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Two new species of *Boaedon* from Ethiopia and Somalia, with a review of the species of East Africa

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Abstract

We conducted a molecular study based on 112 mitochondrial 16S rRNA sequences, which revealed 20 monophyletic species-level groups in Africa, five of these in East and Northeast Africa. Based on genetic data, we describe two new species, *B. broadleyi* **sp. nov.** from Ethiopia and *B. subniger* **sp. nov.** from Somalia, and we elevate *B. fuliginosus arabicus* to full species level. We detected further morphologically divergent specimens that may represent a distinct taxon but refrain from a formal description due to insufficient data. The morphological variation of the recently described *B. montanus* from Central Africa is shown and discussed over its whole distribution area. Moreover, we provide a new country record for Sudan and South Sudan, namely of *B. paralineatus*. Finally, we provide an updated distribution map for all *Boaedon* species occurring in Northeast and East Africa.

Key words: Horn of Africa, East Africa, Yemen, endemism, new species, new country record, 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, distributed throughout Africa, the Seychelles and Yemen. Several new species of this genus were described during the last six years, mainly from West and Central Africa, raising the number of recognized species to 23 (Trape & Mediannikov 2016; Hallermann *et al.* 2020; Ceríaco *et al.* 2021; Trape *et al.* 2022; Uetz *et al.* 2024).

Various molecular studies detected several genetically divergent, but morphologically indistinguishable lineages within *Boaedon*, some of which may represent undescribed cryptic species (Kelly *et al.* 2011; Greenbaum *et al.* 2015; Hallermann *et al.* 2020; Ceríaco *et al.* 2021). Wallach *et al.* (2014) recognized *B. arabicus* Parker, 1930, *B. capensis* Duméril, Bibron & Duméril, 1854, *B. fuliginosus* (Boie, 1827), *B. lineatus* Duméril, Bibron & Duméril, 1854, and *B. maculatus* Parker, 1932 as full species assigned to the *B. lineatus-fuliginosus* species complex, without providing any detailed evidence. The five species recently described by Trape and Mediannikov (2016) were also regarded by those authors as members of this complex. All species of the *B. lineatus-fuliginosus* complex are morphologically very similar, featuring relatively prominent light lateral head stripes and a whitish venter. Earlier taxonomic studies of the *B. fuliginosus* complex using only morphological and morphometric methods regarded *B. fuliginosus* as a pan-African species with variable coloration and pholidosis (Roux-Estève & Guibé 1964, 1965; Thorpe & McCarthy 1978; Hughes 1997) and were unable to provide a satisfactory solution to the remaining taxonomic problems.

The herpetofauna of Ethiopia has not yet been researched to the same extent as that of other areas of Africa. The first zoological research excursion to what was then Abyssinia was carried out by E. Rüppell from 1830-34 (Rüppell 1839). In the 19th century there were mainly explorers from Italy, such as Prince Eugenio Ruspolli in 1891, Enrica Calabresi, Vittorio Bottego, Vincenzo Ragazzi, Captain A. Gasca, Achille Tellini, and the German Baron Carlo von Erlanger, who contributed to the study of the fauna of Ethiopia. In the 20th century, particular mention should be

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made of H. W. Parker (1949), G. Scortecci and F. Testi. More recently, at the end of the 20th and beginning of the 21st century D. W. Yalden, J. B. Rasmussen, M. J. Largen, D. G. Broadley, S. Spawls and B. Lanza contributed significantly to the exploration of the country. Recently described species include *Agama lucyae* Wagner & Bauer 2011, *Bitis harenna* Gower *et al.* 2016, *Hemidactylus afarensis* Šmíd *et al.* 2020, *H. awashensis* Šmíd *et al.* 2015, *H. lanzai* Šmíd *et al.* 2020, *Panaspis annettesabinae* Colston, Pyron & Bauer 2020, *Trachylepis boehmei* Koppetsch, 2020, *Trioceros wolfgangboehmei* Koppetsch, Nečas & Wipfler 2021, *Xenagama wilmsi* Wagner, Mazuch & Bauer 2013 and the amphibians *Leptopelis diffidens* and *L. montanus* Tiutenko & Zinenko, 2021, *L. shebellensis*, *L. xeniae*, several *Ptychadena* (*robeensis*, *beka*, *delphina*, *doro*, *goweri*, *levenorum*, *amharensis)* Goutte *et al.* 2021. Further new, unknown species are apparently still hidden in Ethiopia and have not yet been recorded or described.

In addition to species completely new to science, many species known from neighbouring regions may occur in Ethiopia. Several species previously considered endemic to Somalia have also recently been recorded in Ethiopia, such as *Xenagama taylori*, *X. wilmsi* and *Hemitheconyx taylori* (Largen and Spawls 2006, 2010). Because of the low frequency of collecting attempts within this area, many similar discoveries can be expected in the near future. Concerning the *B. fuliginosus* complex, the most recent comprehensive book on the herpetofauna of Ethiopia by Largen & Spawls (2010) and Spawls *et al.* (2023) mentioned *B. maculatus* and *B. fuliginosus*. Even while the status of *B. fuliginosus* has not yet been fully clarified and the limits of its distribution are still unclear, the occurrence of further *fuliginosus*-like species in Ethiopia seems plausible.

As part of an ongoing review of the genus *Boaedon*, we combined the morphological examination of specimens housed in natural history collections with mitochondrial DNA analysis of fresh samples. Our goal was to detect possible species-level lineages within Northeast and East African *Boaedon*. The recent collection of fresh material from Ethiopia and Somalia and preserved material from MNHN, ZFMK and ZMH allowed us to describe two of these populations as new species. Apart from the Ethiopian population of *Boaedon*, the populations from Rwanda, Uganda and part of Tanzania represent a cryptic species, described recently as *Boaedon montanus* Trape, Mediannikov, Hinkel & Hinkel, 2022. The Sudan and South Sudan populations may belong to two different species: a brown one with two short head stripes, variably lacking, belongs to *B. montanus* and a light brown one with clear head and body stripes belongs to *B. paralineatus.* Another population from western Ethiopia differs morphologically mainly by its black colouration without any light head stripes. This population may also represent a distinct species. Unfortunately, these morphological findings could not be verified by genetic analyses because the amount and quality of extracted DNA from the available museum material was insufficient for sequencing (Logemann 2023, unpublished data).

Material &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); Muséum d'Histoire Naturelle (MHNG), Genève (Switzerland); Leibniz Institute for the Analyses of Biodiversity change (LIB) (Germany), Zoologisches Museum Hamburg (ZMH) (Germany); Museum Koenig (ZFMK), Bonn (Germany); Museum fur̈ Naturkunde (ZMB), Berlin (Germany), Tomáš Mazuch personal Herpetological Collection (TMHC); locality records have mostly 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 micrometre to a precision of 0.1 millimetre. Pholidosis was observed with a Carl Zeiss DRC 475003-9902 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; inter-ocular 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/orbit; the ratio of V and Sc (V/SC) was also recorded. The length and height of the loreal scale (LOR) as well as its ratio (LOR-L/H) were recorded. Snout length is described in relation to the length of the parietal shield on its median contact line (PAR): the PAR is either equal to the distance between the frontal and the rostral scale or longer. Contact of upper preocular with frontal or its separation by contact of prefrontal with supraocular is recorded. 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.

Molecular Genetic Methods

We extracted DNA from muscle tissue preserved in ethanol using a salt extraction protocol (Paxton *et al.* 1996) and amplified a fragment of the mitochondrial 16S rRNA gene using the primers and protocol described in Hawlitschek *et al.* (2012). Newly generated sequences were submitted to GenBank (accession numbers PQ408552 to PQ408563). The newly generated sequences were assembled and aligned to form a set of 124 sequences from GenBank using the MUSCLE (Edgar 2004) algorithm of MEGA 11 (Tamura *et al.* 2011). We then measured genetic p-distances within species and between pairs of species, also in MEGA. We reconstructed phylogenetic relationships, as inferred from the 16SrRNA gene, using the Maximum Likelihood approach in IQtree 2.1.1 (Minh *et al.*, 2019) with 1,000 ultrafast bootstrap repeats and using Bayesian Inference in MrBayes 3.2.7a (Ronquist *et al.*, 2012) under the GTR+G model with two runs, four chains, and 10 M generations sampling every 1,000 generations. MrBayes runs were checked for convergence and normal distribution in Tracer v.1.5.

Results

Phylogenetic Analysis

For the genetic dataset we compiled sequences from 18 currently recognised *Boaedon* species, as well as from two additional new species described herein. Genetic p-distances are shown in Table 1. The mean intraspecific distances among samples range from 0 to 0.015 in *B. variegatus*. Among the species measured here, the shortest interspecific distances are found between *B. broadleyi* **sp. nov.** and *B. radfordi* (0.011), and the longest distances are found between *B. paralineatus* and *B. variegatus*.

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 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: 0.90; see discussion below) receiving lower support. Two potentially undescribed cryptic species were identified as monophyletic lineages: one species from Ethiopia and one species from northern Somalia (both described herein). An eastern-central African clade from Rwanda, Uganda to Tanzania that was recently described as *Boaedon montanus* by Trape *et al.* (2022) includes a well-defined subclade. In this clade an apparently incorrectly determined species "*B. olivaceus*" is nested (GenBank sequence KX277253, Simões et al 2016, Fig. 1). The status of *B. arabicus* as a full species is corroborate by our analysis. This species was long regarded as a subspecies of *B. fuliginosus* until Hughes (1997) proposes its specific status on morphological and biogeographical grounds.

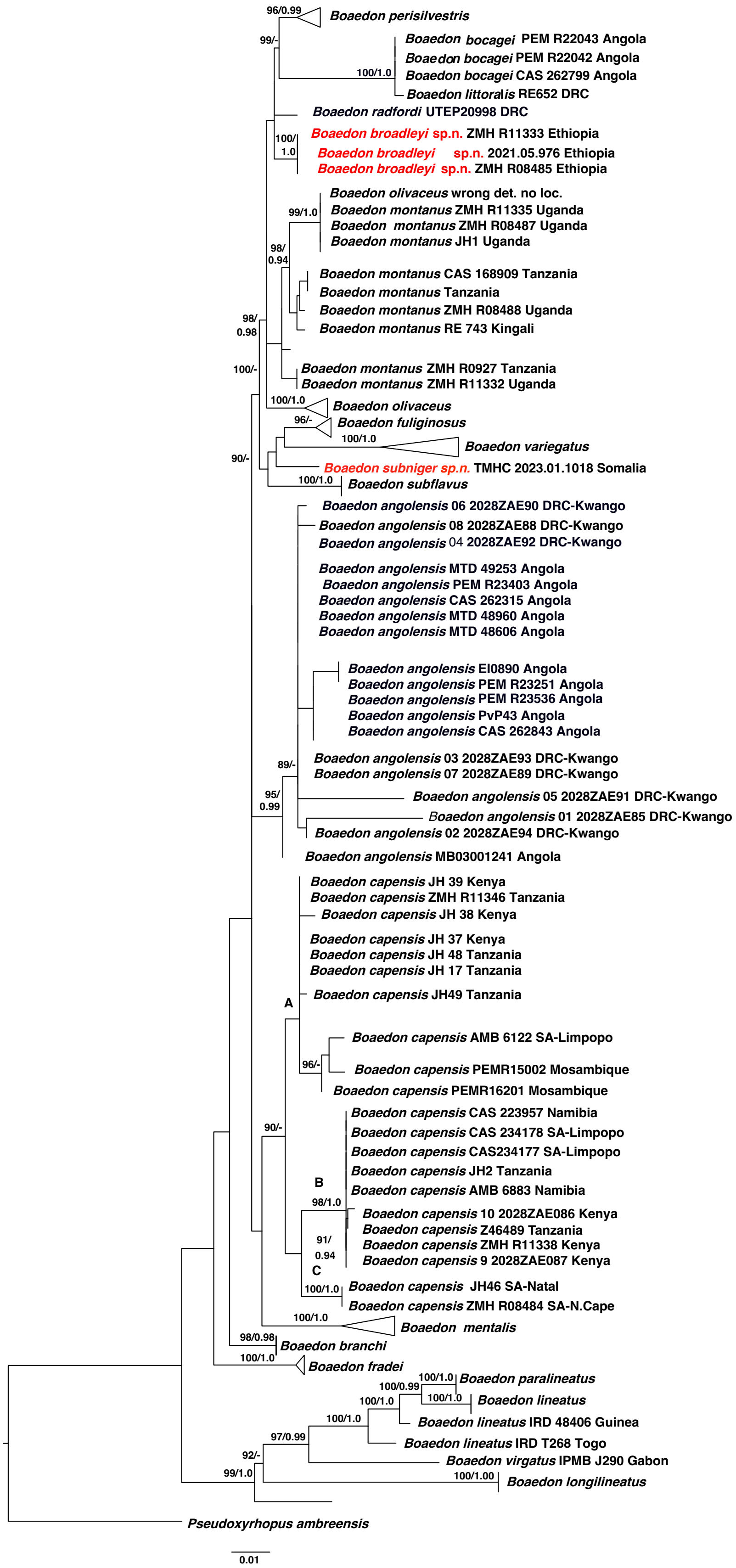

FIGURE 1. Phylogenetic tree (BI/ML) based on the mitochondrial 16S dataset. Numbers at nodes are support values for Bayesian posterior probabilities (above nodes) and ML bootstraps (below node); values below PP <0.5 and ML <50 are not shown. High support values (PP ≥ 0.95 and ML ≥ 70) are marked in bold.

TABLE 1. A matrix of genetic p-distances in selected *Boaedon* species. Values are given as minimum-maximum (mean ± standard deviation). Intraspecific values are given in the first line, interspecific comparisons in the lines below

Taxon	*B. broadleyi* sp.nov.	*B. perisilvestris*	*B. littoralis*	*B. radfordi*	*B. subniger sp.nov.*	*B. fuliginosus*	*B. subflavus*	*B. variegatus*	*B. montanus*	*B. paralineatus*	*B. capensis* s.l.
Intraspecific	0	0–0.006 (0.003±0.002)	0–0.002 (0.001±0.001)	0	0	0–0.006 (0.001±0.002)	0	0–0.023 (0.015±0.005)	0–0.015 (0.009±0.004)	0	0–0.03 (0.013±0.008)
B. broadleyi sp.nov.											
B. perisilvestris	0.011–0.017 (0.013±0.002)										
B. littoralis	0.032–0.038 (0.035±0.002)	0.028–0.039 (0.032±0.003)									
B. radfordi	0.01–0.011 (0.011±0)	0.009–0.016 (0.012±0.003)	0.032–0.037 (0.033±0.002)								
B. subniger sp.nov.	0.012–0.018 (0.015±0.003)	0.021–0.027 (0.024±0.002)	0.039–0.042 (0.04±0.001)	0.022–0.022 (0.022±0)							
B. fuliginosus	0.014–0.019 (0.016±0.001)	0.02–0.029 (0.023±0.002)	0.035–0.043 (0.039±0.002)	0.018–0.022 (0.019±0.001)	0.015–0.022 (0.019±0.002)						
B. subflavus	0.021–0.022 (0.021±0)	0.025–0.031 (0.027±0.002)	0.043–0.047 (0.044±0.002)	0.02–0.02 (0.02±0)	0.019–0.019 (0.019±0)	0.022–0.027 (0.024±0.001)					
B. variegatus	0.036–0.05 (0.041±0.004)	0.039–0.054 (0.045±0.004)	0.048–0.07 (0.057±0.006)	0.04–0.049 (0.043±0.003)	0.039–0.047 (0.042±0.003)	0.029–0.048 (0.037±0.004)	0.042–0.051 (0.046±0.004)				
B. montanus	0.012–0.018 (0.015±0.002)	0.014–0.029 (0.02±0.003)	0.031–0.045 (0.04±0.003)	0.013–0.021 (0.016±0.003)	0.015–0.024 (0.019±0.003)	0.018–0.029 (0.024±0.003)	0.022–0.029 (0.025±0.004)	0.036–0.073 (0.047±0.007)			
B. paralineatus	0.059–0.061 (0.059±0.001)	0.063–0.065 (0.064±0.001)	0.073–0.075 (0.073±0.001)	0.061–0.061 (0.061±0)	0.065–0.065 (0.065±0)	0.057–0.057 (0.057±0)	0.057–0.057 (0.057±0)	0.068–0.081 (0.075±0.004)	0.061–0.078 (0.067±0.005)		
B. capensis s.l.	0.016–0.037 (0.026±0.006)	0.014–0.044 (0.03±0.006)	0.029–0.054 (0.045±0.005)	0.011–0.039 (0.027±0.007)	0.014–0.042 (0.031±0.009)	0.018–0.049 (0.033±0.007)	0.016–0.042 (0.034±0.005)	0.026–0.078 (0.053±0.008)	0.014–0.047 (0.032±0.007)	0.043–0.073 (0.061±0.006)	

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 B: Tanzania, South Africa) and a uniquely southern African group (clade C; Figure 1). The resulting genetic distances between these three clades are comparable to those between previously recognized *Boaedon* species and should therefore be evaluated as putatively distinct species. Trape (pers. com. 2024) noted that the taxa *B. bocagei* Hallermann *et al.*, 2020 and *B. littoralis* Trape & Medianikov, 2016 are valid species corroborated by unpublished studies with new material. Because we have no access to this new DNA material, our analyses did not differentiate the two clades.

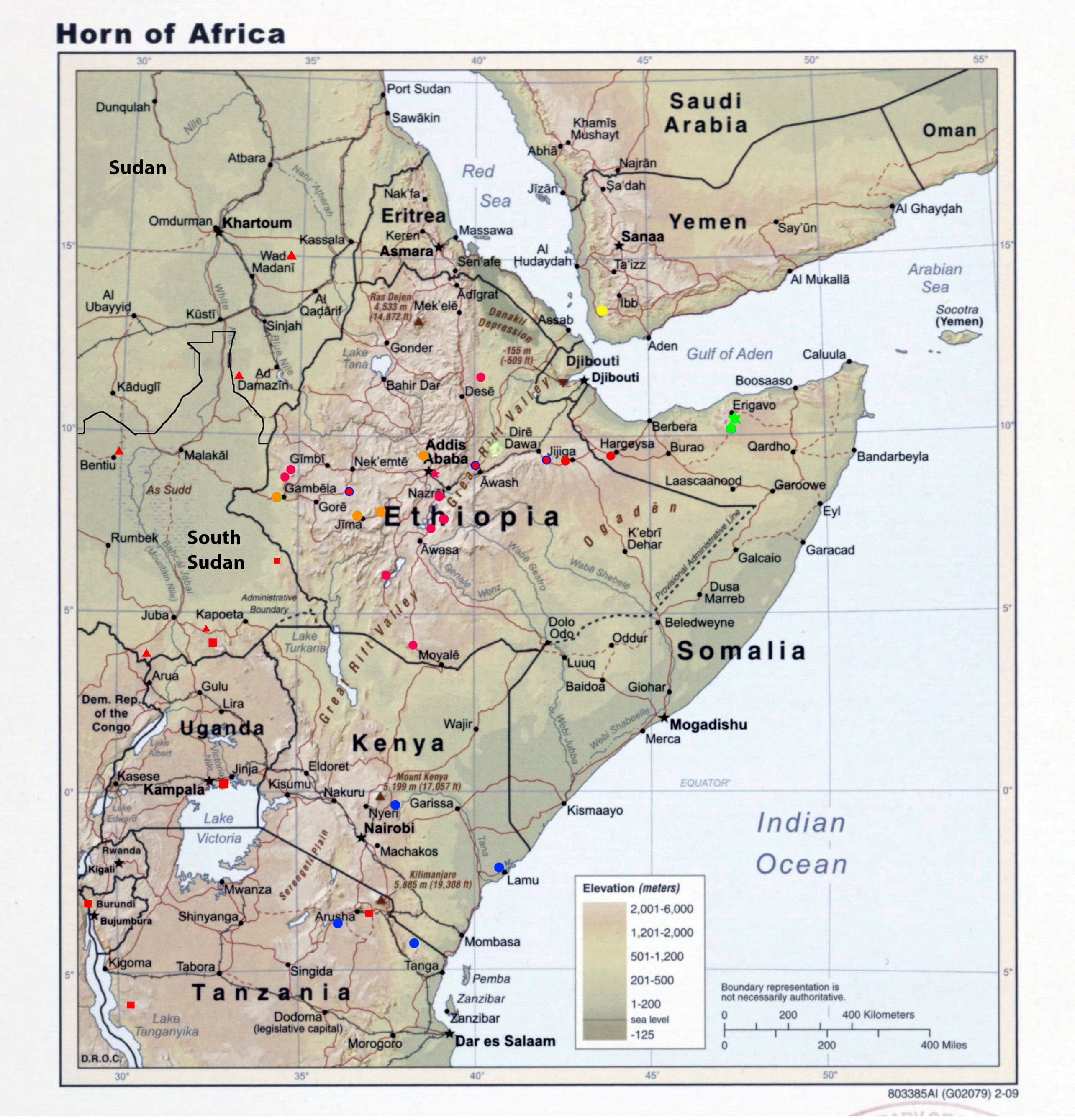

FIGURE 2. Confirmed records of *Boaedon* species in north-eastern and eastern Africa. Red dots: *Boaedon broadleyi* **sp. nov.**; Red star: *Boaedon broadleyi* **sp. nov.** type locality; green dots: *Boaedon subniger* **sp. nov.**; green star: *Boaedon subniger* **sp. nov.** type locality; red square: *Boaedon montanus*; red triangle: *Boaedon paralineatus;* blue dots, *Boaedon capensis* s.l.: orange dots *Boaedon* sp. black form; yellow dot: *B. arabicus*.

Morphological analysis

The results of our morphological analyses are shown in Table 2. Males and females of the newly described species from Ethiopia and Somalia and the species of neighbouring countries differ by a combination of characters from all other congeners in the area (see diagnoses below). Based on these differences and the results of our phylogenetic analyses, we recognise these clades as new species (Figure 3, 5, Tables 3, 4).

Systematics

The House snake genera experienced a confusing taxonomic history full of 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 & Spawls 2010). This classification stood until a 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*. Populations of African House snakes occurring in Ethiopia were recently grouped in three genera and four species: *Pseudoboodon abyssinicus*, *Bofa erlangeri*, *Boaedon maculatus* and *B. fuliginosus* (Tiutenko *et al.* 2022). *Boaedon fuliginosus* is a widespread and highly variable species (Largen & Spawls 2010; Wallach *et al.* 2014; Kelly *et al.* 2015). *P. abyssinicus*, *B. erlangeri* and *B. maculatus* can be easily distinguished from members of the *B. fuliginosus-lineatus* complex by their lower counts of ventral and mid-dorsal scale rows. An integrative taxonomic analysis (molecular genetic and morphological) shows clearly two different *fuliginosus*-like species in Ethiopia and Somalia.

***Boaedon broadleyi* sp. nov.**

(Figs. 3, 4)

Lamprophis fuliginosus Broadley Doria & Wigge 2003*:* 236 Photo 81 from Addis Ababa
Lamprophis fuliginosus Largen & Spawls 2010: 469 Fig. 300
Boaedon fuliginosus Spawls *et al*. 2023: 442, 443 from Lake Langano

Holotype: ZMH R08485 (DNA voucher JH 10): an adult female from near Addis Ababa (Abada) (approx. 09° 01' 48" N 38° 04' 24" E, 2552 m), Oromia Region, collected by Dr. Peter Angenstein during the end of the 1980s, kept in captivity until 2006 by Ralf Hörold and donated to the Zoological Museum Hamburg (ZMH) in Dec. 2006 (Fig. 3)

Paratypes (13): All from Ethiopia: MNHN 4342, an adult female from Ethiopia (Abyssinie) with no specific locality, received by natural produce dealer Deyrolle (Henry or Emile) and collected by A. M. J. Raffray in 1874; ZFMK 16231-32, adult females from Negele (approx. 07° 41' 00" N 39° 15' 00" E, 1575 m), Sidamo Province, Oromia Region, collected by H. Rupp, 28. Feb. 1975; ZFMK 16293, an adult female from Lake Koka (approx. 08° 23' 31" N 39° 05' 00" E, 1595 m) Oromia Region, collected by H. Rupp, Sept. 1973; ZFMK 16294-95, adult female and juvenile respectively from Arba Minch (approx. 06° 02' 00" N 37° 33' 00" E, 1285 m) Southern Nations, Nationalities, and Peoples Region, collected by H. Rupp, 26. Mar. 1975; ZFMK 16799, an adult male from Kaki (approx. 08° 56' 00" N 35° 03' 00" E, 3000 m) Tulu Welel mountains, Oromia Region, collected by G. Nikolaus, 20.Nov. 1975; ZFMK 19159, an adult female from Chifra (Sifra) (approx. 11° 36' 14.2" N 40° 12' 35.86" E, 825 m) Afar Region; ZFMK 84994 a juvenile from Jijiga (approx. 9° 40' 00" N 38° 45' 00" E, 1634 m) Somali Region; ZMH R08486, an adult male, same data as holotype, ZMH R11333 (DNA voucher JH 59), an adult female same data as holotype, ZMH R11341-42, an adult male and female respectively, same data as holotype but donated to the ZMH in 2019.

Diagnosis. *Boaedon broadleyi* **sp. nov.** can be distinguished from most congeners by a beige to light brown to reddish ground colour, with two short white stripes on the sides of the head. The upper stripe begins just behind the eye on the upper postocular, runs through the lower part of the parietal and the upper first temporal and terminates on the second temporal; the lower stripe passes from the lower postocular through the first temporal and terminates on the last supralabial. Frequently three supralabials contact the eye and two preoculars, the upper one much larger than the lower one touching the frontal. PAR is equal to the distance between the frontal and the rostral scale. Middorsal scale rows varies between 27 and 33 (mean 29.1), ventrals are 223–240 in females and 191–224 in males and subcaudals 45–55 and 59–63 respectively. (Table 3)

Within Ethiopian *Boaedon*, *Boaedon broadley* **sp. nov.** differs from Ethiopian *B.* sp. (black form) and Somalian *B. subniger* **sp. nov.** by the combination of its reddish, olive-brown or light brown body colouration with two short head stripes (versus blackish-brown or dark brown body colouration and head stripes missing) with the first two body scale rows uncoloured (versus no dorsals uncoloured) and a higher average of mid-dorsal scale counts of 29.1 (versus 27.0 in *B. subniger* **sp. nov.**). *Boaedon maculatus* has an additional row of scales between the supralabials and loreal between nasal and preocular scale (versus no row of scales) and 10–11 supralabials (versus 8). Extralimital species: *Boaedon montanus* (Trape *et al.* 2022) differs genetically from *B. broadleyi* **sp. nov.** There is no differential diagnostic character to distinguish the species of *B. montanus* in its hole distribution area from *B. broadleyi* because all meristic characters vary in different populations of this species. Within the type series of *B. montanus* one character is different: no contact of the upper preocular with the frontal (versus contact) and PAR longer than distance of frontal to rostral (versus PAR equal to distance from frontal to rostral). Specimens of the Uganda clade (*B. montanus*) and from South Sudan (cf. *montanus*) predominantly have a dark brown coloration (versus light brown in *broadleyi*) and, variably, the preocular is separate from the frontal or in contact with it, predominantly two supralabials touching the eye (91%) (versus 55% in *broadleyi* **sp. nov.**) and frequently a lower mean of MSR of 28.0–28.8 in all populations (versus 29.1in *B. broadleyi* **sp. nov.**) (table 2). *B. perisilvestris* with dark brown colouration and no clear head or body lines (versus headlines present and light brown or olive brown colour in *B. broadleyi* **sp. nov.**) has PAR longer than distance of margin of frontal to end of snout (versus PAR equal in *B. broadleyi* **sp. nov.**). *B. paralineatus* differs in having clearly marginated light headlines anterior and posterior to eye and on anterior part of body (versus short head stripes not well contrasted and no body line in *broadleyi* **sp. nov.**); *B. capensis* species complex differs in having loreal length/high ratio mainly 2 or lower (versus 2 and higher) and a dorsal scale count mean of 27.0 (versus 29.1 in *B. broadleyi* **sp. nov.**).

Description of holotype: Adult female, 1196 mm SVL; head sub-triangular, slightly distinct from the neck, HL 3.3 % of SVL (39.6 mm); interocular distance 13.7 mm, pupil elliptical, eye diameter 3.2 mm; loreal rectangular, about 2.8 x as long (5 mm) as high (1.8 mm); body cylindrical; tail moderately short (10.3 % of SVL). Supralabials 8/8, 3rd, 4th and 5th on both sides contacting orbit; infralabials 9/10, 1st 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 more than two times larger than lower and touching frontal on the left side, on the right head side it is separated from the frontal by the contact of prefrontal with supraocular; 2 postoculars in contact with the lower part of parietal scale caudally, upper postocular in contact with supraocular anterior-dorsally. Lower postocular in contact with 5th and 6th supralabial (both sides of head) ventrally; temporals 1+2+3 on both sides; two internasals; nasal divided; frontal longer (8.3 mm) than wide (4.4 mm); on anterior left border of frontal a small scale is intercalated between frontal and upper preocular; dorsal scales smooth, 22 scale rows one head-length posterior to jaw rictus, 29 scale rows at midbody, 21 scale rows one head length anterior to vent; ventrals 243; anal plate entire; 53 subcaudals, all paired.

Coloration of holotype in life. The coloration is light olive with a creamy venter, first dorsal scale row creamy. Two short white strips on side of head continuing only on head to the end of supralabials and temporals respectively. In **preservative** as above but body and head light brown above, first lower dorsal scale row creamy as venter.

Variation. Variation in measurements and scalation of the paratypes of *B. broadleyi* **sp. nov.** is presented in Table 3. The ground colour of the paratypes in preservative is predominantly light brown in 12 of 13 specimens, one is greyish. Lower 1–3 dorsal scale rows have the same colouration as venter, creamy or whitish. All paratypes have two short white head lines, the extension of the upper head line varies a little, in some specimens it begins on prefrontals runs through preoculars, supraocular, upper postocular, lower part of parietals and terminate on second or third temporals. In others, it begins on upper postocular and runs until first or third temporals. In 5 of 13 paratypes there are three supralabials in contact with the eye. In others only two supralabials are in contact. In all paratypes the upper preocular is in contact with the frontal and two postoculars are in contact with the descending part of the parietal scale. There exist some photo vouchers by Vladimír Tralin from Langano and Filtu which seems to belong to the new species. The colour in life varies from beige, light brown to almost brown. The brown coloured specimen (TMHC 2021.05.976) with two short light headlines from Yabello (DNA voucher TMHC 2021.05.976) belongs definitively to *B. broadleyi* **sp. nov.** (Fig 1).

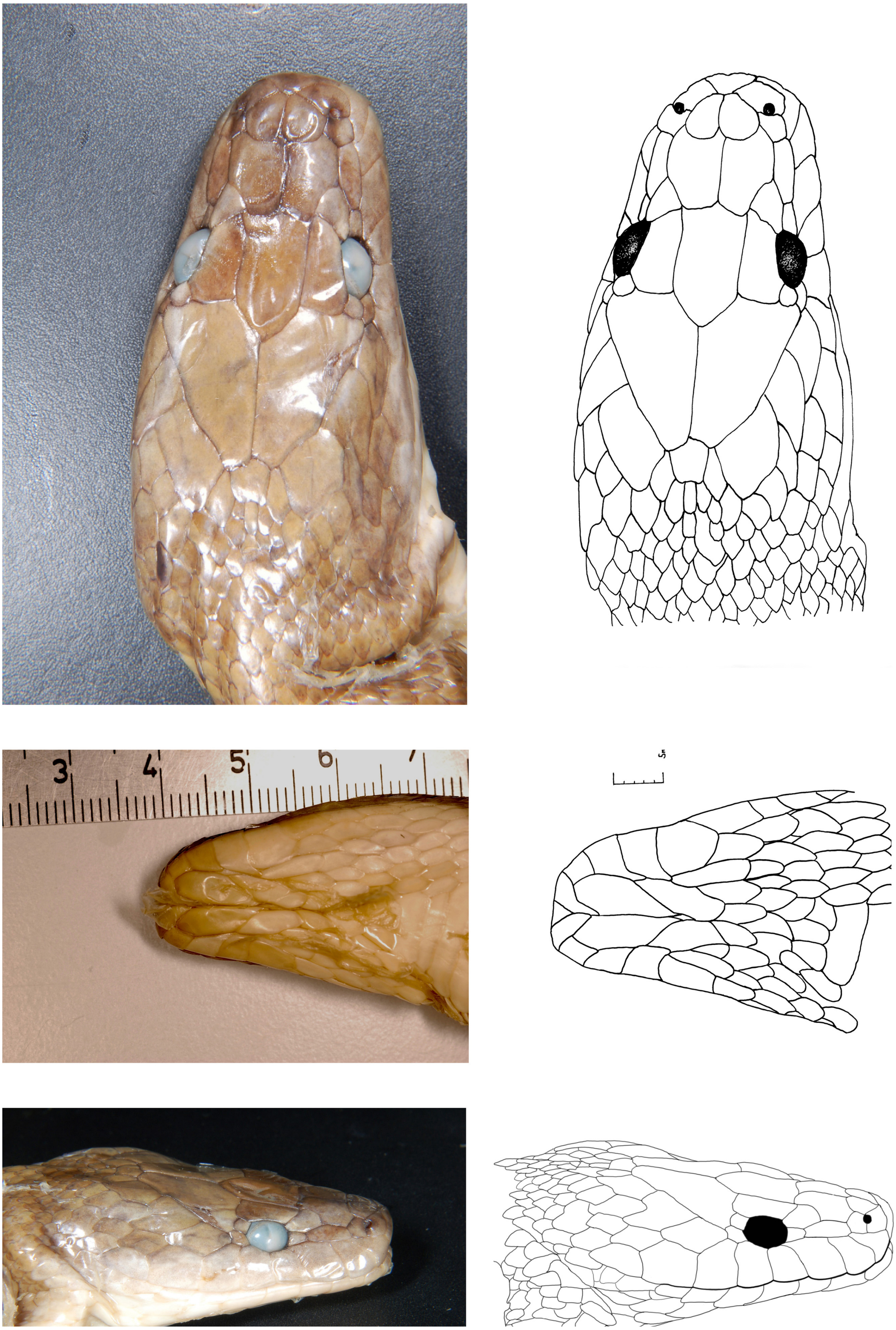

FIGURE 3: Holotype of *Boaedon broadleyi* **sp. nov.** (ZMH R08485) from nearby Addis Ababa, Ethiopia. Left: head in dorsal, ventral and lateral view, right side drawings of the head.

FIGURE 4: Live photo of *Boaedon broadleyi* **sp. nov.** from nearby Lake Oromia region, Ethiopia. Photo by Petr Nečas.

Distribution. The species is currently known from different localities in elevations from approx. 750 m up to 3000 m asl in Ethiopian Regional States in Afar, Oromia, Somali and Southern Nations, Nationalities, and Peoples' National Regional State and most probably in Northern Somalia (Somaliland) (Fig. 2).

Habitat and Natural History notes. The specimens were found in savannas, grasslands and woodlands, absent in arid or semi-arid habitats.

Etymology. The specific epithet is a patronym in the masculine genitive singular name of Donald George (Don) Broadley, a British born Herpetologist and emeritus curator of the Natural History Museum of Zimbabwe in Bulawayo. We honour his extensive work on African reptiles especially on *Boaedon*, which he could not publish before he died in 2016.

Additional Material:

Boaedon broadleyi sp. nov.

Ethiopia: Oromia region: MNHN 1905.0194 (juvenile) Mega (former Abysinie, Mego), (approx. 04° 03' N 38° 18' E); TMHC 2021.05.976 (adult, collector Vladimír Trailin DNA voucher), Yabello (04° 53' N 38° 05' E, 1906 m).

Boaedon subniger sp. nov.

(Figs. 5, 6)

Boaedon fuliginosus Spawls, Mazuch & Mohamad 2023: 443 from Erigavo (Somaliland)

Holotype: ZMH R22350 (DNA voucher **TMHC 2023.01.1018**): a juvenile female from 8.5 km south of Yuffleh (Yufle, Jooflie) (approx. 10° 18' 00" N 47° 10' 58" E, 1758 m), Sanaag region, Somaliland collected by Tomáš Mazuch, 31 August 2017, and donated to the Zoological Museum Hamburg (ZMH) in September 2024 (Figs. 5, 6)

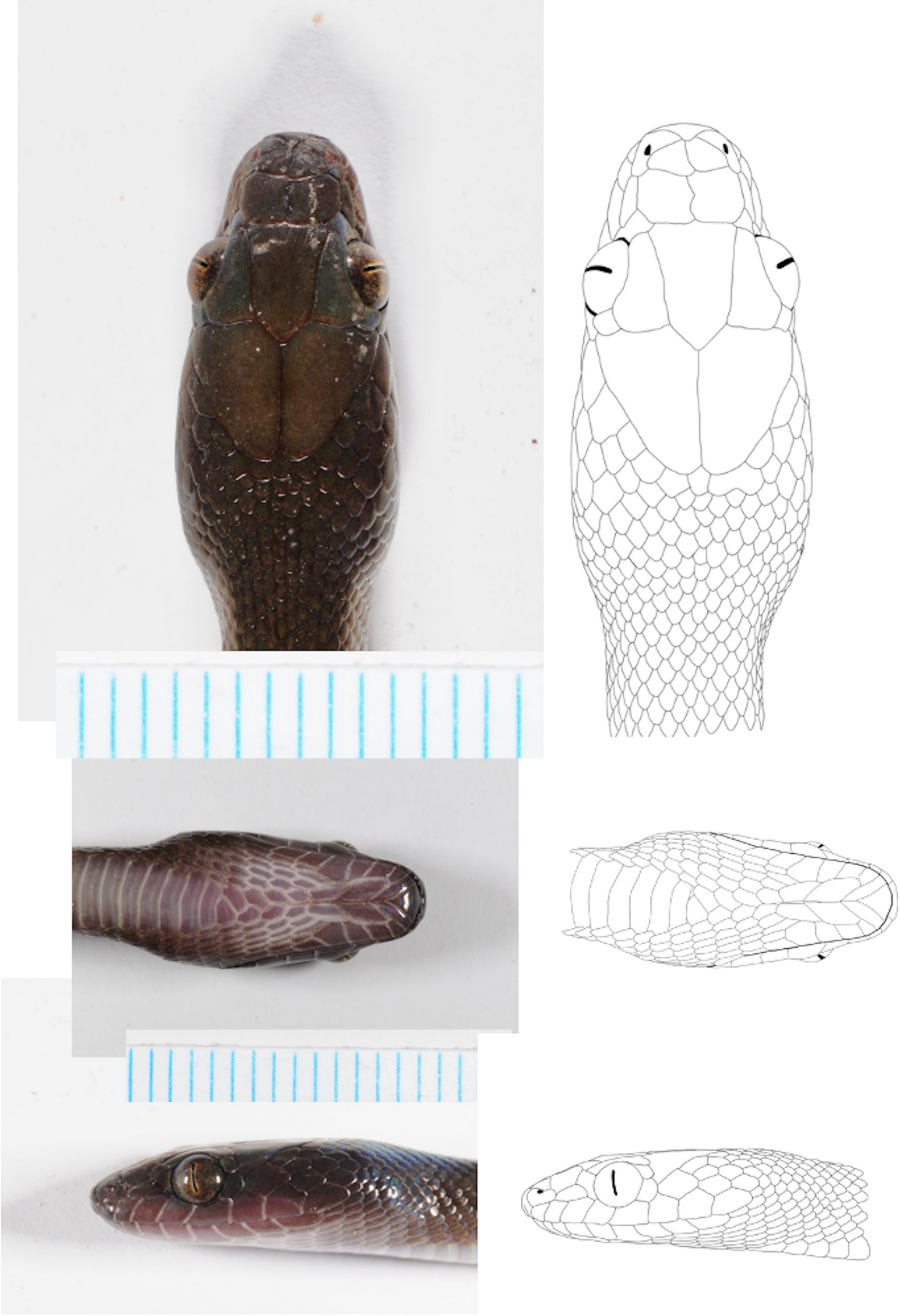

FIGURE 5. Holotype of *Boaedon subniger* **sp. nov.** (ZMH R22350) 8.5 km south of Yuffleh 1758 m, Sanaag region, Somaliland Left: head in dorsal, ventral and lateral view, right side drawings of the head. Photo: Tomáš Mazuch.

FIGURE 6. Live photo of *Boaedon subniger* **sp. nov.** from nearby Yuffleh, Gumbi Hills, Somalia. Photo by Tomáš Mazuch.

Diagnosis. *Boaedon subniger* **sp. nov.** can be distinguished from most congeners by its dark brown to black-brown dorsal colour, without any light head stripes, two supralabials (4th & 5th) touching on eye and one preocular, touching the frontal. PAR is longer than the distance between the frontal and the rostral scale. Venter whitish (for more characters see table 4).

Boaedon subniger **sp. nov.** differs from *B. broadleyi* **sp. nov.** by having fewer MSR (, $\bar{x}$ 27.0, versus 27–33, $\bar{x}$ 29.1, only one preocular (versus two) and its blackish brown or dark brown body colouration without light coloured head stripes (versus reddish, olive-brown or light brown body colouration with two short white head stripes and lips whitish coloured), with no dorsals uncoloured (versus first two rows uncoloured in *broadleyi* **sp. nov.**). *Boaedon maculatus* has an additional row of scales between the supralabials and loreal between nasal and preocular scale, (versus no row of scales) and 10–11 supralabials (versus 8). Extralimital species: *Boaedon montanus* in its whole distribution area differs in having two at least short head lines and whitish upper and lower lips (versus no headlines and no whitish lips), *Boaedon perisilvestris* with similar colouration differs in having more MSR (29–31, $\bar{x}$ 29.4 (versus 27 $\bar{x}$ 27.0 in *B. subniger* **sp. nov.**) and frequently three supralabial scales touching eye (versus two in *B. subniger* **sp. nov.**) and a genetic interspecific distances of 0.024). *B. paralineatus* and *B. capensis* species complex differs in having clear head and/or body lines (versus no head and body lines in *B. subniger* **sp. nov.**) and a brown or reddish colouration (versus blackish brown colouration in *B. subniger* **sp. nov.**)

Description of holotype: Juvenile female, 222 mm SVL; head sub-triangular, slightly distinct from the neck, HL 11.4 mm (5.1 % of SVL (222 mm); interocular distance 4.0 mm, pupil elliptical, eye diameter 2.3 mm; loreal rectangular, about 2.1 x as long (1.5 mm) as high (0.7 mm); body cylindrical; tail moderately short (8.5 % of SVL). Supralabials 8/8, 3th, 4th and 5th on left side of head and 4th and 5th on right side of head contacting orbit; infralabials 9/9, 1st 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; two postoculars in contact with the lower part of parietal scale caudally, upper postocular in contact with supraocular anterior-dorsally. Lower postocular in contact with 5th and 6th supralabial (both sides of head) ventrally; temporals 1+2+3 on both sides;

two internasals; nasal divided; frontal longer (3.5 mm) than wide (1.9 mm); Parietal length (3.8 mm) longer than distance from frontal to rostral (2.3 mm); dorsal scales smooth, 22 SR one head-length posterior to jaw rictus, 27 MSR at midbody, 21 SR one head length anterior to vent; ventrals 225; anal plate entire; 43 subcaudals, all paired.

Colouration of holotype in ethanol: dorsal body colouration dark brown without any light head stripes. Venter whitish, no dorsal scales light coloured, upper and lower labials same colour as dorsum.

Colouration in life (Fig. 6): as above, but colour almost black.

Variation: see Table 4.

Distribution: the species is found only in Northern Somalia (Sanaag region, Somaliland (1760–1780 m asl) (Fig. 2).

Habitat and Natural History notes: The specimens were found in high-altitude semiarid or arid habitats from Somaliland (Sanaag region).

Etymology: The species is named after the Latin word "subniger" for blackish, somewhat dark, from its blackish body coloration without any stripes on head or body.

TABLE 2. Comparison between the different species of *Boaedon* occurring in East-Africa. Measurements in mm.

	Boaedon broadley sp.n. (n= 15: 3/9 +3 juv.)	*Boaedon subniger sp. n.* (n= 1 juv.)	*Boaedon* sp. black ethiopian form (n= 2/2)	*Boaedon montanus* (n= 69 Frade et al 2022	*Boaedon montanus* Uganda, S-Sudan (n=22:10/9+3 juv.)	*Boaedon capensis* n: 24/41
Maximum SVL (♂/♀)	732/1196	-/?	437/732	–/985	500/ 865	605/985
Maximum TL (♂/♀)	130/120	-/?	93/99	18,9%/125(15,4%)	115/ 130	130/ 140
MSR	27–33 x̄ 29,1	27 x̄ 27,0	27–29 x̄ 28.5	25–33 x̄ 28.8	27–31 x̄ 28.8	26–29/25–32 x̄ 27
Ventral scales (♂/♀)	191–224/223–240	-/225	222–235/197–210	201–216 / 215–234	199–228 /207–253	186–216/ 202–230
Subcaudal scales (♂/♀)	59–63/45–55	-/43	58–68/47–50	62–70/45–58	63–70 / 45–57	51–69 /39–63
Subcaudals rows	Double	Double	Double	Double	Double	Double
Preoculars	2	1	2	1–2	1–2	1–2
Postoculars	2	2	2	2	2	2
Supralabials touching the eye	2–3 (45/55%	2/3	2	2	2–3 (95.5/4.5 %)	2–3
Cloacal Plate	entire	entire	entire	entire	entire	entire
Head stripes	present	absent	absent	present	Present 77.3 %	present
Colouration (dorsum)	light brown, olive brown	Blackish-brown	blackish-brown	brownish	Brown Greybrown/ olive brown	brown / reddish
Colouration (ventral)	whitish	whitish	pigmented	whitish	Whitish, 1 pigmented	whitish
Preocular contact frontal	x	x	x	-	86.4 % 13.6% absent or in one point	?
PAR-Rostr/Par.Snout	100%/0	0/100%.	75%/25%	?/100 %	86%/14%	85%/15%

TABLE 3. Morphometric (in mm) and meristic character comparison of *Boaedon broadleyi* **sp. nov.** available material, X: present, –: absent or missing

Examined material	ZMH R08485 **holotype**	MNHN 4342 paratype	ZMH R08486 paratype	ZMH R11333 paratype	ZMH R11341 paratype	ZMH R11342 paratype	ZFMK 16231 paratype	ZFMK 16232 paratype	ZFMK 16293 paratype	ZFMK 16294 paratype	ZFMK 19159 paratype	ZFMK 16299 paratype	MNHN 1905.194	
Sex	Female	Female	Male	Female	Male	Female	Female	Female	Female	Female		Male	Juvenile	
SVL	1196	615	732	713	591	646	635	688	660	560	650	600	236	560–1196 $\bar{x}$ 714.1, n:8 591–732 $\bar{x}$ 641, n:3
Tail length	116	95	130	87	120	80	93	95	86	86	96	120	28.9	
SVL/TL	10.3	6.5	5.6	8.2	4.9	8.1	6.8	7.2	7.7	6.5	6.8	5.0	8.2	
MSR	29	33	31	29	29	29	29	29	29	27	29	27	29	27–33, $\bar{x}$ 29.25 n:8 27–31 $\bar{x}$: 29 n3
Ventral scales (V)	243	232	224	223	191	240	232	231	240	229	231	210	225	223–240 $\bar{x}$ 233.75, n: 8 191–224, $\bar{x}$ 208.3
Subcaudals (SC)	53	55	63	53	63	52	47	51	49	45	54	59	42	
V/SC	4.6	4.2	3.5	3.5	3.0	4.6	5.0	4.5	4.9	5.1	4.3	3.6	5.4	
Supralabials (entering eye)	8	8	8	8	7	8	8	8/9	8/9	8	8	8	8	
Infralabials (touch 1st chin shields)	9/10	9/10	8	10	8/10	8	9	10	10	9	9	9	9	
Loreal length	4.5	3	3.3	3.3	4.5	2.5	3.3	2.8	2.9	3.2	3.1	2.8	1.0	
Loreal height	1.6	1.3	1.4	1.5	1.6	1.1	1.5	1.5	1.3	1.3	1.8	1.8	0.7	
Loreal L/H ratio	2.81	2.3	2.4	2.2	2.8	2.3	2.2	1.9	2.2	2.5	1.7	1.6	1.5	
Preocular	2	2	2	2	2	2	2	2	2	2	2	2	2	
Preocular touch frontal	x	x	x	x	x/-	x	x	x	x	x	x	x	x	
Postocular	2	2	2	2	2	2	2	2	2	2	2	2	2	
Supralabial touch eye	3	3	2	3	3	2	2	2	3	2	3	2	2	
Parietal length equal to distance frontal to rostral	x	x	x	x	x	x	x	x	x	x	x	x	x	

TABLE 4. Morphometric (in mm) and meristic character comparison of *Boaedon subniger* **sp. nov.** available material, X: present, –: absent or missing

Examined material	ZMH R22350 TMHC 2023.01.1018	
Sex	Female juv.	
SVL	222	
Tail length	26	
SVL/TL	8.5	
MSR	27	27, $\bar{x}$ 27.0 n:1
Ventral scales (V)	225	225 $\bar{x}$ 225.0, n: 1
Subcaudals (SC)	43	
V/SC	5.2	
Supralabials (entering eye)	8	
Infralabials (touch 1st chin shields)	9	
Loreal length	1.5	
Loreal height	0.7	
Loreal L/H ratio	2.1	
Preocular	1	
Preocular touch frontal	x	
Postocular	2	
Supralabial touch eye	2/3	
Parietal length equal to distance from frontal to rostral	No, longer	

Discussion

Using an integrative approach, we combined phylogenetic and morphological data, resulting in a better understanding of species richness and diversity of snake species of the *Boaedon fuliginosus* complex in Ethiopia and adjacent countries.

Our phylogenetic results provide evidence for the presence of five strongly supported (≥70% bootstrap values and ≥0.95 BI posterior probabilities) *Boaedon* clades in Ethiopia, Somalia, East Africa (Tanzania, Kenya, Burundi, Rwanda, Kivu region Democratic Republic of Congo, DRC) and Yemen. These correspond to *B. arabicus*, *B. broadleyi* **sp. nov.**, *B. montanus*, *B. subniger* **sp. nov.** and a clade of *B. capensis* s.l.

Some of these taxa are morphologically very similar, and have been confused in the past (e.g., Hughes 1997, Largen & Spawls 2010; Kelly *et al.* 2011; Greenbaum *et al.* 2015 as *B.* cf. *fuliginosus*). Two endemic species in Ethiopia and Somalia were described as new and can be distinguished by morphology and genetic analysis. At present, *Boaedon subniger* **sp. nov.** is restricted to dry habitat in northern Somaliland, wheras *B. broadley* **sp. nov.** is widespread across Ethiopia, including the western border region to Somalia (see map Fig. 2). A morphologically different population without any genetic data available, referred to as "black coloured form" and known from the Gambeli and Kaffa regions, may also be an undescribed species. Without genetic validation, we could not describe it as new.

Boaedon montanus was described by Trape *et al.* (2022) from a population in Rwanda and Kivu region of eastern DRC. The authors mentioned that it may be more widespread in South Sudan, Uganda and Tanzania. This assumption was corroborated by a molecular-genetic analysis of 16S rRNA based on specimens from Uganda and Mount Kilimanjaro, analysed by the senior author (Hallermann *et al.* 2020). Trape *et al.* (2022) gave a diagnosis for the populations from Burundi, Rwanda, and Kivu, albeit not for the species in its whole distribution area because he did not examine any other specimens from Uganda, South Sudan, Sudan or Tanzania. *B. montanus* varies much more in pholidosis characters and coloration than given in its original description (Table 2):

Preocular and frontal are in contact in 86.4%, and not in contact in 13.6% of the specimens studied.

PAR is equal to the distance between the frontal and the rostral scale in 86% and longer in 14% of examined material. Colour in life varies from olive-brown to brownish and in preservative from dark brown to grey-brown, with two short head lines present in 73% of examined material. The distribution of *Boaedon montanus* extends from Kericho in Kenya to around Lake Victoria in Uganda, South Sudan (Equadoria region, Eastern region), Sudan (Darfur region) and Tanzania to Virungas in Eastern DRC and Rwanda. According to Trape *et al.* (2022), 65 specimens collected between 1949 and 1953 and previously studied by Laurent (1956) from Rwanda, Burundi, Kivu (DRC) may also belong to this species, but these have no genetic samples.

Our examined material shows that in South Sudan two different species of the genus *Boaedon* exist, a *lineatus*-like species (*B. paralineatus* in Equadoria province) and a more *fuliginosus*-like species, *B. montanus* (see map, Fig. 2). For Sudan, *B. paralineatus* was proven to occur in the eastern part and North Kordofan state, formerly known only more westwards in Chad (Trape & Mediannikov 2016).

Our phylogenetic analysis shows that *Boaedon angolensis* has a much greater distribution than formerly known and can be found in the Kwango province of DRC. *Boaedon arabicus* is proven clearly to be a distinct species and not conspecific with *B. fuliginosus* (Uetz *et al.* 2024).

Given the morphological conservatism of the genus *Boaedon*, 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.

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Comparative material

Boaedon arabicus: MHNG245676 (Wadi Warazan, Yemen)

Boaedon capensis s.l.*:* ZMB 1784 (Mozambique), ZMB 4233 (Tete, Mozambique), ZMB 4362 (Island of Mozambique, Mozambique), ZMB 6944 (Gerlachshoop, Deutsch-Ostafrika, Tanzania), ZMB 11936 (Tanga, Tanzania), ZMB 13270 (at the foot of Mount Kilimanjaro, Marangu, Deutsch-Ostafrika, Tanzania), ZMB 16711 (Mohoro, Mohorro, Deutsch-Ostafrika, Tanzania), ZMB 17233 (Kitope Village (06° 01' 00" S 39° 16' 00" E), Bagamoyo Kitopeni, Tanzania), ZMB 16693 (plantation, Usambara, Nguelo, Deutsch-Ostafrika, Tanzania), ZMB 16687, ZMB 16697 (Konde (landscape at northern end of Njassa), 525 m, Ipiana, Deutsch-Ostafrika, Tanzania), ZMB 16701 (Ubena, Tanzania), ZMB 5934, ZMB 17237 (Zanzibar, Deutsch-Ostafrika, Tanzania), ZMB 17245 (Nguelo, Handei, Ost Usambara, Tanzania), ZMB 17446

(Mombasa, Kenia), ZMB 17450 (Lamu Island, Kenya), ZMB 17436, ZMB 17567 (Takaungu, small village near Kilifi, Kenya), ZMB 17702 (Handeiberge, E Usambara, Tanzania), ZMB 19713 (Deutsch-Ostafrika, Tanzania), ZMB 20476, ZMB 21103 (Mlalo, Wilhelmstal, Tanzania), ZMB 20343, ZMB 21052 (Langenburg, near Lake Malawi, 1564 m, old Langenburg 09° 34' 00" S 34° 07' 60" E), Deutsch-Ostafrika, Tanzania), ZMB 21481(Nguru, Tanzania), ZMB 21483 (Mlalo, big village of the Waschambaa (s.d.) in western Usambara, Deutsch-Ostafrika, Tanzania), ZMB 21618 (Windhuk, Namibia), ZMB 23479 (Zimba, Kenya), ZMB 23566, ZMB 23568 (Likrange near Tendaguru (mountain in the SE), Tanzania), ZMB 24025 (Nguru Mountains, 1400 m, Deutsch-Ostafrika, Tanzania), ZMB 24585 (Kibonoto = Kibongoto, Kilimanjaro, Tanzania), ZMB 27755 (Mikindani, Bezirk Lindi, Tanzania), ZMB 28005A (Tendaguru, Tanzania), ZMB 17235, ZMB 29056 (Deutsch-Ostafrika), ZMB 29372A, ZMB 29372B (Mikindani, Tanzania), ZMB 52615 (Blantyre, Malawi), ZMB 27615, ZMB 69856, (Morogoro, Morogoro District, Tanzania), ZMB 16698, ZMB 69936, ZMB 69937, ZMB 69938, ZMB 77818 (Kilimanjaro, Deutsch-Ostafrika, Tanzania), ZMH R08035 (Pemba, Mozambique), ZMH R08042 (Lewa, Tanga, Tanzania), ZMH R08050 (Kasanga, Rukwa Region, Tanzania), ZMH R08051-53 (plantation Buschinihof, Pangani, Tanzania), ZMH R08067 (South Africa), ZMH R08233 (Dar es Salaam, Tanzania), ZMH R08332, (plantacao Nangororo, Pemba, Mozambique), ZMH R08339 (East Africa), ZMH R08357-59 (Barikiwa, Donde area, Lindi, Tanzania), ZMH R08366 (Kokotoni (Mkokotoni), Zanzibar), ZMH R08369 (Amani, Usambara, Tanga, Tanzania), ZMH R01738, R08605 (Quelimane (11° 09' 47" S 40° 18' 15" E), Mozambique), ZMH R11346 (East Tanzania).

Boaedon montanus: MNHN 1997.6556 (subad.) (Boma (Village, approx. 06° 24' 40.92" N 34° 43' 0.58" E), South Sudan), ZFMK 26013 (South Sudan), ZFMK 29683, ZFMK 29706, ZFMK 29727-30 (Talanga-Forest, Equadoria, South Sudan), ZFMK 39896 (Darfur, Sudan), ZFMK 47636 (Cyamudongo, Rwanda), ZFMK 61623 (paratype) (Nyungwe (03° 00' 8.85" S 29° 13' 51" E), Rwanda), ZMH R08487-88, ZMH R11331-32, R11335, R11344-45, R11347, R11349, R11351, R11353 (northern coast of Lake Victoria, Uganda).

Boaedon paralineatus: ZFMK 29562 (Equatoria, South Sudan), ZFMK 34534 (Juba to Torit, Equatoria, South Sudan), ZFMK 34535 (juv) (Bahr-el-Ghazal, South Sudan), ZFMK 38417 (Ingessana Hills (11° 40' 53.07" N 33° 53' 4.04" E), Sudan), ZFMK 38418 (Rahad (14° 54' 16.28" N 33° 54' 57.56" E), Sudan).

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary Material: Specimens used for genetic analyses and corresponding GenBank accession numbers.