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Generic affinities of African house snakes revised: a new genus for *Lamprophis inornatus* (Serpentes: Lamprophiidae: Lamprophiinae: Boaedontini)

Arthur Tiutenko[1], Anastasiia Maliuk[2,3] & Claudia Koch[4]

[1] Friedrich-Alexander-Universität Erlangen-Nürnberg, Schlossplatz 4, 91054 Erlangen, Germany
[2] Department of Mechanical Engineering, University College London, WC1E 6BT, London, United Kingdom
[3] National Museum of Natural History, National Academy of Sciences of Ukraine, 15 Bohdan Khmelnytsky Street, 01054 Kyiv, Ukraine
[4] Leibniz Institute for the Analysis of Biodiversity Change (LIB), Museum Koenig, Adenauerallee 160, 53113 Bonn, Germany

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

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Abstract. This article is the second part of a revision of the systematics of Boaedontini Dowling, 1969 and a follow-up to the work by Tiutenko et al. (2022). As a result of morphological and phylogenetic analyses, further taxonomic actions are taken in the genus *Lycodonomorphus* Fitzinger, 1843. *Lamprophis inornatus* Duméril, Bibron & Duméril, 1854, a species initially described in the genus *Lamprophis* and subsequently assigned to *Lycodonomorphus*, is here transferred to a new monotypic genus on a basis of combined criteria including genetic distance, morphology, ecology and biogeography. For improved taxonomic stability of the species and the new genus, a neotype for *L. inornatus* is designated from the specimen ZFMK 032712. The lectotype of *Boodon infernalis* Günther, 1858 is designated from one of three extant syntypes NHMUK 1858.4.11.5 and the type locality of this species, that is currently treated as a junior synonym of *L. inornatus*, is restricted to Durban, South Africa. The name '*infernalis*' should be available if the species status of this northern clade would become restored. *Lycodonomorphus subtaeniatus* Laurent, 1954, another former *Lycodonomorphus* species long assumed to be a member of *Boaedon*, is here formally assigned to this genus and tentatively placed next to *Boaedon upembae* (Laurent, 1954) and *Boaedon virgatus* (Hallowell, 1854) on a basis of pholidosis, cranial morphology and dentition. The tribe Boaedontini now contains nine genera that can be separated by morphological characters according to the proposed key. The genus *Lycodonomorphus* still requires attention of taxonomists, as it contains species, such as *L. bicolor*, *L. laevissimus*, *L. leleupi*, *L. mlanjensis*, *L. obscuriventris*, and *L. whytii*, with uncertain taxonomic position and in this sense has to be viewed as sensu lato.

Key words. Squamata, *Elaiophis*, nomenclature, osteology, skull, taxonomy

Introduction

Lamprophiid snakes comprising the tribe Boaedontini Dowling, 1969, 'African house snakes and allies', typically share such morphological traits as elongate cylindric body, smooth and equally-sized dorsal scales, two postoculars, divided nasal, presence of a loreal scale, undivided anal plate, paired subcaudals, aglyphous teeth, hypapophyses on all dorsal vertebrae. Furthermore, they 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–4th (sometimes the 5th) is in contact with the anterior chin shield. Up-to six anterior maxillary and mandibular teeth are usually enlarged. Obviously, these characters are rather general, and snakes in many other taxonomic groups can match it, if not all of them combined, then at least some combinations. This was the reason why many current members of *Boaedon* Duméril, Bibron & Duméril, 1854, *Lamprophis* Fitzinger, 1843, and *Lycodonomorphus* Fitzinger, 1843 were initially assigned to a variety of unrelated genera, such as *Coelopeltis* Wagler, 1824, *Coluber* Linnaeus, 1758, *Coronella* Laurenti, 1768, *Lycodon* Fitzinger 1826, or *Natrix* Laurenti, 1768. Sometimes new genera were introduced to accommodate such species: *Ablabophis* Boulenger, 1893, *Alopecion* Duméril, Bibron & Duméril, 1854, *Eugnathus* Duméril, Bibron & Duméril, 1854, *Glypholycus* Günther, 1893, *Holuropholis* Duméril, 1856, *Nerophidion* Werner, 1924, and *Pachyophis* Werner, 1924. To some of these genera further snake species were subsequently added that, as we now know, were evolutionary unrelated but just superficially similar. Often it was just this, rather approximate, morphological similarity that encouraged herpetologists to synonymise the genera or to move member species between them. The reasoning of such actions was not always adequately explained. Also, again and again, in the course of revisions, some, even quite obvious, genus-level synapomorphies were overlooked or ignored. Thus, by the end of the 20th century the number of genera in this tribe was reduced to five: *Bothrolycus* Günther, 1874, *Bothrophthalmus* Peters, 1863, *Lamprophis* Fitzinger, 1843, *Lycodonomorphus* Fitzinger, 1843, and *Pseudoboodon* Peracca, 1897.

With the advancement of molecular phylogenetics such morphological traits as pits and grooves on scales, shape of pupils, various dental and cranial features finally began to make sense for taxonomists as characters in morphological genus delimitation. In a little longer than a decade, the number of genera in the tribe grew again – from five to eight. First, Kelly et al. (2011) resurrected the genus *Boaedon* from synonymy of *Lamprophis*, which had been established more than 30 years earlier by Broadley (1983). Then, more recently, Tiutenko et al. (2022), in the first part of this revision of Boaedontini, revived the genus *Alopecion* and erected a new genus *Bofa* Tiutenko, Koch, Pabijan & Zinenko, 2022 for a lamprophiid species, closer related to *Bothrolycus* and *Bothrophthalmus*, that had been initially described as *Boodon erlangeri* Sternfeld, 1908 and subsequently became subsumed to *Lamprophis*. It was showed that such characters as pupil shape, presence of apical pits on dorsal scales, hemipenial morphology, as well as dental and cranial features, correlate with intergeneric genetic distance, hence are diagnostic and can be used for delimitation of the genera, in addition to molecular evidence.

This process is not finalised, and some species still remain misplaced in the genera. It creates a problem because the otherwise distinct morphological and other diagnostic generic characters may be obfuscated by deviant traits of such members. Vague diagnoses, saying that the members of the genus "may or may not" have certain characters, that a trait is "absent or present", are signs of this. If our aim is a stable taxonomy, we should look for ways to accommodate such problematic members in different genera or to introduce subgroups in the current genus. In Boaedontini, *Lycodonomorphus* remains a bundle of such issues.

Fitzinger (1843: 27) established the genus *Lycodonomorphus* in the first volume of his "Systema Reptilium" in just one line of text, assigning *Coluber rufulus* Lichtenstein, 1823 to it. The second volume that perhaps was supposed to contain more extended accounts was never published. The taxon *Coluber rufulus* had been introduced twenty years earlier in a similar manner: just two lines of text describing coloration and the shape of dorsal scales (Lichtenstein 1823: 105). The holotype had not been fixed, but a consensus seems to exist that it is housed in Museum für Naturkunde Berlin with the accession number ZMB 1759 (Loveridge 1958, Bauer 2000, Wallach et al. 2014). If so, then traits of this species described from this and other similar specimens also by other authors should be applicable to the genus as diagnostic. The first comprehensive diagnosis of *Lycodonomorphus rufulus* was provided more than a century later by Loveridge (1958: 20): "Rostral broader than deep, just visible from above; nostril directed upwards, between two nasals; internasals as long as, or longer than, broad, much shorter than the prefrontals; prefrontals moderate; frontal 1½ to 1⅔ times as long as broad, as long as its distance from the end of the snout, shorter than the parietals; loreal longer than deep, well separated from the first labial; preocular 1, rarely 2; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit; lower labials 8, first four in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scales with or without apical pits, in 19 rows; ventrals 160–178 [...]; anal entire; subcaudals 54–78 [...]." Unfortunately, in descriptions of hemipenial morphology, Loveridge just relied on a work by Bogert (1940). According to Bogert and consequently to Loveridge, it is "distally forked", but Zaher showed a photograph and described the hemipenis of this species as not forked (Zaher 1999: 23). We also examined for this study the organ of a male specimen (NMB R10839) and found it unilobal, i.e., not forked (see more in "Results and discussion").

In one and a half centuries of its history, the content of the genus *Lycodonomorphus* changed several times by addition of further members. It currently comprises nine species (Uetz et al. 2025): *L. bicolor* (Günther, 1893), *L. inornatus* (Duméril, Bibron & Duméril, 1854), *L. laevissimus* (Günther, 1862), *L. leleupi* (Laurent, 1950), *L. mlanjensis* Loveridge, 1953, *L. obscuriventris* FitzSimons, 1964, *L. rufulus* (Lichtenstein, 1823), *L. subtaeniatus* Laurent, 1954, and *L. whytii* (Boulenger, 1897). Only three of them were assigned to this genus originally, i.e., upon original description. The rest was transferred to *Lycodonomorphus* from other genera in the course of its history, for various reasons that were not always well explained or evident, and some appear not always justified or correct. As a result, every time when the generic diagnosis of *Lycodonomorphus* was extended with deviant characters of a new member, the diagnosis became increasingly vague.

The first such species was *Glypholycus bicolor* Günther, 1893. Surprisingly, Loveridge found only one morphological difference from *Lycodonomorphus*: "The 4th labial is the only one to normally enter the orbit, whereas in all the other species both 4th and 5th are normal, and the 4th only is very exceptional" (Loveridge 1958: 7). He ignored or overlooked other peculiarities of this snake that Laurent (1954: 41) mentioned two years earlier. Laurent notes that the head and the eyes of *L. bicolor* are smaller ("reduced" in comparison to the head size) than in *L. rufulus*; the pupil is circular and not sub-elliptical as in *Lycodonomorphus* sensu stricto (abbreviated here as 's.s.'); the frontal shield is short; ventral count is lower; the midbody scale count is much higher: 23–25 vs. 19. The latter character (along with the endemism to Lake Tanganyika) serves the identification of *L. bicolor* in the key to *Lycodonomorphus* that Loveridge provides in the same review of the African snake genera (Loveridge 1958: 7). However, he seems

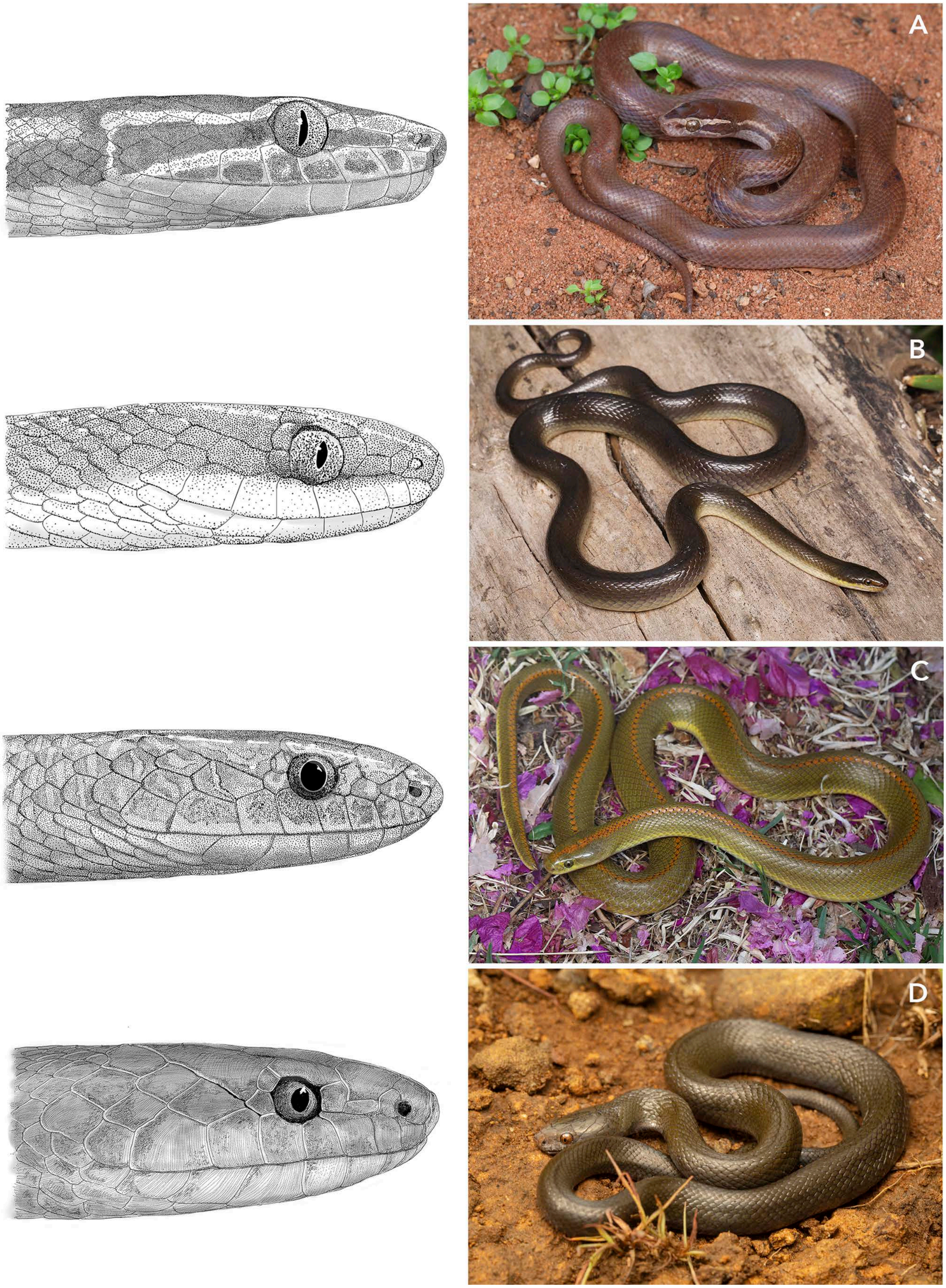

Figure 1. Head morphology details (drawings) and general appearance of *Boaedon capensis* (A), *Lycodonomorphus rufulus* (B), *Lamprophis aurora* (C), *Lycodonomorphus inornatus* (D). Photographs by L. Kemp (A–C) and G. K. Nicolau (D).

not to notice that this and several other characters do not match the generic diagnosis. Perhaps, it was because other members of *Lycodonomorphus* were poorly studied at this time, and the genus officially contained just four species, of which two, i.e., a half of the genus content, had deviant characters. In the same review paper, Loveridge refrained from taking any taxonomic action on *L. subtaeniatus* (with its two subspecies), although its morphological characters are strongly deviant, what he states in the account and the key. Instead, he provides two accounts, one for each subspecies, where he simply adapts the entire morphometry by Laurent (1954) and even cites Laurent's erroneous comment on the hemipenis. Perhaps, it would not have happened if Loveridge had access to the specimens of *L. subtaeniatus*. The generic diagnosis that he provided for *Lycodonomorphus* is obviously a combination of characters found in *L. rufulus*, *L. bicolor* and *L. subtaeniatus*: "Maxillary teeth 18–25, small, subequal; mandibular teeth longest anteriorly. Head slightly distinct from neck; eye moderate, with round or vertically subelliptical pupil; nostril directed upwards, in a semi-divided or divided nasal; a loreal; preoculars 1, rarely 2; lateral head shields separated by an inconspicuous groove from the upper labials. Body cylindrical; scales smooth, with or without apical pits, in 19–25 rows; ventrals rounded; anal entire, rarely divided. Tail moderate, tapering; subcaudals paired." It is, however, unclear what species "rarely" has a divided anal scale because Loveridge does not mention it in the accounts of the genus members. Also, he omits the fact that maxillary teeth in *L. subtaeniatus* are not subequal, but several anterior are enlarged what Laurent clearly states in the initial description (Laurent 1954). FitzSimons (1962: 103) gives a similar diagnosis, but adds the number of pterygoid teeth which is indeed a distinct character of *L. rufulus*, and hence this genus sensu stricto: 30–34. However, he does not mention that their number in *L. bicolor*, *L. laevissimus*, *L. subtaeniatus*, and *L. whytii* is considerably lower. FitzSimons moderates somewhat the confusion about the form of the hemipenis with a statement that it is "not bifurcate or only bifurcate distally."

The addition of *L. inornatus* led to even further confusion about the generic characters. The snake species currently treated as *Lycodonomorphus inornatus* was originally described by Duméril et al. (1854: 434) in the genus *Lamprophis* where it remained for more than 150 years. In 2011, in a phylogenetic study of the subfamily Lamprophiinae Kelly et al. revealed a closer evolutionary relationship of *L. inornatus* to *Lycodonomorphus*. They removed it from *Lamprophis* and preliminary assigned to *Lycodonomorphus*, changing the diagnosis of the genus again to accommodate the characters of this snake that morphologically and superficially more resembles a *Lamprophis*. For example, the statement about extraordinary many pterygoid teeth disappeared while claims about enlarged maxillary teeth (although they are in fact subequal in this species, but just larger than in *Lycodonomorphus*) and shallowly forked hemipenis, along with non-forked, were added. After that, a mixture of characters from three genera – *Lycodonomorphus*, *Lamprophis* and *Boaedon* – in this generic diagnosis was complete. The genus became not diagnosable to such extent that it was even suggested to consider it invalid (Keates et al. 2022: 6). Also, a quite low support of the node *Lamprophis-Lycodonomorphus* (see more on it in "Results and discussion") can be an argument in favour of such measure. Removing the entire genus and merging it with the sister clade (*Lamprophis-Alopecion*) appears, however, not reasonable because its content would then not become phenotypically more homogenous and diagnosable. Nor it would be constructive, because it would obfuscate the biological diversity and evolutionary trends of this taxonomic group. We therefore take here a different way and revise the generic affinities of the *Lycodonomorphus* members non-conforming with the generic diagnosis, to clarify the systematics of the genus and to make it better diagnosable.

In our previous article dedicated to the systematics of this taxonomic group (Tiutenko et al. 2022) we focused our efforts on analysis of the generic affinities of former members of the genus *Lamprophis* – *L. erlangeri* (Sternfeld, 1908) and *L. abyssinicus* Mocquard, 1906. Since these species had been earlier placed in the genera *Boaedon* and *Pseudoboodon*, we investigated the systematic relationships in the whole tribe and found that not only the taxa of our primary interest but some other Boaedontini species are similarly misplaced in the genera and may be separated or moved to different genera with the same approach and methods that we applied to *L. erlangeri* and *L. abyssinicus*. Since we introduced a new genus for the first and moved the second back to *Pseudoboodon*, to complete the review of the genus *Lamprophis*, we reinstated the genus *Alopecion* for *L. guttatus* – the third and last clearly misplaced member. We, however, refrained from such actions in other genera of the tribe considering it out of the scope of our study at that time. This paper is a follow-up of that previously published work and we regard it as the second part of our revision of Boaedontini. To achieve the results presented here, we used the same methods and additional material that we did not include in the first part of this project.

In taxonomic actions we follow the commonly established approaches in delimitation of taxa and adhere to concepts of genus and species most widely accepted and applied in contemporary zoology (Winston 1999, De Queiroz 2007, Zachos 2016, Coyne & Orr 2018, Hillis 2019). Appropriateness is here the main criterion, i.e., considerations whether introduction of a new genus improves the systematics of the group, making it more logical and stable, whether it contributes to our understanding of the evolution of the group, emphasises deeper species divergence, facilitates identification of the member species, etc. In other words, a genus should not be just a clade situated in a phylogeny somewhere above species level and named only for a purpose of establishing a new binomial for its members. Similar considerations were expressed in a number of recent papers dealing with taxonomy and nomenclature of higher categories, such as Smith & Chiszar

(2006), Vences et al. (2013), Cox et al. (2018) and Mahony et al. (2024). Technically, we regard a genus as a definable monophyletic group of species which are closely related and exhibit similar characteristics in morphology, ecology, behaviour, as well as in geographic distribution. Subsuming species to existing or introducing of new genera merely on a basis of a single parameter, such as genetic distance, morphological similarity, spatial or ecological separation, is here avoided. Although the minimum genetic difference of 8% in protein-coding mitochondrial genes and of 0.5% in nuclear, which is a basic threshold for genetic delimitation of Lamprophiidae genera in similar works (Kelly et al. 2011, Broadley et al. 2018, Keates et al. 2019, Tiutenko et al. 2022), serves also us as a starting point, we consider it only a hint and assess all other above-mentioned aspects in order to achieve a robust support of a clade in a genus status. A genus has to be clearly diagnosable by a combination of characters that would allow identification of its members. Although the members of a genus may have other characters or character states that make them distinguishable, they have to share all characters that identify the genus. If a reliable diagnosis cannot be formulated, it may indicate that the genus has either to be split in further genera or subgenera, or merged with a sister genus, or that some of its member species are misplaced and need to be moved to other genera. In other words, when members with deviant states of diagnostic characters are added to a genus, either its content or the generic diagnosis have to undergo a revision.

Material and methods

Since our aim was neither a complete taxonomic revision at species level, nor description of new species, we did not record full morphometry of large numbers of specimens. However, the following eleven morphological characters were assessed and compared during this study in selected series of specimens: Cs = chin shields; Il = infralabials (lower labials); L = total length (SVL + TL); PrO = preoculars; Sc = subcaudal plates; Sl = supralabials (upper labials); Sq = midbody scale rows, rows of dorsal scales at the middle of the body; SVL = snout-to-vent length; T = temporal scales; TL = tail length; V = ventral plates. In most cases, values of these characters that are provided in the initial descriptions or subsequent revisions of the taxa were sufficient for our purposes. When such information in historical sources was incomplete or required confirmation, types and sometimes further (usually topotypic) specimens were examined. In fact, we examined the type material and additional specimens of the majority of species discussed here in six museum collections: Musée Royal de l'Afrique Centrale, MRAC (Tervuren, Belgium); National Museum, NMB (Bloemfontein, South Africa); Natural History Museum, NHMUK (London, United Kingdom); Zoologisches Forschungsmuseum Alexander Koenig, ZFMK (Bonn, Germany). See Supplementary document 1 for the list of specimens examined.

Cranial osteology played an important role throughout this study. Since the skull is a rather conservative, slowly evolving anatomical structure showing no or very minor differences at species level, we consider the geometry of cranial bones among diagnostic characters suitable for genera delimitation as well as for recognition of intrageneric groupings. We performed µCT scans of the skulls of two out of three extant type specimens of *Boodon infernalis* Günther, 1858 that are now treated as syntypes of *Lycodonomorphus inornatus* and of type specimens of *L. bicolor*, *L. laevissimus*, *L. subtaeniatus subtaeniatus*, and *L. whytii* housed in the NHMUK. For comparison with *Lycodonomorphus*, skulls of all three species of *Lamprophis* were scanned, of which two (*L. fiskii*, *L. fuscus*) were type specimens. Specimens loaned from the NHMUK were scanned (by AM) at the Department of Mechanical Engineering, UCL, with use of a Nikon XT H 225 ST scanner (Nikon Metrology Ltd., UK) with an X-ray beam of 65 kV source voltage and 130 mA current, without filters. The magnification setup generated data with an isotropic voxel size of 16.00 µm. The CT data set was reconstructed using XT Software CT Pro 3D. Micro CT images were imported into the image processing software Avizo (Thermo Fisher Scientific, Mass, USA) and rendered in three dimensions. To produce the coloured images of the skulls shown in Figure 5, segmentation was performed in Amira visualisation software (v. 2019.1 by FEI, Thermo Fisher Scientific). The scans of the specimens at the ZFMK were performed (by CK) with the same equipment and technical parameters as given in our previous work (Tiutenko et al. 2022). Additionally, we used for our analyses µCT images of four specimens now publicly available at MorphoSource (www.morphosource.org): three from Musée Royal de l'Afrique Centrale (MRAC) – *Lycodonomorphus leleupi*, *L. subtaeniatus subtaeniatus* and *L. subtaeniatus upembae*, and one from University of Michigan Museum of Zoology (UMMZ) – *Lamprophis aurora*. Accession numbers of these specimens for search in the database are provided in Supplementary document 1.

For cranial features, we use in this article the same terminology as in Tiutenko et al. (2022) that is common for the works on reptilian osteology, such as by Cundall and Irish (2008) or by McDowell (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, mp = maxillary process of palatine, mx = maxilla, na = nasal, of = optic fenestra, pfr = prefrontal, pp = palatine process of maxilla, q = quadrate, occ = occipital condyle, pmx = premaxilla, pro = prootic, psp = parasphenoid rostrum, pt = pterygoid, rp = retroarticular process, mp =

maxillary process of palatine, smx = septomaxilla, so = supraoccipital, st = supratemporal, tr = transverse process of premaxilla, v = vomer, vp = vomerine process of premaxilla. Additionally, for features of the braincase structure that we discuss in this article, we use the following abbreviations adapted from von Szunyoghy (1932): c. par. = carina parietalis (parietal keel), cr. occ = crista occipitalis (occipital crest).

The terminology in hemipenial morphology is after Zaher (1999). Drawings of the hemipenes (Fig. 4) were performed freehand (by AT) from the specimens NMB R6900 (*L. inornatus*) and NMB R10839 (*L. rufulus*). To ensure the correct presentation of morphology, we verified it with the published photographs of the hemipenes of the same species in Visser (1979: 32) and Zaher (1999: 23).

For the phylogenetic analyses, we re-use here the results of our previously published work. See Tiutenko et al. (2022) for the description of the methods that remained unchanged since then. For calculation of the genetic distances and inference of the phylogenetic relationships we used published sequences listed in Supplementary document 1. For economy of space, we provide in this article only a table for ND4 (NADH dehydrogenase subunit 4) protein coding gene (Tab. 2) and refer to the tables of uncorrected pairwise distances (p-distances) for other analysed gene loci shown in Tiutenko et al. (2022). Additionally, a table in the Supplementary document 2 gives information about distances between concatenated sequences of three genes – ND4, cyt b, and c-mos. To obtain the results shown in the Table 1, we performed the estimation of evolutionary distances in MEGA 11 (Tamura et al. 2021) using the Maximum Composite Likelihood model (Tamura et al. 2004). The sequences for these analyses were aligned using the MUSCLE (Multiple Sequence Comparison by Log-Expectation) algorithm (Edgar 2004). Rate variation among sites was modelled using a gamma distribution (shape parameter = 1). Codon positions included were 1st + 2nd + 3rd + non-coding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). This analysis involved 24 nucleotide sequences. There was a total of 660 positions in the final data set.

Nomenclatural acts

This published work and the nomenclatural act it contains were registered in ZooBank, the online registration system for the ICZN. The Life Science Identifier (LSID) for this publication is: urn:lsid:zoobank.org:pub: CD6CFDD4-1327-4556-B92C-6606C5950DE4. The electronic edition of this article 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. It conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under the Code from the electronic edition of this article.

Results and discussion

Kelly et al. (2011), based on preceding works by Bogert (1940), Broadley (1990) and Branch (1998), formulated the following updated diagnosis of *Lycodonomorphus*: "Body cylindrical and moderately elongated; tail moderate to short; head moderate to small, slightly broader than neck and distinct from it; eye moderate, with vertically elliptical or sub-circular to round pupil; midbody scale rows 19–23 (rarely 25), vertebral row not enlarged; dorsal scales smooth, without apical pits or with two pits; ventrals 152–196, without lateral keel; subcaudals paired, 37–89; anal entire (exceptionally divided); maxilla with 18–25 teeth, subequal or slightly smaller or larger posteriorly, diastema absent; hemipenis unforked or very shallowly forked, shaft with feeble basal spines arranged in diagonal rows which change to chevrons distally, spines decrease in size distally; sulcus centrifugal, dividing approximately half way up shaft." It obviously contains some controversial statements, such as maxillary teeth "subequal or slightly smaller or larger posteriorly", "eye with vertically elliptical or sub-circular to round pupil", "dorsal scales smooth, without apical pits or with two pits", "anal entire (exceptionally divided)", indicating that some morphologically quite different snakes are included in the genus. On the other hand, some members of different genera can match this description. For example, *Boaedon virgatus* (Hallowell, 1854) has 23 midbody rows of dorsal scales with two apical pits, vertebral row not enlarged, 192 ventrals, 55 pairs of subcaudals, entire anal plate, no diastema, 21 maxillary teeth, hemipenis shallowly forked distally, moderate eye with vertically elliptical pupil, moderate tail, moderately elongated cylindric body, moderate head that is slightly broader than neck and distinct from it. A member of the genus *Lamprophis* would match this diagnosis as well – for example, the type species *L. aurora* (Linnaeus, 1758): body cylindrical and moderately elongated; tail short; head moderate, slightly broader than neck and distinct from it; eye moderate, with sub-circular pupil; 18 maxillary teeth, no diastema; 23 midbody rows, no apical pits, dorsal row not enlarged; 170–182 ventrals; 37–58 pairs of subcaudals; anal entire; hemipenis shallowly forked. Moreover, the snakes in both genera, *Boaedon* and *Lamprophis*, are known to have enlarged mandibular teeth. In *Lycodonomorphus*, these teeth are similarly enlarged in *L. inornatus* and *L. subtaeniatus*. Maxillary teeth are enlarged in *Boaedon* and similarly enlarged in *L. subtaeniatus*. Furthermore, the attempts to describe the genus as 'aquatic' or 'semiaquatic' cannot be successful because *L. inornatus* and *L. subtaeniatus* – two, out of nine of its members, are not associated with aquatic habitats. While all other Boaedontini genera can be readily separated by combinations of a few characters or even by a single diagnostic character, this does not work with *Lycodonomorphus*. This indicates that the genus is either paraphyletic, containing species that should in fact belong to other existing genera, or it has to be split in further genera, or both. The phylogenetic analyses carried out for the first time by Vidal et al. (2006), and subsequently by Kelly et al.

Table 1. Estimates of evolutionary divergence (uncorrected pairwise distances) between sequences of the ND4 gene in Lamprophiinae genera.

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	*Lycodonomorphus laevessimus* (DQ486314)																							
2	*Lyc. obscuriventris* (OM387032)	0.146																						
3	*Lycodonomorphus whytii* (FJ404375)	0.121	0.146																					
4	*Lycodonomorphus rufulus* (FJ404374)	0.128	0.143	0.126																				
5	*Lycodonomorphus. rufulus* (HQ207160)	0.141	0.162	0.133	0.040																			
6	*Lycodonomorphus rufulus* (HQ207153)	0.132	0.162	0.126	0.038	0.026																		
7	*Elaiophis inornatus* comb. n. (HQ207171)	0.161	0.167	0.152	0.155	0.162	0.164																	
8	*Elaiophis inornatus* comb. n. (HQ207163)	0.168	0.164	0.171	0.166	0.183	0.180	0.121																
9	*Lamprophis aurora* (HQ207167)	0.162	0.168	0.147	0.147	0.158	0.159	0.159	0.180															
10	*Alopecion guttatum* (FJ404366)	0.153	0.158	0.161	0.134	0.170	0.165	0.180	0.164	0.145														
11	*Boaedon virgatus* (FJ404369)	0.176	0.181	0.177	0.187	0.191	0.188	0.182	0.189	0.183	0.188													
12	*Boaedon upembae* (KM519681)	0.164	0.153	0.161	0.158	0.185	0.174	0.176	0.176	0.158	0.165	0.129												
13	*Boaedon capensis 1* (HQ207168)	0.176	0.170	0.188	0.181	0.197	0.192	0.188	0.189	0.186	0.170	0.144	0.152											
14	*Boaedon capensis 2* (HQ207156)	0.191	0.179	0.183	0.200	0.206	0.208	0.194	0.206	0.189	0.179	0.168	0.156	0.108										
15	*Bothrolycus ater* (FJ404347)	0.168	0.175	0.159	0.172	0.177	0.177	0.186	0.194	0.164	0.150	0.180	0.165	0.182	0.195									
16	*Bothrophthalmus lineatus* (FJ404349)	0.208	0.182	0.194	0.189	0.202	0.198	0.192	0.205	0.202	0.177	0.200	0.206	0.208	0.209	0.179								
17	*Bofa erlangeri* (OM162154)	0.174	0.168	0.159	0.162	0.171	0.173	0.186	0.189	0.170	0.159	0.180	0.168	0.195	0.189	0.147	0.171							
18	*Pseudoboodon lemniscatus* (DQ486325)	0.174	0.175	0.164	0.168	0.183	0.186	0.188	0.188	0.171	0.179	0.195	0.180	0.198	0.192	0.185	0.200	0.171						
19	*Mehelya poensis* (FJ404380)	0.189	0.181	0.189	0.155	0.191	0.185	0.206	0.211	0.192	0.180	0.195	0.186	0.203	0.215	0.195	0.195	0.174	0.194					
20	*Limaformosa capensis* (HQ207158)	0.167	0.178	0.183	0.179	0.192	0.189	0.180	0.195	0.174	0.179	0.180	0.171	0.171	0.194	0.179	0.192	0.186	0.200	0.168				
21	*Gracililima nyassae* (HQ207150)	0.182	0.196	0.194	0.189	0.208	0.203	0.197	0.189	0.200	0.192	0.194	0.188	0.191	0.202	0.192	0.202	0.195	0.197	0.159	0.177			
22	*Gonionotophis brussauxi* (FJ404358)	0.194	0.182	0.194	0.193	0.205	0.202	0.205	0.203	0.202	0.195	0.205	0.197	0.186	0.197	0.203	0.195	0.206	0.206	0.171	0.177	0.170		
23	*Hormonotus modestus* (FJ404360)	0.203	0.211	0.198	0.195	0.211	0.209	0.202	0.208	0.200	0.192	0.205	0.214	0.206	0.227	0.200	0.194	0.185	0.198	0.203	0.198	0.215	0.221	
24	*Inyoka swazicus* (HQ207184)	0.200	0.202	0.202	0.191	0.215	0.217	0.209	0.223	0.202	0.198	0.197	0.198	0.226	0.235	0.194	0.214	0.183	0.202	0.191	0.209	0.200	0.211	0.188

Table 2. Differing morphological characters in current diagnoses of *Lamprophis* and *Lycodonomorphus*. * The hemipenis of *Lycodonomorphus bicolor* resembles that of *L. laevissimus*, being shallowly forked (W. Conradie pers. com.). ** The hemipenis of *Lycodonomorphus rufulus* was observed in some specimens to be slightly forked at its tip (W. Conradie pers. com.).

Taxon	Original genus membership	Pupil shape	Sq	Apical pits	V ♂/♀	Sc ♂/♀	Maxillary teeth	Palatine teeth	Pterygoid teeth	Mandibular teeth enlarged anteriorly	Maxillary teeth enlarged anteriorly	Hemipenis forked
Lamprophis		sub-elliptical	19–23	no/yes	168–199	35–74	12–17	8–10	13–23	yes	yes	yes
aurora	*Coluber*	sub-elliptical	23	no/yes?	165–185	46–58/ 35–48	16–17	8	20–23	yes	yes	yes
fiskii	*Lamprophis*	sub-elliptical	21–23	no	178–183	28–34	16	10	13	yes	yes	yes
fuscus	*Lamprophis*	sub-elliptical	19	no	165–199	54–74	12	8	14	yes	yes	yes
Lycodonomorphus		elliptical or sub-elliptical, or circular	19–25	no/yes	154–181/ 152–196	62–86/ 37–79	18–25	8–13	17–39	no/yes	no/yes	no/yes
bicolor	*Glypholycus*	circular	23–25	no	154–164/ 152–166	63–71/ 52–59	18–19	10	24	no	no	yes*
inornatus	*Lamprophis*	sub-elliptical	23–25	yes	170–196	58–70/ 45–56	22–23	10–11	17–19	yes	no	yes
laevissimus	*Natrix*	circular	19	no	172–181/ 172–183	57–78	25	11	25	no	no	yes
leleupi	*Ablabophis*	circular	19–21	no	165–171/ 164–174	65–67/ 52–61	25	10	29	no	no	yes?
mlanjensis	*Lycodonomorphus*	circular	21	no	163–167/ 169	60–71/ 51	–	–	–	no	no	yes?
obscuriventris	*Lycodonomorphus*	sub-elliptical	19	no	158–176/ 159–179	68–86/ 37–69	–	–	–	no	no	no?
rufulus	*Coluber*	sub-elliptical	19	no/yes?	162–175/ 160–178	72–78/ 54–79	25	15	39	no	no	no**
s. subtaeniatus	*Lycodonomorphus*	elliptical	21–23	yes	175–180/ 189–193	59–71/ 50–59	19–20	8	24	yes	yes	yes
s. upembae	*Lycodonomorphus*	elliptical	21–23	yes	172 / 175–188	52–58/ 41–48	19–20	8	24	yes	yes	yes
whytii	*Glypholycus*	circular	19	no/yes?	169/ 160–163	62/ 46–54	23	13	18	no	no	yes?

(2011), Keates et al. (2022) and us (Tiutenko et al. 2022) also support this hypothesis.

Vidal et al. (2006) showed with phylogenies inferred from nuclear (c-mos and RAG2) and mitochondrial (12S, 16S, cytochrome b, and ND4) loci that the genus *Lamprophis*, which at that time included *Boaedon* and *Alopecion*, was paraphyletic with respect to *Lycodonomorphus*. In the phylogeny that they obtained from a combined data set of these six genes *Lycodonomorphus* (represented in their study by *L. rufulus* and *L. whytii*) formed a monophyletic clade with *Lamprophis* (represented by *L. fiskii* and *L. inornatus*) and *Alopecion* (Vidal et al. 2006: 56). Within this clade, *Alopecion* (at that time, *Lamprophis guttatus*), *Lamprophis inornatus*, and *Lycodonomorphus* belonged to the sister lineage of *Lamprophis*, being separated from this and from each other by similarly large p-distances of above 15% in mitochondrial loci. In the phylogeny generated by Kelly et al. (2011) from c-mos, tRNA, cyt b and ND4 data sets, as well as in our tree inferred from c-mos, cyt b and ND4 data sets (Fig. 2), the clade arrangement in the tribe is similar, but *Alopecion* is sister to *Lamprophis*. This inconsistency can be explained by the effect of the 16S rRNA gene. As Main et al. (2024) showed, the concatenation of this gene with protein coding genes, such as NADH, weakened their resolution. On the other hand, the changing position of *Alopecion* in the tree with and without the 16S gene included, while the relationships of other Boaedontini genera remain unchanged, can be another argument in support of the genus status that we proposed in our previous work (Tiutenko et al. 2022). According to the results of all published molecular phylogenetic works in Lamprophiidae and our analyses here (Fig. 2), *L. inornatus* is sister to *Lycodonomorphus* s.s. clade with a p-distance of ca. 18% in cyt b and 15–18% in ND4 mitochondrial genes that is much larger than intrageneric distances in this group (Tab. 2, tables in Tiutenko et al. (2022)). The distance between *L. inornatus* and *Lamprophis* is similar: 15–18%. For comparison, the distance between *Lycodonomorphus* and *Bofa*, not immediately related genera, is just ca. 15% in cyt b and 16–17% in ND4. The distance between *L. inornatus* and *Bofa* in cyt b is 18% and 19% in ND4.

It should be noted that, according to our results, the parent node, i.e., the division between *Lamprophis* and *Lycodonomorphus* clades has a rather low support of 0.55 posterior probability. This can have various reasons, such as problems with alignment of sequences (that are ambiguous or too diverse), different evolution rates of clades, or lack of intermediate taxa in the phylogeny. An even lower posterior probability value of 0.52 is observed, however, between *Bothrolycus* and *Bothrophthalmus*, both distinct genera with very clear morphological diagnoses. For us this phenomenon just means again that molecular results cannot be accepted blindly and always need to be supported by other lines of evidence.

In addition to the molecular phylogenetic results (that admittedly do not yet cover all species of the genus due to lack of data), an assessment of morphological characters (Tab. 2) shows that three species of *Lycodonomorphus* – *L. bicolor*, *L. inornatus*, and *L. subtaeniatus* – do not match the initial generic diagnosis, and thus must be misplaced in this genus for historical reasons, as well as due to limitations of the methodology that the researchers used in the past.

Generic placement of *Lamprophis inornatus*

Superficially *Lamprophis inornatus* (we refer to it by its original binomial here) indeed closer resembles the mem-

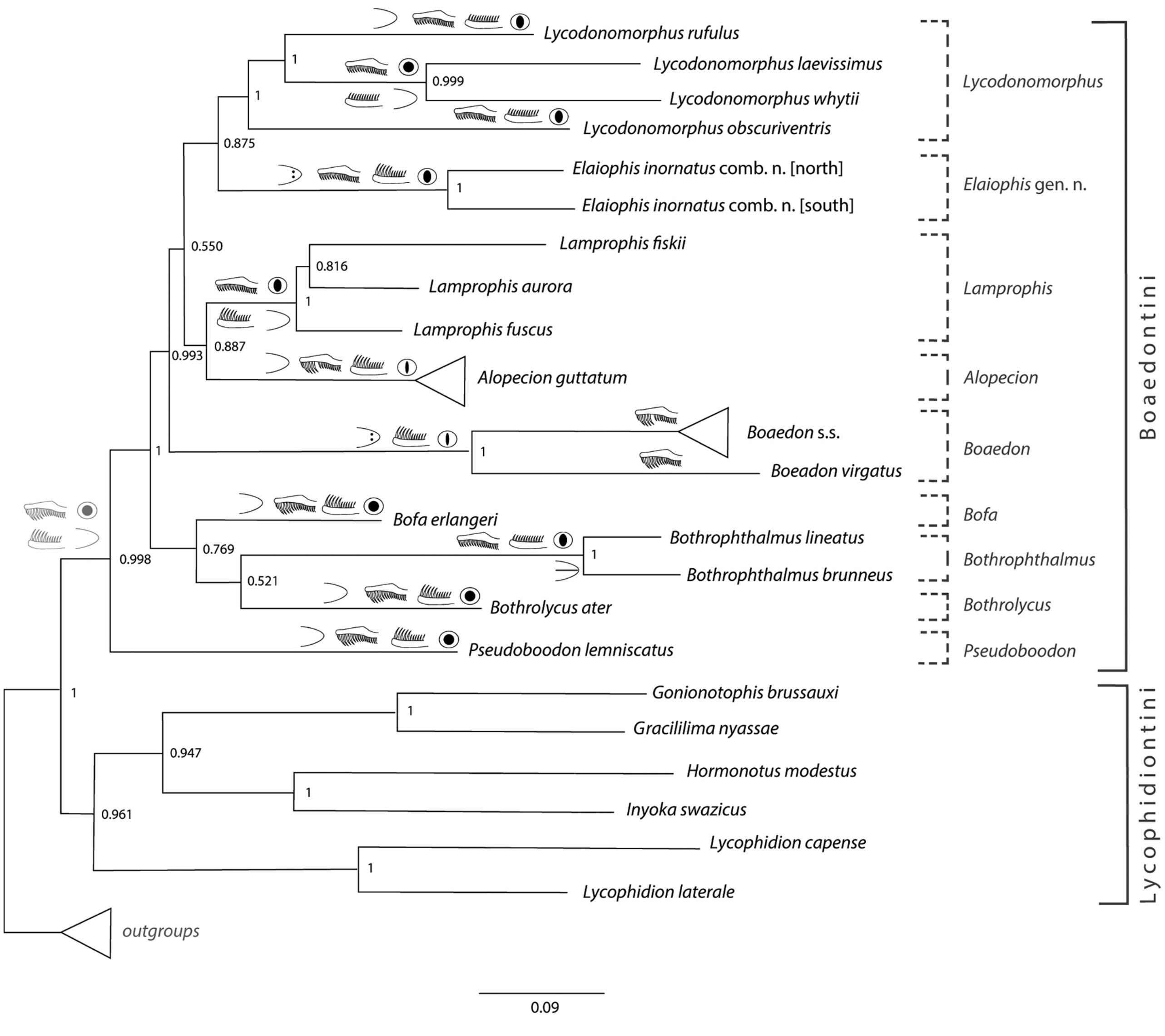

Figure 2. Phylogenetic relationships among Lamprophiinae genera generated from cyt b, ND4 and c-mos data sets based on Bayesian inference. Numbers at nodes represent posterior probabilities from the Bayesian analysis; scale refers to nucleotide substitutions per site. Outgroups, collapsed here to a single branch, included *Aspidelaps scutatus*, *Atractaspis bibroni*, *Buhoma procterae*, *Duberria lutrix*, *Prosymna ruspolii*, *Psammophis crucifer*. Structures in *Alopecion* and *Boaedon* sensu stricto (s.s.) that are not discussed in this article are collapsed as well. For methodology, see Tiutenko et al. (2022). Pictograms at branches in Boaedontini indicate evolutionary trends in dorsal scales morphology, maxillary and mandibular dentition, as well as eye pupil shape discussed in the text.

bers of the genus *Lamprophis* and, unlike *Lycodonomorphus* s.s. that are semi-aquatic and associated with waterbodies, as well as swamps and floodplains, it is a strictly terrestrial snake, preferring mesic habitats including grassland, thicket and forest. FitzSimons (1962) noted that this snake is "similar in habits to the Common Brown House Snake (*Boaedon f. fuliginosus* [= *B. capensis*])." Due to its similarity to *Lamprophis*, this species was initially described by Duméril et al. (1854: 434) as *Lamprophis inornatus*. Four years later Günther described a similar snake, but in the genus *Boaedon* (at that time spelt '*Boodon*'), as *Boodon infernalis* Günther, 1858. Boulenger (1893: 321) synonymised it with *L. inornatus*. Much later, in 1924, Werner introduced a new genus and described *Pachyophis temporalis*, having perhaps overlooked not only the previous names, but also that the genus name '*Pachyophis*' was preoccupied. Therefore, this binomial automatically became invalid but the specific epithet '*temporalis*' has to be considered a junior synonym of '*inornatus*'. The specific epithet '*inornatus*' appeared once again in combination with *Boaedon* as '*Boædon inornatus*' in a paper by Parker (1930: 598), but generally the usage of the combination '*Lamprophis inornatus*' was established and maintained till the second decade of this century, when it was provisionally moved to *Lycodonomorphus* merely on a basis of molecular evidence of its closer phylogenetic relationship to the latter (Kelly et al. 2011).

Not only ecologically, but also morphologically, *L. inornatus* differs from *Lycodonomorphus* s.s. and resembles *Lamprophis*. It has a more robust body, more elongate and more trapezoidal head (Fig. 1), dorsal scales with two apical pits (Fig. 3), strongly enlarged anterior mandibular teeth, smaller number of pterygoid teeth. Its oval pupils seem not to be able to shrink as far as in *Lycodonomorphus* s.s. where they may become small dots in strong light.

Visser (1979: 31–32) compared the hemipenes of *Lamprophis inornatus*, *L. aurora*, *L. fiskii* and *L. fuscus* and found them similar: all organs are belobed, distally shallowly, but conspicuously, forked, with centrifugal sulcus, dividing approximately in the middle of the hemipenial body. Laurent made a confusing remark that the hemipenis of *L. inornatus* is not forked and differs in this from the organ of *Lycodonomorphus rufulus* that is forked (Laurent 1954: 40). We verified it and found the morphology of the hemipenis of *L. inornatus* (NMB R6900) to agree with the description by Visser, whereas the hemipenis of *L. rufulus* (NMB R10839) matched the description by Zaher (1999: 23–24) being unilobed, with a centrolineal sulcus bifurcating closer to the top of the organ (Fig. 4). However, Conradie (pers. com.) reported several specimens of *L. rufulus* having hemipenes with slightly forked tips.

The shape of the parietal bone in the skull of *L. inornatus* (Fig. 5, suppl. document 3) resembles that in *Lamprophis aurora* closer than in *Lycodonomorphus* s.s. (Figs 6.1, 6.2): The carinae parietales are situated closer to each other, notably limiting the dorsal surface of the parietal. Also, the bones of the palatomaxillary arch and of the mandibula resemble more these in *Lamprophis* than in *Lycodonomorphus* s.s. These bones are overall heavier; the dentary stronger curved; the compound bone is posteriorly broader. The dentition also resembles that in *Lamprophis*. *Lamprophis inornatus* has not only fewer pterygoid teeth than *Lycodonomorphus* s.s., but these are longer, stronger and less curved. The maxillary teeth are subequal as well, but larger and fewer than in *Lycodonomorphus* s.s. The six mandibular teeth, after the first, are strongly enlarged, being approximately twice as long as the rest. In both genera

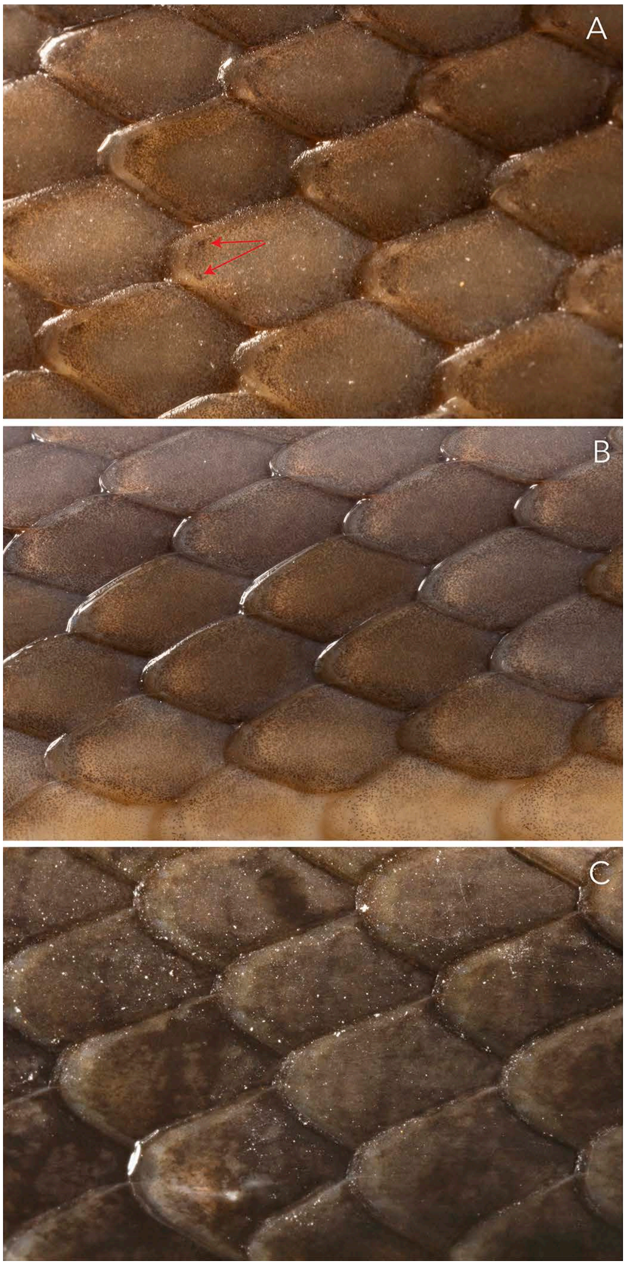

Figure 3. Dorsal scales of *Lycodonomorphus inornatus*, NMB R6900 (A), *L. rufulus*, NMB R10840 (B), *L. laevissimus*, NMB R11137 (C). Note apical pits, visible as two dark dots (indicated by red arrows), on the scales of *L. inornatus*.

(*Lycodonomorphus* and *Lamprophis*) and in *L. inornatus*, all teeth are evenly distributed along the bones; no diastemata are regularly present. In *Lycodonomorphus* s.s. spaces between teeth due to their smaller size and larger number appear smaller.

Lamprophis inornatus is strictly a South-African endemic, with a number of populations whose ranges extend along the coast from the south-western tip of the Western Cape to KwaZulu-Natal and Limpopo (FitzSimons 1962: 114–115, Broadley 1983: 85–86, Bates et al. 2014: 366, Tolley et al. 2023: 557). Some of these populations are significantly spatially separated and exhibit deep phylogenetic divergence. Kelly et al. (2011: 421) showed a high level of divergence and strongly supported phylogenetic structure within *L. inornatus*. They found the genetic distances between the southernmost and northernmost populations that are separated by ca. 1,100 km surprisingly large, substantially larger than maximum intraspecific distances calculated for the species in the related Lamprophiinae clades (Kelly et al. 2011: 424). The presence of two sister clades in *L. inornatus* that may warrant a status of separate species (Fig. 7) was showed also by Keates et al. (2022) in a phylogeny inferred from the same genes, but with *Lycodonomorphus obscuriventris* included in the data set. These authors revealed an intraspecific difference of 6.77% in cyt b gene, i.e., greater than the usual within species in this group, being at a lower level of interspecific distance. For the final decision on the taxonomic status of these clades, further studies are necessary to investigate their phenotypic characters, as well as distribution and boundaries.

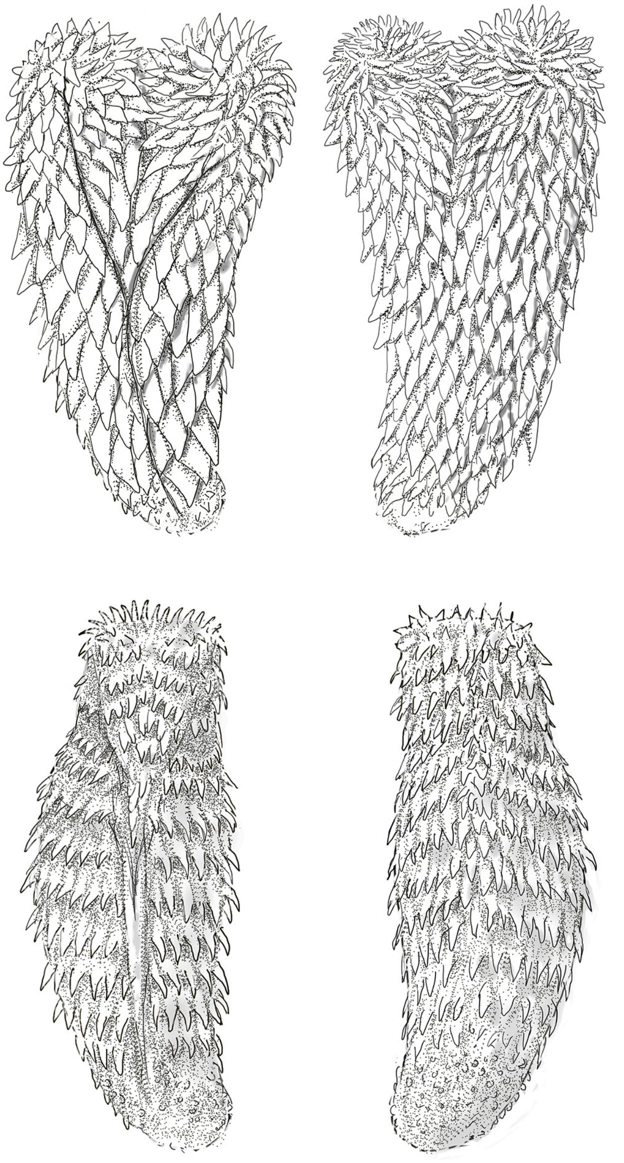
Figure 4. Drawings of hemipenes of *Lycodonomorphus inornatus* (top, NMB R6900) and *L. rufulus* (bottom, NMB R10839) in sulcate (left) and asulcate (right) views.

Lycodonomorphus inornatus is clearly misplaced in the genus *Lycodonomorphus*, but cannot be a member of *Lamprophis* as well, due to its phylogenetic position in a different clade. Hence, with the same approach that was used for delimitation of other genera in this family and tribe, i.e., based on morphological, ecological and genetic evidence discussed above, a placement in a separate new genus appears appropriate.

Description of a new genus
***Elaiophis* gen. n.**

lsid:zoobank.org:act: urn:lsid:zoobank.org:act:246FC9A0-CDA2-4299-93C3-BA6856E342C1

Type species: *Lamprophis inornatus* Duméril, Bibron & Duméril, 1854, by present designation.

Diagnosis: Body cylindric, moderately short. Head moderately depressed. Eye medium-sized to small. Tail short, representing ca. 12–15% of the total length. Head trapezoidal, broader posteriorly, moderately 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 wide sub-elliptical pupil. Anterior chin shields equal in size to the posterior or slightly longer. Loreal single, rectangular, horizontally elongate. No labial pits. No loreal grooves. Dorsal scales with two apical pits, arranged in 23 rows at the middle of the body. Subcaudals paired. Anal entire. 18–19 maxillary, 10–11 palatine, 17–19 pterygoid, 20–23 mandibular teeth. No diastemata. Maxillary teeth subequal. Mandibular teeth 2–7 strongly enlarged. Hemipenis bilobal, shallowly forked; sulcus spermaticus centrifugal, dividing approximately half way up shaft. Dorsal colour olive-green, olive, dark brownish olive, glaucous, dark neutral grey. Ventral colour cream white, or pale neutral grey.

Content: The genus is currently monotypic, containing one species – *Elaiophis inornatus* (Duméril, Bibron & Duméril, 1854) comb. n.

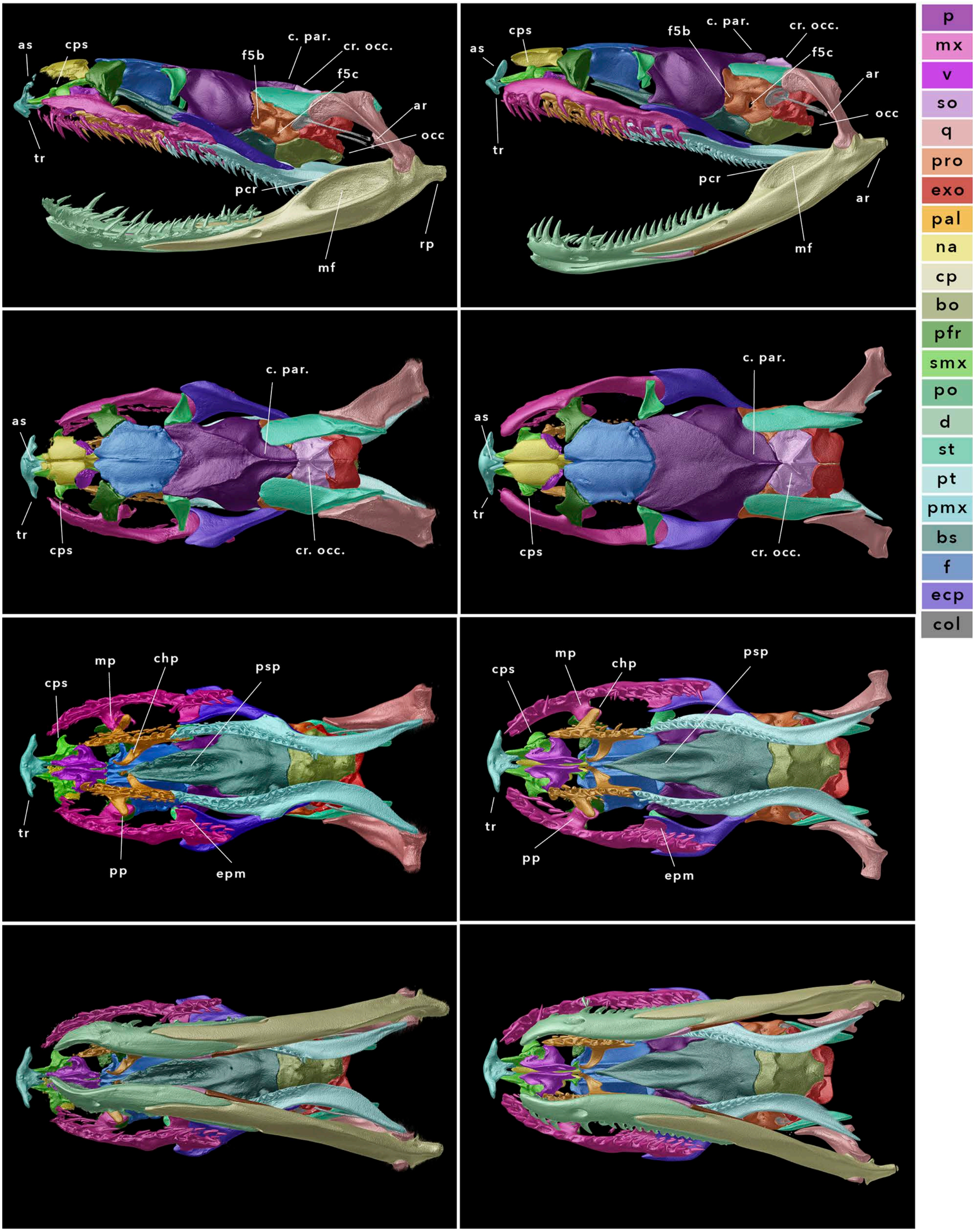

Figure 5. Skulls of the neotype of *Lamprophis inornatus*, ZFMK 032712 (left) and of the lectotype of *Boodon infernalis*, NHMUK 1858.4.11.5 (right).

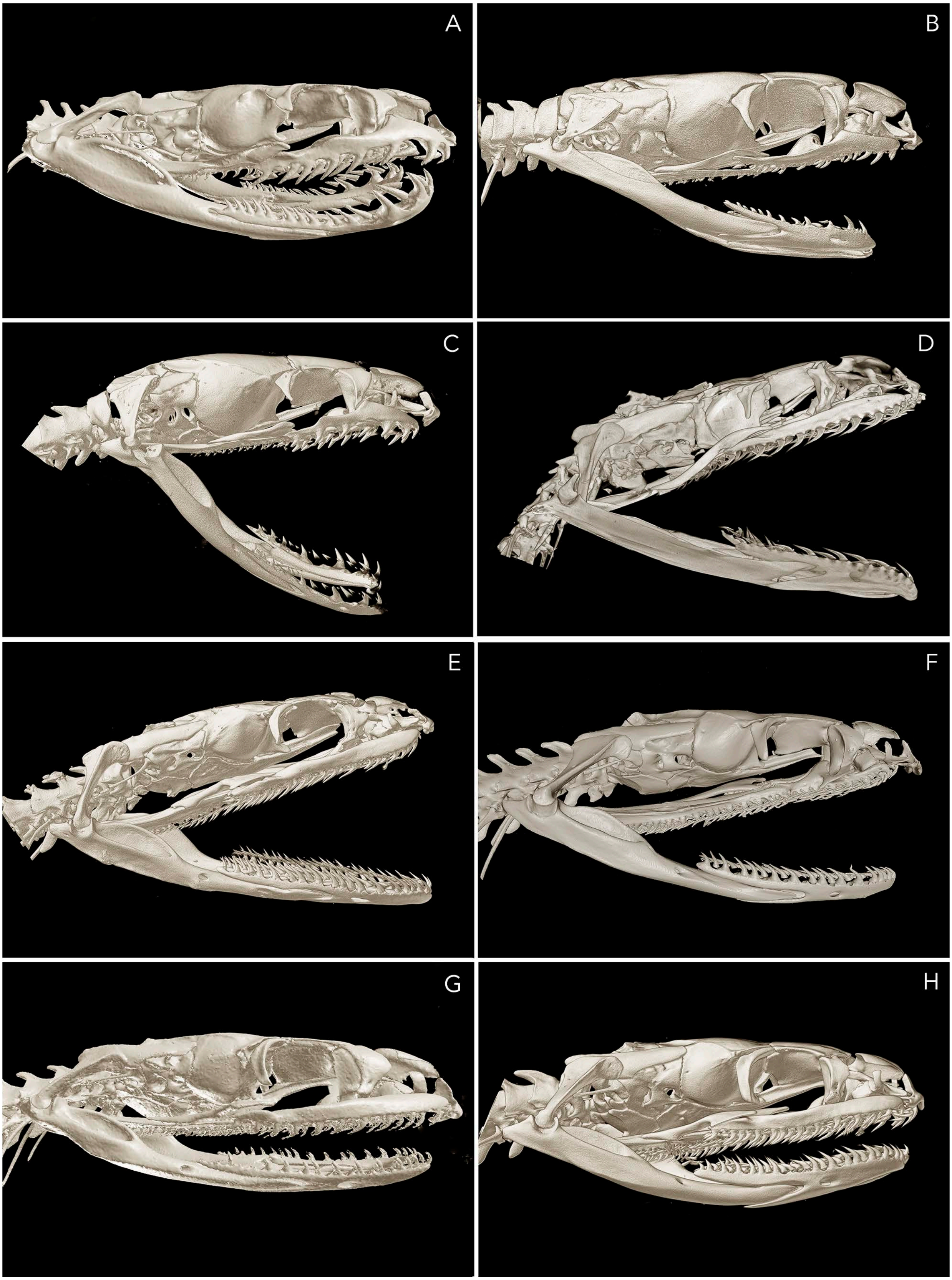

Figure 6.1. Skulls (lateral view) of *Lamprophis aurora*, UMMZ 61580 (A); *Lamprophis fiskii*, NHMUK 1946.1.12.41, holotype (B); *Lamprophis fuscus*, NHMUK 1946.1.12.43, holotype (C); *Lycodonomorphus bicolor*, NHMUK 1946.1.7.81, syntype (D); *Lycodonomorphus laevissimus*, NHMUK 1946.1.23.78, holotype (E); *Lycodonomorphus leleupi*, MRAC R.17637, holotype (F); *Lycodonomorphus rufulus*, UMMZ 126980 (G); *Lycodonomorphus whytii*, NHMUK 1946.1.13.93, holotype (H).

Figure 6.2. Skulls (dorsal view) of *Lamprophis aurora*, UMMZ 61580 (A); *Lamprophis fiskii*, NHMUK 1946.1.12.41, holotype (B); *Lamprophis fuscus*, NHMUK 1946.1.12.43, holotype (C); *Lycodonomorphus bicolor*, NHMUK 1946.1.7.81, syntype (D); *Lycodonomorphus laevissimus*, NHMUK 1946.1.23.78, holotype (E); *Lycodonomorphus leleupi*, MRAC R.17637, holotype (F); *Lycodonomorphus rufulus*, UMMZ 126980 (G); *Lycodonomorphus whytii*, NHMUK 1946.1.13.93, holotype (H).

Etymology: In South Africa where this snake is distributed it is called ‘Olive Snake’ in English, or ’Olyfslang’ in Afrikaans. Both names refer to the dorsal colour. The new genus name ‘Elaiophis’ is a translation of these vernacular names into Latin, being a compound of the Greek words ὄφις (snake) and ἐλαία (olive). Since the head of the nominal compound (‘ophis’) is masculine, the new noun is of the same gender. As English name for the new genus, we suggest ‘African olive snakes’.

The type specimen of *Lamprophis inornatus* had not been fixed in the original description, and we were not able to locate specimens at the Muséum National d’Histoire Naturelle (Paris, France) that Duméril et al. (1854) may have referred to. The three extant syntypes of *‘Boodon infernalis’* housed in the NHMUK (1858.4.11.5, 1855.10.16.354, 1855.10.16.434) were, after the name became a junior synonym of *L. inornatus*, treated in the collection catalogue as syntypes of the latter, even though, strictly speaking, they are not. Since *L. inornatus* is presumably a complex of at least two cryptic species, a designation of a lectotype and restriction of the type locality of *B. infernalis* should prevent future uncertainty about the identity of the initial species. Originally, this type series contained four specimens (Günther 1858: 199), but one juvenile that had the 2nd position in the list seems to be lost. Among the remaining three, there is only one adult female specimen, donated by H. Calloway in 1858, with known collection locality – “Port Natal” [= Durban]. It has the first position in the list of the type series, and its characters agree with the diagnosis provided by Günther. Thus, it is likely to be the ‘main’ specimen he used for the description. We therefore designate this specimen NHMUK 1858.4.11.5 as the lectotype of *Boodon infernalis* Günther, 1858 and restrict the type locality to Durban, KwaZulu-Natal, South Africa. The lectotype hence represents the northern clade (Fig. 7B). Once the species status of this clade is confirmed, the name should be available. For *L. inornatus*, now *E. inornatus* comb. n., whose type locality is “environs du Cap de Bonne-Espérance” [= vicinities of the Cape of Good Hope] according to the original description (Duméril et al. 1854: 455), a designation of a neotype should improve the taxonomic stability of this species and the genus, especially in case of separation of the northern clade. We here designate a topotypic specimen from the collection of the Zoologisches Forschungsmuseum Alexander Koenig as the neotype of *Lamprophis inornatus* and consequently of *Elaiophis inornatus* (Duméril, Bibron & Duméril, 1854) comb. n.

Figure 7. Adult specimens of *Elaiophis inornatus* comb. n. from Makhanda / Grahamstown, Eastern Cape (A), and Haenertsburg, Limpopo (B). Photographs by G. K. Nicolau.

Description of the neotype of *Elaiophis inornatus* (Duméril, Bibron & Duméril, 1854)

Lamprophis inornatus, ZFMK 032712 (Fig. 8), adult female, “Cape: Haut’s Bay, Republic of South Africa” [= Hout Bay, Cape Town, Republic of South Africa, ca. 34°2’ S 18°21’ E], collected in April 1980 by J. Visser, donated in February 1981 by P. van den Elzen.

External morphology: Body cylindrical, SVL 635. Tail moderately tapering, with blunt tip; TL 97 mm, TL/L 0.13. Head trapezoidal, moderately offset from neck; HL 32.4 mm, HW 13.4 mm. Dorsal scales smooth, with two apical pits, Sq 23–23–19. Ventrals rounded, V 183. Sc in 39 pairs. Anal entire. Two preoculars, lower almost half the size of the upper; upper not in contact with frontal. Two postoculars, lower a little smaller than upper. Loreal approximately half as deep as its length. Nasal divided. Rostral large, broader than high, well visible from above. Eight supralabials; 4th and 5th entering the orbit. Temporals 1 + 2. Prefrontals ca. 30% shorter than frontal. Nasals almost half as long as prefrontals. Frontal ca. 30% longer than its maximum breadth. Eight infralabials; four on the left side and five on the right in contact with the anterior chin shield. Both pairs of chin shields approximately equal in length. Gulars between posterior chin shield pair and first ventral irregular.

Colour (in preservative): Dorsum uniformly dark-brown; ventrum and upper labials pale beige. Ventral side of tail brown along medial line.

Dentition: maxillary 16, pterygoid 17, palatine 10, mandibular 23, no diastemata, mandibular teeth 2–7 about 50% longer than the following teeth 8–22, mandibular tooth 23 ca. 50% shorter than teeth 8–22.

Cranial osteology (Fig. 5A): Premaxilla with large ascending process closely approaching nasals. Vomerine process forked, with tips not in contact with vomers. Transverse processes of premaxilla closely approach rostral ends of maxillae. Septomaxillae separated from each other, with posterior ends forming prokinetic joints with frontals. Conchal processes long, sharply bent upward and slighly backward. Nasal bones slightly narrower than the septomaxillae, tightly attached to each other, not fused, approximately half as broad and ca. 40% shorter than frontal bones which they contact with posterior processes. In dorsal view septomaxilae almost entirely hidden under nasals with only conchal processes visible. Medial laminae of nasals contact septomaxillae. Edges of lateral laminae of nasals strongly curved downward, but not approaching conchal processes of septomaxillae. Vomers almost in contact medially, with rostral ends approaching, but not contacting premaxilla. Posterior ends of vomers not approaching choanal processes of palatines. Vomers with globular posterolateral portions, open forward, with narrow processes anteriorly. Lateral laminae of vomers short, triangular, curved downward. Ventral laminae perforated. Cranium elongate, accounting for approximately 3/4 of total skull length. Posterior faces of prefrontal bones curved and slightly concave, forming ante-

Figure 8. Neotype of *Lamprophis inornatus*, ZFMK 032712. Photographs by M. Flecks.

rior borders of orbits. Prefrontals not in immediate contact with frontals and not approaching nasals. Frontals paired, medially nearly contacting and forming long straight suture. Combined, they form hexagon, slightly longer than broad, with lateral margins slightly curved. Frontals ca. 25% narrower than their maximum length, and ca. 30% shorter than parietal, with slightly curved lateral margins, forming dorsal borders of orbits. Posterior faces of frontals angled at ca. 45°, forming ca. 90° insertion in parietal. Frontal ventrally in tight contact, but not fused. Parietal single, slightly longer than maximum breadth, with slightly impressed dorsal surface between parietal ridges, anteriorly with broad U-shaped notch almost seamlessly enclosing matching triangular shape of frontals. Short dorsolateral ridges slightly concave anterolaterally, repeating shape of postorbitals which approach them but do not in contact. Parietal ventrally contacting parabasisphenoid, posteriorly supraoccipital, posterolaterally prootics and anterior ends of supratemporals. Postorbitals triangular, slightly curved, to form posterior border of orbits. Medially impressed flat dorsal surface of the parietal ends posteriorly with sharp parietal keel at approximately 1/3 of its length. Supraoccipital oval, with three occipital crests on its surface. One of them continues parietal keel. Two others originate at both sides of medial crest and end in triangular excrescences of posterior margin of supraoccipital. Supraoccipital with U-shaped notch anteriorly that seamlessly encloses triangular posterior margin of parietal. Exoccipitals contact supraoccipital anterodorsally, prootics anterolaterally, basioccipital ventrally and supratemporals laterally. Exoccipitals irregularly shaped and emarginate dorsally. Foramen ovale situated at each side at suture of prootic and exoccipital. Columella auris inserted into it, with its oval footplate firmly contacting prootic anteriorly and exoccipital posteriorly. Prootics subhexagonal in lateral view. Each with foramina for maxillary and mandibular branches of trigeminal, separated by laterosphenoid. Basioccipital nearly pentagonal, anteriorly in contact with basisphenoid, and posteriorly it forms the ventral border of the foramen magnum. Parasphenoid and basisphenoid fused. Basisphenoid nearly hexagonal in ventral view. One small anterolateral and two posterolateral foramina on each side. Parasphenoid rostrum almost triangular and concave ventrally, tightly enclosed by ventral laminae and anteroventral dentigerous processes of parietal, passes anteriorly between ventral laminae of frontals. Its sharp tip not reaching vomer and choanal processes of palatines. Palatines situated below frontals and in dorsal view are hidden under them. Large hook-shaped choanal processes situated at level of teeth 6–7, almost touching with their tips caudal processes of vomers. Maxillary process a little shorter but thicker than choanal, situated opposite to the palatine process of maxilla and included in its distal end. Palatines straight in ventral view, with rostral ends positioned higher than caudal. Caudal ends forked, forming joints with rostral ends of the pterygoids. Maxillae long, a little shorter than braincase, extending posteriorly almost to 1/4 of their length beyond postorbitals, slightly curved in dorsal and ventral views. Ectopterygoid process large, rectangular, flat, turned downward, situated approximately at teeth 12–14. Palatine process large, rectangular, curved downward and backward, situated opposite to maxillary process of palatine, approximately at teeth 7–8. Pterygoids slender and long, ca. 10% longer than maxillae and approximately 10% shorter than braincase, gradually broaden approximately after tooth 4, wavy in ventral view, coming closest to each other after tooth 17, taper posteriorly and end with narrow tips. Caudal end of ectopterygoid attaches approximately at its middle to broad square process of pterygoid situated at teeth 10–14. Ectopterygoids spade-shaped, curved and slightly forked at their joints with maxillae. Distal margin of forked portion of ectopterygoid angled. Supratemporals elongate, laminar, tapering posteriorly, ending with narrow tips reaching far beyond caudal edge of braincase, closely approaching quadrates with straight posterolateral surfaces but remain separated. Quadrates elongate, slender, slightly curved downward, with dorsal portions broader than ventral. Articulatory processes large, triangular, pointing at columella. Cephalic condyles inserted in glenoid cavity of the compound bone, not approaching caudal tips of pterygoids which point at them. Mandibles nearly straight in dorsal and ventral view. Dentary long, almost equal in length to compound bone, with anterior approximately 1/3 of dentary slightly curved labially. Mental foramen situated at level tooth 6. Dentary forks to upper and lower branches approximately at tooth 10. Upper branch, bearing teeth, slightly longer than lower. Splenial triangular, tapering anteriorly to fine tip and perforated in posterior half by anterior mylohyoid foramen. Splenial attached with angular approximately at level of tooth 17. Posterior mylohyoid foramen situated on this suture. Angular bone slightly shorter and broader than splenial, triangular and directed with its narrower angle posteriorly, entirely lying on labial side of compound bone. Dentary attaches to compound bone approximately at level of tooth 16 via curvy suture. Compound fits with sharp rostral end between branches of dentary. Prearticular crest distinctively higher than surangular, visible in lateral view. Surangular not visible in labial view. Mandibular fossa broad, deep, elongate, oriented dorsally, visible in lateral view. The retroarticular process well-defined and medially directed.

Overall, the skull of this specimen looks almost identical to that of the specimen NHMUK 1855.10.16.354 (Supplementary document 3), but is clearly longer than in NHMUK 1858.4.11.5, the lectotype of *Boodon infernalis* (Fig. 5B). Although all three snakes are adult and of similar size, this difference may be of ontogenetic origin, i.e., the first two specimens could just have been older when they were collected. Otherwise, it can be a distinctive character, potentially useful for separation of two putative species. The collection locality of NHMUK 1855.10.16.354 is unknown, but its pale beige ventral colour may indicate that this animal belongs to the southern clade as well, because the snakes of the northern clade seem to have grey venter. The different shape of the ectopterygoid bone may be another argument in support of this assumption. The ectopterygoid in the specimens from southern clade is almost straight posteriorly and smoothly curved in its anterior broad and forked portion, where it connects to the maxilla. In the specimens from the northern clade, this bone is bent posteriorly at a sharper angle (Fig. 5B). Furthermore, the mandibular fossa is larger in both specimens from the southern clade. The maxilla also differs in these specimens, having a sharper triangular form below the orbit.

The skull of *Elaiophis* gen. n. resembles that of *Lycodonomorphus laevissimus* (Figs 6-1E, 6-2E) but, on the other hand, also surprisingly closely the skull of *Bofa erlangeri* (Tiutenko et al. 2022: 244), although this genus and species belong to a different lineage in Boaedontini. This similarity can be explained by divergence of the main Boaedontini clades in early Oligocene from a common ancestor with *Pseudoboodon* whose skull is also quite similar (Tiutenko et al. 2022: 257). Also, the skulls of *Boaedon* retained most ancestral traits in size and geometry of the bones. More specialised skulls with very different shapes and proportions of the bones, such as in *Alopecion* and the *Bothrolycus*-*Bothrophthalmus* clade, emerged in the course of later radiation in Miocene. The highly specialised skull of *Alopecion* is a result of adaptations that began in the ancestor that it shares with *Lamprophis*. Therefore, the *Lamprophis* skulls that evolved later share some features with *Alopecion*, but differ from the skull of *Elaiophis* gen. n. The more advanced *Lycodonomorphus* species developed rounded parietals, with flat or no crests, longer nasals, shorter maxillae (Figs 6-2B–C).

Generic placement of *Lycodonomorphus subtaeniatus*

Lycodonomorphus subtaeniatus Laurent, 1954 – the third problematic species of *Lycodonomorphus* – is morphologically and ecologically even more deviant from the generic diagnosis. It is already treated by some authors as a member of *Boaedon,* even though no formal revision of its generic placement was yet undertaken.

This species used to comprise two subspecies: *L. s. subtaeniatus* and *L. s. upembae*. Both were described by Laurent (1954) who initially assigned them to the genus *Ablabophis* Boulenger, 1893. However, before Laurent's manuscript was published, Loveridge (1953: 256) synonymised *Ablabophis* with *Lycodonomorphus*. Laurent acknowledged this in the final text of the article and treated the new species as a member of the latter. Earlier, already in 1947, he identified some of the specimens that subsequently became part of the type material of *L. s. subtaeniatus* as *'Boaedon virgatus.'* By this name they are also mentioned in Laurent's earlier paper (1952: 199). The rest of the type series of *L. s. subtaeniatus* and all types of *L. s. upembae* had been initially (in 1930) identified by de Witte as *'Boaedon lineatus'* (de Witte 1933: 86, 1953: 168). From the text of Laurent's article, it is still not clear why the new species had to belong to *Lycodonomorphus*. Laurent compares head size and the geometry of head scales in *L. subtaeniatus*, *L. leleupi* (at that time *L. whytii leleupi*) and *L. inornatus* (at that time a member of the genus *Lamprophis*). He notices several differences from the latter, but does not do the same with *Boaedon* and other *Lycodonomorphus*. Instead, he notices similarities in pholidosis of *L. inornatus* and *L. whytii* (that he grammatically correctly spells as '*whytei*') and perhaps for this reason decides to place the new species in the genus *Lycodonomorphus*. At the same time, Laurent does not consider a possibility that *L. subtaeniatus* is a *Boaedon*, though he mentions a number of traits that they have in common and even emphasises their superficial similarity.

For the first time, a close relationship of *L. subtaeniatus* to *Boaedon*, namely to *B. virgatus*, was confirmed in a more recent phylogenetic study (Greenbaum et al. 2015). Notably, the ventral scale counts that Greenbaum et al. give for their specimens do not match the values provided in the original description of *L. s. upembae* (♂/♀: 175–180/189–197 vs. 172/175–188), but more closely agree with those of the nominal subspecies (175–180/189–193). The authors do not explain how they identified the newly collected specimens as *L. s. upembae*. If the identity was just reasoned from the collection locality, the possibility of misidentification cannot be ruled out.

The main issue with this taxonomic decision is, however, that Greenbaum et al. (2015) transferred only a part of the species to a different genus, i.e., one of its subspecies, and did it rather offhand, having not formally raised the subspecies to a full species rank. Also, Broadley and Cotterill (2004: 48), who mentioned this snake as '*Lycodonomorphus upembae* Laurent, 1954' and called it "sister species" of *L. subtaeniatus*, did not provide any arguments in support of the new status. They only referred to its more robust body form and lower ventral and subcaudal scale counts, i.e., characters that Laurent did not consider significant enough for separation from *L. subtaeniatus*. Furthermore, Broadley and Cotterill borrowed from Laurent (1954) the confusing remark about the hemipenis of this snake that is "bifurcate distally like in *L. rufulus*", even though the organ of *L. rufulus* itself was considered not bifurcate at all or anyway not as much as in *Boaedon* and *L. subtaeniatus*. In a recent book, Trape (2023: 386–387) mentions *B. subtaeniatus* and *B. upembae* again as separate species, but provides a single account for both without any discussion of their taxonomic relationship and explanation of his decision to treat them both as members of *Boaedon*.

The molecular evidence of a closer phylogenetic relationship of *L. s. upembae* to *Boaedon* and absence of such data for *L. s. subtaeniatus* cannot be automatically a reason for taxonomic separation of one subspecies from another. Thus, formally seen, Greenbaum et al. just spread one species across two genera. Meanwhile, this decision seems to have been accepted by some authors who included *upembae* in further *Boaedon* systematics as a species (Trape & Mediannikov 2016, Hallermann et al. 2020, Ceríaco et al. 2021). However, Chippaux and Jackson (2019) did not follow this tendency in their book and maintained both subspecies of *L. subtaeniatus* in the genus *Lycodonomorphus*.

To resolve this taxonomic paradox, we examined and compared the type material of *L. s. subtaeniatus* and *L. s. upembae*. In both subspecies, we found a number of similarities with *Boaedon* that we summarise here.

Pupil shape. Like in *Boaedon*, the pupil is narrow vertically elliptical in both, the nominate subspecies and *L. s. upembae* (Figs 9–10). It is sub-elliptical in *Lycodonomorphus* s.s. Laurent mentions this difference in his description of *L. subtaeniatus* (Laurent 1954: 41) but does not draw any conclusions from it.

Dorsal scales. *Lycodonomorphus subtaeniatus* has 21–23 rows of dorsal scales around the middle of the body. This number is similar in many *Boaedon*, but is normally lower in *Lycodonomorphus* s.s.: 19–21 scales. Only *L. bicolor* has a higher scale count: 23–25. Apical pits are more-or-less clearly visible on dorsal scales of the type specimens of *L. s. subtaeniatus*. The microphotograph of midbody scales of a paratype NHMUK 1953.1.5.51, shown in Figure 9, illustrates this. With some effort, we were also able to recognise them in the type series (22 specimens) of *L. s. upembae* where they are less pronounced (Fig. 10), perhaps due to preservation issues or because they were feeble already in live specimens. The apical pits are generally absent in *Lycodonomorphus* s.s. Although some authors (including Laurent 1954, Loveridge 1958, FitzSimons 1962, Broadley 1983) mention occasionally observed apical pits in *L. rufulus*, we did not find them in the specimens that we examined (Fig. 3).

Cranial features. The cranium in *L. s. subtaeniatus* is of the *Boaedon* type and closely resembles that in *B. virgatus* and in many members of the sister clade. The skulls of both specimens of *L. s. subtaeniatus* that we examined for this study – MRAC R.14864 (Fig. 11) and NHMUK 1953.1.5.51 (Supplementary document 5) – look almost identical with the skulls of *B. bipraeocularis* Günther, 1888 (syntype, NHMUK 1946.1.23.19, suppl. document 4) and *B. olivaceus* (Duméril, 1856) (ZFMK 5405, suppl. document 4). In *L. s. upembae*, parietal keels are more expressed and outline a triangle on the dorsal surface of the parietal bone that is reminiscent of such structure in the parietal of *B. arabicus* Parker, 1930 and *B. lineatus* Duméril, Bibron & Duméril, 1854 (ZFMK 023366, suppl. document 4). However, the latter has generally a more elongate braincase, mainly due to longer nasals and frontals.

Teeth. The number of maxillary teeth in both subspecies (19–20) is lower than in *Lycodonomorphus* s.s. (21–25), but higher than in *L. bicolor* (18–19). The same applies to mandibular teeth. Their number in *L. subtaeniatus* is as in *Boaedon* (20–23) and lower than in *Lycodonomorphus* s.s. (27–31). Only *L. bicolor* has less teeth (20) on the dentary bone than the other members of *Lycodonomorphus*. The examined specimens of *L. s. subtaeniatus* (holotype MRAC R.14864 and paratype NHMUK 1953.1.5.51) have eight palatine teeth. This number agrees with the usual in *Boaedon* (7–8) but is lower than in *Lycodonomorphus* (11). In the holotype (MRAC R.14864) and in a paratype (NHMUK 1953.1.5.51) of *L. s. subtaeniatus* we counted 24 pterygoid teeth. This number corresponds to the usual number of such teeth in *Boaedon* (20–25) but is significantly lower than stated for *Lycodonomorphus* s.s. (30–34). However,

Figure 9. Microphotographs of the head of a paratype of *Lycodonomorphus subtaeniatus subtaeniatus*, NHMUK 1953.1.5.51, in lateral, dorsal and ventral view, and of a fragment of the dorsum. Note the vertically elliptical pupil and apical pits on dorsal scales (indicated by red arrows).

the species of *Lycodonomorphus* in the sister clade to *L. rufulus* have 24–26 pterygoid teeth. We consider these members of the genus problematic and requiring further study (see more on this below). The anterior maxillary and mandibular teeth are enlarged, similarly to all *Boaedon*, but unlike in *Lycodonomorphus* s.s., whose teeth are sub-equal. The size difference between these and the rest of the teeth on the maxilla is, however, much smaller than in other *Boaedon* species, except for *B. virgatus*. Also, similarly to *B. virgatus*, there is no diastema after the enlarged anterior maxillary teeth according to the original description (Laurent 1954) and to our observations. The µCT images of the skulls of the specimens MRAC R.14864 (Fig. 11) and NHMUK 1953.1.5.51 of *L. s. subtaeniatus* confirm this. Although the cranial morphology in *B. bipraeocularis* (syntype, NHMUK 1946.1.23.19, suppl. document 4) and *B. olivaceus* (ZFMK 5405, suppl. document 4) is otherwise almost identical with *L. s. subtaeniatus*, there is a diastema after the sixth maxillary tooth in these two species. In the holotype of *L. s. upembae*, MRAC R.5201, the diastema is absent as well (Fig. 11).

Coloration. Although coloration should not be viewed among primary characters in generic delimitation, its general scheme may give a useful hint. *Lycodonomorphus* s.s. have uniformly brown, blackish or greyish dorsal colour, without any pattern. The majority of currently recognised *Boaedon* members have longitudinal bands on the head and often also on the body. The coloration of *L. s. subtaeniatus* is clearly of the *Boaedon* type, resembling many Central and Western African species, such as *B. virgatus*, *B. littoralis*, *B. fradei*, etc. In both subspecies, canthal, supralabial and temporal bands that are similar to such in the majority of *Boaedon* species are clearly visible. In *L. s. upembae* they are less distinct and barely reach behind the temporal scales. In *L. s. subtaeniatus* these bands are with sharper contours and even continue behind the head, as faint lateral stripes on the anterior of the body.

General form and appearance. *Lycodonomorphus* s.s. have comparatively long bodies, markedly longer than in their closest relatives – *Alopecion*, *Boaedon*, *Lamprophis* (Tiutenko et al. 2022). The body in both subspecies of *L. subtaeniatus* is rather short (Laurent 1954), thus closer resembling that of a *Boaedon* than of a *Lycodonomorphus* s.s. The head is broader posteriorly and has, similarly to a *Boaedon*, a rather trapezoidal shape, compared to more oval heads of *Lycodonomorphus*. Among *Lycodonomorphus* s.s. However,

Figure 10. The head (lateral, ventral and dorsal aspects) and of dorsal scales of the holotype of *Lycodonomorphus subtaeniatus upembae* (MRAC R.5201). Note apical pits barely visible as pairs of spots on the dorsal scales (indicated by red arrows). Courtesy of MRAC.

the head of *L. subtaeniatus* appears slightly shorter than in *B. lineatus* and significantly shorter than in *B. fuliginosus*. The main cause may be the nasal bones which we found shorter in the skulls of *L. subtaeniatus* (compare Fig. 11 and images in suppl. document 5). In *B. upembae* these bones seem to be even shorter than in *L. subtaeniatus*. This makes the braincase also shorter than in *B. virgatus*.

With regard to the aforementioned phenotypic similarities we transfer *Lycodonomorphus subtaeniatus* Laurent, 1954 here to the genus *Boaedon* as *Boaedon subtaeniatus* (Laurent, 1954). Since the morphologically similar *L. s. upembae* was shown by Greenbaum et al. (2015) to be a sister clade to *B. virgatus*, the species *B. subtaeniatus* should preliminarily occupy the same position in the phylogeny of the genus. Some other morphologically similar specimens collected at the same localities as the types of *L. subtaeniatus* and housed in the MRAC under the name '*Boaedon lineatus*' may be conspecific with the latter.

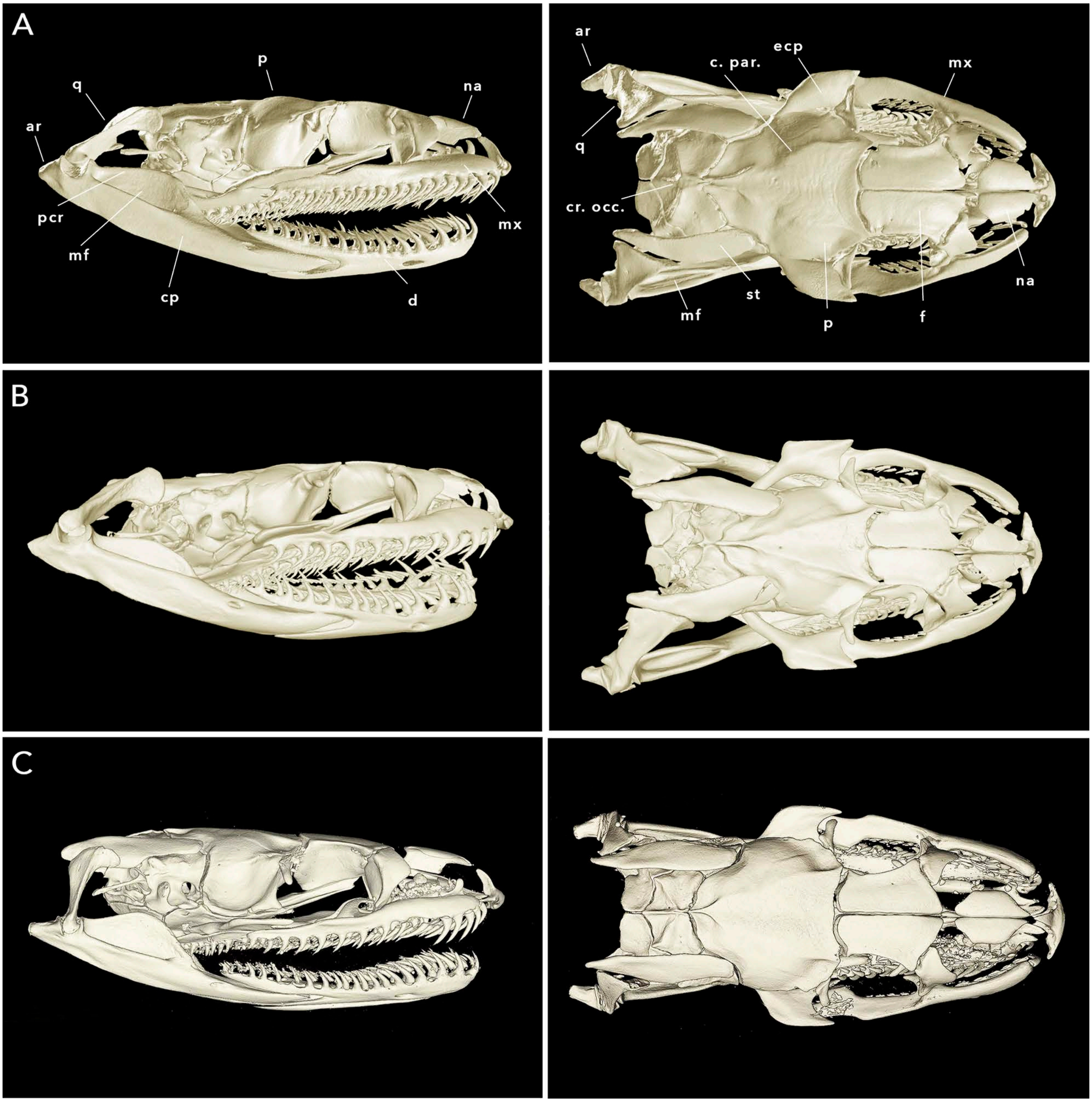

Figure 11. Micro-CT images of the skulls of the holotype specimens of *Lycodonomorphus subtaeniatus subtaeniatus*, MRAC R.14864 (A) and *L. subtaeniatus upembae*, MRAC R.5201 (B), and of a topotypic specimen of *Boaedon virgatus*, ZFMK 75117 (C). Images A–B are courtesy of MRAC.

Final remarks

After *L. subtaeniatus* and *L. inornatus* are removed from *Lycodonomorphus*, this genus can be diagnosed by the following combination of characters (adopted with emendations from Bogert 1940, Loveridge 1958, FitzSimons 1962, Tiutenko et al. 2022). Body cylindrical, elongate; dorsal scales smooth, in 19–21 rows around midbody; ventrals rounded; anal entire; tail moderately long and tapering; subcaudals paired; head oval or slightly trapezoidal, a little broader than neck; eye of moderate size with vertically sub-elliptical pupil capable of shrinking to a dot in strong light; maxillary teeth small, subequal, 20–25 in number, no diastemata; mandibular teeth subequal; inconspicuous groove on either side of the head, between upper labials and lateral head shield; hemipenis not bifurcate or very shallowly bifurcate.

Such external morphological characters, usually mentioned in diagnoses of these genera and their members, as the numbers of temporals (1 + 2), preoculars (one), supralabials (eight, with the fourth and the fifth bordering the orbit) and infralabials (eight, with the first four in contact with the anterior chin shield) are not useful because they are common for Boaedontini. Ventral and subcaudal plate counts are not useful as well due to their large range in *Lycodonomorphus* and variation within Boaedontini genera, especially *Boaedon*.

FitzSimons (1962) mentioned also pterygoid teeth that are subequal, numerous, 30–34 in number. Among five species that we analysed, we observed this, however, only in *L. rufulus* and *L. leleupi*, but not in *L. bicolor*, *L. laevissimus*, and *L. whytii* that had 24–26 pterygoid teeth. Also, we found in all examined *Lycodonomorphus* that the pterygoid teeth are larger anteriorly and gradually decrease in size posteriorly. We therefore remove this character from the genus diagnosis, but consider it important for future taxonomic work that may result in recognition of further groupings.

Enlarged anterior teeth, both mandibular and maxillary, or just the first, seem to be ancestral to this tribe. They are present in *Pseudoboodon*, *Boaedon*, *Bofa*, *Bothrolycus*, *Alopecion* and gradually disappear in more recently diverged clades. In *Bothrophthalmus* and *Elaiophis* gen. n. only mandibular teeth are significantly larger anteriorly, and in *Lycodonomorphus* all teeth are subequal. In the clade *Alopecion-Lamprophis* the first genus has enlarged teeth in both jaws, whereas in the second only mandibular teeth are strongly enlarged. The common ancestor of *Boaedon* and of the clade *Alopecion-Elaiophis-Lamprophis-Lycodonomorphus* is thus likely to have had enlarged anterior maxillary and mandibular teeth.

Since there are otherwise no snake genera with mixed pupil shapes, we consider it among the most useful synapomorphies for genera delimitation in this family. The pupil shape must have evolved at least three times in Lamprophiidae. The ancestral state of it is a uniformly circular pupil, as found in Psammophiinae, Atractaspidinae, Pseudaspidinae, as well as in Elapidae – the sister group to Lamprophiidae. In both tribes of Lamprophiinae, three states of this character occur: circle, wide oval (also called 'sub-elliptical' or 'sub-circular'), and narrow oval (also referred to as 'vertically elliptical' or just 'elliptical'). The circular pupil remains so at all light conditions, whereas the sub-elliptical one may appear as a circle in low light and become a dot when the light is strong, being capable of shrinking and expanding both vertically and horizontally. The vertically elliptical pupil seems not to be able to shrink or to expand as much vertically. It becomes a wide oval in low and a narrow vertical slit in strong light while its height seems to remain more-or-less constant. In Boaedontini, the pupil of this type is characteristic for *Boaedon* and *Alopecion*. The pupil is circular in *Bofa* and *Bothrolycus*. The common ancestor of this and of its sister clade comprising *Alopecion*, *Boaedon*, *Lamprophis*, *Lycodonomorphus* and the new genus described here, must have had circular pupils, too, that it inherited from the common ancestor with its sister – *Pseudoboodon*. That the pupil is circular in some (evolutionary older) members of *Pseudoboodon* and sub-elliptical in others indicates that this genus requires our attention in a future taxonomic study. Generally, it seems that a sub-elliptical pupil is a more advanced trait that is found in more recently diverged Boaedontini genera: *Lamprophis*, *Lycodonomorphus*, *Elaiophis* gen. n., as well as in *Bothrophthalmus* and the more advanced species of *Pseudoboodon*. Snakes having it are usually crepuscular (pers. obs. in *Pseudoboodon*).

The evolution of the apical pits on dorsal scales in Boaedontini seems to coincide with that of the eye pupil. The pits are absent in genera whose members have circular pupils, and are likely to have emerged in the common ancestor of *Alopecion-Elaiophis-Lamprophis-Lycodonomorphus* and *Boaedon* clades along with the vertically elliptical pupil. They are consistently present and well visible in *Boaedon* – nocturnal, terrestrial snakes with vertically elliptical pupils – and gradually disappear in the sister clade whose members (except *Alopecion*) have sub-elliptical pupils. Although apical pits are generally absent in *Lycodonomorphus*, some authors mentioned them as occasionally occurring in *L. rufulus* (Loveridge 1958, FitzSimons 1962) and in *L. whytii* (Rasmussen 2004). In the examined adult specimens of *Lycodonomorphus* (including *L. rufulus*) we did not notice any signs of apical pits, but found them, quite well recognisable, in all, even long preserved, specimens of *Boaedon*. In a comment about a similar case of *Lamprophis aurora*, where apical pits also were only sometimes observed, Broadley (1969) suggested that they may be easier noticeable in live or freshly preserved specimens. We had no access to such material during this study and could not verify this assumption. However, in high-quality and high-resolution live photographs of various specimens of *Lycodonomorphus rufulus* and *Lamprophis aurora* we did not find any signs of apical pits, although they were quite clearly visible in similar images of *Boaedon*.

The range of the genus *Lycodonomorphus* is now limited to the southeast of the continent – to the Great Rift Valley lakes south of the equator, and to South Africa. All members of the genus are more-or-less associated with waterbodies, preying predominantly on fish and amphibians. Currently the genus includes seven species: *L. bicolor*, *L. laevissimus*, *L. leleupi*, *L. mlanjensis*, *L. obscuriventris*, *L. rufulus*, and *L. whytii*. Among them we consider only *L. rufulus* a *Lycodonomorphus* sensu stricto. We tentatively retain *L. bicolor* in *Lycodonomorphus* sensu lato, till its final generic affiliation is clarified. Being ecologically similar, this snake differs from *Lycodonomorphus* s.s. by a number of characters, such as much higher dorsal scale count (23–25); only the 4th supralabial bordering the orbit; lower numbers of maxillary (18–19) and mandibular (19–20) teeth; circular pupil. The definite decision about the taxonomic placement of *L. bicolor* requires a phylogenetic study with use of molecular data comparable to already available for other species. If such a study would prove that this species should belong to a separate genus, the name *Glypholycus* will have to be revived for *L. bicolor* and presumably related 'semiaquatic' species (*L. laevissimus*, *L. leleupi*, *L. mlanjensis*, *L. whytii*) from the synonymy of *Lycodonomorphus*. *Lycodonomorphus obscuriventris* appears to be a special case that may warrant a separate treatment but we do not discuss it here in detail due to a lack of information about this species.

Lycodonomorphus rufulus represents one of more recently diverged clades of Boaedontini (Fig. 2). Keates et al. (2022) noted deep divergence in this species that may indicate a more intensive evolution and cryptic speciation of this genus in South Africa. This may explain also some variation in hemipenial morphology observed in these snakes (W. Conradie pers. com.). Overall, *Lycodonomorphus* is characterised by unusually large interspecific distances, but introduction of further systematic groupings does not appear productive for now. On the other hand, a question about validity of some species in this genus remains relevant. Three poorly studied species – *L. leleupi*, *L. mlanjensis*, *L. whytii* – are still distinguished mainly on a basis of coloration. Their external morphological characters overlap (Tab. 1). Moreover, we found the skulls of the type specimens of *L. leleupi* and *L whytii* (Figs 6.1, 6.2) almost identical, and noticed only small differences in the number of teeth (Tab. 1). Unfortunately, we did not study the skull of *L. mlanjensis* yet, but expect also it to be similar, given the external similarity of the head. Considering that these three snakes have similar ecology, and their distribution areas are likely to overlap, they may indeed belong to a single species – *L. whytii*.

The herpetofauna of the Republic of South Africa has over 200 endemic or nearly-endemic species of reptiles (Bates et al. 2014, Tolley et al. 2023). These include all *Lamprophis* and three species of *Lycodonomorphus*. That three Boaedontini genera, i.e., a third of the tribe content – *Alopecion*, *Elaiophis* and *Lamprophis* – are endemic to this comparatively small region also agrees with the general pattern of South African endemism. This region is home of an extraordinary diversity of endemic genera, both of amphibians and reptiles, as well as of other animals and plants (SANBI 2024). Among 114 reptile genera recorded from South Africa (Tolley et al. 2023) twelve are endemic. Eight of these genera are monotypic. It is hence not unusual that the three South African Boaedontini genera are 'small', of which two are currently monotypic and one contain only three members.

The recognition of smaller genera in Boaedontini follows the current tendency in herpetological systematics. Instead of attempts to establish fewer, but speciose, genera, as it was a more common practice in the 20th century, today large genera are more usually being split into smaller genera, based on a few clear synapomorphies combined with genetic distance and phylogenetic relationship of the members. This is done through resurrection of the genera that were synonymised in the past or through introduction of new genera, and generally results in a more robust and future-proof taxonomy. The genus *Lycodonomorphus* still requires attention of taxonomists, as it contains species with uncertain taxonomic position, such as *L. bicolor*, *L. laevissimus*, *L. leleupi*, *L. mlanjensis*, *L. obscuriventris*, and *L. whytii*, and in this sense has to be viewed as sensu lato. We are of the opinion that these species can be recognised as one or two groups separate from *Lycodonomorphus* s.s. Whether these should become genera or subgenera, would depend on the level of morphological and other difference that future studies may reveal. Depending on criteria applied, an introduction of subgenera may result in another revision of supraspecific affinities in this family. In the absence of such criteria, we here refrain from use of subgenera and from any recommendations regarding it, and adhere to the 'traditional' taxonomic category of genus.

The tribe Boaedontini now contains nine genera that can be distinguished by morphological characters according to the following key.

Key to the genera of Boaedontini

1) A pit present on the 4th and 5th supralabial scales .... *Pseudoboodon*

1') No pits on supralabial scales present 2

2) Anterior mandibular teeth enlarged 3

2') No enlarged mandibular teeth present 4

3) Dorsal scales feebly keeled .... *Bothrophthalmus*

3') Dorsal scales not keeled 5

4) Pupil sub-elliptic, shrinking to a dot in strong light .... *Lycodonomorphus* sensu stricto

4') Pupil circular, shrinking to a dot in strong light .... *Lycodonomorphus* sensu lato

5) Pupil circular 6

5') Pupil not circular 7

6) Conspicuous groove on the loreal scale .... *Bothrolycus*

6') No grooves on head scales .... *Bofa*

7) Pupil sub-elliptical, remaining oval in strong light ... 8

7') Pupil elliptical, shrinking to a narrow vertical slit in strong light 9

8) Maxillary teeth 12–17, anteriorly slightly enlarged .... *Lamprophis*

8') Maxillary teeth 22–23, anteriorly not enlarged .... *Elaiophis*

9) Dorsal scales with two apical pits .... *Boaedon*

9') No pits on dorsal scales present .... *Alopecion*

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Supplementary data

The following data are available online:

Supplementary document 1. List of specimens and GenBank accession numbers of nucleotide sequences used in this study.

Supplementary document 2. Estimates of evolutionary divergence (uncorrected p-distances) between concatenated sequences of three genes: c-mos, ND4 and Cyt b.

Supplementary document 3. Micro-CT images of the skull of a *Boodon infernalis* syntype NHMUK 1855.10.16.354.

Supplementary document 4. Micro-CT images of skulls of some members of the genus *Boaedon*.

Supplementary document 5. Micro-CT images of the skull of a *Lycodonomorphus subtaeniatus subtaeniatus* paratype NHMUK 1953.1.5.51.