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Generic affinities of African house snakes revised: a new genus for *Boodon erlangeri* (Serpentes: Elapoidea: Lamprophiidae: Lamprophiinae)

Arthur Tiutenko[1], Claudia Koch[2], Maciej Pabijan[3] & Oleksandr Zinenko[4]

[1] Friedrich-Alexander-Universität Erlangen-Nürnberg, Schlossplatz 4, 91054 Erlangen, Germany
[2] Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany
[3] Department of Comparative Anatomy, Institute of Zoology and Biomedical Research, Jagiellonian University, 30-387 Kraków, Poland
[4] V. N. Karazin National University, 4 Svobody sq., 61022 Kharkiv, Ukraine

Corresponding author: Arthur Tiutenko, e-mail: arthur.tiutenko@fau.de

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Abstract. *Lamprophis erlangeri* is a lamprophiid snake endemic to moist montane forest remnants and formerly forested areas in the south and south-west of the Ethiopian highlands. Its vernacular name 'Ethiopian House Snake' is a result of century-long speculations about the generic placement of this species. New molecular and morphological data brought evidence that it has been misplaced in both genera of 'African house snakes', *Lamprophis* and *Boaedon*. A new genus is described to accommodate *L. erlangeri*. It represents a sister clade to the Western and Central African genera *Bothrophthalmus* and *Bothrolycus* from which it differs by general body form and proportions, head shape, number of preocular scales, absence of loreal pits, maxillary dentition as well as by a number of cranial features. The type locality of the type species of the new genus, originally 'Somaliland', is restricted in this paper to Abera in Ethiopia. *Lamprophis abyssinicus*, the second Ethiopian endemic in this genus is assigned again to the genus *Pseudoboodon* on a basis of similar external morphology and cranial osteology. In the course of this revision of systematic affinities in *Lamprophis* and *Boaedon*, also the status of the genus *Alopecion*, considered to represent a junior synonym of these genera, is revalidated. It is reinstated as a valid monotypic genus, to include *L. guttatus*, a South-African species with similarly turbulent taxonomic history as of *L. erlangeri*. Cranial osteology of *L. erlangeri*, *L. abyssinicus*, and *L. guttatus* is analysed for the first time. Morphological, ecological and behavioural characters of the related genera *Alopecion*, *Boaedon*, *Bothrolycus*, *Bothrophthalmus*, *Lamprophis*, *Lycodonomorphus, Pseudoboodon*, and of the new genus are reviewed and compared.

Key words. *Alopecion annulifer*, *Boaedon abyssinicus*, *Boaedon erlangeri*, *Boaedon guttatus*, Boaedontini, cranial osteology, *Lamprophis abyssinicus*, *Lamprophis guttatus*, molecular genetics, morphology, osteology, *Pseudoboodon,* skull, Squamata, systematics, taxonomy.

Introduction

The 'Ethiopian House Snake', *Lamprophis erlangeri* (Sternfeld, 1908) is a lamprophiid snake species endemic to moist montane forest remnants and formerly forested areas in the south and south-west of the Ethiopian highlands. This snake occurs neither in houses nor in settlements, and its vernacular name is a result of century-long speculations about its systematic affinities, when it was moved back and forth between two African 'house snake' genera. *Lamprophis* Fitzinger, 1843 and *Boaedon* Duméril, Bibron & Duméril, 1854. This species is uncommon and remains poorly studied; it is rare in museum collections, and few herpetologists have ever had a chance to see *L. erlangeri* in the wild. No new specimens were collected in the past 30 years, and no new information about this snake was published till now, since its rediscovery in 1992 (Nečas et al. 1993).

Sternfeld (1908) described this species as '*Boodon Erlangeri*' from a specimen donated by Erlanger and Neumann, having assigned it, without any explanation, to the genus *Boaedon* (at that time spelt *'Boodon'*, after an emendation by Günther 1858). Broadley (1983) synonymised *Boaedon* with *Lamprophis* when he recognised that the characters originally used for distinguishing these genera were invalid. This decision was followed by Auerbach (1987) and authors of various other books and journal articles who treated *Boaedon* either as a junior synonym of *Lamprophis* or as a separate genus, and moved some or all species, including *L. erlangeri*, from one genus to another

(Meirte 1992: 105, Largen & Rasmussen 1993, Nečas et al. 1993, Nečas 1997, Largen & Spawls 2010: 467).

Subsequently, Kelly et al. (2011) resurrected the genus *Boaedon* and restricted *Lamprophis* to the south and southeast of the continent. They had deliberately left *L. erlangeri* in the genus *Lamprophis*, with an option that it may be assigned to *Boaedon* in future, as soon as more data on this species become available. However, in the book "Snakes of the World" by Wallach et al. (2014: 97), *L. erlangeri* ended up as '*Boaedon erlangeri*' again, without argumentation, presumably because this species had once been in this genus and as a conclusion from the study of Kelly et al. (2011), but also following the established opinion that this snake were similar enough to be a *Boaedon*.

Lamprophis erlangeri is a fairly large representative of the family, probably exceeding 1200 mm in size. It is a slender snake, with a narrow head, rather small black eyes, and a cylindric body covered by glossy scales that show strong blue and violet iridescence in bright light. Hatchlings are entirely black (Nečas 1997), and sometimes the whole bodies and heads of adult animals remain black from above and below, but more usually there is a broad brown or dark yellow stripe along the back that continues from the neck to the tail tip. Sternfeld (1908: 92) describes this species as follows (translated from German): "Rostral broader than high, its upper part = 1/3 of distance from the frontal. Internasals shorter than prefrontals. Frontal 1 1/3 longer than broad, as long as the distance to the snout tip, a little shorter than the parietals. Loreal as long as broad. 1 preocular, not reaching the top of the head. 2 postoculars. 8 upper labials, the 4th and the 5th in contact with eye. T = 2+3 or 3+4. Four lower labials in contact with anterior chinshield, that is larger than the posterior. Nasal divided. Colour: Black-brown above and below. Length 32 cm. Tail 4 cm. 1 specimen. V = 205. Sq = 21. Sc = 46. Somaliland. Erlanger and Neumann."

Notably, Sternfeld (1908) did not compare his new species to other members of the genus, nor did he refer to an important diagnostic character of *Boaedon*: enlarged anterior maxillary teeth (Duméril et al. 1954). Yet, this snake should have somehow reminded him of a 'house snake'. In the 19th and at the turn of the 20th century, a few species of African snakes were misplaced in the genus *Boaedon* in a similar way, according to their general resemblance. Indeed, the majority of Lamprophiinae Fitzinger, 1843 appear similar to each other based on their overall proportions and elongated body form. This certainly applies to *L. erlangeri* as well. Here, we re-examine its morphology for the first time since the initial description of this species and report additional distinctive characters. New molecular results and an amended morphological diagnosis allowed a revision of the systematic position of this species.

Material and methods

On 7 October 2016, we found a juvenile individual of *L. erlangeri* at 6°30'04" N 39°44'42" E, 1480 m a.s.l., in the south of the Harenna Forest, a large forested area that covers the southern slope of the Eastern Highlands in Ethiopia. The specimen was photographed, measured and studied on site. The specific identity of the snake was reasoned in the field from the external characters and the geographic locality, and subsequently confirmed by a comparison with the holotype ZMB 27419, housed in Museum für Naturkunde, Berlin. This specimen was a juvenile female (Fig. 1), with the following measurements: snout–vent length (SVL) 294 mm, tail length (TL) 41.5 mm, head length (HL) 17 mm, head width (HW) 8 mm, head height (HH) 5.2 mm, naris–orbit distance (NOD) 3.5 mm, horizontal eye diameter (ED) 2.2. mm, midbody scale rows (MBR) 23, ventrals (V) 236, subcaudals (SC) 46 pairs, anal entire, upper labials 8 (4th and 5th entering orbit), lower labials 8 (2nd–4th in contact with anterior chinshield), anterior chinshield about twice as long as the posterior, loreal present, nasal divided, preocular 1, postoculars 2, temporals 2+3. Colour: Venter and flanks black, dorsum faintly brown, gular area, labials and snout tip yellow. Five years later, we returned to that record and made it the starting point of this study.

Laboratory procedures

We extracted total genomic DNA according to standard protocols as described previously (Tiutenko & Zinenko 2021) from an ethanol preserved tissue sample that had been taken (by scale clipping) from the aforementioned live specimen. In order to make our results comparable with previous research of other authors (Lawson et al. 2005, Nagy et al. 2006, Vidal et al. 2009, Pyron et al. 2011, Kelly et al. 2011, Greenbaum et al. 2015, Zaher et al. 2019) we sequenced the same four genes: mitochondrial 16S rRNA (16S), cytochrome b (cyt b) and NADH dehydrogenase subunit 4 (ND4), as well as the c-mos proto-oncogene (c-mos) encoded in the nuclear genome. The primers and reaction conditions followed De Queiroz et al. (2002) for cyt b, Burbrink et al. (2000) for 16S; Arévalo et al. (1994) for ND4 and Slowinski & Lawson (2002) for c-mos. The new sequences are available in NCBI GenBank under accession numbers given in the supplementary document.

Phylogenetic analyses

We aligned the newly obtained sequences with publicly available sequence data for representatives of all closely related genera (subfamily Lamprophiinae) as well as *Aspidelaps scutatus*, *Atractaspis bibronii*, *Buhoma procterae*, *Duberria lutrix*, *Prosymna ruspolii*, and *Psammophis crucifer* that served us as outgroups. A list of the NCBI GenBank numbers of all sequences that we have used is given in supplementary document. The alignments of cyt b, ND4 and c-mos were then concatenated, and the best-fitting partitioning scheme was inferred in Partition Finder v2.0 (Lanfear et al. 2017). Although we had sequenced the 16S gene of our sample, we used it only for calculations of genetic distances

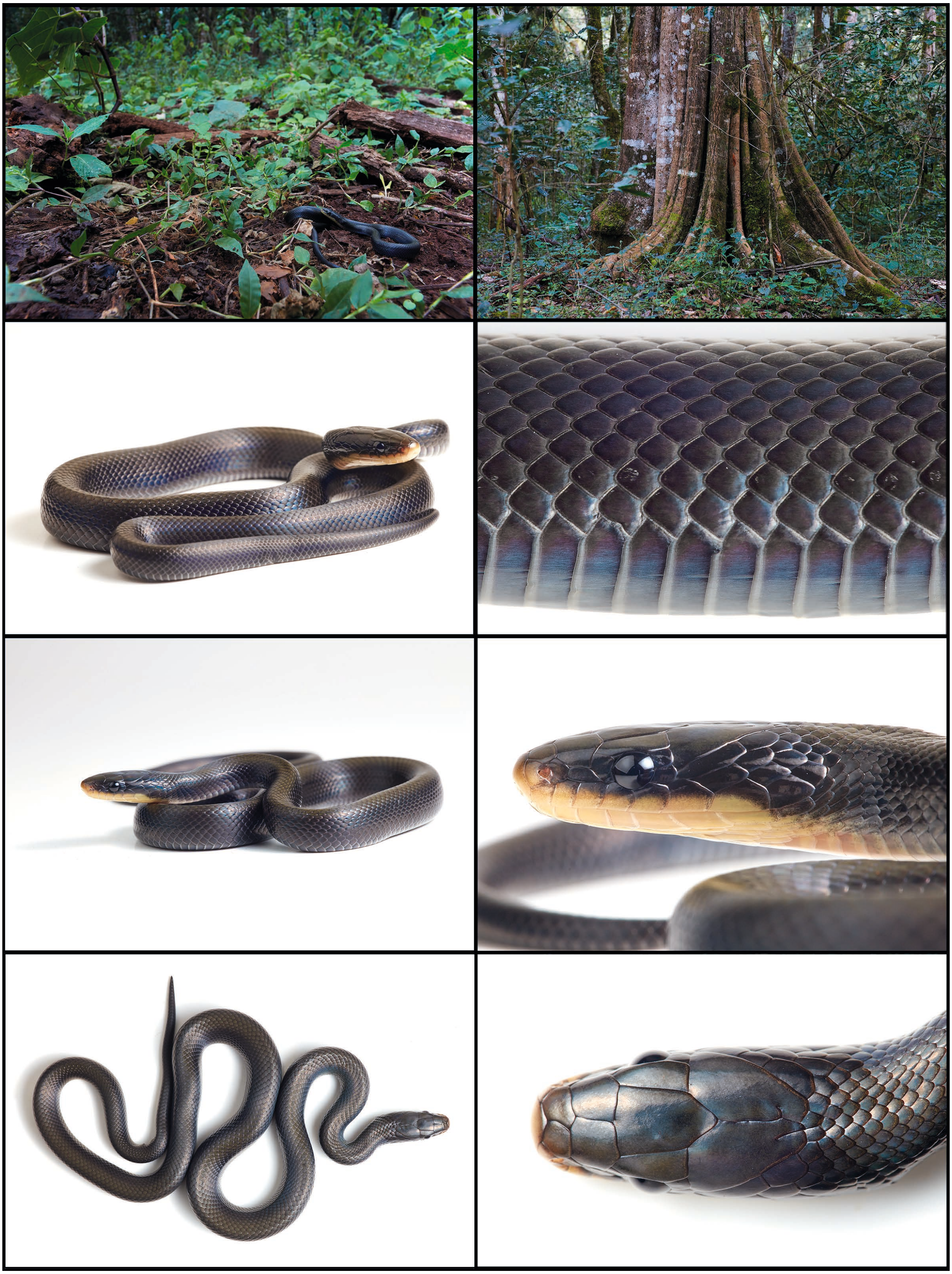

Figure 1. Young *Lamprophis erlangeri*, photographed in situ (at 6°30’04” N, 39°44’42” E, 1,480 m a.s.l., Harenna Forest, Ethiopia), habitat at the locality, and ex situ photographs of the same specimen made in a field studio near the capture site.

and did not include in phylogenetic dataset due to lack of sequences of this locus for the majority of the related taxa. A Bayesian phylogenetic analysis was performed in Mr. Bayes v3.2.2 (Ronquist et al. 2012) with a partitioned matrix of sequences where cyt b and c-mos are treated as one partition and the GTR+G+I substitution model, and ND4 is the second partition with GTR+G substitution model. The analysis included four runs of 300 million generations, with sampling of every 100th generation. We tested for convergence between runs with the use of Tracer v1.6 (Rambaut et al. 2015) by visually inspecting the overlap in likelihood and parameter estimates between runs, as well as the effective sample sizes and the potential scale reduction factor (PSRF) for each run. The resulted consensus tree was visualised in FigTree v1.4.2 (Rambaut 2014). For construction of phylogeny of this taxonomic group, in order to save computation efforts, we chose one representative of each genus (usually of the type species, if available), while in the analyses of genetic diversity all available sequences of each studied gene and genus were used.

The estimates of the evolutionary divergence between and within genera were performed in MEGA X (Kumar et al. 2018). The analysis involved 50 16S, 60 cyt b, 54 c-mos and 47 ND4 nucleotide sequences. There were 562 nucleotide positions in the final 16S data set, 1,117 in cytochrome b, 708 in c-mos, and 672 in ND4.

Morphological analyses

To assess the morphological characters, we examined the holotype ZMB 27419 and other twelve specimens of *L. erlangeri* found in collections of the Natural History Museum (NHMUK), London, UK, of Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany, and of the Museum of Nature, at the V. N. Karazin National University, Kharkiv, Ukraine (KUMN): KUMN Г-1985, vicinity of Manyate, Bale, Oromia; NHMUK 1973.3249, Buyo Village, 14 km S.W. of Jimma, Kaffa; NHMUK 1973.3248, near Shashamane, Shoa; NHMUK 1973.3158–3163, Ghimbi, Wollega; NHMUK 1976.1667, Godare, Illubabor; ZFMK 55533, Bedele, Illubabor; ZFMK 55534, Bedele, Illubabor. Due to COVID-19 pandemic our work with museum collections in 2020 and 2021 was restricted, and we had to refer to photographic images in some cases.

To conclude about the distinctiveness of the external morphological characters of *L. erlangeri*, we studied and compared the published descriptions of the closely-related genera or of their type members. Along with two closest relatives, *Bothrolycus* Günther, 1874, and *Bothrophthalmus* Peters, 1863, we included in our analyses *Boaedon* and *Lamprophis*, both genera that *L. erlangeri* used to be assigned to. For the sake of completeness, we also studied *L. guttatus* (Smith, 1843), a species with similarly controversial taxonomic history, as well as *Lycodonomorphus* Fitzinger, 1843, a closely-related and morphologically similar genus to *Lamprophis*. However, we omitted *Lycodonomorphus inornatus* (Duméril, Bibron & Duméril, 1854), a species with unresolved generic placement, requiring another in-depth study that would go beyond the scope of this article. Finally, we included in our analyses *Pseudoboodon* Peracca, 1897, a genus that is a sister clade to all above-mentioned genera and is sympatric with *L. erlangeri*. This group of six genera represents a monophyletic clade that corresponds to 'Group I' that was recognised by Bogert (1940). Dowling (1969) listed a number of synapomorphies and described a tribe Boaedontini. This has been followed, for instance, by Dowling & Duellman (1978) and Rasmussen & Largen (1992). In more recent works, after all member genera have been moved to Lamprophiidae, the name does not occur. For practical reasons, particularly when we discuss common morphological traits, we find it convenient to treat this group again as Boaedontini Dowling, 1969 – 'African house snakes and allies'. However, we refrain from assigning of the remaining Lamprophiinae, namely Bogert's (1940) 'Group II', to taxonomic categories, mainly due to uncertain position of *Lycophidion* Fitzinger, 1843 (Lawson et al. 2005, Kelly et al. 2011, our results).

The comparative illustrations (Fig. 8) of head morphology of *Lamprophis erlangeri* and of the type species of six Boaedontini genera – *Boaedon capensis* Duméril, Bibron & Duméril, 1854, *Bothrolycus ater* Günther, 1874, *Bothrophthalmus lineatus* Peters, 1863, *Lamprophis aurora* (Linnaeus, 1754), *Lycodonomorphus rufulus* (Lichtenstein, 1823), *Pseudoboodon gascae* Peracca, 1897 – as well as of *Lamprophis guttatus*, are generalised and were performed from several individuals. The illustration of *Lamprophis abyssinicus* Mocquard, 1906, shown in the same plate, is based on the holotype MNHN RA-1905.188 housed in Muséum National d'Histoire Naturelle, Paris, France. Since shapes and proportions considerably differ in each species, the images are approximately adjusted to one size and aligned according to the distance between snout tip and mouth corner.

To conclude about the generic placement of *Lamprophis abyssinicus*, we studied, along with the holotype, an additional specimen: NHMUK 1972.105, Wush-Wush, Kaffa. Since this species was once assigned to the genus *Pseudoboodon*, we examined for comparison the following 15 specimens in collections of Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), of Zoologische Staatssammlung, Munich (ZSM), and of World Museum, Liverpool (LIV): ZFMK 15878–79 (*P. lemniscatus*), ZFMK 16296 (*P. lemniscatus*), ZFMK 55510–12 (*P. lemniscatus*), ZFMK 55532 (*P. lemniscatus*), ZFMK 60544 (*P. lemniscatus*), ZFMK 68421–22 (*P. lemniscatus*), ZSM 2/2017 (*P. gascae*), LIV 2003.47.1–3 (*P. gascae*), LIV 1986.212.242 (*P. lemniscatus*).

An exact comparison of eye sizes is hardly possible when we are not comparing individuals of the same age: Eyes are larger in juvenile snakes and, with increasing age, become smaller relatively to head dimensions. Hence, when we talk about eye size, it is largely our impression that we judge from. Nonetheless, this character seems to make sense because everyone can easily tell which snake species is more bold-eyed, having seen several individuals of different ages. For the purpose of this study, we consider the eye small when its diameter is smaller or equal to half the distance between the anterior border of the orbit and the posterior border of the nostril. An eye is moderately-sized when its diameter is approximately 60–70% of this distance, and large eyes are wider than 70% of the distance eye–nostril.

The osteological analysis of the skull of *L. erlangeri* is based on a high-resolution µCT scan of the specimen ZFMK 55533. The scan was performed with a Bruker SkyScan 1173, with an X-ray beam of 43 kV source voltage and 114 mA current, without filters. Rotation steps of 0.3 were applied with a frame averaging of 4, recorded over a 180° rotation, resulting in 800 projections of 500 ms exposure time each and a total scan duration of 46 min 12 s. The magnification setup generated data with an isotropic voxel size of 19.65 µm. The CT-dataset was reconstructed using N-Recon software version 1.7.1.6 (Bruker MicroCT) and rendered in three dimensions by Amira visualisation software (FEI, Thermo Fisher Scientific). Segmentation to separate and colour the bones was also performed in Amira. Osteological description and terminology follow Cundall & Irish (2008). The following abbreviations are used in figures for osteological features: acq = adductor crest of quadrate, an = angular, ar = articulatory process of quadrate, as = ascending process of premaxilla, chp = choanal process of palatine, col = columella, cp = compound bone, cps = conchal process of septomaxilla, d = dentary, ecp = ectopterygoid, epm = ectopterygoid process of maxilla, exo = exoccipital, p = parietal, pal = palatine; po = postorbital, f = frontal, f5c = foramen for mandibular branch of trigeminal, f5b = foramen for maxillary branch of trigeminal, fo = foramen ovale, ls = laterosphenoid, mp = maxillary process of palatine, mx = maxilla, na = nasal, of = optic fenestra, pfr = prefrontal, pp = palatine process of maxilla, q = quadrate, occ = occipital condyle, pcr = prearticular crest, pmx = premaxilla, pro = prootic, psp = parasphenoid rostrum, pt = pterygoid, rp = retroarticular process, mf = mandibular fossa, mp = maxillary process of palatine, sac = surangular crest of compound bone, smx = septomaxilla, so = supraoccipital, sp = splenial, st = supratemporal, tr = transverse process of premaxilla, v = vomer, vp = vomerine process of premaxilla.

The comparative illustrations of cranial morphology (Fig. 9) are based on a combination of reference images available in printed (FitzSimons 1962, Bourgeois 1968, Chippaux 2006) and digital (Digimorph 2021, MorphoSource 2021) publications, as well as on our own µCT scans of the specimen NHMUK 1982.105 (*Lamprophis abyssinicus*) loaned from the Natural History Museum, London, and of the following specimens housed in Zoologisches Forschungsmuseum Alexander Koenig: ZFMK 55510 (*Pseudoboodon lemniscatus*), ZFMK 74858 (*Lamprophis guttatus*), ZFMK 82159 (*Bothrophthalmus lineatus*). All our scans were performed with the aforementioned equipment and parameters, generating data with an isotropic voxel size of 19.65 µm for ZFMK 55510 and ZFMK 82159, and 17.03 µm for ZFMK 74858 and NHMUK 1982.105.

We visualised a selection of the most relevant morphological differences on mensural, meristic, and qualitative characters as a heatmap using the ggtree package for R (Yu et al. 2017). Complete absence or presence of a character is indicated by '1' (red colour) or '0' (green colour). Decimal fraction values are used for varying characters and result in a colour gradient between green and red.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:83B880B2-B463-417C-9AD0-5351EF867008. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: salamandra-journal.com, zenodo.org.

Results and discussion

The phylogram from the Bayesian analysis of the complete data set that is shown in Figure 2 is similar to the trees presented in previous works dealing with the phylogeny of this group (Vidal et al. 2009, Kelly et al. 2011, Greenbaum et al. 2015). Our analyses revealed that *L. erlangeri* forms a monophyletic clade as sister group to a clade including the genera *Bothrolycus* and *Bothrophthalmus*. Its support is moderate (posterior probability 0.77), but relationships within the clade are weakly resolved, with low support of further clustering of *Bothrolycus*/*Bothrophthalmus* (posterior probability 0.52). Such rather moderate support for nodes in the Lamprophiinae phylogeny was noticed by authors of other studies. For instance, Kelly et al. (2011) recognised noteworthy support only for 72% of in-group nodes. The clade, now containing *Bothrolycus*, *Bothrophthalmus*, and *L. erlangeri*, is sister to another large clade with high posterior support value, containing *Boaedon*, *Lamprophis*, and *Lycodonomorphus*.

The pairwise distances between and within the genera for each of the analysed genes are given in Tables 1–4. Uncorrected genetic p-distances from *L. erlangeri* to the most closely related genera of Lamprophiinae (*Bothrolycus* and *Bothrophthalmus*) correspond to the lower limit of intergeneric distance in Lamprophiinae which usually does not overlap with intrageneric distances (with a notable exception of the genus *Lycophidion* that is probably due to its heterogenic structure and cryptic diversity).

These molecular results clearly demonstrate that *L. erlangeri* is misplaced in the genus *Lamprophis* as well as in the genus *Boaedon*. On the other hand, it cannot be as-

Table 1. Estimates of evolutionary divergence in mitochondrial 16S rRNA (16S) gene sequences (uncorrected p-distances) between selected genera of Lamprophiinae and within *Boaedon* and *Lycodonomorphus* (in bold).

	Bofa gen. n.	*Boaedon*	*Bothrolycus*	*Lycophidion*	*Lycodonomorphus*	*Alopecion*	*Boaedon geometricus*
Bofa gen. n.	–	0.064	0.039	0.031	0.047	0.045	0.075
Boaedon	0.064	**0.027**	0.075	0.069	0.071	0.071	0.051
Bothrolycus	0.039	0.075	–	0.041	0.047	0.061	0.081
Lycophidion	0.031	0.069	0.041	–	0.047	0.049	0.074
Lycodonomorphus	0.047	0.071	0.047	0.047	**0.037**	0.046	0.074
Alopecion	0.045	0.071	0.061	0.049	0.046	–	0.073
Boaedon geometricus	0.075	0.051	0.081	0.074	0.074	0.073	–

signed to any other Boaedontini genus. As a consequence of this finding and with regard to obvious morphological differences that are summarised in Table 5 and that we overview in further detail below we here describe a new genus of snakes in the family Lamprophiidae, subfamily Lamprophiinae, tribe Boaedontini.

Description of a new genus
Bofa gen. n.

lsid:zoobank.org:act:56A821C4-89E5-4656-8C34-C5DD71BF6114

Type species: *Boodon erlangeri* Sternfeld, 1908, by present designation.

Generic diagnosis: Body markedly elongated, slender, cylindric. Tail short, representing ca. 12–15% of the total length. Head narrow, elongated, scarcely distinct from neck. Snout blunt, square-shaped. Rostral rather large, approximately as high as broad, well visible from below and above. Nasal divided. Eye medium-sized, with circular pupil. One preocular, two postoculars. Gular scales large and pairwise symmetrically arranged between posterior chinshields and first ventral shield. Anterior chinshields much larger than posterior. Loreal single, rectangular, horizontally elongate, with no pit. No labial pits. Body scales smooth, shiny, without apical pits. Subcaudals paired. Anal entire. Five to six strongly enlarged and gradually decreasing in size anterior maxillary teeth, followed by smaller

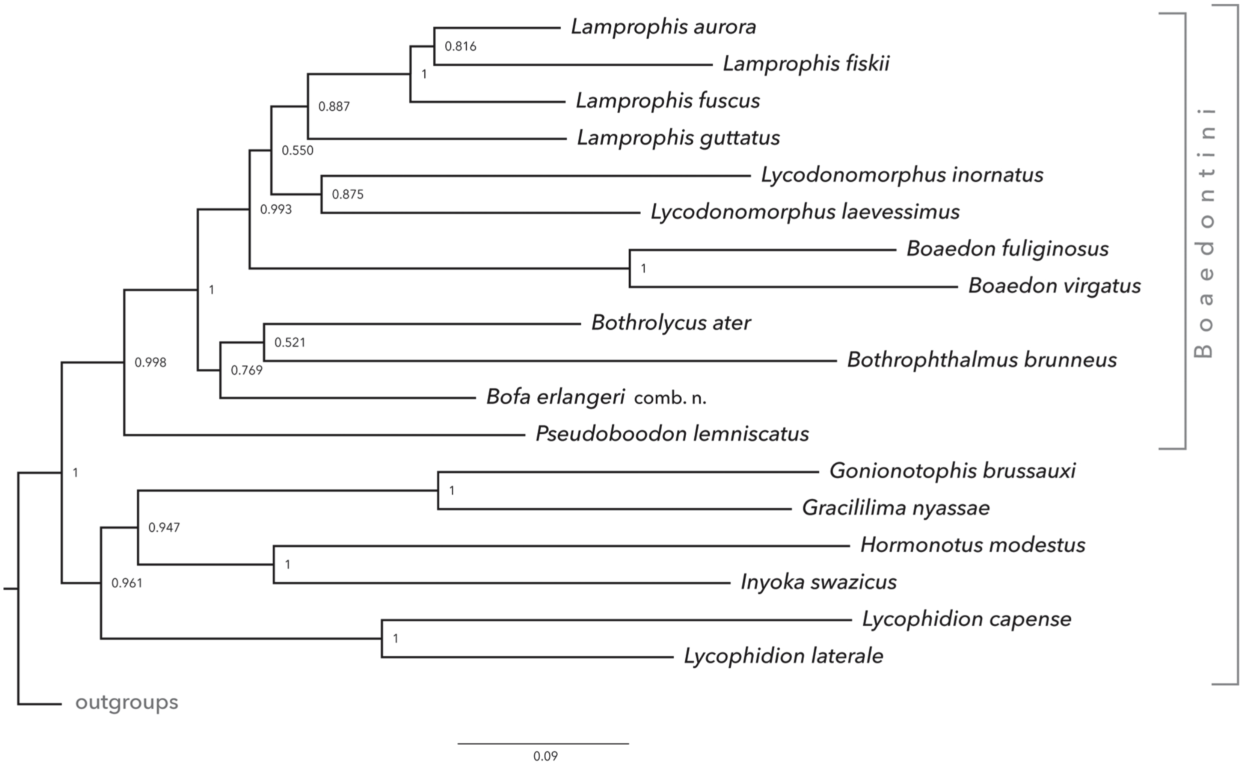

Figure 2. Phylogenetic relationships of Lamprophiinae generated from cyt b, ND4 and c-mos data sets based on Bayesian inference. Outgroups are collapsed to one single branch. Numbers at nodes represent posterior probabilities from the Bayesian analysis; scale refers to nucleotide substitutions per site.

Table 2. Estimates of evolutionary divergence in mitochondrial cytochrome b (cyt b) sequences (uncorrected p-distances) between and within (in bold) selected genera of Lamprophiinae.

	Bofa gen. n.	*Boaedon*	*Bothrolycus*	*Gonionotophis*	*Bothrophthalmus*	*Gracililima*	*Lycodonomorphus* (s.s.)	*Lycophidion*	*Pseudoboodon*	*Lamprophis guttatus*	*Hormonotus*	*Lycodonomorphus inornatus*	*Inyoka*	*Lamprophis* (s.s.)	*Mehelya*
Bofa gen. n.	–	0.180	0.142	0.210	0.173	0.200	0.155	0.180	0.156	0.163	0.203	0.181	0.180	0.146	0.183
Boaedon	0.180	**0.114**	0.185	0.219	0.209	0.218	0.188	0.202	0.207	0.185	0.212	0.203	0.199	0.183	0.199
Bothrolycus	0.142	0.185	–	0.230	0.184	0.202	0.161	0.190	0.168	0.156	0.203	0.179	0.192	0.157	0.204
Gonionotophis	0.210	0.219	0.230	–	0.225	0.180	0.211	0.214	0.205	0.214	0.227	0.224	0.225	0.201	0.176
Bothrophthalmus	0.173	0.209	0.184	0.225	**0.043**	0.214	0.182	0.201	0.200	0.188	0.212	0.207	0.203	0.182	0.216
Gracililima	0.200	0.218	0.202	0.180	0.214	–	0.204	0.209	0.193	0.206	0.208	0.223	0.212	0.205	0.168
Lycodonomorphus (s.s.)	0.155	0.188	0.161	0.211	0.182	0.204	**0.140**	0.196	0.183	0.163	0.197	0.178	0.190	0.154	0.201
Lycophidion	0.180	0.202	0.190	0.214	0.201	0.209	0.196	**0.145**	0.191	0.186	0.206	0.205	0.194	0.189	0.197
Pseudoboodon	0.156	0.207	0.168	0.205	0.200	0.193	0.183	0.191	–	0.179	0.214	0.190	0.188	0.166	0.189
Lamprophis guttatus	0.163	0.185	0.156	0.214	0.188	0.206	0.163	0.186	0.179	**0.089**	0.199	0.173	0.189	0.154	0.198
Hormonotus	0.203	0.212	0.203	0.227	0.212	0.208	0.197	0.206	0.214	0.199	–	0.227	0.187	0.202	0.204
Lycodonomorphus inornatus	0.181	0.203	0.179	0.224	0.207	0.223	0.178	0.205	0.190	0.173	0.227	–	0.208	0.177	0.211
Inyoka	0.180	0.199	0.192	0.225	0.203	0.212	0.190	0.194	0.188	0.189	0.187	0.208	**0.013**	0.188	0.208
Lamprophis (s.s.)	0.146	0.183	0.157	0.201	0.182	0.205	0.154	0.189	0.166	0.154	0.202	0.177	0.188	**0.097**	0.184
Mehelya	0.183	0.199	0.204	0.176	0.216	0.168	0.201	0.197	0.189	0.198	0.204	0.211	0.208	0.184	–

evenly distributed posterior teeth. No diastema. Five anterior mandibular teeth strongly enlarged.

Content: The genus is currently monotypic, containing one species – *Bofa erlangeri* (Sternfeld, 1908) comb. n.

Etymology: The latinised noun 'Bofa' that we introduce here is adopted from the Oromo language where it means 'snake'. We have chosen this name for the new genus because much of its currently known range is in the areas where this language is spoken. In Afaan Oromo 'bofa' has both genders. We adapt this word to Latin grammar as a noun of feminine gender and 1st declension because in Latin most nouns ending with '-a' are feminine.

English name: Obviously, the name 'house snake' is not applicable anymore to this genus. To call it 'Ethiopian forest snakes' appears to be appropriate, since it reflects the distribution and ecology of this genus. Also the word 'Bofa' that can be easily adopted to the grammar and the orthography of almost any language is suitable for use as a vernacular name in English and other languages. Accordingly, the member of the genus may be called in English 'Erlanger's Forest Snake' or just 'Bofa'.

The skull of *Bofa erlangeri* comb. n.

The following description of the skull of the type species of the new genus is based on µCT images of an adult female specimen (ZFMK 55533, Fig. 3).

Snout. The premaxilla has a large ascending process that closely approaches the nasals. The vomerine process is forked. Its tips do not contact the vomers. The flat and sharp-pointed transverse processes closely approach the rostral ends of the maxillae. The septomaxillae are separated from each other. Their posterior ends form prokinetic joints with the frontals. The conchal processes are moderately-sized, sharply bent upward. The nasals are tightly attached to each other, but not fused. They are long, less than 25% shorter than the frontals which they contact with their posterior processes. The nasals are approximately half as broad as the frontals, much narrower than the septomaxillae. The dorsolateral processes of the septomaxillae extend beyond the lateral margins of the nasals and are well visible in dorsal view. The medial laminae of the nasals contact the septomaxillae. The edges of the lateral laminae are strongly curved downward, but do not approach the conchal processes of the septomaxillae. The vomers are almost in contact medially. Their rostral ends approach, but do not contact, the premaxilla. The posterior ends of the vomers approach, but do not contact, the choanal processes of the palatines. The vomers have globular posterolateral portions. These structures are open forward and have narrow processes anteriorly. The lateral laminae of the vomers are short, triangular, curved downward. The ventral laminae are perforated.

Table 3. Estimates of evolutionary divergence in mitochondrial NADH dehydrogenase subunit 4 (ND4) sequences (uncorrected p-distances) between and within (in bold) selected genera of Lamprophiinae.

	Bofa gen. n.	*Bothrolycus*	*Lamprophis*	*Lycodonomorphus*	*Pseudoboodon*	*Limaformosa*	*Boaedon*	*Inyoka*	*Gracililima*
Bofa gen. n.	–	0.146	0.165	0.181	0.171	0.175	0.180	0.184	0.193
Bothrolycus	0.146	–	0.165	0.182	0.184	0.173	0.178	0.193	0.191
Lamprophis	0.165	0.165	**0.117**	0.166	0.179	0.178	0.179	0.201	0.193
Lycodonomorphus	0.181	0.182	0.166	**0.119**	0.186	0.184	0.186	0.213	0.194
Pseudoboodon	0.171	0.184	0.179	0.186	–	0.192	0.189	0.203	0.196
Limaformosa	0.175	0.173	0.178	0.184	0.192	**0.113**	0.178	0.207	0.176
Boaedon	0.180	0.178	0.179	0.186	0.189	0.178	**0.098**	0.218	0.189
Inyoka	0.184	0.193	0.201	0.213	0.203	0.207	0.218	**0.015**	0.203
Gracililima	0.193	0.191	0.193	0.194	0.196	0.176	0.189	0.203	–

Table 4. Estimates of evolutionary divergence in nuclear c-mos proto-oncogene (c-mos) sequences (uncorrected p-distances) between and within (in bold) selected genera of Lamprophiinae.

	Bofa gen. n.	*Boaedon*	*Bothrolycus*	*Gonionotophis*	*Bothrophthalmus*	*Lycophidion*	*Pseudoboodon*	*Limaformosa*	*Lycodonomorphus*	*Lamprophis*	*Mehelya*
Bofa gen. n.	–	0.008	0.011	0.020	0.006	0.022	0.015	0.018	0.007	0.005	0.020
Boaedon	0.008	**0.005**	0.015	0.025	0.011	0.025	0.019	0.022	0.011	0.009	0.017
Bothrolycus	0.011	0.015	–	0.028	0.014	0.029	0.022	0.025	0.013	0.013	0.022
Gonionotophis	0.020	0.025	0.028	–	0.023	0.027	0.024	0.020	0.024	0.021	0.007
Bothrophthalmus	0.006	0.011	0.014	0.023	**0.002**	0.024	0.018	0.020	0.010	0.008	0.016
Lycophidion	0.022	0.025	0.029	0.027	0.024	**0.008**	0.025	0.021	0.024	0.023	0.018
Pseudoboodon	0.015	0.019	0.022	0.024	0.018	0.025	–	0.021	0.018	0.016	0.019
Limaformosa	0.018	0.022	0.025	0.016	0.020	0.021	0.020	**0.002**	0.021	0.019	0.009
Lycodonomorphus	0.007	0.011	0.014	0.024	0.010	0.024	0.018	0.021	**0.003**	0.007	0.017
Lamprophis	0.005	0.009	0.013	0.021	0.008	0.023	0.016	0.019	0.007	**0.006**	0.013
Mehelya	0.020	0.024	0.027	0.012	0.022	0.026	0.023	0.015	0.023	0.020	**0.009**

Braincase. The braincase is elongate, accounting for approximately 3/4 of the total skull length. The prefrontals form the anterior borders of the orbits. Their posterior faces are curved and slightly concave. There is no immediate contact with the frontal: The dorsal margin of the prefrontal does not exactly match the shape of the frontal, so that some distance between them exists. The prefrontals and the nasals do not approach each other. The frontals are paired, medially nearly contacting and forming a long straight suture. Combined, they form a hexagon that is almost as wide as long. Each frontal is ca. 40% narrower than its maximum length, and ca. 30% shorter than the parietal. Their entire lateral margins are slightly curved, to form the dorsal borders of the orbits. The posterior faces of the frontals are angled at ca. 45° and together form a ca. 90° insertion in the parietal. It matches almost seamlessly the shape of the parietal. Ventrally, the frontals are in tight contact, but not fused. Their ventral laminae enclose the parasphenoid rostrum that extends forward at approximately 2/3 of the length of the frontals. The parietal is single, almost as broad as long, with flattened dorsal surface. Anteriorly it has a broad V-shaped notch that almost seamlessly encloses the matching triangular shape of the frontals. Short dorsolateral ridges are slightly concave anterolaterally, repeating the shape of the postorbitals which approach them but do not contact. The parietal contacts the parabasisphenoid ventrally, the supraoccipital posteriorly, the prootics and the anterior ends of the supratemporals posterolaterally. The postorbitals are triangular and slightly curved, to form the posterior border of the orbits. The nearly flat dorsal surface of the parietal ends posteriorly with a sharp medial ridge that extends along the medial line of the parietal at approximately 1/4 of its length, towards the supraoccipital. The latter is oval and has three ridges on its surface. One of them continues the medial ridge of the parietal. Two other, stronger and higher, ridges originate at both sides of the medial ridge and end in triangular excrescences of the posterior margin of the supraoccipital. The supraoccipital has a V-shaped notch anteriorly that seamlessly encloses the triangular posterior margin of the parietal. The jagged posterior margin of the supraoccipital and the indented anterior margins of the exoccipitals match like jigsaw pieces. The exoccipitals contact the supraoccipital anterodorsally, the prootics anterolaterally, the basioccipital ventrally and the supratemporals laterally. Posteriorly they form together the upper and the lateral

Table 5. Differing morphological characters in Boaedontini genera. (The abbreviation 's.s.', i.e. 'sensu stricto', indicates that these characters have not been assessed in *Lycodonomorphus inornatus*.)

	Bofa gen. n.	*Bothrolycus*	*Bothrophthalmus*	*Alopecion*	*Boaedon*	*Lamprophis*	*Lycodonomorphus (s.s.)*	*Pseudoboodon*
Maximum total length (mm)	1,200	720	1,240	620	1,400	900	1,140	950
TL/SVL	0.12–0.13	0.09–0.17	0.16–0.22	0.22–0.27	0.16–0.18	0.18–0.20	0.23–0.33	0.13–0.20
Midbody scale rows	21–23	17–19	23	21–23	23–35	19–25	19–25	15–26
Apical pits on dorsal scales	0	0	0	0	2	0	0	0
Ventrals	217–240	132–152	181–212	186–230	168–246	165–183	152–196	189–214
Subcaudals (pairs)	38–64	17–34	62–85	46–72	38–85	28–74	37–89	32–64
Rostral	large, rectangular, well visible from above	small, trapezoidal, not or barely visible from above	large, trapezoidal, barely visible from above	small, semicircular, not or barely visible from above	moderate, triangular, well visible from above	large, rectangular, well visible from above	moderate, trapezoidal, well visible from above	moderate, trapezoidal, well visible from above
Preoculars	1	2	2 (occasionally 3)	1	1–2	1 (rarely 2)	1–2 (or 0)	1
Loreal pit	absent, but loreal slightly concave	present	present	absent	absent	absent	absent	absent
Labial pit	absent	absent	absent	absent	absent	absent	absent	present
Chinshields length ratio	anterior > posterior	anterior = posterior	anterior >= posterior	anterior > posterior	anterior >= posterior	anterior >= posterior	anterior < posterior	anterior >= posterior
Gulars between chinshields and ventrals	1–3 pairs	irregular	1 pair or irregular	several pairs or irregular	irregular	irregular or 1 pair	irregular or 2 pairs	irregular
Maxillary teeth (total number)	16–19	16–20	23–24	17	17–20	17-19	17–25	19–23
- enlarged teeth	1st–6th	1st–6th	0	3rd–4th or 3rd–5th	1st–5th or 1st–6th	1st–6th	0	1st–6th
- diastema after enlarged teeth	absent	absent or small	absent	present	present	absent or small	absent	absent or small
Maxilla size (relatively to skull length)	long	long	long	short	short	short	short	long
Palatine teeth	9	13	10	11	7	10	11	9
Pterygoid teeth	22	22	23	22	22	21	31	22
Nasals size relatively to frontals	long	long	long	short	short	short	long	long
Head shape	elongated, trapezoidal, not depressed, scarcely broader than neck, a little distinct from it, snout square shaped	in dorsal view triangular, strongly depressed, broader than neck and distinct from it, snout sharp.	elongated, not depressed, trapezoidal, posteriorly broader than neck, distinct from it, snout square shaped	trapezoidal or egg-shaped in dorsal view, strongly depressed, posteriorly much broader than neck, snout square-shaped	depressed, elongated isosceles trapezoidal, broader than neck and distinct from it, in dorsal view appears more or less triangular	oval in dorsal view, not depressed, slightly to moderately broader than neck and distinct from it, snout rounded	oval in dorsal view, slightly broader than neck, not depressed or slightly depressed, snout rounded	elongated, slightly depressed, trapezoidal, posteriorly broader than neck, distinct from it, in dorsal view more or less triangular
Eye size in adults	small to moderate	small to moderate	moderate	moderate to large	moderate to large	moderate	moderate	moderate
Pupil shape	circle	circle	broad oval	narrow oval	narrow oval	broad oval	broad oval	broad oval

borders of the foramen magnum, and their posterolateral corners end with occipital condyles. The exoccipitals are irregularly shaped and emarginate dorsally, to match the shape of the supraoccipital. The foramen ovale is situated at each side at the suture of the prootic and the exoccipital. The columella auris is inserted into it, with its oval footplate firmly contacting the prootic anteriorly and the exoccipital posteriorly. The long thin shaft of the columella is directed toward the articulatory process of the quadrate but remains separated from it. The prootics are subhexagonal in lateral view. Each has foramina for maxillary and mandibular branches of the trigeminal. These are separated by a laterosphenoid. The basioccipital is nearly pentagonal. Anteriorly, it is in contact with the basisphenoid,

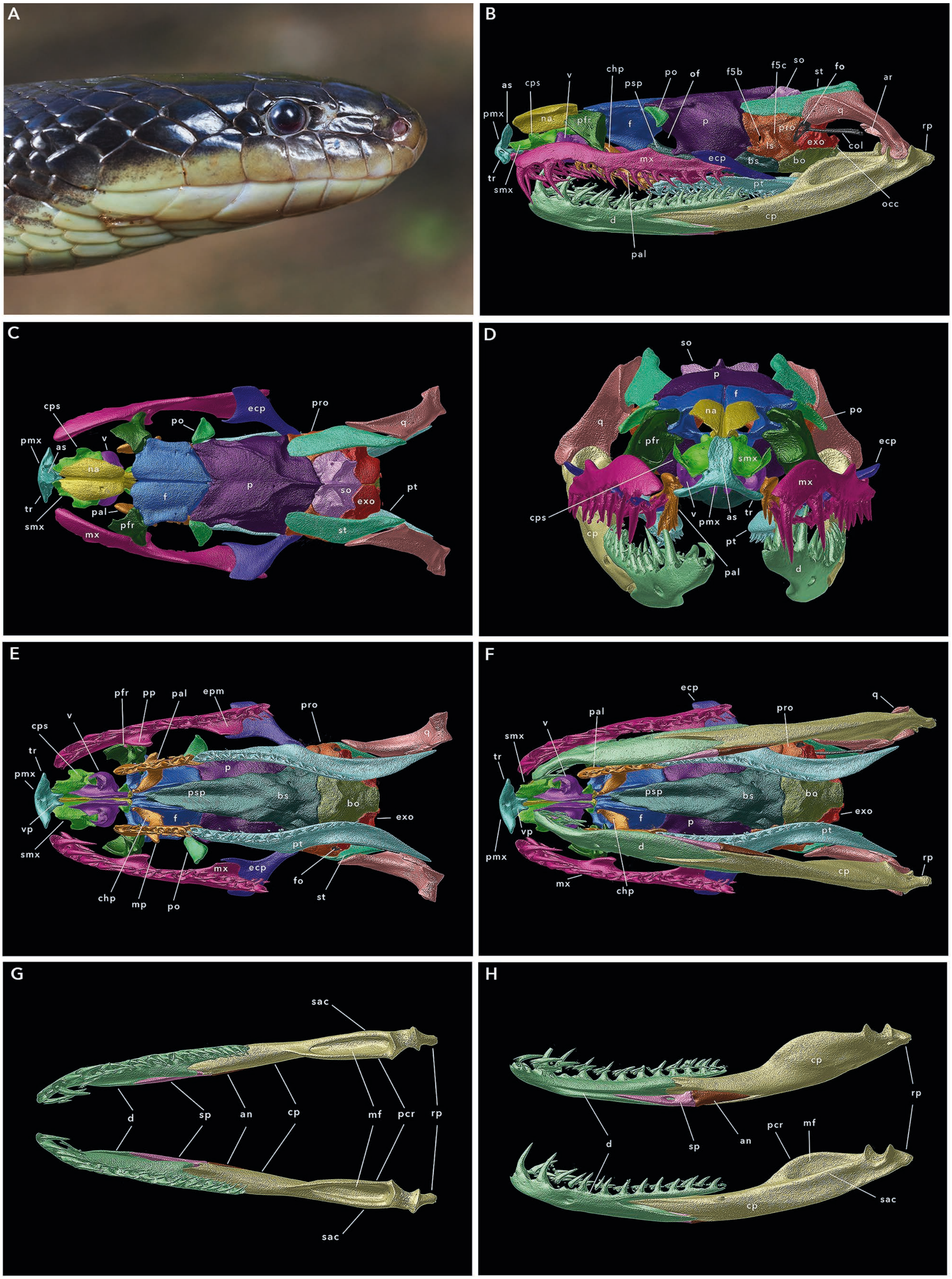

Figure 3. Cranial osteology of *Bofa erlangeri* comb. n. (A) Head of an adult female in life; µCT images of the skull in lateral (B), dorsal (C), frontal (D), ventral (E, F) aspects (with and without mandibles); (G) mandibles in dorsal aspect; (H) right mandible in lingual (top) and left in lateral (bottom) aspects. See "Material and methods" for a key to the abbreviations.

and posteriorly it forms the ventral border of the foramen magnum. The parasphenoid and basisphenoid are fused. The basisphenoid part is nearly hexagonal in ventral view. There are one small anterolateral and two posterolateral foramina on each side. The parasphenoid rostrum is almost perfectly triangular and concave ventrally. It is tightly enclosed by the ventral laminae and anteroventral dentigerous processes of the parietal. Anteriorly, the rostrum passes between the ventral laminae of the frontals but its sharp tip remains at a large distance from the vomer and does not even reach to the choanal processes of the palatines.

Palatomaxillary arch. The palatines have large hook-shaped choanal processes that almost touch with their tips the caudal processes of the vomers. They are situated below the frontals and in dorsal view are hidden under them, so that only the rostral ends and the tips of the maxillary processes are visible. The maxillary process is much smaller than the choanal. It is situated opposite to the palatine process of the maxilla and directed downward. Each palatine has nine subequal teeth. The palatines appear straight in ventral view. Their rostral ends are positioned higher than the caudal that almost contact the rostral ends of the pterygoids from above. The posterior tip is forked and creates a joint with the rostral tip of the corresponding pterygoid. The maxillae are long – almost equal in length to the braincase, and extend posteriorly almost to 1/3 of their length beyond the postorbitals. They are almost straight in dorsal and ventral views, being only slightly curved at their anterior third. The ectopterygoid process is large, rectangular, flat, turned downward. It is situated close to the distal end of the maxilla, approximately at teeth 14–18. The palatine process is triangular, flattened, curved downward and backward. It is situated opposite to the maxillary process of the palatine, approximately at teeth 7–8. There are 19 teeth on each maxilla. The first six teeth are enlarged and gradually decrease in size from tooth 2 to tooth 6. Tooth 2 is the longest, being approximately twice as long as tooth 7. Tooth 1 is slightly shorter than tooth 2, but still much longer than tooth 7. The pterygoids are slender and long, ca. 25% longer than the maxillae and approximately as long as the braincase. Each bears 22 small teeth that decrease in size posteriorly. The pterygoids gradually broaden approximately after the level of tooth 8 and have a wavy shape in ventral view, coming closest to each other at the level of tooth 22. Starting from this point, they taper posteriorly and end with narrow tips. The caudal end of the ectopterygoid attaches to the pterygoid almost in the middle of its length. The ectopterygoids are spade-shaped, slightly forked at their joints with the maxillae.

Suspensorium and mandible. The supratemporals are elongate, laminar, tapering posteriorly and ending with narrow tips that extend far beyond the caudal edge of the braincase. They closely approach the quadrates with their straight posterolateral surfaces but remain separated. The quadrates are elongate, slender, slightly curved downward, with dorsal portions broader than ventral parts. The articulatory processes are large, triangular, pointing at the columella. The cephalic condyles do not approach the caudal tips of the pterygoids that point at them. They are inserted in the glenoid cavity of the compound bone. The mandibles are almost perfectly straight in dorsal and ventral view: Only the anterior approximately 1/3 of the dentary is slightly curved labially. The left dentary has 22, the right 23 teeth, of which the first five (situated on its curved rostral part) are strongly enlarged. The dentary is long: almost equal in length to the compound bone. The mental foramen is at the level of the sixth tooth. Approximately at the level of the tenth tooth, the dentary forks to upper and lower branches. The upper branch that bears teeth is slightly longer than the lower branch that at its labial side seamlessly attaches with the splenial. The splenial is triangular, tapering anteriorly to a fine tip and perforated in the posterior half by the anterior mylohyoid foramen. The splenial is attached with the angular approximately at the level of tooth 17, and the posterior mylohyoid foramen is situated on this suture. The angular is slightly shorter and broader than the splenial. It is triangular and directed with its narrower angle posteriorly, entirely lying on the labial side of the compound bone. The dentary is attached to the compound approximately at the level of tooth 16 via a curvy suture. The compound fits with its sharp rostral end between the branches of the dentary. The prearticular crest is visible in lateral view, being distinctively higher than the surangular, that is not visible in labial view. The mandibular fossa is deep, elongate, moderately broad, oriented dorsally, but visible in lateral view. The retroarticular process is well-defined and medially directed.

Generic affiliation of *Lamprophis abyssinicus*

Lamprophis abyssinicus is the second member endemic to the Ethiopian highlands that has been, already in its initial description, erroneously assigned to this genus (Mocquard 1906). Subsequently *L. erlangeri* and *L. abyssinicus* were mentioned together, as closely related (Largen & Rasmussen 1993, Largen & Spawls 2010). More recently, Wallach et al. (2014) subsumed this snake in *Boaedon*, as usually, without explained reasoning. Although no recently collected specimens and no molecular data are available for *L. abyssinicus*, with our current morphological and phylogeographic concept of *Lamprophis* and *Boaedon*, this species cannot remain in either of these genera and has to be accommodated in a different genus.

Boulenger (1915), Werner (1929) and Parker (1949) had treated this snake as a member of the genus *Pseudoboodon*. Largen & Rasmussen (1993) sorted out this possibility and kept *L. abyssinicus* in the genus *Lamprophis* because it lacked labial pits which are commonly regarded as the most characteristic apomorphy of *Pseudoboodon*. In several aspects of its external morphology this snake resembles *Pseudoboodon* (however, also many other Boaedontini members). Here is the original description of *L. abyssinicus* by Mocquard (1906), translated from French: "Head rather elongated, a little broader than neck; snout narrow, blunt at the tip. Body notably compressed, ventrally rounded. Tail very short. Rostral much broader than high, visible from above; internasals subtriangular, truncated anteriorly, shorter than prefrontals, which are as long as broad; frontal 1 2/3 longer than its breadth; significantly longer than the distance from it to the snout tip, hardly shorter than the parietals, ending anteriorly with sharp angle, broader than supraoculars; nasal divided, rather elongated, anteriorly a little higher; loreal longer than high; one preocular does not enter the dorsal surface of the head and is well separated from the frontal; two equal postoculars; the eye diameter is half as long as the snout; pupil a little elongated vertically; temporals 1+2, the anterior is the largest, contacting the lower postocular with its anterior border; 8 upper labials, 3rd, 4th and 5th bordering the eye, the 7th is the longest; mental triangular, much broader than long; 4 lower labials in contact with chinshield of the first pair, which is longer than of the second pair, the latter are in contact at the median line. Body scales in 21 longitudinal rows, smooth, without apical pits; 174 ventrals; anal entire; 36 divided subcaudals […]".

The main and quite obvious difference of *Pseudoboodon* is an incision in the 4th and 5th labial scales (labial groove) that is characteristic for this genus, but considered to be absent in *L. abyssinicus*. However, we noticed a feeble curvature of these scales in the examined specimens of *L. abyssinicus*. Figure 4 shows the left side of the heads of a small female (SVL 340 mm) of *L. abyssinicus* (NHMUK 1982.105) and of a similarly sized (SVL 427 mm) female of *P. lemniscatus* (ZFMK 68420), for comparison: The labials are feebly, but clearly, curved in the first specimen, although not that much as in the second (red arrows).

Also the skull and the dentition of *L. abyssinicus* closer resemble those of *Pseudoboodon* (see Figure 5 showing µCT images of the skull of an adult female, NHMUK 1982.105). In fact, all bones of the skulls of *L. abyssinicus* and *P. lemniscatus* have almost identical shape, being just longer in the latter. Therefore, we here re-assign this species to the genus *Pseudoboodon* and re-establish the binomial *Pseudoboodon abyssinicus*.

Figure 4. (A–B) Lateral views of heads of preserved specimens of *Lamprophis abyssinicus*, NHMUK 1982.105 (A) and *Pseudoboodon lemniscatus*, ZFMK 68420 (B); labial grooves are indicated by a red arrow. (C) Juvenile *Lamprophis abyssinicus* in life (photograph by R. Gutberlet). (D) Juvenile *Pseudoboodon* cf. *lemniscatus* in life.

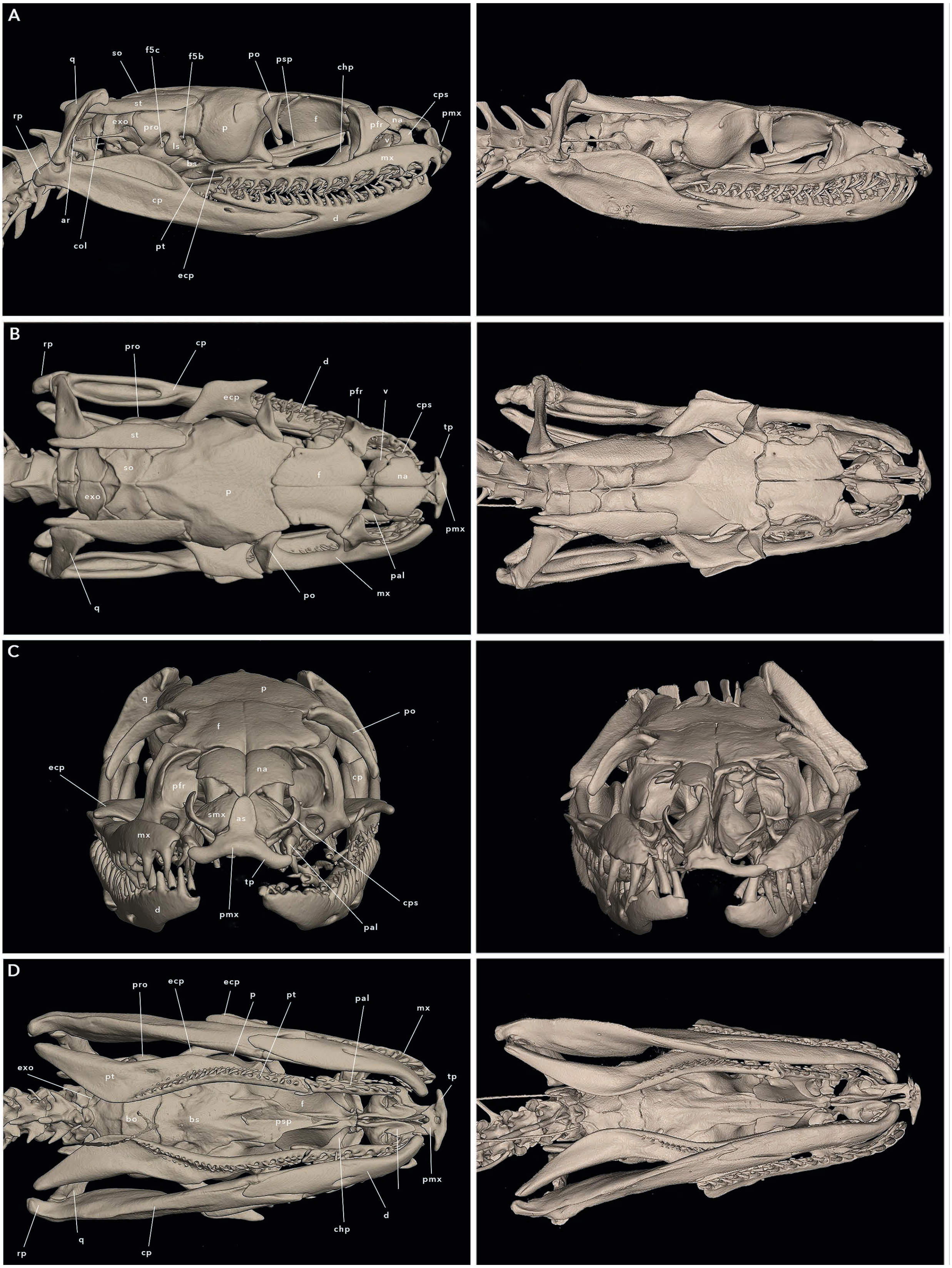

Figure 5. µCT images of skulls of *Pseudoboodon abyssinicus* (left) and *P. lemniscatus* (right): (A) lateral, (B) dorsal, (C) frontal, (D) ventral aspects. See "Material and methods" for a key to the abbreviations.

Revalidation of the genus *Alopecion*

There are two more species in the genus *Lamprophis* with uncertain taxonomic status in the recent past. One of them is *L. geometricus* (SCHLEGEL, 1837), an endemic species of the Seychelles Archipelago that, similarly to *L. erlangeri* and *L. abyssinicus*, has been retained in this genus by KELLY et al. (2011) in order to avoid taxonomic confusion. In a phylogeny using the mitochondrial 16S rRNA gene, *L. geometricus* indeed clusters with the West-African taxa *Boaedon lineatus* DUMÉRIL, BIBRON & DUMÉRIL, 1854, *Boaedon longilineatus* TRAPE & MEDIANNIKOV, 2016, and *Boaedon paralineatus* TRAPE & MEDIANNIKOV, 2016 (HALLERMANN et al. 2020) and should be treated as a member of this genus. This is also consistent with the superficial similarity of this snake with *Boaedon*, especially with representatives of the *B. lineatus* group.

The second problematic species is *L. guttatus*, a much better-known South-African lamprophiid, with a similarly changeful taxonomic history as that of *L. erlangeri*. This snake was originally described as *Lycodon guttatus* SMITH, 1843 in the genus *Lycodon* FITZINGER, 1826, which is now a member of a different family (Colubridae). Apparently having overlooked it, DUMÉRIL et al. (1854: 416) described another species from a specimen of the same series collected by A. SMITH. They assigned it as the type species with the name *Alopecion annulifer* to the genus *Alopecion* DUMÉRIL, BIBRON & DUMÉRIL, 1854 that they had established. Subsequently, also GÜNTHER (1858: 196) used this name for specimens in the collection of the Natural History Museum, even though the holotype of SMITH's *Lycodon guttatus* (NHMUK 1946.1.23.16) was already housed in this institution. Later on, several other representatives of African snake fauna were added to this genus by various authors, but subsequently all of them were moved to other genera. The 'empty' genus *Alopecion* was then treated as a junior synonym of either *Boaedon* or *Lamprophis*, when its type species became assigned to either of these genera.

BOULENGER (1891: 14, 1893: 331) revised the generic placement of *Lycodon guttatus* and assigned it to *Boodon*. Also LOVERIDGE (1936: 22) treated this snake as *Boodon guttatus*, and it occurs, spelt as *Boaedon guttatus*, in the books by HEWITT (1937: 36), ROSE (1950: 276), ISEMONGER (1955: 68), and FITZSIMONS (1962: 116). BOYCOTT (1992) was apparently the first who mentioned this snake among *Lamprophis*. However, this genus included all *Boaedon* at that time. VIDAL et al. (2008) were the first who showed with their molecular study of Lamprophiidae that *Lamprophis* was polyphyletic. In the phylogeny that they presented, *L. guttatus* clustered with species that are now members of *Lamprophis* sensu stricto and not with those that now belong to *Boaedon*. KELLY et al. (2011) confirmed in their study that was dedicated to phylogeny of the subfamily Lamprophiinae a closer phylogenetic relationship of *L. guttatus* to *Lamprophis* and assigned it to a group that they called '*Lamprophis* sensu strictissimo'. They admitted, however, that *L. guttatus* may be moved to a separate genus in future due to genetic and morphologic distinctiveness and proposed to revive *Alopecion* in that case. WALLACH et al. (2014: 98) seem to have overlooked these conclusions or disagreed with them when they treated this species as *Boaedon guttatus*. Nonetheless, *L. guttatus* remained mentioned as a member of the genus *Lamprophis* in all newer herpetological and popular publications.

Indeed, this snake is superficially more similar to *Boaedon* and in its external morphology differs from *Lamprophis* sensu stricto in a number of aspects. This is certainly the reason why it had been more usually associated with *Boaedon* in the past, before a closer relationship to *Lamprophis* was revealed with molecular methods. It differs from *Lamprophis* sensu stricto and from other genera in the subfamily Lamprophiinae by the following combination of external morphological features that should serve as an amended diagnosis of *L. guttatus*: Size small, usually not exceeding 600 mm in total length; body moderately elongated; tail moderate, 18–21% of total length; head of moderate size, in dorsal view egg-shaped or slightly isosceles trapezoidal, posteriorly much broader than neck, markedly depressed; snout blunt, in dorsal view square-shaped, slightly curved down in lateral view; eye moderate to large, with vertically elliptical pupil, capable of shrinking to a thin vertical streak; preocular 1; postoculars 2–3; temporals 1+2; rostral small, semi-circular, not visible or barely visible from above; upper labials 7, 3rd–5th in contact with eye; lower labials 7–9; anterior chinshields significantly (up-to two times) larger than posterior; gulars irregular or arranged in up-to 4 pairs between posterior chinshields and first ventral; midbody scale rows 21–23, vertebral row not enlarged; dorsal scales smooth, without apical pits; ventrals 186–230; subcaudals in 46–72 pairs; anal entire; maxilla with 15–17 teeth; 1st maxillary tooth short, approximately equal in length to the last; teeth 2–6 gradually increase in length up to the 5th which is about twice as long as the 2nd; a well-defined diastema after the 6th tooth, followed by 11–12 smaller teeth, gradually decreasing in length posteriorly; mandibular teeth increase in length from 2nd to 6th (which is the longest) then decrease to 8th which is followed by 11–15 shorter teeth gradually decreasing in length posteriorly; hemipenis not forked. Colour: regionally variable; basic dorsal pattern consists of blotches or spots, arranged in either alternating or adjacent pairs on yellow-brown or grey-brown background; venter off-white or pale-yellow, with occasional greyish spots.

Among Boaedontini *L. guttatus* seems to stand out with its habit to extremely flatten the head (Fig. 6A). This is a useful adaptation for life in rocky habitats that enables the snake to enter narrow cracks when it hunts or hides from enemies. This morphological trait clearly separates *L. guttatus* from the terrestrial and predominantly grassland living *Lamprophis* sensu stricto that have relatively high and rounded heads. Despite the strikingly different appearance of the head, the skull of *L. guttatus* (Fig. 6) resembles the skull of *Lamprophis* closer than that of other Boaedontini (Fig. 9). This is not surprising and should be attributed to a close phylogenetic relationship between

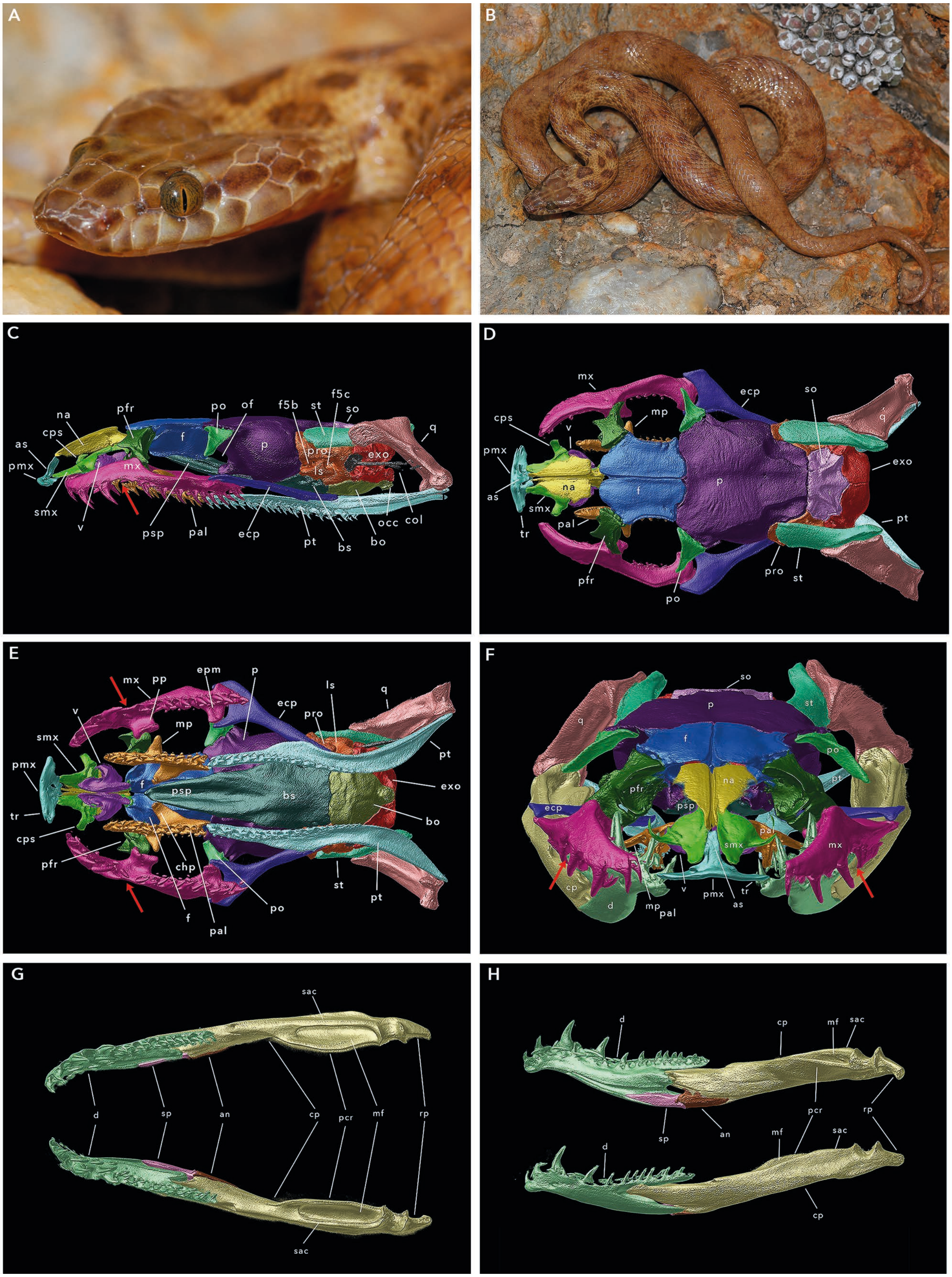

Figure 6. *Alopecion guttatum* comb. n. (A–B) Photographs of a live specimen (courtesy of M. Burger); μ-CT images of the skull in lateral (C), dorsal (D), ventral (E), frontal (F) aspects; (G) both mandibles in dorsal aspect; (H) right mandible in lingual (top) and left in lateral (bottom) aspects. Diastemata are marked with red arrows. See "Material and methods" for a key to the abbreviations.

these taxa. The skull of *L. guttatus* is depressed and more robust, but otherwise looks more or less like the skull of *L. aurora*: The braincase is broader, but its general shape is quite similar. The parietal in this species is almost square-shaped, with nearly equal length and breadth, whereas it is slightly elongated and narrowed caudally in *L. aurora*. The parietal–supraoccipital suture is straight in *L. guttatus*. In *L. aurora* the supraoccipital and the parietal are indented into each other. The exoccipitals are heavier than in *L. aurora*. The frontals are narrower, providing more space for larger eyes. Also the maxillae are stronger curved posteriorly, and the postorbitals are smaller and thinner. Consequently, the orbits are larger. Due to narrower frontals, the eyes of *L. guttatus* are slightly turned upwards and more visible from above, unlike *Lamprophis* sensu stricto, where they are directed more or less horizontally. The bones of the snout – the premaxilla, the septomaxilla, and the nasals – are slightly broader and look much more robust, but are otherwise similar in shape to those of *L. aurora*. There are no significant differences in the palatomaxillary apparatus between *L. guttatus* and *Lamprophis* sensu stricto, except that all bones are heavier. The maxillary dentition, however, differs substantially. The first six teeth in *L. aurora* are usually reported to increase in length up to the fifth or sixth, and sometimes to be followed by a small diastema that separates this group from the rest of the maxillary teeth that are shorter (actually normally-sized), and with length that decreases towards the caudal end of the maxilla. In the specimen of *L. aurora* (MorphoSource 2021: 87602/m4/M57924) that we used for comparison, we did not notice any enlarged interspaces. In the skull of *L. guttatus* a diastema on both maxillae is clearly recognisable (Fig. 6C, 6E, 6F). Since this interspace is large, approximately as wide as one tooth socket, we expect it to be a regular character, similar to the large maxillary diastemata that are characteristic for *Boaedon*. A "small diastema" that is sometimes mentioned for *Lamprophis* could just be a normal interdental space between enlarged teeth that looks like a diastema when it occurs before the normally-sized teeth (see further discussion of this issue in the next subsection). The first and the last teeth on the maxilla of *L. guttatus* are the shortest. The second is a little longer than the first, but approximately as long as the postdiastemal teeth. The next teeth up to the sixth are strongly enlarged, approximately twice as long as the first tooth. Unlike in *Lamprophis* sensu stricto, there is no significant size difference between them: In the examined specimen, the fifth tooth is slightly longer than the sixth and the fourth. The quadrate of *L. guttatus* is also heavier than in *L. aurora*. The mandibles appear similarly curved in dorsal view, but their dentary bones are shorter, and the retroarticular process of the compound bone is significantly longer than in *L. aurora*, resembling those in *Boaedon*.

Certainly, none of the aforementioned characters alone could qualify for genus-level delimitation. However, all of them taken together, and in combination with the genetic data and with differences in ecology argue much stronger for a genus status. *Lamprophis guttatus* is a lineage that is sister to the remainder of the genus *Lamprophis* comprising three species, including the type species *L. aurora*, with the posterior probability 0.89 (Fig. 2). The uncorrected genetic p-distances of *L. guttatus* to *Lamprophis* sensu stricto are similar to the distances between the genera of this tribe and larger than the intrageneric distances (Tables 2–4). With the approach that has been applied so far to delimitation of other Boaedontini genera, to assign *L. guttatus* to a separate genus appears a next logical step. Therefore, we here reinstate *Alopecion* Duméril, Bibron & Duméril, 1854 as a genus in the subfamily Lamprophiinae, family Lamprophiidae, tribe Boaedontini, and assign to it *Lamprophis guttatus* (Smith, 1843) with a new binomial *Alopecion guttatum* (Smith, 1843) comb. n., following the principle of priority for the description of this species by Smith. The initial binomial of the type species, *Alopecion annulifer* Duméril, Bibron & Duméril, 1854, remains in synonymy. The genus is currently monotypic, but since consistent variation in colouration and behaviour, as well as considerable genetic divergence have been observed in different populations throughout the range of this species (Branch 1984, Branch 2006, Kelly et al. 2011, Bates et al. 2014), further species may be added in the course of future studies.

Morphological comparison of Boaedontini

A century ago, when almost any specimen, obtained in this part of the world, was of a new species, not all taxonomists paid attention to less obvious details, such as dentition, eye size, pupil shape, or grooves and pits on scales. *Boaedon lemniscatum* was one of them, a species that Duméril et al. (1854) described simultaneously with the genus *Boaedon* and assigned to it, along with several other snakes that they had found similar. Even after Peracca (1897) had introduced a new genus *Pseudoboodon*, the morphologically similar *B. lemniscatum* remained in the genus *Boaedon* for almost 40 years. Werner (1923) described a species *Pseudoboodon erlangeri* from a specimen that Erlanger donated to Naturhistorisches Museum Wien. Subsequently, it became a junior synonym of *P. lemniscatus* (Duméril, Bibron & Duméril, 1854). *Pseudoboodon*, i.e. 'false *Boaedon*', closely resemble the 'house snakes' with their general habit. Like *Bofa*, *Pseudoboodon* includes endemic species of the Horn of Africa, and at least one species, *P. gascae*, is sympatric and even co-occurs with it at forested localities in southern Ethiopia (Tiutenko 2018). The history of *Pseudoboodon* is another example of how convincing, and misleading at the same time, a general impression can be. Therefore, we here provide a comparative overview of the morphological similarities and differences within this group of genera. A summary of differing characters is given in Table 5 and Figure 10.

With the related lamprophiid genera *Alopecion*, *Boaedon*, *Bothrolycus*, *Bothrophthalmus*, *Lamprophis*, *Lycodonomorphus* and *Pseudoboodon* the new genus shares the fol-

Figure 7. General appearance and body form of Boaedontini in life: (A) *Boaedon capensis*, (B) *Bofa erlangeri* comb. n., (C) *Bothrolycus ater*, (D) *Bothrophthalmus lineatus*, (E) *Lamprophis aurora*, (F) *Alopecion guttatum* comb. n., (G) *Lycodonomorphus rufulus*, (H) *Pseudoboodon* cf. *gascae*. Photographs by M. Burger (C), L. Kemp (A, E, G), G. K. Nicolau (F), M.-O. Rödel (D), S. Spawls (H).

lowing morphological traits: cylindric body, smooth and equally-sized dorsal scales, divided nasal scale, two postoculars, presence of a loreal scale, undivided anal plate, rounded ventrals, paired subcaudals, aglyphous teeth, hypapophyses on all dorsal vertebrae. Also the members of Boaedontini, including the new genus, usually have 7–8 upper labials, of which the 4th and the 5th (sometimes also the 3rd) border the orbit, and 7–9 lower labials, of which 1st to 4th (rarely also the 5th) are in contact with the anterior chinshield. *Bofa* differs from some or all of these genera in a number of aspects that we compare here.

General body form and proportions. The general appearance of the type species of the seven Boaedontini genera is shown in Figure 7. *Boaedon*, *Bothrophthalmus*, *Pseudoboodon*, and *Lycodonomorphus* have a similar body form to *Bofa*, but *Lamprophis* looks shorter and even more conspicuously cylindric. *Bothrolycus* has an 'adder-like' appearance, having a stouter body than in the rest of this group of genera. *Alopecion* has also a shorter and stouter body than the new genus (Figs 4B, 7F).

Bofa erlangeri has a rather short tail, with a TL/SVL ratio of 0.12–0.13. We found a similarly short tail (TL/SVL 0.13) in *Pseudoboodon* cf. *gascae* (from the Harenna Forest) and *P. lemniscatus*, whereas the tails in other representatives of this genus, including *P. abyssinicus*, were slightly longer: TL/SVL 0.15–0.20. The tails of *Lycodonomorphus* are considerably longer than in the new genus: TL/SVL 0.23–0.33. A similar observation applies to *Alopecion*, with the TL/SVL ratio ca. 0.22–0.27. In *Lamprophis* it is 0.18–0.25. The tails of *Boaedon* are slightly shorter than in *Lamprophis*, but still longer than in the new genus with a TL/SVL ratio of 0.16–0.18. In this group of genera, only in *Bothrolycus* the tail is shorter than in *Bofa*, resulting in TL/SVL ratio of ca. 0.09–0.17.

Body scales. In all genera of this group the member species have smooth dorsal scales, except *Bothrophthalmus* in which they are keeled. In *Bofa erlangeri* the dorsal scales are flat and square-shaped (Fig. 1). Similar scales occur, for instance, in *Alopecion*, *Bothrolycus*, *Lamprophis*, *Lycodonomorphus*. From *Boaedon* the new genus differs by the complete absence of apical pits on body scales. Usually two pits, rarely one, are consistently present in *Boaedon*. The dorsal scales of *Lycodonomorphus* sensu stricto lack apical pits while there are two of them in *L. inornatus*. The dorsal scales of *Alopecion*, *Bothrolycus, Lamprophis*, and *Pseudoboodon* have, similarly to *Bofa*, no apical pits.

The members of *Boaedon* have the highest midbody row count among Boaedontini: 23–35. The lowest number is in *Bothrolycus*: 17–19 rows. In *Lamprophis* and *Lycodonomorphus* there are 19–25 rows. In *Bofa*, the midbody row count fits in this range, being 21–23. However, since *Lamprophis* and *Lycodonomorphus* are not distributed in this geographic region, this diagnostic character that was used for separation of *Lamprophis erlangeri* from *Boaedon* (Largen & Rasmussen 1993), remains valid and useful for identification of this species and the new genus.

Head. The head of *Bofa* (Fig. 8A) is narrow, elongated, not depressed (HH/HW 0.65), scarcely distinct from the neck. It appears narrower and somewhat longer than in *Lycodonomorphus* (Fig. 8G) whose heads are rather oval, and much longer than in *Lamprophis* (Fig. 8F). All members of *Boaedon* have moderately broad and somewhat depressed heads, which are strongly distinct from the necks (Fig. 8C). The same applies to an even larger extent to *Alopecion*, with its broad and flat head (Fig. 8A). *Bothrolycus* (Fig. 8D) have a comparatively larger and strongly depressed head that is conspicuously broader posteriorly, and sharper angled laterally than in *Boaedon* and *Alopecion*. The snout in *Bothrolycus* is significantly sharper than in other genera, with the rostral that is rather small and not visible or barely visible from above. In *Bothrophthalmus* (Fig. 8E), the head is rather square-shaped, with a broader snout than in other genera of this group, moderately depressed, and not much broader than the neck.

Eye size. The eyes of *Bofa* are rather moderately-sized or even appear small (ED/NOD 0.52–0.63), particularly in old individuals. They are usually not visible from below, and, in mature individuals, barely visible from above. *Boaedon* have conspicuously larger eyes than the new genus with ED/NOD up-to ca. 0.80. They become, however, moderately-sized in old snakes. In *Alopecion* (Fig. 8A) and *Lycodonomorphus rufulus* (Fig. 8G) the eyes are also larger (ED/NOD ca. 0.75–0.80). In *Lamprophis* (Fig. 8F) the eyes appear large in younger individuals, but are moderately-sized in older snakes. The members of *Pseudoboodon* have moderately-sized eyes which are however larger than in *Bofa* (Figs 1, 3A, 8).

Pupil shape. The eye of *Bofa erlangeri* is very dark in life, and the pupil can be seen only at close examination in bright light. In preserved specimens it turns white and is therefore well visible. The circular pupil in this species is a rather distinct character. Among the compared genera, only *Bothrolycus* have such circle-round pupils.

The pupils of *Lamprophis* and of *Lycodonomorphus* are wide ovals. They are capable to shrink to a tiny oval or a dot in bright light and become almost circular in a dark environment. Nonetheless, they still can be considered elliptical at all conditions. A similar pupil is found in the genus *Bothrophthalmus*, as well as in *Pseudoboodon*, where it has been noted to be "round at all conditions save intense sunlight, when it closes to a vertical slit" (Spawls 2004). Only in *Boaedon* and *Alopecion* the pupil remains always clearly elliptical, and turns into a narrow vertical slit, but never to a dot, in bright light.

Gular scales. In *Pseudoboodon* (Fig. 8H, 8I) and *Bothrolycus* (Fig. 7D) there are four or more smaller, irregular gular scales between the posterior chinshield pair and the first ventral shield. *Bofa* (Fig. 8B) usually has one to three pairs of large gulars ('false chinshields'), immediately followed by the first ventral. The holotype of *Bofa erlangeri* has two pairs. In *Bothrophthalmus* (Fig. 8E) there is usually one pair

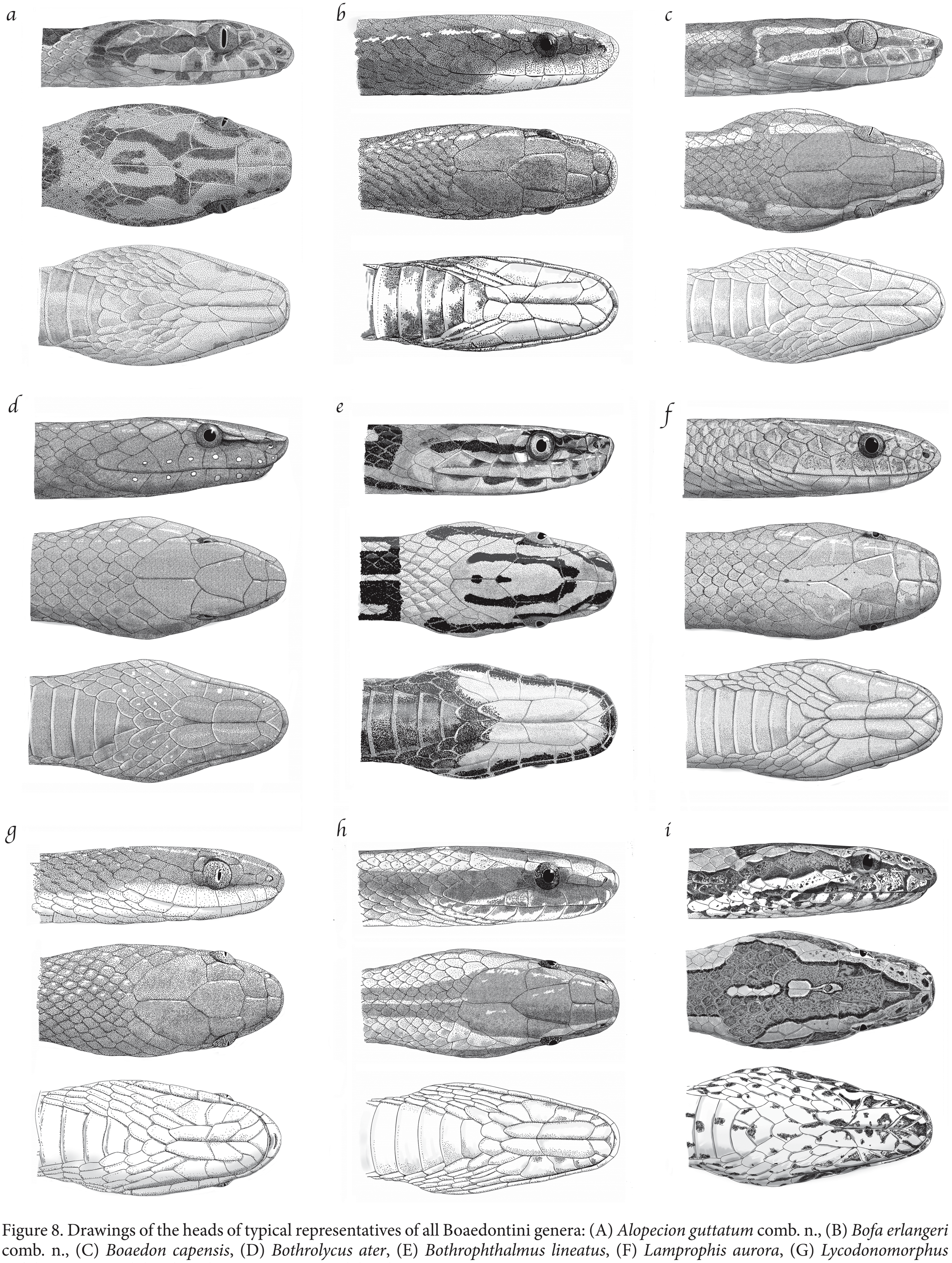

Figure 8. Drawings of the heads of typical representatives of all Boaedontini genera: (A) *Alopecion guttatum* comb. n., (B) *Bofa erlangeri* comb. n., (C) *Boaedon capensis*, (D) *Bothrolycus ater*, (E) *Bothrophthalmus lineatus*, (F) *Lamprophis aurora*, (G) *Lycodonomorphus rufulus*, (H) *Pseudoboodon abyssinicus*, (I) *Pseudoboodon gascae*.

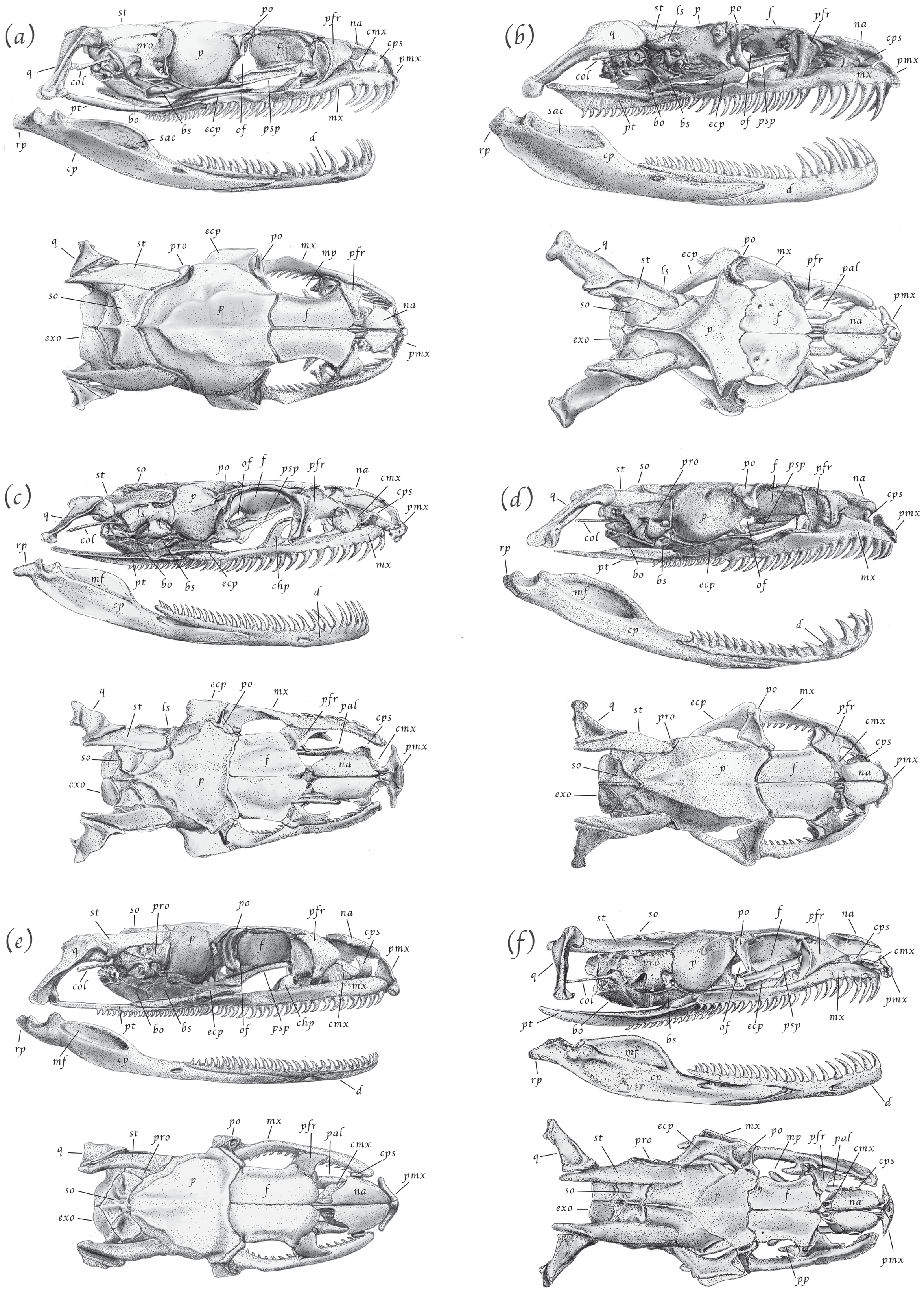

Figure 9. Drawings of the skulls of Boaedontini: (A) *Boaedon fuliginosus*, (B) *Bothrolycus ater*, (C) *Bothrophthalmus lineatus*, (D) *Lamprophis aurora*, (E) *Lycodonomorphus rufulus*, (F) *Pseudoboodon lemniscatus*. See "Material and methods" for abbreviations.

of large gulars as well. Some *Lamprophis* (Fig. 8F) and *Lycodonomorphus* (Fig. 8G) may have just two gulars behind the posterior chinshields, but usually not as large and symmetrically arranged as in *Bofa*. In *Alopecion* (Fig. 8A) and *Boaedon* (Fig. 8C), the gulars situated between chinshields the first ventral are either irregular or arranged in more than two pairs. The arrangement and the number of gular scales correlate with the head breadth: In *Alopecion*, *Boaedon*, *Bothrolycus*, and *Pseudoboodon* the heads are broader posteriorly, hence more gular scales fit across the throat.

Chinshields. In *Bofa* the anterior chinshield is approximately twice as long as the posterior (Fig. 8B). Similarly to *Bofa*, the posterior chinshields in *Alopecion* (Fig. 8A) and *Boaedon* (Fig. 8C) are much shorter than the anterior. This applies also to *Bothrophthalmus* (Fig. 8D) and *Pseudoboodon* (Fig. 8H, 8I), but apparently not to such extent. In *Bothrolycus* (Fig. 8D) and *Lamprophis* (Fig. 8F), the anterior and posterior chinshields are of approximately equal length. In *Lycodonomorphus rufulus*, i.e. *Lycodonomorphus* sensu stricto, the anterior pair is shorter (Fig. 8G), whereas it is slightly longer than the posterior in *L. inornatus*. The length of the anterior pair seems to depend in this group on the snout length.

Other head scales. *Bothrolycus* have two preoculars instead of a single, as in *Bofa* and other genera of this group. A single loreal scale is present in all genera. In *Bofa* it is lower than broad: Although Sternfeld (1908) described it as square (having "equal breadth and height"), we found it horizontally elongate also in the holotype. *Bothrolycus* and *Bothrophthalmus* stand out in this group, having a conspicuous loreal groove, which reminds of the thermoreceptor of a pit-viper, but is of unknown purpose. Although *Bofa* lacks such grooves, the loreal of *B. erlangeri* is slightly concave (Fig. 3A), thus may be a transient feature from completely flat loreals of other Boaedontini to the groove found in the sister lineage of this genus.

All four currently recognised members of *Pseudoboodon* also share an unusual morphological trait that is unique for this genus: a triangular pit incised in the fifth and sixth upper labial scales. No such morphological peculiarities are found in *Bofa* and in other related genera. The members of the new genus, especially *Bofa erlangeri*, have a large rostral scale that is visible from above. In *Alopecion*, *Boaedon*, *Lamprophis*, *Lycodonomorphus* and *Pseudoboodon* the rostral is much smaller and in dorsal view not or barely visible. Due to a rather sharply pointed snout, in *Bothrolycus* the rostral is the smallest in this group and typically is not visible from above.

Teeth and jaws. Dowling (1969) recognised as characteristic for this tribe that the maxillary teeth are "longer anteriorly, with a tendency to have 5–7 anterior teeth which increase in length posteriorly, a diastema, then 11–16 smaller subequal teeth". However, this seems to be fully applicable only to the members of the genera *Boaedon* (Fig. 9A) and *Alopecion* (Fig. 6). These snakes have indeed a rather pronounced diastema after the fifth or the sixth anterior tooth, followed by the rest of the teeth that are smaller and subequal.

In the remaining taxa of the Boaedontini genera it is a matter of interpretation whether an enlarged interspace is present or not. Moreover, its size may vary individually and depend on the age of the snake. This interspace seems to be caused by the size difference between the anterior group of enlarged teeth and the rest of teeth on the maxilla: It is usually equal to the spaces between enlarged teeth, being in fact the last such interdental space that precedes the normally-sized posterior teeth. For *Bothrolycus* (Fig. 9B), Boulenger (1893: 345) states that the teeth are evenly distributed and presents a drawing of a maxilla that shows this, albeit there is in fact a small interspace after the sixth tooth in the holotype, according to the original genus description by Günther (1874: 444). Dowling (1969) mentions a diastema after six enlarged teeth in this genus as well, and in the specimen of *B. ater* UMMZ 56291, housed in the Museum of Zoology of the University of Michigan, there is also a well noticeable interspace between the last enlarged (6th) and the first normally-sized (7th) teeth (MorphoSource 2021: 87602/m4/M70139). The same applies to *Bothrophthalmus* whose teeth are generally considered gapless (Bourgeois 1968: 22), but a slightly larger interspace between the last enlarged and the first normally-sized teeth is shown in Bourgeois' (1968) monograph. In the specimen of *B. lineatus* ZFMK 82159 we found no enlarged interspaces (Fig. 9C). In *Lycodonomorphus* sensu stricto (Fig. 7E) all maxillary teeth are of approximately equal length and more or less evenly arranged along the maxilla. They seem to be shorter than in the rest of Boaedontini genera. A diastema was also reported for *Pseudoboodon* (Bogert 1940: 25, Rasmussen & Largen 1992: 69, 73). However, we did not find one in the specimen of *P. lemniscatus* ZFMK 55510 (Figs 4, 9F). Also according to Rasmussen & Largen (1992: 69), a diastema is not consistently present in snakes of this genus. In *Lamprophis* the maxillary teeth seem to be a little shorter anteriorly, gradually increase in length up to the sixth tooth, and then decrease again. FitzSimons (1962: 112) mentions a "small interspace after a group of six anterior teeth, which increase in size up to the fifth". This interspace seems to be of similar kind as in *Bothrolycus*, i.e. caused by a larger tooth that is followed by smaller teeth. It may be absent, as in the specimen of *L. aurora* UMMZ 61580 (MorphoSource 2021: 87602/m4/M57924).

The maxilla is 'short' (i.e. equal to or shorter than a half of the total skull length, measured as a distance from the rostral face of the premaxilla to the caudal ends of the supratemporals) in the clade that comprises *Alopecion*, *Boaedon*, *Lamprophis*, *Lycodonomorphus*, and 'long' (i.e. longer than a half of total skull length) in *Bofa*, *Bothrolycus*, *Bothrophthalmus*, and *Pseudoboodon*. Accordingly, the dentary is shorter in the first four genera as well. The maxillary length as well as the teeth number and size have been hypothesised to depend on prey capture method (Westeen et al. 2020). Although it may be valid for the adaptive radiation among the families of snakes, especially concerning the venom teeth evolution, this hypothesis does not explain such differences between and within genera of snakes sharing the same feeding modes and prey capture methods. All Boaedontini constrict a prey that they ether ambush or actively find, and all species use both these preying modes to greater or lesser extent. Hence, it appears more likely that the differences in their palatomaxillary apparatus are a result of adaptations for different diet.

The enlarged anterior maxillary and mandibular teeth are not unique for Boaedontini and are found in many groups of alethinophidians. In fact, this trait is also more or less present in the sister group of Boaedontini, Bogert's (1940) 'Group II', that includes such genera as *Lycophidion*, *Mehelya* and several others (Dunger 1966, Broadley et al. 2018). It is certainly an adaptation to a feeding mode when the snake has to catch and immobilise prey that is covered by hairs or feathers. Therefore, such teeth are present in genera whose diet includes to a large extent birds and mice: *Boaedon*, *Pseudoboodon*, and *Bofa*. The natural history of *Bothrolycus* is the least known among Boaedontini, but its huge anterior teeth and the strong maxillae indicate that this terrestrial snake may be specialised in preying on comparatively large furry or feathered animals, such as rats and birds that descend to the ground. The relatively thick and stout body of *Bothrolycus* may be an adaptation to ambush-preying (similarly to ground-dwelling vipers or pythons), being of an advantage when the snake has to grab and restrain the prey. Also the strong quadrate and pterygoid bones of *Bothrolycus* argue for this hypothesis. Overall, the shape of the mandible and its suspensorium in this snake, as well as thick and strong maxillae, resemble the anatomical apparatus in Pythonidae that is responsible for an extraordinary gape diameter (Cundall & Greene 2000). In *Alopecion*, the rather exceptional dentition may be an adaptation for restraining spiny prey – girdled lizards (*Cordylidae*), that, along with geckos and rodents, at least in some populations, seem to constitute a substantial part of this snake's diet (FitzSimons 1962, Branch & Burger 1991, Taft et al. 2017, Huysteen & Petford 2018). The anterior teeth are not as strongly enlarged in *Bothrophthalmus* and *Lamprophis* and not enlarged at all in *Lycodonomorphus*, snakes that typically feed on amphibians, fish and lizards, i.e. a prey with smoother skin surfaces.

The palatines of *Bothrolycus* are long, bearing 13 teeth, and surprisingly thin for a snake with such robust jaws, being the thinnest in this group of genera. The mandibular and the choanal processes are situated in this genus at the same level together, each at the opposite side of the palatine. This is similar in *Bofa erlangeri*, while the choanal process is closer to the caudal end of the palatine in the rest of Boaedontini. The examined *Boaedon fuliginosus* specimen had just seven teeth on both palatines, i.e. the smallest tooth number and perhaps the shortest palatines in this group. In the remainder of the genera the number of teeth seems to be within the range 9–11: In *Pseudoboodon* the palatine bears, as in *Bofa*, nine teeth; *Alopecion* and *Lycodonomorphus* have palatines with eleven teeth; in the examined specimens of *Lamprophis aurora* and *Bothrophthalmus lineatus* we counted ten teeth. There are 21 to 23 small, curved and posteromedially directed pterygoid teeth in all genera except *Lycodonomorphus*. The examined specimen UMMZ 126980 of *L. rufulus* (MorphoSource 2021: 87602/m4/M75082) has 31 small teeth on each pterygoid. The pterygoid and palatine teeth are known to play an important role in intraoral movement and manipulation of prey, and the difference in their number and length, as well as the shape of the bones, result from the need to consume the prey in specific environmental circumstances. In the case of *Lycodonomorphus*, for example, longer palatines and pterygoids, with a larger number of small teeth may be of advantage when slippery prey is consumed in an aquatic environment. The snakes in the remaining Boaedontini genera are terrestrial and anatomically adapted to consume almost any vertebrate animal of suitable size that is available in their habitat and ecological niche. Therefore, their palatine and pterygoid teeth are not as highly specialised.

The quadrates in Boaedontini are generally rather short, if compared with other groups of colubroid and elapoid snakes, but their shape considerably varies. This again supports the idea of diet-driven adaptive evolution of skull traits. Evolutionary relationships, at least at the level of genera, do not seem to play any role: *Bothrolycus* has the largest and strongest quadrates whereas they are thinnest and shortest in its closest relative *Bothrophthalmus*. In both, these bones are straight, whereas they are slightly curved in their close relative *Bofa*. In the latter, the quadrates are of similar size as in the rest of Boaedontini.

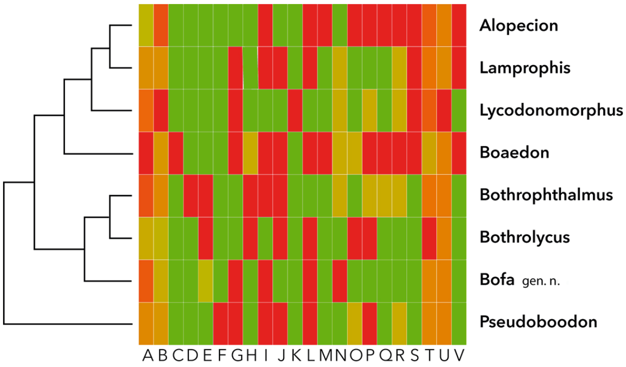

Figure 10. Graph visually comparing different character combinations in Boaedontini: A – body size, B – tail length, C – apical pits on dorsal scales, D – dorsal scales keeled, E – loreal pits, F – labial pits, G – rostral visible from above, H – number of preoculars, I – anterior chinshields larger, J – length of chinshield pairs equal, K – anterior chinshields smaller, L – anterior maxillary and mandibular teeth enlarged, M – diastema after enlarged maxillary teeth, N – gulars paired, O – head flattened, P – head much broader than neck, Q – eye size (in adults), R – pupil elliptic, S – maxilla size, T – palatine teeth number, U – pterygoid teeth number, V – nasals large (relatively to frontals). Pure colours indicate presence (red) or absence (green) of the character. Intermediate states are shown with mixed colours when a shift towards red means greater and towards green lesser strength of the character.

Other cranial features. In all genera, except *Bothrolycus* and *Bothrophthalmus* the frontals are in dorsal view significantly longer than their breadth. In *Bothrolycus* they are nearly as broad as long, and only slightly longer in *Bothrophthalmus*. In these genera the frontals are also almost equal in length to the nasal bones, hence being relatively small or at least shorter in comparison with the other Boaedontini.

The size and the shape of the postorbital, rather than of the prefrontal, appear to consistently correlate with the eye size, and can be used for assessment of this character: The larger the eye, the smaller and thinner is the postorbital. Among examined specimens, the postorbitals were the thinnest and the shortest in *Boaedon fuliginosus* and *Alopecion guttatum*, both snakes with comparatively large eyes. *Bothrolycus* is an exception here again: The postorbital of this relatively small-eyed snake is rather thin, but long – almost reaching the maxilla with its lower end.

The posterior part of the parietal (that contains the optic tectum) is notably narrower and lower in *Bothrolycus ater* and *Bofa erlangeri*, the only species in this group that have circular pupils. This could be another indication that these still poorly-known snakes have different activity patterns. Generally, for the clade *Bofa*/*Bothrolycus*/*Bothrophthalmus*, parietals with a narrow posterior part and sharp lateral and medial ridges are characteristic. This trait reaches its extreme in *Bothrolycus* (Fig. 9B) where the anterior half of the parietal is almost twice as broad as the posterior. It is nearly triangular in dorsal view and posteriorly outlined by sharp and high ridges merging to a single medial ridge that passes through the much lower and narrower posterior half of the parietal and ends at the suture with the supraoccipital. In *Bothrophthalmus* the anterior ca. 2/3 of the parietal are similarly broad as in *Bothrolycus*, but with not as sharp ridges, and the fall-off to the posterior low and narrow 1/3 is not as strong. In *Bofa*, the parietal is not extremely broad anteriorly, but similar sharp ridges are present, and, like in *Bothrophthalmus*, the posterior 1/3 is much narrower than the anterior 2/3.

In *Bothrolycus*, the parietal deeply enters the supraoccipital with its posterior margin. The latter is extremely narrow in the middle and has two high ridges which originate at the contact point with the medial parietal ridge and extend laterally to the exoccipitals, where they are followed by similarly high exoccipital ridges. The third supraoccipital ridge is much lower and extends medially across it from the anterior to the posterior border. The ridges on the exoccipitals cause deep folds at their posterior sides, making

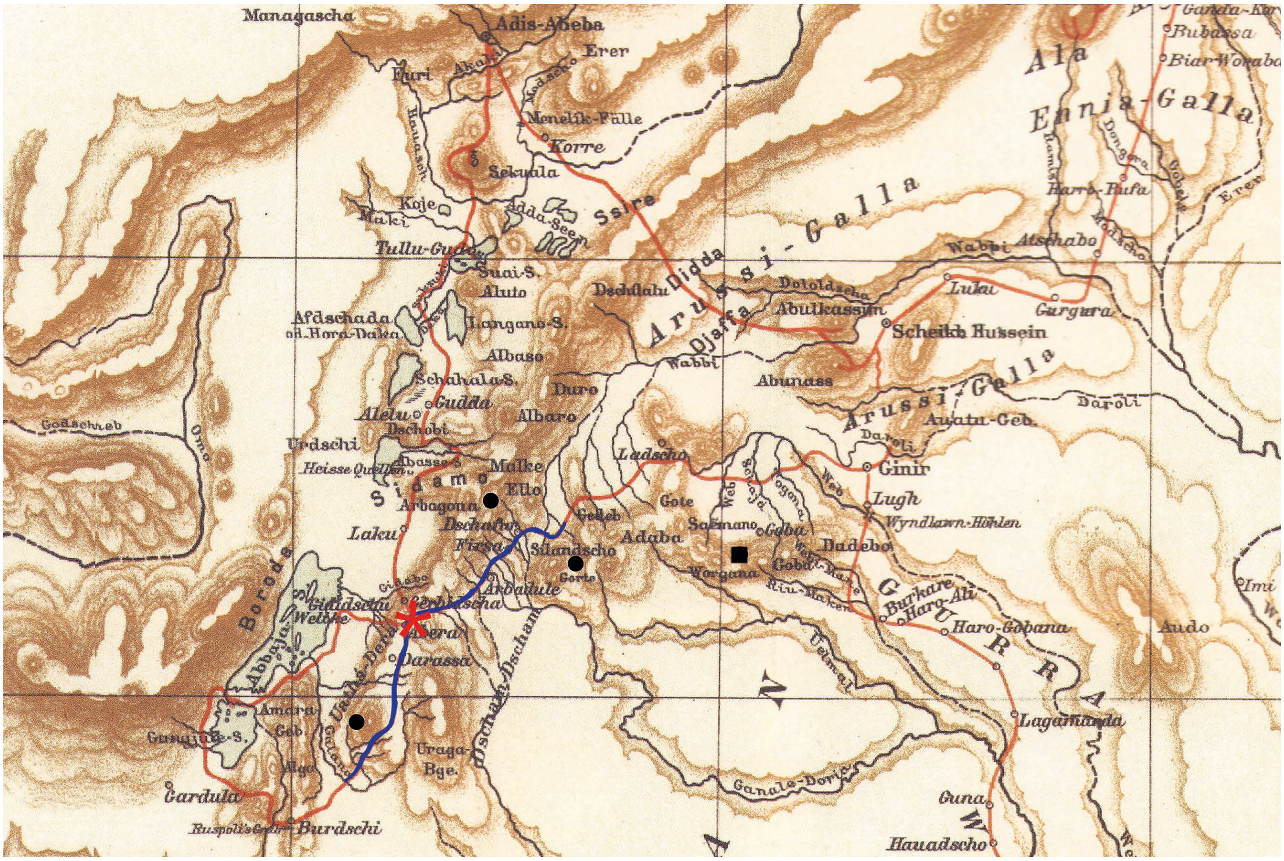

Figure 11. Fragment of a map from the final report of Erlanger's expedition (Erlanger 1904). The part of the route within the distribution area of *Bofa erlangeri* comb. n. is marked with blue colour. Localities where this species was recorded east of the Rift Valley are marked with black circles. Black square – our record; red asterisk – proposed restriction of type locality.

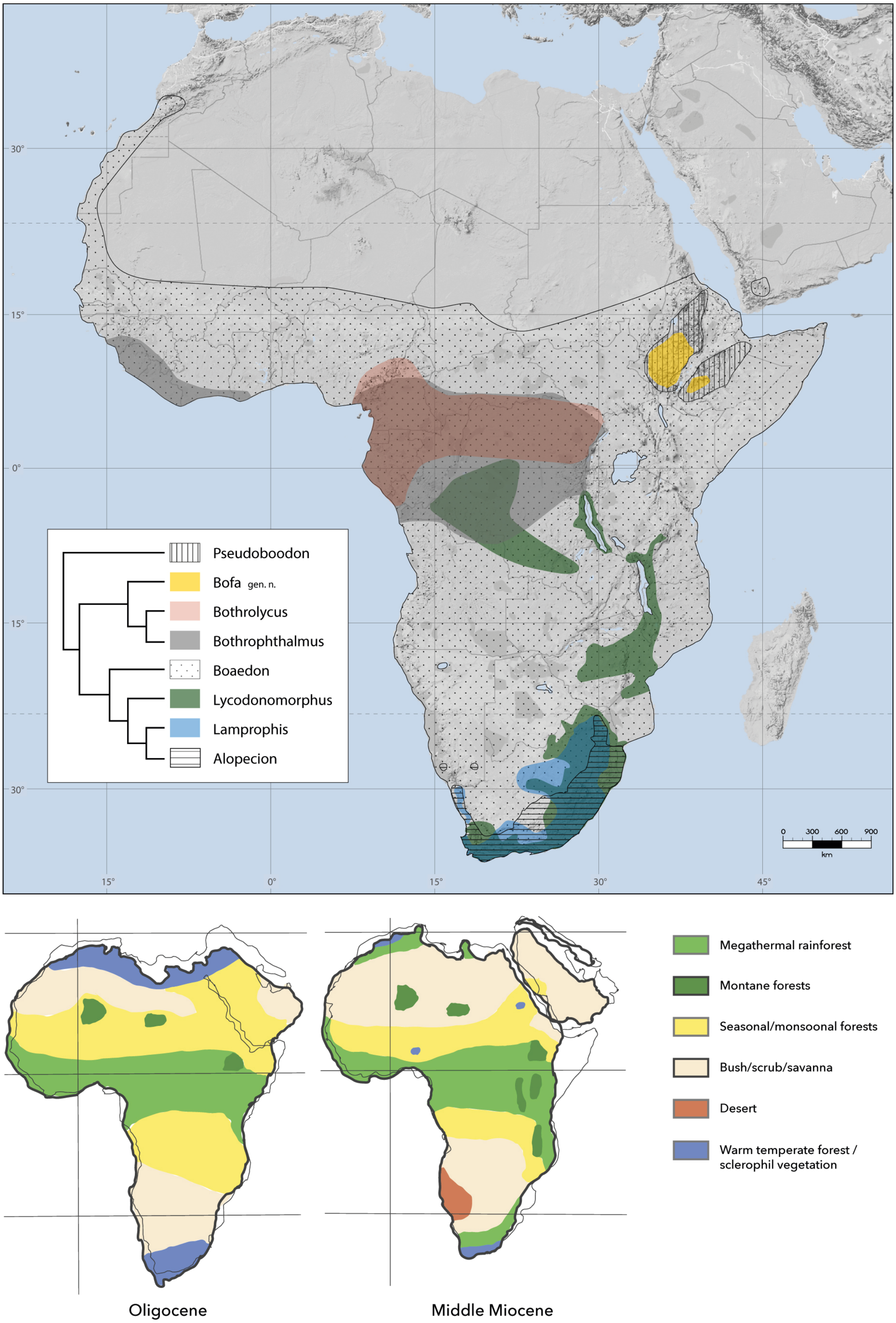

Figure 12. Top: Map of Africa showing the currently known approximate ranges of the member genera of Boaedontini. Bottom: Tentative vegetation maps for Oligocene, following the terminal Eocene cooling event, and for middle Miocene, coinciding with the Miocene thermal maximum (after Morley & Kingdon 2013, with modifications).

the exoccipitals appear smaller in dorsal view than in the rest of Boaedontini.

All these morphological differences are visualised in Figure 10. Apparently, some of the aforementioned characters are related to phylogenetic affinities, but the majority result from adaptive radiation within the tribe. Some singleton characters may reappear separately in different clades of the Boaedontini, and even in other groups of Lamprophiinae, but combinations of them unambiguously define each of the genera compared here. Figure 10 also demonstrates that *Alopecion* and *Boaedon* are the most morphologically derived genera in the tribe. This may be, at least partially, related to the ecological specialisation of the first (*Alopecion*) and evolutionary success leading to expansion across the continent and beyond (*Boaedon*). *Bofa* has a significant number of morphological differences from other genera and shares character states both with the oldest lineage of the tribe (*Pseudoboodon*) and with the genera *Bothrolycus* and *Bothrophthalmus*, with which it is allied.

Type locality of *Bofa erlangeri*

The type species of the new genus, *B. erlangeri*, occurs both, east and west of the Great Rift Valley. Its type locality was imprecisely specified in a way typical for the time – as "Somaliland", even though it was in Abyssinia. Since the route of Erlanger's expedition is exactly known (Erlanger 1904), we can estimate the location of possible collection sites by matching it to better documented localities where specimens of this snake were collected or observed later. We know that, after Erlanger and his people had left Addis Ababa, they went south and explored the areas in the Great Rift Valley and east of it. Although they travelled along the western shore of Lake Chamo, they did not go west far enough to reach the currently known distribution area of *B. erlangeri*. Thus, it is much more likely that the holotype was collected in the east where the main route of the expedition was, more precisely somewhere in the vicinity of Abera, where Erlanger and his people had a longer stay at a residence of the local dejazmach, and that he extensively describes in his report (Erlanger 1904). Therefore, we propose to treat Abera, ca. 6°27' N 38°26' E, as the restricted type locality of *B. erlangeri* (Fig. 11). Today, this place (in Dara district of Southern Nations, Nationalities, and People's Region) is not a singleton settlement but a number of small villages that are situated approximately at equal distance from the localities where further specimens of *B. erlangeri* have been collected in the second half of the 20th century.

Biogeographic remarks

The new genus is endemic to the Ethiopian highlands. Throughout its range the single species of the genus is not sympatric with any *Boaedon* species, having different habitat preferences and ecology. From other related genera which are distributed in equatorial Africa or south of the equator (*Bothrophthalmus*, *Bothrolycus*, *Lamprophis*, *Lycodonomorphus*), the new genus is separated ecologically, being confined to montane forests, and spatially, by a large geographical distance (see map in Fig. 12). The main radiation of Boaedontini took place in eastern and southern Africa that is mostly a plateau 1,000 m and more above sea level that derived from an ancient uplift left over from the break-up of Gondwana, but some parts of it were augmented by later tectonic processes. One of them was Ethiopia where the vulcanism that began ca. 30 mya (Burke 1996) produced an extensive highland area. That the range of the genus *Pseudoboodon* is limited to the Horn of Africa and that the oldest among the now known genera in its sister clade *Bofa*, is endemic to the Ethiopian highlands may indicate that the initial divergence, i.e. between *Pseudoboodon* and the common ancestor of the rest of the tribe, took place in this geographic region during Eocene-Oligocene transition 30–35 million years ago (Zheng & Wiens 2016, McCartney et al. 2021). After the rise of the Ethiopian highlands, new habitats evolved providing conditions for subsequent radiation of *Pseudoboodon* across plateaus as far north as Eritrea and northern Somalia. The evolution of the remaining Boaedontini genera continued at lower altitudes and, similarly to some other widespread groups of African snakes (Barlow et al. 2019, Engelbrecht et al. 2021), probably was driven by a climatic and biome shift. This period in Europe, the so-called "Grande Coupure", is characterised by mass extinction and floral and faunal turnover. Also in tropical regions, at the end of the Eocene, the flora underwent a change, with disappearance of forests from mid-latitudes as a result of global cooling (Morley 2000, 2011). The split between the lowland forest genera *Bothrolycus* and *Bothrophthalmus* and the highland forest genus *Bofa* took place in the middle of the Oligocene (Greenbaum et al. 2015), possibly as a result of retraction of tropical forests toward the equator. At that time a forest covered the area of the contemporary open savannah between the western Ethiopian highlands and the Congo Forest, where the ancestral population of the clade *Bothrolycus*/*Bothrophthalmus* may have lived, while *Bofa* remained confined to the low-altitude montane forests lying further north (Fig. 12). In the upper Oligocene, the older lineages of *Boaedon* may also have evolved in the equatorial forest. The later radiation of Boaedontini took place in the Miocene and likely was driven by biome shift at margins of their ranges.

Being associated with forested or recently forested habitats in a region where less than 4% of natural forests survived deforestation (Billi 2015), *Bofa erlangeri* may be extinct in most parts of its historical range, especially at the majority of localities east of the Great Rift Valley, including the type locality. Despite intensive photographic tourism, birdwatching and other citizen-science activities in this region, observations of *B. erlangeri* are seldom and limited to the west of the Rift Valley. As with other endemic forest snakes in Ethiopia, an urgent action is required to assess the status of the populations of *B. erlangeri* in order to take adequate conservation measures before this species, and thus the entire genus of snakes, is gone forever.

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Supplementary data

The following data are available online:

Supplementary document. GenBank accession numbers of nucleotide sequences used in the phylogenetic analyses of this study.