

ORIGINAL ARTICLE

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

Amarasinghe A. Thasun Amarasinghe^{1,2}  | Rafaqat Masroor³  |
 Hmar T. Lalremsanga⁴  | Sanjaya Weerakkody⁵  | Natalia B. Ananjeva⁶  |
 Patrick D. Campbell⁷  | Stevie R. Kennedy-Gold^{8,9}  | Sanjaya K. Bandara¹⁰  |
 Andrey M. Bragin^{11,12}  | Atthanagoda K. A. Gayan¹³  | Vivek R. Sharma¹⁴  |
 Amit Sayyed¹⁵  | Lal Biakzuala⁴  | Andradige S. Kanishka¹⁰  |
 Sumaithangi R. Ganesh¹⁶  | Ivan Ineich¹⁷  | Anslem de Silva¹⁸  |
 Lakshman J. M. Wickramasinghe¹⁹  | Sampath S. Seneviratne⁵  |
 Nikolay A. Poyarkov^{11,12}  | Gernot Vogel²⁰  | Daniel Jablonski²¹ 

¹Herpetology Lab, Museum Zoologicum Bogoriense (MZB), Research Center for Biosystematics & Evolution, The National Research & Innovation Agency (BRIN; Government of Indonesia), Cibinong, Indonesia

²Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Indonesia, Depok, Indonesia

³Zoological Sciences Division, Pakistan Museum of Natural History, Islamabad, Pakistan

⁴Developmental Biology and Herpetology Laboratory, Department of Zoology, Mizoram University, Aizawl, Mizoram, India

⁵Laboratory for Molecular Ecology and Evolution, Department of Zoology & Environment Sciences, Faculty of Science, University of Colombo, Colombo, Sri Lanka

⁶Division of Herpetology and Ornithology, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

⁷Science Department, Darwin Centre, Natural History Museum, London, UK

⁸Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

⁹Department of Herpetology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

¹⁰Taprobanica Nature Conservation Society, Homagama, Sri Lanka

¹¹Department of Vertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, Moscow, Russia

¹²Joint Russian-Vietnamese Tropical Research and Technological Center, Hanoi, Vietnam

¹³Institute of Biochemistry, Molecular Biology and Biotechnology, University of Colombo, Colombo, Sri Lanka

¹⁴Department of Zoology, Government Model Science College, Jabalpur, Madhya Pradesh, India

¹⁵Wildlife Protection and Research Society, Maharashtra, India

¹⁶Chennai Snake Park, Chennai, Tamil Nadu, India

¹⁷Institut de Systématique, Évolution et Biodiversité, Muséum National d'Histoire Naturelle, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, CNRS, Paris, France

¹⁸Amphibia and Reptile Research Organization of Sri Lanka (ARROS), Gampola, Sri Lanka

¹⁹Herpetological Foundation of Sri Lanka, Wattala, Sri Lanka

²⁰Society for Southeast Asian Herpetology, Heidelberg, Germany

²¹Department of Zoology, Comenius University in Bratislava, Bratislava, Slovakia

Correspondence

Amarasinghe A. Thasun Amarasinghe,
Department of Biology, Faculty of
Mathematics and Natural Sciences,
Universitas Indonesia, Kampus UI,
Depok, 16424, Indonesia.
Email: thasun.amarasinghe@ui.ac.id

Daniel Jablonski, Department of
Zoology, Comenius University in
Bratislava, Ilkovičova 6, Mlynská do-
lina, 842 15 Bratislava, Slovakia.
Email: daniel.jablonski@uniba.sk

Funding information

Slovak Research and Development
Agency, Grant/Award Number:
APVV-19-0076; Asian Herpetological
Association (AHA), Asosiasi
Herpetologi Asia, Grant/Award
Number: AHA-2022/AATA/01;
Russian Science Foundation, Grant/
Award Number: 22-14-00037; Russian
State Theme, Grant/Award Number:
ZISP122031100282-2; Department of
Science & Technology (DST), Science
& Engineering Research Board, New
Delhi, India, Grant/Award Number:
EEQ/2021/000243; Scientific Grant
Agency of the Slovak Republic, Grant/
Award Number: VEGA1/0242/21;
Rufford Foundation, UK, Grant/Award
Number: 36737-1; Ministry of Science
and Higher Education of the Russian
Federation, Grant/Award Number:
075-15-2021-1069

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 (~356 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 Transcaspiya, 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, Transcaspiya (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); Zoologisches 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 | Genetic data

Total genomic DNA was extracted from the tissue samples (blood, liver, or muscle biopsies from ethanol-preserved 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°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+I+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+I+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) mid-body and (iii) one head length prior to cloacal plate]. We counted ventral scales without preentrals 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 μm and we recorded data for every 0.4° rotation for 360° with (AL) 1 mm filter. The source voltage for the scan was 65 kV and the source current was 153 μA . 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: $\log X_{\text{adj}} = \log(X) - \beta[\log(\text{SVL}) - \log(\text{SVL}_{\text{mean}})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population and SVL_{mean} = overall average SVL of all populations (Chan & Grismer, 2022; Leonart 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

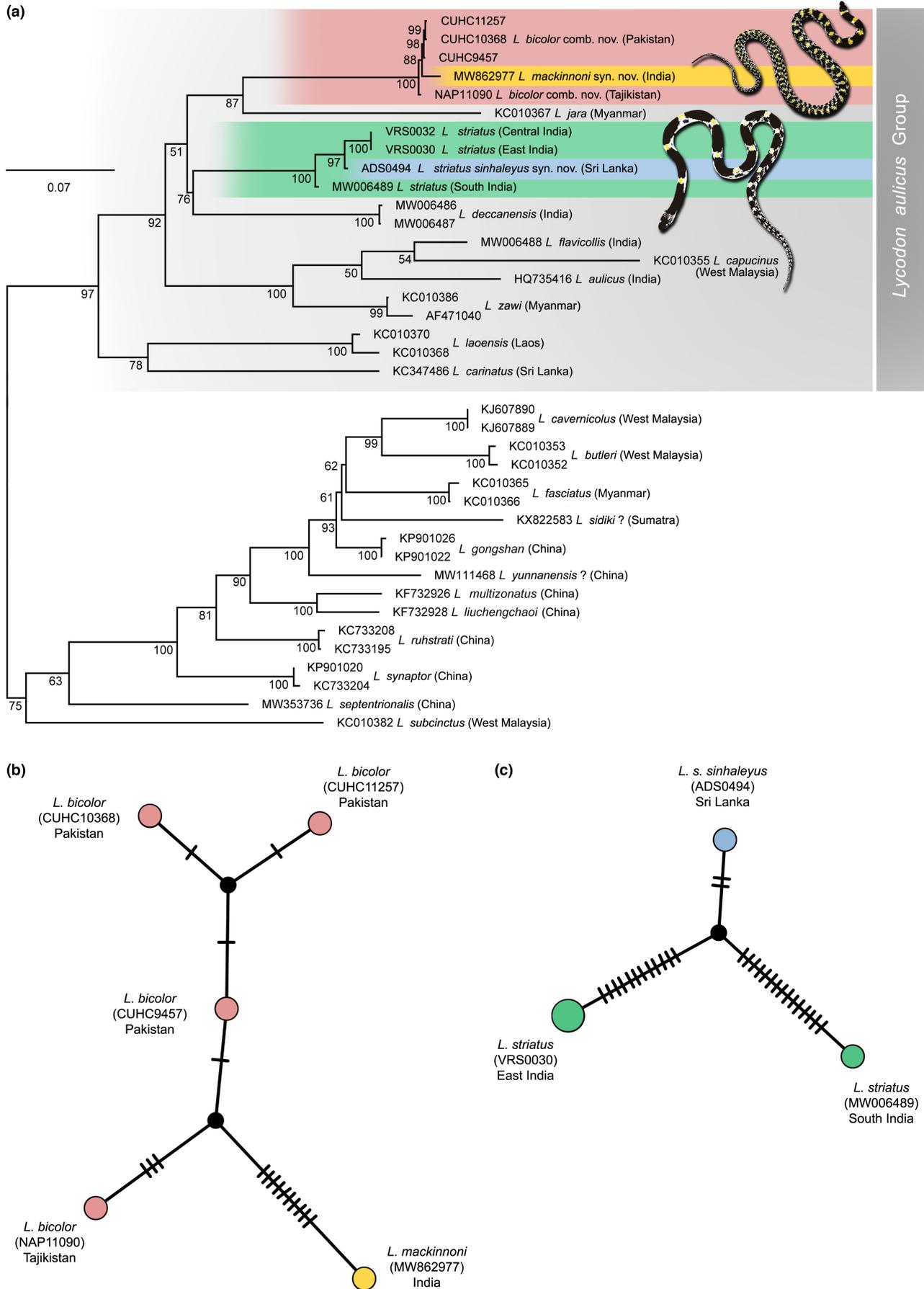


FIGURE 1 (a) Maximum likelihood (ML) phylogeny of the genus *Lycodon* based on 1096 bp of the mitochondrial *Cyt b* gene. Topologies of ML and Bayesian analyses were similar (Figure S1). Haplotype networks reconstructed for (b) *L. bicolor* and (c) *L. striatus*.

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*.

No.	Species	Species																
		1	2	3	4	5	6	7	8	9	10	11	12					
1	<i>L. laoensis</i>	0																
2	<i>L. carinatus</i>	12.3	0															
3	<i>L. mackinnoni</i>	14.6	13.9	0														
4	<i>L. bicolor</i> comb. nov.	15.8	14.6	1.4	0													
5	<i>L. jara</i>	18.0	16.5	14.3	14.8	0												
6	<i>L. deccanensis</i>	16.7	15.0	14.5	15.2	15.8	0											
7	<i>L. s. sinhaleus</i>	12.5	14.6	14.1	14.0	14.7	13.2	0										
8	<i>L. striatus</i> s. str.	11.1	13.2	12.7	12.6	14.4	11.4	2.1	0									
9	<i>L. capucinus</i>	17.3	15.3	17.6	17.9	16.9	16.5	16.7	15.0	0								
10	<i>L. flavicollis</i>	16.7	15.6	14.7	16.2	16.6	15.2	14.0	12.6	15.1	0							
11	<i>L. zawi</i>	16.7	14.8	14.5	15.7	15.9	15.5	13.7	13.2	13.7	11.7	0						
12	<i>L. aulicus</i>	18.1	18.2	17.1	18.0	17.2	17.4	16.0	14.8	15.1	8.5	8.9	0					

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 ($\chi^2 = 14.73$, $p = .0001$) 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. sinhaleus* 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 re-evaluation 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 different-sized 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

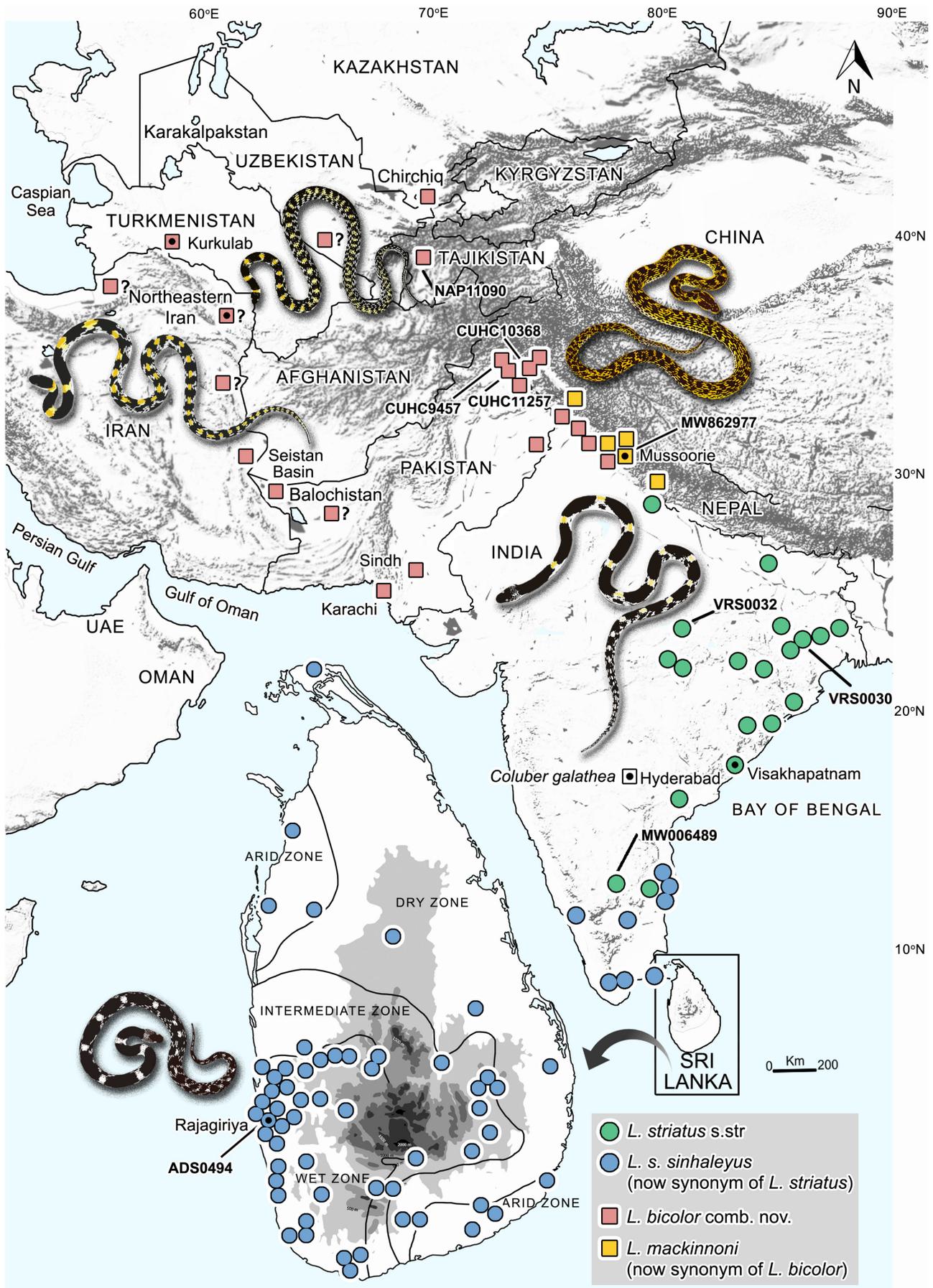
genus *Lycodon*, restrict its type locality to Kurkulab in Turkmenistan based on Nikolsky (1903) and consider its distribution as being the region stretching from Pakistan towards Central Asia. Furthermore, the comparison of *Lycodon bicolor* comb. nov. with *L. striatus* sensu stricto from eastern India 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.

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.



- *L. striatus* s.str
- *L. s. sinhaleyus*
(now synonym of *L. striatus*)
- *L. bicolor* comb. nov.
- *L. mackinnoni*
(now synonym of *L. bicolor*)

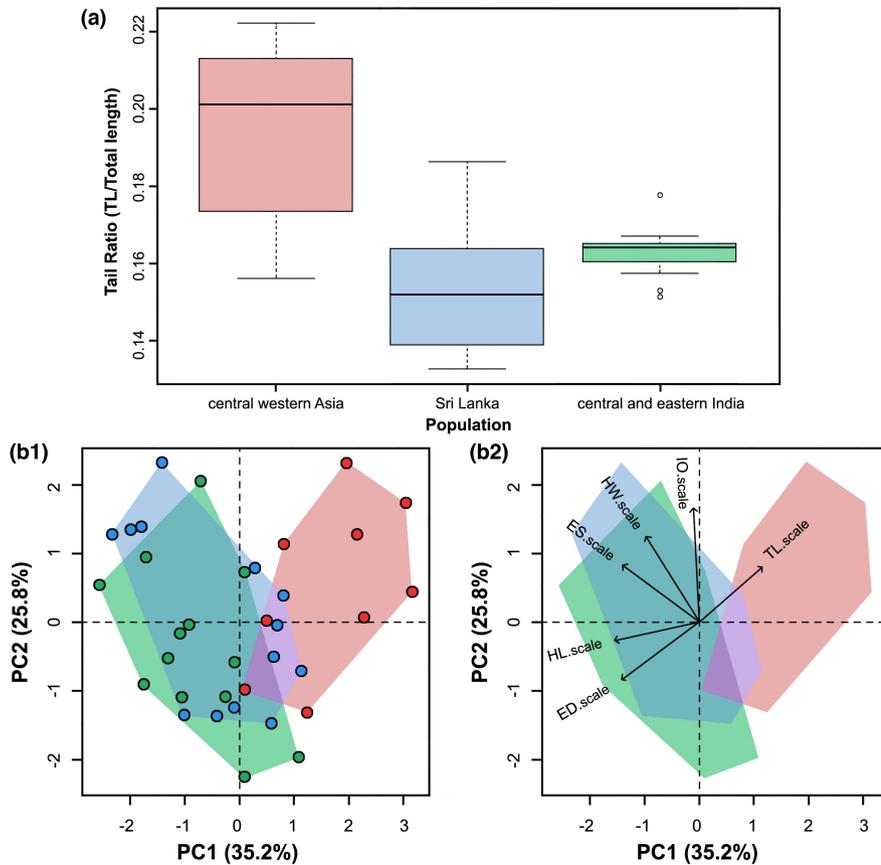


FIGURE 3 (a) Boxplots showing the tail ratio of *Lycodon striatus* sensu lato in eastern India, central western Asia, and Sri Lanka; top, middle and bottom lines of the boxes indicate 75th percentile, median and 25th percentile respectively. Principal component analysis (PCA) biplot of morphometric variation 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.

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 (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 north-eastern 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 ~356 mm SVL (now lost, probably a female due to its high ventral count, 74 fide Russell [1796:22]) collected from 'Vizagapatam' (now Visakhapatnam; 17°41'12.54"N, 83°13'06.53"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	<i>L. striatus</i> sensu stricto			<i>L. bicolor</i> comb. nov.		
	India	Sri Lanka	Himalayas	Western Asia and Pakistan	Other (<i>n</i> = 11)	
	(<i>n</i> = 31)	Neotype of <i>L. s. sinhaleys</i> NMSL 2022.03.01	Holotype of <i>L. mackinnoni</i> NHMUK 1946.1.13.81	Syntypes of <i>L. bicolor</i> ZISP 10006, 13		
Snout-vent length	110.0–312.0	282.0	309.0	190.0, 300.0	117.0–386.0	
Tail length (TL)	25.0–65.0	37.0	--	40.0, 60.0	48.0–83.0	
TL/total length % in males	15.2–17.8 (<i>n</i> = 12)	--	--	--	20.1–22.2 (<i>n</i> = 4)	
Head length	8.5–13.3	10.3	10.4	--	9.2–13.3	
Head width	5.4–7.5	5.7	6.1	--	5.3–6.9	
Interorbital width	3.1–3.9	3.9	3.4	--	3.3–4.3	
Snout length	3.3–4.4	2.9	2.6	--	3.4–4.9	
Eye diameter	1.5–2.0	1.6	1.2	--	1.5–2.2	
Ventrals	161–184	161	185	185, 186	176–192	
Subcaudals	41–51	38	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			Anal	Sup	Ventrals	Subcaudals	Preocular & frontal	Head	Collar mark	Scales between 1st cross mark & parietal		Dorsal colouration of adults
	16	9	d								180–215	57–78	
<i>L. aulicus</i> s.l. (SW India & Sri Lanka)	16	9	d	180–215	57–78	c	wl	p	16–26	Dark blackish-brown/creamy white crossbars			
<i>L. bicolor</i> 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			
<i>L. bicolor</i> comb. nov. (Uttarakhand, ' <i>L. mackinnoni</i> ')	?	7, 8	d	162–187	48–57	s	ns	a	12–14	Dark brown/yellow striated cross marks			
<i>L. carinatus</i> (Sri Lanka)	15	8, 9	e	188–193	53–60	s	wl	p	23–25	Black/white serrated crossbars			
<i>L. decanensis</i> (SC India)	?	9, 10	e	181–214	66–78	s	ns	p	12–14	Brown/white crossbars			
<i>L. fasciatus</i> (NE India & Myanmar)	11	8, 9	e	182–220	62–79	s	wl	p	12–14	Dark brown/pale brownish white crossbars			
<i>L. fasciolatus</i> (East India & Sri Lanka)	?	9	d	174–204	60–73	s, c	ns	a	7–10	Reddish-brown/creamy yellow crossbars			
<i>L. flavicollis</i> (SW India)	?	8, 9	d	210–224	65–74	c	ns	p	—	Uniform light brown/no crossbars			
<i>L. flavomaculatus</i> (NW India)	?	9	d	165–183	55	s	ns	p	12–14	Dark brown or black/yellow spotted cross marks			
<i>L. gammiei</i> (NE India & Bhutan)	?	7–9	?	205–220	98–111	s	ns	p	12–14	Dark brown/brownish-yellow crossbars			
<i>L. hypsirrhinoides</i> (Andaman)	?	9	d	188–213	61–75	c	wl	a	—	Uniform dark brown/no crossbars			
<i>L. jara</i> (NE India)	?	8	d	167–188	52–76	s	ns	p	—	Glossy greenish-purple/yellow spots			
<i>L. laoensis</i> s.s. (Laos)	?	9	d	163–187	60–76	c	ns	p	21–25	Dark brown/white or yellow crossbars			
<i>L. septentrionalis</i> (east Himalayas)	8	8	e	207–217	81–92	s	ns	p	28–32	Purplish-black/white crossbars			
<i>L. striatus</i> s.str. (central & east India)	9	8	d	161–184	41–51	s	ns	p	18–20	Blackish-brown/white striated crossbars			
<i>L. striatus</i> (Sri Lanka & south India)	13	7, 8	d	142–165	33–45	s	ns	p	16–18	Blackish-brown/white crossbars			
<i>L. subcinctus</i> s. str. (Java)	8–14	8	d	208–227	62–89	—	wl	p	27–30	Black/white crossbars			
<i>L. tivarii</i> (Nicobar)	?	9	d	218–234	60–94	c	wl	p	—	Uniform brown/no crossbars			
<i>L. iravancoricus</i> (SW India)	?	8, 9	e	168–206	54–73	c	wl	p	17–23	Dark purplish-brown/faint cream crossbars			
<i>L. zawi</i> (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 3rd–5th 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,

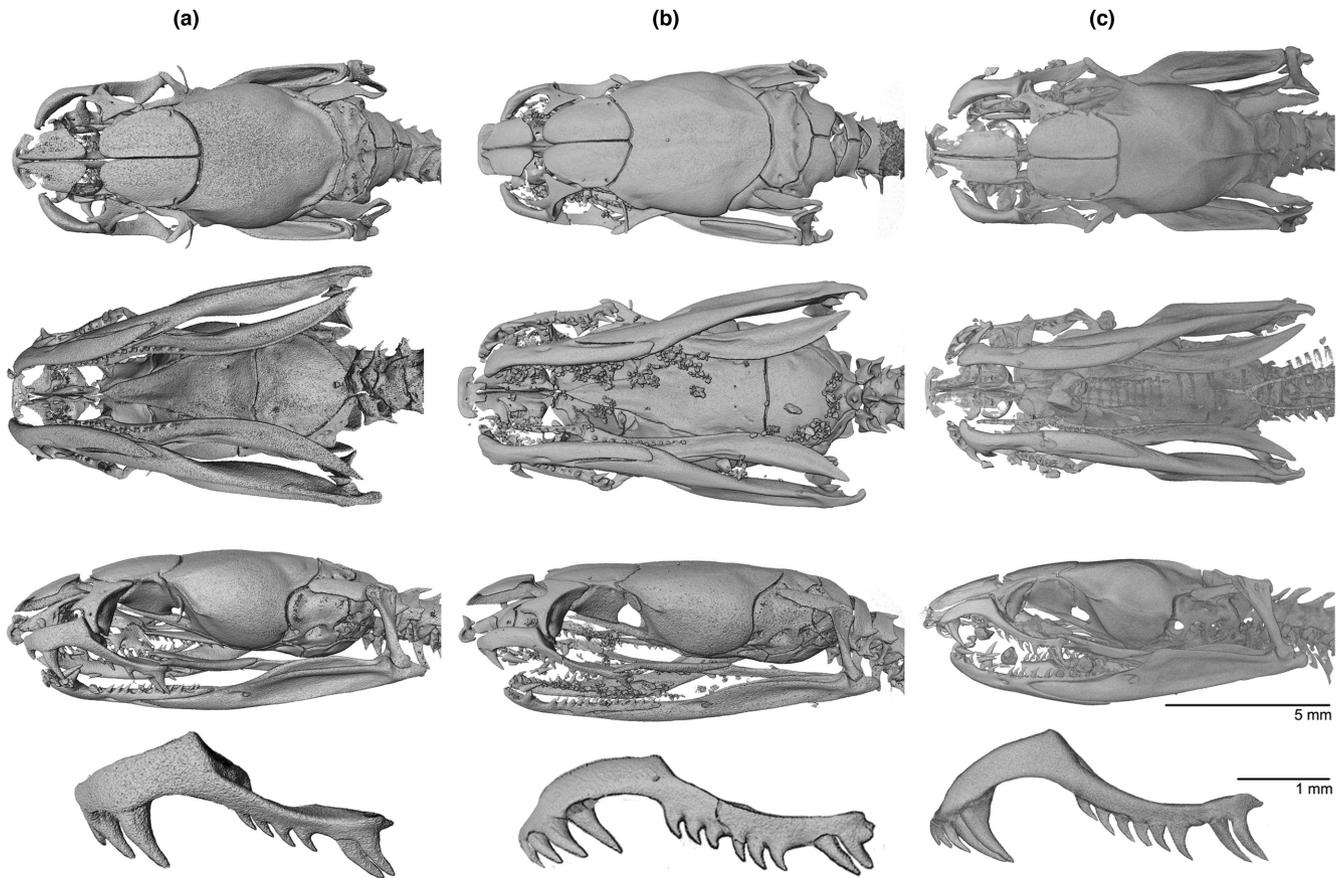


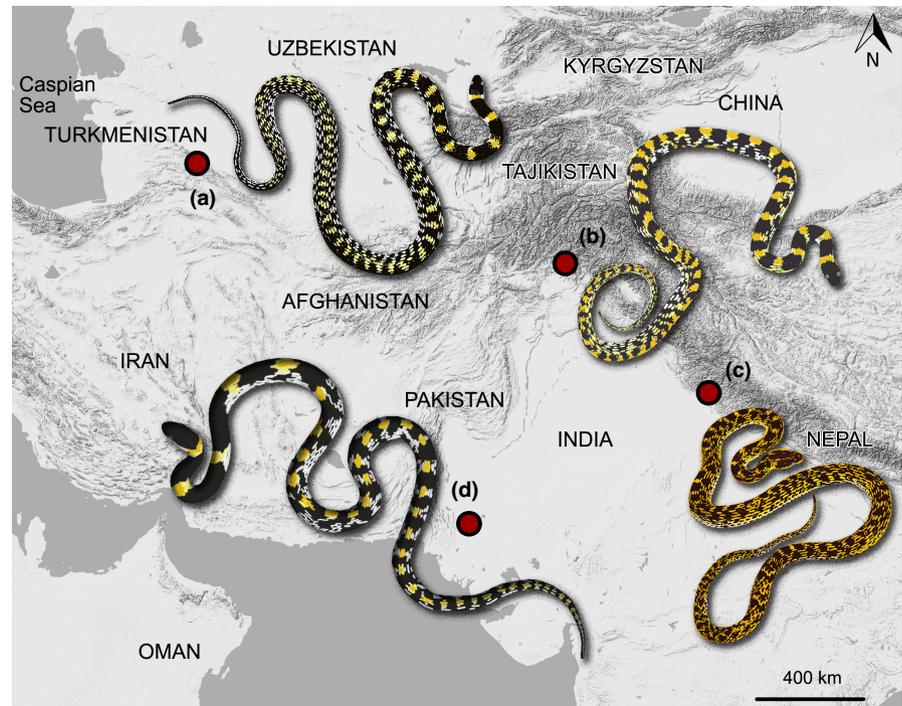
FIGURE 5 Dorsal, lateral and ventral skull views (scale = 5 mm) and the maxilla (scale = 1 mm) of (a) a voucher of *L. striatus* sensu stricto from India (NHMUK 1882.8.26.20), (b) a voucher of *L. bicolor* comb. nov. (NHMUK 1891.10.6.39) from 'Transcaspia' and (c) a voucher of *L. striatus* from Sri 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) Nagpur-Seoni 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 Mareduhilli 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 look-alike 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 penneplain 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 night-fall. 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 mm long and 10–12 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°21'13.83"N, 57°23'16.08"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.

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-Grumzhimailo from Dzhilyantau (Baldzhuan in Tajikistan) in the 1880s during the last

century; (ii) ZISP 10160, collected by E. Fiipovich 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 Afghan–Iranian 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 mm × 9–11 mm (Minton, 1966), or between two to four eggs 26–30 mm × 9–10 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 sinhalayus* 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 'similar-looking' 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 (*Euphyctis*: 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 penneplains 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 re-evaluate 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.

ACKNOWLEDGEMENTS

Fieldwork in Pakistan (by RM and DJ) was performed under the permit (No. PMNH/EST1(89)/05) of the Pakistan Museum of Natural History, Islamabad; and fieldwork in Sri Lanka (by LJM and ADS) was performed under the permits (Nos: WL/3/2/2/13 and WL/3/1/8/5) of the Department of Wildlife Conservation and (No: R&E/RES/NFSRCM/2018-02) of the Department of Forestry. We thank B. Pandav, R. Khot and O. Adhikari (BNHS); J. Vindum and A. Leviton (CAS); A. Resetar and H. Voris (FMNH); Silke Schweiger and Georg Gassner (NHW); N. Wickramasinghe, S. Kasthuriarachchi, L. Somaratne, C. Kothalawala, C. Munasinghe, T. Gamage, R. Dasanayake, R. Wickramanayake, P. Gunasiri (NMSL); G. Köhler and L. Acker (SMF, Germany); D. Rödder and W. Böhme (ZFMK, Germany); N.L. Orlov (ZISP); M.O. Rödel and F. Tillack (ZMB, Germany); V.F. Orlova and R.A. Nazarov (ZMMU); K. Venkataraman, K. Chandra, K.A. Subramanian, S. Kumar, K. Deuti, P.G.S. Sethy, S. Raha, P. Bag and S. Debnath (ZSI); A.O. Latifi, M.H. Vohidov and R.S. Muratov (IZIP, Tajikistan) for providing in-house facilities / loan / pictures of specimens under their care. B. Clark (NHMUK, London) is acknowledged for assistance in MicroCT scanning; J. Poláková (Department of Zoology, Comenius University in Bratislava, Slovakia) for help with the molecular lab work; the Executive Chairman and the Board of Trustees of the Chennai Snake Park Trust are acknowledged for their support and encouragements to SRG. We also thank Lee Grismer (La Sierra University, USA), S. Karunarathna (Sri Lanka) and an anonymous reviewer for their valuable comments to

improve the draft. Finally, we thank Junichi Fujinuma (University of Tartu, Estonia); J. Supriatna and the staff of the Research Center for Climate Change, University of Indonesia, for their support.

FUNDING INFORMATION

Slovak Research and Development Agency (Grant No: APVV-19-0076); Scientific Grant Agency of the Slovak Republic (Grant No. VEGA 1/0242/21); Russian Science Foundation (RSF Grant No: 22–14-00037); Department of Science and Technology (DST), Science and Engineering Research Board, New Delhi, India (Grant No. EEQ/2021/000243); Rufford Foundation, UK (Grant No. 36737-1) and Asian Herpetological Association (Asosiasi Herpetologi Asia), Indonesia (Grant No: AHA-2022/AATA/01).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

ORCID

Amarasinghe A. Thasun Amarasinghe  <https://orcid.org/0000-0002-4151-1806>
 Rafaqat Masroor  <https://orcid.org/0000-0001-6248-546X>
 Hmar T. Lalremsanga  <https://orcid.org/0000-0002-3080-8647>
 Sanjaya Weerakkody  <https://orcid.org/0000-0002-6178-887X>
 Natalia B. Ananjeva  <https://orcid.org/0000-0003-2288-0961>
 Patrick D. Campbell  <https://orcid.org/0000-0001-7473-7740>
 Stevie R. Kennedy-Gold  <https://orcid.org/0000-0003-1729-7878>
 Sanjaya K. Bandara  <https://orcid.org/0000-0003-0434-8525>
 Andrey M. Bragin  <https://orcid.org/0000-0002-3621-9763>
 Atthanagoda K. A. Gayan  <https://orcid.org/0000-0003-3301-4081>
 Vivek R. Sharma  <https://orcid.org/0000-0001-9049-9201>
 Amit Sayyed  <https://orcid.org/0000-0002-1244-7809>
 Lal Biakzuala  <https://orcid.org/0000-0001-5142-3511>
 Andradige S. Kanishka  <https://orcid.org/0000-0002-3842-9414>
 Sumaithangi R. Ganesh  <https://orcid.org/0000-0002-1947-8093>
 Ivan Ineich  <https://orcid.org/0000-0003-1235-1505>
 Anslem de Silva  <https://orcid.org/0000-0001-7899-5237>
 Lakshman J. M. Wickramasinghe  <https://orcid.org/0000-0002-9597-7070>

Sampath S. Seneviratne  <https://orcid.org/0000-0003-2159-4410>

Nikolay A. Poyarkov  <https://orcid.org/0000-0002-7576-2283>

Gernot Vogel  <https://orcid.org/0000-0002-4542-518X>

Daniel Jablonski  <https://orcid.org/0000-0002-5394-0114>

REFERENCES

- Agarwal, I., Bauer, A. M., Gamble, T., Giri, V. B., Jablonski, D., Khandekar, A., Mohapatra, P. P., Masroor, R., Mishra, A., & Ramakrishnan, U. (2022). The evolutionary history of an accidental model organism, the leopard gecko *Eublepharis macularius* (Squamata: Eublepharidae). *Molecular Phylogenetics & Evolution*, 168, 107414. <https://doi.org/10.1016/j.ympev.2022.107414>
- Amarasinghe, A. A. T., Bandara, S. K., Weerakkody, S., Campbell, P. D., Marques, D. A., Danushka, A. D., de Silva, A., & Vogel, G. (2022). Systematics of the Sri Lankan water snakes of the genus *Fowlea* Theobald, 1868 (Reptilia: Natricidae). *Herpetologica*, 78, 201–219. <https://doi.org/10.1655/Herpetologica-D-22-00004>
- Amarasinghe, A. A. T., & Campbell, P. D. (2016). On the resolution of a long standing issue surrounding the holotype of *Cnemaspis podihuna* Deraniyagala, 1944 (Reptilia: Gekkonidae). *Zootaxa*, 4137, 296–300. <https://doi.org/10.11646/zootaxa.4137.2.12>
- Amarasinghe, A. A. T., Karunarathna, S., Campbell, P. D., Gayan, A. K. A., Ranasinghe, W. D. B., de Silva, A., & Mirza, Z. A. (2022b). The hidden diversity and inland radiation of Sri Lanka's ground-dwelling geckos of the genus *Cyrtodactylus* (Reptilia: Gekkonidae). *Systematics and Biodiversity*, 20, 1–25. <https://doi.org/10.1080/14772000.2022.2039319>
- Amarasinghe, A. A. T., Karunarathna, S., Campbell, P. D., Madawala, M., & de Silva, A. (2021). A new species of *Hemidactylus* Goldfuss, 1820 (Reptilia: Gekkonidae) from Sri Lanka with re-description of *H. hunae* Deraniyagala, 1937. *Herpetologica*, 77, 259–272. <https://doi.org/10.1655/Herpetologica-D-21-00003.1>
- Annandale, N. (1906). Notes on the fauna of a desert tract in southern India. Part. I. Batrachians and reptiles, with remarks on the reptiles of the desert region of the North-West Frontier. *Memoirs of the Asiatic Society of Bengal Calcutta*, 1, 183–202.
- Bandara, S. K., Ganesh, S. R., Kanishka, A. S., Danushka, A. D., Sharma, V. R., Campbell, P. D., Ineich, I., Vogel, G., & Amarasinghe, A. A. T. (2022). Taxonomic composition of the *Oligodon arnensis* (Shaw, 1802) species complex (Squamata: Colubridae) with the description of a new species from India. *Herpetologica*, 78, 51–73. <https://doi.org/10.1655/Herpetologica-D-21-00026.1>
- Barbour, T. (1912). A contribution to the zoogeography of the east Indian islands. *Memoirs of the Museum of Comparative Zoology*, 44, 1–204.
- Bauer, A. M. (2015). Patrick Russell's snakes and their role as type specimens. *Hamadryad*, 37, 18–65.
- Beddome, R. H. (1862). Notes upon the land and fresh-water snakes of the Madras Presidency. Madras Quart. *Journal of the Medical Sciences*, 5, 1–31.
- Bouckaert, R. R. (2010). DensiTree: Making sense of sets of phylogenetic trees. *Bioinformatics*, 26, 1372–1373. <https://doi.org/10.1093/bioinformatics/btq110>
- Boulenger, G. A. (1890). *The Fauna of British India, including Ceylon and Burma. Reptilia and Batrachia*. Taylor & Francis.
- Boulenger, G. A. (1891). Notes on Transcaspian reptiles. *Proceedings of the Zoological Society of London*, 1, 628–633.
- Burbrink, F. T., Lawson, R., & Slowinski, J. B. (2000). Mitochondrial DNA phylogeography of the polytypic north American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. *Evolution*, 54, 2107–2118. [https://doi.org/10.1554/0014-3820\(2000\)054\[2107:mdpotp\]2.0.co;2](https://doi.org/10.1554/0014-3820(2000)054[2107:mdpotp]2.0.co;2)
- Cantor, T. E. (1847). Catalogue of reptiles inhabiting the Malayan peninsula and islands. *Journal of the Asiatic Society of Bengal*, 16, 608–954.
- Chan, K. O., & Grismer, L. L. (2022). GroupStruct: An R package for allometric size correction. *Zootaxa*, 5124(4), 471–482. <https://doi.org/10.11646/zootaxa.5124.4.4>
- Chernov, S. A. (1935). New material on the distribution of the Indian snake *Lycodon striatus* (Shaw) (Ophidia, Colubridae) in soviet middle Asia [in Russian]. *Comptes Rendus (Doklady) de l'Académie Des Sciences de l'URSS*, 3, 189–192.
- Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: A computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657–1659. <https://doi.org/10.1046/j.1365-294x.2000.01020.x>
- Constable, J. D. (1949). Reptiles from the Indian peninsula in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology at Harvard*, 103, 59–160.
- Daniel, J. C. (2002). *The book on Indian Reptiles and Amphibians*. Bombay Natural History Society. Oxford Press.
- Daudin, F. M. (1803). *Histoire Naturelle, Générale et Particulière des Reptiles; Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et Partie du Cours Complet d'Histoire Naturelle Rédigé par C.S. Sonnini, membre de plusieurs sociétés savantes*. Tome sixième. F. Dufart.
- Das, I. (2002). *A photographic guide to snakes and other reptiles of India*. New Holland Publisher.
- Das, I., & De Silva, A. (2005). *A photographic guide to snakes and other reptiles of Sri Lanka*. New Holland Publisher.
- Deraniyagala, P. E. P. (1953). *A coloured atlas of some vertebrates from Ceylon vol. 2 Tetrapod Reptilia*. Ceylon Government Press.
- de Silva, A. (2009). *Snakes of Sri Lanka: A coloured atlas*. Vijitha Yapa Publications.
- De Silva, P. H. D. H. (1969). Taxonomic studies on Ceylon snakes of the family Colubridae. *Spolia Zeylanica*, 31, 431–546.
- De Silva, P. H. D. H. (1980). *Snake Fauna of Sri Lanka with special reference to skull, Dentition and Venom in Snakes*. National Museum of Sri Lanka.
- Deraniyagala, P. E. P. (1955). *A colored atlas of some vertebrates from Ceylon, Volume 3: Serpentine reptilia*. Ceylon National Museums.
- Dowling, H. G. (1951). A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–98.
- Dowling, H. G., & Savage, J. M. (1960). A guide to the snake hemipenis: A survey of basic structure and systematic characteristics. *Zoologica*, 45, 17–28.
- Dubey, B., Meganathan, P. R., Vidal, N., & Haque, I. (2012). Molecular evidence for the nonmonophyly of the Asian natriacid genus *Xenochrophis* (Serpentes, Colubroidea) as inferred from mitochondrial and nuclear genes. *Journal of Herpetology*, 46, 263–268.
- Dufresnes, C., Mahony, S., Prasad, V. K., Kamei, R. G., Masroor, R., Khan, M. A., Al-Johany, A. M., Gautam, K. B., Gupta, S. K., Borjesson, L. J., Melnikov, D. A., Rosanov, J. M., Skopinov, D. V., Borzee, A., Jablonski, D., & Litvinchuk, S. N. (2022). Shedding light on taxonomic chaos: Diversity and distribution of south Asian skipper frogs (Anura, Dicroglossidae,

- Euphlyctis). *Systematics and Biodiversity*, 20, 2102686. <https://doi.org/10.1080/14772000.2022.2102686>
- Duméril, A. M. C., Bibron, G., & Duméril, A. H. A. (1854). *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome 7 (Première partie)*. Librairie Encyclopédique de Roret.
- Faiz, A. U. H., Abbas, F., Bagaturov, M. F., Zahra, L., Hassan, M. U., & Akahter, T. (2018). A first finding and a new species of Wolf-Snake (*Lycodon mackinnoni* Wall, 1906) of the Ophidian Fauna of Azad Kashmir (Pakistan). *Current Studies in Herpetology*, 18, 153–158. <https://doi.org/10.18500/1814-6090-2018-18-3-4-153-158>
- Ferguson, W. (1877). *Reptile Fauna of Ceylon. Letter on a Collection Sent to the Colombo Museum*. Colombo, Sri Lanka.
- Ganesh, S. R., Amarasinghe, A. A. T., & Vogel, G. (2020). Redescription of *Lycodon travancoricus* (Beddome, 1870) (Reptilia: Colubridae), an Indian endemic snake, with a review of its geographic range. *Taprobanica*, 9, 50–58. <https://doi.org/10.47605/tapro.v9i1.221>
- Ganesh, S. R., Deuti, K., Punith, K. G., Achyuthan, N. S., Mallik, A. K., Adhikari, O., & Vogel, G. (2020). A new species of *Lycodon* (Serpentes: Colubridae) from the Deccan plateau of India, with notes on the range of *Lycodon travancoricus* (Beddome, 1870) and a revised key to peninsular Indian forms. *Amphibian & Reptile Conservation*, 14, 74–83.
- Ganesh, S. R., & Vogel, G. (2018). Taxonomic reassessment of the common Indian wolf snakes *Lycodon aulicus* (Linnaeus, 1758) complex (Squamata: Serpentes: Colubridae). *Bonn Zoological Bulletin*, 67, 25–36.
- Gans, C., Gaunt, A. S., & Adler, K. (Eds.). (2008). *Biology of the Reptilia, Volume 20: Morphology H, the skull of Lepidosauria*. Society for the Study of Amphibians and Reptiles.
- Gowande, G., Pal, S., Jablonski, D., Masroor, R., Phansalkar, P., D'Souza, P., Jayarajan, A., & Shanker, K. (2021). Molecular phylogenetics and morphology of the widespread agamid species *Calotes versicolor* (Daudin, 1802) (Squamata, Agamidae) support taxonomic reassessment across South Asia. *Vertebrate Zoology*, 71, 669–696. <https://doi.org/10.3897/vz.71.e62787>
- Green, E. E. (1904). *Lycodon Striatus* in Ceylon. *Spolia Zeylanica*, 2, 205.
- Günther, A. C. L. G. (1863). Third account of new species of snakes in the collection of the British museum. The Annals and Magazine of Natural History. *Zoology, Botany, and Geology*, 2, 348–367.
- Günther, A. (1858). *Catalogue of Colubrine snakes in the collection of the British Museum*. Board of Trustees.
- Günther, A. C. L. G. (1864). *The reptiles of British India*. Taylor and Francis.
- ICZN (International Code of Zoological Nomenclature). (1999). *International code of zoological nomenclature* (4th ed.). International Trust for Zoological Nomenclature.
- Ingoldby, C. M. (1923). Notes on a collection of Reptilia from Waziristan and the adjoining portion of the N.W. Frontier Province. *Journal of the Bombay Natural History Society*, 29, 117–130.
- Jablonski, D., Masroor, R., & Hofmann, S. (2021). Revisited molecular phylogeny of the genus *Sphaerotheca* (Anura: Dicoglossidae): The biogeographic status of northernmost populations and further taxonomic changes. *Diversity*, 13, 216. <https://doi.org/10.3390/d13050216>
- Jablonski, D., Masroor, R., & Hofmann, S. (2022). On the edge of the Shivaliks: An insight into the origin and taxonomic position of Pakistani toads from the *Duttaphrynus melanostictus* complex (amphibia: Bufonidae). *Zoosystematics & Evolution*, 98, 275–284. <https://doi.org/10.3897/zse.98.79213>
- Jablonski, D., Masroor, R., Khan, M., & Altaf, M. (2019). Addition to the snake fauna of Pakistan: Mackinnon's wolf Snake, *Lycodon mackinnoni* Wall, 1906. *Herpetological Bulletin*, 147, 21–23. <https://doi.org/10.33256/hb147.2123>
- Jan, G. (1863). *Elenco Sistematico degli Ofidi descritti e disegnati per l'Iconografia Generale*. A. Lombardi.
- Jerdon, T. C. (1854). Catalogue of the Reptiles inhabiting the Peninsula of India, Part 2. *Journal of the Asiatic Society of Bengal*, 22, 522–534.
- Kalki, Y., Gowda, S., Agnivamshi, M., Singh, K., Patel, H., & Mirza, Z. A. (2020). On the taxonomy and systematics of the recently described *Lycodon deccanensis* Ganesh, Deuti, Punith, Achyuthan, Mallik, Adhikari, Vogel, 2020 (Serpentes, Colubridae) from India. *Evolutionary Systematics*, 4, 109–118. <https://doi.org/10.3897/evolsyst.4.60570>
- Karunarathna, D. M. S. S., & Amarasinghe, A. A. T. (2011). A preliminary survey of the reptile fauna in Nilgala forest and its vicinity, Monaragala District, Sri Lanka. *Taprobanica*, 3, 69–76. <https://doi.org/10.47605/tapro.v3i2.49>
- Karunarathna, D. M. S. S., & Amarasinghe, A. A. T. (2012). Reptile diversity in Beraliya Mukalana proposed forest reserve, Galle District, Sri Lanka. *Taprobanica*, 4, 20–26. <https://doi.org/10.47605/tapro.v4i1.61>
- Karunarathna, D. M. S. S., Amarasinghe, A. A. T., Gabadage, D. E., Bahir, M. M., & Harding, L. E. (2010). Current status of faunal diversity in Bellanwila–Attidiya sanctuary, Colombo District - Sri Lanka. *Taprobanica*, 2, 48–63. <https://doi.org/10.47605/tapro.v2i1.27>
- Karunarathna, D. M. S. S., Henkanathgedara, S. M., Amarasinghe, A. A. T., & de Silva, A. (2013). Impact of vehicular traffic on herpetofaunal mortality in a savannah forest, eastern Sri Lanka. *Taprobanica*, 5, 111–119. <https://doi.org/10.47605/tapro.v5i2.106>
- Kazemi, E., Nazarizadeh, M., Fatemizadeh, F., Khani, A., & Kaboli, M. (2021). The phylogeny, phylogeography, and diversification history of the westernmost Asian cobra (Serpentes: Elapidae: *Naja oxiana*) in the Trans-Caspian region. *Ecology and Evolution*, 11, 2024–2039.
- Khan, M. S. (2002). *Guide to the snakes of Pakistan*. Edition Chimaira.
- Khan, M. S. (2003). Key and checklist to the snakes of Pakistan with special reference to the venomous snakes. *Pakistan Journal of Zoology*, 1, 1–53.
- Khan, M. S. (2006). *Amphibians and reptiles of Pakistan*. Krieger Publishing Company.
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA 7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. <https://doi.org/10.1093/molbev/mss020>
- Lanza, B. (1999). A new species of *Lycodon* from The Philippines, with a key to the genus (Reptilia: Serpentes: Colubridae). *Tropical Zoology*, 12, 89–104.
- Lawson, R., Slowinski, J. B., Crother, B., & Burbrink, F. (2005). Phylogeny of the Colubroidea (Serpentes): New evidence from

- mitochondrial and nuclear genes. *Molecular Phylogenetics & Evolution*, 37, 581–601. <https://doi.org/10.1016/j.ympev.2005.07.016>
- Lei, J., Sun, X., Jiang, K., Vogel, G., Booth, D. T., & Ding, L. (2014). Multilocus phylogeny of *Lycodon* and the taxonomic revision of *Oligodon multizonatum*. *Asian Herpetological Research*, 5, 26–37. <https://doi.org/10.3724/SP.J.1245.2014.00026>
- Leigh, J. W., & Bryant, D. (2015). PopART: Full-feature software for haplotype network construction. *Methods in Ecology & Evolution*, 6, 1110–1116. <https://doi.org/10.1111/2041-210X.12410>
- Leviton, A. E., & Anderson, S. C. (1970). The amphibians and reptiles of Afghanistan, a checklist and key to the Herpetofauna. *Proceedings of the California Academy of Sciences*, 38, 163–206.
- Lleonart, J., Salat, J., & Torres, G. J. (2000). Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205, 85–93.
- Lohani, A., Kadariya, R., Paudel, U., Shrestha, B. P., & Bahadur, K. C. R. (2022). A survey of Snake diversity in Bardiya National Park and associated corridor Forest in Nepal. *Reptiles & Amphibians*, 29, 182–186. <https://doi.org/10.17161/landa.v29i1.16293>
- Mallik, A. K., Srikanthan, A. N., Pal, S. P., D'Souza, P. M., Shanker, K., & Ganesh, S. R. (2020). Disentangling vines: A study of morphological crypsis and genetic divergence in vine snakes (Squamata: Colubridae: *Ahaetulla*) with the description of five new species from peninsular India. *Zootaxa*, 4874, 1–62. <https://doi.org/10.11646/zootaxa.4874.1.1>
- Manhas, A., Wanganeo, R. R. N., & Wanganeo, A. (2015). First record of Himalayan wolf snake (*Lycodon mackinnoni* Wall, 1906) in Doda District of lower Himalayas, Jammu and Kashmir, India. *World Research Journal Biology of Biological Sciences*, 1, 2–4.
- Minh, B. Q., Nguyen, M. A. T., & von Haeseler, A. (2013). Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30, 1188–1195. <https://doi.org/10.1093/molbev/mst024>
- Minton, S. A. (1966). A contribution to the herpetology of the Western Pakistan. *Bulletin of the American Museum and Natural History*, 134, 27–184.
- Mohapatra, P. P., Ingle, M., & Chandra, K. (2021). *Snakes of Central India*. Zoological Survey of India.
- Murray, J. A. (1884). *The vertebrate zoology of Sind: A systematic account, with descriptions of all the known species of mammals, birds, and reptiles inhabiting the province observations on their habits; tables of their geographical distribution in Persia, Beloochistan, and Afghanistan; Punjab, north-west provinces, and the peninsula of India generally*. Education Society's Press Byculla.
- Nawani, S., Deepak, V., Gautam, K., Gupta, S., Boruah, B., & Das, A. (2021). Systematic status of the rare Himalayan wolf snake *Lycodon mackinnoni* Wall, 1906 (Serpentes: Colubridae). *Zootaxa*, 4966, 305–320. <https://doi.org/10.11646/zootaxa.4966.3.3>
- Nikolsky, A. M. (1903). Sur trois nouvelles espèces de reptiles, recueillies par Mr. N. Zarudny dans la Perse orientale en 1901 [In Russian and Latin]. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Pétersbourg*, 8, 95–98.
- Orlov, N. L., Atayev, C. A., Ananjeva, N. B., Shammakov, S. M., & Shestopal, A. A. (2018). *Pieces of tropical mesophilic herpetofauna in the deserts of Turkmenistan. Herpetological and ornithological research: Current aspects. Dedicated to the 100th anniversary of A.K. Rustamov (1917–2005)*. KMK Scientific Press.
- Pandey, D. P., Jelic, D., Sapkota, S., Lama, H. M., Lama, B., Pokharel, K., Goode, M. J., & Kuch, U. (2018). New records of snakes from Chitwan National Park and vicinity, Central Nepal. *Herpetology Notes*, 11, 679–696.
- Pyron, R. A., Kandambi, D. H. K., Hendry, C. R., Pushpamal, V., Burbrink, F. T., & Somaweera, R. (2013). Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Molecular Phylogenetics & Evolution*, 66, 969–978. <https://doi.org/10.1016/j.ympev.2012.12.004>
- R Core Team. (2021). *R: A language and environment for statistical computing, version 4.0.4*. R Foundation for Statistical Computing <https://www.R-project.org/>
- Rambaut, A. (2014). *FigTree Version 1.4.2*. University of Edinburgh <http://tree.bio.ed.ac.uk/software/figtree/>
- Rambaut, A., & Drummond, A. J. (2009). *Tracer: MCMC trace analysis tool, version 1.5*. University of Oxford.
- Rawat, Y., Bhattarai, S., Poudyal, L., & Subedi, N. (2020). Herpetofauna of Shuklaphanta National Park, Nepal. *Journal of Threatened Taxa*, 12, 15587–15611. <https://doi.org/10.11609/jott.5611.12.5.15587-15611>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B. R., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sánchez-Gracia, A. (2017). dnap 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution*, 34, 3299–3302. <https://doi.org/10.1093/molbev/msx248>
- Russell, P. (1796). *An account of Indian serpents, collected on the coast of Coromandel; containing descriptions and drawings of each species; together with experiments and remarks on their several poisons*. George Nicol.
- Sabaj, M. H. (2020). Codes for natural history collections in ichthyology and herpetology. *Copeia*, 108(2), 593–669. <https://doi.org/10.1643/ASIHCODONS2020>
- Sclater, W. L. (1891). Notes on a collection of snakes in the Indian museum, with descriptions of several new species. *Journal of the Asiatic Society of Bengal*, 60, 230–250.
- Seshadri, K. S. (2017). *Lycodon striatus* (barred Wolf Snake) diet. *Herpetological Review*, 48, 676–677.
- Shaw, G. (1802). *General zoology or systematic natural history, Volume 3, Part 2*. G. Kearsley, Thomas Davison.
- Siler, C. D., Oliveros, C. H., Santanen, A., & Brown, R. M. (2013). Multilocus phylogeny reveals unexpected diversification patterns in Asian wolf snakes (genus *Lycodon*). *Zoologica Scripta*, 42, 262–277. <https://doi.org/10.1111/zsc.12007>
- Sindaco, R., Venchi, A., & Grieco, C. (2013). *The reptiles of the Western palearctic 2: Annotated checklist and distributional atlas of the snakes of Europe, North Africa, the Middle East and Central Asia, with an update to the Volume 1*. Societas Herpetologica Italica.
- Smith, M. A. (1943). *The Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese subregion. Reptilia and Amphibia: Volume III, Serpentes*. Taylor & Francis.
- Somaweera, R. (2005). A bark gecko (*Hemidactylus leschenaultii*) preying on a wolf snake (*Lycodon striatus sinhaleysus*). *Gekko*, 4, 8–10.

- Somaweera, R. (2006). *Snakes of Sri Lanka [In Sinhalese]*. Wildlife Heritage Trust of Sri Lanka.
- Soubrier, J., Steel, M., Lee, M. S., Der Sarkissian, C., Guindon, S., Ho, S. Y., & Cooper, A. (2012). The influence of rate heterogeneity among sites on the time dependence of molecular rates. *Molecular Biology and Evolution*, *29*, 3345–3358. <https://doi.org/10.1093/molbev/mss140>
- Stamatakis, A. (2014). RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Szczerbak, N. N. (2003). *Guide to the reptiles of the eastern palearctic* (1st ed.). Krieger Publication Co.
- Terentjev, P. V., & Chernov, S. A. (1949). *Key to amphibians and reptiles*. Israel Program for Scientific Translations.
- Theobald, W. (1876). *Descriptive catalogue of the reptiles of British India*. Thacker Spink & Co.
- Thompson, J. D., Gibson, T. J., & Higgins, D. G. (2003). Multiple sequence alignment using ClustalW and ClustalX. *Current Protocols in Bioinformatics*, *2003*, 2.3.1–2.3.22. <https://doi.org/10.1002/0471250953.bi0203s00>
- Vogel, G., & David, P. (2019). A new species of the *Lycodon fasciatus* complex from the Khorat plateau, eastern Thailand (reptiles, Squamata, Colubridae). *Zootaxa*, *4577*, 515–528. <https://doi.org/10.11646/zootaxa.4577.3.6>
- Voris, K. H. (2000). Maps of Pleistocene Sea levels in South Asia: Shorelines, river systems and time durations. *Journal of Biogeography*, *27*, 1153–1167. <https://doi.org/10.1046/j.1365-2699.2000.00489.x>
- Wagner, P., Bauer, A. M., Leviton, A. E., Wilms, T. M., & Böhme, W. (2016). A checklist of the amphibians and reptiles of Afghanistan. Exploring herpetodiversity using biodiversity archives. *Proceedings of the Californian Academy of Sciences*, *63*, 457–565.
- Wall, F. (1909). A popular treatise on the common Indian snakes. *Journal of the Bombay Natural History Society*, *19*, 87–106.
- Wall, F. (1921). *Ophidia Taprobanica or the snakes of Ceylon*. Sri Lanka.
- Wall, F. (1923). A hand-list of the snakes of the Indian Empire. *Journal of the Bombay Natural History Society*, *29*, 598–632.
- Wallach, V., Williams, K. L., & Boundy, J. (2014). *Snakes of the world: A catalogue of living and extinct species*. CRC Press.
- Wang, K., Yu, Z., Vogel, G., & Che, J. (2021). Contribution to the taxonomy of the genus *Lycodon* H. Boie in Fitzinger, 1827 (Reptilia: Squamata: Colubridae) in China, with description of two new species and resurrection and elevation of *Dinodon septentrionale chapaense* angel, Bourret, 1933. *Zoological Research*, *42*, 62–86. <https://doi.org/10.24272/j.issn.2095-8137.2020.286>
- Whitaker, R., & Captain, A. (2004). *Snakes of India: The field guide*. Draco Books.
- Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Prentice Hall Inc.

SUPPORTING INFORMATION

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

How to cite this article: Amarasinghe, A. A. T., Masroor, R., Lalremsanga, H. T., Weerakkody, S., Ananjeva, N. B., Campbell, P. D., Kennedy-Gold, S. R., Bandara, S. K., Bragin, A. M., Gayan, A. K. A., Sharma, V. R., Sayyed, A., Biakzuala, L., Kanishka, A. S., Ganesh, S. R., Ineich, I., de Silva, A., Wickramasinghe, L. J. M., Seneviratne, S. S. ... Jablonski, D. (2023). Integrative approach resolves the systematics of barred wolf snakes in the *Lycodon striatus* complex (Reptilia, Colubridae). *Zoologica Scripta*, *00*, 1–24. <https://doi.org/10.1111/zsc.12587>