

Taxonomic status of *Lycodon subcinctus* sensu lato in China (Serpentes, Colubridae)

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Abstract

The Malayan Banded Wolf Snake *Lycodon subcinctus* Boie, 1827 once included three subspecies, namely *L. s. subcinctus* Boie, 1827, *L. s. sealei* Leviton, 1955, and *L. s. maculatus* (Cope, 1895). Thereafter, *L. s. sealei* has been elevated to species level, and the taxonomic status of *L. s. maculatus* has not been resolved. We sequenced the mitochondrial cytochrome b (cytb) gene fragments of eight specimens of *L. s. maculatus* from China, including three from the adjacent areas of its type locality. Combining the sequences obtained from GenBank, we reconstructed a molecular phylogeny and reevaluated the taxonomic status of *L. s. maculatus*. Phylogenetic analysis revealed three highly divergent lineages within *L. subcinctus* sensu lato which correspond to *L. subcinctus* sensu stricto, *L. sealei*, and *L. s. maculatus*, respectively. Coupled with morphological comparison, we elevate *L. s. maculatus* to full species and redescribe it based on the type and freshly collected material.

Key Words

cytochrome b, morphology, phylogeny, subspecies, systematics, Wolf Snake

Introduction

Lycodon subcinctus Boie, 1827, a species originally described from Java, was subsequently considered to be widespread, ranging from almost the entire South-east Asia to southern China and the Nicobar Islands of

India (Boulenger 1893; Pope 1935; Smith 1943; Taylor 1965; Zhao 2006; Nguyen et al. 2009; Harikrishnan et al. 2010; Siler et al. 2013; Geissler et al. 2019; Reilly et al. 2019). Cope (1895) once dissected a snake specimen (Cat. No. 7339, U.S.N.M.) from Hong Kong, China, and gave it the name *Anoplophallus maculatus* Cope,

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1895. Stejneger (1926) considered the specimen dissected by Cope (1895) to belong to *L. subcinctus*, and therefore, the name *A. maculatus* was taken as a junior synonym of *L. subcinctus*. Leviton (1955) described a subspecies of *L. subcinctus* from the Philippines, namely *L. s. sealei* Leviton, 1955. Afterwards, Lanza (1999) recognized three subspecies within *L. subcinctus*: *L. s. subcinctus* Boie, 1827, mainly distributed in West Malaysia, Indonesia (Java, Sumatra), Singapore, Vietnam, Laos, Cambodia, and Thailand; *L. s. sealei*, mainly distributed in the Philippines, Brunei, and Borneo; and *L. s. maculatus* (Cope, 1895), mainly distributed in southern China. Currently, *L. s. sealei* has been elevated to full species (Leviton et al. 2018; Weinell et al. 2019) whereas *A. maculatus* is still treated as a junior synonym of *L. subcinctus* (e.g., Uetz et al. 2023) or by some authors, with a subspecific rank of *L. subcinctus* (e.g., Poyarkov et al. 2023).

In China, *Lycodon subcinctus* was recorded from Fujian, Guangdong, Hainan, Hunan, Sichuan, and Yunnan provinces, Guangxi Autonomous Region, and Hong Kong and Macao special administrative regions, and no subspecies has been recognized (Pope 1935; Zhao et al. 1998; Zhao 2006; Li et al. 2011; Francis 2021; Huang 2021; Wang 2021; Guo et al. 2022).

When studying *Lycodon* species in China, we found that there are some morphological differences between the snakes identified as *L. subcinctus* from China and *L. subcinctus* from the type locality in Java and the adjacent areas. In addition, molecular result revealed three

strongly supported, highly divergent clades within *L. subcinctus* sensu lato, corresponding to the three subspecies previously considered, namely *L. s. subcinctus*, *L. s. sealei*, and *L. s. maculatus*. Since *L. sealei* has been treated as a separate species, *Anoplophallus maculatus* should also be regarded as a valid species, which we presently refer to as *Lycodon maculatus* comb. nov. (Cope, 1895).

Materials and methods

Total genomic DNA was extracted from liver tissue samples. A fragment of mitochondrial cytochrome b (cytb) gene was amplified using newly designed primer pairs SubF1: 5'-GCCAATATTGACTTAGCCTT-3' and SubR1: 5'-ATTGAAAATGTTTGGGGTGA-3'. Polymerase Chain Reaction (PCR) amplification and sequencing were completed by Tsingke Biotechnology Co., Ltd. Sequences were edited and manually managed using SeqMan in Lasergene 7.1 (DNASTAR Inc., Madison, WI, USA). The new sequences have been deposited in GenBank, homologous sequences were downloaded from GenBank (Table 1). Sequences of *Boiga cynodon* (Boie, 1827) and *Dasypeltis atra* Sternfeld, 1912 were used as outgroups according to Wang et al. (2021). The technical computation methods for sequence alignment, genetic distance calculation, the best substitution model selection, and Bayesian inference (BI) and maximum likelihood (ML) phylogenetic analyses were the same as those in Liu et al. (2023).

Table 1. Cytochrome b (cytb) sequences used in the phylogenetic analysis.

Species	Voucher	Locality	GenBank
<i>Lycodon albofuscus</i>	LSUHC 3867	Tioman, Pahang, Malaysia	KX660500
<i>Lycodon alcalai</i>	KU 327847	Bataan, Philippines	KC010344
<i>Lycodon anakradaya</i>	SIEZC 20247	Song Giang, Khanh Hoa, Vietnam	OM674283
<i>Lycodon aulicus</i>	/	Jabalpur, Madhya Pradesh, India	HQ735416
<i>Lycodon banksi</i>	VNUF R.2015.20	Phou Hin Poun, Khammouane, Laos	MH669272
<i>Lycodon bibonius</i>	KU 304589	Cagayan, Philippines	KC010351
<i>Lycodon butleri</i>	LSUHC 9136	Bukit Larut, Perak, Malaysia	KC010353
<i>Lycodon capucinus</i>	LSUHC 9277	Nam Du, Kien Giang, Vietnam	KC010356
<i>Lycodon carinatus</i>	RAP 0447	Kanneliya, Galle, Sri Lanka	KC347486
<i>Lycodon cathaya</i>	SYS r001542	Huaping, Longsheng, Guangxi, China	MT602075
<i>Lycodon cavernicolus</i>	LSUHC 9985	Gua Wang Burma, Perlis, Malaysia	KJ607889
<i>Lycodon chapaensis</i>	VNUF R. 2017.23	Nam Dong, Thanh Hoa, Vietnam	MK585007
<i>Lycodon chrysoprateros</i>	KU 307720	Dalupiri, Cagayan, Philippines	KC010360
<i>Lycodon davisonii</i>	LSUHC 8479	O'Lakmeas, Pursat, Cambodia	KX660497
<i>Lycodon deccanensis</i>	BNHS 3610	Tumkur, Karnataka, India	MW006486
<i>Lycodon dumerilli</i>	KU 319989	Agusan del Sur, Mindanao, Philippines	KC010361
<i>Lycodon effraenis</i>	LSUHC 9670	Kedah, Malaysia	KC010376
<i>Lycodon fasciatus</i>	CAS 234957	Midat, Chin, Myanmar	KC010366
<i>Lycodon flavicollis</i>	/	Devarayanadurga, Karnataka, India	MW006488
<i>Lycodon flavozonatus</i>	SYS r000640	Huangganshan, Jiangxi, China	MK201413
<i>Lycodon futsingensis</i>	SYSr 000923	Guangdong, China	MK201432
<i>Lycodon gongshan</i>	KIZ 035112	Dulongjiang, Nujiang, Yunnan, China	MW353748
<i>Lycodon jara</i>	CAS 235387	Kachin, Myanmar	KC010367
<i>Lycodon laoensis</i>	FMNH 258659	Salavan, Laos	KC010368
<i>Lycodon liuchengchaio</i>	JK 201704	Ningshan, Shaanxi, China	MK201563
<i>Lycodon mackinnoni</i>	ADR 197	Mussoorie, Uttarakhand, India	MW862977
<i>Lycodon meridionalis</i>	VNUF R.2017.54	Cuc Phuong, Ninh Binh, Vietnam	MH669268
<i>Lycodon muelleri</i>	DLSUD 031	Cavite, Luzon, Philippines	KC010373
<i>Lycodon multizonatus</i>	KIZ 01623	Luding, Sichuan, China	KF732926

Species	Voucher	Locality	GenBank
<i>Lycodon nympha</i>	RAP 0536	Kandalam, Matale, Sri Lanka	KC347476
<i>Lycodon obvelatus</i>	KIZ 040146	Panzhihua, Sichuan, China	MW353745
<i>Lycodon pictus</i>	IEBR 4166	Trung Khanh, Cao Bang, Vietnam	MT845093
<i>Lycodon rosozonatus</i>	SYS r001617	Jianfengling, Hainan, China	MK201531
<i>Lycodon rufozonatus</i>	SYS r001770	Taizhou, Zhejiang, China	MT625858
<i>Lycodon ruhstrati</i>	GP 285	Junlian, Sichuan, China	KC733195
<i>Lycodon sealei</i>	KU 327571	Barangay Estrella, Palawan, Philippines	KC010384
<i>Lycodon sealei</i>	KU 309447	Barangay Irawan, Palawan, Philippines	KC010385
<i>Lycodon semicarinatus</i>	/	Ryukyu, Japan	AB008539
<i>Lycodon septentrionalis</i>	CIB 117521	Medog, Nyinchi, Tibet, China	MW353736
<i>Lycodon serratus</i>	KIZ 038335	Deqin, Yunnan, China	MW353746
<i>Lycodon sidiki</i>	MZB 5980	Ache, Sumatra, Indonesia	KX822583
<i>Lycodon stormi</i>	JAM 7487	Air Terjun Moramo, Sulawesi, Indonesia	KC010380
<i>Lycodon striatus</i>	/	Savandurga, Karnataka, India	MW006489
<i>Lycodon subannulatus</i>	LSUHC 5576	Sibu, Johor, Malaysia	KX660499
<i>Lycodon subcinctus</i>	UTA-R 62972	Jawa Barat, Indonesia	KX822580
<i>Lycodon subcinctus</i>	MZB.Ophi.5398	Sumatera, Utara, Indonesia	KX822581
<i>Lycodon subcinctus</i>	UTA-R 62266	Sumatera, Utara, Indonesia	KX822579
<i>Lycodon subcinctus</i>	UTA-R 63046	Bengkulu, Indonesia	KX822582
<i>Lycodon subcinctus</i>	LSUHC 5016	Sungai Lembing, Pahang, Malaysia	KC010382
<i>Lycodon subcinctus</i>	MVZ291678	Lesser Sundas	MK844529
<i>Lycodon subcinctus</i>	MVZ291679	Lesser Sundas	MK844530
<i>Lycodon subcinctus</i>	MVZ291680	Lesser Sundas	MK844531
<i>Lycodon subcinctus</i>	MVZ291681	Lesser Sundas	MK844532
<i>Lycodon subcinctus</i>	MVZ291682	Lesser Sundas	MK844533
<i>Lycodon subcinctus</i>	MVZ291683	Lesser Sundas	MK844534
<i>Lycodon subcinctus</i>	MVZ291684	Lesser Sundas	MK844535
<i>Lycodon subcinctus</i>	MVZ291685	Lesser Sundas	MK844536
<i>Lycodon synaptor</i>	HS11006	Mengzi, Yunnan, China	MK201304
<i>Lycodon tristigatus</i>	FMNH 269033	Bintulu, Sarawak, Malaysia	KX660474
<i>Lycodon truongi</i>	SIEZC 20249	Song Giang, Khanh Hoa, Vietnam	OM674282
<i>Lycodon zawi</i>	CAS 239944	Kaaukpyu, Rakhine, Myanmar	KC010386
<i>Lycodon zayuensis</i>	KIZ 032400	Chayu, Tibet, China	MW199792
<i>Lycodon maculatus</i> comb. nov.	SYS r001155	Shenzhen, Guangdong, China	MT625846
<i>Lycodon maculatus</i> comb. nov.	SYS r001943	Qingyuan, Guangdong, China	MT625859
<i>Lycodon maculatus</i> comb. nov.	SYS r001430	Guangdong, China	MK201493
<i>Lycodon maculatus</i> comb. nov.	HS15028	Fujian, China	MK201314
<i>Lycodon maculatus</i> comb. nov.	SYS r001621	Diaoluoshan, Hainan, China	MK201534
<i>Lycodon maculatus</i> comb. nov.	HS13005	Jiguanshan, Sichuan, China	MK201313
<i>Lycodon maculatus</i> comb. nov.	KIZ014158	Xishuangbanna, Yunnan, China	MK201560
<i>Lycodon maculatus</i> comb. nov.	KU 328531	Nakhon Ratchasima, Thailand	KC010383
<i>Lycodon maculatus</i> comb. nov.	KIZ2009061301	Hechi, Guangxi, China	OR823820
<i>Lycodon maculatus</i> comb. nov.	KIZ20190902	Hechi, Guangxi, China	OR823821
<i>Lycodon maculatus</i> comb. nov.	KIZ2023029	Guangzhou, Guangdong, China	OR823822
<i>Lycodon maculatus</i> comb. nov.	KIZ2023030	Putian, Fujian, China	OR823823
<i>Lycodon maculatus</i> comb. nov.	KIZ2023031	Xishuangbanna, Yunnan, China	OR823824
<i>Lycodon maculatus</i> comb. nov.	KIZ2023032	Shenzhen, Guangdong, China	OR823825
<i>Lycodon maculatus</i> comb. nov.	KIZ2023034	Xishuangbanna, Yunnan, China	OR823826
<i>Lycodon maculatus</i> comb. nov.	KIZ2023044	Dongguan, Guangdong, China	OR823827
<i>Boiga cynodon</i>	KU 324614	Negros Occidental, Philippines	KC010340
<i>Dasypeltis atra</i>	CAS 201641	Kabale, Uganda	AF471065

Measurements and scale counts were taken following Nguyen et al. (2022). SVL: snout-vent length, TaL: tail length, HL: head length, HW: head width, HH: head height, ED: eye diameter, SnL: snout length, EN: eye to narial distance, InD: internarial distance, SL: supralabials, IL: infralabials, SL-E: SL contacting the eye, LoR: loreals, LoR-E: LoR contacting the eye, PrO: preoculars, PtO: postoculars, aTMP: anterior temporals, pTMP: posterior temporals, DSR: dorsal scale rows at one head length posterior to the head, midbody, and one head length anterior to the vent, Ven: ventral scales, SC: subcaudals, Prec: cloacal plate, BB: light-colored body bands, TB: light-colored tail bands.

Results

The resulting topologies from BI and ML analyses are consistent (Fig. 1). All sequences of *Lycodon subcinctus* sensu lato formed a monophyletic lineage comprising three clades. Clade A included the sequence from the type locality of *L. subcinctus*, Java, and the sequences from Sumatra, Bengkulu, and the Lesser Sundas (Indonesia), and Pahang (West Malaysia); clade B included the sequences from the type locality of *L. sealei*, namely Palawan Island, the Philippines; and clade C included the sequences from the adjacent areas of the type locality of *Anoplophallus maculatus* in Guangdong, and the

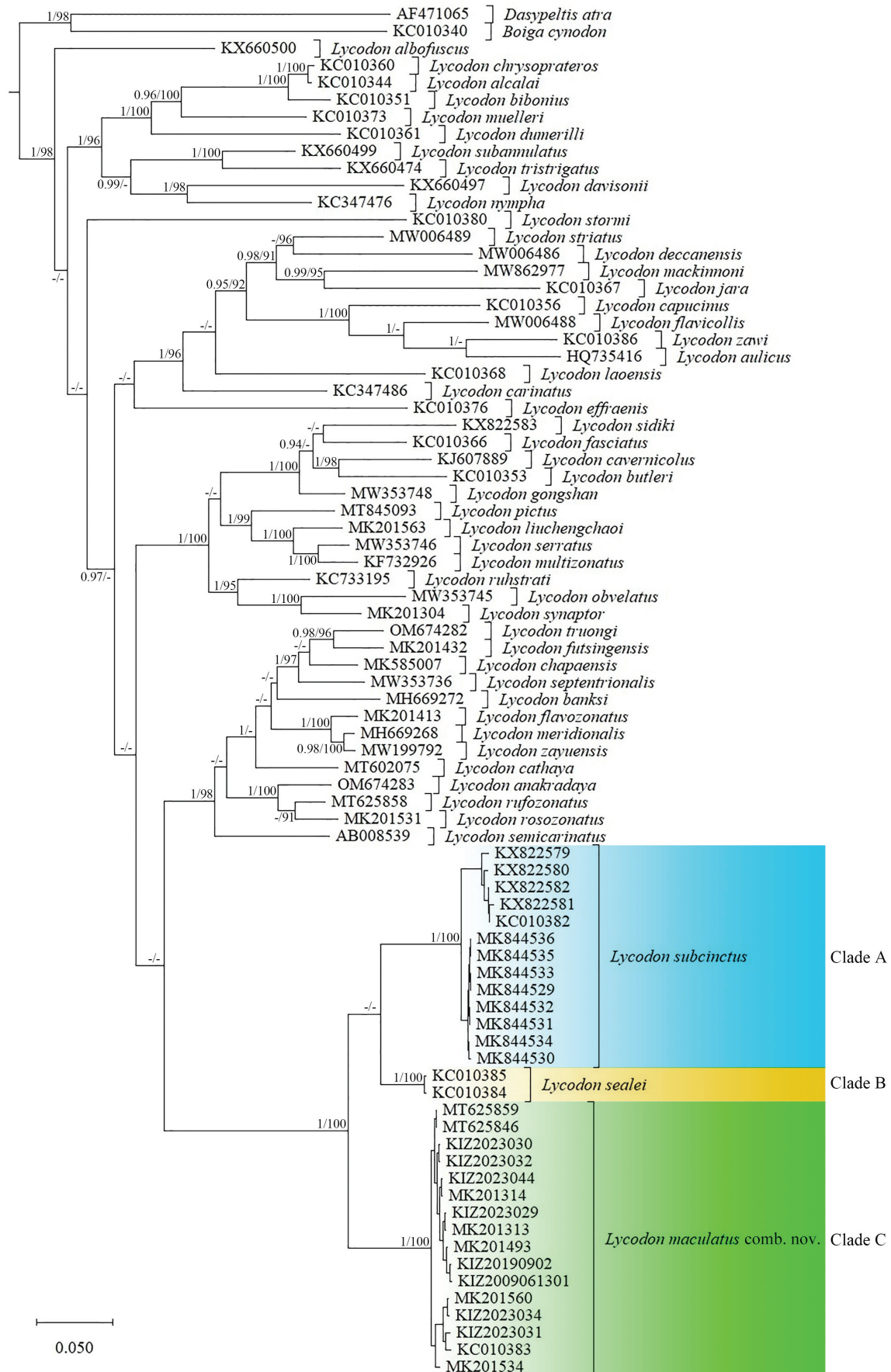


Figure 1. Bayesian phylogenetic tree of *Lycodon* inferred from the mitochondrial cytb sequences. Numbers before slashes indicate Bayesian posterior probabilities (>0.90) and numbers after slashes indicate ML bootstrap supports (>90).

sequences from Guangxi, Fujian, Sichuan, Hainan, and Yunnan, China, and Nakhon Ratchasima, Thailand. The average genetic distance (uncorrected p-distance) between clades A and B was 6.6%, the average genetic distance (uncorrected p-distance) between clades A and C was 8.8%, and the average genetic distance (uncorrected p-distance) between clades B and C was 8.9%. Therefore, we consider clade C, namely *A. maculatus*, to be a valid species instead of a strict synonym or a subspecies of *L. subcinctus*.

***Lycodon maculatus* comb. nov. (Cope, 1985)**

Figs 2, 3

Type material. *Holotype*. USNM 7339, adult male.

Type locality. Hong Kong Special Administrative Region, China.

Diagnosis. Body size relatively small, slender; 17–17–15 dorsal scale rows; eight supralabials, 3rd–5th or 3rd–6th contacting eye; 8–9 infralabials; no preocular; prefrontal contacting eye; two postoculars; one loreal contacting eye; one anterior temporal and two posterior temporals in most individuals; ventral scales less than 205; subcaudal scales more than 70, paired; cloacal plate divided; dorsal scale feebly keeled; anterior part of head dark grey or black; posterior lateral parts of head white in juveniles and dark gray or grayish black in adults; 20–27 distinct white bands on dorsal body and tail in juveniles; 5–8 grayish white bands gradually blur backward on anterior part of body in adults; no bands on posterior part of body and tail in adults.

Redescription of the holotype. Head flattened, somewhat elongate, HL 17.1 mm, HW 9.3 mm, HH 6.7 mm, HL/HW 1.84, HW/HH 1.39, distinct from the neck; snout relatively elongate, SnL 5.4 mm, SnL/HL 0.32, nostril closer to snout than to eye, internarial distance large, InD 4.2 mm, InD/HW 0.45; eye moderately sized, ED 2.0 mm, ED/HL 0.12, with a nearly rounded pupil; rostral approximately triangular, visible from above; two nearly triangular internasals; two large parallelogram-like prefrontals; single shield-shaped frontal; two large, elongate parietals; 1\1 nearly trapezoidal supraocular; no preocular; 2\2 small postoculars, upper one slightly larger than lower one; 1\1 narrow, elongate loreal entering orbit, in contact with nasal anteriorly, prefrontal dorsally, second and third supralabials ventrally; 8\8 supralabials; first and second supralabials in contact with nasal; third, fourth, and fifth supralabials in contact with eye; 1\1 anterior temporal; 2\2 posterior temporals; 8\8 infralabials; first pair infralabials contact medially forming a deep, medial groove; first three infralabials in contact with first pair of chinshields; first pair of chinshields elongate, bearing a deep, medial grooves contiguous with groove separating first pair of infralabials.

Body slender; SVL 428 mm; tail incomplete; 191 ventrals; cloacal plate divided; dorsal scales in 17–17–15 rows; vertebral row not enlarged; no apical pits.

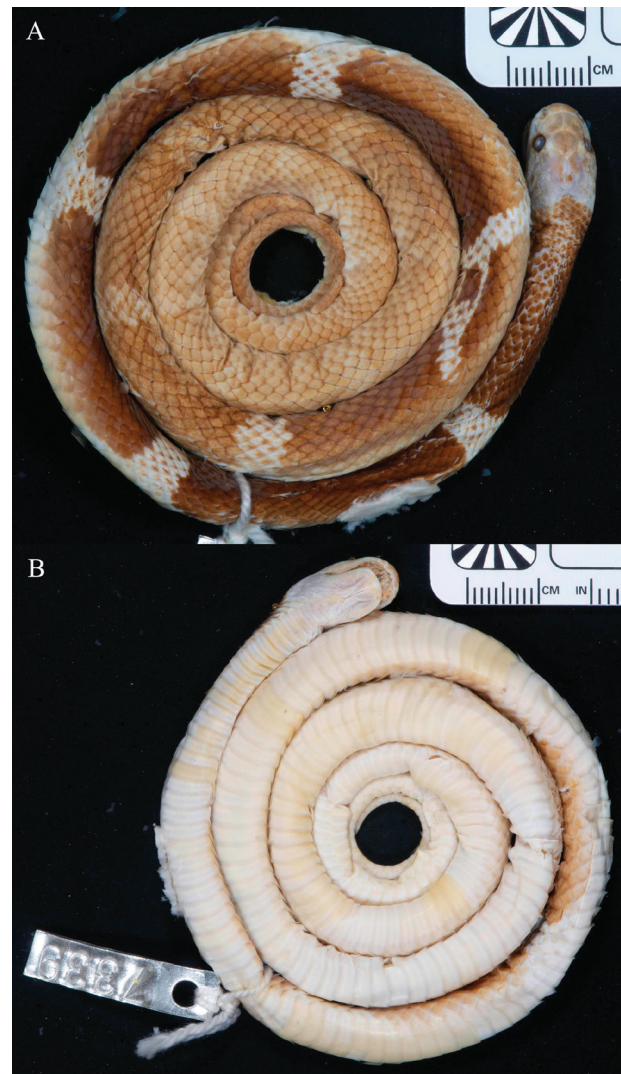


Figure 2. The holotype (USNM 7339) of *Lycodon maculatus* comb. nov. in preservative. **A.** Dorsal view; **B.** Ventral view. Photos are obtained from the website of National Museum of Natural History. Photographer: Teresa Hsu from Division of Amphibians & Reptiles, National Museum of Natural History, Smithsonian Institution.

After long-term immersion in preservative, head almost entirely white with a little light reddish brown on top; dorsal surface of anterior body reddish brown with seven white bands, first six distinct and last one indistinct; dorsal surface of posterior body and tail pale brown with no bands; ventral surface of head, body, and tail white.

Other specimens examined. We examined eight specimens in Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ) and two specimens in Museum of Herpetology, Chengdu Institute of Biology, Chinese Academy of Sciences (CIB). KIZ2009061301, adult male, from Tian'e County, Hechi City, Guangxi Autonomous Region, China (Exact locality unknown); KIZ20190902, adult female, from Leyi Village, Chuanshan Town, Huanjiang County, Hechi City, Guangxi Autonomous Region, China (25°5'56"N, 108°0'9"E, at an elevation



Figure 3. *Lycodon maculatus* comb. nov. from China in life. **A.** The adult female (KIZ20190902) from Hechi City, Guangxi Autonomous Region; **B.** The adult female (KIZ2023029) from Guangzhou City, Guangdong Province; **C.** The adult female (KIZ2023030) from Putian City, Fujian Province; **D.** The adult male (KIZ2023031) from Xishuangbanna Prefecture, Yunnan Province; **E.** The adult male (KIZ2023032) from Shenzhen City, Guangdong Province; **F.** An uncollected juvenile from Qingyua City, Guangdong Province.

of 570 m); KIZ2023029, adult female, from Huangpu District, Guangzhou City, Guangdong Province, China (23°5'45"N, 113°16'52"E, at an elevation of 200 m); KIZ2023030, adult female, from Hanjiang District, Putian City, Fujian Province, China (Exact locality unknown); KIZ2023031, adult male, from Menglun Town, Mengla County, Xishuangbanna Prefecture, Yunnan Province, China (21°56'9"N, 101°15'10"E, at an elevation of 550 m); KIZ2023032, adult male, from Luohu District,

Shenzhen City, Guangdong Province, China (22°34'7"N, 114°14'9"E, at an elevation of 240 m); KIZ2023034, adult male, from Jinghong City, Xishuangbanna Prefecture, Yunnan Province, China (Exact locality unknown); KIZ2023044, juvenile, from Xiegang Town, Dongguan City, Guangdong Province, China (22°54'20"N, 114°14'19"E, at an elevation of 260 m); and CIB 78124 and CIB 9820, two adult females, both from Sanya City, Hainan Province, China (Exact locality unknown) (Fig. 4).

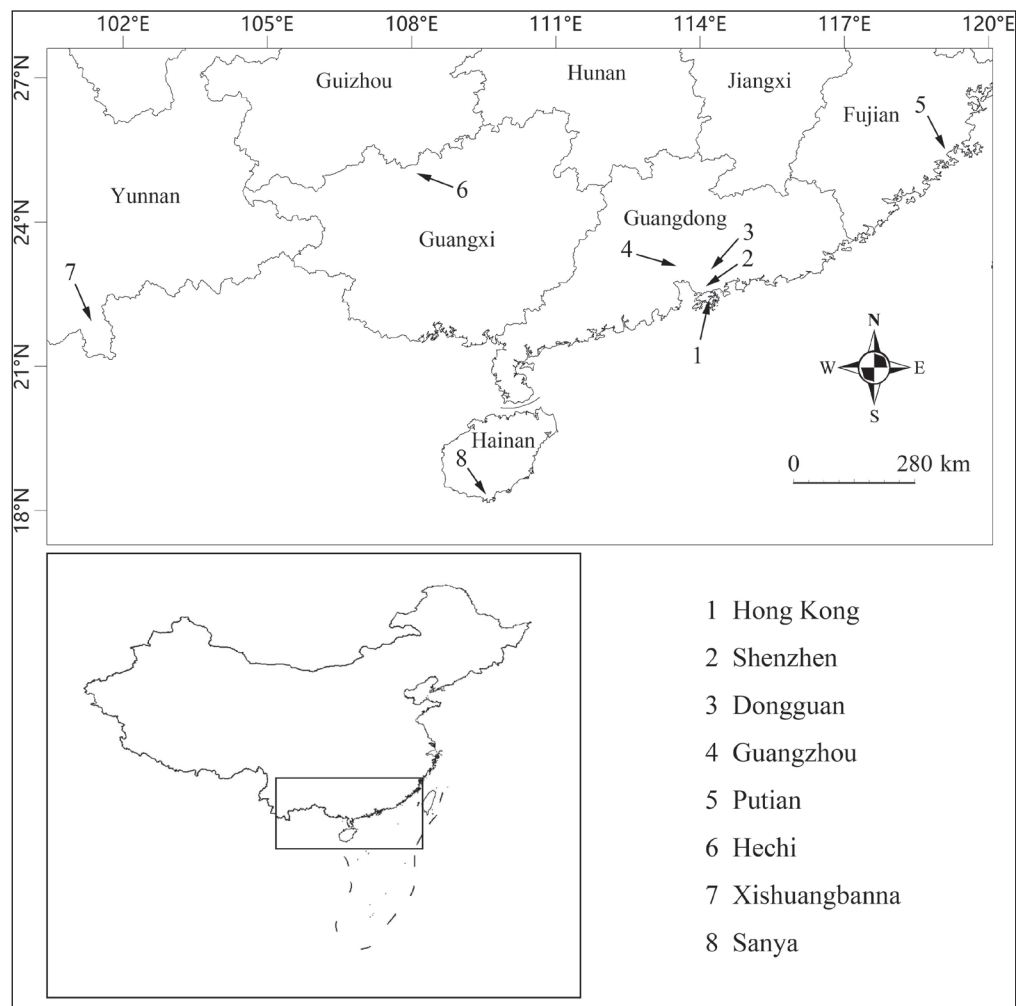


Figure 4. Map showing the type locality of *Lycodon maculatus* comb. nov. in Hong Kong Special Administrative Region, China (1) and the localities of the specimens examined in this study (2–8).

Variation. The morphological data of other specimens are presented in Table 2. All specimens resemble the holotype except that third, fourth, fifth, and sixth supralabials contact eye in some individuals, anterior and posterior temporals vary from one to two, nine infralabials in some individuals, first four infralabials in contact with first pair of chinshields, ventrals vary from 189 to 203, subcaudals vary from 71 to 84, and the bands on dorsal body vary from five to eight in adults and 14 bands on dorsal body and 12 bands on dorsal tail in the juvenile.

Morphological comparison. *Lycodon maculatus* comb. nov. differs from *L. subcinctus* by having fewer ventral scales, namely less than 205 vs. more than 205. *Lycodon maculatus* comb. nov. differs from *L. sealei* by subcaudal scales more than 70 vs. less than 70. In addition, the number of bands on dorsal body and tail is significantly different, although the bands become indistinct in adults, they are usually distinct in juveniles. According to the figures in Siler et al. (2013), Leviton et al. (2018), Francis (2021), and Huang (2021), and Fig. 3F and Table 2 in this paper, the total number of bands on dorsal body and tail of juveniles is less than 15 in *L. sealei* and more than 40 in *L. subcinctus*, whereas the number is 20–27 in *Lycodon maculatus* comb. nov.

Distribution. *Lycodon maculatus* comb. nov. is currently known to be distributed in southern China and Nakhon Ratchasima, Thailand. As Nakhon Ratchasima is located in central southern Thailand and the nearest confirmed distribution site of *Lycodon maculatus* comb. nov. is in Xishuangbanna, Yunnan, China, it can be assumed that the species is likely to occur in the area between Nakhon Ratchasima and Xishuangbanna, specifically in northern Thailand and central and northern Laos. In addition, it is likely that the population in northern Vietnam, previously considered to be *L. subcinctus*, also belongs to *Lycodon maculatus* comb. nov.

Discussion

The name *Anoplophallus maculatus* was synonymized with the name *Lycodon subcinctus* shortly after its proposal (Stejneger 1926) and later this taxon was considered one of the subspecies of *L. subcinctus* (Lanza 1999). At present, “The Reptile Database” (Uetz et al. 2023) regarded this taxon as a synonym of *L. subcinctus*, and Poyarkov et al. (2023) recognized it as a subspecies of *L. subcinctus*. All literature sources on the snakes of China

Table 2. Measurements (in mm) and scalation data of the examined specimens. For abbreviations see Materials and methods. “/” represents injured and incomplete.

	KIZ2009061301	KIZ20190902	KIZ2023029	KIZ2023030	KIZ2023031	KIZ2023032	KIZ2023034	KIZ2023044	CIB 78124	CIB 9820
Sex	Male	Female	Female	Female	Male	Male	Male	Juvenile	Female	Female
SVL	526	464	432	635	425	456	414	237	578	562
TaL	/	108	112	143	114	/	109	56	156	151
HL	18.4	16.6	16.0	20.9	15.9	16.1	15.5	11.5	20.4	17.2
HW	10.3	10.3	9.9	12.1	9.2	9.1	7.4	/	11.7	9.8
HH	7.5	7.8	6.2	8.7	5.3	6.2	5.6	/	7.1	7.0
ED	2.4	2.1	2.2	2.5	2.5	2.0	2.0	1.6	2.6	2.1
SnL	6.5	5.7	5.5	7.0	5.2	5.5	5.2	3.8	6.8	5.9
EN	3.6	3.1	3.3	4.2	2.9	3.1	2.6	1.8	3.6	3.3
InD	4.8	4.1	4.0	5.1	4.0	4.1	4.2	2.0	5.2	4.0
SI	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8
IL	9/9	9/9	9/9	9/9	8/9	9/8	9/8	9/9	8/8	9/8
SL-E	345/345	345/345	3456/3456	3456/3456	345/345	3456/3456	345/345	3456/3456	3456/3456	345/345
LoR	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
LoR-E	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
PrO	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
PtO	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2
aTMP	1/1	1/1	1/1	1/1	1/1	1/1	2/2	1/1	1/1	1/1
pTMP	2/2	2/1	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2
DSR	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15
Ven	199	195	192	199	200	196	202	/	203	189
SC	/	72	76	71	84	/	82	74	74	71
Prec	divided	Divided	divided	divided	divided	divided	divided	divided	divided	divided
BB	8	6	7	5	7	8	7	14	7	7
TB	0	0	0	0	0	0	0	12	0	0

(e.g., Zhao et al. 1998; Zhao 2006; Zhang 2009; Li et al. 2011; Shi et al. 2011; Wang et al. 2020, 2021; Zhu and Rao 2020; Francis 2021; Huang 2021; Wang 2021) report that *L. subcinctus* occurs in China, but do not specify any subspecies. Our phylogenetic analysis revealed three lineages within *L. subcinctus* sensu lato. The first lineage includes sequences from Indonesia (including the Lesser Sundas) and Malaysia and refers to *L. subcinctus* sensu stricto. The second lineage includes sequences from the Philippines that are related to *L. sealei*. The last lineage contains sequences of specimens originating from China and Thailand and refers to *Lycodon maculatus* comb. nov. Currently, *L. subcinctus* sensu stricto is known to be distributed in Indonesia and Malaysia and their adjacent areas, while *L. sealei* is known only in the Philippines, and all populations previously considered being *L. subcinctus* from China belong to *Lycodon maculatus* comb. nov. Therefore, we remove *L. subcinctus* from the herpetofauna of China. Since we have not obtained samples from Laos, Vietnam, Cambodia, region of Thailand except Nakhon Ratchasima, and the Nicobar Islands, we are currently unable to determine the taxonomic status of the populations identified as *L. subcinctus* in these areas. Further studies are needed to clarify what species they belong to.

Many records of *Lycodon subcinctus* (now *Lycodon maculatus* comb. nov.) in China are known from the literature. Pope (1935) described three specimens of this species, two from Hainan and one from Fujian, China. He recorded the ventral scales as 197 and 199 in the Hainan specimens and 221 in the Fujian specimen, and the subcaudal scales as 77 and 78 in the Hainan specimens and

77 in the Fujian specimen, respectively. It is worth noting that two of the three specimens described by Pope (1935) are juveniles, one from Hainan and the other from Fujian. He described the juvenile from Hainan as having 13 light cross-bands on the body, but did not mention any bands on the tail. However, he described the juvenile from Fujian as having 16 distinct light cross-bands throughout. For this species, there are 20–27 light bands throughout in juveniles. Since Pope (1935) only described the bands on the body without mentioning the bands on the tail of the juvenile from Hainan, we cannot know the total number of bands on this specimen. However, the total number of bands on the juvenile from Fujian obviously does not match the characteristics of this species. Therefore, we speculate that the juvenile from Fujian described by Pope (1935) does not belong to this species, and the record of 221 ventral scales is questionable. Zhao et al. (1998) recorded the ventral scales of this species as 193–202 and subcaudal scales as 71–78 based on eight voucher specimens from China. Zhao (2006) recorded the ventral scales of this species as 196–227 and subcaudal scales as 72–105 based on seven specimens from Hainan, China, but did not provide the voucher numbers of the specimens. Li et al. (2011) recorded the ventral scales of this species as 193–202 and subcaudal scales as 71–78, but did not provide voucher specimens details from which this data was derived. Shi et al. (2011) recorded that this species has one preocular and 227 ventral scales, and 105 subcaudal scales based on one specimen from Hainan, China, but also did not provide the voucher number of the specimen. An important diagnosis of *Lycodon maculatus* comb. nov. is the absence of preocular, so it is obvious

that Shi et al. (2011) relied on a misidentified specimen, and thus, the numbers of ventral and subcaudal scales they recorded do not belong to this species. Coincidentally, the maximum numbers of ventral and subcaudal scales recorded by Zhao (2006) are the same as those recorded by Shi et al. (2011), and all specimens of this species in Zhao (2006) and Shi et al. (2011) are from Hainan. Thus, the maximum numbers of ventral and subcaudal scales recorded by Zhao (2006) may come from the same specimen as in Shi et al. (2011), which was misidentified as *L. subcinctus* at that time. In this way, the records of 227 ventral scales and 105 subcaudal scales are also not credible. Currently, there are no reliable records of the number of ventral scales exceeding 205.

Conclusion

Based on molecular and morphological data, we resurrect and elevate the junior synonym subspecies, *Lycodon subcinctus maculatus*, as a full, valid species, which we refer to as *Lycodon maculatus* comb. nov. This species is currently confirmed to be distributed in Hong Kong Special Administrative Region, Guangxi Zhuang Autonomous Region, and Guangdong, Fujian, Hainan, Sichuan, and Yunnan provinces, China, and Nakhon Ratchasima, Thailand, based on molecular data. As for whether the populations in the other parts of Thailand and in Laos, Vietnam, Cambodia, and the Nicobar Islands, that were previously considered *L. subcinctus*, also belong to *Lycodon maculatus* comb. nov., further research is needed to verify.

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