# Integrative approach resolves the systematics of barred wolf snakes in the Lycodon striatus complex (Reptilia, Colubridae) 

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#### Abstract

We reviewed the systematics of Lycodon striatus (Shaw, 1802), including all available name-bearing types of its synonyms after evaluating phylogeographic (genetics), morphological (morphometry, meristic, and hemipenes), osteological and distribution evidence. Lycodon striatus sensu lato is widely distributed throughout South and Central Asia and mimics elapids. Based on phylogenetic analyses of mitochondrial DNA, we demonstrate that populations from (i) eastern and central Peninsular India plus Sri Lanka and (ii) south-western parts of Central Asia form two different clades representing two distinct species: $L$. striatus sensu stricto and $L$. bicolor comb. nov. respectively. These two clades are sisters to $L$. deccanensis (in the case of $L$. striatus) and $L$. jara (in the case of $L$. bicolor) and together form two main sister radiations. Although the external morphological variability is high in both species, the genetic variability is higher only in L. striatus but not distinct enough to represent more than one species if using the phylogenetic or biological species concept. The phylogeny of the L. aulicus group hints at Sri Lankan L. striatus, likely having evolved in continental Asia through a probable overland dispersal across the Bay of Bengal (present Palk Strait) into Sri Lanka. This dispersal may have been facilitated by low sea levels during the Pleistocene glaciations when Sri Lanka was connected to mainland India. After considering genetic divergence (with a $p$-distance of $1.8 \%-2.1 \%$ in the mitochondrial cytochrome $b$ gene) and morphological evidence, we synonymize the Sri Lankan subspecies, L. s. sinhaleyus Deraniyagala, 1955, with L. striatus sensu stricto. The eastern and central Indian L. striatus (i.e. L. striatus sensu stricto) is morphologically distinct and deeply divergent genetically compared to Tajik and Pakistani $L$. bicolor with a $p$-distance of $13.6 \%$ in cytochrome $b$ gene (mtDNA). Interestingly, L. bicolor is conspecific (p-distance $1.4 \%$ ) with L. mackinnoni, a western Himalayan endemic, and it reveals intraspecific clinal variation.


## KEYWORDS

Asia, iconotype, Lycodon mackinnoni, Lycodon striatus sinhaleyus, neotype, nomen dubium, subspecies

## 1 | INTRODUCTION

The striated (barred) wolf-snake, Coluber striatus Shaw, 1802 , is currently considered a widely distributed species in South and Central Asia, including peninsular India, Sri Lanka, Nepal, Pakistan, Iran, Turkmenistan, Uzbekistan, West Tajikistan and possibly Afghanistan (Sindaco et al., 2013; Wallach et al., 2014; Wagner et al., 2016). Shaw (1802: 527) named the species based on a 14 -inch ( $\sim 356 \mathrm{~mm}$ ) specimen illustrated and described by Russell (1796) as 'Gajoo Tutta' (page 22 and plate 16), hence an iconotype. Russell (1796: 22) further stated the specimen was found from 'Vizagapatam' (=Visakhapatnam, Andhra Pradesh), India, although it was rare and had 174 ventrals and 40 subcaudals. A year after the description
of C. striatus, Daudin (1803) named the same species depicted and described by Russell (1796) as C. malignus. In the same publication, Daudin (1803) named another species C. galathea based on another illustration on plate 26 in Russell's publication (1796: page 32). Russell (1796: 32) stated that this specimen was found in Hyderabad, India, and had 171 ventrals and 41 subcaudals. Later, Wall (1921) synonymized both species with Shaw's Lycodon striatus.

Duméril et al. (1854: 384) described another possibly similar species as $L$. napei based on a single specimen in the Muséum National d'Histoire Naturelle Paris (MNHN-RA), but without any data on its origin or pholidosis. This species was also synonymized with $L$. striatus by Wall (1921). Another species similar to $L$. striatus was described by Nikolsky (1903:96) as Contia bicolor based on two specimens
from Persia and Transcaspia, and he stated that one of them had 202 ventrals and 65 subcaudals. Later, it was placed in the genus Lycodon and considered a subspecies of $L$. striatus by subsequent authors (e.g. Khan, 2002, 2003; Lanza, 1999; Minton, 1966). Deraniyagala (1955) described two subspecies (i) L. s. sinhaleyus from Rajagiriya (Colombo), Sri Lanka, and (ii) L. s. nordicus from Baluchistan, Persia, Transcaspia (i.e. Turkmenistan) towards Calcutta (Northeast India). Deraniyagala (1955) stated that the Sri Lankan subspecies had 144-160 ventrals and 35-40 subcaudals, while L. s. nordicus had 163-195 ventrals and 44-58 subcaudals. In these early descriptions, the males and females were not separated for meristic characters. However, the latter subspecies was synonymized with the forma typica by Lanza (1999).

Although there were several attempts to understand the morphological variation using the number of body scales, e.g. ventrals and subcaudals (e.g. Deraniyagala, 1955; Wall, 1921, 1923; Smith, 1943), L. striatus has long been considered a single species widely distributed in South and Central Asia (Boulenger, 1891; Wallach et al., 2014). Therefore, based on the type material and additional voucher specimens from India and Sri Lanka, we revisit the taxonomic status of $L$. striatus sensu lato which involves the examination of the type material of all its synonyms. After taking morphological, meristic, and morphometric characters into consideration with the geographical distribution of examined specimens ( $n=73$ ), we recognize that $L$. striatus represents a species complex that needs comprehensive taxonomic evaluation.

## 2 | MATERIALS AND METHODS

For this study, we collected morphological, osteological, genetic, and distribution data for Lycodon striatus sensu lato, which we compared to publicly available data. We compared the type specimens (or iconotypes) of all the species/subspecies (including synonyms) of Lycodon striatus sensu lato, with specimens and the descriptions of other known congeners (see Appendix S1). When diagnosing and re-describing the species, we scored specimens for the same morphological and morphometric characters used in recent descriptions of the genus Lycodon (e.g. Ganesh, Amarasinghe, et al., 2020; Ganesh, Deuti, et al., 2020; Ganesh \& Vogel, 2018; Vogel \& David, 2019).

### 2.1 Tissue collection and specimen examination

Our fieldwork in Central and South Asia took place from 1980 to 2022. We collected some specimens by hand, euthanized the specimens with sodium pentobarbital, and
fixed the specimens in a $10 \%$ buffered formalin solution prior to their storage in $70 \%$ ethanol. Prior to fixation, we preserved tissue samples for DNA analysis in $95 \%$ ethanol, and the respective vouchered specimens were deposited in the herpetological collection at the Pakistan Museum of Natural History, Islamabad, Pakistan (PMNH); Department of Zoology, Comenius University in Bratislava, Slovakia (CUHC); Department of Vertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, Moscow, Russia; and the National Museums of Sri Lanka, Colombo (NMSL). We also examined specimens (see Appendix S1) from the Bombay Natural History Society, Mumbai, India (BNHS); California Academy of Sciences, San Francisco, USA (CAS); Carnegie Museum of Natural History, Pittsburgh, USA (CM); Field Museum of Natural History, Chicago, USA (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Departmental Museum of Zoology, Mizoram University, Aizawl, India (MZMU); the Natural History Museum, London, UK, (NHMUK); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL); Pakistan Museum of Natural History, Islamabad, Pakistan (PMNH); Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK); Zoologicheskii Institut, Rossiiskoi Akademii Nauk, St. Petersburg, Russia (ZISP); Museum für Naturkunde, Berlin, Germany (ZMB); Zoological Museum of Mikhail V. Lomonosov, Moscow State University, Moscow, Russia (ZMMU); and Zoological Survey of India, Kolkata, India (ZSI). Museum acronyms are those of Sabaj (2020). We obtained morphological, morphometric, and meristic data for species comparisons, and distribution data from examined specimens, published literature as well as georeferenced photographic vouchers from iNaturalist, a citizen science platform.

## $2.2 \mid$ Genetic data

Total genomic DNA was extracted from the tissue samples (blood, liver, or muscle biopsies from ethanolpreserved museum specimens and road-killed animals) using the NucleoSpin Tissue kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions. For molecular genetic analyses, we used fragments of cytochrome $b$ (Cyt b) using primers L14910 and H16064 (Burbrink et al., 2000). We used standard PCR protocols with annealing temperature and elongation time of $46^{\circ} \mathrm{C}$ and 1:30 min. The purified PCR products were sent for sequencing to Macrogen Inc. (Amsterdam, The Netherlands; http://www.macrogen-europe.com or Seoul, South Korea; http://macrogen.com).

New sequences of Cyt $b$ ( 1096 bp ) generated for this work were deposited in GenBank and combined with data taken from previously published studies (Table S1; Dubey et al., 2012; Kalki et al., 2020; Pyron et al., 2013; Siler et al., 2013; Nawani et al., 2021; Wang et al., 2021). Following sequences AF471054 (Ptyas mucosa), KC347453 (Ahaetulla nasuta), and KF732930 (Oligodon chinensis) were used as outgroups (Lawson et al., 2005; Lei et al., 2014; Pyron et al., 2013). The sequences were aligned in MEGA 7 (Kumar et al., 2016) using ClustalW (Thompson et al., 2003) with default settings.

The Bayesian inferences (BI) and maximum likelihood (ML) methods were adopted for constructing the phylogenetic trees. We used MrBayes v3.2.6 (Ronquist et al., 2012) to construct BI tree and RAxML GUI v1.5 incorporated into RAxML v8 (Randomized Axelerated Maximum Likelihood; Stamatakis, 2014) to construct ML tree. We carried out a log-likelihood ratio test with and without enforcing the molecular clock in MEGA 7. The molecular clock test rejected the null hypothesis at a $5 \%$ significant level, and hence, a relaxed clock under log-normal distribution was used as the prior for the clock model. We ran the output .xml file constructed in BEAUTi v2.6.3 in Markov Chain Monte Carlo (MCMC) algorithm for 100 million iterations, sampling every 10,000 generations in Yule Coalescent model. The effective sample size (ESS) values for the priors were checked using Tracer software v1.7.1 (Rambaut \& Drummond, 2009), and a value $>200$ was used as the threshold. The initial $10 \%$ of the trees were discarded as the burn-in, as suggested by Tracer v1.7.1, and we produced the maximum clade credibility tree at mean heights in Tree Annotator (Rambaut \& Drummond, 2009). We also employed DensiTree v2.2.7 (Bouckaert, 2010) to come by the different topologies in the sets of Cyt $b$ gene trees. For the partitioned BI phylogeny, the MCMC was run with four chains (one cold and three hot chains) for 20 million generations by sampling every 5000 generations with a relative burn-in of $25 \%$ of the trees in MrBayes v3.2.6 (Ronquist et al., 2012). For the partitioned BI tree inference, PartitionFinder v1.1.1 (Lanfear et al., 2012) was used to determine the best nucleotide substitution model and the best partitioning scheme using the 'all' algorithm under the Bayesian information criterion (BIC). The software selected the models HKY $+\mathrm{I}+\mathrm{G}$ for the first and second codon positions and GTR +G for the third codon position.

The ML analysis was also performed based on the partitioned Cyt $b$ dataset by allowing FreeRate heterogeneity (Soubrier et al., 2012) at 10,000 Ultrafast Bootstrap (UFB) replicates (Minh et al., 2013) using the best partitioning schemes selected by PartitionFinder. The models selected (GTR $+\mathrm{I}+\mathrm{G}$ for the first and second codon positions; GTR + G for the third codon position) were based
on BIC values in PartitionFinder. Trees obtained from ML and BI analyses were visualized using FigTree v1.4.3 (Rambaut, 2014).

The uncorrected $p$-distances were calculated in MEGA 7 and DnaSP 6 (Rozas et al., 2017), and missing data and gaps were dealt with using the pairwise deletion option. For presentation of intra-lineage variability of two detected lineages representing L. s. bicolor, L. mackinnoni, $L$. striatus and L. s. sinhaleyus, we built haplotype networks using PopArt (Leigh \& Bryant, 2015) with the implemented parsimony network algorithm of TSC (Clement et al., 2000), with a $95 \%$ connection limit.

## 2.3 | Morphological character data

We measured the following characters with a Mitutoyo digital caliper and Leica M50 (Leica Microsystems Inc.) or AmScope SM-1BZ-RL (10-90×; United Scope LLC) or Carl Zeiss DRC 475003-9902 dissecting microscope (Carl Zeiss AG): eye diameter (ED, horizontal diameter of eye); eye-nostril length (distance between anterior-most point of eye and middle of nostril); snout length (ES, distance between anterior-most point of eye and snout tip); internarial distance (IN, least distance between nostrils measured dorsally); interorbital width (IO, least distance between upper margins of orbits); head length (HL, distance between posterior edge of mandible and tip of snout); head width (HW, maximum width of head measured dorsally); snout-vent length (SVL, measured from tip of snout to anterior margin of vent) and tail length (TL, measured from posterior margin of vent to tail tip).

Meristic characters were taken as follows: supralabials (SUP) and infralabials (first labial scale to last labial scale bordering gape); dorsal scale rows [DSR, counted around the body from one side of ventrals to the other in three positions: (i) one head length behind neck, (ii) midbody and (iii) one head length prior to cloacal plate]. We counted ventral scales without preventrals according to Dowling's method (Dowling, 1951) and subcaudal scales from the first subcaudal scale following the cloacal plate to the scale before the tip of the tail, the tail tip scale being excluded from the count.

Sex of the specimens was identified by examining everted hemipenes or by ventral tail dissection. We examined the basic structure and systematic characteristics of the hemipenes according to the method described by Dowling and Savage (1960). We evaluated the dorsal cross markings, especially the number of black cross markings of each individual. The number of cross marks on the body was counted from the first band posterior to the marking on the nape up to the last marking clearly visible and separated from the background colouration. Body colour
pattern is considered a reliable character only when a drawing/description/photograph of a live animal or dead specimen is available to us. We considered the number of vertebral scales in between cross markings at the anterior body as a reliable character for species diagnosis.

We examined features of the skull and counted the number of maxillary, palatine, pterygoid and mandibular teeth of Lycodon striatus sensu lato based on MicroCT scans of museum specimens. MicroCT scan was generated using a Bruker Skyscan 1272 (Bruker BioSpin Corporation) scanner. The head was scanned for 210 min at a resolution of $5.4 \mu \mathrm{~m}$ and we recorded data for every $0.4^{\circ}$ rotation for $360^{\circ}$ with (AL) 1 mm filter. The source voltage for the scan was 65 kV and the source current was 153 uA . Volume rendering was performed with CTVox (Bruker BioSpin Corporation) and images were edited in Adobe Photoshop CS6. The osteological description is based on volume renders retrieved from CTVox following terminology of the skull described by Gans et al. (2008).

## 2.4 | Morphometric analysis

Statistically informative tests could not be performed on separate sexes due to the smaller sample sizes of females representing the different regions, insufficient for this purpose. Juveniles were excluded to avoid the bias of allometry for statistical analysis. Boxplots were generated for tail ratio (TL/total length) to visualize the range, mean, median, and degree of differences between different populations bearing statistically different mean values. We performed separate Kruskal-Wallis one-way analysis of variance tests on the tail length ratio to detect any significant difference between different populations, (i) eastern and central India $=13$, (ii) Pakistan $=9$ and (iii) Sri Lanka $=14$. We used this test due to the small sample size (Zar, 2010). Variation in adult size was normalized using the following equation: $\log X_{a d j}=\log (X)-$ $\beta\left[\log (\mathrm{SVL})-\log \left(\mathrm{SVL}_{\text {mean }}\right)\right]$, where $\mathrm{X}_{\text {adj }}=$ adjusted value; $X=$ measured value; $\beta=$ unstandardized regression coef ficient for each population and $\mathrm{SVL}_{\text {mean }}=$ overall average SVL of all populations (Chan \& Grismer, 2022; Lleonart et al., 2000) prior to multivariate analyses on seven morphometric characters, SVL, TL, HL, HW, ES, ED and IO. The scaled morphometric characters were treated as the dependent variable and the population as the predictor variable for multivariate analysis.

Multivariate analysis was conducted using principal component analysis (PCA) to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables, i.e. principal components (PC). We used the princomp function in the R statistical software program (v4.0.4; R Core Team, 2021). A biplot of the first
two principal component scores was used to examine the degree of the relative influence of each morphometric character on the data set. All statistical analyses were conducted using the R statistical software program (v4.0.4; R Core Team, 2021). Boxplots were generated for tail ratios (TL/total length) to visualize the range, mean, median, and degree of differences between the above three populations.

## 3 | RESULTS

## 3.1 | Molecular phylogenetic and genetic variability

The molecular analyses of mitochondrial DNA using maximum likelihood (ML) and Bayesian inference (BI; Figure 1a and Figure S1) showed eight lineages within the Lycodon aulicus group. These lineages represent different taxa with sequence divergence (uncorrected $p$ distances) between $8.5 \%$ (L.flavicollis and L. aulicus) and $18.2 \%$ (L. aulicus and L. carinatus; Table 1 and Table S2). The basal position of the $L$. aulicus group, representing a single-clade sister to the $L$. laoensis $+L$. carinatus lineage, includes eight lineages: (1) L. mackinnoni $+L$. striatus sensu lato in Central Asia (now L. bicolor comb. nov. see below) from India and Pakistan, respectively, (2) L. jara from Myanmar, (3) L. deccanensis from India, (4) L. striatus sensu stricto + L. s. sinhaleyus from Sri Lanka, (5) L. capucinus from West Malaysia, (6) L. flavicollis from India, (7) L. zawi from Myanmar and (8) L. aulicus from India (Figure 1a and Figure S1). We tentatively included $L$. laoensis $+L$. carinatus also into the $L$. aulicus group. The uncorrected genetic distance (\%) between targeted taxa represents one evolutionary lineage. For example, the uncorrected genetic distance between L. mackinnoni from Mussoorie (type locality) in India and L. striatus sensu lato from Tajikistan and Pakistan (hereafter L. bicolor comb. nov.) is $1.4 \%$, and the genetic distance between $L$. striatus sensu stricto from India and L. s. sinhaleyus from Rajagiriya (type locality), Sri Lanka, is $1.8 \%-2.1 \%$ (Table 1 and Table S2). Therefore, these should be considered as closely related entities, representing intraspecific variability. This also supports the results based on intra-lineage haplotype networks. Sequences including L. mackinnoni and L. striatus sensu lato from Pakistan are formed by four haplotypes - the Pakistani population is distant from the Indian by 11 to 14 mutation steps, whereas the difference between the Pakistani and Tajik populations is only four to seven mutation steps (Figure 1b). Similarly, the distance between $L$. striatus sensu stricto from India and L. s. sinhaleyus from Sri Lanka is formed by 14 to 17 mutation


FIGURE 1 (a) Maximum likelihood (ML) phylogeny of the genus Lycodon based on 1096 bp of the mitochondrial Cyt $b$ gene. Topologies of ML and Bayesian analyses were similar (Figure S1). Haplotype networks reconstructed for (b) L. bicolor and (c) L. striatus.
TABLE 1 Uncorrected mean $p$-distance (sequence divergence) for mitochondrial cytochrome $b$ gene calculated for members of Lycodon aulicus group and its basal sister species, L. laoensis and $L$. carinatus.

steps (Figure 1c). Together with the data obtained from the morphology of these snakes, we thus propose taxonomical changes for $L$. striatus sensu lato in the L. aulicus group as outlined below.

## 3.2 | Morphometric distinctness

Based on 36 examined specimens of Lycodon striatus sensu lato (see map in Figure 2), five of six morphometric ratio comparisons showed significant differences ( $p<.05$ ) between western central Asian and central + eastern Indian (forma typica) populations. However, the morphometric ratios of the Sri Lankan populations were not significantly different from the forma typica, except for the tail ratio (TL/total length; $\chi^{2}=7.05, p=.007 ; n=12$ ). Although the tail ratio (13.3-17.0) of the Sri Lankan population was generally smaller than the forma typica, and the differences were statistically significant, the range of tail ratios showed partial overlap with its forma typica in India (Figure 3a). In contrast, the tail ratio (TL/total length) of the western central Asian population (17.1-22.2, $n=9$ with mixed sex) was significantly larger $\left(\chi^{2}=14.73\right.$, $p=.0001$ ) compared to the tail ratio of the forma typica (15.1-16.7, $n=12$ ) and their range showed partial overlap.

The principal component analysis also showed distinct overall differences in morphometric characters between western central Asian and central + eastern Indian populations, with distinct and overlapping clusters (Figure 3b). However, the cluster of the Sri Lankan population significantly overlaps with the forma typica in the first two principal components. Principal components 1 and 2 collectively explained $61.0 \%$ of the variation in the morphometric data matrix (Figure 3b; Table S3). Scaled morphometric ED and HL loaded negatively with both PCs, whereas ES, IO and HW only loaded negatively with PC1.

We present diagnostic morphological, morphometric, and meristic data taken for each of the above three populations in Table 2 and compared them to the Lycodon species in Sri Lanka and India in Table 3.

## 3.3 | Systematics

Currently, there are six junior synonyms under L. striatus sensu lato (including nominotypical subspecies): Coluber malignus, C. galathea, L. napei, L. striatus bicolor, L. s. sinhaleyus and L. s. nordicus. Except for the syntypes of $L$. bicolor, our attempts to trace type specimens of other taxa in other depositories (e.g. MNHN-RA, NHMUK, NMSL, ZSI, etc.) proved unsuccessful. Therefore, the only available original materials for those nomina are the original descriptions and associated illustrations based on the original
specimens. Coluber striatus was described based on a specimen depiction by Russell (1796: plate 16; see Figure S2A). The illustration was based on a single specimen (holotype by monotypy), and we examined the available dry skin catalogued as holotype (NHMUK 1904.7.27.67; not holotype fide Bauer, 2015). We restrict the type locality of $L$. striatus to Visakhapatnam, Andhra Pradesh, India, based on the holotype (now lost) fide Russell (1796) and Shaw (1802), and consider its distribution as being from eastern towards northwest and south India including Sri Lanka. Coluber malignus was described based on the same specimen illustrated (iconotype) of $C$. striatus, hence it is to be regarded as a junior objective synonym of $C$. striatus. Coluber galathea was also described based on specimens depicted by Russell (1796: plate 26; see Figure S2B). The illustration was probably based on several specimens (syntypes; holotype fide Bauer, 2015), and we examined two available dry skins catalogued as syntypes (NHMUK 1904.7.27.61-62; not syntypes fide Bauer, 2015). After examining several live specimens, and studying several photographic materials, we reveal that C. galathea most likely corresponds to a juvenile life stage of $C$. striatus sensu stricto. In contrast, we have observed some adult individuals from south-central India (surrounding Bangalore) that have similar colouration resembling the juvenile colouration of $C$. striatus. Therefore, we only tentatively synonymize C. galathea with C. striatus sensu lato, leaving it for future taxonomists to further examination and reevaluation of inter-population distinctions using additional integrative taxonomic approaches. Lycodon napei is a dubious species where neither a type specimen nor a type locality has been recognized. Although the original description implies that it might be a Lycodon species, it is impossible to assign it with certainty to any taxonomic group because the description is insufficient for identification and the type specimen no longer exists. Therefore, we consider the nomen $L$. napei as a nomen dubium.

A comparison of the syntypes of Contia bicolor with the other known members of the genus Contia showed that C. bicolor shares characteristics with the genus Lycodon and not with the genus Contia. Based on phylogeny as well as skull morphology, e.g. the curvature characteristic in maxillary bone with differentsized teeth separated by a diastema (i.e. toothless) gap in C. bicolor vs. subequal-sized teeth with no diastema in the genus Contia, we assign the species to the genus Lycodon, restrict its type locality to Kurkulab in Turkmenistan based on Nikolsky (1903) and consider its distribution as being the region stretching from Pakistan towards Central Asia. Furthermore, the comparison of Lycodon bicolor comb. nov. with L. striatus sensu stricto from eastern India and other known Lycodon species (Table 2) leads us to recognize it as a distinct species.

Therefore, we resurrect $C$. bicolor from the synonymy of L. striatus and elevate it to the species level. The subspecies, L. s. nordicus proposed by Deraniyagala for Central Asia and northeast India has no designated type material and the nomen was referred to the specimens examined by Wall (1921). The assigned subspecies represents both species $L$. bicolor comb. nov. and L. striatus sensu stricto in pholidosis as well as its biogeographic distribution; hence, we synonymize it with both species.

Interestingly, the syntypes of L. bicolor comb. nov. and the individuals from Tajik and Pakistani populations have no distinctive morphological or meristic character variations. Therefore, it is confirmed that $L$. bicolor comb. nov. is a widely distributed species-see distribution under species account below. Further comparison between the specimens of $L$. bicolor comb. nov. (including the syntypes) and L. mackinnoni (including the syntypes; see Appendix S1) revealed that there are no distinct morphological characters to distinguish these two species, excluding the colouration (colour morphs) and, mainly, the dorsal striated pattern (see Figures 4 and 6).

Moreover, the uncorrected genetic distance between $L$. mackinnoni from Mussoorie (type locality) in India and L. striatus sensu lato from Tajikistan and Pakistan (hereafter $L$. bicolor comb. nov.) is $1.4 \%$ and thus represents the same evolutionary lineage. Based on both morphological and genetic evidence, we consider L. mackinnoni as conspecific to L. bicolor comb. nov. Therefore, in accordance with the principle of priority sensu Article 23 of the Code (ICZN, 1999), here we synonymize L. mackinnoni with $L$. bicolor comb. nov.

The Sri Lankan population of $L$. striatus shows several minor differences in body colouration and meristic characters (e.g. lower number of subcaudals). Therefore, such populations can be re-evaluated to see the overall pattern of genetic divergence through phylogenies of both the mitochondrial and autosomal DNA, and we leave it to future taxonomic workers to re-evaluate the inter-population distinctions with further integrative taxonomic approaches. Hence, here we state that (i) a name-bearing type is needed to define this nominal taxon objectively due to the designated holotype by monotypy of L. s. sinhaleyus (NMSL RS.15, fide Deraniyagala, 1955) and the other vouchers listed as lost, (ii) the available description is not detailed enough for future taxonomic comparisons, especially with the remaining populations in Peninsular India, and (iii) the clarification of the taxonomic status of the nomen sensu Article 75.3.1 (ICZN, 1999) through neotype designation qualifies with all the conditions of Article 75.3 (ICZN, 1999). The herein designated neotype (NMSL 2022.03.01) is consistent with what is known of the former name-bearing type according to its original description sensu Article 75.3.5 (ICZN, 1999), and it is distinguishable from the other known Lycodon species


FIGURE 2 Current distribution showing the museum collection/personal observation/photographic evidence localities of Lycodon striatus sensu stricto in blue and green circles; and $L$. bicolor comb. nov. in red and yellow squares. The type locality of $C$. galathea ( $L$. striatus) shows in an open square. The localities of $L$. mackinnoni (now a junior synonym of $L$. bicolor comb. nov.) are marked with yellow squares. The symbols with dots in the middle represent the type locality of the respective species. Imprecise localities retrieved from historical publications are marked with a '?' symbol. The localities of genetic samples are marked with GenBank accession numbers.

FIGURE 3 (a) Boxplots showing the tail ratio of Lycodon striatus sensu lato in eastern India, central western Asia, and Sri Lanka; top, middle and bottom lines of the boxes indicate 75 th percentile, median and 25th percentile respectively. Principal component analysis (PCA) biplot of morphometric variation between the above three populations with (b1) combined sexes shows the morphological distinctiveness; (b2) the same base biplots with vectors associated with species clusters. Each point in b1 represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity. ED, eye diameter; ES, snout length; HL, head length; HW, head width; IO, interorbital width; PC, principal component; TL, tail length.

(Article 75.3.2, ICZN, 1999). In agreement with Article 75.3.6 (ICZN, 1999), the designated neotype was collected from the holotype's type locality. The neotype is already deposited at NMSL following Article 75.3.7 (ICZN, 1999), and we provide its description based on external characters (see Appendix S2), satisfying the requirements of Article 75.3.3 (ICZN, 1999). See Appendices S3-S6 for English translations of the historical species descriptions (including synonyms) that were originally written in languages other than English.

The Sri Lankan population of $L$. striatus sensu lato (i.e. L. s. sinhaleyus), including the designated neotype, is morphologically and genetically conspecific with L. striatus sensu stricto. Therefore, in accordance with the principle of priority sensu Article 23 of the Code (ICZN, 1999), we synonymize L. s. sinhaleyus with L. striatus. Based on current evidence, we thus consider L. striatus sensu stricto as a widely distributed species from central and eastern India (including some lower elevations of northern and northeastern India) to Sri Lanka.

## 3.4 | Taxonomy

### 3.4.1 | Lycodon striatus (Shaw, 1802) sensu stricto (Figures 1-5, S1-S3; Tables 1 and 2)

## Holotype (by monotypy)

An adult specimen of $\sim 356 \mathrm{~mm}$ SVL (now lost, probably a female due to its high ventral count, 74 fide Russell [1796:22]) collected from 'Vizagapatam' (now Visakhapatnam; $17^{\circ} 41^{\prime} 12.54^{\prime \prime} \mathrm{N}, \quad 83^{\circ} 13^{\prime} 06.53^{\prime \prime} \mathrm{E}$, datum $=$ WGS84; 169 m above sea level), Andhra Pradesh, India. The specimen was depicted by Russell (1796) on Plate 16 (see Figure S2A).

## Diagnosis (redefined herein)

Lycodon striatus sensu stricto is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL of 355 mm ; a single
TABLE 2 Morphological, morphometric, and meristic characters of Lycodon striatus sensu stricto, L. bicolor comb. nov. including types (see Appendix S1 for accession data).

| Character | L. striatus sensu stricto |  |  | L. bicolor comb. nov. |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | India$(n=31)$ | Sri Lanka |  | Himalayas <br> Holotype of $L$. <br> mackinnoni NHMUK 1946.1.13.81 | Western Asia and Pakistan |  |
|  |  | Neotype of $L$. s. sinhaleyus NMSL 2022.03.01 | Other ( $n=12$ ) |  | Syntypes of $L$. bicolor ZISP 10006, 13 | Other ( $n=11$ ) |
| Snout-vent length | 110.0-312.0 | 282.0 | 134.0-304.0 | 309.0 | 190.0, 300.0 | 117.0-386.0 |
| Tail length (TL) | 25.0-65.0 | 37.0 | 25.0-63.0 | -- | 40.0, 60.0 | 48.0-83.0 |
| TL/total length \% in males | $15.2-17.8(n=12)$ | -- | 18.5-18.6 $(n=5)$ | -- | -- | 20.1-22.2 $(n=4)$ |
| Head length | 8.5-13.3 | 10.3 | 10.1-13.2 | 10.4 | - | 9.2-13.3 |
| Head width | 5.4-7.5 | 5.7 | 5.5-7.2 | 6.1 | - | 5.3-6.9 |
| Interorbital width | 3.1-3.9 | 3.9 | 2.9-4.0 | 3.4 | - | 3.3-4.3 |
| Snout length | 3.3-4.4 | 2.9 | 3.0-3.7 | 2.6 | - | 3.4-4.9 |
| Eye diameter | 1.5-2.0 | 1.6 | 1.5-1.8 | 1.2 | - | 1.5-2.2 |
| Ventrals | 161-184 | 161 | 142-163 | 185 | 185, 186 | 176-192 |
| Subcaudals | 41-51 | 38 | 33-45 | 54 | 65, 65 | 51-67 |
| Temporals | $2+2$ | $2+2$ |  | $2+2$ | $2+2$ |  |
| Supralabials | 8 | 8 |  | 8 | 8 |  |
| Infralabials | 9 | 8 |  | 9 | 9 |  |
| Preocular | 1 | 1 |  | 1 | 1 |  |
| Postocular | 2 | 2 |  | 2 | 2 |  |
| Loreal | 1 | 1 |  | 1 | 1 |  |
| Clear bands on the dorsum | 12-16 | 8-12 |  | 20 | above 20 |  |
| White collar on the nape (in subadults) | Distinct | Indistinct |  | Indistinct | Distinct |  |

Abbreviation: --, not measured/not applicable.
TABLE 3 Main characters of the Lycodon species with 17 DSR (L. aulicus group) at midbody recorded in India and Sri Lanka.

| Species (distribution) | Maxillary teeth | Sup | Anal | Ventrals | Subcaudals | Preocular <br> \& frontal | Head | Collar mark | Scales between 1st cross mark \& parietal | Dorsal colouration of adults |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L. aulicus s.l. (SW India \& Sri Lanka) | 16 | 9 | d | 180-215 | 57-78 | c | wl | p | 16-26 | Dark blackish-brown/creamy white crossbars |
| L. bicolor comb. nov. (Pakistan to SE of Caspian Sea) | 12, 13 | 8 | d | 176-192 | 51-67 | s | ns | p | 12-14 | Reddish-brown/white striated crossbars |
| L. bicolor comb. nov. (Uttarakhand, ' $L$. mackinnoni') | ? | 7,8 | d | 162-187 | 48-57 | s | ns | a | 12-14 | Dark brown/yellow striated cross marks |
| L. carinatus (Sri Lanka) | 15 | 8,9 | e | 188-193 | 53-60 | s | wl | p | 23-25 | Black/white serrated crossbars |
| L. deccanensis (SC India) | ? | 9, 10 | e | 181-214 | 66-78 | s | ns | p | 12-14 | Brown/white crossbars |
| L. fasciatus (NE India \& Myanmar) | 11 | 8,9 | e | 182-220 | 62-79 | S | wl | p | 12-14 | Dark brown/pale brownish white crossbars |
| L. fasciolatus (East India \& Sri Lanka) | ? | 9 | d | 174-204 | 60-73 | S, c | ns | a | 7-10 | Reddish-brown/creamy yellow crossbars |
| L. flavicollis (SW India) | ? | 8,9 | d | 210-224 | 65-74 | c | ns | p | - | Uniform light brown/no crossbars |
| L. flavomaculatus (NW India) | ? | 9 | d | 165-183 | 55 | s | ns | p | 12-14 | Dark brown or black/yellow spotted cross marks |
| L. gammiei (NE India \& Bhutan) | ? | 7-9 | ? | 205-220 | 98-111 | s | ns | p | 12-14 | Dark brown/brownish-yellow crossbars |
| L. hypsirhinoides (Andaman) | ? | 9 | d | 188-213 | 61-75 | c | wl | a | - | Uniform dark brown/no crossbars |
| L. jara (NE India) | ? | 8 | d | 167-188 | 52-76 | s | ns | p | - | Glossy greenish-purple/yellow spots |
| L. laoensis s.s. (Laos) | ? | 9 | d | 163-187 | 60-76 | c | ns | p | 21-25 | Dark brown/white or yellow crossbars |
| L. septentrionalis (east Himalayas) | 8 | 8 | e | 207-217 | 81-92 | s | ns | p | 28-32 | Purplish-black/white crossbars |
| L. striatus s.str. (central \& east India) | 9 | 8 | d | 161-184 | 41-51 | s | ns | p | 18-20 | Blackish-brown/white striated crossbars |
| L. striatus (Sri Lanka \& south India) | 13 | 7,8 | d | 142-165 | 33-45 | s | ns | p | 16-18 | Blackish-brown/white crossbars |
| L. subcinctus s. str. (Java) | 8-14 | 8 | d | 208-227 | 62-89 | - | wl | p | 27-30 | Black/white crossbars |
| L. tiwarii (Nicobar) | ? | 9 | d | 218-234 | 60-94 | c | wl | p | - | Uniform brown/no crossbars |
| L. travancoricus(SW India) | ? | 8, 9 | e | 168-206 | 54-73 | c | wl | p | 17-23 | Dark purplish-brown/faint cream crossbars |
| L. zawi (NE India \& Myanmar) | ? | 8,9 | d | 179-207 | 45-75 | s, c | wl | a | 23-25 | Dark brown/narrow white crossbars |

Note: Exceptional values are placed in parentheses.
Abbreviations: -, not applicable; ?, unknown; a, absent; c, in contact; d, divided; e, entire; NE, northeast; ns, narrow and small; NW, northwest; p, present; s, separated; SC, south-central; SE, southeast; SW, southwest; wl, wide \& large.


FIGURE 4 Live photographs of L. bicolor comb. nov. from (a) Chanor, Tajikistan, and (b) Sanghar, Khyber Pakhtunkhwa, Pakistan; L. striatus from (c) Jabalpur, Central India and (d) Homagama, Colombo, Sri Lanka. Photographs by AB, DJ, VRS, and SKB.
preocular, not reaching frontal; two postoculars; a single elongate loreal scale, in contact with internasal but not in contact with eye; prefrontal not reaching postnasal but in contact with supraocular; divided cloacal plate; divided nasal scale, with anterior nasal slightly larger than posterior; ventrals 142-178 $(n=21)$ in males and 149-178 $(n=12)$ in females; undivided subcaudals $33-51(n=33)$ in both males and females combined; temporals $1+2$ or $2+2$; eight supralabials with 3 rd- 5 th in contact with eye; dorsal scale rows $17-17-15$; tail length $15.2 \%-18.6 \%$ of total length in males; dark brown or black dorsum with around 8-16 clearly visibly white striated bands along the body with posterior bands vaguely diffuse, compared to the anterior bands, in both sexes; and collar band more prominent in Sri Lankan population compared to the Indian population.

## Redescription of the species (see Appendix S2)

## Skull and dentition

A complete and robust skull displays a general colubrid pattern (Figure 5); premaxilla single, round anteriorly, with a broad ascending process, a flat nasal crest, and a relatively long transverse process; nasals elongate, triangular, lateral processes tapering anteriorly to form a blunt process, but slightly bifurcates at the point of articulation with the ascending process; and parietals rough, anterior process curved backward. The anterior maxillary teeth (three) and posterior maxillary teeth (six) are separated by a diastema equal or greater in length to the longest
anterior maxillary tooth; among the posterior maxillary teeth, posterior most teeth (two) are enlarged; palatine with 10 teeth; pterygoid with 14 or 15 teeth and mandible with a total of 16 or 17 teeth separated by a narrow diastema with anteriorly four enlarged teeth and posteriorly 12 or 13 teeth.

## Hemipenis (based on Figure S3)

The organ is single and bulbous in shape, relatively long, robust and non-capitate. The inverted hemipenis extends to 13th subcaudal level; the simple oblique sulcus spermaticus shallow and centripetal extends directly to apex; lobes blunt, apical lobe less evident; acalyculate organ with a specialized ornamentation forms spines on the proximal portion of the hemipenis greatly enlarged with basal hooks; spines on the upper basal areas enlarged and decreasing the size slightly towards the proximal portion; the lobe is spinose on both the sulcate and asulcate surfaces; apical region not separated from the basal portion and apical part of the hemipenis is spinose; and sulcate and asulcate expansion pleat naked.

## Distribution

Lycodon striatus sensu stricto is distributed in Sri Lanka, southern and eastern India up to Nepal (Karunarathna et al., 2010; Karunarathna \& Amarasinghe, 2011, 2012; Lohani et al., 2022; Mohapatra et al., 2021; Pandey et al., 2018; Rawat et al., 2020) and some parts of Central India (Figure 2), including northern parts of Andhra Pradesh, Odisha, West Bengal, Bihar, Jharkhand,


FIGURE 5 Dorsal, lateral and ventral skull views $(s c a l e=5 \mathrm{~mm})$ and the maxilla (scale $=1 \mathrm{~mm})$ of $(\mathrm{a})$ a voucher of $L$. striatus sensu stricto from India (NHMUK 1882.8.26.20), (b) a voucher of L. bicolor comb. nov. (NHMUK 1891.10.6.39) from 'Transcaspia' and (c) a voucher of $L$. striatus from Sri Lanka (NHMUK 1905.3.25.96). Some of the maxillary teeth on the lateral view are not visible due to the old age of the specimen, decalcification or an artefact of the scan. Note the distinct differences between the parietal and its anterior curved process, premaxilla, ascending process of nasals and maxillary teeth.

Chhattisgarh and eastern parts of Madhya Pradesh. In addition, the populations in the eastern parts of Rajasthan, Gujarat and Maharashtra states and western Madhya Pradesh might also represent the same species. Based on the reliable localities for this species (at least from photographic evidence), it occurs in a wide range of habitats including open canopy, secondary deciduous forests, scrublands, grasslands, home gardens and cultivated habitats below 600 m above sea level. Lycodon striatus sensu stricto has been reported as widespread (partly in Daniel, 2002; Das, 2002; Das \& de Silva, 2005; Deraniyagala, 1955; De Silva, 1969, 1980; Somaweera, 2006; Whitaker \& Captain, 2004) and as a human commensal species. Our observations revealed that $L$. striatus sensu stricto has a robust distribution in eastern Peninsular India, covering the northern part of the Eastern Ghats, parts of the Chota Nagpur Plateau, Brahmaputra Basin and Indo Gangetic Plateau. The species is also known from the foothills of western Himalaya to the mangrove swamps of Circar Coast and the Sal Forests of Chota Nagpur Plateau. It is also widespread and scattered across (i) the Terai
landscape covering northern Uttar Pradesh, (ii) NagpurSeoni Hills (in eastern Maharashtra / southern Madhya Pradesh) and (iii) Chota Nagpur Plateau (in western Orissa, southern Jharkhand and Chattisgarh). The range of this species covers the western Himalayan foothills near Ludhiana up to Visakhapatnam (here we restrict the type locality) of the Circar Coast, in the southeast. Within its range, we have failed to observe this species from Kanpur in Terai or close to the Maredumilli Hills in the Eastern Ghats. Additionally, although there have been reports of sightings from other outlying areas such as Bangladesh, the region south of Khasi Hills (Shillong) and the east of Manipur, and Chindwin River of Myanmar, these reports are most probably misidentifications of some other lookalike species, e.g. L. septentrionalis.

Our observations also revealed low-altitudinal areas in southern India and Sri Lanka as potential distribution envelope. It is evident that these areas have low-to-moderate rainfall conditions. Most of the specimens were recorded from the lower peneplain between the southern parts of the Coromandel Coast and the Eastern Ghats across the Kaveri


FIGURE 6 Colouration variability of Lycodon bicolor comb. nov. may relate to the variety of habitats along the gradient of elevation (clinal variation). The four colour morphs so far identified within its distribution range are as follows: (a) typical morph; (b) Pakistani morph; (c) Mackinnon's morph and (d) Sindh morph; Illustration by A.A.T. Amarasinghe.

River tracts and delta. The westernmost record locality is from the Davengere/Shivamogga regions. It seems that the Palk Strait separating the Indian Peninsula and Sri Lanka is not a barrier as this species can be found on both sides of the strait. In Sri Lanka, most of the specimens are reported from the southwestern lowland and are less frequently reported in the lowland dry zone. The montane regions of the Western Ghats in India and the highlands of Sri Lanka were recognized as unsuitable areas for this species.

## Natural history

Although Lycodon striatus sensu stricto is a non-venomous species, it is mostly found at twilight or the onset of nightfall. It is a crepuscular and terrestrial species, but not as good at climbing when compared to its congeners. During the mid-day heat, it is often found hidden under leaf litter, fallen logs, loose soil mounds, wall crevices and piles of rubble (de Silva, 2009). It is oviparous and females lay two to five eggs at a time (De Silva, 1969). Eggs are elongate, $25-30 \mathrm{~mm}$ long and $10-12 \mathrm{~mm}$ wide (Wall, 1921). De Silva (1969) collected two gravid females in May and June, and both had three eggs each. Diet includes small tetrapod reptiles such as skinks (e.g. Lankascincus sp. and juvenile Eutropis sp.), geckos and lacertid lizards (Seshadri, 2017) and we once observed cannibalism, probably of its own weak hatchlings. Compared to the abundance of other wolf snakes, it is a common species in India and relatively less abundant in Sri Lanka. It is less defensive in nature when disturbed, preferring to coil the body and hide the head within the coils formed. Tail vibration (not tail twitching to attract prey) has been observed as a defensive response. Somaweera (2005) reported a Hemidactylus leschenaultii gecko preying on L. striatus. Due to their
higher abundance around human settlements, domestic cats have been identified as a major threat to this species (Amarasinghe, personal observation). In addition, data collected from social media platforms in Sri Lanka reveal that it is one of the top five species often killed by humans due to misidentification. The presence of cross bands is frequently the reason this harmless colubrid gets misidentified as the highly venomous elapid krait (Bungarus sp.). In both South India and Sri Lanka, this species has been regularly listed in snake rescue projects and vehicular traffic mortalities (Karunarathna et al., 2013).

## Lycodon bicolor (Nikolsky, 1903) comb. nov. (Figures 1-5, S1, S2, Tables 1-3.)

## Syntypes

Adult female, ZISP 10013, SVL 300 mm , collected from Kulkulab, Transcaspia (Kurkulab; $38^{\circ} 21^{\prime} 13.83^{\prime \prime} \mathrm{N}$, $57^{\circ} 23^{\prime} 16.08^{\prime \prime} \mathrm{E}$, datum = WGS84; 280 m above sea level), Turkmenistan, by Bilkewitsch in 1902 (the head is damaged and it has therefore been difficult to obtain several diagnostic characters); ZISP 10006, juvenile male, SVL 190 mm, collected from 'Eastern Persia' (eastern Iran), by N.A. Zarudny in 1901.

### 3.4.2 | Diagnosis

Lycodon bicolor comb. nov. is distinguished from other congeners by having the following combination of characters: adults reaching a maximum SVL of 386 mm ; a single preocular, not reaching frontal; two postoculars; a
single elongate loreal scale, in contact with internasal but not in contact with eye; prefrontal not reaching postnasal but in contact with supraocular; divided cloacal plate; divided nasal scale, anterior nasal twice as large as posterior nasal; ventrals 178-181 $(n=6)$ in males and 186-192 ( $n=3$ ) in females; undivided subcaudals 51-67 ( $n=9$ ) in both males and females combined; temporals $2+2$; eight supralabials with 3rd-5th in contact with eye; dorsal scale rows $17-17-15$; tail length $20.1 \%-22.2 \%$ of total length in males ( $n=6$ ); bronze brown dorsum with over 20 clearly visible white striated bands along the body with posterior bands vague compared to the anterior bands in both sexes; and collar band prominent.

## Redescription of the species (see Appendix S2)

We have identified four morphs of colouration in adults of this species:
(i) the typical morph (Figure 6a) has over 20 clearly visible striated crossbars on the body, including a very distinct collar band on the nape; the anterior crossbars are arranged comparatively with a wider distance between each other, and the posterior crossbars (nearly half of the body length) are highly striated and diffused. The yellow markings on the mid-crossbars are bright golden yellow. We report this colouration morph as the 'typical morph', and this morph is mostly distributed in the drier and mid-elevated area of western Central Asia;
(ii) the eastern Pakistani population (Figure 6b) has over 30 clearly visible striated crossbars on the body including a very distinct collar band on nape; the anterior crossbars are arranged comparatively with the narrow distance between each other and the posterior crossbars (nearly one-third of the body length) are moderately striated and diffused. The yellow markings on the mid-crossbars are bright yellow. We report this morph of coloration as the 'Pakistani morph', and this morph is mostly distributed in the cold, high-elevated area of the Himalayas region in eastern Pakistan;
(iii)the northwest Indian population along the western Himalayas (Figure 6c) has irregular striated crossbars on the body and no collar band on nape; the anterior crossbars are arranged with a very narrow distance between each other and the posterior crossbars (nearly three-fourths of the body length) are highly striated and diffused. The yellow markings on the mid-crossbars are yellowish-orange. We report this colouration morph as the 'Mackinnon's morph', and this morph is mostly distributed in the cold mid- to the high-elevated area of the western Himalayas region in north-western India;
(iv) the western and southern Pakistani population (Figure 6d) has over 20 clearly visible striated crossbars on the body including a very distinct collar band on nape; the anterior crossbars are arranged comparatively with a very wide distance between each other and the posterior crossbars (nearly one-third of body length) are moderately striated and diffused. The yellow markings on the mid-crossbars are pale-to-bright yellow. We report this morph of colouration as the 'Sindh morph', and this morph is mostly distributed in the drier and low-elevated areas of southern and western Pakistan.

## Skull and dentition

Based on the syntype (ZISP 10006) and NHMUK 1891.10.6.39 from 'Transcaspia' (Figure 5), a complete and robust skull displaying a general colubrid pattern; premaxilla single, flat anteriorly, with a broad ascending process, a flat nasal crest and a relatively short transverse process; nasals short, trapezoid, lateral processes tapering anteriorly to form a pointed process, but bifurcates at the point of articulation with the ascending process; parietals smooth, anterior process curved and slightly pointed forward in between frontals. The anterior maxillary teeth (four or five) and posterior maxillary teeth (eight or nine) are separated by a diastema equal or greater in length to the longest anterior maxillary tooth; among the posterior maxillary teeth, posterior most teeth (two) are enlarged; palatine with 10 teeth; pterygoid with $11-13$ teeth and mandible with a total of 16-18 teeth separated by a diastema with four enlarged teeth anteriorly and 10-14 teeth posteriorly.

## Distribution

Based on both of its syntypes, we restrict the type locality of Lycodon bicolor comb. nov. to the bordering region of eastern Iran and Turkmenistan, and more precisely restrict it to Kulkulab (Kurkulab) in Turkmenistan based on the adult female syntype, ZISP 10013. Lycodon bicolor comb. nov. has been known as $L$. striatus (sensu lato) from the Central Asia region even before its description in 1903 (see Boulenger, 1891). The subsequent authors (Chernov, 1935; Leviton \& Anderson, 1970; Minton, 1966; Terentjev \& Chernov, 1949) reported this species from the south-western parts of Central Asia (Figure 2) including the eastern and north-eastern Iran, Uzbekistan (exclusive of the Republic of Karakalpakstan) north to the Chirchik (Chirchiq) River, western Tajikistan and from Balochistan (Pakistan; see Orlov et al., 2018; Sindaco et al., 2013). There are three more specimens in the ZISP collections: (i) ZISP 6909, donated by Grum-Grmzhimailo from Dzhilyantau (Baldzhuan in Tajikistan) in the 1880s during the last
century; (ii) ZISP 10160, collected by E. Fiippovich from the environment of Astrabad (Gorgan in Iran); and (iii) ZISP 12447, collected in 1928 from the vicinity of Termez (southern Uzbekistan) by the staff of Prof. E. Pavlovsky during the Central Asian Expedition. In 1934, A. Gvozdev, G. Georgievsky and one of the authors of this work (N.B. Ananjeva) found live individuals from Gissar Valley in Tajikistan during the Parasitological expedition of the Tajik base of the Academy of Sciences of the USSR.

However, the species has not been reported from Afghanistan except from the Seistan Basin on the AfghanIranian border (Leviton \& Anderson, 1970) and the border areas of Waziristan in Pakistan (Ingoldby, 1923; Khan, 2006). Khan (2006) also reported the species from southern and north-eastern Pakistan based on museum collections and field observations. Based on the reliable observations and localities for that species (resulting from observations with photographic evidence), it seems to be a common, widespread and human commensal snake occurring in both hot dry plains and deserts as well as mountains at elevations up to 2000 m average sea level (Jablonski, personal observation). Szczerbak (2003) suggests the species also resides in rocky areas with scant semi-desert vegetation and mountains. Khan (2006) collected the species in cultivated land as well as open fields with sparse bushes in mesic habitats. As the nomen L. mackinnoni is now synonymized with $L$. bicolor comb. nov., its distribution also includes the foothills of the Himalayas in the Indian territory, Shiwaliks (Nawani et al., 2021).

## Natural history

Minton (1966) observed the species in agricultural lands, desert scrubs and in oases during humid evenings and after rain. Breeding occurs in early months of the year and females lay four eggs measuring 25$28 \mathrm{~mm} \times 9-11 \mathrm{~mm}$ (Minton, 1966), or between two to four eggs $26-30 \mathrm{~mm} \times 9-10 \mathrm{~mm}$ in size at the end of June or in July (Szczerbak, 2003). Khan (2006) mentioned four to eight eggs hatched within a month. According to Szczerbak (2003), this species feeds on small lizards. We observed this species in Tajikistan and Pakistan mostly during wet nights (after 9 p.m.), after or during a drizzle. For information from Indian populations, see Nawani et al. (2021).

## 4 | DISCUSSION

## 4.1 | The taxonomic confusion of Lycodon striatus

The taxonomy and nomenclature of Lycodon striatus sensu lato has long been neglected due to the
unavailability of molecular data as well as the limited number of specimens available in museum collections. Shaw's original description in 1802 went unnoticed when Daudin (1803) described Coluber malignus based on the same specimens depicted by Russell (1796; page 22 and plate 16). Daudin's second species, C. galathea, is also barely discernible from L. striatus, although the type materials originated from two different biogeographic regions, 'Vizagapatam' (Coromandel Coast) and Hyderabad (Deccan Plateau) respectively. However, C. galathea has not been recognized by subsequent authors (e.g. Cantor, 1847; Günther, 1858) and the later treatises clarified the situation (e.g. Boulenger, 1890, 1893; Günther, 1864). Theobald (1876) did not mention the type locality of L. striatus and grossly stated 'Coromandel' as the distribution of the species, as did Murray (1884). Owing to the lack of specimens from Southern India in the Indian Museum, Sclater (1891) erroneously assumed that L. travancoricus might entirely replace L. striatus in Southern India. Boulenger (1893) reported this species from Russelconda (=Odisha, India) although not from 'Hyderabad', India. Although Wall (1909) summarized the distribution throughout its range, Barbour (1912) incorrectly listed L. striatus among the Southeast Asian fauna. Constable (1949) misquoted both Vizagapatam and Hyderabad as type localities, considering C. galathea as a junior synonym.

Ferguson (1877) first listed L. striatus from Sri Lanka but considered it a variety of L. aulicus. The renowned entomologist Edward Ernest Green (1861-1949) recorded L. striatus from Sri Lanka with a confirmation of an eleven and half inch specimen captured from a termite mound (Green, 1904). Prior to that, Jan (1863) mentioned the Sri Lankan population as $L$. napei. Our attempts to trace any Lycodon specimens that Giorgio Jan (1791-1866) referred to from the Naturhistorisches Museum Basel and Museo Civico di Storia Naturale di Milano failed. Jerdon (1854) and Beddome (1862) failed to provide any clarification under which nomen they referred the Sri Lankan population of L. striatus sensu lato. Günther (1863) reported that R. H. Beddome collected this species in the Anamallay Mountains, in the Southern Western Ghats, India. Although Deraniyagala (1955) clearly designated a single type (holotype by monotypy) of $L$. striatus sinhaleyus and assigned the western and central populations to this trinomen, he did not mention the status of the dry zone population of Sri Lankan L. striatus, he probably was not aware of its distribution in the eastern and northern parts of the island. There are several examples that some of the other reptile type specimens mentioned by Deraniyagala $(1953,1955)$ were believed to have been deposited in the NMSL and then subsequently considered lost; however, Deraniyagala had already deposited
them at the NHMUK (similarly Cnemaspis podihuna, see Amarasinghe \& Campbell, 2016; Hemidactylus hunae, see Amarasinghe et al., 2021). However, there is no evidence that the holotype of L. s. sinhaleyus has ever been deposited at NHMUK. Deraniyagala (1955) provided pholidosis for four specimens (including the holotype), but after an extensive search of Deraniyagala's entire snake collection at the NMSL and the NHMUK, we were unable to find any of these specimens. Therefore, we are forced to conclude that the holotype of $L$. s. sinhaleyus is lost or destroyed. Annandale (1906) first reported on the similarity between the populations from Tamil Nadu and Sri Lanka, when he remarked that the snake he found from 'Pamben' (=Pamban, Rameswaram) was 'practically identical' to Green's (1904) description from Sri Lanka.

## 4.2 | A land bridge dispersion of Lycodon striatus to Sri Lanka?

Although Indian and Sri Lankan populations are conspecific, some body characteristics (e.g. number of subcaudals) of Sri Lankan populations are slightly different from the typical form of the eastern Indian populations. This is likely due to the biogeographical isolation of the Sri Lankan population though having genetically shallow divergence (although only mtDNA) between those populations. Probably, the Sri Lankan population is yet to be evolved to the species level. Although several recent studies emphasized the importance of biogeography in shaping the cryptic diversity among 'similarlooking' snake species in eastern India in contrast to Sri Lanka, e.g. Oligodon russelius vs. O. arnensis (see Bandara et al., 2022) and Fowlea piscator vs. F. unicolor (see Amarasinghe, et al., 2022), we are not confident enough to consider L. s. striatus and L. s. sinhaleyus as two distinct species.

The phylogeny of the $L$. aulicus group hints at the Sri Lankan L. striatus as likely having been evolved in continental Asia through a probable overland dispersal across the Bay of Bengal (present Palk Strait) onto the island. Multiple dispersal events probably occurring over a land bridge into Sri Lanka gave rise to the Sri Lankan members (L. striatus and L. aulicus) in this group. This dispersal could have been facilitated by low sea levels during the Pleistocene when the island was connected to mainland India (Voris, 2000). This is evident from the phylogenetic position and genetic distances of lineages represented by L. striatus sensu stricto and 'sinhaleyus' populations being very low compared to other taxa in the genus. Interestingly, the Sri Lankan populations have a shallow genetic distance from eastern and central Indian populations compared to southwest Indian populations,
and it hints at probable multiple dispersal events from the southern part of the Western Ghats into the west zone of Sri Lanka and again into the Eastern Ghats via the island's dry zone. Several researchers on the reptile fauna highlighted the possibility of Pleistocene dispersion to Sri Lanka from the Indian subcontinent (e.g. Mallik et al., 2020; Amarasinghe, Karunarathna, et al., 2022). Therefore, such a pattern of shallow divergence is rather surprising as Sri Lanka is considered as having one of the most phylogenetically diverse and unique island snake faunas in the world (Pyron et al., 2013).

The basal lineage of the $L$. aulicus group points to $L$. jara, which is a species from south-eastern Asia, as the possible centrum of the genus' evolution, a predicted scenario yet to be tested with emphasis on the diversification on a temporal scale (like in Pyron et al., 2013; Siler et al., 2013) after incorporation of autosomal DNA analysis of widely distributed $L$. aulicus from throughout its range. It is still preliminary but it could be hypothesized that the lineage of $L$. striatus sensu lato (in the sense of morphology) evolved in southeast Asia (probably Myanmar) and dispersed along the Himalayan foothills (Shiwaliks) towards central and western Asia (see similar patterns of evolution and dispersion in other groups of amphibians or reptiles in Agarwal et al., 2022; Dufresnes et al., 2022; Jablonski et al., 2021, 2022). The other lineage seems to have dispersed towards Sri Lanka, through the lower peneplains (0-500) of central and eastern India and evidently evolved as L. deccanensis and L. striatus. However, it does not explain why L. striatus is less abundant in the highly biodiverse Western Ghats in India, while it is distributed in both the wet and dry zones of Sri Lanka. A possible explanation for this might be niche competition with a cortege of congeners that are more affiliated to elevated landscapes in the Western Ghats - such as L. travancoricus, L.flavicollis and L. deccanensis. Whereas in Sri Lanka, this role is solely played by $L$. carinatus, confined to the mid-elevations of the southwestern wet zone of the island. Therefore, a similar pattern of varied biogeographic histories can be constructed for L. striatus in western India, especially in the north-western part of India and isolated or cryptic populations that may still exist. However, this requires additional field explorations.

## 4.3 | Range, clinal variation and dispersal of Lycodon bicolor into Central Asia

Although Nawani et al. (2021) correctly presented that the lineage representing L. mackinnoni is different from L. striatus sensu stricto, missing comparative material from Pakistan and Central Asia prevented the authors
from showing that this Indian taxon is the junior synonym of L. bicolor comb. nov. In recent times, Manhas et al. (2015), Faiz et al. (2018) and Jablonski et al. (2019) reported L. bicolor comb. nov. as L. mackinnoni from the Azad Kashmir Province in north-eastern Pakistan. Our results suggest that $L$. bicolor comb. nov. is conspecific with $L$. mackinnoni and most probably with all populations of this species through Pakistan, Iran, Tajikistan and Central Asia (Figure 2). It was Boulenger (1891) who first reported on Boettger's collection of L. striatus sensu lato from Transcaspia (NMHUK 1891.10.6.39), remarking with great interest on the occurrence of the species from the far west. Boulenger (1893) reported this species from Puli Hatun, Transcaspia and 'Kurrachee' (=Karachi, Pakistan), which all now refer to the Central Asian member of $L$. striatus sensu lato, $L$. bicolor comb. nov. Ingoldby (1923) reported a species from Waziristan (north-eastern Pakistan) at 3500-5000 feet elevation with $32-35$ cross bands between its head and tail base (also see Smith, 1943), which evidently refer to L. bicolor comb. nov. Khan (2006) reported L. aulicus, L. s. striatus and $L$. s. bicolor from Pakistan, supplemented by photographic evidence. However, the presented distribution pattern suggests that the identification of some of these snakes was not correct and we can thus expect that some of the records of $L$. aulicus may represent $L$. bicolor comb. nov., especially those from the Palearctic part of the country. Hypothetically, the Indus River may form a natural distribution barrier between $L$. aulicus and L. bicolor comb. nov., a scenario that should be resolved through improved sampling from Pakistan and India in the future. A similar distribution pattern was recently reported for amphibians (Euphlyctis: Dufresnes et al., 2022) and lizards (Calotes: Gowande et al., 2021), so we can also expect similar parallels in snakes. Thus, some of the current records of L. bicolor comb. nov. from Sindh Province in southern Pakistan should be taken with caution as they could refer to L. aulicus. However, we evidently report the existence of true L. bicolor from southern Pakistan with slight morphological variation (Figure 6). On the other hand, we can move the eastern range border of $L$. bicolor comb. nov. further to northern India where the species range corresponds to the Shiwalik mountains and meets the range of $L$. striatus in Uttarakhand (Figures 5 and 6). This is because $L$. mackinnoni, a similar-looking highland congener mentioned from north-eastern Pakistan and northern Indian regions (Nawani et al., 2021) indeed represents a clinal variation in L. bicolor comb. nov. (Figure 6). Populations of $L$. bicolor comb. nov. (including L. mackinnoni) are different in body colouration (e.g. having a collar band with clear anterior bands with wider distances vs. completely absent in L. mackinnoni), however, the pholidosis
of $L$. bicolor comb. nov. in Turkmenistan has no distinct variation compared to the $L$. mackinnoni in the western Himalayas (Table 2). Thus, we conclude that this is a case of clinal variation probably due to the varied environment and various habitats along the gradient of elevation, a phenomenon also seen in other snake species in the region (e.g. Oligodon russelius; see Bandara et al., 2022).

The taxonomy and distribution patterns resulting from our analyses are not as surprising as they may first seem. Although we cannot exactly define the range borders among L. aulicus, L. striatus and L. bicolor comb. nov. in the northern part of the Indian subcontinent (Figures 5 and 6), several recent studies showed that this region is a meeting point of different evolutionary lineages among closely related reptile species (e.g. Agarwal et al., 2022; Gowande et al., 2021). We can thus expect that contact borders between these Lycodon species could be related to this area. Moreover, we can deduce that, like the genera Calotes or Eublepharis, Lycodon could colonize central Asia from the Indian subcontinent following plains, semi-deserts, or river valleys up to the north and across to the west. It is most probable that rapid colonization was affected by suitable local environmental conditions in the past which changed later. This could be the reason why the current range in Central Asia seems interrupted (see Sindaco et al., 2013), whereas populations considered as L. mackinnoni (now Mackinnon's morph) appear to be uncommon and restricted to limited areas of the Himalayan foothills (Shiwaliks) mostly above 800 m elevations (Faiz et al., 2018; Nawani et al., 2021). Lycodon bicolor comb. nov. (Pakistani morph) in western parts of its range is a common species distributed at middle and lower elevations below 2000 m (Figures 5 and 6). Similarly, several studies highlighted that the same species is distributed throughout both ranges of the lower peneplains of central Western Asia and Western Himalayas, e.g. the Asian cobras, Naja oxiana (Kazemi et al., 2021). Thus, it would be interesting to study environmental variables affecting species distribution of L. bicolor comb. nov. in this part of Asia together with the unstudied level of genetic variability and so far unknown past refugial areas.

## 5 | CONCLUSIONS

The $L$. aulicus group is now recognized by 16 distinct taxa (Figure 1, Table 3) inhabiting three discrete regions in Asia, which emphasizes how biogeography shapes cryptic diversity among 'similar-looking' snake species. Among these taxa, the members with striated (barred) body colouration (L. striatus complex) represent two distinct clusters (and
clades): (i) L. striatus - eastern and central India and, particularly in this case, towards south India and Sri Lanka; and (ii) L. bicolor - northwest India, West Himalayas, towards Central Asia. Although our study revealed the existence of two distinct species of striated (barred) wolf snakes within Peninsular India, isolated or cryptic populations may still exist, especially in south-western India but this requires additional field explorations to uncover them. Therefore, we leave this task for future taxonomists to reevaluate the inter-population distinctions using genomic and wealthier morphometric datasets.

## AUTHOR CONTRIBUTIONS

Amarasinghe A. Thasun Amarasinghe, Gernot Vogel, and Daniel Jablonski designed the study and its concept. Material preparation, data collection, and analysis were performed by all authors. The first draft of this manuscript was prepared by Amarasinghe A. Thasun Amarasinghe. All authors commented on and improved particular versions of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

 The authors declare that they have no conflict of interest.
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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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# Integrative approach resolves the systematics of barred wolf snakes in Lycodon striatus complex (Reptilia: Colubridae) 

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Figure S1. The molecular phylogeny of the members of the genus Lycodon (mitochondrial cytochrome $b$ gene) using a Bayesian Inference.


Figure S2. Illustrations of several historical specimens: (A) the holotype of Coluber striatus Shaw, 1802 (depicted by Russell 1796: Plate 16, resized); (B) the syntype of C. galathea Daudin, 1803 (depicted by Russell 1796: Plate 26, resized); (C) a voucher of Contia bicolor Nikolsky, 1903 (depicted by Nikolsky 1916: Plate 4, resized); and (D) the neotype of Lycodon striatus sinhaleyus Deraniyagala, 1955 (illustration by AATA).


Figure S3. Sulcate view of the fully erected left hemipenis (in situ) of Lycodon striatus sensu stricto (road killed specimen after injecting ethanol) from (A) Jabalpur, Central India and (B) Rajagiriya, Sri Lanka. Photographs by VRS and AKAG.


Table S1. Locality data and sequence accession numbers of Lycodon species used in phylogenetic analysis.

| Species | Voucher Number | Sequence Location | Cyt b | Source |
| :---: | :---: | :---: | :---: | :---: |
| Ahaetulla nasuta | RAP0517 | Norton Bridge, Sri Lanka | KC347453 | Pyron et al. 2013 |
| Lycodon aulicus | - | Jabalpur, India | HQ735416 | Dubey et al. 2012 |
| L. bicolor | ZMMU- NAP11090 | Chanor, Magmurud District, Tajikistan | NAP11090 | This study |
| L. bicolor | CUHC9457 | Kanju, Khyber Pakhtunkhwa, Pakistan | OQ282987 | This study |
| L. bicolor | PMNH4249 | Dadar, Khyber Pakhtunkhwa, Pakistan | OQ282988 | This study |
| L. bicolor | CUHC11257 | Sanghar, Khyber PakhtunkhwaSindh, Pakistan | OQ282989 | This study |
| L. butleri | LSUHC8066 | Fraser's Hill, Malaysia | KC010352 | Siler et al. 2013 |
| L. butleri | LSUHC9136 | Bukit Larut, Malaysia | KC010353 | Siler et al. 2013 |
| L. cavernicolus | LSUHC9985 | Perak, Malaysia | KJ607889 | Grismer et al. 2014 |
| L. cavernicolus | - | Perak, Malaysia | KJ607890 | Grismer et al. 2014 |
| L. capucinus | LSUHC5725 | Pulau Rawa, Johor, West Malaysia | KC010355 | Siler et al. 2013 |
| L. carinatus | RAP0447 | Galle, Sri Lanka | KC347486 | Pyron et al. 2013 |
| L. deccanensis | BNHS3610 | Savandurga, India | MW006486 | Kalki et al. 2020 |
| L. deccanensis | NCBS-NRCAA-0010 | Savandurga, India | MW006487 | Kalki et al. 2020 |
| L. fasciatus | CAS234875 | Chin, Myanmar | KC010365 | Siler et al. 2013 |
| L. fasciatus | CAS234957 | Chin, Myanmar | KC010366 | Siler et al. 2013 |
| L. flavicollis | - | Devarayanadurga, India | MW006488 | Kalki et al. 2020 |
| L. gongshan | GP3516 | Yunnan, China | KP901022 | Guo et al. 2015 |
| L. gongshan | GP3548 | Yunnan, China | KP901026 | Guo et al. 2015 |
| L. jara | CAS235387 | Kachin, Myanmar | KC010367 | Siler et al. 2013 |
| L. laoensis | FMNH258659 | Salavan, Laos | KC010368 | Siler et al. 2013 |
| L. laoensis | LSUHC8481 | Pursat, Cambodia | KC010370 | Siler et al. 2013 |
| L. liuchengchaoi | DL14315 | China | KF732928 | Lei et al. 2014 |
| L. mackinnoni | ADR197 | Mussoorie, India | MW862977 | Nawani et al. 2021 |
| L. multizonatus | KIZ01623 | Luding, China | KF732926 | Lei et al. 2014 |
| L. ruhstrati | GP2243 | Guangdong, China | KC733208 | Guo et al. 2013 |
| L. ruhstrati | GP285 | Sichuan, China | KC733195 | Guo et al. 2013 |
| L. septentrionalis | CIB117521 | Tibet, China | MW353736 | Wang et al. 2021 |
| L. sidiki? | MZB5980 | Aceh, Sumatra, Indonesia | KX822583 | Direct submission |
| L. sinhaleyus | NMSL2022.03.01 | Rajagiriya, Colombo, Sri Lanka | ADS0494 | This study |
| L. striatus | - | Jharkhand, India | VRS0030 | This study |
| L. striatus | - | Madhya Pradesh, India | VRS0032 | This study |
| L. striatus | - | Savandurga, India | MW006489 | Kalki et al. 2020 |
| L. subcinctus | LSUHC5016 | West Malaysia | KC010382 | Siler et al. 2013 |
| L. synaptor | GP2188 | Yunnan, China | KC733204 | Guo et al. 2013 |
| L. synaptor | - | China | KP901020 | Guo et al. 2013 |
| L. yunnanensis? | KIZYPX46120 | China | MW111468 | Xu et al. 2021 |
| L. zawi | CAS239944 | Myanmar | KC010386 | Siler et al. 2013 |
| L. zawi | CAS210323 | Saigang, Myanmar | AF471040 | Lawson et al. 2005 |
| Oligodon chinensis | DL12672 | China | KF732930 | Lei et al. 2014 |
| Ptyas mucosa | CAS208434 | Mandalay, Myanmar | AF471054 | Lawson et al. 2005 |

Table S2. Uncorrected mean p-distance for the mitochondrial cytochrome $b$ gene calculated for species of Lycodon aulicus group.

| No | Lycodon species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| :--- | :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 1 | laoensis | 0 |  |  |  |  |  |  |  |  |  |
| 2 | carinatus | 11.9 | 0 |  |  |  |  |  |  |  |  |
| 3 | bicolor + mackinnoni | 14.5 | 13.9 | 0 |  |  |  |  |  |  |  |
| 4 | jara | 17.1 | 16.3 | 14.5 | 0 |  |  |  |  |  |  |
| 5 | deccanensis | 15.8 | 15.0 | 14.7 | 15.3 | 0 |  |  |  |  |  |
| 6 | striatus + sinhaleyus | 12.1 | 14.3 | 13.6 | 14.4 | 12.4 | 0 |  |  |  |  |
| 7 | capucinus | 16.6 | 15.2 | 17.4 | 16.8 | 16.6 | 15.8 | 0 |  |  |  |
| 8 | flavicolis | 15.8 | 15.4 | 14.7 | 16.1 | 14.8 | 13.3 | 11.4 | 0 |  |  |
| 9 | zawi | 16.3 | 14.8 | 14.8 | 15.7 | 15.2 | 13.7 | 13.6 | 11.6 | 0 |  |
| 10 | aulicus | 17.8 | 18.1 | 17.4 | 17.2 | 16.9 | 15.3 | 15.2 | 8.5 | 9.0 | 0 |

Table S3. Principal Component Analysis (PCA) and loadings for the Lycodon striatus sensu stricto from eastern India, western central Asia (now L. bicolor comb. nov.), and Lycodon sinhaleyus from Sri Lanka. Principal components (PC) 1 and 2 collectively explained $61.0 \%$ of variation. $\mathrm{TL}=$ tail length; $E D=$ eye diameter; $E S=$ snout length; HL = head length; $I O=$ Interorbital distance; and HW = head width.

| PCA variable | PC 1 | PC 2 | PC 3 | PC 4 | PC 5 | PC 6 |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| Standard deviation | 1.4526 | 1.2449 | 0.8517 | 0.7981 | 0.72731 | 0.67004 |
| Proportion of variance | 0.3517 | 0.2583 | 0.1209 | 0.1062 | 0.08816 | 0.07483 |
| Cumulative percentage\% | 35.2 | 61.0 | 73.1 | 83.7 | 92.5 | 100.0 |
| Loadings |  |  |  |  |  |  |
| TL.scale | 0.39061 | 0.3124 | -0.8137 | 0.0472 | -0.2911 | 0.0262 |
| ED.scale | -0.4833 | -0.3308 | -0.3792 | 0.0876 | 0.1336 | 0.6983 |
| ES.scale | -0.4765 | 0.3263 | -0.3244 | 0.0445 | 0.5829 | -0.4685 |
| HL.scale | -0.5281 | -0.1086 | -0.1052 | -0.4598 | -0.6319 | -0.2956 |
| IO.scale | -0.0354 | 0.6582 | 0.1808 | -0.5749 | 0.0995 | 0.4386 |
| HW.scale | -0.3266 | 0.4913 | 0.2120 | 0.6679 | -0.3851 | 0.1118 |

Appendix 1. Specimens examined
L. aulicus.—India: Andhra Pradesh: NHMUK 82.8.26.22; Assam: NHMUK 1908.5.23.15, ZSI 8940, 18559, 20850, 22448, 25519, 25532; Bihar: ZSI 25186; Karnataka: NHMUK 1921.6.15.3, 1955.1.3.11, ZSI 23435; Kerala: NHMUK 74.429.958, 1904.10.18.5, 1924.10.13.9, ZSI 24301, 13793; Madhya Pradesh: CAS 12263, FMNH 606447, ZSI 23974, 24064, 24280; Maharashtra: FMNH 8650, NHMUK 69.8.28.94, NHMW 37406.1-2, ZSI 22120, 22122, 22138-9, 22834-5, 23434, 26049; Odisha: ZSI 22773, 23980A-B, 25654, 25774; Sikkim: ZSI 16441, 18669; Rajasthan: ZMB 9956; Sikkim: ZSI 16441; Tamil Nadu: MCZ R3877, R4783, NHMUK 1936.1.3.4; Uttar Pradesh: SMF 324663, ZSI 21102, 24528; West Bengal: FMNH 161469, 165107-8, NHMW 14487.1, 14488, ZMB 1790-1, 1806, ZSI 19228, 22835, 22970, 23929-30, 23957, 24059-60, 24178, 24230, 26140-1; Bangladesh: ZSI 18578; Nepal: FMNH 62427, 83090, NHMUK 1936.7.2.2, 1984.1216, 80.11.10.138, ZSI 16027; Pakistan: SMF 64484; Myanmar: CAS 205000, 215387, 219800, 245960, NHMUK 1928.1.4.1, NHMW 14483, 21699.1, 21702.2, ZMB 10258, 11625; Thailand: ZSI 12780; Sri Lanka: FMNH 123906-7, NHMW 14486, 14487.1-3, 21689.1-2, 21689.5-7, 21701.1, ZFMK 52137, 52510, 52511, CM 67639, 67701-4, 67824, 67949-50, 83598, 83605, 89932, 22535.
L. bicolor comb. nov.-Transcaspia (east of the Caspian Sea in Central Asia): ZISP 10013 (syntype), NHMUK 1891.10.6.39. Persia Oriental (Estarabad, eastern Iran): ZISP 10006 (syntype); Tajikistan: ZISP 6909; Uzbekistan: ZISP12447; Turkmenistan: ZMMU uncat.; Pakistan: CAS 101495, ZSI 7973, 8406, 14811, NHMUK 1929.4.29.6, 1940.2.24.29, PMNH 4249; India: Uttarakhand: NHMUK 1946.1.13.81 (holotype of L. mackinnoni); ZSI 16686, 17291-2.
L. carinatus.-CM 67945.
L. deccanensis.—India: Tamil Nadu: ZSI 13271 (paratype).
L. fasciatus.—Myanmar: NHMUK 1901.4.26.1 (neotype), 91.11.26.31, 1900.9.20.5-6, 1901.4.26.1, 1904.4.26.7, 1908.6.23.9-11, 1908.6.23.14, 1925.4.2.28, 1925.9.17.10-11, 1925.12.22.1516, 1937.2.1.12, 1940.3.3.3, BNHS 1218, 1222-4, 1228, CAS 245498; India: Assam: BNHS 1219-21, 1229, NHMUK 92.1.25.1, 94.10.4.2, 1907.12.16.28-29, 1908.6.23.6, 1908.6.23.8, ZSI 4003, 8656, 13637-8, 14879, 14940; Meghalaya: ZSI 3853, 13543; Eastern Himalaya: ZSI 18675.
L. fasciolatus.—India: Kerala: NHMUK 1904.10.18.2-4, 1924.10.13.7, NHMW 21707; Tamil Nadu: NHMUK 1946.1.14.92, MCZ R2232; Sri Lanka: FMNH 25927, MHNG 744.7, 1198.70, NHMW 21689.4, ZFMK 32253.
L. flavicollis.-India: Tamil Nadu: ZSI 25641 (holotype), 25642-3 (paratypes).
L. flavomaculatus.—India: Karnataka: NHMUK 1906.7.27.2 (syntype), 1946.1.13.83 (syntype); Maharashtra: ZSI 25868.
L. gammiei.-West Bengal: ZSI 8447 (holotype).
L. hypsirhinoides.—India: Andaman: ZSI 8145 (holotype); 25227-8, 25253, 25261.
L. jara.—India: Arunachal: ZSI 23616; Assam: ZSI 4131, 8007, 8010-12, 8014, 8017-8, 13813, 17360, 11364, 14751, 14754; Uttar Pradesh: ZSI 14747; West Bengal: ZSI 8015, 8943, 18531, 18686, 19472-3.
L. laoensis.—Laos: NHMUK 1946.1.13.64 (holotype); India: Arunachal: ZSI 24109.
L. ruhstrati.-Taiwan: NHMW 22794:1-16, 18, FMNH 14067-14068, CAS 18874-75.
L. striatus sensu stricto.-India: Odisha: ZSI 7976, 12941, NHMUK 1882.8.26.18-20; Jharkhand: NHMUK 1927.8.9.4, ZSI uncat. 1-2; Madhya Pradesh: ZSI uncat. 3-9; Bihar: ZSI 17557; Uttarakhand: ZSI 16403; Tamil Nadu: NHMUK 1861.12.30.17, 1861.12.30.22, 1861.12.30.66, 1861.12.30.68, 1874.4.29.123-125, 1882.8.26.35-36; Karnataka: NHMUK 1862.8.14.27-28, 1874.4.29.43; Maharashtra: BNHS 1092a-b, 3186; Sri Lanka: NHMUK 1905.3.25.96 (neotype, designated in this study); WHT 0262, FMNH 167013, ZFMK 52138, CM 67641-42, 67705-6, 67951-3, 67997-8.
L. tiwarii.—India: Nicobar: ZSI 20849 (holotype), 20851 (paratype), 25587-9.
L. travancoricus.-India: Kerala: NHMUK 1946.1.13.75 (syntype), ZSI 13396, 13695-6, 17693, CAS 15967, FMNH 217705; Karnataka: ZSI 13531, 13694, 13698.
L. zawi.—Myanmar: CAS 210323 (holotype); India: Mizoram: MZMU 930, 1058.

## Appendix 2.

Lycodon striatus (Shaw, 1802) sensu stricto
(Figs. 2-5, S1, Tables 1, 2)
Coluber striatus Shaw, 1802
Coluber galathea Daudin, 1803
Coluber malignus Daudin, 1803
Lycodon malignus - Boie, 1827
Lycodon galathea - Boie, 1827
Lycodon striatus - Stoliczka 1870, Nicholson 1874, Müller 1887, Sclater 1891, Wall 1921,
Boulenger 1894, Green 1904, Wall 1921, Smith 1943, Taylor 1950, De Silva 1980,
Somaweera 2006, Wallach et al. 2014
Lycodon striatus nordicus Deraniyagala, 1955 [Partim]
Lycodon striatus sinhaleyus Deraniyagala, 1955
Lycodon striatus striatus - Deraniyagala 1955, Lanza 1999, Murthy 2010
Lycodon striatus sinhaleyus — Lanza 1999, de Silva 2009

## Holotype (by monotypy)

An adult specimen of $\sim 356$ mm SVL (dry skin, NHMUK 1904.7.27.67, probably a female due to high ventral count, 74 fide Russell [1796:22]) collected from "Vizagapatam" (now Visakhapatnam; $17^{\circ} 41^{\prime} 12.54$ "N, $83^{\circ} 13^{\prime} 06.53$ " E , datum = WGS84; 169 m above sea level), Andhra Pradesh, India. The specimen was depicted by Russell (1796) on Plate 16 (see Fig. S2A).

## Redescription of the species

Based on examined preserved materials from eastern and central India (Appendix I, $n=12$ ) adults with SVL 245.0-355.0 mm, tail length 50.0-63.0 mm; head elongate, nearly twice as long as wide, mildly depressed, distinct from neck; snout elongate, moderate, flattened and wide in dorsal view, blunt and rounded in lateral profile, forming an oval shape, rather depressed, mildly produced anteriorly, the muzzle marginally exceeding the mentum.

Rostral shield moderate, hemispherical, distinctly visible from above, rounded posteriorly, notched ventrally, protruding beyond mental, as wide as posterior border of internasals; nostrils large, placed in a suture between anterior and posterior nasal scales; nasals divided, shortened, subequal; anterior nasal in contact with rostral and internasal dorsally, $1^{\text {st }}$ supralabial ventrally; posterior nasal in contact with internasal and loreal dorsally separating from prefrontal, $1^{\text {st }}$ and $2^{\text {nd }}$ supralabials ventrally; internasals subpentagonal; prefrontal rather large, nearly twice as large as internasals, wider than long, and subpentagonal, in broad contact with loreal ventrally and with preocular, supraocular and frontal posteriorly, posteriorly not in line with posterior border of preoculars; frontal large, subhexagonal, elongate posteriorly beyond the posterior margin of supraoculars, slightly longer than wide, slightly longer than internasals and prefrontals together; supraoculars wide, elongated, subrectangular; parietals large, elongate, butterfly and wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, upper anterior and posterior temporals, and six dorso-nuchal scales posteriorly; single loreal scale, elongate, in contact with posterior nasal and internasal anteriorly, prefrontal dorsally, post ocular posteriorly, and $2^{\text {nd }}$ and $3^{\text {rd }}$ supralabials ventrally; eye large, round, larger than internasal, pupil rounded; one preocular, vertically shortened, subpentagonal, in contact with prefrontal and loreal anteriorly, prefrontal and supraocular dorsally, and $3^{\text {rd }}$ supralabial ventrally; two postoculars, subequal in size, subcircular, upper post ocular in contact with supraocular, parietal, upper anterior temporal, and lower postocular; lower postocular in contact with both anterior temporals posteriorly, $5^{\text {th }}$ and $6^{\text {th }}$ supralabials ventrally; temporals $2+2$.

Supralabials eight, $6^{\text {th }}-7^{\text {th }}$ larger in size, $7^{\text {th }}$ being the largest, $3^{\text {rd }}-5^{\text {th }}$ contacting the eye; $1^{\text {st }}$ supralabial triangular, in contact with rostral and both nasals anteriorly and dorsally, $2^{\text {nd }}$ supralabial with posterior nasal and loreal dorsally, $3^{\text {rd }}$ supralabial with loreal, preocular and orbit dorsally, $4^{\text {th }}$ supralabial with orbit, $5^{\text {th }}$ supralabial with orbit and the lower postocular dorsally, $6^{\text {th }}$ supralabial with lower postocular and lower anterior temporal dorsally, and $7^{\text {th }}-8^{\text {th }}$ supralabials with temporals and body scales dorsally. Mental small, triangular, wider than long; first infralabial pair enlarged, elongate, and in broad contact with each other, in contact with anterior chin shield posteriorly; nine infralabials, $1^{\text {st }} 5^{\text {th }}$ in contact with first chin shield, $5^{\text {th }}$ infralabial largest in size and in contact with both anterior and posterior chin shields; $6^{\text {th }}-9^{\text {th }}$ infralabials in contact with gular scales; both two larger anterior chin shields and two smaller posterior chin shields in broad contact each other; posterior chin shields bordered posteriorly by six gular scales.

Body robust, elongate, subcylindrical and rather uniform in girth; costal scales in 17-17-15 rows, all smooth and bluntly pointed; 162-178 ventral scales in males ( $n=18$ ) and 168-178 ( $n=7$ ) in females, laterally angulate; cloacal plate divided. Tail cylindrical, tapering to a fine point, long [15.2$19.2 \%$ of total length in males ( $n=18$ ) and $14.3-16.7 \%$ in females ( $n=7$ )], robust and thick; 41-51 ( $n=25$ ) paired subcaudals.

## Colouration

In the preservative, dorsally brown with faint off-white striated crossbars; ground colour and crossbars more intense anteriorly, obscure posteriorly, bifurcating laterally; crossbars fading out on tail; 12-16 crossbars on the body clearly visible; supra- and infralabials pale white with no speckles; posterior parietal distinct (indistinct in most adults) white, striated collar band on nape; underside of head white; venter lacking pattern and uniformly white.

In life, same as in preservative, but the ground dorsal colour varies from dark chocolate-brown to black; in some populations a yellow (pale or bright) colour is visible medially on the crossbars.

Lycodon bicolor (Nikolsky, 1903) comb. nov.
(Figs. 2-5, S1, Tables 1, 2)
Contia bicolor Nikolsky, 1903
Lycodon mackinnoni Wall, 1906 syn. nov.
Ophites mackinnoni - Wall, 1923
Lycodon striatus nordicus Deraniyagala, 1955 [Partim]
Lycodon striatus bicolor - Minton 1966, Lanza 1999, Khan 2002, 2003

## Syntypes

Adult female, ZISP 10013, SVL 300 mm, collected from Kulkulab, Transcaspia (Kurkulab; $38^{\circ} 21^{\prime} 13.83 " \mathrm{~N}, 57^{\circ} 23^{\prime} 16.08$ "E, datum = WGS84; 280 m above sea level) Turkmenistan, by Bilkewitsch in 1902 [the head is damaged and it has therefore been difficult to obtain several diagnostic characters]; ZISP 10006, juvenile male, SVL 190 mm, collected from "Eastern Persia" (eastern Iran), by N.A. Zarudny in 1901.

## Redescription of a syntype

Juvenile male, ZISP 10006, SVL 190 mm, tail length 40 mm ; head elongate, twice as long as wide, mildly depressed, distinct from neck; snout elongate, moderate, flattened and wide in dorsal view, blunt and rounded in lateral profile, forming an oval shape, rather depressed, mildly produced anteriorly, the muzzle marginally exceeding the mentum.

Rostral shield moderate, hemispherical, distinctly visible from above, rounded posteriorly, notched ventrally, protruding beyond mental, as wide as posterior border of internasals; nostrils large, placed in a suture between anterior and posterior nasal scales; nasals divided, shortened, posterior nasals half in size of anterior; anterior nasal in contact with rostral and internasal dorsally, $1^{\text {st }}$ supralabial ventrally; posterior nasal in contact with internasal and loreal dorsally separating from prefrontal, $1^{\text {st }}$ supralabial ventrally; internasals subpentagonal; prefrontal rather large, thrice as large as internasals, wider than long, and subpentagonal, in broad contact with loreal ventrally and with preocular, supraocular and frontal posteriorly, posteriorly in line with posterior border of preoculars; frontal large, subhexagonal, elongate posteriorly beyond the posterior margin of supraoculars, longer than width, slightly longer than internasals and prefrontals together; supraoculars wide, elongated, subrectangular; parietals large, elongate, butterfly and wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, upper anterior and posterior temporals, and six dorso-nuchal scales posteriorly; single loreal scale, elongate, in contact with posterior nasal and internasal anteriorly, prefrontal dorsally, post ocular posteriorly, and $1^{\text {st }}-3^{\text {rd }}$ supralabials ventrally; eye large, round, larger than internasal, pupil rounded; one preocular, vertically shortened, subpentagonal, in contact with prefrontal and loreal anteriorly, prefrontal and supraocular dorsally, and $3^{\text {rd }}$ supralabial ventrally; two postoculars, subequal in size, subcircular, upper post ocular in contact with supraocular, parietal, upper anterior temporal and lower postocular; lower postocular in contact with anterior temporals posteriorly, $5^{\text {th }}$ and $6^{\text {th }}$ supralabials ventrally; temporals 2+2.

Supralabials eight, $5^{\text {th }}-7^{\text {th }}$ larger in size, $7^{\text {th }}$ being the largest, $3^{\text {rd }}-5^{\text {th }}$ contacting the eye; $1^{\text {st }}$ supralabial triangular, in contact with rostral and both nasals anteriorly and dorsally, $2^{\text {nd }}$ supralabial with loreal dorsally, $3^{\text {rd }}$ supralabial with loreal, preocular and orbit dorsally, $4^{\text {th }}$ supralabial with orbit, $5^{\text {th }}$ supralabial with orbit and the lower postocular dorsally, $6^{\text {th }}$ supralabial with lower postocular and lower anterior temporal dorsally, and $7^{\text {th }}-8^{\text {th }}$ supralabials with temporals and body scales dorsally. Mental
large, triangular, wider than long; first infralabial pair enlarged, elongate, and in broad contact with each other, in contact with anterior chin shield posteriorly; ten infralabials, $1^{\text {st }}-5^{\text {th }}$ in contact with first chin shield, $5^{\text {th }}$ infralabial in narrow contact with the anterior chin shield and in broader contact with the posterior chin shield; $6^{\text {th }}$ infralabial largest in size in narrow contact with posterior chin shield, $6^{\text {th }}-9^{\text {th }}$ infralabials in contact with gular scales; both of the two larger anterior chin shields and two smaller posterior chin shields in broad contact each other; posterior chin shields bordered posteriorly by six gular scales.

Body robust, elongate and subcylindrical of rather uniform girth; costal scales in 17-17-15 rows, all smooth and bluntly pointed; pre-ventrals damaged; 185 ventral scales, laterally angulate; cloacal plate divided. Tail cylindrical, tapering to a fine point, long (17.4\% of total length), robust and thick; 69 paired subcaudals.

## Colouration

In the preserved syntype (ZISP 10006), dorsally dark rufous brown with faint off-white crossbars; ground colour and crossbars more intense anteriorly, obscure posteriorly; crossbars fading out on tail, those on body spaced out more (inter-bar distance 5 to 7 scales) anteriorly and closer ( 3 or 4 scales apart) posteriorly, bifurcating laterally along the outer 1-5 scale rows; over 20 clearly visible crossbars on the body; first five crossbars well defined, and amorphous afterwards; supra and infralabials pale white with no speckles; two scales behind the parietal a three scale wide distinct white collar band on nape; underside of head white; venter white and lacking pattern.

In life, same as in the preserved syntype, but dorsally black.

Lycodon striatus sinhaleyus Deraniyagala, 1955
(Figs. 2-6, Tables 2, 3)

## Holotype

Adult female, NMSL RS. 15, total length 256 mm, from Rajagiriya, Colombo, Sri Lanka (lost).

## Neotype (designate herein)

Adult female, NMSL 2022.03.01, SVL 282 mm , from Rajagiriya, $\left(6^{\circ} 54^{\prime} \mathrm{N}, 79^{\circ} 52^{\prime} \mathrm{E}\right.$, datum = WGS84; 10 m above sea level), Colombo District, Western Province, Sri Lanka.

## Description of the neotype

Adult female, SVL 282 mm , tail length 37 mm ; head elongate, twice as long as wide HW $55.4 \%$ of HL , mildly depressed, distinct from neck; snout elongate ES $34.5 \%$ of HL , moderate, round and wide in dorsal view, pointed in lateral profile, forming an oval shape, rather depressed, mildly produced anteriorly, the muzzle marginally exceeding the mentum.

Rostral shield moderate, hemispherical, distinctly visible from above, rounded posteriorly, notched ventrally, protruding beyond mental, as wide as posterior border of internasals; nostrils large, placed in a suture between anterior and posterior nasal scales; nasals divided, shortened, posterior nasals slightly smaller than anterior; anterior nasal in contact with rostral and internasal dorsally, $1^{\text {st }}$ supralabial ventrally; posterior nasal in contact with internasal and loreal dorsally separating from prefrontal, $1^{\text {st }}$ supralabial ventrally; internasals subpentagonal; prefrontal rather large, twice as large as internasals, wider than long, and subpentagonal, in broad contact with loreal ventrally and with preocular, supraocular and frontal posteriorly, posteriorly not in line with posterior border of preoculars; frontal large, subtriangular, elongate posteriorly beyond the posterior margin of supraoculars, slightly longer than width, slightly longer than internasals and prefrontals together; supraoculars wide, elongated, subrectangular; parietals large, elongate, butterfly and wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, upper anterior and posterior temporals, and seven dorso-nuchal scales posteriorly; single loreal scale, elongate, in contact with posterior nasal and internasal anteriorly, prefrontal dorsally, post ocular posteriorly, and $2^{\text {nd }}$ and $3^{\text {rd }}$ supralabials ventrally; eye large, round, larger than internasal, pupil rounded; one preocular, vertically shortened, subpentagonal, in contact with prefrontal and loreal anteriorly, prefrontal and supraocular dorsally, and $3^{\text {rd }}$ supralabial ventrally; two postoculars, subequal in size, subcircular, upper post ocular in contact with supraocular, parietal, and lower postocular; lower postocular in contact with upper anterior temporal posteriorly, $5^{\text {th }}$ and $6^{\text {th }}$ supralabials ventrally; temporals $2+2$.

Supralabials eight, $5^{\text {th }}-7^{\text {th }}$ larger in size, $7^{\text {th }}$ being the largest, $3^{\text {rd }}-5^{\text {th }}$ contacting the eye; $1^{\text {st }}$ supralabial triangular, in contact with rostral and both nasals anteriorly and dorsally, $2^{\text {nd }}$ supralabial with loreal dorsally, $3^{\text {rd }}$ supralabial with loreal, preocular and orbit dorsally, $4^{\text {th }}$ supralabial with orbit, $5^{\text {th }}$
supralabial with orbit and the lower postocular dorsally, $6^{\text {th }}$ supralabial with lower postocular and lower anterior temporal dorsally, and $7^{\text {th }}-8^{\text {th }}$ supralabials with lower temporals and body scales dorsally. Mental large, triangular, wider than long; first infralabial pair enlarged, elongate, and in broad contact with each other, in contact with anterior chin shield posteriorly; eight infralabials, $1^{\text {st }}-5^{\text {th }}$ in contact with first chin shield, $5^{\text {th }}$ infralabial largest in size and in contact with both anterior and posterior chin shields; $6^{\text {th }}-8^{\text {th }}$ infralabials in contact with gular scales; both of the two larger anterior chin shields plus two smaller posterior chin shields in broad contact each other; posterior chin shields bordered posteriorly by four gular scales.

Body robust, elongate and subcylindrical and of rather uniform girth; costal scales in 17-1715 rows, all smooth and bluntly pointed; 161 ventral scales, laterally angulate; cloacal plate divided. Tail cylindrical, tapering to a fine point, fairly short ( $11.6 \%$ of total length), robust and thick; 38 paired subcaudals.

## Coloration

In the preservative, dark brown dorsally with faint off-white striated crossbars; ground colour and crossbars more intense anteriorly, obscure posteriorly, bifurcating laterally; crossbars fading out on tail; 8-12 clearly visible crossbars on the body visible clearly; supra and infralabials pale white with no speckles; posterior parietal faded white, striated collar band on nape; underside of head white; venter lacking pattern and uniformly white.

In life, same as in preservative, but the ground dorsal colour varies from dark brown to black; in some populations a yellow colour is visible medially on the crossbars.

Skull and dentition (based on NHMUK 1905.3.25.96, SVL 229 mm)
A complete and robust skull displays a general colubrid pattern (Fig. 5C); premaxilla single, round anteriorly, with a broad ascending process, a flat nasal crest, and a relatively long transverse process; nasals elongate, triangular, lateral processes tapering anteriorly to form a pointed process, but slightly bifurcates at the point of articulation with the ascending process; parietals smooth, anterior process straight; the apical process of parietal and ascendant process of supraoccipital prominent. The anterior maxillary teeth (five) and posterior maxillary teeth (eight) are separated by a diastema equal or greater in length to the longest anterior maxillary tooth; among the posterior maxillary teeth, posteriormost teeth (two) are enlarged; palatine with 12 teeth; pterygoid with 18 teeth; and mandible with total of 20 teeth separated by a diastema with anteriorly four enlarged teeth and posteriorly 16 teeth.

Hemipenis (based on Fig. S3)
The organ is single and bulbous in shape, relatively short, robust, non-capitate, and the inverted hemipenis extends to $5^{\text {th }}$ subcaudal level; simple oblique sulcus spermaticus shallow and centripetal, extends directly to apex; lobes blunt, apical lobe less evident; acalyculate organ with a specialized ornamentation forms spines on the proximal portion of the hemipenis greatly enlarge to basal hooks; spines on the upper basal areas enlarged and decreasing the size slightly towards the proximal portion; the lobe is spinose on both the sulcate and asulcate surfaces; apical region not separated from the basal portion, apical part of the hemipenis is spinose; sulcate and asulcate expansion pleat naked.

Appendix 3. English translation of the original French description of Coluber malignus Daudin, 1803 (now junior objective synonym of Lycodon striatus)
[Page 46] THE SMART SNAKE ${ }^{1}$.
RUSSEL has given, in his work on the serpents of the Coromandel, the description and the figure of a species which seems to me to have great relations with vipers; but since this author does not positively assure that it has poisonous fangs, I have tentatively placed it among colubrids.

The head is oval, depressed, obtuse, a little more enlarged than the neck, covered with nine plates above its anterior half, and furnished behind with scales similar to those of the back. The mouth is small, with [page 47] its jaws of equal length, furnished with numerous teeth, pointed and curved back on marginal and palatal branches. Russel noticed that the front teeth of the marginal branches of the upper jaw are longer than the others.

The body is cylindrical, furnished above with oval, enlarged, overlapping scales; it is terminated in a small, slender, pointed tail, one seventh of the total length, which is one foot two inches. The neck circumference is one inch three lines, and the body thickness is about two inches.

The color of the head is dark green and without spots. Body and tail are blackish, varying in hues of dark green, and all over the back is a row of twenty or so narrow spots of yellowish white with two longitudinal rows on the sides of the body and the the [sic] base of the tail, formed of small white lines. Large ventral plates under the body, of a bluish white, are one hundred and seventy-four, and forty doubles under the tail.
[Page 48] Russel concludes the description of this snake, noting that it closely resembles the blue krait in color, although the spots are arranged differently. He adds that he did not take a good look at the long front teeth of the upper jaw, and that they could be mistaken for poisonous hooks. The inhabitants of Bengal call this serpent gajou-tutta; it is rare in Vizagapatam, and is arguably not as dangerous as it is believed in the country.

[^0]Appendix 4. English translation of the original French description of Coluber galathea Daudin, 1803 (now junior subjective synonym of Lycodon striatus)

## [Page 55] THE GALATHEA COLUBRID ${ }^{1}$

Plate LXXXII, figure 2.
Russel figured this pretty snake in his work on Coromandel serpents, under the name of karetta, which is given to it by the Indians. He counted a hundred and seventy-one large abdominal plates, and forty one subcaudal; but he did not give its description, because he lost the one he did; but as the figure of this snake is well executed, it is easy to indicate its principal characters.

The head is oval, depressed, covered [page 56] with nine plates as in other snakes. We see above, from the occiput to the end of the tail, about fifteen large black, oval, regular and spaced spots, on a flesh-colored background, which appears reddish and mottled; and on the back, between these spots, we can see a narrow, longitudinal, reddish band. The tail is very short and pointed.

[^1]Appendix 5. English translation of the original Russian description of Contia bicolor Nikolsky, 1903 (now Lycodon bicolor comb. nov.)

Contia bicolor sp. nov.
№ 10006. Persia orientalis 1901. ZARUDNY. 1 specimen.
№ 10013. Transcaspia. Kulkalab. 1902. BILKEWITSCH. 1 specimen.
The width of the interorbital shield barely exceeds its height, from above this shield is barely visible, the nasal shield is semi-divided, divided only above the nostril; length of suture between internasal scales at least 2 times less than length of suture between prefrontal ones, length of frontal scales almost $11 / 2$ times its width, almost equal to distance of this scale from end of snout and much less than length of parietal scales; the width of the frontal shield is 2 times the width of the supraorbital, the zygomatic shield is very long, its length is 3 times the height; 1 preorbital shield, 2 postorbitals, $2+2$ temporals, 8 supralabials, of which the 4 th and 5 th touch the eye; the pupil is vertically oval; among the infralabials five anterior scales touch the anterior mandibular; the posterior mandibular scales are at least half the size of the anterior scales and touch each other; scales smooth in 15 longitudinal rows, 202 ventral scales, anal shield divided, 65 subcaudals; the body and head are black above; in the anterior third there are 6 white transverse stripes, the width of which is more than half the width of the black spaces; in the second third, white stripes are interrupted in two places, and in the back third, each scale is black with white lateral edges; the entire underside is pure white, the entire length is 360 mm ., found in eastern Persia; there was no label with the specimen, thus the exact location is unknown. Later, Bilkevich sent me one specimen of this snake from Kulkulab in the Caspian region.

Appendix 6. English translation of the original French description of Lycodon napei Duméril, Bibron and Duméril, 1854 (now nomen dubium)
[page 384] 6. LYCODON DE NAPĖE. Lycodon Napei. Nobis.
CHARACTERS. The entire upper part of the trunk a reddish-brown color, with large white, rounded dorsal spots distributed at roughly equal intervals, four to five times as wide as the spots themselves; the underside of the trunk of a fine pure white, but intermixed with brown on the sides.
[page 385] DESCRIPTION.
We found this species referred to by this name in the collection [note from the translator: the MNHN collection], without any indication of its origin, nor of the donor. Its size is half that of Müller's Lycodon, with which it has some analogy. Besides the great apparent resemblance to the background of the shade presented by the top of the trunk and even the lower region, there is this remarkable difference that the underside of the tail is in the individual which we have under the eyes, of a milk white and not strewn with small brown spots, as in the so-called Müller species, and that the top of the head is here without any spot, while it is, in the individual described above, motley or veined with white on a reddish background.

We have no information on this Serpent, whose label only bore the sign $\delta$ and a point of doubt on the origin, of the writing of our collaborator Bibron.


[^0]:    ${ }^{1}$ Coluber malignus ; suprà nigricans, maculis transversis albidis circà 20 suprà dorsum, cum lineâ albâ in utroque latere, subtùs coerulescente albidus ; caudâ 1/7.

    Scutis abdom. 174. - Scutellis subcaud. 40-214.
    Gajou-tutta. Russel, Hist. nat. of serpents Corom. and Indian, $\mathrm{n}^{\circ} 16$, pl. clxi.

[^1]:    ${ }^{1}$ Coluber galathea ; suprù rufescens cum maculis nigris ovatis et magnis circà 15 ; caudâ ...
    Scutis abdom. 171. - Scutellis subcaud. 41-212.
    Karetta. Russel , Hîst. nat. of Coromand. and Indian serpents, p. 52 , n ${ }^{\circ} 26$, pl. xxvi.

