



A new stiletto snake (Lamprophiidae, Atractaspidinae, Atractaspis) from Liberia and Guinea, West Africa

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Abstract

We describe a new stiletto snake, *Atractaspis*, from western Liberia and southeastern Guinea. The new species shares with morphologically similar western African *Atractaspis* species, *A. reticulata* and *A. corpulenta*, the fusion of the 2nd infralabial with the inframaxillary. From *A. corpulenta* the new species differs by a more slender body (276–288 ventrals and 19 or 20 dorsal scale rows versus 178–208 ventrals with 23–29 dorsal scale rows), a divided anal plate and divided subcaudal scales (both non-divided in *A. corpulenta*). The new species differs from most *A. reticulata* by having 19 or 20 dorsal scale rows at midbody (versus 21–23, rarely 19), and a lower ventral count (276–288 versus 304–370). The new species thus has a relatively longer tail: snout-vent-length / tail-length in the female holotype (15.7) and paratype (21.5) versus a mean of 23.6 in seven female *A. reticulata*. The new *Atractaspis* likely is endemic to the western part of the Upper Guinea forest zone and thus adds to the uniqueness of this diverse and threatened biogeographic region.

Introduction

The stiletto snakes or burrowing asps, genus *Atractaspis* Smith, 1849, currently comprise 22 (Wallach et al. 2014), or 21 (Uetz et al. 2018) valid species. Most species are restricted to sub-Saharan Africa where they occur in a wide range of habitats from semi-deserts to rainforests (Spawls and Branch 1995); only two occur in the Middle East and Arabia (Wallach et al. 2014; Grossmann et al. 2018). These fossorial and venomous snakes are famous for their unique skull anatomy and venom delivery system, enabling them to use a single fang to bite, with closed mouth, in a lat-

eral stabbing movement (Broadley 1990; Greene 1997; Cundall and Irish 2008; McDowell 2008). Various herpetologists have already been suffering from this behavior, making it impossible to hold the snakes in the usual way behind the head without being bitten (see Wagner et al. 2009). Their systematic position was matter of a constant debate and the snakes have been placed for instance within Viperidae, within Aparallactinae as subfamily of Colubridae, as a separate family Atractaspididae, and most recently as a subfamily Atractaspidinae within the Lamprophiidae (Broadley 1990; Vidal et al. 2007; Wallach et al. 2014; Uetz et al. 2018; Portillo et al. 2018).

From West and western Central Africa 11 Atractaspis species are known: A. aterrima Günther, 1863, A. boulengeri Mocquard, 1897, A. coalescens Perret, 1960, A. congica Peters, 1877, A. corpulenta (Hallowell, 1854), A. dahomeyensis Bocage, 1887, A. irregularis (Reinhardt, 1843), A. microlepidota Günther, 1866, A. micropholis Günther, 1872, A. reticulata Sjöstedt, 1896, and A. watsoni Boulenger, 1908 (Chippaux 2001; Chirio and LeBreton 2007). On recent surveys in north-western Liberia and south-eastern Guinea, we collected stiletto snakes deviating from all other known Atractaspis species. These snakes are described here as a species new to science. In addition, we redescribe the holotype of A. reticulata, the species which is morphologically most similar to our new species, and summarize its known distribution.

Material and methods

The holotype was euthanized by smearing a benzocaine cream into its mouth. The paratype and one additional specimen were found dead. From the holotype and paratype we collected tissue samples, which were preserved in 97% ethanol. The snakes were preserved in 75% ethanol and are inventoried in the herpetological collections of the Museum für Naturkunde, Berlin, Germany (ZMB; holotype), the Museo di Storia naturale del Salento, Calimera, Italy (MSNS; paratype), or will be inventoried at the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB; additional specimen, see below). Measurements and assessment of morphological characters of the new species and comparative material, including its pholidosis, has been done by one person (CK). Ct-scanning and measurements of skull bones have been compiled by KM. Dorsal scale rows were counted at three points along the trunk, i.e. at one head length posterior to the end of the head, at midbody (at half of the snout-vent length), and at one head length anterior to the anal scale. Dorsal scale row reduction formulae were based on Dowling (1951a). the formulae for the supracaudal scales are analogous to this procedure. We added a 'x' to the formulae if no fusion or reduction takes place. Ventral counts are according to Dowling (1951b). Preventrals are the scales anterior to the ventrals, characterized as being broader than long. The terminal scale was not included in the subcaudal count and is given as '+1'. Values for symmetric characters are given as left/right. Measurements of snout-vent length and tail length were rounded to the nearest millimeter, all other to the nearest 0.1 millimeter. Sex was determined by a small incision at the base of the tail. Comparative measures have been compiled from the literature, material housed at ZMB and the holotype of A. reticulata from the Naturhistoriska Rijkmuseet, Section for Vertebrate Zoology, Stockholm, Sweden (NRM 1796 collected in "Kamerun, Ekundu" by Sjöstedt; Tables 1, 2). Wallach et al. (2014) and Uetz et al. (2018) erroneously cited the Zoological Museum of the University of Uppsåla, Sweden (ZMUU), as the repository of the holotype of A. reticulata.

The heads of the holotype and paratype of the new species, the *A. reticulata* holotype and further comparative material were subjected to micro-tomographic analysis at the Museum für Naturkunde Berlin, using a Phoenix nanotom X-ray|s tube at 80–100 kV and 100–230 μA, generating 1000–1440 projections with 750 ms per scan. The different kV-settings depended on the respective specimen size. Effective voxel size, i.e. resolution in three-dimensional space, ranged from 5.71–15.67 μm. The cone beam reconstruction was performed using the phoenix|x-ray datos|x version 2.2 software (GE Sensing and Inspection Technologies GMBH) and the data were visualized in VG Studio Max, version 3.1.

We sequenced 509 bp of the 16S ribosomal RNA of the types of the new species, following the procedures and using the primers as described in Portillo et al. (2018). We compared the two sequences to each other and to the sequences of the other *Atractaspis* species from which 16S have been published (Portillo et al. 2018): *Atractaspis boulengeri* (IPMB J355; GenBank AY611833), *A. corpulenta* (IPMB J369; GenBank AY611837), *A. irregularis* (UTEP 21655; GenBank MG746901) and *A. micropholis* (IPMB J283; GenBank AY611823). We also received an unpublished 16S sequence from *A. reticulata heterochilus* (UTEP 21664; Democratic Republic of the Congo, Tshopo Province: road between Nia Nia and Kisangani; Portillo et al. submitted) for comparison. The sequences of the new species have been deposited at GenBank.

Results

Species description

Atractaspis branchi sp. n.

http://zoobank.org/990E7C05-947C-4ED7-A8A8-97BFCD77A29F Figures 1–4; Tables 1–3

Holotype. ZMB 88529 (field and tissue number RG97; 16S GenBank MK501382), female, Liberia, Lofa region, Foya Forest, 08°01'16.2"N, 010°25'31.4"W, 317 m a.s.l., near a small rocky creek in primary lowland rainforest, 6 April 2018, coll. M.-O. Rödel, G. Sambolah & J. Glos.

Paratype. MSNS Rept 280 (field number 9294X, skull broken; 16S GenBank MK501383), female, Guinea, Nzérékoré Region, Koyakoélé, 07°44'54"N, 009°11'28"W, 393 m a.s.l., 26 December 2011, coll. L. Chirio.

Additional material. IRSNB not yet accessioned (field number 9314X), Guinea, Nzérékoré Region, Belefanin, 07°55'28"N, 009°01'33"W, 486 m a.s.l., coll. L. Chirio (voucher, only head and anterior part of body; snake still in Africa and thus not available to us).

Diagnosis. External morphology, skull anatomy and molecular data (see below) clearly supports the position within the genus *Atractaspis*. The new species can be only mistaken morphologically with species from

Table 1. Morphology and pholidosis of *A. branchi* sp. n. and the three subspecies of *Atractaspis reticulata*, based on literature data, the *A. branchi* and *A. reticulata* types and vouchers from ZMB collection; SVL = snout-vent length; TL = tail length; na = no data available; measures in mm, for scale counts see material & method section; museum acronyms: AMNH = American Museum of Natural History, New York, USA; KUZ= Department of Zoology, Kyoto University, Kyoto, Japan; MBG = Mission Biologique au Gabon, Makokou, Gabon; MNHN = Museum National d'Histoire Naturelle, Paris, France; MSNS = Museo di Storia naturale del Salento, Calimera, Italy; NRM = Naturhistoriska Rijkmuseet, Stockholm, Sweden; RGMC= Musée Royal de l'Afrique Centrale, Tervuren, Belgium (now MRAC); SMF = Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Germany; USNM = Smithsonian Institution, National Museum of Natural History, Washington, USA; ZMB = Museum für Naturkunde, Berlin, Germany; ZMH = Zoologisches Museum Hamburg, Hamburg, Germany; ZSM = Zoologische Staatssammlung München, Munich, Germany; * = error according to Laurent (1950).

Taxon	Accession number	Status	Sex	SVL	TL	Dorsals	Ventrals	Subcaudals	Source
A. branchi sp. n.	ZMB 88529	Holotype	9	267	17	17-19-17	3+276	25/25+1	this study
	MSNS Rept 280	Paratype	9	689	32	19-20-19	5+288	19/19+1	this study
A. r. reticulata	NRM 1796	Holotype	na ♀	765 712	35 33	?-19-? 17-19-17	308 4+304+1/2	21/21 21/21+1	Sjöstedt 1897 this study
	ZMB 14724		na ♂	1095 1075	40 40	?-21-? 19-21-17	328 1+327	19/19 20/19+1	Werner 1899 this study
	ZMB 21725		9	855	37	17-21-17	6+322	21/21+1	this study
	ZMB 28500		9	483	5+?	19-21-17	5+320	4/4+?	this study
	ZMB 30714		9	600	23	17-21-17	3+338	21/21+1	this study
	ZMB? (not found)		na	na	na	?-21-?	330	20	Sternfeld 1908
	ZMH R11274		8	485	25	?-21-?	327	27/28+1	Werner 1913
A. r. brieni	RGMC 2706	Syntype	8	na	na	19-23-19	345	28	Laurent 1945 / 1956a
	RGMC 2694	Syntype	9	na	na	19-23-19	370	22 (1× simple)	Laurent 1945 / 1956a
	RGMC 21577		8	717	35	23-23-19	347	25 (2× simple)	Laurent 1960
	AMNH 11901		8	786	30	19-23-19	353	23	Schmidt 1923
A. r. heterochilus	KUZ R8330		na	273	13	19-23-19	327	22/22	Ota et al. 1987
	MBG 0644		8	507	23	?-23-?	339	22	Knoepffler 1966
	MNHN 1964.566		9	706	30	19-23-?	337	21/21	Roux-Estève 1965
	MNHN 1963.899		9	783	39	19-23-?	344	23/23	Roux-Estève 1965
	RGMC 608	Holotype Holotype	9	497 na	23 na	19-23-? 19-23-19	341 342	22 21	Boulenger 1901/1919 Laurent 1945
	RGMC 1686		9	na na	na na	?-23-? 19-23-19	359 350	21 21	Boulenger 1919 Laurent 1945
	RGMC 6614		9	na	na	19-23-19	344	na	Laurent 1945
	RGMC 8003		9	na	na	19-23-19	346	na	Laurent 1945
	RGMC 8252		9	na	na	19-23-19	349	24	Laurent 1945
	RGMC 8764		9	na	na	19-23-19	350	23	Laurent 1945
	RGMC 8767		9	na	na	19-23-19	355	24	Laurent 1945
	RGMC 16214		3	na	na	19-23-19	319	26	Laurent 1956a
	? (Cameroon)		9	na	na	?-21-?	336	21	Boulenger 1919
	BMNH (Cameroon)		9	na	na	?-21-?	356*	20	Boulenger 1919
	? (Cameroon)		9	na	na	?-23-?	339	22	Boulenger 1919
	SMF 52361		3	na	na	?-23-?	319	24/24+1	Perret and Mertens 1957
	USNM 565138		3	730	45	19-23-19	4+318	2/2+1+26/26	Pauwels and Sallé 2009
	ZMH R11275		9	730	25	?-23-?	326	4/4+2+11/11+1	Werner 1913
	ZSM 111/1954		8	640 564	31 32	19-23-21 19-23-19	328 6+331	1+25/25+1 1+25/25+1	Hellmich 1957 this study
	Summary data		33				313-327		Laurent 1956a
	Summary data		99				326-353		Laurent 1956a

Laurent's (1950) section 'D', his *reticulata*-group. In particular it differs from all other species of the genus, except *A. reticulata* and *A. corpulenta* (including the West African *A. c. leucura*), by the fusion of the 2nd infralabial with the inframaxillary. From *A. corpulenta* it differs by a much higher ventral count (276–288 vs 178–208), lower number of dorsal scale rows at midbody (19 vs 23–29), divided anal plate and subcaudals, and the absence of a white colored tail tip (present

in *A. c. leucura*); from *A. reticulata* it can be distinguished by a lower ventral count (276–288 vs 304–370), and 19 (the paratype has mostly 19 scale rows, but 20 at midbody) dorsal scales rows at midbody (19 scale rows present in the *A. reticulata* holotype, other vouchers having 21–23 rows) (Table 1). The new species further differs from *A. corpulenta* by a more slender body and from *A. reticulata* by a longer tail compared to body length.

Table 2. Morphological ratios in some *Atractaspis* species. SVL = snout-vent length; TL = tail length; EM / VE = distance lower eye margin to mouth / vertical eye diameter; EN / HE = distance anterior eye margin to nostril / horizontal eye diameter; HW / VE = head width (distance of outer margins of supraoculars) at mid eye level / vertical eye diameter; * head damaged, no measures possible; measures in mm.

Taxon	Accession number	sex	SVL / TL	HW / VE	EM / VE	EN / HE
A. branchi sp. n.	ZMB 88529 (Holotype)	9	267.0 / 17.0 = 15.7	4.5	2.5	1.9
	MSNS Rept 280 (Paratype)	9	689.0 / 32.0 = 21.5	6.2	3.6	2.4
A. r. reticulata (Cameroon, Ekundu)	NRM 1796 (Holotype)	9	712.0 / 33.0 = 21.6	6.4	4.2	2.3
A. r. reticulata (Cameroon, Johann-Albrechtshöhe)	ZMB 28500	9	483.0 / 5+ = ?	6.3	3.6	2.6
A. r. reticulata (Cameroon, Victoria)	ZMB 21725	9	855.0 / 37.0 = 23.1	6.1	3.8	2.9
A. r. reticulata (Cameroon, Ajoshöhe)	ZMB 30714	9	600.0 / 23.0 = 26.1	6.4	3.5	3.0
A. r. reticulata (Cameroon, Yaoundé)	ZMB 14724	3	1075.0 / 40.0 = 26.9	*	*	*
A. r. heterochilus (Angola, Piri Dembos)	ZSM 111/1954	3	564.0 / 32.0 = 17.6	4.9	2.6	2.1
A. bibronii rostrata (Mozambique)	ZMB 2821	2	565.0 / 33.0 = 17.1	5.5	3.0	2.2
A. bibronii rostrata (Tanzania)	ZMB 16799	9	177.0 / 13.0 = 13.6	4.5	1.8	2.0
A. bibronii rostrata (Tanzania, Sanya)	ZSM 60/1993	9	272.0 / 17.0 = 16.0	4.6	2.0	1.9
A. bibronii rostrata (Tanzania, Sanya)	ZSM 60/1993	9	432.0 / 25.0 = 17.3	5.0	2.4	2.4
A. c. congica (Angola, Belavista)	ZSM 113/1954	3	395.0 / 32.0 = 12.3	5.7	2.7	2.2
A. c. congica (Angola, Piri Dembos)	ZSM 112/1954/2	3	508.0 / 36.0 = 14.1	5.4	2.7	2.4
A. i. irregularis (Liberia, Nimba County)	ZMB 88015	2	241.0 / 18.0 = 13.4	4.6	1.7	1.8
A. i. irregularis (Liberia, Nimba County)	ZMB 87809	2	550.0 / 41.0 = 13.4	5.1	2.4	1.8

Holotype description. Subadult female; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 267 mm; tail length 17 mm (ratio snout-vent length / tail length = 15.7); head length 7.7 mm (tip of snout to angle of jaws) / 7.1 mm (tip of snout to end of parietal suture); head width 5.7 mm (at widest point) / 3.6 mm (distance between the outer margins of supraocular at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 2.9 mm; small eyes directed dorsolaterally; eye diameter 1.0 mm (horizontal) / 0.8 mm (vertical), pupil roundish; distance from lower border of eye to mouth 2.0 mm; distance between anterior edge of eye to posterior edge of nostril 1.9 mm; 5 supralabials, the 4th being the largest, the 3rd and 4th in contact with eye; 5 infralabials, the 1st and 3rd touching the inframaxillary, the 2nd fused with the inframaxillary, the 3rd being the largest; the 1st pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1st to 3rd supralabial and preocular, nostril nearly completely situated in the anterior part of nasal: loreal absent: 1 small preocular, not in contact with frontal, touching 3rd supralabial; 1 postocular distinctly larger than preocular, touching temporal and 4th supralabial; 1 small supraocular (length 1.6 mm); 1 very large anterior temporal (length 2.7 mm) followed by 2 posterior temporals; beside the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of distinctive inframaxillaries touched by 3 gular scales; mental groove present; top of head covered by 9 scales; suture of internasals 0.7 mm long; suture of prefrontals 0.8 mm long; frontal slightly longer than wide (3.1 mm vs 2.8 mm); suture of parietals 1.8 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally, apical pits absent, but all dorsal

scales with a single little pore near the center of the scale; 3 preventrals, 276 rounded ventral scales; anal plate divided; subcaudals divided, 25/25+1; ratio ventrals / subcaudals: 11.0; dorsal scale rows straight.

Dorsal scale row reduction:

$$19 \frac{4+5(8)}{4+5(8)} 17 \frac{6 \rightarrow 6+7(66)}{6 \rightarrow 6+7(64)} 19 \frac{5+6(240)}{6+7(239)} 17(276)$$

Supracaudal scale row reduction:

$$14 \frac{2+3(2)}{3+4(4)} 12 \frac{-4(5)}{5+6(5)} \frac{4+5(17)}{4+5(16)} \frac{3+4(22)}{3+4(22)} \frac{-3(25)}{-3(24)} 4(25)$$

Color in life: dorsal scales of uniform, shiny, purple-brown with light grey margins, venter marginally lighter, broad tongue fleshy (Fig. 1). Color in preservation: dorsally uniform dark grey with a purplish hue; all scales with lighter margins, venter lighter; mental, first pair of infralabials and lower margin of the rostral pale.

Paratype description. Adult female, skull broken; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 689 mm; tail length 32 mm (ratio snout-vent length / tail length = 21.5); head length 7.7 mm (tip of snout to angle of jaws) / 11.7 mm (tip of snout to end of parietal suture); head width 10.3 mm (at widest point) / 6.2 mm (distance between the outer margins of supraocular at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 4.7 mm; small eyes directed dorsolaterally; eye diameter 1.5 mm (horizontal) / 1.0 mm (vertical), pupil roundish; distance from lower border of eye to mouth 3.6 mm; dis-



Figure 1. Life coloration of the Atractaspis branchi sp. n. holotype (ZMB 88529).

tance between anterior edge of eye to posterior edge of nostril 3.6 mm; 5 supralabials, the 4th being the largest, the 3rd and 4th in contact with eye; 5 infralabials, the 1st and 3rd touching the inframaxillary, the 2nd fused with the inframaxillary, the 3rd being the largest; the 1st pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1st to 3rd supralabial and preocular on the right side (left side preocular is fused with the prefrontal), nostril nearly completely situated in the anterior part of nasal; loreal absent; 1 small preocular on the right side (left side missing), not in contact with frontal, touching 3rd supralabial; 1 postocular little larger than preocular, touching temporal and 4th supralabial; 1 small supraocular (length

2.6 mm); 1 very large anterior temporal (length 5.2 mm) followed by 2 posterior temporals; beside the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of distinctive inframaxillaries touched by 3 gular scales; mental groove present; top of head covered by 9 scales; suture of internasals 1.4 mm long; suture of prefrontals 1.6 mm long; frontal slightly longer than wide (4.9 mm vs 4.8 mm); suture of parietals 2.8 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally, apical pits absent, but all dorsal scales with a single little pore near the center of the scale; 5 preventrals, 288 rounded ventral scales; anal plate divided; subcaudals divided, 19/19+1; ratio ventrals/subcaudals: 15.6; dorsal scale rows oblique.

Dorsal scale row reduction:

$$19 \frac{4+5(14)}{4+5(10)} \frac{5-5+6(64)}{17} \frac{x}{20} \frac{x}{19} \frac{x}{19} \frac{x}{19} \frac{x}{20} \frac{x}{19} \frac{5+6(274)}{19} \frac{17}{19} \frac{17$$

Supracaudal scale row reduction:

Color: Dorsal and ventral scales of freshly dead individual a dark grey with lighter grey to almost white margins; dorsal scales with slight rainbow shimmer (Fig. 2).

Additional material. The only available data, collected in the field, of this specimen (Fig. 2; only head and anterior body left), were sublinguals fused on each side with the 2^{nd} infralabials; 4/4 infralabials (including the ones fused with the sublinguals); 2 preventrals + > 56 ventrals).

Skull anatomy. The skull anatomy of most *Atractaspis* species is unknown, as is the phylogenetic relationships of our new species. We here compare ct-scans and measurements of the holotype and paratype of *Atractaspis*

branchi sp. n. to the morphologically most similar Atractaspis species, A. reticulata (NRM 1796, holotype of A. r. reticulata; and ZMB 28500), and two other Atractaspis species, A. boulengeri matschiensis (ZMB 11040) and A. aterrima (ZMB 8016). In general, skull shape was very similar (Figs 3-5; Table 3). However, the short and stout skull of the new species can be distinguished from the representatives of the three other species by shorter frontals compared to skull length with only a shallow inclusion of the nasals (ratio length of frontals to skull length: 0.25-0.26 vs 0.28-0.31) and a higher number of palatine teeth (3 vs 0 or 2). Furthermore A. branchi sp. n. differs from A. boulengeri matschiensis and A. aterrima by the extension of the nasals anteriorly, being longer than level of premaxilla (vs nasals shorter than level of premaxilla), and from A. boulengeri matschiensis by a transverse anterior border of the premaxilla in dorsal view (vs a convex anterior border). However, we examined only one or two (A. branchi and A. reticulata) individuals of each taxon, and intraspecific variability so far has not been investigated in any Atractaspis species, but it might be expected. For instance, the measurements and scans of the two types of A. branchi sp. n. indicate that smaller specimens may have shorter fangs and larger eyes (Table 2).



Figure 2. Atractaspis branchi sp. n. paratype (MSNS Rept 280) and head and anterior part of body of a further, not yet accessioned specimen (field number 9314X) from south-eastern Guinea.

Table 3. Skull anatomy of some *Atractaspis* species; given are measures and ratios of bones, collected from ct-scans; *Atractaspis branchi* sp. n. has a comparatively short frontale; measures in mm (compare Material and methods and Figs 3–5).

Species / character	branchi sp. n. (Holotype)	<i>branchi</i> sp. n. (Paratype)	reticulata (Holotype)	reticulata	aterrima	boulengeri matschiensis ZMB 11040	
Accession number	ZMB 88529	MSNS Rept 280	NRM 1796	ZMB 28500	ZMB 8016		
Head length	8.46	14.74	13.17	9.98	12.89	14.22	
Nasale length	1.88	3.43	3.22	2.43	3.3	2.91	
Nasale width	1.83	2.96	2.64	2.41	2.15	2.82	
Frontale length	2.15	3.88	4.01	3.09	3.67	4.14	
Vomer length	1.41	2.43	2.3	1.82	2.1	2.53	
Vomer width	0.99	1.52	1.35	1.15	1.28	1.71	
Lower jaw length	8.24	15.85	15.29	11.09	14.62	17.44	
Length of fang	2.98	7.14	7.42	4.02	6.02	5.51	
Quadratum length	2.45	5.66	4.49	3.79	5.67	6.6	
Angulare length	1.46	2.84	2.77	2.13	3.27	3.16	
Spleniale length	1.31	3.08	2.28	2.08	2.45	2.71	
Nasale / head length	0.22	0.23	0.24	0.24	0.26	0.20	
Frontale / head length	0.25	0.26	0.30	0.31	0.28	0.29	
Nasale width / length	0.97	0.86	0.82	0.99	0.65	0.97	
Vomer width / length	0.70	0.63	0.59	0.63	0.61	0.68	
Lower jaw / head length	0.97	1.08	1.16	1.11	1.13	1.23	
Fang / head length	0.35	0.48	0.56	0.40	0.47	0.39	
Quadratum / head length	0.29	0.38	0.34	0.38	0.44	0.46	
Angulare / Spleniale	0.90	1.08	0.82	0.98	0.75	0.86	

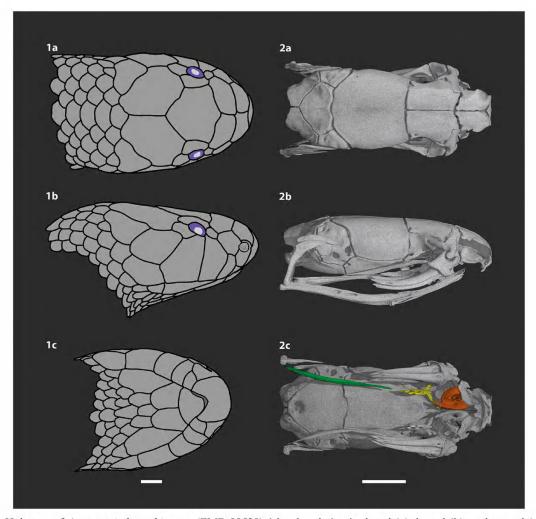


Figure 3. Holotype of *Atractaspis branchi* sp. n. (ZMB 88529) **1** head scalation in dorsal (**a**), lateral (**b**), and ventral (**c**) views **2** ct-scan of skull in dorsal (**a**), lateral (**b**), and ventral (**c**) views; lower jaw virtually removed; green: pterygoid, yellow: palatine, orange: vomer. Scale bar: 1 mm.

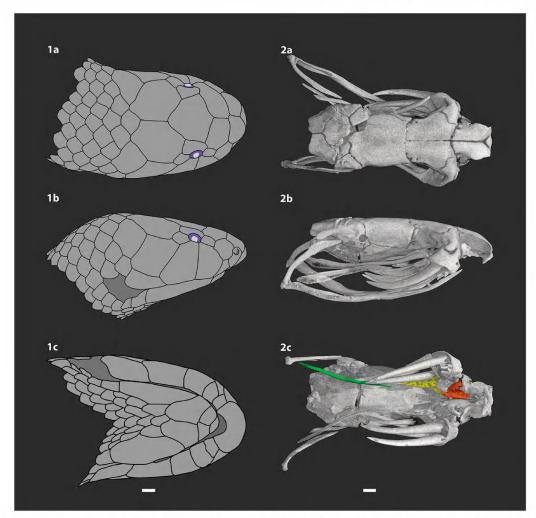


Figure 4. Paratype of *Atractaspis branchi* sp. n. (MSNS Rept 280) **1** head scalation in dorsal (**a**), lateral (**b**), and ventral (**c**) views; **2** ct-scan of skull in dorsal (**a**), lateral (**b**), and ventral (**c**) views; lower jaw virtually removed; green: pterygoid, yellow: palatine, orange: vomer. Scale bar: 1 mm.

Broadley (1990: fig. 121) figured an *A. bibroni*i Smith, 1849 that possesses one fang (no replacement teeth) on each maxilla, but small teeth on palatine (4) and dental (3) bones. Cundall and Irish (2008: fig. 2.87D) figured functional and replacement fangs and two palatine teeth.

Molecular data. The 16S sequences of the two type specimens of *Atractaspis branchi* sp. n. were almost identical (1% difference, 509 bp used for comparisons). Uncorrected pairwise comparisons to the respective part of 16S sequences of other *Atractaspis* revealed the following differences (first number refers to comparison with *A. branchi* holotype, the second to the paratype): *Atractaspis boulengeri* (4–3%, 499 bp, 485 bp), *A. corpulenta* (7–6%, 501 bp, 487 bp), *A. irregularis* (8–7%, 509 bp, 505 bp), *A. micropholis* (5%, 502 bp, 488 bp), and *A. reticulata heterochilus* (7–6%, 521 bp, 505 bp).

Natural history. We found the holotype at night. It was slowly moving along the steep slope of the bank of a

small rocky creek in primary lowland evergreen rainforest (Fig. 6). When handled, the snake first tried to hide its head below body loops; the head was bend down at an almost right angle and with fangs partly visible outside of the mouth. In this head position, the snake repeatedly tried to strike. Either it tried to move slowly away from the human observers or it abruptly coiled and uncoiled, often jumping distances equaling almost its entire body length, similar to wolf snakes of the genus *Lycophidion* (Rödel et al. 1995; Greene 1997). The two snakes from south-eastern Guinea were collected in plantations of banana, manioc and coffee, which were planted under the few remaining high trees of the former forest. No other data on biology and ecology of the new species are known.

Distribution. So far the new species is known from the type locality and two additional sites in south-eastern Guinea. These latter two sites are about 27 km apart (Fig. 7).

Etymology. We name this new snake to honor our recently deceased friend and colleague, William Roy "Bill"

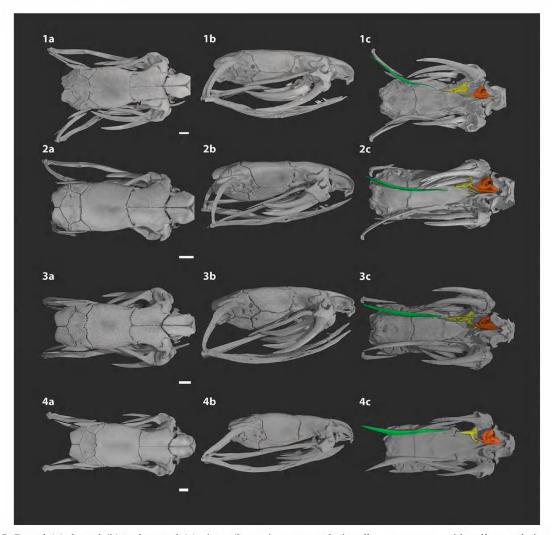


Figure 5. Dorsal (a), lateral (b) and ventral (c) views (lower jaw removed virtually, green: pterygoid, yellow: palatine, orange: vomer) of the skulls of 1 Atractaspis reticulata (NRM 1796, holotype); 2 Atractaspis reticulata (ZMB 28500); 3 Atractaspis aterrima (ZMB 8016); and 4 Atractaspis boulengeri matschiensis (ZMB 11040). Scale bar: 1 mm.

Branch, for his outstanding contributions to African herpetology. MOR and OSGP are particularly pleased to name the species in memory of Bill. We remember our outstanding field trips with him, unforgettable discussions with a large portion of special humor, and his friendship. The dedication of this species of stiletto snake to Bill is particularly appropriate. After Bill turned from cancer research to herpetology (see "William R. Branch" in Li Vigni 2013), the subject of his first herpetological research, on the serotaxonomy and hemipeneal morphology of stiletto snakes, was presented in two contributions at a symposium of herpetology and ichthyology in Kruger National Park in 1975 (Branch 1975a, b). As the vernacular name, we suggest Branch's Stiletto Snake.

Redescription of the holotype of *Atractaspis reticulata reticulata* Sjöstedt, 1896 (NRM 1796) (Fig. 8)

Adult female; slender snake with moderately robust body and short and rounded head; no constriction between head and body; snout-vent length 712 mm; tail length 33 mm (ratio SVL / TailL = 21.6); head length 16.4 mm (tip of snout to angle of jaws) / 11.7 mm (tip of snout to end of parietal suture); head width 13.8 mm (at widest point) / 5.8 mm (distance between outer margins of supraoculars at the level of mid eye); nostrils directed laterally; dorsally measured distance between nostrils 4.5 mm; small eyes directed dorsolaterally; eye diameter 1.3 mm (horizontal) / 0.9 mm (vertical), pupil roundish; distance from lower border of eye to mouth 3.8 mm; distance between anterior edge of eye to posterior edge of nostril 3.0 mm; 5 supralabials, the 4th being the largest, the 3rd and 4th in contact with eye; 5 infralabials, the 1st and 3rd touching the inframaxillary, the 2nd fused with the inframaxillary, the 3rd being the largest; the 1st pair of infralabials in contact behind mental; rostral visible from above, rounded in lateral and dorsal views; nasal divided, touching 1st to 3rd supralabial and preocular, nostril nearly completely situated in the anterior part of nasal; loreal absent; 1 small preocular, not in contact with frontal, touching 3rd supralabial; 1 postoc-

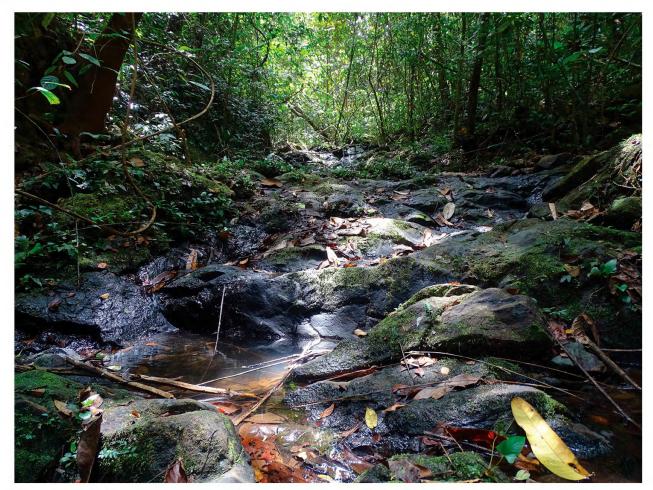


Figure 6. Type locality of *Atractaspis branchi* sp. n. in north-western Liberia. The holotype specimen was found at night. It was moving along the steep slope on the left bank of the small creek.

ular only slightly larger than preocular, touching temporal and 4th supralabial; 1 small supraocular (length 2.4 mm); 1 very large anterior temporal (length 5.0 mm) followed by 2 posterior temporals; other than the temporals only 3 further scales touching the posterior borders of parietals; 1 pair of inframaxillaries, mental groove present; top of head covered by 9 scales; suture of internasals 1.4 mm long; suture of prefrontals 1.3 mm long; frontal slightly longer than wide (5.1 mm vs 4.5 mm); suture of parietals 2.9 mm long; dorsal scales smooth, rhombic shaped, decreasing gradually in size dorsally; apical pits absent, but all dorsal scales with a single little pore near the center of the scale; 4 preventrals, 304+1/2 rounded ventral scales; anal divided; subcaudals divided, 21/21+1; ratio ventrals/ subcaudals: 14.5; dorsal scale rows oblique.

Dorsal scale row reduction:

$$19 \frac{3+4(2)}{4+5(4. \text{ PreV})} 17 \frac{5 \rightarrow 5+6(70)}{5 \rightarrow 5+6(68)} 19 \frac{-5(268)}{5+6(263)} 17 \frac{5 \rightarrow 5+6(268)}{x} 18 \frac{4+5(272)}{x} 17(304)$$

Supracaudal scale row reduction:

$$15 \frac{1+2(1)}{3+4/6+7(1)} 12 \frac{2+3(2)}{3+4(2)} 10 \frac{4+5(6)}{4+5(5)} 8 \frac{3+4(13)}{3+4(13)} \frac{2+3(19)}{2+3(18)} 4(21)$$

Color in preservation: Dorsally uniform dark greyish blue, all scales with thin lighter margins; venter and head appear slightly lighter with a olive hue; most of the mental, and lower margin of the rostral pale.

Distribution of Atractaspis reticulata subspecies

Three subspecies of *A. reticulata* are currently recognized (Wallach et al. 2014): the nominate form *A. reticulata reticulata* Sjöstedt, 1896, *A. reticulata heterochilus* Boulenger, 1901, and *A. reticulata brieni* Laurent, 1956.

The definitions of these subspecies are still unclear. The holotype of *A. r. reticulata* is the only known specimen with 19 midbody dorsal scale rows. Boulenger (1901) described *A. heterochilus* based on 23 midbody dorsal scale rows and more ventrals (341 vs "308" [304 according to method of Dowling 1951b]). Laurent (1950) assigned *A. heterochilus* as a subspecies to *A. reticulata*. Laurent (1956a) described *A. r. brieni* based on higher ventral counts in both sexes. The taxonomic classification of specimens with 21 dorsal scale rows at midbody remains difficult. All of them were found in southern Cameroon (ZMB material; Werner 1913; Boulenger 1919). The four examined ZMB specimens (ZMB 14724,

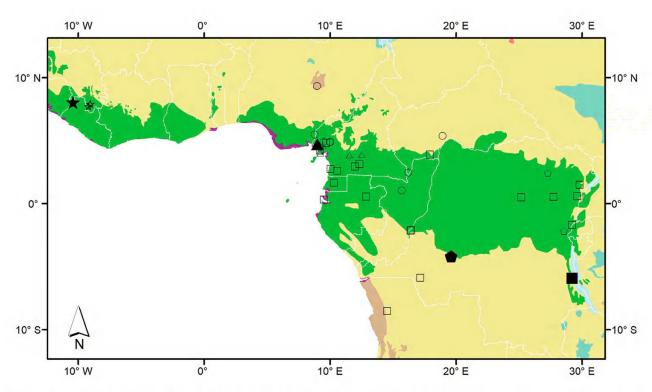


Figure 7. Localities of *Atractaspis branchi* sp. n. and *A. reticulata* ssp. Records are based on museum specimens, literature and database (GBIF) records; large closed symbols represent the type localities of the different taxa, stars: *A. branchi* sp. n., circles: *A. reticulata* records without reference to subspecies; triangles: *A. r. reticulata*; quadrats: *A. r. heterochilus*; diamonds: *A. r. brieni*; country borders indicted as white lines; background of map: major biomes based on Olson et al. (2001).

21725, 28500, 30714) were determined as *A. r. reticulata*. Based on the published data (23 midbody scale rows), the record of the nominate subspecies *A. r. reticulata* from the Republic of Congo by Ota et al. (1987) is recognized here as *A. r. heterochilus*. The *A. r. heterochilus* record in Schmidt (1923) from Medje, Haut-Uele Province, Democratic Republic of Congo, is identifiable as *A. r. brieni* (female with 353 ventrals).

We here summarize data from the literature. GBIF database, and some museum records of A. reticulata (Fig. 7). Atractaspis reticulata is a terrestrial forest snake (Hughes 1983; Lasso et al. 2002; Herrmann et al. 2005). Data for altitudinal range are given for Cameroon: 0-1800 m a.s.l. (Herrmann et al. 2005; Chirio and LeBreton 2007; Gonwouo et al. 2007), and Gabon: 0-500 m a.s.l. (Pauwels and Vande weghe 2008). According to Frétey and Blanc (2004), this species occurs in Cameroon, the Central African Republic, Equatorial Guinea, Gabon, Republic of Congo, and the Democratic Republic of the Congo. Hughes (1983, 1988) listed this species also for Ghana and Nigeria, however without locality or collection data. Barry Hughes wrote in an email to OSGP, "The mention of Atractaspis reticulata from Ghana is based on the examination of a single individual in poor condition, whose head scalation corresponds with the description of that species" (B. Hughes pers. comm. September 2018). Unfortunately, we could not examine that specimen, and the record for Ghana must be regarded as doubtful (see Discussion). In addition to recent records of four specimens from south-eastern Nigeria (Eniang and Ijeomah 2011), there is one voucher from the Bauchi plateau in Central Nigeria in the British Museum of Natural History (BMNH 1934.7.7.45, don. Hamilton Liddiard). Furthermore, this species was recorded from Angola (Hellmich 1957). Pitman (1938) included Atractaspis reticulata and A. heterochilus in a key to Ugandan snakes because of records from the neighboring northeast Democratic Republic of Congo. However, until now, no voucher of these snakes has become known from east of the African rift valley. Here we summarize the records which have been published, using the subspecies affiliation as mentioned in the respective literature (Fig. 7). In various cases the subspecies mentioned in the respective papers cannot be verified with the presented data or figures!

Atractaspis reticulata ssp. records without reference to subspecies and without published scalation data are from **Ghana**: without precise locality (Hughes 1983, 1988); **Nigeria**: without precise locality (Hughes 1983; Butler and Reid 1990); Cross River Province: Oban Division of Cross River National Park (Eniang and Ijeomah 2011); Plateau Province: "Bauchi" (GBIF: BMNH 1934.7.7.45); **Cameroon**: Sud-West Province: Kumba-Nguti road,

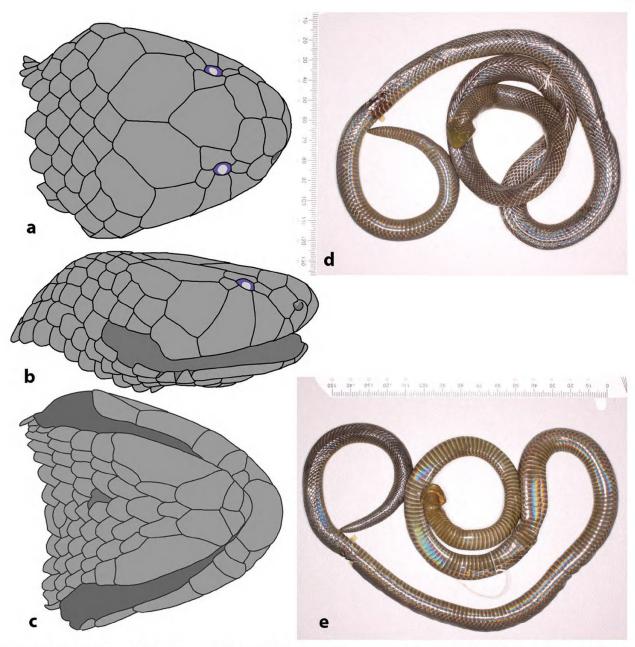


Figure 8. Dorsal (a), lateral (b) and ventral (c) views of the head *Atractaspis reticulata* (NRM 1796, holotype); dorsal (d) and ventral (e) views of the entire snake.

58.3 km south of Nguti (Lawson 1993: UTA R 31311); Littoral Province: Nguéngué (1140 m a.s.l.) and Mount Nlonako (Herrmann et al. 2005: ZFMK 75261, HWH [private collection Herrmann] 639, 714, 765); Central African Republic: Sangha-Mbaéré Province, Parc National de Dzangha-Ndoki (GBIF: MNHN 2011.281); Republic of Congo: Sangha Province: Liouesso (Trape and Roux-Estève 1995); Democratic Republic of Congo: Kwilu Province: Kafumba (GBIF: SDNHM 63850).

Atractaspis reticulata reticulata records are restricted to southern and south-western **Cameroon** (between sea level and ca 700 m a.s.l.): Sud-West Province: "Ekundu" [= Ekundu Titi] (Sjöstedt 1896: NRM 1796, type locality; locality according to map in Mertens 1938); Buea

(Werner 1913: ZMH R11274); Victoria (Sternfeld 1908: ZMB? no identifiable voucher present, ZMB 21725); Johann-Albrechtshöhe (ZMB 28500); Central Province: "Ajoshöhe am Nyong" [= Ayos] (ZMB 30714); Yaoundé (Sternfeld 1908: ZMB 14724).

Atractaspis reticulata heterochilus was likewise reported from Cameroon: Sud-West Province: Nyasoso (photographic record in Dobiey and Vogel 2007); Mount Cameroon area (Gonwouo et al. 2007); Sud Province: "Ngam" [= Ngan] (Perret and Mertens 1957: SMF 52361); Bitye (Laurent 1950, but 21 midbody scale rows); Campo Reserve (Ota et al. 1987: KUZ R8330); Central African Republic: Lobaye Province: Boukoko, (Roux-Estève 1965: MNHN 1963.899, MNHN 1964.566); Equatorial Guinea: Cen-

tro-Sur Province: Monte Alén, (Lasso et al. 2002); Gabon: Ogooué-Maritime Province: Yenzi, Gamba, Ndougou Department (Pauwels and Sallé 2009: USNM 565138); Ogooué-Ivindo Province: Makokou (Knoepffler 1966: MBG 0644); Estuaire Province: "Gabun" [= probably Gabon estuary] (Werner 1913: ZMH R11275); Democratic **Republic of the Congo**: Tshopo Province: "Stanleyville" [= Kisangani] (Laurent 1945: RGMC 6614, 8003, 8252); Tanganyika Province: "Albertville" [= Kalemie] (Boulenger 1901: RGMC 608, type locality); Ituri Province: "Makele" [= Makala, according to Christy 1915], (Boulenger 1919; Laurent 1945: RGMC 1686); Irumu (de Witte 1953); North Kivu Province: "N'Goma" [= Goma], (Schouteden 1933; de Witte 1941: RGMC 4068); "Kartoushi" [= near Oicha, according to map in Gyldenstolpe 1924] (de Witte 1941); Mai-Ndombe Province: "Ndwa" [= Bolobo, according to Chapin 1954] (Laurent 1956a: RGMC 16214); "Kunungu" [= Bolobo, according to Chapin 1954] (Laurent 1945: RGMC 8764, 8767); Kwango Province: "Imbela" [= Kimbele] (GBIF: RBINS 12278); Angola: Cuanza Norte Province: Piri Dembos (Hellmich 1957: ZSM 111/1954). The Angolan record of Hellmich (1957) was doubted by Branch (2018). However, the specimen was re-examined by us and could be confirmed as being A. reticulata heterochilus.

Atractaspis reticulata brieni was reported from **Democratic Republic of the Congo**: Kwilu Province: Ipamu, (Laurent 1945, 1956a: RGMC 2694, 2706, type locality); South Kivu Province: Mushofi (1300 m asl), near Bunyakiri, (Laurent 1960: RGMC 21577); Haut-Uele Province: Medje (Schmidt 1923: AMNH 11901).

It is apparent from this list and Figure 7 that the distributions of the *A. reticulata* "subspecies", and in particular the nominate form and *A. r. heterochilus*, are not in accordance with any logical pattern of biogeographic regions or barriers. We would not be surprised if *A. reticulata* proves to be actually a complex of various cryptic species, but proofing this hypothesis is beyond the goal of the present study.

Discussion

The phylogenetic relationships within the genus *Atractaspis* are still unclear. Two recent contributions included only some species of *Atractapis* (Underwood and Kochva 1993; Moyer and Jackson 2011). The study by Underwood and Kochva (1993) deviates in its phylogenetic conclusions partly from Laurent's (1950) species grouping. However, for morphological comparisons between species Laurent's (1950) paper is still the most useful. Our new species morphologically falls within Laurent's (1950) section "D" (*reticulata* group) of the genus. Together with *A. reticulata* and *A. corpulenta* it shares the fusion of the 2nd infralabial with the inframaxillary. This character likewise distinguishes these two species and *A. branchi* sp. n. from all other congeners.

Atractaspis corpulenta is a comparatively very robust, heavily built snake (only 178–208 ventrals with 23–29

dorsal scale rows at midbody vs 276-288 ventrals and 19 or 20 dorsal scale rows in A. branchi) and has a non-divided anal plate and subcaudal scales (both divided in A. branchi). Its West African rainforest subspecies, A. corpulenta leucura, has a white tail tip (see fig. 3 in Rödel and Mahsberg 2000), which is lacking in A. branchi. Atractaspis branchi thus can be only confused with A. reticulata, from which it differs by a lower ventral count while having simultaneously a higher number of subcaudals and, thus, a relatively longer tail: snout-vent length / tail length in A. branchi: 15.7 and 21.5; in A. reticulata: mean = 22.3, minimum = 16.2, maximum = 29.2 (N =15). The two A. reticulata with the comparatively longest tails (16.2 and 17.6) originate from Gabon and Angola, respectively, and are both males. The seven A. reticulata females, for which we could calculate a snout-vent length / tail length ratio, had a mean of 23.6 (Tables 1, 2).

The new species has 19 dorsal scales rows at midbody (the paratype has mostly 19 rows but rarely 20 around midbody) and thus differs from almost all A. reticulata vouchers investigated by us and reported in the literature by having 21–23 rows (Table 1). However, the holotype of A. reticulata reticulata has only 19 scale rows and mid-body scale rows. thus numbers of scales at mid-body is not diagnostic for these two taxa. Apart from ventral and subcaudal scale counts, differences in skull anatomy between the new species and A. reticulata are a shorter frontale and a greater number of palatine teeth in the new species. An additional diagnostic character might be larger eyes in A. branchi compared to A. reticulata (Table 2). However, the holotype is a young female and relative eye size seems to diminish with body size, as indicated by the two types and our measurements of other differently sized Atractaspis, including variously sized A. reticulata (Table 2). The types of the new species indicate other potential ontogenetic changes in characters, i.e. body colour changing from brown to grey, fang length increasing with body length, and rows of the dorsal body scales changing from perfectly straight in the smaller holotype to oblique in the larger, and presumably older, paratype.

However, confusion of *A. branchi* with *A. reticulata* taxa seems unlikely, as they most probably do not overlap geographically. From West Africa sensu stricto (Senegal to the Nigerian Cross River; see Penner et al. 2011 for discussion), *A. reticulata* has been reported from Nigeria (Eniang and Ijeomah 2011: Oban Division, Cross River National Park, Cross River Province; Butler and Reid 1990 and Hughes 1983: without further details) and Ghana (Hughes 1983). The Ghanaian record is of particular interest, as it might be conspecific, based on biogeographic arguments, with the new species. Unfortunately, this snake could not be investigated.

The Cross River area is zoogeographically part of the Lower Guinea forest zone. It is not yet clear where the zoogeographic barrier between the West and Central African fauna exactly runs: at the Cross River, the Niger Delta, or the Dahomey Gap. Nor has it been clarified what exact processes are responsible for the separation of fauna

and flora, and what is the time scale during which taxa in both areas evolved (see Penner et al. 2011; Jongsma et al. 2018 and studies cited therein). The geographic scale, processes and time most likely varies between taxa (see Bell et al. 2017 for Central African examples). However, it is becoming more evident that there is only very little to almost no overlap in occurrences between forest species of the Upper and Lower Guinea realms. Indeed, many studies, mostly recent, either have discovered related but distinct species in both forest blocs or have shown that "widespread" taxa actually comprise cryptic species complexes, including species that either occur in West or Central African rainforests. Examples of recent discoveries of species pairs within amphibians are Sclerophrys taiensis and S. tuberosus (Bufonidae; Rödel and Ernst 2000); Acanthixalus sonjae and A. spinosus (Hyperoliidae; Rödel et al. 2003); Cardioglossa occidentalis and C. leucomystax (Arthroleptidae; Blackburn et al. 2008); and Amnirana "albolabris-West" and Amnirana albolabris (Ranidae; Jongsma et al. 2018). Among reptiles different species in West and Central Africa have been discovered in the crocodile genera Mecistops and Osteolaemus (Crocodylidae; Shirley et al. 2014); the turtles Pelusios cupulatta and P. gabonensis (Pelomedusidae; Rhodin et al. 2017); the cobras Naja guineensis and N. melanoleuca (Elapidae; Wüster et al. 2018); and the vipers Atheris hirsuta and A. squamigera (Viperidae; Ernst and Rödel 2002). Among birds there are for instance Picathartes gymnocephalus and P. oreas (Picathartidae; Treplin 2006); and among mammals there are different West and Central African species within the antelope genera (*Neotragus* spp., Tragelaphus spp.; Philantomba spp.; Hernández Fernández and Vrba 2005; Moodley and Bruford 2007; Colyn et al. 2010), within small carnivores (Genetta johnstoni and G. piscivora; Gaubert et al. 2004), otter shrews (Micropotamogale spp.), or within various bats such as the genus Rhinolophus (Fahr et al. 2002). Many more examples have been published (Huntley et al. 2019) and several more examples, still unpublished, are known to us.

Apart from a species-level uniqueness of Upper Guinean forest assemblages, it is also evident, that this region is an important area for old endemic lineages. Prominent herpetological examples comprise the frog family Odontobatrachidae (Barej et al. 2014), and the frog genera *Pseudhymenochirus* (Pipidae; Evans et al. 2004) and *Morerella* (Hyperoliidae; Rödel et al. 2009). Therefore, the discovery of a new and presumably endemic species of fossorial snake from the western Upper Guinea forests is not very surprising. However, further surveys are needed to determine the geographic range of the new snake species and to gather more information about its ecological needs and biological properties.

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References

Barej MF, Schmitz A, Günther R, Loader SP, Mahlow K, Rödel M-O (2014) The first endemic West African vertebrate family – a new anuran family highlighting the uniqueness of the Upper Guinean biodiversity hotspot. Frontiers in Zoology 11: 8. https://doi.org/10.1186/1742-9994-11-8

Bell RC, Parra JL, Badjedjea G, Barej MF, Blackburn DC, Burger M, Channing A, Dehling JM, Greenbaum E, Gvoždík V, Kielgast J, Kusamba C, Lötters S, McLaughlin PJ, Nagy ZT, Rödel M-O, Portik DM, Stuart BL, VanDerWal J, Zassi-Boulou AG, Zamudio KR (2017) Idiosyncratic responses to climate-driven forest fragmentation and marine incursions in reed frogs from Central Africa and the Gulf of Guinea Islands. Molecular Ecology 26: 5223–5244. https://doi.org/10.1111/mec.14260

Blackburn DC, Kosuch J, Schmitz A, Burger M, Wagner P, Gonwouo LN, Hillers A, Rödel M-O (2008) A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. Copeia 2008: 603–612. https://doi.org/10.1643/CH-06-233

Boulenger GA (1901) Matériaux pour la faune du Congo. Reptiles nouveaux. Annales du Musée du Congo (Zoologie, Série 1) 2: 7–14. [pls 3–5]

Boulenger GA (1919) Batraciens et reptiles recueillis par le Dr. C. Christy au Congo Belge dans les districts de Stanleyville, Haut-

- Uelé et Ituri en 1912–1914. Revue zoologique Africaine 7: 1–29. https://doi.org/10.5962/bhl.part.15108
- Branch WR (1975a) Serotaxonomic studies on southern African snakes, with particular reference to the status of the genus *Atractaspis*. Abstract of a contribution presented at the 'Symposium of Herpetology and Ichthyology', Kruger National Park, 1–5 Sept 1975. Journal of the Herpetological Association of Africa 14: 7–8. https://doi.org/10.1080/04416651.1975.9650872
- Branch WR (1975b) Hemipeneal morphology of southern African snakes: a taxonomic review. Abstract of a contribution presented at the 'Symposium of Herpetology and Ichthyology', Kruger National Park, 1–5 Sept 1975. Journal of the Herpetological Association of Africa 14: 10. https://doi.org/10.1080/04416651.1975.9650877
- Branch WR (2018) Snakes of Angola: an annotated checklist. Amphibian & Reptile Conservation 12: 41–82.
- Broadley DG (1990) Fitzsimons' Snakes of Southern Africa. Jonathan Ball & AD Donker Publishers, Parklands, South Africa, 423 pp.
- Butler JA, Reid JC (1990) Records of snakes from Nigeria. The Nigerian Field 55: 19–40.
- Chippaux J-P (2001) Les Serpents d'Afrique Occidentale et Centrale.
 Collection Faune et Flore tropicales 35. IRD éditions, Paris, 292 pp.
- Chirio L, LeBreton M (2007) Atlas des reptiles du Cameroun. Patrimoines naturels 67. Muséum national d'Histoire naturelle/IRD éditions, Paris, 688 pp.
- Chapin JP (1954) Gazetteer for "The Birds of the Belgian Congo". Bulletin of the American Museum of Natural History 75B: 638–738.
- Christy C (1915) The Ituri river, forest, and pygmies. The Geographical Journal 46: 200–213. https://doi.org/10.2307/1779389
- Colyn M, Hulselmans J, Sonet G, Oudé P, De Winter J, Natta A, Nagy ZT, Verheyen E (2010) Discovery of a new duiker species (Bovidae: Cephalophinae) from the Dahomey Gap, West Africa. Zootaxa 2637: 1–30. https://doi.org/10.11646/zootaxa.2637.1.1
- Cundall D, Irish F (2008) The snake skull. In: Gans C, Gaunt AS, Adler K (Eds) Biology of the Reptilia, Volume 20, Morphology H, The Skull of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 349–692.
- Dobiey M, Vogel G (2007) Venomous snakes of Africa / Giftschlangen Afrikas. Edition Chimaira, Terralog 15, Frankfurt am Main, 149 pp.
- Dowling HG (1951a) A proposed method of expressing scale reductions in snakes. Copeia 1951: 131–134. https://doi.org/10.2307/1437542
- Dowling HG (1951b) A proposed standard of counting ventrals in snakes. British Journal of Herpetology 1: 97–99.
- Eniang EA, Ijeomah HM (2011) Diversity of ophidian species in Oban Division of the Cross River National Park, Nigeria. Production Agriculture and Technology Journal 7: 188–201.
- Ernst R, Rödel M-O (2002) A new *Atheris* species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. Herpetological Journal 12: 55–61.
- Evans BJ, Kelley DB, Tinsley RC, Melnick DJ, Cannatella DC (2004) A mitochondrial DNA phylogeny of African clawed frogs: phylogeography and implications for polyploid evolution. Molecular Phylogenetics and Evolution 33: 197–213. https://doi.org/10.1016/j. ympev.2004.04.018
- Fahr J, Vierhaus H, Hutterer R, Kock D (2002) A revision of the *Rhinol-ophus maclaudi* species group with the description of a new species from West Africa (Chiroptera: Rhinolophidae). Myotis 40: 95–126.
- Frétey, T, Blanc CP (2004) Liste des reptiles d'Afrique centrale. Les dossiers de l'ADIE, Serie Biodiversité "2" [= 3]: 1–73.

- Gaubert P, Fernandes CA, Bruford MW, Veron G (2004) Genets (Carnivora, Viverridae) in Africa: an evolutionary synthesis based on cytochrome b sequences and morphological characters. Biological Journal of the Linnean Society 81: 589–610. https://doi.org/10.1111/j.1095-8312.2004.00309.x
- Gonwouo NL, LeBreton M, Chirio L, Ineich I, Tchamba NM, Ngassam P, Dzikouk G, Diffo JL (2007) Biodiversity and conservation of the reptiles of the Mount Cameroon Area. African Journal of Herpetology 56: 149–161. https://doi.org/10.1080/21564574.2007.9635560
- Greene HW (1997) Snakes: the Evolution of Mystery in Nature. University of California Press, Berkeley, 351 pp.
- Grossmann W, Zwanzig BM, Kowalski T, Zilger HJ, Colacicco F, Ballandat S (2018) Die Erdviper *Atractaspis andersonii* Boulenger, 1905 im Sultanat Oman. Sauria 40: 3–19.
- Gyldenstolpe N (1924) Zoological results of the Swedish Expedition to Central Africa 1921. Vertebrata. I. Birds. Kungliga Svenska Vetenskapsakademiens handlingar (3. Ser.) 1(3): 1–326. [1 pl., 1 map]
- Hellmich W (1957) Die Reptilienausbeute der Hamburgischen Angola-Expedition. Mitteilungen aus dem Hamburger Zoologischen Museum und Institut 55: 39–80.
- Hernández Fernández M, Vrba ES (2005) A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews of the Cambridge Philosophical Society 80: 269–302. https://doi.org/10.1017/ S1464793104006670
- Herrmann H-W, Böhme W, Euskirchen O, Herrmann PA, Schmitz A (2005) African biodiversity hotspots: the reptiles of Mt Nlonako, Cameroon. Revue Suisse de Zoologie 112: 1045–1069. https://doi.org/10.5962/bhl.part.80336
- Hughes B (1983) African snake faunas. Bonner zoologische Beiträge 34: 311–356.
- Hughes B (1988) Herpetology in Ghana (West Africa). British Herpetological Society Bulletin 25: 29–38.
- Huntley JW, Keith KD, Castellanos AA, Musher LJ, Voelker G (2019) Underestimated and cryptic diversification patterns across Afrotropical lowland forests. Journal of Biogeography early view. https://doi.org/10.1111/jbi.13505
- Jongsma GFM, Barej MF, Barratt CD, Burger M, Conradie W, Ernst R, Greenbaum E, Hirschfeld M, Leaché AD, Penner J, Portik DM, Zassi-Boulou A-G, Rödel M-O, Blackburn DC (2018) Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. Molecular Phylogenetics and Evolution 120: 274–285. https://doi.org/10.1016/j.ympev.2017.12.006
- Knoepffler L-P (1966) Faune du Gabon (amphibiens et reptiles). I. Ophidiens de l'Ogooué-Ivindo et du Woleu N'tem. Biologia Gabonica 2(1): 3–23.
- Lasso CA, Rial AI, Castroviejo J, De la Riva I (2002) Herpetofauna del Parque Nacional de Monte Alén (Rio Muni, Guinea Ecuatorial). Graellsia 58(2): 21–34. https://doi.org/10.3989/graellsia.2002.v58.i2.276
- Laurent RF (1945) Contribution à la connaissance du Genre *Atractaspis*A. Smith. Revue de Zoologie et de Botanique Africaines 38: 312–343.
- Laurent RF (1950) Révision du genre *Atractaspis* A. Smith. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 38: 1–49.
- Laurent RF (1956a) Notes herpétologiques africaines. Revue de Zoologique et de Botanique Africaines 53: 229–256.
- Laurent RF (1956b) Contribution à l'herpétologie de la région des Grands Lacs de l'Afrique centrale. Annales du Musée Royal du Congo belge (Sciences Zoologiques) 48: 1–390.

- Laurent RF (1960) Notes complémentaires sur les chéloniens et les ophidiens du Congo oriental. Annales du Musée Royal du Congo Belge (Sciences Zoologiques) 84: 1–86.
- Lawson DP (1993) The reptiles and amphibians of the Korup National Park project, Cameroon. Herpetological Natural History 1(2): 27–90.
- Li Vigni F (2013) A Life for Reptiles and Amphibians, Vol. 1. Edition Chimaira, Frankfurt am Main, 495 pp.
- McDowell SB (2008) The skull of Serpentes. In: Gans C, Gaunt AS, Adler K (Eds) Biology of the Reptilia, Volume 21, Morphology I, The Skull and Appendicular Locomotor Apparatus of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 467–620.
- Mertens R (1938) Herpetologische Ergebnisse einer Reise nach Kamerun. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 442: 1–52. [10 pls.]
- Moodley Y, Bruford MW (2007) Molecular biogeography: towards an integrated framework for conserving Pan-African biodiversity. PLoS ONE 2(5): e454. https://doi.org/10.1371/journal.pone.0000454
- Moyer K, Jackson K (2011) Phylogenetic relationships among the stiletto snakes (genus *Atractaspis*) based on external morphology. African Journal of Herpetology 60: 30–46. https://doi.org/10.1080/21 564574.2010.520034
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the World: a new map of life on Earth. BioScience 51: 933–938.
- Ota H, Hikida T, Barcelo J (1987) On a small collection of lizards and snakes from Cameroon, West Africa. African Study Monographs 8: 111–123.
- Pauwels OSG, Sallé B (2009) Miscellanea Herpetologica Gabonica III. Hamadryad 34: 22–27.
- Pauwels OSG, Vande Weghe JP (2008) Les Reptiles du Gabon. Smithsonian Institution, Washington DC, 272 pp.
- Penner J, Wegmann M, Hillers A, Schmidt M, Rödel M-O (2011) A hotspot revisited a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077–1088. https://doi.org/10.1111/j.1472-4642.2011.00801.x
- Perret J-L (1960) Une nouvelle et remarquable espèce d'*Atractaspis* (Viperidae) et quelques autres serpents d'Afrique. Revue Suisse de Zoologie 67: 129–139. https://doi.org/10.5962/bhl.part.75262
- Perret JL, Mertens R (1957) Etude d'une collection herpétologique faite au Cameroun de 1952–1955. Bulletin de l'Institut Français d'Afrique Noire, Série A, Sciences Naturelles 19: 548–601.
- Pitman CRS (1938) A guide to the snakes of Uganda part XI. The Uganda Journal 5(3): 160–244.
- Portillo F, Branch WR, Conradie W, Rödel M-O, Penner J, Barej MF, Kusamba C, Muninga WM, Aristote MM, Bauer AM, Trape JF, Nagy ZT, Carlino P, Pauwels OSG, Menegon M, Burger M, Mazuch T, Jackson K, Hughes DF, Behangana M, Zassi-Boulou A-G, Greenbaum E (2018) Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophidae). Molecular Phylogenetics and Evolution 127: 288–303. https://doi.org/10.1016/j.ympev.2018.03.019
- Rhodin AGJ, Iverson JB., Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP (2017) Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Edition). Chelonian Research Foundation, Lunenburg, 292 pp.

- Rödel M-O, Ernst E (2000) *Bufo taiensis* n. sp., eine neue Kröte aus dem Taï-Nationalpark, Elfenbeinküste. herpetofauna 22(125): 9–16.
- Rödel M-O, Grabow K, Böckheler C, Mahsberg D (1995) Die Schlangen des Comoé-Nationalparks, Elfenbeinküste (Reptilia: Squamata: Serpentes). Stuttgarter Beiträge zur Naturkunde, Serie A 528: 1–18.
- Rödel M-O, Kosuch J, Grafe TU, Boistel R, Assemian NE, Kouamé NG, Tohé B, Gourène G, Perret J-L, Henle K, Tafforeau P, Pollet N, Veith M (2009) A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). Zootaxa 2044: 23–45.
- Rödel M-O, Kosuch J, Veith M, Ernst R (2003) First record of the genus *Acanthixalus* Laurent, 1944 from the Upper Guinean rain forest, West Africa, with the description of a new species. Journal of Herpetology 37: 43–52.
- Rödel M-O, Mahsberg D (2000) Vorläufige Liste der Schlangen des Tai-Nationalparks / Elfenbeinküste und angrenzender Gebiete. Salamandra 36: 25–38.
- Roux-Estève R (1965) Les serpents de la région de La Maboké-Boukoko. Cahiers de la Maboké 3: 51–92.
- Schmidt KP (1923) Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part II. Snakes, with field notes by Herbert Lang and James P. Chapin. Bulletin of the American Museum of Natural History 49: 1–146.
- Schouteden H (1933) Contribution á la faune des reptiles et des batraciens de la région méridionale du Parc Albert (Kivu). Revue de Zoologique et de Botanique Africaines 23: 233–238.
- Shirley MH, Vliet KA, Carr AN, Austin JD (2014) Rigorous approaches to species delimitation have significant implications for African crocodilian systematics and conservation. Proceedings of the Royal Society B 281: 20132483. https://doi.org/10.1098/rspb.2013.2483
- Sjöstedt Y (1896) *Atractaspis reticulata*, eine neue Schlange aus Kamerun. Zoologischer Anzeiger 19: 516–517.
- Sjöstedt Y (1897) Reptilien aus Kamerun West-Afrika. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar 23(4): 1–29. [pls 1–3]
- Spawls S, Branch B (1995) The Dangerous Snakes of Africa. Natural history. Species Directory. Venoms and Snakebite. Blandford, London, 192 pp.
- Sternfeld R (1908) Die Schlangenfauna von Kamerun. Mitteilungen aus dem Zoologischen Museum in Berlin 3: 397–432.
- Trape JF, Roux-Estève R (1995) Les serpents du Congo: liste commentée et clé de détermination. Journal of African Zoology 109: 31–50
- Treplin S (2006) Inference of phylogenetic relationships in passerine birds (Aves: Passeriformes) using new molecular markers. Dissertation, University of Potsdam, Germany, 131 pp.
- Vidal N, Delmas A-S, David P, Cruaud C, Couloux A, Hedges SB (2007) The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. Comptes Rendus Biologies 330: 182–187. https://doi.org/10.1016/j.crvi.2006.10.001
- Uetz P, Freed P, Hošek J (2018) The Reptile Database. http://www.reptile-database.org [Accessed on: 2018-9-14]
- Underwood G, Kochva E (1993) On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). Zoological Journal of the Linnean Society 107: 3–64. https://doi.org/10.1111/j.1096-3642.1993.tb01252.x

- Wagner P, Townsend E, Barej M, Rödder D, Spawls S (2009) First record of human envenomation by *Atractaspis congica* Peters, 1877 (Squamata: Atractaspididae). Toxicon 54: 368–372. https://doi.org/10.1016/j.toxicon.2009.04.019
- Wallach V, Williams KL, Boundy J (2014) Snakes of the World: A Catalogue of Living and Extinct Species. Taylor & Francis, CRC Press, London, New York, Boca Raton, 1209 pp. https://doi.org/10.1201/ b16901
- Werner F (1899) Ueber Reptilien und Batrachier aus Togoland, Kamerun und Deutsch-Neu-Guinea grösstentheils aus dem k. Museum für Naturkunde in Berlin. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 49: 132–157.
- Werner F ("1912" [1913]) Neue oder seltene Reptilien und Frösche des Naturhistorischen Museums in Hamburg. Reptilien der Ostafrika-Expedition der Hamburger Geographischen Gesellschaft 1911/12. Leiter: Dr. E. Obst. Reptilien und Amphibien von Formo-

- sa. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 30 2. Beiheft: 1–39, 40–45, 45–51.
- de Witte GF (1941) Exploration du Parc National Albert. Batraciens et reptiles. Institut des Parcs Nationaux du Congo Belge, Brussels, xviii + 261 pp. [+ xxvi pls]
- de Witte GF (1953) Exploration du Parc National de l'Upemba. Reptiles. Institut des Parcs Nationaux du Congo Belge, Brussels, 322 pp. [+ xli pls +1 map]
- de Witte GF (1962) Genera des serpents du Congo et du Ruanda-Urundi. Annales du Musée Royal d'Afrique Centrale 104: 1–203.
- Wüster W, Chirio L, Trape J-F, Ineich I, Jackson K, Greenbaum E, Barron C, Kusamba C, Nagy ZT, Storey R, Hall C, Wüster CE, Barlow A, Broadley DG (2018) Integration of nuclear and mitochondrial gene sequences and morphology reveals unexpected diversity in the forest cobra (*Naja melanoleuca*) species complex in Central and West Africa (Serpentes: Elapidae). Zootaxa 4455: 68–98. https://doi.org/10.11646/zootaxa.4455.1.3



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