



A revision of *Lycodon tristrigatus* (Serpentes: Colubridae) in Borneo, with the description of a new species from Gunung Penrissen, Sarawak

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Abstract. We present a systematic revision of *Lycodon tristrigatus* based on morphological and genetic data. A recent study found that the Gunung Penrissen population (western Sarawak, Borneo) is highly divergent from other Bornean populations based on genetic analyses. Here, we reanalysed the published mtDNA and SNP data and conducted additional morphological assessments to clarify the taxonomic status of this population. Our results show that the Gunung Penrissen population forms a distinct genetic lineage and is diagnosable by a unique combination of morphological characters relative to *L. tristrigatus* sensu stricto and closely related congeners. We therefore describe the Gunung Penrissen population as a new species. This discovery underscores Gunung Penrissen as an important centre of reptile endemism in Borneo.

Key words. Malaysia, MIG-seq, phylogeny, Sundaland, taxonomy.

Introduction

The genus *Lycodon* is one of the most species-rich members of Colubridae, currently comprising nearly 80 species distributed from eastern Iran to China and Japan, and southward to the Philippines and the Indo-Australian Archipelago (SILER et al. 2013, NGUYEN et al. 2025). Several genera (e.g., *Cercaspis*, *Dinodon*, *Dryocalamus*, and *Lepturophis*) were historically recognized as distinct, but recent phylogenetic studies have mostly treated them as junior synonyms of *Lycodon* because they are phylogenetically nested within it (GUO et al. 2013, SILER et al. 2013, FIGUEROA et al. 2016, WOSTL et al. 2017). Nevertheless, this taxonomic treatment remains debated, as *Dryocalamus* and *Lepturophis* have each been reported to form well-supported clades that are genetically divergent from other *Lycodon* species (WOSTL et al. 2017, WICKRA-

MASINGHE et al. 2020, BERNSTEIN et al. 2026). Here we use the term “*Dryocalamus* group” as a convenient, informal designation for seven species that were previously assigned to *Dryocalamus*: *Lycodon chithrasekarai*, *L. davisonii*, *L. gracilis*, *L. nympha*, *L. subannulatus*, *L. philippinus*, and *L. tristrigatus*. Members of this group are small arboreal snakes distributed from South Asia (India and Sri Lanka) through the Indochinese region, and the Thai-Malay Peninsula to Sumatra, Borneo, Java, and the Philippines (DAS 2015, WICKRAMASINGHE et al. 2020).

Within Borneo, two members of the *Dryocalamus* group – *L. subannulatus* and *L. tristrigatus* – have been reported historically. *Lycodon tristrigatus* is considered common, whereas *L. subannulatus* has been documented only a few times (STUEBING 1991, STUEBING et al. 2014). Recently, FUKUYAMA et al. (2025) concluded that the two nominal taxa in Borneo are morphologically and genetically indis-

tinguishable, and that Bornean “*L. subannulatus*” should be treated as a colour morph of *L. tristrigatus*. Under that interpretation, the distribution of *L. subannulatus* would be restricted to the Thai-Malay Peninsula (including the Tanintharyi Region of Myanmar), Sumatra, and Java (there are also unconfirmed records from Palawan in the Philippines) and *L. tristrigatus* would be the only member of the group occurring in Borneo (GRISMER et al. 2013, LEE et al. 2018, FUKUYAMA et al. 2025, LEE et al. 2025). However, FUKUYAMA et al. (2025) also reported that a sample identified as *L. tristrigatus* from Gunung Penrissen (western Sarawak, Borneo) is highly divergent from other Bornean samples based on genetic analyses. This observation raises an unresolved taxonomic question: namely, whether the Gunung Penrissen population represents deep intraspecific structure within *L. tristrigatus* or an independently evolving lineage consistent with an undescribed species.

In this study, we reanalyse the genetic dataset provided by FUKUYAMA et al. (2025) and conduct additional molecular phylogenetic and morphological assessments to clarify the taxonomic status of the Gunung Penrissen population. Our results demonstrate that the population is both genetically distinct and morphologically diagnosable from *L. tristrigatus* sensu stricto and other congeners, supporting its recognition as a new species, which we describe herein.

Materials and methods

We examined the morphology of the specimens of *Lycodon subannulatus* and *L. tristrigatus* deposited in the Graduate School of Human and Environmental Studies, Kyoto University (KUHE), Museum Zoologicum Bogoriense (MZB), Osaka Museum of Natural History (OMNH), the Sarawak Forestry Corporation (SFC-GRB), Sarawak Museum (SM), the Sarawak Research Collection, Forest Department Sarawak (SRC), Thailand Museum of Natural History (THNHM) and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum at The National University of Singapore (ZRC).

Snout-vent length (SVL) and tail length (TaL) were measured to the nearest 1 mm, using a flexible measuring tape. Scale terminology followed VOGEL et al. (2009). The number of ventral scales was counted according to the method described by DOWLING (1951). The terminal scute was excluded from the number of subcaudals. Dorsal scale row counts are given at one head length behind the head, at midbody and at one head length before the vent. Values for paired head characters are given in left/right order. The pale body bands were counted on the left side of the body. Incomplete bands were counted as one band, whereas two fused bands were counted as two. Tail bands were not counted because they become indistinct posteriorly. Sex was determined by the presence or absence of hemipenes. This was assessed by dissection of the ventral base of the tail or, when dissection was not possible, inferred from tail shape. Some of the morphological data used in

the study was already reported in FUKUYAMA et al. (2025). Information on morphological characters was also taken from previous studies (TAYLOR 1922, SMITH 1943, WICKRAMASINGHE et al. 2020).

We reanalysed the genetic data of *L. tristrigatus* published by FUKUYAMA et al. (2025). For mtDNA data, we conducted phylogenetic analyses of the mitochondrial cytochrome b (cyt b) region, which is the most widely used gene fragment for taxonomic studies of the genus *Lycodon*. In addition to the cyt b data published by FUKUYAMA et al. (2025), we used cyt b sequences of *Lycodon* species in the *Dryocalamus* group and the Philippine group assigned by WOSTL et al. (2017) as ingroup samples, while *L. albofuscus* and *L. subcinctus* were used as outgroups (Table 1). Sequences were aligned using MAFFT (KATO & STANDLEY 2013) with the default settings. We used maximum-likelihood (ML) methods to conduct phylogenetic analyses. Suitable models were selected using Modeltest-NG (DARRIBA et al. 2020), based on the Bayesian Information Criterion (BIC). The ML analysis was conducted using RAXML-NG (KOZLOV et al. 2019). Support values for internal branches of the ML tree were evaluated based on 1000 bootstrap replicates. We regarded tree topologies with BS of 70% or greater as sufficiently supported (HUELSENBECK & HILLIS 1993). Uncorrected p-distances among the sequences were calculated using MEGA X with the pairwise deletion option (KUMAR et al. 2018). For nuDNA SNP data, we used 1692 genomic SNP loci obtained from 12 individuals using multiplexed inter-simple sequence repeat (ISSR) genotyping by sequencing (MIG-seq; SUYAMA & MATSUKI 2015). SNP calling and genotyping were performed using ipyrad v0.9.61 (EATON & OVERCAST 2020). Reads were clustered at a similarity threshold of 85% (clust_threshold = 0.85). The minimum read depth required for statistical base calling was set to 6 (mindepth_statistical = 6). Only loci present in at least 7 of the 12 individuals were retained for downstream analyses (min_samples_locus = 7). Additional details of the data processing pipeline are provided in FUKUYAMA et al. (2025). We constructed a Neighbour-Net network based on concatenated SNP sequences using SplitsTree 4 (HUSON & BRYANT 2006).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:B3784F53-C5A8-4E51-A246-AFoF207FF787. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: salamandra-journal.com, zenodo.org.

Table 1. Samples used for molecular analysis in this study together with the information on voucher specimens, collection locality, and GenBank accession numbers. Samples 1–4 and 6–13 were used for MIG-seq analysis also. Voucher abbreviations: FMNH = Field Museum of Natural History; KU = University of Kansas Natural History Museum; KUHE = Graduate School of Human and Environmental Studies, Kyoto University; LSUHC = La Sierra University Herpetological Collection; PNM = Philippine National Museum Herpetological Collections; SRC = Sarawak Research Collection, Sarawak Forest Department; USMHC = Universiti Sains Malaysia Herpetological Collection; UTA = University of Texas at Arlington.

Species	Voucher	Locality	DRA Biosample ID for MIG-seq data	cytb	Genbank Reference
1 <i>Lycodon penrissenensis</i> sp. n.	SRC 00890	Malaysia, Sarawak, Penrissen	SAMD00751782	LC798237	FUKUYAMA et al., 2025
2 <i>Lycodon tristrigatus</i>	KUHE 57392	Malaysia, Sarawak, Kubah	SAMD00751773	LC798239	FUKUYAMA et al., 2025
3 <i>Lycodon tristrigatus</i>	SRC 00922	Malaysia, Sarawak, Kubah	SAMD00751783	LC798236	FUKUYAMA et al., 2025
4 <i>Lycodon tristrigatus</i>	KUHE 59841	Malaysia, Sarawak, Bako	SAMD00751774	LC798235	FUKUYAMA et al., 2025
5 <i>Lycodon tristrigatus</i>	KUHE 62439	Malaysia, Sarawak, Bako	–	LC798232	FUKUYAMA et al., 2025
6 <i>Lycodon tristrigatus</i>	SRC 00596	Malaysia, Sarawak, Mulu	SAMD00751775	LC798234	FUKUYAMA et al., 2025
7 <i>Lycodon tristrigatus</i>	SRC 00809	Malaysia, Sarawak, Lambir	SAMD00751776	LC798238	FUKUYAMA et al., 2025
8 <i>Lycodon tristrigatus</i>	SRC 00819	Malaysia, Sarawak, Lambir	SAMD00751777	LC798233	FUKUYAMA et al., 2025
9 <i>Lycodon tristrigatus</i>	SRC 00844	Malaysia, Sarawak, Lambir	SAMD00751778	LC798231	FUKUYAMA et al., 2025
10 <i>Lycodon tristrigatus</i>	SRC 00855	Malaysia, Sarawak, Lambir	SAMD00751779	LC798230	FUKUYAMA et al., 2025
11 <i>Lycodon tristrigatus</i>	SRC 00875	Malaysia, Sarawak, Lambir	SAMD00751780	LC798229	FUKUYAMA et al., 2025
12 <i>Lycodon tristrigatus</i>	SRC 00883	Malaysia, Sarawak, Lambir	SAMD00751781	LC798240	FUKUYAMA et al., 2025
13 <i>Lycodon tristrigatus</i>	SRC 201908–S270	Malaysia, Sarawak, Lambir	SAMD00751784	–	FUKUYAMA et al., 2025
14 <i>Lycodon tristrigatus</i>	FMNH 269033	Malaysia, Sarawak, Bintulu	–	KX660474	FIGUEROA et al., 2016
15 <i>Lycodon subannulatus</i>	LSUHC 5051	Malaysia, Pahang, Tioman Island	–	KX660498	FIGUEROA et al., 2016
16 <i>Lycodon subannulatus</i>	LSUHC 5576	–	–	KX660499	FIGUEROA et al., 2016
17 <i>Lycodon davisonii</i>	FMNH 255034	Laos, Khammouan	–	KX660473	FIGUEROA et al., 2016
18 <i>Lycodon davisonii</i>	LSUHC 8479	Cambodia, Cardamom	–	KX660497	FIGUEROA et al., 2016
19 <i>Lycodon nympha</i>	RAP 0536	Sri Lanka, Matale	–	KC347477	PYRON et al., 2013
20 <i>Lycodon alcalai</i>	KU 327847	Philippines, Bataan Peninsula	–	KC010344	SILER et al., 2013
21 <i>Lycodon alcalai</i>	KU 327848	Philippines, Sabtang Island	–	KC010345	SILER et al., 2013
22 <i>Lycodon bibonius</i>	KU 304589	Philippines, Camiguin Norte Island	–	KC010351	SILER et al., 2013
23 <i>Lycodon chrysoprateros</i>	KU 307720	Philippines, Dalupiri Island	–	KC010360	SILER et al., 2013
24 <i>Lycodon dumerilii</i>	KU 305168	Philippines, Dinagat Island	–	KC010362	SILER et al., 2013
25 <i>Lycodon dumerilii</i>	PNM 7751	Philippines, Leyte Island	–	KC010363	SILER et al., 2013
26 <i>Lycodon muelleri</i>	KU 323384	Philippines, Luzon Island	–	KC010374	SILER et al., 2013
27 <i>Lycodon muelleri</i>	KU 313891	Philippines, Luzon Island	–	KC010385	SILER et al., 2013
28 <i>Lycodon albofuscus</i>	USMHC 1457	Malaysia, Penang	–	KX822584	WOSTL et al., 2017
29 <i>Lycodon subcinctus</i>	UTA–R 63046	Indonesia, Bengkulu	–	KX822582	WOSTL et al., 2017

Results

The ML phylogenetic tree inferred from mitochondrial cyt b data supported a clade comprising *L. subannulatus* and *L. tristrigatus* (BS = 100%) (Fig. 1A). This clade was separated into three groups corresponding to *L. tristrigatus* from Gunung Penrissen, *L. subannulatus*, and *L. tristrigatus* excluding Gunung Penrissen. These latter two groups were recovered as sister to one another, while *L. tristrigatus* from Gunung Penrissen was the earliest diverging lineage in the clade although the relationships among the three lin-

eages were poorly resolved (BS = 51%). The clade containing *Lycodon tristrigatus* excluding Gunung Penrissen consisted of two subclades, one composed of samples from eastern Sarawak (Mulu, Lambir, Bintulu) and the other composed of samples from western Sarawak (Bako and Kubah). The uncorrected cyt b p-distances between *L. tristrigatus* from Gunung Penrissen and *L. subannulatus* were 7.8–7.9%, whereas those between *L. tristrigatus* from Gunung Penrissen and *L. tristrigatus* populations outside Gunung Penrissen were 8.4–10.2%. The Neighbour-Net based on the nuclear SNPs showed that *L. tristrigatus* consists of three

clusters corresponding to *L. tristrigatus* from Gunung Penrissen, *L. tristrigatus* from eastern Sarawak and *L. tristrigatus* from western Sarawak (excluding Gunung Penrissen), and that the Gunung Penrissen lineage was highly divergent from the other two groups (Fig. 1B). In addition, *L. tristrigatus* from Gunung Penrissen can be distinguished from all other species of the genus by several morphological characters. Thus, we describe this lineage as a new species below.

Taxonomy

Lycodon penrissenensis FUKUYAMA & NISHIKAWA sp. n. Figs 2–4

ZooBank LSID: urn:lsid:zoobank.org:act:4F8EC75A-14AA-449C-A7EC-F96F60F7D5B9

Dryocalamus subannulatus: DAS et al. 2016.

Dryocalamus tristrigatus: FUKUYAMA et al. 2025.

Holotype: Adult female (SRC 00890; field number: KUHE 201811-S90) collected by Ibuki Fukuyama at 21:00 h on 1 January 2019 at Gunung Penrissen, Padawan, Kuching, Sarawak, Malaysia (1.12259° N, 110.22866° E; 1035 m above sea level).

Paratype: Adult female (SFC-GRB-01225; field number: TH1981) collected by Kanto Nishikawa at about 17:45 h on 21 February 2012 at the same locality as holotype.

Etymology: The specific epithet *penrissenensis* is derived from Gunung Penrissen, where this species occurs.

Diagnosis: *Lycodon penrissenensis* sp. n. can be distinguished from all other members of the genus *Lycodon* by a combination of the following morphological characters: SVL 320–428 mm; relative tail length (TaL/TL) = 27.3–27.8% in females; 15 dorsal scale rows at midbody; cloacal plate undivided; 203–205 ventrals all with a strong lateral keel; 98–105 paired subcaudals in females; no preocular and two postoculars; seven supralabials, third and fourth entering orbit; seven or eight infralabials (Table 2, S1).

Description of the holotype: Female, SVL 320 mm; TaL 120 mm, relative tail length 27.3%; head length (HL) 10.6 mm from anterior edge of rostral to posterior end of mandible; head width (HW) 6.4 mm at broadest point; head distinct from neck; snout 3.8 mm from front of rostral to anterior edge of eye; eye large, 1.9 mm in length; pupil slightly vertically elliptical; rostral width 2.7 mm; internasals 1.3 mm in length and 1.5 mm in width, contacting only the na-

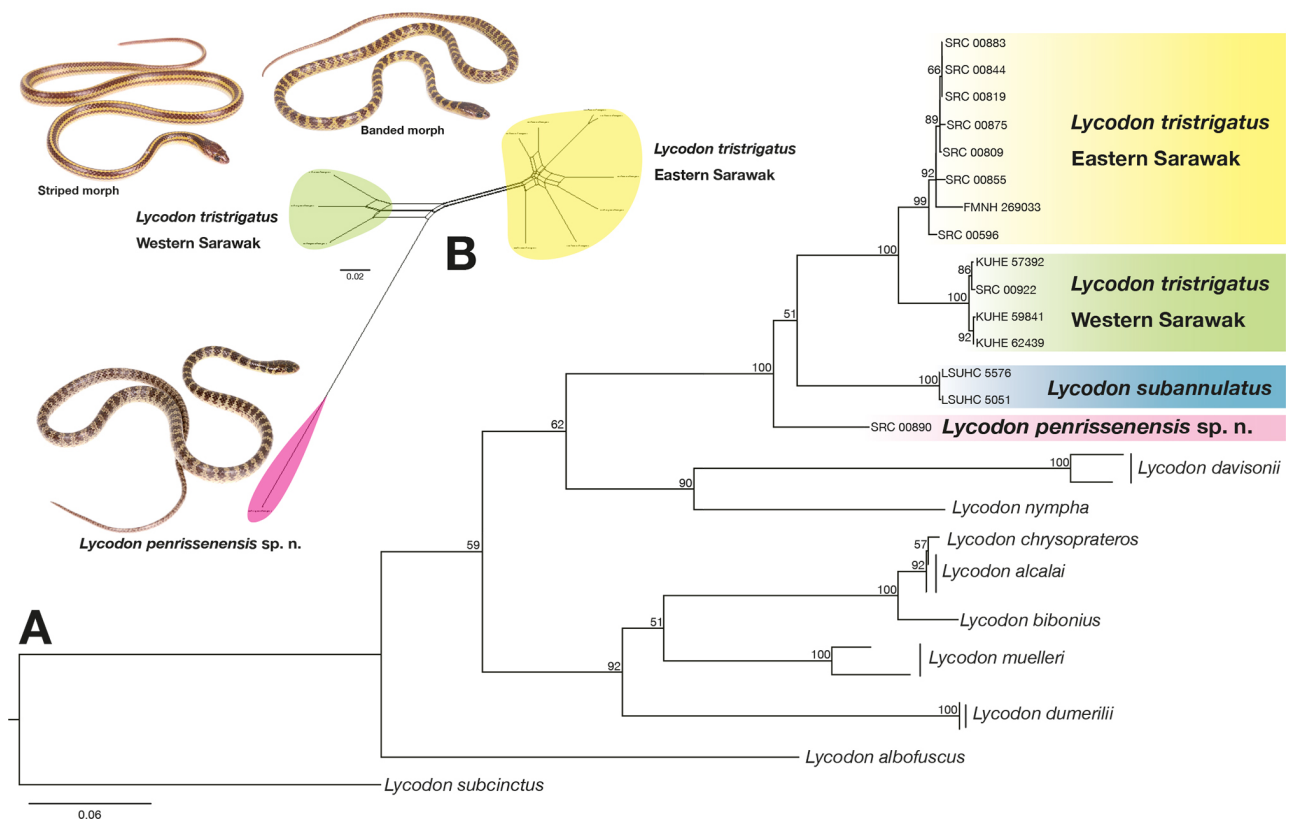


Figure 1. (A) Maximum likelihood tree based on the mitochondrial cyt b gene for samples of *Lycodon*. Numbers above or below branches represent bootstrap supports. (B) Neighbour-Net network of *Lycodon tristrigatus* and *Lycodon penrissenensis* sp. n. based on 1692 genomic SNP loci obtained by MIG-seq.

sals laterally; length of internasal suture 1.0 mm; prefrontals wider than long, in contact laterally with nasal, loreal, and supraocular; length of prefrontal suture 1.2 mm; frontal 4.4 mm in length and 2.8 mm in width; supraoculars 2.9 mm in length and 1.5 mm in width; parietals 5.0 mm in length

and 3.0 mm in width; length of parietal suture 3.1 mm; 2 + 2 temporals, touching parietal laterally; no preocular; two postoculars; 1 loreal, 1.5 mm in length and 0.6 mm in width, in contact with nasal, prefrontal, supraocular, eye, and 2nd and 3rd supralabials; 7/7 supralabials, 1st and 2nd in contact



Figure 2. Dorsal (A) and ventral (B) views of holotype of *Lycodon penrissenensis* sp. n. (SRC 00890). Scale bar = 50 mm.

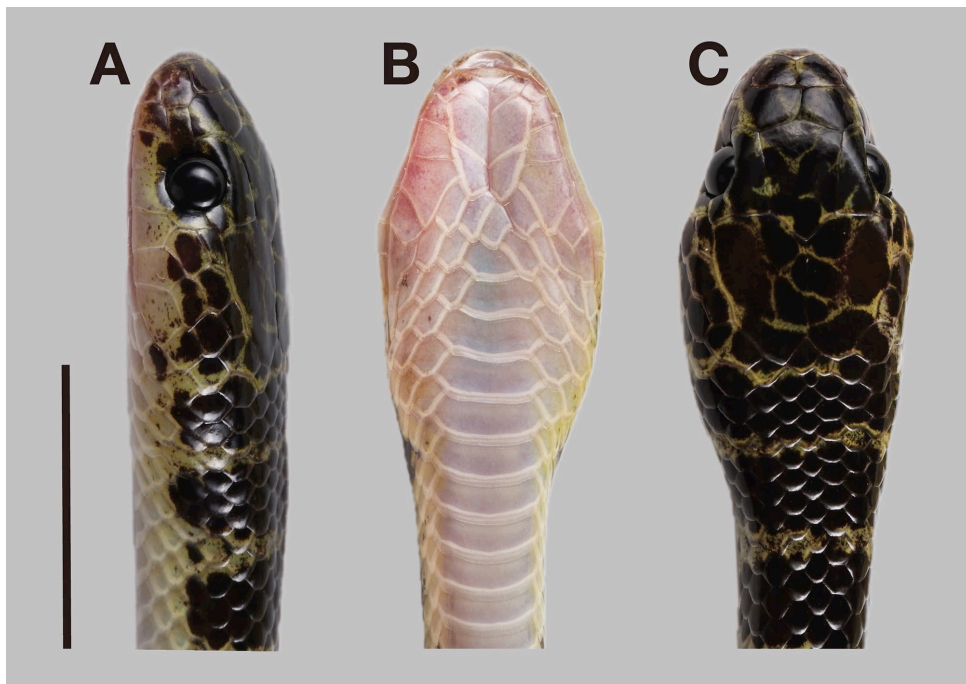


Figure 3. Left lateral (A), ventral (B) and dorsal (C) views of the head of holotype of *Lycodon penrissenensis* sp. n. (SRC 00890). Scale bar = 10 mm.

with nasal, 3rd in contact with loreal and orbit, 4th below orbit and contacting lower postocular, 5th in contact with lower postocular and anterior temporal, 6th longest vertically and in contact with anterior and posterior temporal, 7th widest horizontally in contact with anterior temporal and one dorsal scale; mental 1.7 mm in length and 1.1 mm in width; anterior chin shields 2.4 mm in length and 1.3 mm in width; posterior chin shields 1.8 mm in length and 1.1 mm in width; 8/8 infralabials, 1st pair in contact behind mental,

2nd small, 2nd to 4th touching anterior chin shields, 5th largest and contacting posterior chin shields and 1st sublabial and one gular scale, 6th and 7th contacting 2nd sublabial; 1st sublabial touching posterior chin-shield; two gular and two prefrontals (wider than long) at midline between posterior chin-shields and 1st ventral; eight maxillary teeth on each upper jaw; dorsal scales in 15/15/15 rows, smooth, unreduced; 205 ventrals, with a strong lateral keel; cloacal plate undivided; 98 subcaudals, paired; tail complete.



Figure 4. *Lycodon penrissenensis* sp. n. in life: (A) SRC 00890 (holotype); (B) SFC-GRB-01225 (paratype).

Table 2. Diagnostic characteristics of *Lycodon penrisseensis* sp. n., *L. tristrigatus*, and *L. subannulatus*.

Species	<i>Lycodon penrisseensis</i> sp. n.	<i>Lycodon tristrigatus</i>	<i>Lycodon tristrigatus</i>	<i>Lycodon subannulatus</i>	<i>Lycodon subannulatus</i>	<i>Lycodon subannulatus</i>	<i>Lycodon subannulatus</i>
Locality	Gunung Penrisse	Borneo	Borneo	Sumatra	Sumatra	Thai-Malay	Thai-Malay
N	2	4	14	2	1	6	16
Sex	Female	Male	Female	Male	Female	Male	Female
Max SVL (mm)	428	420	488	391	456	568	517
Max TL (mm)	593	583	630	516	589	825	685
TaL/TL (%)	27.3–27.8	23.3–28.1	22.7–25.4	24.2–25.6	22.6	24.8–33.2	22.8–27.2
Ventral	203–205	214–227	213–234	221–231	231	236–245	217–237
Subcaudals	98–105	93–111	86–102	98–101	97	108–112	92–110
Supralabials	7/7	7/7	7/7	7/7	7/7	7/7	7/7
Supralabials touch	3–4 th /3–4 th	3–4 th /3–4 th	3–4 th /3–4 th	3–4 th /3–4 th	3–4 th /3–4 th	3–4 th /3–4 th	3–4 th /3–4 th
Ocular							
Infralabials	8/8 or 8/7	8/8	8/8	8/8	8/8	8/8	8/8 (n=15) or 7/8 (n=1)
Preocular	0	0 (n=3) or 1 (n=1)	0 (n=13) or 1 (n=1)	1	1	1	1
Postoculars	2/2	2/2	2/2	2/2	1/2	2/2 (n = 5) or 3/3 (n = 1)	2/2 (n=15) or 2/1 (n=1)
Cloacal plate	1	1	1	1	1	1	1
Body color pattern	Banded	Striped (n=3) or Banded (n=1)	Striped (n=11) or Banded (n=3)	Banded	Banded	Striped (n = 1) or Banded (n = 5)	Striped (n = 4) or Banded (n = 12)
Vermiform or vermiculate markings on the crown	Present	Absent	Absent	Absent	Absent	Absent	Absent

In life, the dorsal surface is dark brown, with 86 narrow pale olive-green crossbands on the body. Dark brown speckles are present within each crossband dorsally and laterally, together with dark brown spots on the lateral portions of each crossband. The crossbands are wider ventrolaterally, are connected to one another at the outermost dorsal scale rows, and become indistinct on the tail. On the lateral side, the crossbands are 1.5–2.0 dorsal scales long, and on the dorsal side, 0.5–1.5 vertebral dorsal scales long. Head dark brown; the edges of each head scale are yellowish, and yellowish vermiculate markings are present on the frontal and parietals. Supralabial region cream white, with dark brown blotches on the upper portions of the 1st to 4th and 6th supralabials. Ventral surface plain white, with irregular pale brown spots posteriorly. Ventral surface of the tail pale brown.

In preservative, the body crossbands and the ventral ground colour changed to cream white. Other colours and patterns did not significantly differ from colouration in life.

Variation: The female paratype is generally similar to the holotype in morphology. It is larger (SVL = 428, TaL = 165, HL = 12.8, HW = 7.3) than the holotype (SVL = 320, TaL = 120, HL = 10.6, HW = 6.4), has a slightly longer tail

(TaL = 27.8% of TL vs. 27.3% in the holotype), fewer ventrals (203 vs. 205), more subcaudals (105 vs. 98), and fewer body bands (78 vs. 86). In addition, the paratype has seven infralabials on the right side but eight on the left, whereas the holotype has eight infralabials on both sides. The female paratype has yellowish vermiform markings on the frontal and parietals, whereas the corresponding markings are vermiculate in the holotype.

Comparisons: *Lycodon penrisseensis* sp. n. can be distinguished from all other species of the genus *Lycodon* except *L. kundui* and the *Dryocalamus* group (*L. chithrasekarai*, *L. davisonii*, *L. gracilis*, *L. nympha*, *L. subannulatus*, *L. philippinus*, and *L. tristrigatus*) by having 15 midbody scale rows (more than 15 in all other species). *Lycodon penrisseensis* sp. n. differs from *L. kundui* by having longer tail (27.3–27.8% of TL vs. 17.4%), higher number of ventrals (203–205 vs. 183) and subcaudals (98–105 vs. 70), and absence of preocular (vs. present); from *L. chithrasekarai* by having undivided cloacal plate (vs. divided) and lower numbers of ventral (203–205 vs. 228); from *L. davisonii* by having 15 midbody scale rows (vs. 13) and lower numbers of ventrals (203–205 vs. 233–255); from *L. gracilis* by having a higher number of subcaudals (98–105 vs. 75–87), and absence of preocular (vs. usually present); from *L. nympha*

by having 15 midbody scale rows (vs. 13), undivided cloacal plate (vs. divided), higher numbers of subcaudals (98–105 vs. 65–88), and absence of preocular (vs. present); from *L. subannulatus* by having longer tail in females (27.3–27.8% of TL vs. 22.6–27.2%), lower numbers of ventrals (203–205 vs. 217–245), absence of preocular (vs. present), and presence of vermiform or vermiculate markings on the crown (vs. the pale temporal marking may extend onto the parietals but does not form discrete vermiform or vermiculate markings) (Fig. 6, Table 2, S1); from *L. philippinus* by having longer tail (27.3–27.8% of TL vs. 23.5–23.7%), lower numbers of postoculars (two vs. usually three), and lower numbers of ventrals (203–205 vs. 216–225); and from *L. tristrigatus* by having longer tail in females (27.3–27.8% of TL vs. 22.7–25.4%), lower numbers of ventrals (203–205 vs. 213–234), and presence of vermiform or vermiculate markings on the crown (vs. the edges of each head scale are often yellowish but do not form discrete vermiform or vermiculate markings on the frontal or parietals) (Figs. 5, 6, Table 2, S1).

Distribution: *Lycodon penrissenensis* sp. n. is known only from Gunung Penrissen, Kuching Division, Sarawak, Malaysian Borneo (Fig. 7).

Natural history: The holotype specimen was found at night on a herbaceous plant ca. 50 cm above the ground in a primary forest at an elevation of 1035 m a.s.l. The paratype was found beneath a pile of dead branches at the forest edge at an elevation of 1000 m a.s.l. in the late afternoon. The species is likely to be arboreal as other species of the group.

Discussion

FUKUYAMA et al. (2025) revealed that *L. tristrigatus* exhibits marked colour dimorphism, with striped and banded morphs. Similarly, *L. subannulatus* is generally banded, but is known to be locally dimorphic in southern Thailand (Cox 1991). The only two known specimens of *L. penrissenensis* sp. n. are banded; however, given its phylogenetic



Figure 5. *Lycodon tristrigatus* from Lambir Hills National Park, Sarawak (A: SRC 00855; B: SRC 00809), *L. tristrigatus* from Mulu National Park, Sarawak (C: SRC 00596), and *L. tristrigatus* from Kubah National Park, Sarawak (D: SRC 00922).

affinity with these two species, it is possible that *L. penrissenensis* sp. n. also exhibits striped and banded colour dimorphism. DAS et al. (2016) provided a list of reptiles from Gunung Penrissen that included *L. tristrigatus*, but we lack sufficient evidence to determine whether that record represents (i) the striped morph of *L. penrissenensis* sp. n. or (ii) a true occurrence of *L. tristrigatus*, implying sympatry of the two taxa on the area. Therefore, additional sampling and genetic confirmation of “*L. tristrigatus*” from Gunung Penrissen are essential to evaluate these issues.

Several reptile species have been discovered and described from Gunung Penrissen, including *Cnemaspis leucura*, *Larutia kecil*, *Sphenomorphus shelfordi*, *Tytthoscincus batupanggang* and *T. leproauricularis* (BOULENGER 1900, KARIN et al. 2016, KURITA et al. 2017, FUKUYAMA et al. 2019). All of these species, as well as *L. penrissenensis* sp. n., are currently known only from this region, and several reptile species reported from the mountain – *Calliophis nigrotaeniatus*, *Gekko rhacophorus*, and *Stoliczka borneensis* – are known to exhibit disjunct distributions, occurring

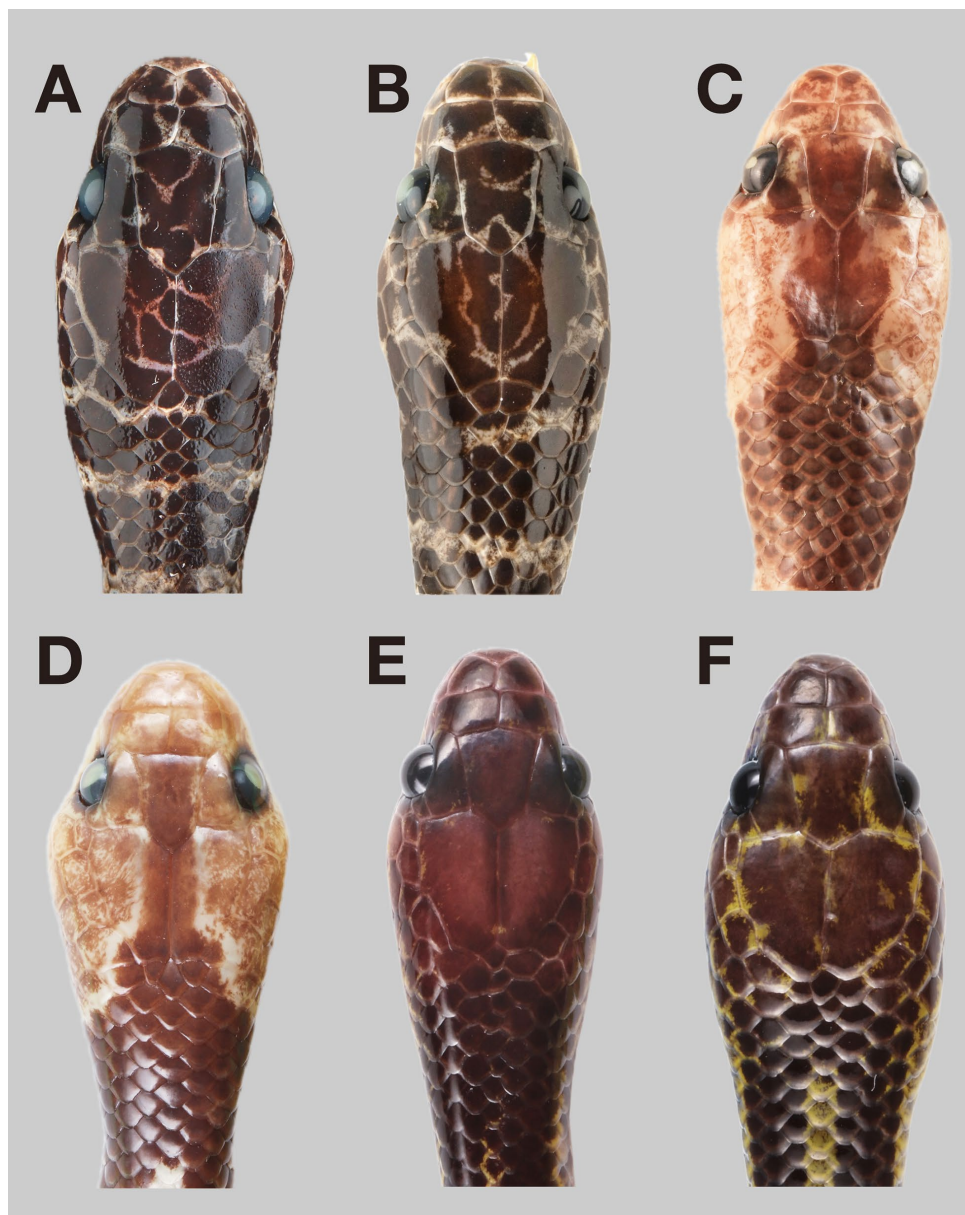


Figure 6. Dorsal views of the head of three species of *Dryocalamus* group, *Lycodon penrissenensis* sp. n. in preservative (A: SRC 00890), *Lycodon penrissenensis* sp. n. in preservative (B: SFC-GRB-01225), *L. subannulatus* from Sumatra in preservative (C: MZB Ophi 3709), *L. subannulatus* from Thai-Malay Peninsula in preservative (D: THNHM 03242), *L. tristrigatus* from Western Sarawak in life (E: KUHE 62439), and *L. tristrigatus* from Eastern Sarawak in life (F: SRC 00855). Only *L. penrissenensis* sp. n. has vermiform or vermiculate markings on the crown.

at Gunung Penrissen and in other highlands of northeastern Borneo (PUI & DAS 2012, DAS et al. 2016, FUKUYAMA et al. 2020). Gunung Penrissen is the only known locality for these species in western Borneo. The discovery of *L. penrissenensis* sp. n. further highlights the biogeographic distinctiveness of the reptile fauna of Gunung Penrissen.

KARIN et al. (2016) suggested that Pleistocene climatic fluctuations may have contributed to the co-occurrence of genetically divergent montane lineages at Gunung Penrissen. Under this hypothesis, populations initially diverged while isolated on separate mountains. During cooler glacial periods, the downslope expansion of montane forests may have increased habitat connectivity and permitted dispersal among mountains. Subsequent warming and the upward contraction of montane habitats would then have isolated these populations again at higher elevations. Repeated cycles of range expansion and contraction could

therefore have promoted both allopatric divergence and secondary contact among previously differentiated lineages, potentially accounting for the coexistence of divergent lineages at Gunung Penrissen. A broadly comparable model has been proposed for the mountains of Peninsular Malaysia, where many reptile lineages show pronounced mountain-specific differentiation and where intervening lowlands appear to restrict contemporary gene flow. These montane habitats have consequently been described as a “sky-island archipelago” (GRISMER et al. 2015, GRISMER et al. 2016, GRISMER et al. 2018). The montane regions extending from Mount Kinabalu in northern Borneo to the Sarawak–Kalimantan border, including Gunung Penrissen, may represent a similar biogeographic system. However, this hypothesis remains to be tested through geographically comprehensive sampling and comparative phylogeographic studies.

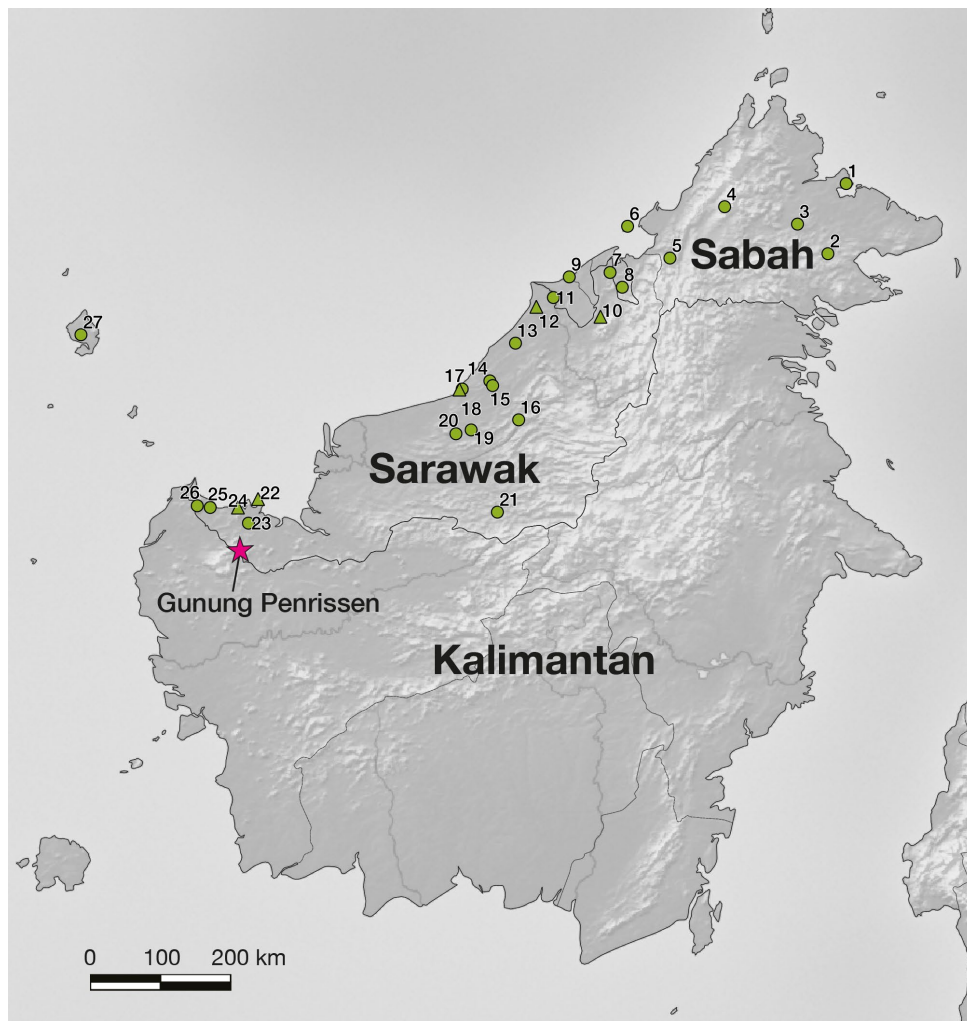


Figure 7. Map of Borneo, showing the known localities of *Lycodon tristrigatus* (green circle and triangle) and *Lycodon penrissenensis* sp. n. (pink star). Samples of *L. tristrigatus* from green triangle designated localities are used for phylogenetic analyses. Locality data of *Lycodon tristrigatus* were obtained from DE ROOIJ (1917), STUEBING (1991), DEHLING & DAS (2006), STUEBING et al. (2014), PUI et al. (2017), FUKUYAMA et al. (2025) (see Supplementary Table S2 for locality details).

Many Bornean montane areas along the Sarawak–Kali-mantan border remain inadequately surveyed for reptiles. The continued discovery of new reptile species in Bornean montane habitats (KARIN et al. 2016, FUKUYAMA et al. 2019, QUAH et al. 2019, KAISER et al. 2020, QUAH et al. 2021) suggests that substantial undescribed diversity may remain in these regions. Further field surveys, combined with taxonomic and phylogeographic studies, should clarify the distribution of *L. penrissenensis* sp. n. and provide insights into the historical processes underlying reptile diversification at Gunung Penrissen and in other Bornean montane regions.

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References

- BERNSTEIN, J. M., C. C. AUSTIN, J. A. SOTO-CENTENO, T. HUANG, J. R. ROBERTS, J. A. MCGUIRE, D. T. ISKANDAR, B. IOVA, J. H. FREDERICK, M. B. SANGUILA, J. L. WEINELL, R. M. BROWN & S. RUANE (2026): Diversification and colonisation in the Indo-Australian Archipelago: Genomic insights from colubrid snakes. – *Journal of Biogeography*, **53**: e70202.
- BOULENGER, G. A. (1900): Descriptions of new reptiles and batrachians from Borneo. – *Proceedings of the Zoological Society of London*, **1900**: 182–187.
- COX, M. J. (1991): *Snakes of Thailand and Their Husbandry*. – Krieger Publishing Company, Florida, 566 pp.
- DARRIBA, D., D. POSADA, A. M. KOZLOV, A. STAMATAKIS, B. MOREL & T. FLOURI (2020): ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. – *Molecular Biology and Evolution*, **37**: 291–294.
- DAS, I. (2015): *A Field Guide to the Reptiles of South-East Asia*. – Bloomsbury Publishing, London, 376 pp.
- DAS, I., Y. M. PUI, A. SHABRANI, B. R. KARIN & H. BREUER (2016): Reptiles. – pp. 109–119 in: MOHD-AZLAN, J., A. A. TUEN & I. DAS (eds): *Life from Headwaters to the Coast: Gunung Penrissen the Roof of Western Borneo*. – Natural History Publications (Borneo), Kota Kinabalu, 182 pp.
- DE ROOIJ, N. (1917): *The Reptiles of the Indo-Australian Archipelago. II, Ophidia*. – E. J. Brill, Leiden, 334 pp.
- DEHLING, J. M. & I. DAS (2006): *Dryocalamus tristrigatus* (Three-lined Tree Snake). – *Herpetological Review*, **37**: 497.
- DOWLING, H. G. (1951): A proposed standard system of counting ventrals in snakes. – *British Journal of Herpetology*, **1**: 97–99.
- EATON, D. A. R. & I. OVERCAST (2020): ipyrad: Interactive assembly and analysis of RADseq datasets. – *Bioinformatics*, **36**: 2592–2594.
- FIGUEROA, A., A. D. MCKELVY, L. L. GRISMER, C. D. BELL & S. P. LAILVAUX (2016): A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. – *PLoS One*, **11**: e0161070.
- FUKUYAMA, I., T. HIKIDA, M. Y. HOSSMAN & K. NISHIKAWA (2019): A new species of the genus *Larutia* (Squamata: Scincidae) from Gunung Penrissen, Sarawak, Borneo. – *Zootaxa*, **4661**: 522–532.
- FUKUYAMA, I., M. Y. HOSSMAN, Y. FUKU, M. GUMAL & K. NISHIKAWA (2025): Banded or striped? Significant colour dimorphism of a bridal snake in Borneo. – *Zoologica Scripta*, **54**: 133–143.
- FUKUYAMA, I., G. VOGEL, M. MATSUI, K. ETO, M. MUNIR, M. Y. HOSSMAN, A. HAMIDY & K. NISHIKAWA (2020): Systematics of *Calliophis intestinalis* with the resurrection of *Calliophis nigrotaeniatus* (Elapidae, Serpentes). – *Zoological Science*, **37**: 586–594.
- GRISMER, L. L., A. C. DIESMOS, J. M. DEHLING & D. T. ISKANDAR (2013): *Dryocalamus subannulatus*. – The IUCN Red List of Threatened Species 2013: e.T183191A44271883.
- GRISMER, L. L., E. S. H. QUAH, P. L. WOOD JR., S. ANUAR, A. MUIN, H. R. DAVIS, M. L. MURDOCH, J. L. GRISMER, M. COTA & A. J. COBOS (2016): Dragons in the mist: three new species of *Pseudocalotes* Fitzinger (Squamata: Agamidae) from the sky island archipelago of Peninsular Malaysia. – *Zootaxa*, **4136**: 461–490.
- GRISMER, L. L., P. L. WOOD, S. ANUAR, E. S. H. QUAH, M. A. MUIN, C. K. ONN, A. X. SUMARLI & A. I. LOREDO (2015): Repeated evolution of sympatric, palaeoendemic species in closely related, co-distributed lineages of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) across a sky-island archipelago in Peninsular Malaysia. – *Zoological Journal of the Linnean Society*, **174**: 859–876.
- GRISMER, L. L., P. L. WOOD, E. S. H. QUAH, S. ANUAR, E. B. NGADI, N. A. M. IZAM & N. AHMAD (2018): Systematics, ecomorphology, cryptic speciation and biogeography of the lizard genus *Tytthoscincus* Linkem, Diesmos & Brown (Squamata: Scincidae) from the sky-island archipelago of Peninsular Malaysia. – *Zoological Journal of the Linnean Society*, **183**: 635–671.
- GUO, P., L. ZHANG, Q. LIU, C. LI, R. A. PYRON, K. JIANG & F. T. BURBRINK (2013): *Lycodon* and *Dinodon*: One genus or two? Evidence from molecular phylogenetics and morphological comparisons. – *Molecular Phylogenetics and Evolution*, **68**: 144–149.
- HUELSENBECK, J. P. & D. M. HILLIS (1993): Success of phylogenetic methods in the four-taxon case. – *Systematic Biology*, **42**: 247–264.
- HUSON, D. H. & D. BRYANT (2006): Application of phylogenetic networks in evolutionary studies. – *Molecular Biology and Evolution*, **23**: 254–267.

- KAISER, C. M., J. LAPIN, M. O'SHEA & H. KAISER (2020): Carefully examining Bornean *Stegonotus* (Serpentes, Colubridae): the montane groundsnake population in Sabah is a new and distinct species. – *Zootaxa*, **4894**: 53–68.
- KARIN, B. R., I. DAS & A. M. BAUER (2016): Two new species of diminutive leaf-litter skinks (Squamata: Scincidae: *Tytthoscincus*) from Gunung Penrissen, Sarawak, Malaysia (northern Borneo). – *Zootaxa*, **4093**: 407–423.
- KATO, K. & D. M. STANDLEY (2013): MAFFT multiple sequence alignment software version 7: improvements in performance and usability. – *Molecular Biology and Evolution*, **30**: 772–780.
- KOZLOV, A. M., D. DARRIBA, T. FLOURI, B. MOREL & A. STAMATAKIS (2019): RAXML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. – *Bioinformatics*, **35**: 4453–4455.
- KUMAR, S., G. STECHER, M. LI, C. KNYAZ & K. TAMURA (2018): MEGA X: molecular evolutionary genetics analysis across computing platforms. – *Molecular Biology and Evolution*, **35**: 1547–1549.
- KURITA, T., K. NISHIKAWA, M. MATSUI & T. HIKIDA (2017): A new species of Rock Gecko genus *Cnemaspis* (Squamata: Gekkonidae) from Western Sarawak, Malaysia. – *Zootaxa*, **4258**: 525–538.
- LEE, J. L., A. H. MILLER, G. M. CONNETTE, K. S. OO, G. R. ZUG & D. G. MULCAHY (2018): First record of the Malaysian Bridle Snake, *Dryocalamus subannulatus* (Duméril, Bibron & Duméril, 1854), in Myanmar (Reptilia, Serpentes, Colubridae). – *Check List*, **14**: 341–345.
- LEE, J. L., T. V. NGUYEN, M. T. CHIT, N. A. POYARKOV & G. VOGEL (2025): Taxonomic notes on the wolf snakes *Lycodon* (Fitzinger, 1826) of Myanmar: new records, redescription, and an annotated key (Squamata: Colubridae). – *Zoological Research: Diversity and Conservation*, **2**: 125–152.
- NGUYEN, T. V., N. A. POYARKOV & G. VOGEL (2025): Taxonomic reassessment of the *Lycodon rufozonatus* species complex (Serpentes, Colubridae), with re-evaluation of *Dinodon rufozonatum walli*, and description of a new species from north-central Vietnam. – *ZooKeys*, **1251**: 293–322.
- PUI, Y. M. & I. DAS (2012): A significant range extension for the Kinabalu Parachute Gecko, *Ptychozoon rhacophorus* (Boulenger, 1899) (Squamata: Gekkonidae) and a new state record from Sarawak, northwestern Borneo. – *Herpetology Notes*, **5**: 177–179.
- PUI, Y. M., R. ZAINUDIN, T. WAHAB, K. K. P. LIM, S. HASSAN & I. DAS (2017): A Field Guide to the Amphibians and Reptiles of Bako National Park. Second Edition. – Sarawak Forestry Corporation, Kuching, 75 pp.
- PYRON, R. A., H. K. D. KANDAMBI, C. R. HENDRY, V. PUSHAMAL, F. T. BURBRINK & R. SOMAWEERA (2013): Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. – *Molecular Phylogenetics and Evolution*, **66**: 969–978.
- QUAH, E. S. H., L. L. GRISMER, K. K. P. LIM, M. S. S. ANUAR & A. Y. IMBUN (2019): A taxonomic reappraisal of the Smooth Slug Snake *Asthenodipsas laevis* (Boie, 1827) (Squamata: Pareidae) in Borneo with the description of two new species. – *Zootaxa*, **4646**: 501–526.
- QUAH, E. S. H., K. K. P. LIM & L. L. GRISMER (2021): On the taxonomic status of *Asthenodipsas vertebralis* (Boulenger, 1900) (Squamata: Pareidae) in Borneo with the description of a new species. – *Zootaxa*, **4949**: 24–44.
- SILER, C. D., C. H. OLIVEROS, A. SANTANEN & R. M. BROWN (2013): Multilocus phylogeny reveals unexpected diversification patterns in Asian wolf snakes (genus *Lycodon*). – *Zoologica Scripta*, **42**: 262–277.
- SMITH, M. A. (1943): Fauna of British India, Amphibia and Reptilia, Vol. III. Serpentes. – Taylor and Francis, London, 583 pp.
- STUEBING, R. B. (1991): Checklist of snakes of Borneo. – *Raffles Bulletin of Zoology*, **39**: 323–362.
- STUEBING, R. B., R. F. INGER & B. LARDNER (2014): A Field Guide to the Snakes of Borneo. Second Edition. – Natural History Publications (Borneo), Kota Kinabalu, 310 pp.
- SUYAMA, Y. & Y. MATSUKI (2015): MIG-seq: an effective PCR-based method for genome-wide single-nucleotide polymorphism genotyping using the next-generation sequencing platform. – *Scientific Reports*, **5**: 16963.
- TAYLOR, E. H. (1922): The Snakes of the Philippine Islands. – Bureau of Printing, Manila, 312 pp.
- VOGEL, G., P. DAVID, O. S. G. PAUWELS, M. SUMONTHA, R. HENDRIX, N. T. VU & T. ZIEGLER (2009): A revision of *Lycodon ruhstrati* (Fischer 1886) auctorum (Squamata Colubridae), with the description of a new species from Thailand and a new subspecies from the Asian mainland. – *Tropical Zoology*, **22**: 131–182.
- WICKRAMASINGHE, L. J. M., D. R. VIDANAPATHIRANA, V. PUSHAMAL & N. WICKRAMASINGHE (2020): A new species of *Dryocalamus* (Serpentes: Colubridae) endemic to the rainforests of southwestern Sri Lanka. – *Zootaxa*, **4748**: 248–260.
- WOSTL, E., A. HAMIDY, N. KURNIAWAN & E. N. SMITH (2017): A new species of wolf snake of the genus *Lycodon* H. Boie in Fitzinger (Squamata: Colubridae) from the Aceh Province of northern Sumatra, Indonesia. – *Zootaxa*, **4276**: 539–553.

Supplementary data

The following data are available online:

Supplementary Table S1. Measurements and scale counts of *Lycodon penrissenensis* sp. n., *L. tristrigatus*, and *L. subannulatus*.

Supplementary Table S2. Known localities of *Lycodon tristrigatus*.