

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

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ABSTRACT

While considerable progress has been made in the taxonomic studies of the genus *Lycodon* in Asia, questions remain to be clarified regarding the taxonomy of certain groups, particularly those containing species in China. Not only do many regions in China remain overlooked by herpetologists, resulting in the possibility of undiscovered new species, but the surveyed areas also have suspicious records of recognized congeners that require taxonomic confirmations. Combining both morphological and genetic data, we tackle these outstanding issues in the taxonomy of *Lycodon* in China. In particular, we discover two new species of *Lycodon*: one from the previously neglected hot-dry valley in the northern Hengduan Mountain Region close to Tibet, and another reclusive and cryptic species from the *L. fasciatus* complex in

the downtown park of a major city in southern Sichuan Province. Additionally, we clarify the distribution of *L. septentrionalis* in China and resurrect and elevate its junior synonym subspecies, *Dinodon septentrionale chapaense*, as a full, valid species, and we synonymize the recently described *L. namdongensis* to the resurrected *L. chapaensis* **comb. nov.** *Lycodon chapaensis* **comb. nov.** thus represents a new national record of reptilian fauna of China. Lastly, based on literature review, we also correct some of the erroneous records of *L. fasciatus*

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and *L. ruhstrati* in China, point out remaining taxonomic issues of the genus for future research, and update the dichotomous key and distribution of the 20 species of *Lycodon* currently recorded from China.

Keywords: Erroneous records; Guangdong; Hunan; Misidentification; Serpentes; Sichuan; Wolf Snake; Yunnan

INTRODUCTION

After major generic revisions (Guo et al., 2013; Siler et al., 2013), Wolf Snakes of the genus *Lycodon* Fitzinger, 1826 represent one of the most diverse snake radiations in Asia, including 66 recognized species to date (Ganesh et al., 2020; Uetz et al., 2020). Majority of the currently recognized taxa are known inhabiting tropical to subtropical forests at a mid-to-low elevation (Luu et al., 2018; Vogel & Brachtel, 2008; Vogel et al., 2009; Wang et al., 2020a), where species of the genus are known to feed heavily on reptiles, particularly on lizards (Zhang & Wang, 2014; Zhao et al., 1998).

In China, 17 species have been recorded (Janssen et al., 2020; Wang et al., 2020b), including *L. aulicus* (Linnaeus, 1758), *L. cathaya* Wang, Qi, Lyu, Zeng, Wang, 2020, *L. fasciatus* (Anderson, 1879), *L. flavozonatus* (Pope, 1928), *L. futsingensis* (Pope, 1928), *L. gongshan* Vogel, Luo, 2011, *L. laoensis* Günther, 1864, *L. liuchengchaoi* Zhang, Jiang, Vogel, Rao, 2011, *L. multizonatus* (Zhao, Jiang, 1981), *L. meridionalis* (Bourret, 1935), *L. pictus* Janssen, Pham, Ngo, Le, Nguyen, Ziegler, 2019, *L. ruhstrati* (Fischer, 1886), *L. rosozonatus* (Hu, Zhao, 1972), *L. rufozonatus* Cantor, 1842, *L. septentrionalis* (Günther, 1875), *L. subcinctus* Boie, 1827, and *L. synaptor* Vogel, David, 2010. In the Hengduan Mountain Region (HMR) in Southwest China alone, seven recognized species have been recorded from Yunnan and Sichuan Provinces, namely *L. fasciatus*, *L. gongshan*, *L. liuchengchaoi*, *L. ruhstrati*, *L. multizonatus*, *L. septentrionalis*, and *L. synaptor* (Chen et al., 2018a, 2018b; Guo et al., 2007; Vogel & David, 2010; Vogel & Luo, 2011; Yang & Rao, 2008; Zhang et al., 2011b; Zhao, 2004; Zhao & Yang, 1997). Of these seven species found in the HMR, only *L. multizonatus* is from the high-elevation regions in the northeast (Lei et al., 2014). As most parts of the HMR have not been surveyed in details for herpetological diversity, and given previous studies already suggested that the northern parts of the HMR actually harbor a surprising number of undocumented reptilian diversity (Peng et al., 2014b; Wang et al., 2021), it is likely that the diversity of *Lycodon* in the northern HMR is also underestimated.

In relation to the overlooked diversity, many recognized species have outstanding taxonomic issues. Species currently recorded from HMR are known by having wide distribution ranges that expand across distinct zoogeographic regions (Zhao & Adler, 1993), particularly *L. fasciatus*, *L. ruhstrati*, and *L. septentrionalis* (Zhao, 2006; Zhao et al., 1998). As studies have suggested that cryptic diversity and misidentification of

recognized congeners explain some of the existing suspicious records (Vogel & David, 2010; Vogel & Luo, 2011; Vogel et al., 2009), the current remaining records of these species across China and Southeast Asia warrant further confirmations.

In this study, we combined both morphological and genetic data to shed lights into the current taxonomy of *Lycodon* in China. As results, we discover two new species of *Lycodon*: one species from northern HMR that has never been documented before, and another one from the previously identified population of *L. fasciatus* in Panzhihua, Sichuan. Additionally, we found that the previously identified "*L. septentrionalis*" in Yunnan Province represent the same lineage as the recently described species *L. namdongensis* from northern Vietnam, and this lineage matches the diagnosis of an existing synonym, *Dinodon septentrionale chapaense* Angel, Bourret, 1933 (= *Lycodon septentrionalis chapaensis* after generic revision), which we resurrect and elevate to full species status. We provide an expanded description of the poorly known *L. chapaensis* **comb. nov.** based on additional specimens from China. Furthermore, we confirm that the questionable records of "*L. fasciatus*" from Hunan and Guangdong represent misidentifications over *L. liuchengchaoi*, and records of "*L. ruhstrati*" in Yunnan represent clear misidentifications over *L. chapaensis* **comb. nov.** and *L. gongshan*. Lastly, we provide an updated dichotomous key and distribution to the recognized species in China and discuss some remaining taxonomic issues for future studies.

MATERIALS AND METHODS

Taxonomic sampling

A total of 13 specimens and a non-vouchered genetic tissue of the genus *Lycodon* were collected from Southwest China between 2016 and 2020 (Figure 1; Table 1; Appendix I, II). Liver or muscle tissues were taken after the specimens were euthanized, and the voucher specimens were fixed in 10% buffered formalin in the field, transferred to 70% ethanol after 48h for permanent storage, and deposited at the Zoological Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ).

Specimens of recognized congeners were examined in museum collections, including Natural History Museum (BMNH), California Academy of Sciences (CAS), Chengdu Institute of Biology, Chinese Academy of Sciences (CIB), Field Museum of Natural History (FMNH), KIZ, and Henan University (HENU) (Appendix II). For species that we could not examine in person, data were obtained from literature (Angel & Bourret, 1933; Boulenger, 1893; Janssen et al., 2019; Luu et al., 2019; Peng et al., 2014a, 2015, 2017; Vogel et al., 2009; Wang et al., 2020a; Zhang, 2019). Additional abbreviations of voucher collections included herpetological collection of Dr. Guo Peng at Yibin University (GP), Muséum National d'Histore Naturelle (MNHN), and Vietnam National University of Forestry (VNUF). Photos of the holotype of *Dinodon septentrionale chapaense* were obtained from the

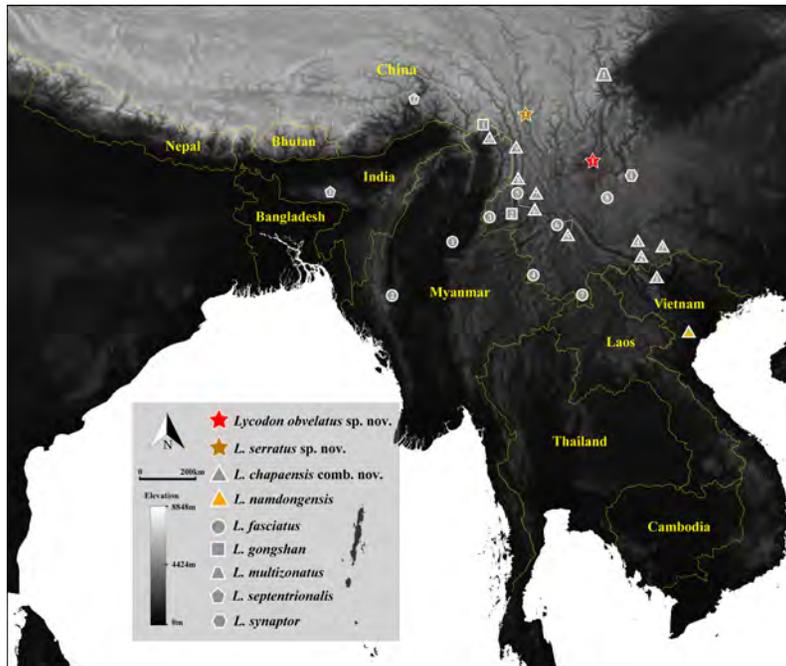


Figure 1 Distributions of focal members of the genus *Lycodon* in Southwest China and nearby countries for this paper

Different shapes represent different species, and numbers indicate different localities where the species have been recorded (details see Appendix I). Number 1 always indicates the type locality of that given species. Bifurcating white lines indicate sympatric distribution of two species at the same site. *Lycodon serratus* sp. nov. (brown star): Geyading, Deqin County, Yunnan, China. *Lycodon obvelatus* sp. nov. (red star): Panzhihua City, Panzhihua, Sichuan, China. *Lycodon chapaensis* comb. nov. (triangle): the orange triangle indicates the type locality of its junior synonym, *L. namdongensis* at Quan Son, Thanh Hoa Province, Vietnam; gray triangle indicates remaining localities of the species. *Lycodon fasciatus* sensu stricto (circle); *L. gongshan* (square); *L. multizonatus* (trapezoid); *L. septentrionalis* sensu stricto (pentagon); and *L. synaptor* (hexagon).

website of MNHN (<https://science.mnhn.fr/institution/mnhn/collection/ra/item/1933.11?listIndex=25&listCount=253>).

Morphological data

With the exception of total length, snout–vent length, and tail length, which were taken using a string and a ruler to the nearest 1mm, measurements were taken using a digital caliper to the nearest 0.1mm. Morphometric and pholidosis characters and their measurement/counting methods followed Wang et al. (2020a) and include: eye diameter (ED), head length (HL), head width (HW), snout–vent length (SVL), TaL (Tail length), total length (ToL); supralabial count (SL), infralabial count (IL), chin shield count (CS), preocular count (PrO), postocular count (PtO), loreal count (LoR), loreal entering orbit (LoR-E), temporal count (TMP), preventral scale count (PrV), ventral scale count (VEN), subcaudal count (SC), dorsal scale rows at one head length posterior to the neck (DSRH), dorsal scale rows at midbody (DSRM), dorsal scale rows at one head length anterior to the vent (DSRV), number of maxillary teeth (MT), body scale texture (BST; smooth vs. keeled), numbers of light bands on the dorsum (NDB; which excludes the collar-band on head), and numbers of light bands on the tail (NTB). All paired head pholidosis characters were given in the left/right order. Maxillary teeth formula are recorded as A-B-C format, where from left to right each letter represents the number of teeth in that specific tooth group

from anterior end to posterior end of maxillary bone, and “-” indicates the presence of a gap. Hemipenis morphology was described based on Dowling & Savage (1960), and the color description followed Köhler (2012) for maximum comparability.

For SL, scale count was given in “A-B-C” format, where A is the number of anterior SL that do not enter the orbit, B is number of SL that enter the orbit, and C is the number of remaining SL that are posterior to and do not contact the orbit. For IL, scale counts were given in “A(B)” format, where A is the total number of IL, and B is the number of IL that are in contact with the anterior chin shield. For TMP, scale count was given in “A+B” format, where A and B are the number of anterior and posterior temporal scales, respectively. For posterior temporal scale count, paraparietal scale was included.

Additionally, the following morphological characters were also recorded: vertical eye diameter (VED), measured linearly between superior most and inferior most points of eye; distance between head and first body cross-band (DHB), measured between the posterior meeting point of parietal and the anterior edge of first dorsal cross-band along the vertebral line; position of first body cross-band (PBB), recorded as the number of the anterior most ventral scale at which the first body cross-band is located; paraparietal scale count (PPT), defined as the number of enlarged scales bordering the partial

Table 1 Samples and their Genbank accession Nos. in the present study

Genus	Species	Voucher No.	Locality	GenBank accession No.
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 035013	Lushui, Nujiang Prefecture, Yunnan, China	MW353742
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 038282	Fugong, Nujiang Prefecture, Yunnan, China	MW353744
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 035113	Dulongjiang, Nujiang Prefecture, Yunnan, China	MW353743
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 027593	Tengchong, Baoshan, Yunnan, China	MW353741
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 034331	Xichou, Wenshan Prefecture, Yunnan, China	MW353739
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 006753	Mengzi, Honghe Prefecture, Yunnan, China	MW353737
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 049166	Daweishan, Honghe Prefecture, Yunnan, China	MW353738
<i>Lycodon</i>	<i>chapaensis</i> comb. nov.	KIZ 047084	Jingdong, Puer, Yunnan, China	MW353740
<i>Lycodon</i>	<i>gongshan</i>	KIZ 035112	Dulongjiang, Nujiang Prefecture, Yunnan, China	MW353748
<i>Lycodon</i>	<i>gongshan</i>	KIZ 035114	Dulongjiang, Nujiang Prefecture, Yunnan, China	MW353749
<i>Lycodon</i>	<i>gongshan</i>	/	Yunlong Nature Reserve, Dali, Yunnan, China	MW353747
<i>Lycodon</i>	<i>obvelatus</i> sp. nov.	KIZ 040146	Panzhuhua, Sichuan, China	MW353745
<i>Lycodon</i>	<i>septentrionalis</i>	CIB 117521	Medog, Nyinchi Prefecture, Tibet, China	MW353736
<i>Lycodon</i>	<i>serratus</i> sp. nov.	KIZ 038335	Deqin, Yunnan, China	MW353746
<i>Boiga</i>	<i>cynodon</i>	KU324614	Negros Occidental, Philippines	KC010340
<i>Dasypeltis</i>	<i>atra</i>	CAS 201641	Kabale, Uganda	AF471065
<i>Lycodon</i>	<i>albofuscus</i>	USMHC 1457	–	KX822584
<i>Lycodon</i>	<i>alcalai</i>	KU327848	Municipality of Sabtang, Batanes, Philippines	KC010345
<i>Lycodon</i>	<i>banksi</i>	VNUF R.2015.20	Khammouane, Laos	MH669272
<i>Lycodon</i>	<i>bibonius</i>	KU304589	Cagayan, Philippines	KC010351
<i>Lycodon</i>	<i>butleri</i>	LSUHC 9137	Perak, Malaysia	KJ607891
<i>Lycodon</i>	<i>butleri</i>	LSUHC 8365	Perak, Malaysia	KJ607892
<i>Lycodon</i>	<i>capucinus</i>	MVZ 291704	–	MK844523
<i>Lycodon</i>	<i>capucinus</i>	MVZ 291703	–	MK844522
<i>Lycodon</i>	<i>cathaya</i>	SYS r001542	Longsheng County, Guangxi, China	MT602075
<i>Lycodon</i>	<i>cavernicolus</i>	LSUHC 10500	Perlis, Malaysia	KJ607890
<i>Lycodon</i>	<i>cavernicolus</i>	LSUHC 9985	Perlis, Malaysia	KJ607889
<i>Lycodon</i>	<i>chapaensis</i> comb. nov. (<i>septentrionalis</i>)	–	Yunnan, China	MK201305
<i>Lycodon</i>	<i>chrysoprateros</i>	KU 307720	Cagayan, Philippines	KC010360
<i>Lycodon</i>	<i>dumerillii</i>	PNM7751	–	KC010363
<i>Lycodon</i>	<i>dumerillii</i>	KU 305168	–	KC010362
<i>Lycodon</i>	<i>effraenis</i>	LSUHC 9670	–	KC010376
<i>Lycodon</i>	<i>effraenis</i>	KU 328526	Karome, Nakhon Si Thammarat, Thailand	KC010364
<i>Lycodon</i>	<i>fasciatus</i>	CAS 234875	Mindat, Chin State, Myanmar	KC010365
<i>Lycodon</i>	<i>fasciatus</i>	CAS 234957	Mindat, Chin State, Myanmar	KC010366
<i>Lycodon</i>	<i>fasciatus</i>	SYS r001654	Xishuangbanna, Yunnan, China	MK201559
<i>Lycodon</i>	<i>fasciatus</i>	KIZ 014125	Xishuangbanna, Yunnan, China	MK201557
<i>Lycodon</i>	<i>flavozonatus</i>	SYSr000640	Huangganshan, Jiangxi, China	MK201413
<i>Lycodon</i>	<i>flavozonatus</i>	HS15101	Huangshan, Anhui, China	MK201312
<i>Lycodon</i>	<i>gongshan</i>	GP3548	Lingcang, Yunnan, China	KP901026
<i>Lycodon</i>	<i>gongshan</i>	GP3547	Lingcang, Yunnan, China	KP901025
<i>Lycodon</i>	<i>gongshan</i>	GP3546	Lingcang, Yunnan, China	KP901024
<i>Lycodon</i>	<i>gongshan</i>	GP3516	Lingcang, Yunnan, China	KP901022
<i>Lycodon</i>	<i>jara</i>	CAS 235387	Putao, Kachin, Myanmar	KC010367
<i>Lycodon</i>	<i>laoensis</i>	KU 328529	Karome, Nakhon Si Thammarat, Thailand	KC010371
<i>Lycodon</i>	<i>laoensis</i>	FMNH 258659	Salavan, Laos	KC010368
<i>Lycodon</i>	<i>liuchengchaoi</i> (<i>fasciatus</i>)	GP 2094	Nanling, Guangdong, China	KC733201
<i>Lycodon</i>	<i>liuchengchaoi</i> (<i>fasciatus</i>)	GP 2097	Chebaling, Guangdong, China	KC733202
<i>Lycodon</i>	<i>liuchengchaoi</i>	JK 201704	Ningshan, Shaanxi, China	MK201563
<i>Lycodon</i>	<i>liuchengchaoi</i>	SYS r001654	Shennongjia, Hubei, China	MK201580

Continued

Genus	Species	Voucher No.	Locality	GenBank accession No.
<i>Lycodon</i>	<i>liuchengchaoi</i>	DL 14315	–	KF732928
<i>Lycodon</i>	<i>meridionalis</i>	VNUF R.2017.123	Thanh Hoa, Vietnam	MH669270
<i>Lycodon</i>	<i>meridionalis</i>	VNUF R.2012.4	Bac Kan, Vietnam	MH669271
<i>Lycodon</i>	<i>multizonatus</i>	SyS r002411	Baishuijiang National Nature Reserve, Longnan, Gansu, China	MT625863
<i>Lycodon</i>	<i>multizonatus</i>	KIZ 01623	Luding, Sichuan, China	KF732926
<i>Lycodon</i>	<i>multizonatus</i> (<i>liuchengchaoi</i>)	HS 11252	Sanjiazhai, Yunnan, China	MK201303
<i>Lycodon</i>	<i>chapaensis</i> comb. nov. (<i>namdongensis</i>)	VNUF R. 2017.23	Thanh Hoa, Vietnam	MK585007
<i>Lycodon</i>	<i>pictus</i>	ZFMK93747	Cao Bang, Vietnam	MN395830
<i>Lycodon</i>	<i>pictus</i>	ZFMK93746	Cao Bang, Vietnam	MN395829
<i>Lycodon</i>	<i>rufozonatus</i>	LSUMZ 44977	–	AF471063
<i>Lycodon</i>	<i>rufozonatus</i>	GP133	Tongjiang, Sichuan, China	KC733194
<i>Lycodon</i>	<i>ruhstrati</i>	GP2243	Ruyuan, Guangdong, China	KC733208
<i>Lycodon</i>	<i>ruhstrati</i>	GP2049	Chebaling, Guangdong, China	KC733200
<i>Lycodon</i>	<i>ruhstrati</i>	GP991	Gongcheng, Guangxi, China	KC733197
<i>Lycodon</i>	<i>ruhstrati</i>	GP285	Junlian, Sichuan, China	KC733195
<i>Lycodon</i>	<i>ruhstrati</i>	YSr001631	Huangping, Guangxi, China	MK201538
<i>Lycodon</i>	<i>ruhstrati</i>	YSr001555	Yangmeiao, Guangxi, China	MK201521
<i>Lycodon</i>	<i>ruhstrati</i>	YSr001309	Jiuliashan, Jiangxi, China	MK201473
<i>Lycodon</i>	<i>ruhstrati</i>	YSr001275	Jiangshi, Fujian, China	MK201467
<i>Lycodon</i>	<i>ruhstrati</i>	HS12069	Chebaling, Guangdong, China	MK201310
<i>Lycodon</i>	<i>ruhstrati</i>	DL12678	–	KF732925
<i>Lycodon</i>	<i>sealei</i>	KU327571	Palawan, Philippines	KC010384
<i>Lycodon</i>	<i>sealei</i>	KU309447	Palawan, Philippines	KC010385
<i>Lycodon</i>	<i>semicarinatus</i>	–	Ryukyu Archipelago, Japan	AB008539
<i>Lycodon</i>	<i>sidiki</i>	MZB.Ophi.5980	–	KX822583
<i>Lycodon</i>	<i>stormi</i>	JAM7487	–	KC010380
<i>Lycodon</i>	<i>striatus</i>	FBRC_DNA205	–	MK089444
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291678	Indonesia	MK844529
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291679	Indonesia	MK844530
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291680	Indonesia	MK844531
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291681	Indonesia	MK844532
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291682	Indonesia	MK844533
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291683	Indonesia	MK844534
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291684	Indonesia	MK844535
<i>Lycodon</i>	<i>subcinctus</i>	MVZ291685	Indonesia	MK844536
<i>Lycodon</i>	<i>subcinctus</i>	LSUHC5016	Pahang, West Malaysia	KC010382
<i>Lycodon</i>	<i>synaptor</i>	GP2188	Yunnan, China	KC733204
<i>Lycodon</i>	<i>synaptor</i>	SYS r001775	Darongshan, Guangxi, China	MK201582
<i>Lycodon</i>	<i>synaptor</i>	SYS r001800	Dawuling, Guangdong, China	MK201581
<i>Lycodon</i>	<i>synaptor</i>	HS13002	Honghe, Yunnan, China	MK201309
<i>Lycodon</i>	<i>synaptor</i>	HS12087	Kunming, Yunnan, China	MK201308
<i>Lycodon</i>	<i>synaptor</i>	HS11006	Mengzi, Yunnan, China	MK201304
<i>Lycodon</i>	<i>synaptor</i>	GP3515	Lingcang, Yunnan, China	KP901021
<i>Lycodon</i>	<i>synaptor</i>	GP3288	Maandi, Yunnan, China	KP901020
<i>Lycodon</i>	<i>synaptor</i>	GP3270	Daweshan, Yunnan, China	KP901019
<i>Lycodon</i>	<i>synaptor</i>	GP3545	Yunnan, China	KP901023
<i>Lycodon</i>	<i>zawi</i>	CAS 239944	Kyaukpyu, Rakhine State, Myanmar	KC010386
<i>Lycodon</i>	<i>zawi</i>	CAS 210323	Thabakesay, Saging, Myanmar	AF471040

New sequences are indicated in bold. Species name in parentheses indicates the previous synonym or misidentified species name used for the given sequence. “/” indicates non-voucher data, “–” indicates that information is not available or could not be located.

scales on each side, excluding the anterior temporal and frontal scales; nuchal scale (NS), defined as the total number of small nuchal scales bordering the posterior end of parietal; presence or absence of collar-band of occipital head (NCB), were also recorded.

Genetic data

The genomic DNA was extracted from liver or muscle tissues with a standard three-step phenol-chloroform extraction method (Sambrook et al., 1989). The fragment of the mitochondrial cytochrome b (*cyt b*) gene was targeted using published primers (Burbrink et al., 2000), and PCR and sequencing protocols followed Wang et al. (2020a). Data were filtered and trimmed manually using Geneious v. 10.0, and the final sequence for alignment contains 1 117 bp, and all newly generated sequences were deposited in GenBank (accession No. MW353736–353749; Table 1).

In addition, available sequences of congeners were downloaded from Genbank (Table 1). *Boiga cynodon* and *Dasypeltis atra* were selected as outgroups following previous phylogenetic studies (Lei et al., 2014; Siler et al., 2013). Sequences were edited and aligned using Geneious v. 10.0.

Both maximum likelihood analyses (ML) and Bayesian inferences (BI) were conducted on the final *cyt b* alignment. Partitioned Bayesian analyses were conducted using MRBAYES v. 3.2.7a (Ronquist et al., 2012) on CIPRES (Miller et al., 2010). Sequence data was partitioned by three codon positions, and the best model of nucleotide substitution was selected for each partition by the Akaike Information Criterion (AIC), implemented in JMODELTEST2 v. 2.1.10 (Darriba et al., 2012), which was GTR+ Γ for all three partitions. Two independent Markov chain Monte Carlo analyses were run, each with four Metropolis-coupled chains. Bayesian analyses were run for 90 million generations, with parameters and topologies sampled every 1 000 generations. Stationarity and convergence were assessed with TRACER v. 1.6.0 (Rambaut et al., 2013), and the first 20% of samples were discarded as burn-in.

Partitioned Maximum Likelihood analyses were performed using RAxML-VI-HPC v. 8.2.10 (Stamatakis, 2014) using the same partition strategy as for the Bayesian analyses. The most complex model (GTR+ Γ) was applied for all the partitions, with 1 000 replicate ML inferences run. Each inference was initiated with a random starting tree, and nodal support was assessed with 1 000 bootstrap pseudoreplicates. Nodes having ML bootstrap values of 70 and above and BI posterior probabilities of 0.95 and above were considered well supported. Pairwise uncorrected genetic distances were calculated using PAUP v. 4.0 b10 (Swofford, 2002).

RESULTS

Molecular results

ML and BI yield overall similar topology, although some nodes have different level of supports (strongly supported in one but not in the other) (Figure 2). Overall, with addition of most

available Indian and Southeast Asian taxa (i.e., *L. alcalai*, *L. chrysoprateros*, *L. dumerilii*, *L. jara*, and *L. zawi*), our phylogeny shows similar topology as to recent studies for the well-supported nodes (Luu et al., 2019; Wang et al., 2020a) (Figure 2). Although the genus *Lycodon* is still recovered as monophyletic, the current dataset could not resolve higher relationships among major clades (polytomy in BI and/or low bootstrap support <60 in ML).

The samples of “*L. septentrionalis*” from China and holotype of *L. namdongensis* together from a monophyletic clade (Clade A, 0.93/93), with two distinct, genetically diverged groups recovered within this clade: first group includes the sample from southern Tibet, which is close to and in the same zoogeographic region of the type locality (i.e., Khasi Hills in East Himalaya) of *L. septentrionalis*; and the second group (Clade B, 1.00/100) contains the specimens of “*L. septentrionalis*” from western and southern Yunnan and the holotype of *L. namdongensis*, with *L. namdongensis* nested within the Yunnan “*L. septentrionalis*” (Figure 2). The Yunnan populations of “*L. septentrionalis*” show minimal divergence from the holotype of *L. namdongensis* (uncorrected genetic distance 0%–1.8%), but they have considerable divergences from the Tibetan population of true *L. septentrionalis* (5.7%–7.4%) (Table 2).

The putative new species from northern HMR is recovered sister to *L. multizonatus* with strong supports (Clade D, 1.00/98), and it shows a considerable genetic divergence from *L. multizonatus* (3.6%–4.0%). The previously reported sample of “*L. liuchengchaoi*” from Yunnan, China is nested within *L. multizonatus* (1.00/99). Samples that are currently identified as *L. fasciatus* are polyphyletic, consisting of three major groups: the first well-supported group (1.00/100) contains samples true *L. fasciatus* from Myanmar, southern Yunnan and western Yunnan, which is within the close proximity of the type locality of the species, and this group forms a strongly supported clade with *L. butleri*, *L. gongshan*, *L. cavernicolus*, and *L. sidiki* (Clade C; 1.00/100), although relationships within Clade C remain unresolved (Figure 2); the second group includes samples of “*L. fasciatus*” from Guangdong, which are nested within *L. liuchengchaoi* (Clade E, 1.00/100); and the third group includes the sample of the putative new species from Panzhihua, which forms a monophyletic group with *L. synaptor* (Clade G, 1.00/100). These three groups are genetically diverged: the Guangdong samples of “*L. fasciatus*” are nearly identical to *L. liuchengchaoi* ($\leq 0.2\%$) and show substantial genetic divergence from the true *L. fasciatus* from Myanmar and Yunnan (9.4%–11.7%); the Panzhihua sample is also substantially diverged from the true *L. fasciatus* (13.3%–13.6%), and it is also substantially diverged from its sister species *L. synaptor* (8.6%–9.5%; Table 2).

Morphological results and taxonomic conclusion

All examined specimens of the currently identified “*L. septentrionalis*” from Yunnan have overlapping body sizes and tail ratios, same head pholidosis characters, similar dorsal pholidosis characters, and same body coloration and

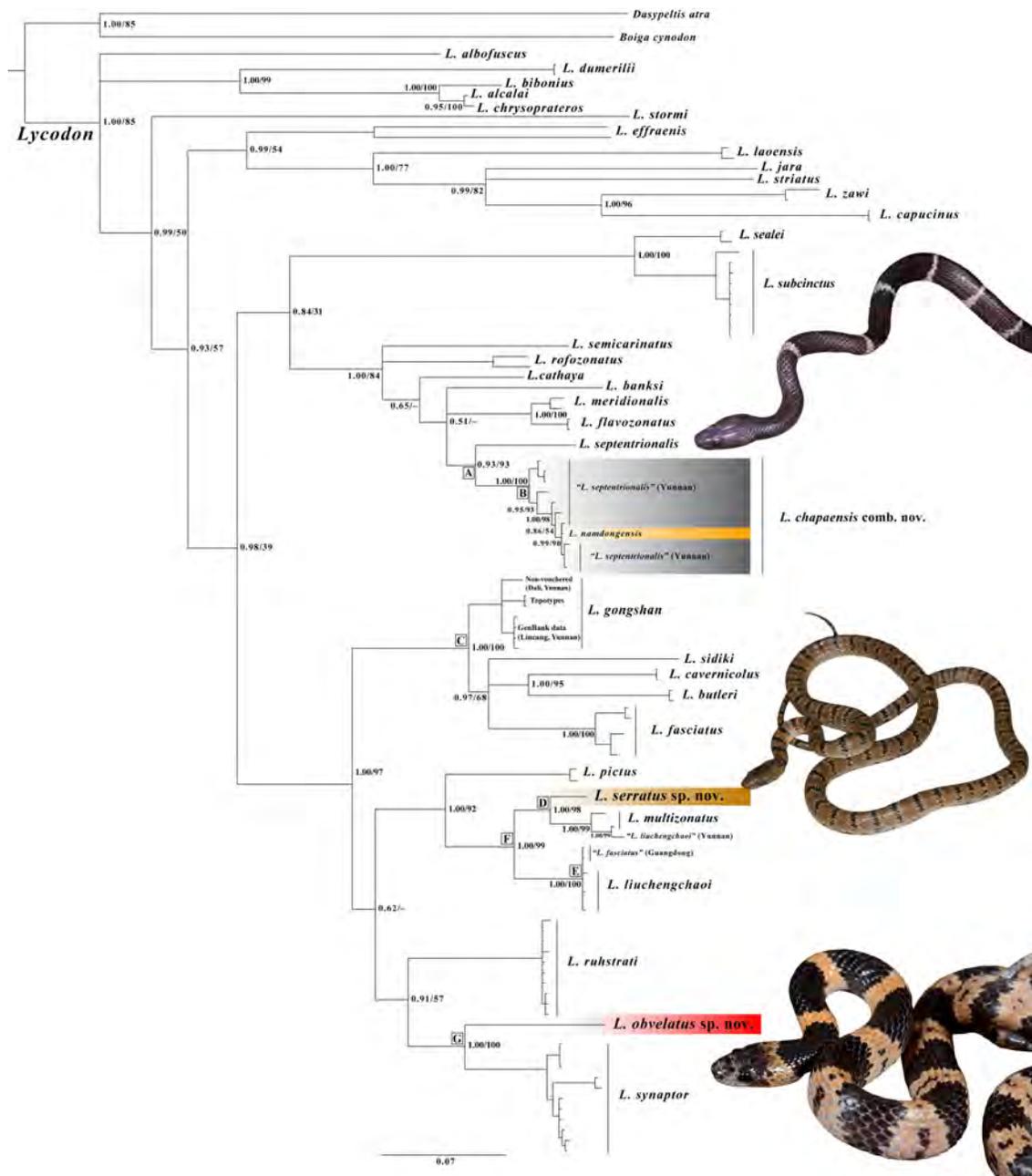


Figure 2 Phylogenetic trees of the genus *Lycodon* inferred by Bayesian analyses (BI) based on 1 117 bp of mitochondrial gene *cyt b*

Both bootstrap supports (BS) and Bayesian posterior probabilities (BPP) are indicated on each of the corresponding node. “-” indicates a differential topology between ML and BI results. Support values for strongly supported (BS \geq 70, BPP \geq 0.95) intraspecific nodes were omitted, except few cases where the nodes are specifically referred in text.

ornamentation with respect to the holotype of *L. namdongensis* and the holotype of *Dinodon septentrionale chapaense* (Figures 3, 5; Table 3). On the other hand, specimens of *L. septentrionalis* from southern Tibet, which is close to its type locality, differs from the above Yunnan and Vietnam populations by having multiple rows of keeled dorsal scales (vs. smooth or only posterior vertebral row feebly

keeled) and different number of maxillary teeth (8 vs. 11 or 12). Such morphological differentiation suggests that the Yunnan population of “*L. septentrionalis*”, the holotype of *L. namdongensis*, and the holotype of *D. septentrionale chapaense* represent the same lineage, which is different from true *L. septentrionalis*.

The specimen of the putative new species from the northern

Table 2 Uncorrected genetic distance (%) based on 1 117 bp fragment of *cyt b* among selected members of the genus *Lycodon*

	1	2	3	4	5	6	7	8	9	10	11
1 <i>L. serratus</i> sp. nov.	-										
2 <i>L. obvelatus</i> sp. nov.	11.9	-									
3 <i>L. septentrionalis</i>	14.3	14.2	-								
4 <i>L. namdongensis</i>	14.8	14.9	6.6	-							
5 “ <i>L. septentrionalis</i> ”	13.7–15.2	14.3–15.0	5.7–7.4	0.1–1.7	0–1.8						
6 <i>L. gongshan</i>	10.1–10.6	11.3–12.3	12.5–14.6	12.5–14.5	11.3–14.7	0–2.2					
7 <i>L. fasciatus</i>	9.9–11.1	13.3–13.6	12.4–14.1	12.9–14.1	12.4–14.4	5.7–8.0	0–2.4				
8 <i>L. pictus</i>	8.3–8.4	12.2–12.3	13.5–13.7	13.0	12.5–13.3	10.5–11.4	10.7–12.0	0.6			
9 <i>L. liuchengchaoi</i>	5.2–5.4	11.1–11.5	12.6–14.2	13.2–14.5	12.9–14.6	8.1–10.5	9.4–11.7	7.9–8.4	0–0.2		
10 <i>L. multizonatus</i>	3.6–4.0	11.3–12.0	12.5–14.0	13.1–14.3	12.8–14.6	8.2–11.2	9.4–11.7	8.2–8.9	5.4–6.4	0.5–2.2	
11 <i>L. synaptor</i>	10.9–12.6	8.6–9.5	12.1–13.8	12.7–14.1	11.4–14.2	8.5–12.1	10.1–12.0	9.4–11.1	10.5–12.5	10.9–12.8	0–3.0

The diagonal values are intraspecific genetic distances for the species with multiple available specimens.

HMR is morphologically most similar to *L. multizonatus* (i.e., coloration), but it shows morphological differentiations from the latter and all remaining recognized species, including different head shape, more IL, more DSRH, smooth DST, and distinct ornamentation patterns (details see comparison section in the taxonomic account below; Figures 4, 5; Table 4).

The specimen of “*L. fasciatus*” from Panzhihua in southern Sichuan Province is morphologically similar to the true *L. fasciatus*, but it can be differentiated from the true *L. fasciatus* readily by having a smaller body size, smooth dorsal scales, fewer infralabials, and a distinct collar-band on neck in adult (details see comparison section in the taxonomic account below; Figures 4, 5; Table 4). Additionally, the Panzhihua specimen differs from the type of *Dinodon yunnanensis*, which is currently considered as a junior synonym of *L. fasciatus* but was believed to be valid (Vogel & David, 2010; details see comparisons in the taxonomic account below).

In conclusion, the *Lycodon* specimens from northern HMR and from Panzhihua represent two distinct evolutionary lineages that cannot be assigned to any recognized species. Hence we describe them as two new species. Additionally, populations of “*L. septentrionalis*” from Yunnan Province represent the same lineage as *L. namdongensis* and *Dinodon septentrionale chapaense* from northern Vietnam, which are distinct and diverged from the true *L. septentrionalis* from the East Himalaya both morphologically and genetically. We resurrect *D. septentrionale chapaense* and elevate it as a full species, *L. chapaensis* comb. nov., and synonymize *L. namdongensis* as its junior synonym. The distribution of *L. chapaensis* comb. nov. in Yunnan hence represents a new national record of reptilian fauna of China.

Taxonomic account

Lycodon chapaensis comb. nov. (Angel, Bourret, 1933) (Figures 3C–G, 5F, G)

Proposed Chinese common name: 沙坝白环蛇 (Pinyin: Sha Ba Bai Huan She)

Proposed English common name: Chapa Wolf Snake

Chresonyms: *Dinodon septentrionale chapaense* Angel & Bourret, 1933

Dinodon septentrionalis Smith, 1943 (in part); He & Zhou, 2000; Zhang et al., 2002

Dinodon septentrionale: Zhao & Yang, 1997; Zhao et al., 1998; He & Zhou, 2002; Zhao, 2006; Yang & Rao, 2008

Lycodon septentrionalis: Siler et al., 2013; Guo et al., 2013; Cai et al., 2015 (in part); Jiang et al., 2016; Wang et al., 2020b

Lycodon cf. *septentrionalis* Yang et al., 2019

Lycodon namdongensis Luu et al., 2019

Holotype: MNHN-RA-1933.0011, adult female, from 20 km SW of Lao-Kay (=Lao Cai), Tonkin, Vietnam. Collected by Bourret R. on 01 July 1931.

Additional referred specimens: VNUF R. 2017.23 (holotype of *L. namdongensis*) from Nam Dong Nature Reserve, Thanh Hoa Province, Vietnam; KIZ 06753, female from Mengzi, Honghe Prefecture, Yunnan, China; KIZ 35113, male from Dulongjiang, Gongshan Prefecture, Yunnan, China; KIZ 035594, male from Yongping, Dali, Yunnan, China; KIZ 027593, male from Tengchong, Baoshan, Yunnan, China; KIZ 038282, male from Fugong, Nujiang Prefecture, Yunnan, China; and KIZ 035045, subadult female from Lushui, Gongshan Prefecture, Yunnan, China.

Diagnosis: *Lycodon chapaensis* comb. nov. differs from congeners by a combination of the following characters: (1) body size large, ToL 691–1114 mm; (2) tail length moderate, TaL 17.1%–20.5% ToL; (3) dorsal scale rows 17-17-15, mostly smooth, except the posterior vertebral row, which very feebly keeled; (4) VEN 200–225; (5) SC 74–84; (6) cloacal plate entire; (7) loreal short, not entering orbit; (8) SL 7 or 8, 2-3-3, 3-2-3, or 2-2-3; (9) IL 8–10, first 4 or 5 in contact with anterior chin shield; (10) preocular single, in contact with supraocular and prefrontal; (11) postocular 2; (12) temporal 2+2 or 2+3; (13) paraparietal much enlarged, single; (14) maxillary teeth 11 or 12, forming four distinct groups separated by three gaps (3-1-1-6 or 5-1-1-5), fourth and fifth tooth largest, about 2.5 times larger than first; first gap twice as wide as between the first two teeth; second gap largest,



Figure 3 Comparisons between true *Lycodon septentrionalis* (A, B); *L. namdongensis* (C), and Yunnan specimen of “*D. septentrionalis*” (D–G)

A, B: Closeup and dorsolateral overview of a un-vouchered individual from Medog, Tibet, China; C: Holotype of *L. namdongensis* (VNUF R. 2017.23) from Quan Son, Thanh Hoa, Vietnam; D: Un-vouchered individual from Daweishan Nature Reserve, Honghe Prefecture, Yunnan; E: Vouchered adult male from Yongping County, Dali, Yunnan, China (KIZ 035594); F: Vouchered adult male from Tengchong County, Baoshan, Yunnan (KIZ 027593); G: Hemipenis of KIZ 027593 after preservation. Photos of *L. namdongensis* taken from Luu et al. (2019), remaining photos by Chao Wu, Kai Wang, Shaobin Hou, Weiliang Xie, and Zhongbin Yu.

about four times as wide as between the first two teeth; third gap in same width as in first gap; (15) hemipenis single, not forked at tip, bulbous shaped, with medium sized spines on distal end of stem, and spinose and calyculate with spinulate ridges on bulb, apical nude; (16) dorsal Jet Black (Color 300) or dark Indigo (Color 190) in life, with 23–37 white cross-bands on dorsum, 11–16 on tail; (17) cross-bands with rather

clearly defined edges, not serrated or only slightly serrated, single scale width dorsally, widen ventrolaterally; and (18) ventral white, with black transverse bands or irregular speckles.

Comparisons: *Lycodon chapaensis* **comb. nov.** differs from true *L. septentrionalis* by having smooth or only feebly keeled vertebral scale row on posterior body (vs. much more



Figure 4 The dorsolateral view (1) and ventral view (2) of the holotype of *Lycodon serratus* sp. nov. (KIZ 038335) (A) and *L. obvelatus* sp. nov. in life (KIZ 040146) (B) (Photos by Wen-Jie Dong and Kai Wang)

distinctively keeled on medial 3–5 rows), more maxillary teeth (11 or 12 vs. 8), and different maxillary teeth formula (3-1-1-6 or 5-1-1-5, fourth and fifth teeth largest, second gap widest, as four times of distance as in between first two teeth vs. 4-2-2, last two teeth largest, two gaps about same length, as twice as in between first two teeth).

Additionally, *L. chapaensis* comb. nov. further differs from *L. butleri*, *L. cavemicolus*, *L. davisonii*, *L. dumerilii*, *L. fasciatus*, *L. gibsonae*, *L. gongshan*, *L. gracilis*, *L. liuchengchaoi*, *L. multizonatus*, *L. nymphea*, *L. orientalis*, *L. philippinus*, *L. pictus*, *L. sealei*, *L. sidiki*, *L. subcinctus*, *L. submaculatus*, and *L. tristrigatus* by having loreal not entering orbit (vs. entering); from *L. albofuscus*, *L. aulicus*, *L. capucinus*, *L. flavicollis*, *L. flavomaculatus*, *L. hypsirhinoides*, *L. jara*, *L. kundui*, *L. laoensis*, *L. mackinnoni*, *L. meridionalis*, *L. stratus*, *L. tessellatus*, *L. tiwartii*, and *L. zawi* by having a single cloacal plate (vs. divided); from *L. alcalai*, *L. banksi*, *L. cathaya*, *L. bibonius*, *L. cardamomensis*, *L. carinatus*, *L. chrysoprateros*, *L. davidi*, *L. effraenis*, *L. fausti*, *L. ferroni*, *L. flavozonatus*, *L. futsingensis*, *L. gammiei*, *L. kundui*, *L. muelleri*, *L. multifasciatus*, *L. rosozonatus*, *L. rufozonatus*, *L. ruhstrati*, *L. semicarinatus*, *L. solivagus*, *L. stormi*, *L. synaptor*, *L. travancoricus*, *L. zoosvictoriae* by having a larger maximum body size (ToL >1 000 mm vs. <1 000 mm); and from *L. paucifasciatus* by having lower number of dorsal scale rows at midbody (17 vs. 19); and from *L. ophiophagus* by having a shorter tail (TaL 17.1%–18.4% vs. 20.1%–22.8%).

Description of *L. chapaensis* comb. nov. based on holotype and referred materials: Large *Lycodon*, maximum

ToL 1 114 mm; tail moderate, TaL 17.1%–20.5% ToL; head oval, rather wide, moderately distinct from neck; eye large, oval in shape, not laterally compressed. Rostral large, broader than height, pentagonal, visible from above; nasal divided, anterior half bordering rostral, first supralabial, and internasal, posterior half bordering first and second supralabials, loreal, internasal, and prefrontal; internasal paired, roughly rectangular, wider than long or subequal to, much smaller than prefrontals; prefrontal paired, hexagonal, bordering preocular, supraocular, and frontal posteriorly; loreal rather short, longer than wide, bean-shaped or spear-shaped, separated from orbit by preocular and third supralabial; preocular single, taller than wide; supralabials 8 (rarely 7), third to fifth or third and fourth entering orbit; postocular 2, superior one larger; anterior temporal 2, superior one longer and narrower, inferior one shorter and wider; posterior temporal 2 or 3 (including paraparietal); frontal pentagonal, spear-like tip pointing posteriorly; supraocular elongated; parietal paired, inlaying spear tip of frontal anteriorly, bordering supraocular and superior postocular anteriorly, paraparietal and 1–4 nuchal scales posteriorly; paraparietal single, much enlarged and elongated. Infralabials 8–10, anterior most pair enclosing mental and meeting medioposteriorly; 5 or 6 infralabials bordering chin shields, first to fourth or fifth bordering anterior chin shield, fifth or sixth bordering posterior chin shield, respectively; anterior chin shield much longer, forming V-shape, inlaying tip of first pair of infralabials anteriorly; posterior chin shields slightly smaller, not separated from each other by distinct mental groove. Dorsal body scales smooth,



Figure 5 Comparisons of (1) dorsal overview, (2) ventral overview, (3) lateral head, (4) dorsal head, (5) ventral head, and (6) dorsum close-up among *Lycodon serratus* sp. nov. (KIZ 038335; holotype) (A), *L. obvelatus* sp. nov. (KIZ 040146; holotype) (B), *L. multizonatus* (KIZ 01623; topotype) (C), *L. fasciatus* (KIZ 74110262) (D), *L. gongshan* (KIZ 730034; holotype) (E), “*L. septentrionalis*” (KIZ 035594; from Dali, Yunnan, China) (F), *L. chapaensis* comb. nov. (MNHN-RA-1933.0011, holotype; from Chapa, Tonkin, Vietnam) (G), and *L. septentrionalis* (CIB 117521; from Medog, Tibet, China) (H) (Photos of the holotype of *L. chapaensis* comb. nov. are obtained from the website of Muséum National d’Histoire Naturelle, remaining photos by Zhong-Bin Yu and Jin-Long Ren)

except vertebral row that only feebly keeled toward very posterior portion in some individuals; dorsal scale rows 17 at one head-length posterior to neck, 17 at midbody, 15 one-head length anterior to vent. Preventral 1 or 2; ventrals 200–225, angulate; cloacal plate entire; subcaudal paired, 74–85 excluding tail tip. DHB 4.5%–7.9% SVL, PBB at 15th–22th ventral scale.

Maxillary teeth 11 or 12, forming four distinct groups separated by three gaps. First three or five teeth in first group,

gradually enlarged; single tooth in second and third group, respectively, both significantly enlarged (about 2.5 times of second tooth); remaining six or four teeth in last group, gradually decrease in size, eventually about the same size as first or second tooth. First gap twice as wide as regular width between first two teeth; second gap largest, about four times wider as regular; last gap about same as in first gap. Most teeth curved posteriorly towards tip, except first two or three.

Hemipenis morphology based of KIZ 027593: hemipenis

Table 3 Comparisons between holotype of *Dinodon septentrionale chapaense*, holotype of *Lycodon namdongensis*, true *L. septentrionalis* from Tibet, and “*L. septentrionalis*” from Yunnan Province

Species	<i>Lycodon septentrionalis</i>	<i>Dinodon septentrionale chapaense</i>	<i>L. namdongensis</i>	“ <i>L. septentrionalis</i> ”
Voucher No.	CIB 117521, CIB M20150607	MNHN-RA-1933.0011 (holotype)	VNUF R. 2017.23 (holotype)	KIZ 006753, 027593, 035594, 038282, 034331
Sample size	2 (1)	1	1	5
ToL	1 187	1 051+	723	691–1 114
SVL	945–955	890	575	564–915
TaL	242	161 (incomplete)	148	127–199
TaL/ToL	20.4%	–	20.5%	17.1%–18.4% (average 17.6%)
DSRH	17	17	17	17
DSRM	17	17	17	17
DSRV	15	15	15	15
SL	8 (2-3-3)	8 (2-3-3)	8 (2-3-3)	7 or 8 (2-3-3, 3-2-3, or 2-2-3)
IL	9 (4)	9 (5)	10 (5)	8–10 (first 4 or 5 in contact with anterior chin shield)
PrO	1	1	1	1
PtO	2	2	2	2
LoR	1	1	1	1
LoR-E	No	No	No	No
TMP	2+3	2+3	2+3	2+2 or 2+3
VEN	207–212	224	218	200–225
SC	78	56+	85	74–84
Cloacal Plate	Entire	Entire	Entire	Entire
MT	8	–	12	11 or 12
NCB	Absence	Absence	Absence	Absence
NDB	33–35	28	23	23–37
NTB	19	11	14	11–14
BST	Keeled	Smooth	Smooth	Smooth or only posterior vertebral row feebly keeled

Abbreviations are explained in methods. “–” indicates data not available. The number in parentheses for the Sample size row indicate differential sample size for total length and tail length due to the incomplete tail of one of the specimen (CIB M20150607). Except the holotype of *L. namdongensis*, all remaining specimens were examined in person by authors.

single, bulbous shape, with single sulcus spermaticus; rather short, reaching only fifth caudal scale from cloaca when everted, length unknown at retracted state; proximal 1/4 length with some shallow transverse flounces; middle 1/4 densely covered with medium sized spines; distal bulbous structure large, about 1/2 of total length, spinose toward basal end, gradually transition to calyculate with spinulate ridges toward 2/3 of bulbous, and eventually back to flounced toward very tip; apical nude (Figure 3).

Coloration: The dorsal surfaces of the head and body are Jet Black (Color 300) or sometimes dark Indigo (Color 190). A single white collar-band is present on the occipital region of juveniles, but not in adults. White cross-bands are single-scale broad dorsally and widen into triangular shape ventrolaterally. A total of 23–37 cross-bands are present on the body and 11–16 on the tail. The ventral surface of the head and body is white, with some Medium Neutral Gray (Color 298) patches on the anterior infralabials and the gular region. The ventral surface of the body is white to Light Buff (Color 2), with Dark Neutral Gray (299) to Jet Black (Color 300) cross-bands,

transverse groups of speckles, or random speckles. Ventral surface of the tail is nearly completely Dark Neutral Gray (299) to Jet Black (Color 300), with white to Light Buff (Color 2) cross-bands, transverse groups of speckles, or random speckles.

Natural history: *Lycodon chapaensis comb. nov.* inhabits subtropical and tropical evergreen and sometime mixed forests (i.e., with planted coniferous trees in Dali, Yunnan) at mid to low elevation (from 616 m at Nam Fong Nature Reserve, Quan Son District, Thanh Hoa Province, Vietnam, to 2 030 m at Dahaoping, Tengchong, Yunnan, China). The species is nocturnal, where all individuals were found at night actively foraging when collected in China. Unlike other congeners that feed heavily on reptiles, *L. chapaensis comb. nov.* have been reported to feed mostly on rodents, and sometimes frogs (Yang & Rao, 2008; Zhao & Yang, 1997). Yang & Rao (2008) stated the specimens from Yunnan are often found in areas near agriculture fields where rodents are abundant, and individuals from Lushui in western Yunnan were observed actively hunting for rodents in village houses.

Table 4 Comparison of key morphological characters between the holotypes of *Lycodon serratus* sp. nov., *L. obvelatus* sp. nov., and morphologically similar congeners that are also found in the Hengduan Mountain Region (i.e., *L. gongshan*, *L. fasciatus*, *L. multizonatus*, and *L. liuchengchaoi*)

Species	<i>Lycodon serratus</i> sp. nov.	<i>L. obvelatus</i> sp. nov.	<i>L. multizonatus</i>	<i>L. gongshan</i>		<i>L. fasciatus</i>		<i>L. liuchengchaoi</i>	
Sex	M	M	M	M	F	M	F	M	F
Sample size	1 (holotype)	1 (holotype)	4	2	2	1	3	2 (1)	5 (3)
ToL	628	551	440–520	928–963	753–1003	696	418–613	747	389–615
SVL	480	447	350–428	691–740	589–798	553	341–493	595–676	309–481
TaL	148	104	90–96	223–237	164–207	143	71–120	152	80–138
TaL/ToL	23.6%	18.9%	17.7%–20.5%	23.1%–23.2%	21.8% (n=1)	20.5%	17.0%–19.6%	20.3%	20.6%–24.8%
DSRH	19	17	17	17	17	17	17	17	17
DSRM	17	17	17	17	17	17	17	17	17
DSRV	15	15	15	15	15	15	15	15	15
SL	8 or 9 (2-3-3 or 2-4-3)	8 (2-3-3)	8 (2-3-3)	8 (2-3-3)	8 (2-3-3)	8 (2-3-3)	8 (2-3-3)	7 (2-3-2) or 8 (2-3-3)	8 (2-3-3)
IL	10 (5)	8 (4 or 5)	8 (4)	9 (4)	9 (4)	9 (5)	9 (4) or 9 (5)	8 (4)	8 (4)
PrO	1	1	1	1	1	1	1	1	1
PtO	2	2	2	2	2	2	2	2	2
LoR	1	1	1	1	1	1	1	1	1
LoR-E	Yes	Yes	Yes	Yes	Yes	Yes	Yes/No (*)	Yes	Yes
TMP	2+2	2+2 or 2+3	2+3	2+2 or 2+3	2+2	2+2	2+2 or 2+3	1+2 or 2+2	1+2, 2+2, or 2+3
VEN	198	199	191–195	210–212	209–215	198	205–211	202–204	200–228
SC	84	76	63–75	94–96	92(n=1)	84	66–95	68–69+	75–81
Cloacal plate	Divided	Entire	Divided	Entire	Entire	Entire	Entire	Divided	Divided
MT	12 (6-1-1-4 or 6-1-2-3)	11 (7-1-1-2)	11 (no distinct gap) (n=2)	10 (7-1-2) or 11 (7-2-2)	11 (5-3-3) (n=1)	12 (8-2-2)	12 (8-2-2)	8	–
CB in adults	Presence	Presence	Presence	Absence	Absence	Absence	Absence	Presence	Presence
NDB	66	31	55–62	37 or 38	32–36	34	31–37	40–45	33–45
NTB	26	13	11–19	15 or 16	13 (n=1)	16	11–17	10–15	11–13
BST	Smooth	Smooth	Keeled	Keeled	Keeled	Keeled	Keeled	Keeled	Keeled

Abbreviations can be found in methods. “–” indicates not available due to incomplete tail. “*” indicates only loreals of a single specimen (KIZ 751473) do not enter orbit. The number in parentheses for the Sample Size row indicates differential sample size for total length and tail length for *L. liuchengchaoi*. Data for the female of *L. gongshan* and for all *L. liuchengchaoi* were obtained from literature (*L. gongshan*: Vogel & Luo, 2011; *L. liuchengchaoi*: Peng et al., 2014, 2017, 2018; Zhang et al., 2011b; Zhang et al., 2019). M: Male; F: Female.

Currently *L. chapaensis* **comb. nov.** has been recorded from western (Gaoligong Mountain Range, including Baoshan, Dali, Dehong Prefecture, and Nujiang Prefecture), south central (Puer and Lincang Prefectures), and southeastern (Honghe and Wenshan Prefectures) Yunnan Province in China and Lao Cai and Thanh Hoa Provinces in northern Vietnam (Luu et al., 2019). Based on the reported questionable records of “*L. septentrionalis*” in eastern Myanmar, northern Laos, and northern Thailand, it is likely that the species is also found in these countries as well (see Discussion below).

Lycodon serratus **sp. nov.** (Figures 4A, 5A; Table 2)

ZooBank LSID: 355B3EDA-546E-417B-9E16-7BC92789DE81
Proposed Chinese common name: “锯纹白环蛇” (Pinyin: Ju Wen Bai Huan She)

Proposed English common name: Serrate-banded Wolf Snake
Holotype: KIZ 038335, adult male, collected by Zhong-Bin Yu and Wen-Jie Dong on 25 July 2020 from the Jinsha River Valley near Geyading Village, Deqin County, northwest Yunnan Province, China (N28.7720°, E99.1128°, WGS84, elevation 2 200 m a.s.l.).

Etymology: The Latin species name *serratus* means “serrated”, which describes the diagnostic narrow, serrated black cross-band of the new species.

Diagnosis: *Lycodon serratus* **sp. nov.** can be diagnosed from recognized congeners by a combination of the following morphological characters: (1) body size moderate, slender, ToL 628 mm, SVL 480 mm; (2) tail long, TAL 23.6% ToL; (3) head flat, distinct from neck, snout narrow; (4) eye large, vertical ellipse in shape; (5) dorsal body scales smooth, 19 rows at one-head-length behind the neck, 17 rows at midbody, and 15 rows at one-head-length before vent; (6) ventral scale

count 198; (7) subcaudal scale count 84; (8) cloacal plate divided; (9) supralabials 8 or 9, 2-3-3 or 2-4-3; (10) infralabials 10(5); (11) preocular single, postocular 2; (12) loreal scale entering orbit; (13) enlarged paraparietal 2, bordered by 7 additional nuchal scales other than posterior upper temporal and parietal; (14) maxillary teeth 12 in four groups (6-1-1-4 or 6-1-2-3), sixth and seventh much larger, first and second gap about same size, twice as distance between first two teeth; (15) dorsal surface dirty Tawny Olive (Color 17) with narrow, strongly serrated Jet Black (Color 300) cross-bands, two-scale broad middorsally at anterior 1/7 of body, single-scale broad for the remaining ones; (16) single collar-band on neck, 66 cross-bands on dorsum, 26 on tail; (17) first dorsal cross-band at 10th ventral scale; (18) anterior 1/3 of ventral surface uniform white, remaining 2/3 of ventral body and whole tail speckled with Dark Neutral Gray (Color 299).

Comparisons: *Lycodon serratus* **sp. nov.** is morphologically most similar and closely related to *L. multizonatus*, where both species have divided cloacal plate, large eyes, and similar number of black bands across the body. However, the new species can be differentiated from *L. multizonatus* by having more DSRH (19 vs. 17), more IL (9 or 10 vs. 8), more IL-aCS (5 vs. 4), a flatter head that is distinct from the neck (vs. robust and indistinct), a narrower snout (vs. wide), much narrower black bands on the middle to posterior body (mostly single scale broad, rarely two vs. ≥ 3 scales), more black bands on the tail (26 vs. 11–19), and a distinct ventral ornamentation patterns (irregular speckles vs. regularly paired black spots or complete black bands) (Figure 5).

For remaining species that are found in the close proximity in the Hengduan Mountain Region (*L. fasciatus*, *L. gongshan*, *L. liuchengchaoi*, *L. ruhstrati*, *L. chapaensis* **comb. nov.**, and *L. synaptor*), *L. serratus* **sp. nov.** differs from all by having more DSRH (19 vs. 17), smooth dorsal scales (vs. feebly or distinctively keeled medially), a narrow snout (vs. robust and wide), larger and laterally compressed eyes (ED 15.2% HL, VED 17.5% HL vs. not laterally compressed, <12%), more cross-bands on the body and tail (66 on body, 26 on tail vs. *L. fasciatus* 19–37 on body, 7–21 on tail; *L. gongshan* 32–40 on body, 13–15 on tail; *L. liuchengchaoi* 40–45 on body, 10–15 on tail; *L. ruhstrati* 33–46 on body, 14–28 on tail; *L. chapaensis* **comb. nov.** 23–37 on body, 11–16 on tail; *L. synaptor* 30 or 31 on body, 9 on tail), different-shape and width of the bands (narrow (mostly single-scale broad) and strongly serrated vs. broader (mostly two- to three-scale broad and less serrated) and less serrated), and a distinct body coloration (Tawny Olive (Color 17) with Jet Black (Color 300) bands vs. Jet Black (Color 300) with white or yellowish bands). Additionally, *L. serratus* **sp. nov.** differs from *L. fasciatus*, *L. gongshan*, and *L. ruhstrati* by having divided cloacal plate (vs. entire), presence of neck collar-band in adult (vs. absence), and a distinct ventral ornamentation pattern (randomly speckled vs. regular transverse bands (*L. fasciatus*, *L. gongshan*) or mostly uniform white (*L. ruhstrati* and *L. chapaensis* **comb. nov.**)); from all but *L. fasciatus* and *L. chapaensis* **comb. nov.** by having more IL-aCS (5 vs. 4); from

all but *L. chapaensis* **comb. nov.** by having non-overlapping SC (84 vs. *L. gongshan* 92–96; *L. liuchengchaoi* 68–77; *L. ruhstrati* 97–114; *L. synaptor* 68 or 69); from *L. liuchengchaoi* by having fewer VEN (198 vs. 202–206); from *L. chapaensis* **comb. nov.** and *L. synaptor* by having loreal entering orbit (vs. separated) and a divided cloacal plate (vs. entire). For the junior synonym of *L. fasciatus* that is currently available, *L. serratus* differs from *Dinodon yunnanensis* Werner, 1922 by more DSRH (19 vs. 17), smooth or feebly keeled dorsal body scale rows (strongly keeled), a divided cloacal plate (vs. entire), and more cross-bands on the dorsum (66 vs. 23).

For remaining three species that have genetic data and are in the same clade (i.e., *L. butleri*, *L. pictus*, and *L. cavernicolus*), *L. serratus* **sp. nov.** differs from all by having a distinct body coloration (Tawny Olive (Color 17) with Jet Black (Color 300) bands vs. Jet Black (Color 300) with white or yellowish bands). Additionally, the new species differs from *L. pictus* by more DSRH (19 vs. 17), a divided cloacal plate (vs. entire), more cross-bands on the body (66 vs. 28 or 29) and tail (26 vs. 13), much narrower cross-bands (mostly single scale-broad, rarely two vs. 2–4 scale broad), and by the presence of collar band in adult (vs. absence); from *L. cavernicolus* by having smooth dorsal scales (vs. keeled), fewer SL (8 vs. 9 or 10), and more NDB (66 vs. 36–45); and from *L. butleri* by having smooth dorsal scales (vs. keeled) and a divided cloacal plate (vs. entire).

For all the remaining 55 species of the genus, *L. serratus* **sp. nov.** differs from all by having a distinct dorsal coloration (Tawny Olive (Color 17) with Jet Black (Color 300), strongly serrated bands vs. black or brownish with white, yellow, or red cross-bands that are less serrated or smooth, or with no complete cross-bands but reticulated ornamentations). Additionally, *L. serratus* **sp. nov.** differs from all except 18 species (i.e., *L. cardamomensis*, *L. carinatus*, *L. flavozonatus*, *L. futsingensis*, *L. hypsirrhinoides*, *L. jara*, *L. laoensis*, *L. mackinnoni*, *L. meridionalis*, *L. nympa*, *L. orientalis*, *L. sealei*, *L. septentrionalis*, *L. sidiki*, *L. striatus*, *L. tessellatus*, *L. tiwarii*, and *L. zawi*) by having a divided cloacal plate (vs. entire). For the excluded 17 species, the new species differs from *L. cardamomensis*, *L. carinatus*, *L. flavozonatus*, *L. meridionalis*, *L. nympa*, *L. sealei*, and *L. sidiki* by having smooth dorsal scales (vs. keeled); from *L. futsingensis*, *L. hypsirrhinoides*, *L. jara*, *L. laoensis*, *L. mackinnoni*, *L. striatus*, *L. tessellatus*, and *L. zawi* by having more DSRH (19 vs. 17); from *L. orientalis* by the presence of preocular scale (vs. absence); and from *L. tiwarii* by having fewer ventral scales (198 vs. 218–237).

Description of holotype: KIZ 038335, Adult male, medium sized *Lycodon*, SVL 480mm, TaL 148mm. Body slender; tail long, TaL 23.6% of ToL; head elongated, flat, snout narrow, HW 9.7mm, HL 12.2mm, distinct from neck; eye large, slightly compressed laterally, ED 2.4mm, VED 2.8mm, ED 19.9% HL, VED 23.0% HL; pupil vertically oriented. Rostral pentagonal, broader than height, visible from above; nasal laterally elongated, divided, anterior one bordering rostral, first supralabial, and internasal, posterior one bordering first and second supralabials, loreal, internasal, and prefrontal;

internasal pentagonal; prefrontal paired, hexagonal, larger than internasal; loreal elongated tear shape, entering orbit, bordering posterior nasal, prefrontal, second and third supralabials, and preocular; preocular single; supralabials 8/9, third to fifth entering orbit on left, third to sixth entering orbit on right; postocular 2; temporal 2+2 (including paraparietal), inferior one of first pair much larger; frontal pentagonal, spear-like tip pointing posteriorly; supraocular elongated; parietal paired in V-shape, inlaying spear-tip of frontal anteriorly, bordering supraocular and superior postocular anteriorly, paraparietal, and 7 nuchal scales posteriorly; paraparietal single, enlarged. Infralabials 10/10, anterior most pair enclosing mental and meeting medialposteriorly; anterior 5 infralabials bordering anterior chin shield on both sides, fifth and sixth bordering posterior chin shield on both sides; 2 pairs of chin shield, anterior pair much elongated, meeting medially, forming V-shape and inlaying meeting tip of first pair of infralabials anteriorly; posterior chin shield much narrower and shorter, separated from each other by rather wide section of mental groove. Dorsal body scales smooth, 19 rows one-head-length behind neck, 17 rows midbody, 15 rows one-head-length before vent. Single preventral; ventral 198, angular; cloacal plate divided; subcaudal paired, 84 excluding tail tip. DHB 10.4mm, 2.1% SVL; PBB at 5th ventral scale.

Maxillary teeth 12 (fifth lost), forming 4 distinct groups separated by three gaps on both sides. Six teeth (first to sixth) in first group: first four gradually increase in size, followed by much enlarged sixth; single (seventh) tooth in second group, also much enlarged, same size as sixth; single (eighth) tooth in third group, same size as fourth; last four (ninth to twelfth) in last group, ninth and tenth same size as fourth, eleventh and twelfth same as second. Three gaps present between sixth and seventh teeth (about 1.8 times regular width), seventh and eighth (twice regular width), eighth and ninth (twice regular width).

The hemipenis only partially everted, single; very proximal end free of spines; remaining part filled with small to medium sized spines.

Coloration: In life, the background coloration of the dorsal and lateral surfaces of the head and body is Tawny Olive (Color 17). The dorsal surface of the head is speckled with Dark Neutral Gray (Color 299), particularly on the frontal and parietal scales. A single Jet Black (Color 300) collar-band on neck, 66 cross-bands of the same color are present on the dorsum, and another 26 cross-bands are present on the tail. Cross-bands on the anterior 1/7 of SVL are broader, expanding across two dorsal scales in width, and the remaining bands are rather narrow, expanding only a single dorsal scale in width. All bands are strongly serrated. The immediate bordering margins of each black band are Pale Buff (Color 1). Ventral surface of the head is white. The immediate bordering regions between infralabials and between infralabials and chin shields are speckled with Dark Neutral Gray (Color 299). The ventral surface of the body and tail is white: the anterior 1/7 of the SVL is uniform white with no patterns, and the remaining section of the ventral body and

the tail is speckled with Dark Neutral Gray (Color 300), with the tail more heavily speckled. Coloration and ornamentation patterns remain mostly the same after short-term preservation (one month).

Distribution, natural history and conservation: Besides *L. multizonatus*, *L. serratus* **sp. nov.** is the only known species of the genus that inhabits hot-dry valley habitats at high elevation in the northern HMR. Currently *L. serratus* **sp. nov.** is known from the type locality in Yunnan Province only, however, an individual of the same species was photographed but not captured in Derong County of Sichuan Province, which is about 21 km linearly southeast from the type locality (personal communication with Mr. Di-Hao Wu). The habitats consist of open rock outcrops and low bushes, and the annual precipitation is very low (Figure 6A). While the distribution range of the species remains unknown, habitat destructions from road constructions were observed at and near the type locality of the new species (Wang et al., 2021). We recommend Data Deficient (DD) for the IUCN status of the new species, and we call for population studies to assess its conservation status in the near future.

The new species is sympatric with *Diploderma* sp., *Gekko scabridus*, and *Scincella monticola* (Wang et al., 2021; Yang & Rao, 2008), and the holotype of *L. serratus* **sp. nov.** was found at night searching for food on a bush, where several individuals of *Diploderma* sp. were sleeping on. As the genus *Lycodon* is known to feed predominantly on lizards (Zhao et al., 1998), it is likely that these sympatric lizard species constitute main preys of the new species. Other herpetofauna that are sympatric with the new species include *Elaphe carinata*, *E. taeniura*, *Protobothrops xiangchengensis*, *Amolops jingshaensis*, *Bufo gargarzans*, and *Scutigera* sp..

Lycodon obvelatus **sp. nov.** (Figures 4B, 5B; Table 4)

Zoobank LSID: D15F4F07-FADF-43D5-94B8-EA746655727B

Chresonyms: *Lycodon fasciatus*: Deng et al., 1991; Wu et al., 1997; Zhao et al., 1998; Zhao, 2002, 2004, 2006

Proposed Chinese common name: 隐士白环蛇 (Pinyin: Yin Shi Bai Huan She)

Proposed English common name: Recluse Wolf Snake

Holotype: KIZ 040146, adult male, collected by Kai Wang and Ben-Fu Miao from Panzhihua City Park, Panzhihua, Sichuan, China (N26.5751°, E101.7174°, WGS84, elevation 1 243 m a.s.l.) on 19 April, 2018.

Etymology: The Latin species name, *obvelatus*, means “hidden” or “concealed”, which not only describes the taxonomic confusions of the cryptic new species over *L. fasciatus*, but it also highlights the fact that new species can be hidden even in major urban areas.

Diagnosis: *Lycodon obvelatus* **sp. nov.** can be diagnosed from congeners by a combination of the following characters: (1) body size small, ToL 551 mm; (2) tail moderate, TaL 18.9% ToL; (3) dorsal scale rows 17-17-15, all smooth; (4) VEN 199; (6) SC 76; (7) cloacal plate entire; (8) loreal long and narrow, entering orbit; (9) SL 8, 2-3-3; (10) IL 8(4 or 5);

(11) preocular single, in contact with supraocular and prefrontal; (12) postocular 2; (13) temporal 2+2 or 2+3; (14) paraparietal enlarged, single; (15) frontal bordering 4 nuchal scales; (16) maxillary teeth 11 in four groups (7-1-1-2), seventh largest, first gap widest, four times wide as distance between first two teeth; (17) hemipenis single clavate, nip at distal end, spinose except very proximal end; spines larger toward proximal end; (18) distinct collar band present on occipital head, Salmon Color (Color 251); (18) dorsal Jet Black (Color 300) in life, with 31 Salmon Color (Color 251) cross-bands on dorsum, 13 on tail; (19) cross-bands with serrated edges, 2- or 3-scale broad medially, widen slightly toward ventrolateral side; (20) first dorsal cross-band at 4th ventral scale, DHB 14.1 mm; and (21) ventral pale Salmon Color (Color 251), with more or less regular black transverse bands and some irregular speckles.

Comparisons: The new species is morphologically most similar and was confused as *L. fasciatus*, but it can be differentiated from the latter by having smooth dorsal scales (vs. keeled), fewer infralabials (8 vs. 9 in most individuals), and the presence of distinct collar band on head in adults (vs. absence) (Figure 5). *Lycodon obvelatus* sp. nov. further differs from *Dinodon yunnanensis*, which is still considered the junior synonym of *L. fasciatus* but believed to be valid, by having smooth dorsal scales (vs. keeled), more ventral scale (199 vs. 193), more dorsal cross-band on body (32 vs. 23), and fewer supralabials (8 vs. 9).

For species that are also similar to *L. fasciatus*, *L. obvelatus* sp. nov. differs from *L. gongshan* by having smooth dorsal scales (vs. keeled), fewer subcaudals (76 vs. 92–96), and a smaller body size (ToL 551mm vs. maximum 963mm); from *L. liuchengchaoi* by having smooth dorsal scales (vs. keeled), an entire cloacal plate (vs. divided), and fewer dorsal cross-bands (31 vs. ≥ 40); from *L. pictus* by having fewer ventrals (199 vs. 212–218), presence of collar-band in adults (vs. absence), and a distinct coloration (dorsal Jet Black (Color 300), with Salmon Color (Color 251) cross-bands vs. dorsal Brick Red (Color 36) to Warm Sepia (Color 40), with dirty white cross bands); and from *L. synaptor* by having loreal entering orbit (vs. separated from orbit by preocular), smooth dorsal scales (vs. keeled), and wider dorsal cross-band (2- or 3-scale broad dorsally vs. single scale broad).

Lycodon obvelatus sp. nov. differs from *L. serratus* sp. nov. by having fewer infralabials (8 vs. 10), fewer ASR (17 vs. 19), far fewer dorsal cross-bands (31 on dorsum, 13 on tail vs. 66 on dorsum, 26 on tail), a distinct coloration (dorsal Jet Black (Color 300) with Salmon Color (Color 251) cross-bands vs. dorsal dirty Tawny Olive (Color 17) with Jet Black (Color 300) cross-bands), and wider cross-bands (expanding 2- or 3-scale wide dorsally vs. mostly single-scale broad) (Figure 3).

For remaining species, *L. obvelatus* sp. nov. differs from all members of the *L. ruhstrati* species group (*L. cathaya*, *L. chapaensis* comb. nov., *L. futsingensis*, *L. multifasciatus*, *L. ophiophagus*, *L. paucifasciatus*, *L. ruhstrati*, and *L. septentrionalis*) and *L. alcalai*, *L. banksi*, *L. bibonius*, *L.*

cardamomensis, *L. carinatus*, *L. chrysoprateros*, *L. davidi*, *L. ferroni*, *L. flavozonatus*, *L. gammiei*, *L. kundui*, *L. muelleri*, *L. rufozonatus*, *L. rosozonatus*, *L. solivagus*, *L. stormi*, *L. travancoricus*, and *L. zoosvictoriae* by having loreal entering orbit (vs. separated); from *L. effraenis* by the presence of loreal scale (vs. absence); from *L. subannulatus* by having more DSRH (17 vs. 15) and DSRM (17 vs. 15); from *L. albofuscus*, *L. aulicus*, *L. capucinus*, *L. flavicollis*, *L. flavomaculatus*, *L. hypsirrhinoides*, *L. jara*, *L. laoensis*, *L. mackinnoni*, *L. meridionalis*, *L. multizonatus*, *L. nympa*, *L. orientalis*, *L. sealei*, *L. sidiki*, *L. striatus*, *L. subcinctus*, *L. tessellatus*, *L. tiwarii*, and *L. zawi* by having an entire cloacal plate (vs. divided); from *L. anamallensis* by fewer temporals (2+2 or 2+3 vs. 3+4); and from *L. philippinus* by more MT (11 vs. 8) and fewer ventral scales (199 vs. 216–225).

Description of holotype: KIZ 040146, adult male, medium sized *Lycodon*, ToL 551 mm, SVL 447 mm. Body slender, tail moderate, TaL 18.9% ToL; head moderate, flat, snout narrow, HL 11.3 mm, HW 9.4 mm, distinct from neck; eye large, not laterally compressed, ED 2.1 mm, 18.6% HL; pupil vertically oriented. Rostral pentagonal, broader than height, slightly visible from above; nasal divided, anterior half rectangular, small, bordering rostral, first supralabial, and internasal, posterior half hexagonal, much larger, bordering first and second supralabials, loreal, internasal, and prefrontal; prefrontal paired, hexagonal, much larger than internasal, separated from orbit by preocular; loreal much elongated, entering orbit, bordering posterior nasal, prefrontal, second and third supralabials, and preocular; preocular single; supralabials 8/8, third to fifth entering orbit; postocular 2; temporals 2+3/2+2, inferior one of first pair much larger; frontal pentagonal, spear-like tip pointing posteriorly; supraocular elongated; parietal paired in V-shape, relatively wide, inlaying spear-tip of frontal anteriorly, bordering supraocular and superior postocular anteriorly, paraparietal, and four smaller nuchal scales posteriorly; paraparietal single, enlarged. Infralabials 8/8, anterior most pair enclosing mental and meeting medioposteriorly; anterior 5 infralabials bordering anterior chin shield on left, 4 on right; fifth and sixth bordering posterior chin shields on left, fourth and fifth on right; two pairs of chin shield, anterior pair wider, meeting medially, forming V-shape and inlaying meeting tip of first pair of infralabials anteriorly; posterior chin shields much narrower and elongated, separated from each other by rather wide section of mental groove. Dorsal body scales smooth, 17 rows one-head-length behind neck, 17 rows midbody, 15 rows one-head-length before vent. Single preventral; ventral 199, angular; cloacal plate entire; subcaudal paired, 76 excluding tail tip. DHB 14.1 mm, 3.1% SVL, PBB at 4th ventral scale.

Maxillary teeth 11, forming 4 distinct groups separated by three gaps. Seven teeth in first group: first five gradually increase in size, followed by much enlarged sixth and seventh; smaller eighth tooth in second group, same size as third; ninth tooth in third group, same size as eighth; last two (tenth and eleventh) in last group, same size as fifth. Three gaps present,

namely between seventh and eighth teeth (largest, about 4 times regular teeth width), eighth and ninth (1.5 times regular width), ninth and tenth (twice regular width).

Hemipenis only partially everted, single clavate, nip at distal end, spinose except very proximal end; spines enlarged toward proximal end; very proximal end free of spines.

Coloration: In life, the dorsal and lateral surfaces of the head are Jet Black (Color 300), except the anterior portion of the head: the internasal, prefrontal and anterior frontal are speckled with Pale Neutral Gray (Color 296); and the posterior half of nasal, loreal, and first four supralabials are nearly uniform Pale Neutral Gray (Color 296). A distinct collar band on occipital region of the head, dirty Salmon Color (Color 251). Dorsal surface of the body is Jet Black (Color 300). Salmon Color (Color 251) cross-bands are present on the dorsal and lateral surfaces of body and tail. Cross-bands have jagged edges, and they are two- to three-scale broad dorsally and are further widen ventrolaterally. A total of 31 cross-bands are present on the body, and 13 are on the tail. Starting at the fifth cross-bands from the head, most Salmon Colored (Color 251) cross-bands of the body has a transverse row of black speckles running through the middle, some of which even forms a narrow and almost complete black transverse streak (i.e., in number 20 and 21 cross-bands from the head). The ventral surfaces of the head, body, and tail are pale Light Flesh Color (Color 250) to white. Anterior five infralabials, mental, and anterior portion of the anterior chin shields are Medium Neutral Gray (Color 298). Dark Neutral Gray (Color 299) to Jet Black (Color 300) cross-bands, transverse groups of patches, or irregular speckles are present on the ventral body, with the anterior nine cross-bands clearly defined. A total of twelve Jet Black (Color 300) cross-bands are present on ventral tail.

The ornamentations remain the same after two-year of preservation, but coloration fades away. Specifically, the Salmon Color (Color 251) of dorsal cross-bands becomes pale Light Flesh Color (Color 250), and the ventral color becomes almost Light Buff (Color 2).

Distribution, natural history, and conservation: Although *L. obvelatus* sp. nov. is currently only known from the Panzhuhua City Park, it is possible that the new species is also found in the nearby regions in Panzhuhua and in the adjacent north-central Yunnan Province (i.e., in Yongren County). The habitat consists of both natural and horticultural plants of both deciduous and evergreen species, and roads and other tourist infrastructures fragmented the habitats (Figure 6B). The holotype was found actively hunting for geckos on a stone parapet at night. Other reptiles that are sympatric in the city park include *Naja kaouthia*, *Ptyas nigromarginata*, *Elaphe taeniura*, *Achalinus* sp., *Pareas* sp., *Indotyphlops braminus*, *Diploderma dymondi*, *Gekko* sp., *Hemidactylus bowringii*, and *Sphenomorphus indicus*; and amphibian includes *Kaloula verrucosa*, *Polypedates* sp., *Odorrana grahami*, and *Duttaphrynus melanostictus*.

Although the type locality is at the center of a major city (about 10.8 million people), the oasis in the city park provides

habitats for a surprisingly diverse group of reptiles and amphibians. The natural habitats around the Panzhuhua City have been deforested in the mid 1900s, and the self-recovering process of the fragile valley ecosystem is particularly slow. The City Park of Panzhuhua preserved few of the remaining natural montane evergreen forests in the area, which provide important habitats for local wildlife. The discovery of the new species highlights the conservation importance of the remaining habitats in the city park. Unfortunately, the current maintenance practice of the park is not ecofriendly, with rapid developments for tourist infrastructure, replacements of native plants with exotic horticultural plants, and the wide usage of pesticides. We recommend the park modify its current practices and conserve the remaining natural habitats for the native wildlife.

DISCUSSION

Additional cryptic diversity in the northern HMR

The discovery of our two new species supports the notion that the reptilian diversity in the northern HMR is still underestimated. As the suitable habitats of reptiles (i.e., hot-dry valleys) in the HMR are isolated and fragmented by continuous mountain ranges over 4 000 m of elevation, populations in different river valleys are allopatric to each other, despite the short linear distance among them (Figure 1). Therefore, it is likely that nearby valleys along the upper Mekong, Salween, and Yalong Rivers also harbor additional undiscovered diversity of the genus *Lycodon*. Further surveys are needed to better inventory of the reptilian diversity and assess their conservation statuses in the northern HMR.

Problematic records of *Lycodon* species in China and SE Asia

***Lycodon fasciatus* and *L. liuchengchaoi*:** For the recognized species of the genus *Lycodon* in China, great confusions exist in published literature regarding the taxonomic identification and the resulting distribution range, particularly for *L. fasciatus* (Vogel & David, 2010; Vogel & Luo, 2011). Much similar to other groups of reptiles from the HMR that represent species complexes (i.e., *Gloydus strauchi*, *Diploderma flaviceps*; Shi et al., 2018; Wang et al., 2019a, 2021), *L. fasciatus* was and still is considered as a widespread taxon, despite increasing evidence suggesting the existence of cryptic diversity (Vogel & David, 2010; Vogel & Luo, 2011; Zhang et al., 2011b). As the results of taxonomic confusions, misidentifications and erroneous records of species are prevalent in literature.

Kang et al. (2009) reported *L. fasciatus* as a new record of snake in Hunan Province based on specimens from Hupingshan Nature Reserve. Later Bai et al. (2018) reported *L. liuchengchaoi* from the very same nature reserve. Closer examination of the corresponding descriptions reveals that the referred specimens by Kang et al. (2009) and Bai et al. (2018) both possess a divided cloacal plate, which matches the diagnosis of *L. liuchengchaoi* but not *L. fasciatus* (Zhang et al.,



Figure 6 The habitats at the type locality of *Lycodon serratus* sp. nov. near Geyading Village, Deqin County, Yunnan Province, China (A) and *L. obvelatus* sp. nov. in Panzhihua City Park, Panzhihua, Sichuan, China (B) (Photos by Zhong-Bin Yu and Ben-Fu Miao)

2011b). In addition to the presence of a yellow collar-band on the neck in figures of both Kang et al. (2009) and Bai et al. (2018), which again contradict to the diagnosis of *L. fasciatus* but align with *L. liuchengchaoi*, it is clear that the previous record of *L. fasciatus* from Hunan Province by Kang et al. (2009) represent a misidentification of *L. liuchengchaoi*.

Li et al. (2012) first recorded *L. fasciatus* from Guangdong Province, and the authors stated that the tail length of Guangdong specimens is 24.8%–25.8% of the total length in sub-adults, which are much longer than the true *L. fasciatus* ($\leq 22.5\%$; Vogel & Luo, 2011; Table 4). Later Guo et al. (2013) provided the genetic data of *L. fasciatus* from Guangdong, but at the time there is no genetic data from totypic *L. fasciatus* to compare against. Recently, Peng et al. (2018) reported *L. liuchengchaoi* from Guangdong based on morphological and molecular evidence of *cyt b* gene, and the authors stated that

the *cyt b* data of their specimens of *L. liuchengchaoi* from Guangdong is nearly identical to the published sequence of *L. liuchengchaoi* on GenBank and share the same haplotype with previously published data of *L. fasciatus* from Guo et al. (2013). As results, Peng et al. (2018) confirms the previous record of *L. fasciatus* in Guangdong represents misidentification of *L. liuchengchaoi*. However, Peng et al. (2018) did not submit their new data to GenBank, nor did they conduct phylogenetic analyses of the mentioned samples.

Our phylogenetic study of available sequences supports the conclusion by Peng et al. (2018), where the Guangdong samples of “*L. fasciatus*” from Guo et al. (2013) are nested within available data of *L. liuchengchaoi*; and with the newly available totypic samples of *L. fasciatus*, the Guangdong samples are confirmed to be paraphyletic with respect to the true *L. fasciatus* from Yunnan (Figure 2). In addition to our revision of “*L. fasciatus*” in Panzhihua, it is clear that the current records of “*L. fasciatus*” outside of Yunnan Province in China (i.e., in Anhui, Gansu, Guizhou, Hubei, Shaanxi, and Zhejiang; Zhao et al., 1998) are distant from the range of the true *L. fasciatus*, and these questionable records likely represent either misidentifications of recognized congeners, or additional cryptic diversity that warrant further investigations. Future studies should focus on confirming the taxonomic statuses of the questionable records of “*L. fasciatus*” outside of Yunnan Province in China. Currently, *L. fasciatus* sensu stricto has been confirmed in Yunnan Province of China and Myanmar (Vogel & Luo, 2011; present study).

Regarding *L. liuchengchaoi*, Li et al. (2020) reported a sample of “*L. liuchengchaoi*” from “Sanjiazhai” in Yunnan Province, which would expand the distribution range of the species further southwestward and represents a new record of herpetofauna of Yunnan Province. However, our phylogeny shows that the referred sample of “*L. liuchengchaoi*” by Li et al. (2020) is phylogenetically distinct from the true *L. liuchengchaoi*, and it actually represents a misidentification of *L. multizonatus* instead (Figure 2). With this correction of taxonomy, this record in Yunnan still represents a range extension of the *L. multizonatus* and a new record of Yunnan Province. However, Li et al. (2020) did not provide complete information regarding the county or prefecture of the locality name “Sanjiazhai”. As multiple localities in Yunnan Province are under this very same name, the distribution of *L. multizonatus* in Yunnan remains unknown. Future studies should verify the record.

For the remaining confirmed record of *L. liuchengchaoi*, it is important to note that there are considerable discrepancies of key morphological characters between the type series of the species and the later reported records in China, particularly regarding the number of dorsal cross-band and the state of cloacal plate (Peng et al., 2018; Zhang et al., 2011b). Future population-level studies are needed to better understand the morphological variation and diagnosis of *L. liuchengchaoi*.

***Lycodon ruhstrati* in Yunnan Province:** Guo et al. (2007) first reported *L. ruhstrati* as the new record of reptilian fauna of Yunnan Province from the Gaoligong Mountains in far western

Yunnan. However, examination of the description and photos by Guo et al. (2007) reveals that all three referred specimens by Guo et al. (2007) do not agree with the diagnosis of *L. ruhstrati*: the first specimen (HNU 200505001) has a much shorter tail (TaL/ToL 18.7%), fewer ventral scales (VEN 203), fewer subcaudal scales (SC 68), and distinctively banded ventral surface of the body throughout (vs. in true *L. ruhstrati*, TaL/ToL 20.8%–24.8%, VEN 214–233, SC 90–116, and ventral body either uniformly colored or speckled without distinct cross-bands; Vogel et al., 2009); and the remaining two specimens (HNU 200505002 and 200609001) both have loreals entering orbits (vs. in true *L. ruhstrati* not entering orbit; Vogel et al., 2009; Zhao et al., 1998). Furthermore, the later two specimens have much longer tails (TaL/ToL 21.5–25.5%) and more subcaudals (92–94) than the first specimen. Therefore, even based on the reported morphological data by Guo et al. (2007) alone, it is clear that the three referred specimens are neither true *L. ruhstrati*, nor do they even represent the same taxa: HNU 200505001 is similar to *L. chapaensis*, while HNU 200505001 and 200609001 matches diagnosis of *L. gongshan*.

A year after Guo et al. (2007), Yang & Rao (2008) also recorded *L. ruhstrati* from Yunnan. This time the record is based on a different vouchered specimen, which has no detailed locality information (KIZ 8300012, “from Yunnan”; Yang & Rao, 2008). Unfortunately, we could not locate the referred specimen at KIZ (possibly lost), but upon review of the description by Yang & Rao (2008), we found that the specimen does not agree with the diagnosis of the true *L. ruhstrati*, including having fewer SC (81 vs. 90–116), different dorsal scale texture (feebly keeled vs. distinctively keeled), and by the presence of white collar-band on neck (vs. absence in adults). Therefore, based on the current published data, all reported voucher specimens of “*L. ruhstrati*” from Yunnan do not agree with the diagnosis of true *L. ruhstrati*, and there is no evidence confirming the presence of *L. ruhstrati* in Yunnan Province as of to date.

***Lycodon gongshan* in Yunnan and Sichuan:** *Lycodon gongshan* was described based on morphological characters only, and the type series was collected from far western Yunnan Province in the Dulongjiang Valley and adjacent Nujiang valley (Vogel & Luo, 2011). Later Guo et al. (2015) recorded the species from Lincang, Southwestern Yunnan Province and provided genetic data of the species. Our newly collected topotypic materials from Dulongjiang confirm the taxonomic identification by Guo et al. (2015) (Figure 2; Table 2). Furthermore, our phylogenetic analyses confirm that our non-vouchered genetic sample from Yunlong Nature Reserve in Yunlong County, Dali is also *L. gongshan*, which expand its range eastwards (Figure 1).

Although our results expand the range of *L. gongshan* further eastwards, the species is still endemic to Yunnan only, and the existing records of the species in Sichuan Province require further confirmation. Chen et al. (2018a) recorded *L. gongshan* based on two specimens from Hongbao Village and

Daheishan National Forest in Panzhihua, Sichuan. However, the images that Chen et al. (2018a) provided show obvious difference from the type series of *L. gongshan* in terms of ornamentation pattern, and the recorded numbers of dorsal cross-bands do not match with the bands of the actual specimen in the photographs. Based on morphological data alone, we cannot assign these two specimens to our new species *L. obvelatus* from Panzhihua City (i.e., Hongbao individuals have keeled dorsal scales, where dorsal scales of *L. obvelatus* is smooth). It is likely that there are two species of *Lycodon* in Panzhihua, similar to the genus *Diploderma* (i.e., *D. dymondi* is found in Panzhihua City, where *D. swild* is found in Hongbao Village; Wang et al., 2019b), but whether the Hongbao population represents morphological variation of *L. gongshan* or a distinct new species would require future confirmation.

Remaining records of “*L. septentrionalis*” in SE Asia and validity of *L. ophiophagus*: *Lycodon septentrionalis* has been recognized to have a wide distribution range, from the Himalaya (i.e., India (Boulenger, 1893; Smith, 1943) and Bhutan (Tshewang & Letro, 2018)) across Myanmar (Dowling & Jenner, 1988) and Yunnan of China (Zhao et al., 1998; Zhao, 2006) to Southeast Asia (including Vietnam (Smith, 1943; Van Sang et al., 2009), Laos (Deuve et al., 1961), and Thailand (David et al., 2004)). Similar to the above-discussed congeners that also have wide distribution ranges, the current records of *L. septentrionalis* likely contain misidentifications of different lineages, particularly in Southeast Asia. With our resurrection of *L. chapaensis*, it leaves the remaining records of *L. septentrionalis* in Laos, Vietnam, and Thailand questionable. The taxonomic position of the Southeast Asian populations of “*L. septentrionalis*” should be reconsidered in future studies.

Additionally, our morphological comparison shows overwhelmingly similar morphology between *L. chapaensis* and *L. ophiophagus*. The only differences are the relative tail length (17.1%–20.5% in *L. chapaensis* vs. 20.1%–22.8% in *L. ophiophagus*) and number of subcaudal scales (74–85 vs. 87–90). However, given the small sample size ($n=2$) and the lack of molecular data of *L. ophiophagus*, we cannot conclude on its taxonomic validity. Future integrative taxonomic studies are needed to confirm the validity of *L. ophiophagus* with respect to *L. chapaensis*.

Records of *L. aulicus* and *L. capucinus* in China: Owing the nearly indistinguishable morphology and the lack of genetic materials from topotypic individuals, taxonomists have not reached agreements regarding the validity of *L. capucinus*: whether it is junior synonym of *L. aulicus*, valid but only as a subspecies, or valid as a full species (O’Shea et al., 2018; Ota, 2000; Siler et al., 2013; Wostl et al., 2017). Although the overall distributions of *L. capucinus* and *L. aulicus* have been relatively consistent in literature (*L. aulicus* is from South Asia, where *L. capucinus* is from Southeast Asia, and both species are hypothesized to be sympatric in Myanmar; David & Vogel, 1996; Lanza, 1999; Smith, 1943), the distribution of both

species near the hypothesized contacting region remain unclear, particularly in China (O’Shea et al., 2018).

While considering *L. capucinus* as a subspecies of *L. aulicus*, both *L. a. capucinus* and the nominate subspecies *L. a. aulicus* have been recorded from Hong Kong (Pope, 1935; Romer, 1979). Most of the later authors did not consider the subspecies or species status of *L. capucinus*, and only *L. aulicus* have been recorded from China, with its distribution ranging from southwestern Yunnan, Fujian, to Guangdong Provinces (Wang et al., 2020b; Zhao & Adler, 1993; Zhao et al., 1998; Zhao, 2006). In contrary, Zhang et al. (2011b) only record *L. capucinus* from China, without discussing the past record of *L. a. aulicus* from Hong Kong (Pope, 1935) or the possible distribution of *L. aulicus* from the Myanmar border regions in Southwest Yunnan.

Images of live individuals of the *L. aulicus-capucinus* complex from China-Myanmar border in Yunnan and from Hong Kong show nearly identical ornamentation patterns (Figure 7), which matches the current diagnosis of *L. capucinus* (O’Shea et al., 2018). Unfortunately, vouchered genetic materials of the *L. aulicus-capucinus* complex from China and from the type localities of the two corresponding names are still unavailable to date. Given the *L. aulicus-capucinus* complex is known by its profound variability in ornamentation patterns (O’Shea et al., 2018), we cannot determine the taxonomic identity of the Chinese populations with confidence. Based on the current diagnosis of both species, we here consider the Chinese populations as *L. capucinus*, and we propose to maintain its Chinese common name as 白环蛇. Later taxonomic studies are needed to further verify the validity of *L. capucinus* and confirm the identity of the related Chinese populations.

Updated key and distribution of the genus *Lycodon* in China: To facilitate future taxonomic studies of the genus *Lycodon* in China, we provide an updated dichotomous key and the distributions of the 20 recognized species of *Lycodon* species in China. The distribution data are based of Zhao et al. (1998) and are further modified with new findings in this present study and additional literatures published after 1998 (Appendix III). “?” indicates possible but not yet confirmed

records based on photographic evidence or published sequences with vague locality and no morphological data; and “!” indicate possible erroneous records that warrant future confirmations. “Dorsal background coloration” is defined as the same coloration of the dorsal surface of the head.

Key to the species of *Lycodon* in China:

- 1a) Dorsal background coloration yellowish brown, dark brown, or reddish brown; dorsal cross-bands Jet Black (Color 300), relatively narrow and serrated, not widen towards ventrolateral sides; cloacal plate divided; loreal entering orbit.....2
- 1b) Dorsal background coloration blackish, with white, gray, yellowish, pinkish, or reddish dorsal cross-bands, usually widen toward ventrolateral sides; or dorsal brownish with no cross-bands but reticulated patterns; cloacal plate divided or entire; loreal entering orbit or not.....3
- 2a) Head distinct from neck; eyes laterally compressed; dorsal scale rows 19 at one-head length behind neck; first five infralabials in contact with anterior chin shield; black cross-bands on the anterior dorsum strongly serrated, mostly single scale broad, rarely two.....*L. serratus* (Yunnan; Sichuan?)
- 2b) Head indistinct from neck; eyes not laterally compressed; dorsal scale rows 17 at one-head length behind neck; first four infralabials in contact with anterior chin shield; black cross-bands on the anterior dorsum less serrated, mostly 2- or 3-scale broad.....*L. multizonatus* (Gansu, Sichuan, Yunnan?)
- 3a) Dorsal scale rows 19 at one-head length behind neck... ..4
- 3b) Dorsal scale rows 17 at one-head length behind neck... ..5
- 4a) Dorsal scale rows 19 at mid-body; dorsal cross-bands wide, 28–35 on dorsum, 8–13 on tail.....*L. rosozonatus* (Hainan)
- 4b) Dorsal scale rows mostly 17 at mid-body, rarely 19; dorsal cross-bands narrow, 51–87 on dorsum, 12–30 on tail*L. rufozonatus*



Figure 7 Photos of live *Lycodon aulicus-capucinus* complex from China

A: From Hong Kong, China; B: From Yingjiang County, Yunnan, China. Photos by Jin-Long Ren and Franco Leung Ka Wah.

(Anhui, Beijing, Chongqing, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Henan, Hebei, Hubei, Hunan, Heilongjiang, Jilin, Jiangsu, Jiangxi, Liaoning, Sichuan, Shandong, Shanghai, Shanxi, Shaanxi, Taiwan, Tianjin, Yunnan, Zhejiang)

5a) Cloacal plate entire.....6
 5b) Cloacal plate divided.....16
 6a) Dorsal body scale smooth.....7
 6b) Dorsal body scale feebly keeled or strongly keeled.....10

7a) Ventrals 212–218; subcaudals 90 or 91; infralabials 9 or 10; loreal entering orbit; maxillary teeth 13 or 14.....*L. pictus* (Guangxi)
 7b) Ventrals≤210; subcaudals<90; infralabials ≥8; loreal entering orbit or not.....8
 8a) Infralabials 8; loreal always entering orbit; maxillary teeth 11; dorsal cross-bands Salmon color (Color 251) in life.....*L. obvelatus* (Sichuan; Yunnan?)
 8b) Infralabials 9 or more; loreal mostly not entering orbit; dorsal cross-bands Pale Rose Pink (Color 243), with dense but faint gray speckles.....9
 9a) Dorsal cross-bands connecting with each other laterally, separating ground black coloration into ellipse patches; maxillary teeth 10.....*L. cathaya* (Guangxi)
 9b) Dorsal cross-bands separated from each other; maxillary teeth 12–15.....*L. futsingensis* (Fujian, Guangdong, Guangxi, Jiangxi, Zhejiang, Hong Kong)
 10a) Loreal entering orbit; dorsal cross-bands wide (usually 3-scale wide) with strongly jagged edges.....11
 10b) Loreal not entering orbit; dorsal cross-bands narrow (usually 1- to 2-scale wide) with smother edges (except *L. ruhstrati*).....12
 11a) Tail long, TaL 23.1%–23.2% ToL in males, 21.5% in female.....*L. gongshan* (Sichuan?, Yunnan)
 11b) Tail short, TaL 19.8%–22.5% in males, 19.0%–21.9% in females.....*L. fasciatus* (Yunnan, Anhui!, Gansu!, Guizhou!, Hubei!, Shaanxi!, Zhejiang!)
 12a) Dorsal cross-bands bright Sulphur Yellow (Color 80) in life, 50–96 on dorsum.....*L. flavozonatus* (Anhui, Chongqing, Fujian, Guangdong, Guangxi!, Guizhou, Hainan, Hunan, Jiangxi, Sichuan, Zhejiang)
 12b) Dorsal cross-bands white or gray, <50 on dorsum.....13
 13a) Dorsal cross-bands dirty white (speckled with Dark Neutral Gray (Color 300)) or Cinnamon Drab (Color 259), increasingly more dirty posteriorly, 19–46 on dorsum, 3–4 dorsal-scale wide for most parts; intercepted black segments rather short.....*L. ruhstrati* (Anhui, Beijing, Chongqing, Fujian, Gansu, Guangdong,

Guangxi, Guizhou, Hainan, Henan, Hong Kong, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Shaanxi, Taiwan, Tianjin, Zhejiang)

13b) Dorsal cross-bands clear white, 25–31 on dorsum, 1 or 2 scale wide on most parts; intercepting black segments long.....14
 14a) Body size small, ToL 463–487mm; subcaudal 68 or 69; maxillary teeth 10, forming three groups, group one and three each with two significantly enlarged teeth.....*L. synaptor* (Yunnan)
 14b) Body size large, ToL >1 000 mm; subcaudal 74–85.....15
 15a) Medial 5–7 rows of dorsal scale keeled; maxillary teeth 8.....*L. septentrionalis* (Tibet)
 15b) Dorsal body scale completely smooth or only very posterior portion of vertebral row feebly keeled; maxillary teeth 11 or 12.....*L. chapaensis* (Yunnan)
 16a) Dorsal body scales smooth and glassy.....17
 16b) Medial rows of dorsal body scales strongly or feebly keeled.....18
 17a) Frontal in contact with preocular; reticulated patterns absent on body.....*L. laoensis* (Yunnan)
 17b) Frontal not in contact with preocular; light reticulated patterns present on lateral and sometimes dorsal body...*L. aulicus-capucinus* complex (Fujian, Guangdong, Hong Kong, Yunnan)
 18a) Loreal not entering orbit; dorsal cross-bands Sulphur Yellow (Color 80) to Olive Sulphur Yellow (Color 90); distinct speckles and reticulated patterns present on dorsal and lateral head;*L. meridionalis* (Guangxi, Yunnan)
 18b) Loreal entering orbit; speckles and reticulated patterns absent on dorsal and lateral head.....19
 19a) Preocular absent; prefrontal entering orbit; dorsal cross-bands white.....*L. subcinctus* (Fujian, Guangdong, Guangxi, Hainan)
 19b) Preocular present; prefrontal not entering orbit; dorsal cross-band creamy Dark Spectrum Yellow (Color 78) to creamy Light Chrome Orange (Color 76).....*L. liuchengchaoi* (Beijing?, Guangdong, Henan, Hunan, Sichuan, Shanxi, Shaanxi, Zhejiang)

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The electronic version of this article in portable document format represents a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone (see Articles 8.5–8.6 of the Code). This

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SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Collections of all animals used for this present study obey the Wildlife Protection Act of China. Collection permits were issued by Kunming Institute of Zoology, Chinese Academy of Sciences (BBCJ-2014-001).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

K.W. and J.C. conceived the study. K.W. and Z.B.Y. conducted the field surveys. Z.B.Y. and V.G. collected morphological data. Z.B.Y. collected genetic data. K.W. analyzed the data and prepared the manuscript, with other authors' inputs. All authors read and approved the final version of the manuscript.

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Appendix I

Detailed locality information in Figure 1.

Lycodon chapaensis **comb. nov.** (triangle): 1. Laocai, Tonkin, Vietnam; 2. Daweishan, Honghe Prefecture, Yunnan, China; 3. Xichou County, Wenshan Prefecture, Yunnan, China; 4. Mengzi, Yunnan, China; 5. Jingdong County, Puer, Yunnan, China; 6. Tengchong County, Baoshan, Yunnan, China; 7. Yunlong County, Dali, Yunnan, China; 8. Lushui, Nujiang Prefecture, Yunnan, China; 9. Fugong, Nujiang Prefecture, Yunnan, China; 10. Dulongjiang, Nujiang Prefecture, Yunnan, China.

L. fasciatus (circle): 1. Mogok, Mandalay, Myanmar; 2. Mindat, Chin State, Myanmar; 3. Longchuan, Dehong Prefecture, Yunnan, China; 4. Menglian County, Puer, Yunnan, China; 5. Tengchong, Baoshan, Yunnan, China; 6. Jingdong County, Puer, Yunnan, China; 7. Mengla, Xishuangbanna, Yunnan, China; 8. Kunming, Yunnan, China (type locality of junior synonym, *Dinodon yunnanensis*)

L. gongshan (square): 1. Dulongjiang, Gongshan County, Yunnan, China; 2. Xiaoheishan, Longling County, Yunnan, China; 3. Yunlong Nature Reserve, Dali, Yunnan, China.

Lycodon multizonatus (trapezoid): 1. Pengba, Luding County, Sichuan, China.

Lycodon septentrionalis (pentagon): 1. Khasi Hills, Meghalaya State, India; 2. Medog, Nyinchi Prefecture, Tibet, China.

Lycodon synaptor (hexagon): 1. Dongchuan, Yunnan, China.

Appendix II

Examined specimens of recognized species. Museum abbreviations see method.

Lycodon chapaensis **comb. nov.** ($n=8$): MNHN-RA-1933.0011 (holotype), from 20 km SW of Lao-Kay (=Lao Cai), Tonkin, Vietnam; KIZ 027593, Tengchong, Yunnan, China; KIZ 035594, Yongping, Dali, Yunnan, China; KIZ 006753, Mengzi, Yunnan, China; KIZ 035045, Lushui, Gongshan, Yunnan, China; KIZ 038282, Fugong, Nujiang, Yunnan, China; KIZ 035113, Dulongjiang, Gongshan, Yunnan, China; KIZ 034331, Xichou, Wenshan, Yunnan, China.

L. fasciatus ($n=4$): KIZ 74110262, 74110263, Tengchong County, Yunnan, China; 7410145, Husa, Longchaun County, Yunnan, China; 751473, Menglian County, Yunnan, China.

L. gongshan ($n=4$): KIZ 730034 (holotype), 730008 (paratype), 35112 (topotype), 35114 (topotype), Dulongjiang, Gongshan County, Yunnan, China.

L. liuchengchaoi ($n=1$): HENU 001, Nanyang, Neixiang County, Henan, China.

L. multizonatus ($n=4$): CIB 9964 (holotype), CIB 9965 (paratype), Pengba, Luding County, Sichuan, China; KIZ 01623, Luding, Sichuan, China; KIZ 0911051, Shimian, Sichuan, China.

L. ruhstrati ($n=8$): NMW 22794:1, 22994:3, 22794:4, 22794:10, 22794:15, 22794:18, FMNH 140167, 140168, CAS 18874, all from Taiwan.

L. septentrionalis ($n=2$): CIB 117521, CIB M20150607, Medog, Tibet, China.

L. synaptor ($n=1$): BMNH 1905.1.30.63 (holotype), Dongchuan, Yunnan, China.

Appendix III

Literature used for the updated distribution of *Lycodon* species in China. For full citation refer to the literature cited section.

L. aulicus-capucinus complex: Ades & Kendrik, 2004

L. cathaya: Wang et al., 2020a

L. fasciatus: Yan et al., 2004; Kang et al., 2009; Li et al., 2012

L. flavozonatus: Orlov & Ryabov, 2004; Luo et al., 2010

L. futsingensis: Vogel et al., 2009; Zhang et al., 2011a; Peng et al., 2015

L. gongshan: Vogel & Luo, 2011; Guo et al., 2015; Chen et al., 2018a

L. liuchengchaoi: Zhang et al., 2011b, 2015; Peng et al., 2014, 2017, 2018; Bai et al., 2018; Zhao et al., 2018; Zhang, 2019

L. multizonatus: Lei et al., 2014; Yao & Gong, 2012; Li et al., 2020

L. meridionalis: Orlov & Ryabov, 2004

L. pictus: Jessen et al., 2020

L. ruhstrati: Yuan & Wei, 2000; Wang et al., 2003; Ades & Kendrik, 2004; Wang & Zheng, 2005; Chen et al., 2006; Guo et al., 2007; Yang & Rao, 2008; Zhang et al., 2017

L. rufozonatus: Zhao, 2006

L. septentrionalis: Chen et al., 2018b

L. synaptor: Vogel & David, 2010