habitats or sheltering in rock crevices. Specimen LMPC 1026, a subadult, had a juvenile *Chondrodactylus pulitzeriae* (Schmidt, 1933) in its stomach when collected.

Boaedon angolensis Bocage, 1895

(Figures 2, 7A, 7B).

Boaedon lineatus var. *angolensis* (Bocage 1895: 80; 1897: 112; Ferreira 1900: 51)

Boodon lineatus (Ferreira 1897: 244; 1906: 167; Monard 1937: 113)

Boaedon lineatus lineatus [part] (Hellmich 1957a: 71; 1957b: 60)

Boaedon lineatus (Wallach et al. 2014: 96)

Boaedon capensis-fuliginosus-lineatus complex (Branch 2018: 57)

Boaedon fuliginosus [part] (Marques et al. 2018: 329).

Boaedon cf. *angolensis*: (Ceriaco et al. 2018a: 425)

Boaedon angolensis [part] (Marques et al. 2018: 327; Baptista et al. 2019a: 118; Butler et al. 2019: 237; Branch et al. 2019c: 323)

Bocage (1895) described this form as an ‘Angolan high plateau’ variety of *Boaedon lineatus*, based on material from Duque de Braganca [currently Kalandula Falls], St. Salvador de Congo [currently M’Banza Congo], Ambaca, Quissange, Cahala, Galanga, Caconda, Biballa, Huilla, Gambos, Humbe, and Cahata. Unfortunately, all type material was destroyed during the Museu Bocage fire in 1978 and no extant syntypes have yet been located in any other museum collection. The original description of *B. lineatus* var. *angolensis* by Bocage (1895) differentiated the new taxon from the nominotypical form by its more elongate and slender body, a more elongated head, less distinct from the body, and a different head colouration (Bocage 1895). No scale characters or measurements were noted. Conradie et al. (2016) were the first to use the nomen *B. angolensis* as a full species (as *Boaedon* cf. *angolensis*), based on specimens from Cuando Cubango Province. Later, Ceriaco et al. (2018a) considered the specimens from Cangandala National Park, Malanje Province as *B. cf. angolensis*, noting that the species boundaries of this group were being evaluated (present paper). Branch (2018) also noted that the status of *B. lineatus* var. *angolensis* was under investigation. Marques et al. (2018), Baptista et al. (2019a), Butler et al. (2019) and Branch et al. (2019c) further referred to the taxon as *B. angolensis*. Our phylogenetic results demonstrate that the name *B. cf. angolensis* applied by Conradie et al. (2016) to one of the specimens they mentioned (PEM R21846) is not conspecific with our current understanding of *B. angolensis*, but rather represents a new species (see *Boaedon branchi* sp. nov. account below), but that of Cangandala National Park mention by Ceriaco et al. (2018a) does conform to the nominotypical form.

Due to the destruction of the original type material, it has been impossible to allocate the nomen *B. angolensis* to a distinct taxon known to occur in Angola. The only surviving specimen labelled by Bocage as *Boodon quadrilineatus* var. *angolensis* was donated to the Zoological Museum Hamburg in 1887, but has no specific locality other than ‘Angola.’ This specimen shares morphological diagnostic characters that agree with both Bocage’s original description and our recently collected material and group together as a well-supported clade in our phylogeny. Furthermore, the type localities noted by Bocage (1895) are consistent with those of our recently collected material. Given that our morphological and phylogenetic results allow us to unambiguously associate this form with different places in the highlands, and the fact that all syntypes have been lost (the collections with which Bocage was known to have exchanged or donated typical material, e.g. ZMB and BMNH, were thoroughly checked), we choose to designate a neotype for *Boaedon angolensis* Bocage, 1895, in order to stabilise the application of this nomen, which has been confused with other nominal taxa in the genus *Boaedon*. Based on the morphological and phylogenetic results, we formally treat this taxon as a full species.

Neotype: MTD 48606 (field no. MHA 62; Figures 15–16), an adult male from Uíge (town), Campus-Fazenda of Universidade Kimpa Vita (−7.59747°, 14.98092°, 817 m), Uíge Province, Angola, collected by Monique Hölting on 12 October 2013.

Additional Material: Huíla Province: CAS 262843, an adult male from Bicuar National Park (−15.10106°, 14.83986°, 1 247 m), collected by Mariana P Marques, Luis MP Ceríaco, Suzana Bandeira, Timóteo Júlio, Brett Butler and Matthew Heinicke on 28 July 2017. Malanje Province: CAS 262315, an adult female from Bola-Cassaxi (−9.77363°, 16.82283°, 1 089 m), Cangandala National Park, collected by Luis MP Ceríaco, Mariana P Marques, Suzana Bandeira, Edward L Stanley and Jens J Vindum on 30 September 2015; MB03-001241, a subadult male from Laúca (−9.737671°, 15.138884°, 870 m), collected by Luis MP Ceríaco and Marina P Marques on 30 March 2017. Uíge Province: MTD 48960, an adult female from Planalto de Mucaba (−7.42978°, 15.16779°, 1 198 m), Municipality of Mucaba, collected by Raffael Ernst on 9 November 2014; MTD 49253, an adult female from Uíge District, road near Quipembe (−7.223972°, 15.097028°, 1 224 m), collected by Thea Lautenschläger on 26 July 2015; Kwanza Norte Province: ZMH R08064 a juvenile male from Piri-Dembos, Roça Novo Douro, coffee plantation, (−8.56667°, 14.50000°, 750 m), collected by GA von Maydell on 4 March 1953; Huambo Province: ZSM 105/54, an adult female from Sanguengue ‘Eukalyptus-plantage’ (−12.36667°, 16.20000°, 1 800 m), Bela-Vista, collected by GA von Maydell on 12 December 1952. Cuando Cubango Province: PEM R23251, an adult male from 65 km south of Menongue (−15.26050°, 17.677614°, 1 246 m), collected by Werner Conradie on 24 March 2016; PEM R23403, an adult female from Menongue HALO compound (−14.66313°, 17.66522°, 1 385 m), collected by John Hilton on 24 May 2017; PEM R23536, a subadult female from 60 km West of Menongue on EN280 (−14.67253°, 17.14700°, 1 378 m), collected by Luke Verburgt on 3 November 2016. ZMH R08036, an adult female from Angola, without a specific locality.

Additional non-vouchered genetic material: One tissue sample (EI_0890) from Longonjo (−12.90189°, 15.2444°, 1 429 m), Huambo Province, Angola, collected by Luke Verburgt on 25 April 2019; a second tissue sample (PVP 43) from Ngola (−14.16944°, 14.44861°, 1 550 m), Huíla Province, Angola, collected by Pedro Vaz Pinto on 9 April 2013.

Diagnosis: *Boaedon angolensis* (Figures 7A, 7B) can be distinguished from most congeners by the following combination of characters: presence of a dark grey (dark brown in life) or pale brown (pale olive in life) ground colour; thin lower white stripe (in life and preservative) on the upper labial scales, in most specimens continuing, interrupted for 4 to 5 body scales as a thin broken white stripe laterally for the first 20% of the body, occasionally terminating at the angle of the jaw; an upper thin white (red or pale orange in life) stripe present only on the upper temporals behind eye.



Figure 7. A: Neotype of *Boaedon angolensis* (MTD 48606) from Uíge town, Uíge Province, north-western Angola. B: Live photo of the *Boaedon angolensis* neotype MTD 48606 from Uíge town, Uíge Province north-western Angola. Photo by Monique Hölting.

Boaedon angolensis can be distinguished from other Angolan *Boaedon* species as follows: from *B. variegatus* by having a lower number of MSR (25–28 versus 27–30), a lower number of ventral scales in males (198–204 versus 218–220), the upper preocular not touching the frontal, two supralabials touching eye (versus three) and a different body colouration (uniform dark brown to pale olive versus white reticulate markings on the body in *B. variegatus*); from *B. olivaceus* by having a double row of subcaudals (versus a single row); from *B. fuliginosus* by having a shorter snout (length of the parietals is longer than the distance between frontal and end of snout versus parietal length is equal to the length between the frontal and end of snout); from *B. virgatus* by having 25–28 MSR (versus 25 or less), 198–204 ventral scales in males (versus fewer than 200) and a whitish venter (grey laterally pigmented in *B. virgatus*); from *B. mentalis sensu stricto* by having 215–224 ventral scales in females (versus 204–214) and second chin shields not separated (versus frequently entirely separated from each other by the anterior chin shields), and a dark grey (dark brown in life) or pale brown (pale olive in life) dorsal colouration (versus light brown).

Boaedon angolensis can be distinguished from other species occurring in the region by the following combination of characters: from the nominotypical *B. lineatus* by a higher number of subcaudal scales (50–72 versus <50), thinner white stripes on side of head, and a lower number of MSR (25–28 versus 29–31); from *B. capensis* by having a shorter snout (the parietal length is equal to the distance between frontal and rostral), the loreal length to height ratio is greater than 2 (versus less than 2 in *B. capensis*), and the presence of two thin white stripes on the head (versus broad white stripes); from *B. upembae* by having more ventral scales (>198 versus 175–197 in *B. upembae*) and by having 25–28 MSR (versus 21–23); and it can be distinguished from *B. radfordi* by having a double row of subcaudals (versus a single row).

Boaedon angolensis can be distinguished from *B. littoralis* by having 1–2 preoculars (versus only one), a lower number of ventral scales in females (215–224 versus 223–234); it can be distinguished from *B. subflavus* by having fewer ventral scales in both males and females (males: 198–204 versus 213–229 and females: 215–224 versus 234–247), 25–28 MSR (versus more than 29), and a dark grey (dark brown in life) or pale brown (pale olive in life) dorsal colouration (versus yellowish dorsal colouration); it can be differentiated from *B. perisilvestris* by having fewer MSR (25–28 versus >29), and by having a thin white stripe on flanks (versus no light stripe on flanks); it can be distinguished from *B. parolineatus* by having fewer ventral scales in both males and females (<224 versus 225–250 in *B. parolineatus*), 25–28 MSR (versus >31), no preocular contact with frontal (versus upper preocular in contact with frontal), a thin longitudinal stripe reaching only the first quarter of the body (versus longitudinal light stripes along complete body); it can be differentiated from *B. longilineatus* by having fewer ventral scales in females (215–224 versus 226–233), more subcaudals in females (50–62 versus 42–49), and thin stripes on head and first quarter of flanks (versus broad temporal head and body stripes).

Description of neotype: See Table 4 for summary of measurements. Adult male, 602 mm SVL; head subtriangular, slightly distinct from the neck, 3.9% of SVL (23.8 mm HL); interocular distance 7.0 mm, pupil elliptical, eye diameter 3.0 mm; loreal rectangular, 1.6 times longer (2.2 mm) than high (1.4 mm); body cylindrical; tail moderately short (24.2% of SVL). Supralabials 8/8, 4th and 5th touching the eye on both sides of the head; infralabials 8/9, first on both sides 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; 2 preoculars on left side, upper larger than lower, one preocular on right side, not touching frontal; 2

Table 4. Morphometric (in mm) and meristic character comparison of *Boaedon angolensis* (Bocage, 1895) neotype and comparative material. X: present, -: absent or missing data.

Examined material	MTD 48606 Neotype	MTD 48960	MTD 49253	ZSM 105/1954	CAS 262315	MB03-001241	CAS 262843	ZMH R08064	ZMH R08036	PEM R23403	PEM R23251	PEM R23536
Sex	Male	Female	Female	Female	Female	Male	Male	Male	Female	Female	Male	Female
SVL	610	725	760	690	840	335	250	248	625	882	460	472
Tail length	158	117	127	96	120	67	55	50	107	134	140	77
SVL/TL	3.9	6.2	6.0	7.2	7.0	5.0	4.6	5.0	5.8	6.5	3.3	6.1
MSR	27	25	27	27	27	27	27	27	27	28	28	28
Ventral scales (V)	204	219	216	215	217	202	201	198	218	224	203	224
Subcaudals (SC)	72	62	50	52	50	67	58	68	51	56	67	54
V/SC	2.8	3.6	4.3	4.1	4.3	3.0	3.5	2.9	4.3	4.0	3.0	4.1
Sublabials	8	8	8	9-8	8	8	8	8	9	8 (4-5)	8 (4-5)	8 (4-5)
Infralabials	8	8	9	9-8	8	9	8	8	10	9 (1-4)	9 (1-4)	9 (1-4)
Loreal length	2.7	3	3.9	3.5	3.5	1.6	-	1.3	3.7	3.7	2.9	2.4
Loreal height	2.9	1.5	1.7	1.4	1.7	0.9	-	0.7	1.5	1.8	1.5	1.4
Loreal L/H ratio	1.0	2.0	2.2	2.5	2.1	1.8	1.2	1.9	2.5	2.0	1.9	1.71
Preocular	1	1	2	1	2	1	1	1	2	1	1	1
Postocular	1-2	1	2	2	2	2	2	2	2	2	2	2
Supralabials touching eye	2	2	2	2	2	2	2	2	2	2	2	2
Parietal length longer than distance from frontal to rostral	X	X	X	X	X	X	X	X	X	X	X	X

postoculars on left side, one on right side, contacting 5th supralabial (both sides of head); temporals 1 + 2 + 3 both sides; two internasals; nasal divided; frontal slightly longer (6.0 mm) than wide (4.9 mm); dorsal scales smooth, 23 scale rows one head-length posterior to jaw rictus, 27 MSR, 21 scale rows one head length anterior to vent; ventral scales 204; cloacal plate entire; 72 subcaudals, first seven subcaudals single, all others paired.

Colouration of neotype in life: Dorsum of head, neck, body and tail dark brown (Figure 7B). Ventral scales completely white and entire ventral surface of tail white. Thin upper head stripe orange, extending from above nasal scale through prefrontal, interrupted for a short distance, then extending through supraocular, upper postocular, upper first, middle second and middle third temporals. The lower head stripe white, beginning at nasal scale, extending through loreal and 4th to 8th supralabials, interrupted on 4th to 5th body scales, but continuing as a thin white lateral stripe on the first 20% of the body. Iris orange-brown. In preservative, as above, but upper orange head stripe is white or whitish.

Variation: Variation in measurements and scalation of the additional material studied is presented in Table 4. Colouration of specimens MTD 49253, MTD 48960, ZSM 105/54, ZMH R08036 head and body dark grey, ventral side of head, body and tail whitish, no dark pigment on venter. CAS 262315 head and body grey-brown, venter and tail whitish without dark pigment. Two male specimens, MB03-001241 and ZMH R08064, dark brown with thin white head stripes, no dorsal body scales white. In CAS 262843 the colouration is pale brown (pale olive in life), with a creamy venter, lower dorsal scales creamy and one thin white stripe extending from snout, above the eye, to behind temporal region. A non-vouchered road-killed specimen (tissue sample PVP 43) from N'gola, Huíla Province exhibited a pale olive brown dorsal colouration.

Distribution: The species is restricted to Angola and was found in the Provinces of Cuando Cubango, Uíge, Malanje, Huambo, Kwanza Norte, Huíla, and potentially extends into Benguela and Cunene Provinces. The latter two areas were represented in the original type series (Bocage 1895; Figure 2) and were noted by Monard (1937), but have not been verified by recent material. It is also expected that the species may occur in the Provinces of Bengo and Kwanza Sul, especially in areas with a similar elevation to those typical of the Angolan Plateau.

Habitat and natural history notes: *Boaedon angolensis* has been recorded from fallow land in peri- and urban localities at mid-elevation (neotype locality MTD 48606 in Uíge town at around 800 m elevation) to higher elevation open savannah habitats on the plateau of Mucaba (on average 1 200 m elevation, MTD 48960 and MTD 49253). The later locality comprises human dominated farmbush savannah habitats that are frequently burnt, as well as mixed forest-savannah mosaics with occasional calciferous outcrops. Specimens collected in both Cangandala National Park, Malanje Province (CAS 262315) and Bicuar National Park (CAS 262843) were found in open areas in a mosaic of Miombo woodlands. The specimen collected in Laúca (MB03-001241), was collected in a disturbed area near the construction of a hydroelectric dam, although the surrounding areas were dominated by Miombo woodlands. The tissue sample EI_0890 was taken from a specimen killed on the road in the town of Longonjo.

***Boaedon bocagei* sp. nov.**

(Figures 2, 8A, 8B).

Boaedon lineatus lineatus [part] (Bocage 1895: 78)

Boodon lineatus [part] (Ferreira 1903: 114)

Boaedon fuliginosus complex [part] (Marques et al. 2018: 329)

Boaedon capensis-fuliginosus-lineatus complex [part] (Branch 2018: 57)

Populations of *Boaedon* occurring in the western lowlands of Luanda and Bengo Provinces have not been addressed in any taxonomic context. Although, Bocage (1895) noted that specimens collected by Anchieta from the coastal zone north of Quanza (Kwanza) are the typical form of *B. lineatus* and gave some morphological characters for these specimens. Furthermore, he considered specimens received from Toulon from Luanda to be different from the nominate form and described them as *Alopecion variegatum* (Bocage 1867), although he later (Bocage 1895) treated this material as a new variety: *Boaedon lineatus* var. *lineolata* (see above under systematics of *B. variegatus*).

Holotype: CAS 262799 (field no. AMB 10121; Figures 8A, 8B), an adult female from Kissama National Park at Kawa Camp, (−9.183383°, 13.371144°, 136 m), Bengo Province, collected by Luis MP Ceríaco, Aaron M Bauer and David C Blackburn on 15 December 2015.

Paratypes: PEM R22042 (field no. PVP 19), a subadult and PEM R22043 (field no. PVP 20), a juvenile female from Samba (−8.88222°, 13.184167°, 67 m), Luanda Province, collected by Pedro Vaz Pinto in March 2015; MB03-0001118, a subadult from Caop Velha, Cacuaco (−8.784722°, 13.46805°, 5 m) Bengo Province, collected by Luis MP Ceríaco on 2 April 2012; PEM R20914 (field no. ID# 13-23), an adult female from Soyo (−6.23167°, 12.33389°, 5 m) Zaire Province, collected by Warren Klein in March 2015; MHNCUP/REP 166-168 (3 specimens from Novo Redondo [= Sumbe] (−11.20605°, 13.84371°, 10 m), Kwanza Sul Province, Angola, collected by Francisco Newton in 1903.

Diagnosis: *Boaedon bocagei* sp. nov. (Figures 8A, 8B) can be distinguished from most congeners by the presence of olive to brown ground colour, with two white, dark brown bordered stripes on the sides of the head. The upper stripe starts from just behind nasals, continuing above eye and extending along first quarter of the body on both sides; the lower stripe from loreal through supralabials to the posterior temporals; three supralabials contacting the eye; and usually one preocular, when two are present, the upper one touches the frontal.

Among Angolan congeners, *B. bocagei* sp. nov. differs from *B. fuliginosus* by having a shorter snout (length of the parietals longer than the distance between frontal and end of snout versus the parietal length is equal to the length between the frontal and end of snout) and the loreal length to height ratio is less than 2 (versus greater than 2); it differs from *B. angolensis* by having a higher number of ventral scales in females (221–229 versus 215–224) and males (208–211 versus 198–204); it may be distinguished from *B. variegatus* by having a lower number of MSR (25–27 versus 27–30); it can be differentiated from *B. virgatus* by having 25–27 MSR (versus 23–25), more than 208 ventral scales (versus fewer than 200) and a whitish venter (versus grey pigmented venter); from *B. mentalis sensu stricto* by its olive brown or brown ground colour (versus light brown) and by having the second chin shields in contact with each other (versus frequently completely separated from each other by the

anterior chin shields); and it can be distinguished from *B. olivaceus* by having a double row of subcaudals (versus a single row).

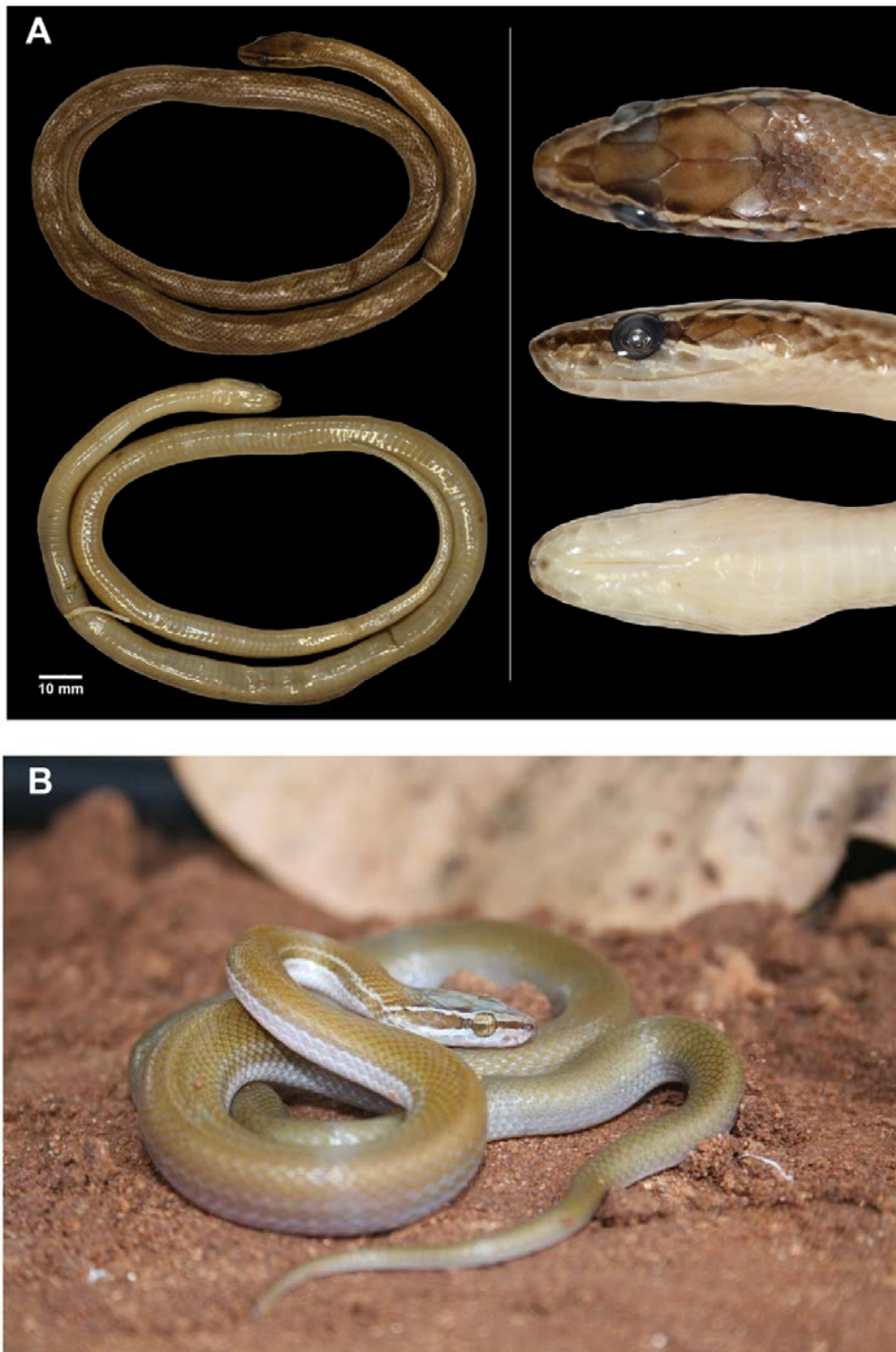


Figure 8. A: Holotype of *Boaedon bocagei* sp. nov. (CAS 262799) from Kawa camp, Kissama National Park, Luanda Province, north-western Angola. B: Live photo of the *Boaedon bocagei* sp. nov. holotype CAS 262799, from Kawa camp, Kissama National Park, Luanda Province, north-western Angola. Photo by Luis MP Ceriaco.

It can be distinguished from other congeners occurring in the region as follows: from the nominotypical *B. lineatus* by its lower number of MSR (25–27 versus 29–31), and by its olive brown or brown ground colour (versus dark brown); from *B. capensis* by having the length of the parietals longer than the distance between frontal and end of snout (versus not longer than the distance between frontal and end of snout); from *B. littoralis* by having 1–2 preocular (versus only one) and 25–27 MSR (versus 27–31); from *B. subflavus* by having a lower number of ventral scales in males (208–211 versus 213–229) and females (221–229 versus 234–247), 25–27 MSR (versus more than 29), and olive brown or brown ground colour (versus overall yellowish colouration); from *B. perisilvestris* by having 25–27 MSR (versus >29), and by having lateral head stripes (versus no light lateral stripes); from *B. parolineatus* by having fewer ventral scales in males (208–211 versus 225–243) and females (221–229 versus 239–250), 25–27 MSR (versus more than 31); from *B. longilineatus* by lower ventral scale counts in females (221–229 versus 226–233), higher subcaudal scale counts (48–66 versus 42–49), and by having thin stripes on head and first quarter of flanks (versus broad head and body stripes); from *B. upembae* by having more ventral scales in males (208–211 versus 175–180) and females (221–229 versus 189–197), and 25–27 MSR (versus 21–23); and from *B. radfordi* by having a double row of subcaudals (versus a single row).

Description of holotype: Adult female (Figures 8A, 8B), 435 mm SVL; head subtriangular, slightly distinct from the neck, HL 3.8% of SVL (16.9 mm); interocular distance 4.3 mm, pupil elliptical, eye diameter 3 mm; loreal rectangular, twice as long (2 mm) as high (1 mm); body cylindrical; tail moderately short (22% of SVL). Supralabials 9/9, 3rd, 4th and 5th on both sides touching the eye; infralabials 10/10, 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; 2 preoculars on both sides, upper one larger than lower and not touching frontal; 2 postoculars, in contact with 5th supralabial (both sides of head); temporals 1 + 2 + 3 on both sides; two internasals; nasal divided; frontal longer (5.6 mm) than wide (3.2 mm); dorsal scales smooth, 22 scale rows one head-length posterior to jaw rictus, 27 MSR, 19 scale rows one head length anterior to vent; ventral scales 229; cloacal plate entire; 48 subcaudals, all paired.

Colouration of holotype in life: The colouration is yellowish-olive with a whitish venter, lowest dorsal scale row whitish (Figure 8B). Two clear white stripes on side of head continuing on first quarter of flanks. In preservative as above, but body and head light brown dorsally (Figure 8A).

Variation: Variation in measurements and scalation of the paratypes of *B. bocagei* sp. nov. are presented in Table 5. Paratypes PEM R22042, PEM R22043 and MB03-0001118 show clear white stripes on the head continuing onto the first quarter of body. The ground colour of two of the subadult specimens is brown, whereas the others are olive-brown. Three supralabials are in contact with the eye in all specimens.

Table 5. Morphometric (in mm) and meristic character comparison of *Boaedon bocagei* sp. nov. Tails truncated in PEM R22042 and R22043, X: present, –: absent or missing data.

Examined material	CAS 262799 Holotype	MB03-0001118 Paratype	PEM R22042 Paratype	PEM R22043 Paratype	PEM R20914 Paratype	MHNCUP/Rep 166 Paratype	MHNCUP/Rep 167 Paratype	MHNCUP/Rep 168 Paratype
Sex	Female	Male	Male	Female	Female	Juvenile	Juvenile	Unsexed
SVL	435	234	306	221	451	430	276	620
Tail length	70	46	47	21	71	78	58	105
SVL/TL	6.2	5.1	–	–	6.4	5.5	4.7	5.9
MSR	27	25	25	25	27	24	27	26
Ventral scales (V)	229	211	208	229	221	212	209	216
Subcaudals (SC)	48	66	46 (tip gone 3–4 subcaudals)	30 (truncated)	53	50	62	50
V/SC	4.8	3.2	–	–	4.2	4.2	3.4	
Sublabials (entering eye)	9	8	8 (3–5)	8 (3–5)	8 (3–5)	8	9	8
Infralabials (touch 1st chin shields)	10	9	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)
Loreal length	–	1.1	1.3	1.1	1.0	–	1.4	3.3
Loreal height	–	0.8	0.8	0.8	0.7	–	0.8	1.8
Loreal L/H ratio	1.6	1.4	1.6	1.3	1.6		1.7	1.8
Preocular	2	2	1	1	1	1	1	1
Postocular	2	2	2	2	2	2	2	2
Supralabials touching eye	3	3	3 (3–5)	3 (3–5)	3 (3–5)	3 (3–5)	3 (3–5)	3 (3–5)
Parietal length longer than distance from frontal to rostral	X	X	X	X	X	X	X	X

Distribution: This species is currently known only from the coastal lowland areas of Luanda, Bengo, Zaire, and Cuanza Sul Provinces (Figure 2).

Habitat and natural history notes: The holotype was collected in Kissama National Park at night. The habitat of the type locality is a typical western Angolan savannah, with sandy soils dominated by *Adansonia digitata*, *Euphorbia conspicua*, *Acacia* [= *Senegalia*] *welwitschii* and *Combretum* sp., together with good grass cover (Grandvaux-Barbosa 1970). The species is also found in the Luanda city area, a massive metropolis of more than 8 million inhabitants, especially in disturbed areas with some vegetation.

Etymology: The specific epithet is a patronym in the masculine genitive singular named after the Portuguese zoologist José Vicente Barbosa du Bocage (1823–1907), ancestor of Angolan herpetology, in honour of his significant taxonomic contributions on the Angolan and African herpetofauna. We propose the English name ‘Bocage’s Brown House Snake’ and the Portuguese name ‘Serpente Castanha de Bocage’ for this species.

***Boaedon branchi* sp. nov.** (Figures 2, 9A, 9B).

Boaedon cf. *angolensis* [part] (Conradie et al. 2016: 22)

Boaedon capensis-fuliginosus-lineatus complex [part] (Branch 2018: 57)

Boaedon angolensis [part] (Marques et al. 2018: 327; Branch et al. 2019c: 323)

Conradie et al. (2016) reported one specimen from Cuando Cubango Province collected in 2015 that they considered as potentially being representative of *B. angolensis*. Although its body scale counts fall within the variation of *B. angolensis* (see Table 4, 6), its colouration is different. Phylogenetic and morphological analyses of the specimen support its recognition as a new species. The Cuando Cubango specimen appears sister to all remaining *Boaedon* analysed in this study (Figure 1).

Holotype: PEM R21846 (field no. ANG 15 56; Figures 9A, 9B) an adult male from about 47.5 km E of Menongue on road to Cuito Cuanavale (−14.59517°, 18.07111°, 1 497 m), Cuando Cubango Province, Angola collected by William R. Branch on 8 June 2015.

Paratype: PEM R23538 (field no. WC-4652) subadult male from Longa River (−14.55956°, 18.41406°, 1 319 m), Cuando Cubango Province, Angola, collected on 4 November 2016 by unknown collector and presented to Luke Verburgt.

Diagnosis: *Boaedon branchi* sp. nov. (Figures 9A, 9B) can be distinguished from most congeners by its yellowish-olive ground life colour, with two fine white stripes on the side of the head, an upper stripe from above the eye to the posterior temporal region and a lower stripe from the lower preocular to the posterior supralabial, no lateral stripes on body and the first 1–3 dorsal scale rows immaculate white.

Table 6. Morphometric (in mm) and meristic character comparison of *Boaedon branchi* sp. nov. and *Boaedon fradei* sp. nov., X: present, –: absent or missing data.

Examined material	PEM R21846 Holotype	PEM R23538 Paratype	PEM R23487 Holotype	PEM R23486 Paratype	PEM R19894 Paratype	PEM R23985 Paratype	IICT R 40–1959 Paratype	IICT R 5–1959 Paratype	IICT R 410–1959 Paratype	IICT 341–1959 Paratype	IICT R 404–1959 Paratype
Taxon	<i>Boaedon branchi</i> sp. nov.	<i>Boaedon branchi</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.	<i>Boaedon fradei</i> sp. nov.
Sex	Male	Male	Female	Female	Male	Male	Male	Female	Male	Female	Female
SVL	508	346	738	476	450	608	480	719	384	698	232
Tail length	125	75	122	79	106	143	108	114	90	135	36
SVL/TL	4.1	4.6	6.1	6.0	4.2	4.3	4.4	6.3	4.3	5.1	6.4
MSR	29	29	29	28	27	28	25	27	27	27	26
Ventral scales (V)	197	210	211	214	219	201	193	221	193	215	217
Subcaudals (SC)	67	64	50	52	63	65	65	50	69	52	46
V/SC	2.9	3.3	4.2	4.1	3.5	2.2	3.0	4.4	2.8	4.1	4.7
Sublabials (entering eye)	8 (4–5)	8 (4–5)	9 (5–6)/8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)	8 (4–5)
Infralabials (touch 1st chin shields)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9 (1–4)	9	9	9	8
Loreal length	2.6	2.2	3.0	2.2	2.1	2.2	2.8	3.4	2.1	3.8	1.6
Loreal height	1.3	1.0	2.1	1.8	1.2	3.0	1.6	1.9	1.5	1.81	0.91
Loreal L/H ratio	2.0	2.2	1.4	1.2	1.8	1.4	1.7	1.8	1.5	2.1	1.7
Preocular	2	1	1	1	1/2	1	1	2	1	1	2
Postocular	2	2	2	2	2	2	2	2	1	2	2
Supralabials touching eye	2	2	2	2	2	2	2	2	2	2	2
Parietal length longer than distance from frontal to rostral	X	X	X	X	X	X	X	X	X	X	X



Figure 9. A: Holotype of *Boaedon branchi* sp. nov. (PEM R21846) from Menongue, Cuando Cubango Province, south-eastern Angola. B: Live photo of the *Boaedon branchi* sp. nov. holotype PEM R21846, from Menongue, Cuando Cubango Province, south-eastern Angola. Photo by WR Branch.

Among Angolan species, *B. branchi* sp. nov. can be distinguished from *B. fuliginosus* by having a shorter snout (the length of the parietals is longer than the distance between the frontal and the end of snout versus the parietal length is equal to the length between the frontal and end of snout). *B. branchi* sp. nov. differs from *B. angolensis* in lacking a thin white stripe on lower side of neck (versus stripe present in most specimens in *B. angolensis*), its yellowish-olive ground colour in life (versus brown or olive ground colour) and by having 29 MSR in males (versus 25–28). It can be distinguished from *B. bocagei* sp. nov., by having 29 MSR (versus 25–27) by lacking a dark bordered head stripe (versus a dark bordered head stripe present) and two supralabials touching eye (versus three supralabials touching eye). It can be distinguished from *B. variegatus* by having a lower number of ventral scales (197–210 versus 218–240), and 1–2 preoculars (versus one), the upper of which, when present, is in contact with the frontal at one point, and a yellowish olive colouration (versus brown colouration with looping white or yellowish markings). It can be differentiated from *B. virgatus* by having 29 MSR (versus 25 or fewer), and a whitish venter (versus pigmented venter); from *B. mentalis sensu stricto* by not having the second chin shields separated from each other (versus second chin shields often completely separated from each other by the anterior chin shields) and its yellowish ground colour (versus light brown ground colour); and from *B. olivaceus* by having a double row of subcaudals (versus a single row). It differs from *B. fradei* sp. nov. by the lower 2–3 dorsal scales rows being immaculate white (versus pigmented) and by its yellowish ground colour (versus dark brown to olive ground colour).

Boaedon branchi sp. nov. can be distinguished from other congeners occurring in the region by the following combinations of characters: from the nominotypical *B. lineatus* by its lower number of MSR (29 versus 29–31 in *B. lineatus*) and a yellowish-olive ground colour and no lateral stripes on body (versus predominantly brown colouration with stripes on the side of the body); from *B. capensis* by the parietals longer than the distance between frontal and end of snout (versus the length of the parietals is no longer than the distance between frontal and end of snout) and loreal length to height ratio greater than 2 (versus less than 2); from *B. littoralis* by a yellowish body colouration (versus light brown); from *B. subflavus* by having fewer ventral scales in males (197–210 versus 213–229) and 29 MSR (versus 29–31); from *B. perisilvestris* by having 29 MSR (versus 29–31) and by its yellowish-olive colouration (versus dark brown); from *B. paralineatus* by having fewer ventral scales in males (197–210 versus 225–243), 29 MSR (versus more than 31), fine white stripes present only on head (versus stripes on head and body); from *B. longilineatus* by having no stripes on neck and body and yellowish colouration (versus broad upper head and body stripes on first quarter of body and a brown body colouration); from *B. upembae* by having more ventral scales in males (197–210 versus 175–180), and by having 29 MSR (versus 21–23); and from *B. radfordi* by having a double row of subcaudals (versus a single row).

Description of holotype: The specimen is a road kill with some visible external damage (Figure 9A). Adult male, 508 mm SVL + 123 mm TL = 631 mm total length; head (21.1 mm length) subtriangular, slightly distinct from the neck, pupil elliptical; loreal rectangular 2.0 times longer than high (2.6 × 1.3 mm); body cylindrical; tail moderately short (24.2% of SVL). Supralabials 8/8, 4th and 5th in contact with eye on both sides; infralabials 9/9, first on both sides in contact behind the mental, first three on both sides in contact with anterior chin shields and 4th in contact with posterior chin shields on both sides; a single preocular on each side, the upper part touching the frontal at one point; 2 postoculars, the lower in contact with 5th and 6th supralabials below and with parietal above (both sides of head); temporals 1 + 2 + 4 on right side and 1 + 2 + 3 on left side; two internasals in broad contact; nasal divided; frontal longer than wide (5.6 mm × 3.9 mm); dorsal scales smooth, 25 scale rows

one head-length posterior to jaw rictus, 29 MSR, 19 scale rows one head length anterior to vent; ventral scales 197; cloacal plate entire; 67 subcaudals, all paired. Four enlarged anterior maxillary teeth followed posteriorly after a small diastema by seven smaller maxillary teeth (due to specimen damage some teeth are broken off or missing).

Hemipenis: Only the right hemipenis is fully everted and it is typical of the genus *Boaedon* (Zaher 1999). Distal ornamentation is spinose; 10–12 rows of spines encircle the basal section, whereas an additional 10 rows encircle the distal two-thirds of the arms; the spines are ossified, not webbed, and increase in size proximally; the proximal third of the basal section is constricted, and covered with small, scattered spines. The fully everted hemipenis extends to the 12th subcaudal, with bifurcation at the 10th subcaudal and the centrolineal sulcus present at the 5th subcaudal.

Colouration of holotype: Head and body with a pale yellow-olive dorsal colouration and a whitish venter. Lowest 2–3 dorsal scale rows are immaculate white, distinct separation from other pale yellow-olive dorsal scales. Two thin white stripes on sides of head, the upper running from rostral through prefrontal and upper preocular above eye to upper 2nd temporal row. Lower stripe starts on supralabials 1 to 4 as an interrupted white stripe, on supralabial 5 runs from 6th supralabial to 8th supralabial. Colouration in preservative light brown above, venter creamy, no contrasting colouration between venter and dorsum, head stripes white as described above (in life).

Variation: See Table 6 for measurements of the type material. The colouration of the paratype is very similar to holotype, but is light brown in dorsal colouration, the upper white dorsal stripe extends to the middle scale of the 3rd row of temporal scales and only 1–2 lower dorsal scale rows are immaculate white. The paratype has six enlarged anterior maxillary teeth followed posteriorly after a small diastema by twelve smaller sized maxillary teeth. The hemipenis structure is very similar to the holotype.

Distribution: The species is currently only known from the region east of the town of Menongue in south-eastern Cuando Cubango Province of Angola (Figure 2). It is expected that the species may also occur more widely in the region and into northern Namibia and adjacent Zambia.

Habitat and natural history notes: The region where the species occurs is dominated by low Miombo woodlands, characterised by *Brachystegia spiciformis* var. *latifoliolata*, *Julbernardia* sp. and *Brachystegia glaberrima* on sandy soils (Grandvaux-Barbosa 1970). The stomach content of the male paratype contained an unidentified rodent.

Etymology: The specific epithet is a patronym in the masculine genitive singular named after our dear colleague, the British-born South African herpetologist William (Bill) Roy Branch (1946–2018), in honour of his inspiring work on the Angolan herpetofauna. Bill was a collaborator on this work for many years, but died in October 2018, as the manuscript was drawing near to completion. We propose the English name ‘Branch’s Brown House Snake’ and the Portuguese name ‘Serpente Castanha de Branch’ for this species.

***Boaedon fradei* sp. nov.**

(Figures 2, 10A, 10B, 11).

Boaedon lineatus lineatus [part] (Laurent 1964: 93)

Boaedon fuliginosus fuliginosus (Manaças 1973: 58)

Boaedon fuliginosus [part] (Marques et al. 2018: 329)

Boaedon cf. *angolensis* [part] (Conradie et al. 2016: 22)

The eastern Angolan populations of *Boaedon* (in Lunda Sul and Moxico Provinces) have been historically assigned to *Boaedon lineatus* (Laurent 1964) and *B. fuliginosus* (Manaças 1973). Specimens from Moxico Province reported by Manaças (1973) are currently housed in the IICT collections (Lisbon, Portugal). Specimens reported by Laurent (1964) from Alto Chicapa, Lunda Sul Province and Lac Calundo [= Lake Calundo], Moxico Province represent *Boaedon fuliginosus* (see *B. fuliginosus* account). The collection of fresh material in Moxico Province during the National Geographic Okavango Wilderness Project (2015–2019), together with the re-examination of the historical specimens reported by Manaças (1973), allowed us to identify this population as a new species.

Holotype: PEM R23487 (field no. WC-4699; Figures 10A, 10B) an adult female from the source lake of the Quembo River (−13.13544°, 19.04397°, 1 375 m), Moxico Province, Angola collected by Werner Conradie on 1 November 2016.

Paratypes: PEM R23486 (field no. WC-4667) a subadult female from the same locality as the holotype, collected by Werner Conradie and Luke Verburgt on 28 October 2016; PEM R23985 an adult male from campsite near to bridge over Lungwebungu River (−12.58013°, 18.66740°, 1 304 m), Moxico Province, Angola, collected by Werner Conradie and Alexander Rebelo on 22 April 2018; PEM R19894 (field no. TB29) an adult male from a village nearby Chiri Camp, Saurimo (−9.42333°, 20.45194°, 1 030 m), Lunda Sul Province, Angola, collected on 7 November 2015 by Thomas Branch; IICT 40-1959, unsexed individual collected on 28 October 1959; IICT 5-1959, an adult female collected on 14 January 1959; IICT 341-1959, unsexed adult collected on 1 November 1959; IICT 404-1959, juvenile unsexed collected in 1959; and IICT 410A-1959, unsexed juvenile collected on 17 November 1959. All above IICT specimens from Calombe, Luso (−11.83000°, 19.91660°, 1 362 m) Moxico Province, Angola, and collected by Fernando Frade.

Additional Angolan Material: Based on geographical proximity the following Angolan material is assigned to the new species, but carries no formal type status: IICT 150-1958, adult female, IICT 350-1959, an adult male, IICT 400-1959 an adult male, IICT 340-1968, an unsexed adult, all from Rio Calombe (−11.83000°, 19.91660°, 1 362 m) Moxico Province, Angola, collected by Fernando Frade between 1 November 1958 and 3 March 1968; IICT 240-1968, unsexed adult from Luso [= Luena] (−11.783000°, 19.31600°, 1 257 m) collected by António Américo on 3 March 1969; PEM R25338 (field no. WC-7056), a juvenile from Lake Hundo (−14.97431°, 21.62966°, 1 100 m), Moxico Province, Angola, male collected by Werner Conradie and Chad Keates on 4 December 2019.



Figure 10. A: Holotype of *Boaedon fradei* sp. nov. (PEM R23487) from source lake of the Quembu River, Moxico Province, eastern Angola. B: Live photo of the *Boaedon fradei* sp. nov. holotype PEM R23487, from Quembu River source, Moxico Province, south-eastern Angola. Photo by W Conradie.

Additional non-vouchered genetic material: Two samples (EI_0761–762) from near Saurimo (−9.65476°, 20.38723°, 1 060 m and −9.70143°, 20.28413°, 1 066 m, respectively), Lunda Sul Province, Angola, collected by Luke Verburgt on 9 October 2018.

Diagnosis: *Boaedon fradei* sp. nov. (Figures 10A, 10B, 11) can be distinguished from most congeners by its dark brown ground colour (in preservative), with two thin white stripes on the side of the head and relatively low ventral scale counts of 193–219 in males

Among Angolan congeners, *B. fradei* sp. nov. differs from *B. fuliginosus* by having a shorter snout in which the length of the parietals is longer than the distance between the frontal and the end of snout (versus the parietal length is equal to the length between the frontal and end of snout), and the loreal length to height ratio is lower than or equal to 2 (versus greater than 2); it differs from *B. angolensis* by its dark brown ground colour (in preservative) with two contrasting white head stripes (in preservative; versus grey to olive brown with thin head stripes continuing on first quarter of the sides of the body); it differs from *B. branchi* sp. nov. by its dark brown ground colour (versus yellowish ground colour and lower 1–3 dorsal scale rows immaculate white). It can be distinguished from *B. bocagei* sp. nov., by having only two supralabials touching the eye (versus 3). *Boaedon fradei* sp. nov. may be distinguished from *B. variegatus* by having a lower number of ventral scale rows (193–221 versus 218–240) and brown body colouration (in preservative) without white or yellowish looping markings in adults (versus white or yellowish looping markings on brown ground colouration); from *B. virgatus* by having 25–29 MSR (versus 25 or fewer), and an unpigmented venter (versus pigmented venter); from *B. mentalis sensu stricto* by having the second chin shields in contact with each other (versus second chin shields often completely separated from each other by the anterior chin shields) and dark brown body colouration (in preservative; versus light brown ground colour); and from *B. olivaceus* by having a double row of subcaudals (versus a single row).

Boaedon fradei sp. nov. may be distinguished from other *Boaedon* occurring in the region by the following combinations of characters: from the nominotypical *B. lineatus* by its lower number of MSR (25–29 versus 29–31) and by the absence of light stripes on side of the body (versus stripes present on the side of the body); from *B. capensis* by the short snout (versus the length of the parietals is not much longer than the distance between frontal and end of snout). It can be distinguished from *B. littoralis* by having 1–2 preoculars (versus only one), preocular in contact with frontal (versus preocular often separate from the frontal); from *B. subflavus* by having fewer ventral scales in males (193–219 versus 213–229) and females (211–221 versus 234–247), 25–29 MSR (versus >29); from *B. perisilvestris* by having 25–29 MSR (versus >29) and two supralabials touching eye (versus three); from *B. parolineatus* by having fewer ventral scales in males (193–219 versus 225–243) and females (211–221 versus 239–250), 25–29 MSR (versus >31), longitudinal light stripes present only on head (versus longitudinal light stripes on head and body); from *B. longilineatus* by lower ventral scale counts in females (211–221 versus 226–233), and by having no stripes on neck and body and dark brown to olive ground colour (in life) (versus a broad upper head and body stripes reaching first quarter of body and a brown body colouration); from *B. upembae* by having more ventral scales in males (193–219 versus 175–180) and females (211–221 versus 189–197), and 25–29 MSR (versus 21–23); and from *B. radfordi* by having a double row of subcaudals (versus a single row).

Description of holotype: Adult female (Figures 10A, 10B), 738 mm SVL + 122 mm TL = 860 mm total length; head (30.3 mm length) subtriangular, slightly distinct from the

neck, pupil elliptical; loreal rectangular 1.4 times longer than high (3.0×1.4 mm); body cylindrical; tail moderately short (16.5% of SVL). Supralabials 9/8, 5th and 6th/4th and 5th 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 contacting posterior chin shields on both sides; a single preocular on each side touching the frontal at one point; 2 postoculars, the lower in contact with 6th and 7th/5th and 6th supralabial below and with parietal above (both sides of head); temporals 1 + 2 + 4 on right side and 1 + 2 + 3 on left side; two internasals; nasal divided; frontal longer than wide (7.1 mm \times 5.3 mm); dorsals smooth, 29 MSR; ventral scales 211; cloacal plate entire; 50 subcaudals, all paired. Five enlarged anterior maxillary teeth followed posteriorly, after a small diastema, by 10 smaller maxillary teeth or tooth loci.

Colouration of holotype: Head and body dark brown to olive ground colour with yellowish flanks (in life; Fig 10 B), venter cream with yellow blotches that fades in preservatives. Two white stripes on each side of head, the upper running from the rostral through the prefrontal, the upper part of preocular above the eye, through the upper postocular to the posterior upper temporal. The lower stripe starts on supralabial 3 as an interrupted white stripe continuing to supralabials 4–5 under eye, begins again on the lower postocular and runs across supralabials 9/8 and ends five scales onto the neck. Colouration in preservative is brown above strongly contrasting with a creamy venter.

Variation: See Table 6 for variation in measurements and scalation of the paratypes and additional material of *Boaedon fradei* sp. nov. All specimens have the same dark brown to olive dorsal colouration as the holotype with minimal variation in the white head stripes.

Hemipenis: Description based on male paratype PEM R23985 with fully everted hemipenis. The hemipenis is typical of the genus *Boaedon* (Zaher 1999). Distal ornamentation is spinose; 9–10 rows of spines encircle the basal section, whereas an additional 10–11 rows encircle the distal two-thirds of the arms; the spines are ossified, not webbed, and increase in size proximally; the proximal third of the basal section is constricted, and covered with small, scattered spines. The fully everted hemipenis extends to the 11th subcaudal, bifurcates at the 9th subcaudal, with the centrolineal sulcus present at 5th subcaudal.

Distribution: In Angola, based on material examined here the new species is known to occur in the eastern Provinces of Moxico and Lunda Sul (Figure 2). Additional cytochrome b (cytb) sequences produced for the types (PEM R23486 and PEM R23487) BLAST (<https://blast.ncbi.nlm.nih.gov/uplib.idm.oclc.org>) to 97.5–99.0% similarity to previous published cytb sequences from eastern Angola (HQ207146.1; paratype PEM R19894 from near Saurimo, Lunda Sul Province, Angola; Kelly et al. 2011), Botswana (HQ207113.1; Kelly et al. 2011), and eastern DRC (KM519701.1; Greenbaum et al. 2015), and unpublished sequences from north-eastern Namibia, Zambezi Region (MCZ R188214; Figure 11). This indicates that this newly described species occurs over a much wider distribution range from eastern Angola, northern Botswana to the eastern DRC, potentially encompassing most of Zambia and north-eastern Namibia.



Figure 11. *Boaedon fradei* sp. nov. (MCZ R188214) from 88.6 km SW of Katima Mulilo, Zambezi Region, Namibia. Photo by WR Branch.

Habitat and natural history notes: The region where the species occurs is dominated by low Miombo woodlands on sandy soils, characterised by *Brachystegia spiciformis* var. *latifoliolata*, *Julbernardia* sp. and *Brachystegia glaberrima* (Grandvaux-Barbosa 1970). Manaças (1973) reported the presence of a small rodent in the stomach of one of the specimens from Calombe, Luso.

Etymology: The species epithet is formed in the masculine genitive singular and honours the Portuguese naturalist and first director of the Zoological Section of Junta das Missões Geográficas e de Investigações Coloniais (later renamed Junta de Investigação Científica do Ultramar, and subsequently Instituto de Investigação Científica Tropical) Fernando Frade Viegas da Costa (1898–1983), usually known as Fernando Frade, who collected four of the paratypes of this new species. Frade was the first to collect herpetological material in Moxico Province, and his collection of amphibians and reptiles remains the largest collection available from that province. His contributions to African zoology, especially to those of former Portuguese colonies in Africa, are scattered among dozens of papers and monographs, and his name is commemorated in patronyms of several invertebrate taxa. We propose the Portuguese common name of ‘Serpente Castanha de Frade’, and the English common name of ‘Frade’s Brown House Snake’ for this species.

Discussion

Using an integrative approach, combining phylogenetic and morphological data, and a thorough revision of the taxonomic and nomenclatural history of the genus in Angola, the results of the present work more than double the number of *Boaedon* species recorded in the country. The four taxa mentioned in the most recent revisions of Angolan herpetofauna

(Marques et al. 2018; Branch 2018; Branch et al. 2019c) have now been increased to nine taxa, of which three are new to science. These results follow on from recent works dealing with Angolan herpetology, which are contributing to a better understanding of the diversity of the country's herpetofauna (Conradie et al. 2012a, 2012b, 2013; Stanley et al. 2016; Ceriaco et al. 2018b, 2020a, 2020b; Branch et al. 2019a; Marques et al. 2019a, 2019b).

Our phylogenetic results provide evidence for the presence of seven strongly supported ($\geq 70\%$ bootstrap values and ≥ 0.95 BI posterior probabilities) *Boaedon* clades in Angola. These correspond to *B. angolensis*, *B. bocagei* sp. nov., *B. variegatus*, a clade of *B. mentalis sensu stricto*, *B. olivaceus*, *B. branchi* sp. nov. and *B. fradei* sp. nov. Some of these taxa are morphologically very similar, and have been confused in the past (e.g. Manaças 1973; Kelly et al. 2011; Greenbaum et al. 2015; Marques et al. 2018). The southern (Namibia, South Africa) and a northern (Namibia, southern Angola) clades of *B. mentalis sensu lato* are presently only differentiated genetically, as a more detailed morphological revision of this species-pair is going to be addressed elsewhere (Hallermann et al. in prep.). In addition to the taxa covered by our phylogenetic results, *B. fuliginosus* and *B. virgatus*, for which phylogenetic results were not available, were confirmed by traditional morphological analysis. *Boaedon fuliginosus* is still one of the most taxonomically challenging groups within the genus. The Angolan population, which we restricted to the northern parts of the country, seems to be in accordance with our most updated and informed interpretation of what 'true' *B. fuliginosus* really is (Trape and Mediannikov 2016; Chippaux and Jackson 2019). However, as noted in its respective account, additional research is needed to fully address the taxonomic and nomenclatural doubts surrounding the group. Regarding *B. virgatus*, the presence of this taxon in Angola is confirmed by the identification of three preserved specimens from Cabinda Province housed in ZMB collection. These historical specimens, collected in the late nineteenth century by the 'Africanischen Gesellschaft', have gone unnoticed until now. The re-identification of these specimens allowed us to record an additional species previously unknown to occur in the country, which reinforces the importance of historical collections for current biological research. Besides these taxa, our results also provide new country records for *B. angolensis*, *B. variegatus* and *B. olivaceus*. A potential tenth taxon requires additional attention, namely *Lycodonomorphus subtaeniatus* Laurent, 1954. This taxon was described by Laurent (1954), based on a type series of 13 specimens. The type series consists of one holotype from 'Keseki, près de Kwamouth', Democratic Republic of the Congo (RGMC 14864), eight other paratypes from different localities in the Democratic Republic of the Congo all of which are housed in the collections of the RGMC (14856-57, 11862, 14678, 14578, 2625, 3062, 3077), and four paratypes (two male and two female) from 'Dundo', Lunda Norte Province, north-eastern Angola) housed in the Museu Regional do Dundo (MD 2026, 2028, 2038, and 2041). Following the description of *L. s. subtaeniatus*, Laurent (1954a) described a subspecies of the former, *L. s. upembae*, based on one specimen from 'Nyonga' and 'Kina Mwena' (Democratic Republic of the Congo), housed in the collections of the RGMC. This later taxon has recently been included in a phylogenetic work and it is considered as a full species and has been transferred to the genus *Boaedon* (Greenbaum et al. 2015). It is possible that the nominotypical form also belongs to the genus *Boaedon*, however, no fresh material is currently available for the required phylogenetic comparisons. At this stage of investigation, we follow Greenbaum's interpretation: based on 'different subcaudal scale counts and the distal bifurcation in the hemipenis (present in *L. s. upembae* and absent in *L. s. subtaeniatus*) used by Laurent (1954) to diagnose the subspecies, we hypothesise that these populations are not sister taxa. Additional phylogenetic studies are needed to confirm the taxonomic status and generic placement of *L. s. subtaeniatus*. However, in the interest of taxonomic stability and clarity,

we retain *L. subtaeniatus* in the genus *Lycodonorphus*, and recognise *Boaedon upembae* as a distinct species.’ If *L. subtaeniatus* turns out to belong to the genus *Boaedon*, then it will be differentiated from all other Angola *Boaedon* in having a unique lateral pigmentation consisting of a darker lateral line and an undivided hemipenis.

Given the morphological conservatism of the genus, and the historical lack of objectivity and consensus regarding the diagnostic characters used by different authors dealing with these animals, it is nearly impossible to unambiguously allocate historical records to the presently reviewed taxa without a detailed morphological analysis of the specimens. For this reason, we opted to exclude mapping and the use of historical literature records for which we had not personally analysed the specimen or the reported data for a specimen. Although some of these specimens may be revisited in additional studies and securely allocated to the taxa referred and/or described here (or to additional undescribed species), for some historical records this will be impossible, as a result of the destruction and loss of the specimens (e.g. Bocage specimens that were destroyed in the Museu Bocage fire in 1978). The same applies to records based on observations or even voucher photos.

Apart from Angolan populations, our results also allow the revision and recognition of additional diversity in other parts of the continent and neighbouring islands. The phylogenetic data of the recently described species by Trape and Mediannikov (2016) were reviewed in our study. The validity of *B. perisilvestris* was verified through comparisons with our own material from Kinshasa, but *B. paralineatus* and *B. lineatus* should be re-analysed. More material for morphological and phylogenetic analyses is needed to establish the species status of these recently described species. A more detailed analysis of these newly recognised taxa will be presented as soon as new study material becomes available (Hallermann et al. in prep.). Additional cryptic *Boaedon* species from Ethiopia and Uganda are currently being described elsewhere (Hallermann et al. in prep.). Cryptic diversity was also found within the *B. capensis* group. What is currently recognised as *B. capensis*, is a diverse species complex, as shown in our phylogeny (Figure 1). For the purpose of the present paper, and namely for our morphological comparisons, we treated it as *B. capensis sensu lato*, which requires additional study.

Finally, the generic status of the endemic Seychellois *Boaedon geometricus* as part of *Boaedon* is confirmed by our phylogenetic results. Kelly et al. (2011) had suggested that this species might be referable to *Boaedon* and this was followed by Wallach et al. (2014).

Identification key to the Angolan species of *Boaedon* (compiled mostly by using preserved material)

- 1) Subcaudals
single *B. olivaceus*
- 1a) Subcaudals
divided 2
- 2) Venter pigmented with broad central greyish or yellowish stripe, 23–25 scales around
midbody *B. virgatus*
- 2a) Venter immaculate white, creamy or with scattered yellow scales, 25–30 around
midbody 3

- 3) Parietal length equal to distance between frontal and rostral, dark black ground colour *B. fuliginosus*
- 3a) Parietal length longer than distance between frontal and rostral, lighter brown ground colour 4
- 4) Light head stripes are broad and dark edged, terminating at least one quarter down the body *B. bocagei* sp. nov.
- 4a) Light head stripes are narrow and not dark edged, terminating just behind the head 5
- 5) Second chin shields (posterior maxillary scale) separate from one another in most specimens, light brown *B. mentalis sensu stricto* (northern clade)
- 5a) Second chin shields in contact 6
- 6) Three supralabials touching the eye, dark brown ground colour, white or yellow line loops on body in adults (in life) *B. variegatus*
- 6a) Two supralabials touching the eye, no looping markings 7
- 7) Lower 2–3 dorsal scale rows pigmented 8
- 7a) Lower 2–3 dorsal scale rows unpigmented *B. branchi* sp. nov.
- 8) White head stripes extending onto side of neck that are sometimes interrupted *B. angolensis*
- 8a) Narrow yellow to white head stripes extending just past anterior supralabial *B. fradei* sp. nov.

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