

A new species of *Lycodon* Boie, 1826 (Serpentes: Colubridae) from central Laos

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Abstract: We describe a new species of the genus *Lycodon* Boie based on an adult male specimen from Khammouane Province, central Laos. *Lycodon banksi* **sp. nov.** is distinguished from its congeners by a combination of the following characters: (1) dorsal scales in 17-17-15 rows, dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; (2) supralabials 8; (3) infralabials 10; (4) loreal in contact with the eye; (5) cloacal single; (6) ventral scales 241; (7) dorsal surface of body with 87 greyish yellow blotches; (8) ventral surface of body and tail uniformly grey cream. Based on the molecular comparison, *Lycodon banksi* **sp. nov.** is placed in a clade with other species previously considered to be members of the genus *Dinodon*. The new species is at least 9% genetically divergent from other species within this clade as shown by a fragment of the mitochondrial cytochrome *b*. This discovery increases the number of *Lycodon* species known from Laos to eleven.

Keywords: New species - *Lycodon* - Laos - karst forest - morphology - phylogeny - taxonomy.

INTRODUCTION

The genus *Lycodon* Boie is one of the most diverse genera of colubrid snakes, with 50 currently recognized species (Uetz *et al.*, 2017). The members of this genus have a broad distribution from eastern Iran to southern China and Japan, southward to the Philippines as well as the Indo-Australian Archipelago (Lanza, 1999; Siler *et al.*, 2013; Neang *et al.*, 2014). Six species of *Lycodon* have been described within the last five years, namely *Lycodon synaptor* Vogel & David, 2010, *L. gongshan* Vogel & Luo, 2011, and *L. liuchengchaoi* Zhang, Jiang, Vogel & Rao, 2011 from China; *L. davidi* Vogel, Nguyen,

Kingsada & Ziegler, 2012 from Laos; *L. zoosvictoriae* Neang, Hartmann, Hun, Souter & Furey, 2014 from Cambodia; and *L. cavernicolus* Grismer, Quah, Anuar, Muin, Wood & Nor, 2014 from Malaysia.

From Laos, ten species of *Lycodon* have been reported to date, comprising *L. capucinus* (Boie, 1827), *L. davidi* Vogel, Nguyen, Kingsada & Ziegler, 2012, *L. fasciatus* (Anderson, 1879), *L. futsingensis* (Pope, 1928), *L. laoensis* Günther, 1864, *L. meridionalis* (Bourret, 1935), *L. rufozonatus* Cantor, 1842, *L. ruhstrati abditus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009, *L. septentrionalis* Günther, 1875, and

L. subcinctus Boie, 1827 (Deuve, 1970; Vogel *et al.*, 2012; Siler *et al.*, 2013; Luu *et al.*, 2013; Teynié *et al.*, 2014).

Our recent field survey in the karst forest of Phou Hin Poun National Protected Area (NPA), Khammouane Province, central Laos led to the discovery of a snake, which could be identified as a member of the genus *Lycodon* based on the following characters: eye with a vertically elliptical pupil; nostril enlarged; robustly arched upper maxillary bone with an inward curve in the anterior part; anterior and posterior maxillary teeth interrupted by a diastema; dorsal scales smooth or weakly keeled, in 17 rows anteriorly and at midbody, and 15 rows posteriorly; ventral scales weakly notched (Lanza 1999; Grismer *et al.*, 2014). Although only a single specimen was collected, it proved to be morphologically distinct. Our finding is corroborated by another record, a closely resembling specimen photographed in about 12.4 km distance. The morphological results are further supported by molecular analyses so that we describe the single adult male from Phou Hin Poun, Khammouane Province, central Laos as a new *Lycodon* species.

MATERIAL AND METHODS

Sampling: The field survey was conducted by Vinh Quang Luu and Thomas Calame in Phou Hin Poun NPA, Khammouane Province, central Laos in April 2016. The collected specimen was fixed in approximately 85% ethanol, and subsequently transferred to 70% ethanol for permanent storage. Liver tissue sample was preserved separately in 95% ethanol. The specimen from Phou Hin Poun NPA, central Laos was deposited in the collections of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam. Another specimen was photographed on 22 July 2016 by an arachnology team led by Peter Jaeger, in ca. 12.4 km distance from the type locality.

Morphological analysis: Measurements were taken following Vogel *et al.* (2009) with a digital caliper to the nearest 0.1 mm, except body and tail lengths. These measurements included: head length (HL, from snout tip to jaw angles); head width (HW, maximum head width at posterior margin of parietals); head height (HH, vertical height between upper and under sides of head were measured at HW); interorbital distance (IO, the distance between outer edges of supraoculars); eye-nostril distance (EN, from anterior edge of the orbit to posterior edge of nostril); internarial distance (IN, horizontal diameter between nostrils); eye diameter (ED, horizontal diameter of the orbit); snout length (SnL, from the tip of rostral to the anterior edge of the orbit); snout-vent length (SVL, from tip of snout to the vent); tail length (TaL); ratio of tail length / total length (TaL/TL); total length (TL).

Scale counts were taken following Vogel *et al.* (2009).

Ventral scales (VEN) were counted according to Dowling (1951); dorsal scale rows (DSR): number of dorsal scale rows at neck (ASR, at one head length behind head), number of dorsal scales at midbody (MSR), and number of dorsal scale rows before the vent (PSR, at one head length before the vent); supralabials (SL, counted on upper lips); infralabials (IL, counted on lower lips); loreals (Lor); loreal scale touching the orbit (yes or no); preoculars (PreOc); postoculars (PosOc); temporals (Temp, counted immediately behind postoculars and between posterior SL and parietals). Bilateral scale counts were given as left/right. Keel (keeled dorsal scale rows); PreVEN (preventral scales); VEN notched (present or absent); VEN keeled (present or absent); SC (subcaudal scales); numbers of pattern-units (like crossbars or vertebral blotches) are provided as number on body + number on tail.

For comparisons, we referred to the data provided by Boulenger (1893), Smith (1943), Orlov & Ryabov (2004), Neang *et al.* (2014), and Grismer *et al.* (2014); studied specimens are listed in the Appendix.

Museum abbreviations are as follows: CAS-California Academy of Sciences; GP-Specimens in the collection of Peng Guo; LSUMZ-The Louisiana State University Museum of Natural Science; MNHN-Muséum National d'Histoire Naturelle, Paris, France; VNUF-Vietnam National University of Forestry.

Molecular data and phylogenetic analyses: The mitochondrial cytochrome *b* gene was employed in this study, because it has been widely used in previous molecular analyses of *Lycodon* (e.g., Guo *et al.*, 2013, Siler *et al.*, 2013). We included six new sequences from samples collected in Laos and Vietnam (Table 1). Other sequences of related species were obtained from GenBank. Three species, *Ahaetulla prasina*, *Boiga cynodon*, and *Dispholidus typus*, were assigned as outgroups based on their phylogenetic relationships to the genus *Lycodon* (Guo *et al.*, 2013, Siler *et al.*, 2013) (Table 1).

We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial cytochrome *b* was amplified using the primer pair L14910/H16064 (Burbrink *et al.*, 2000). After sequences were aligned by Clustal X v2 (Thompson *et al.*, 1997), data were analyzed using maximum parsimony (MP) and maximum likelihood (ML) as implemented in PAUP*4.0b10 (Swofford, 2001) and Bayesian analysis (BA) as implemented in MrBayes v3.2 (Ronquist *et al.*, 2012). Settings for these analyses followed Le *et al.* (2006), except that the number of generations in the Bayesian analysis was increased to 1×10^7 and the number of bootstrap replicates in ML to 1000. The optimal model for nucleotide evolution was set to TrN+I+G for ML and combined Bayesian analyses as selected by Modeltest v3.7 (Posada & Crandall, 1998). The cutoff point for the burn-in function was set to 19 in

the Bayesian analysis, as $-\ln L$ scores reached stationarity after 19,000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as estimated in PAUP and posterior probability (PP) in MrBayes v3.2. $BP \geq 70\%$ and $PP \geq 95\%$ are regarded as strong support for a clade. Uncorrected pairwise divergences were calculated in PAUP*4.0b10 (Table 2).

RESULTS

Molecular data, Phylogenetic analysis: The final matrix consisted of 1100 aligned characters, of which 440 were parsimony informative. The alignment did not contain gaps. Maximum parsimony analysis of the dataset recovered two most parsimonious trees with

Table 1. *Lycodon* samples used in the molecular analyses (for abbreviations see Material and methods); * = listed as *L. aulicus* in Siler *et al.* (2013); ** = listed as *L. fasciatus* in genbank but as *L. cf. fasciatus* in the CAS catalogue.

Species	GenBank no.	Locality	Voucher number
<i>Ahaetulla fronticinta</i>	AF471072	Myanmar: Ayeyarwady Division	CAS 204966
<i>Ahaetulla prasina</i>	KC010339	Philippines: Palawan Province	KU 326673
<i>Boiga cynodon</i>	KC010340	Philippines: Negros Occidental Province	KU:324614
<i>Dispholidus typus</i>	AY188012	Not reported	Not reported
<i>Lycodon capucinus</i> *	KC010350	Philippines: Romblon Province	KU:315378
<i>L. capucinus</i> *	MH669273	Laos: Bolikhamxay Province	VNUF R.2015.15
<i>L. butleri</i>	KJ607892	Malaysia: Perak	LSUHC:8365
<i>L. butleri</i>	KJ607891	Malaysia: Perak	LSUHC:9137
<i>Lycodon banksi</i> sp. nov.	MH669272	Laos: Khammouane Province	VNUF R.2015.20
<i>L.cf. fasciatus</i> **	KC010366	Myanmar: Chin State	CAS 234957
<i>L.cf. fasciatus</i> **	KC010365	Myanmar: Chin State	CAS 234875
<i>L. futsingensis</i>	KC733206	China: Zhejiang Province	GP 2216
<i>L. futsingensis</i>	KC733207	China: Guangdong Province	GP 2226
<i>L. 'flavozonatus'</i>	KC733199	China: Guangxi Province	GP1939
<i>L. 'flavozonatus'</i>	KC733210	China: Guangdong Province	GP2279
<i>L. laoensis</i>	KC010368	Laos: Salavan Province	FMNH 258659
<i>L. laoensis</i>	KC010370	Cambodia: Pursat Province	LSUHC 8481
<i>L. meridionalis</i>	MH669271	Vietnam: Bac Kan Province	VNUF R.2012.4
<i>L. meridionalis</i>	MH669268	Vietnam: Ninh Binh Province	VNUF R.2017.54
<i>L. meridionalis</i>	MH669269	Vietnam: Ninh Binh Province	VNUF R.2017.88
<i>L. meridionalis</i>	MH669270	Vietnam: Thanh Hoa Province	VNUF R.2017.123
<i>L. rufozonatus</i>	KC733194	China: Sichuan Province	GP 133
<i>L. rufozonatus</i>	AF471063	Not reported	LSUMZ:44977
<i>L. ruhstrati</i>	KC733208	China: Guangdong	GP2243
<i>L. ruhstrati</i>	KC733200	China: Guangdong	GP2249
<i>L. semicarinatus</i>	AB008539	Not reported	Not reported
<i>L. subcinctus</i>	KC010385	Philippines: Palawan Province	KU 309447
<i>L. subcinctus</i>	KC010384	Philippines: Palawan Province	KU 327571
<i>L. subcinctus</i>	KC733203	China	GP2191
<i>L. synaptor</i>	KC733204	China: Yunnan Province	GP 2188

Table 2. Uncorrected ("p") distance matrix showing percentage pairwise genetic divergence (cytochrome *b*) between new and closely related species.

Species name	1	2	3	4	5
1. <i>Lycodon banksi</i> sp. nov.	-				
2. <i>L. meridionale</i> & <i>L. 'flavozonatus'</i>	9.0-9.2	-			
3. <i>L. futsingensis</i>	9.6	8.5-8.7	-		
4. <i>L. rufozonatus</i>	10.6-11.1	7.4-8.2	8.7-9.2	-	
5. <i>L. semicarinatus</i>	10.9	9.8-10.3	10.3	9.3-10.2	-

1649 steps (CI = 0.46; RI = 0.65). In the ML analysis, the score of the single best tree found was 8329.12 after 2678 arrangements were tried. The topology derived from the Bayesian analysis (Fig. 1) was similar to that in Guo *et al.* (2013), but nodes of the phylogeny received lower statistical support. The new species was recovered in a clade together with other species, which were previously placed in the genus *Dinodon* (see Siler *et al.*, 2013; Guo *et al.*, 2013). This clade was strongly supported by both MP and Bayesian analyses (BP = 86%, PP = 97%) (Fig. 1). The new species is most closely related to a clade containing '*L. flavozonatus*', *L. futsingensis*, *L. meridionalis* in terms of genetic distance based on cytochrome *b*, and is diverged at least about 9.0-9.2% from the latter species (Table 2).

TAXONOMIC ACCOUNT

Lycodon banksi sp. nov.

Figs 2-5, Table 3

Holotype: VNUF R.2015.20 (field number: TK 20.15), adult male, collected on 4 April 2015 by Vinh Quang Luu and Thomas Calame in the karst forest, at the mouth of a cave, Phou Hin Poun NPA, Hinboun District, Khammouane Province, central Laos, at an elevation of 167 m a.s.l.

Diagnosis: *Lycodon banksi* sp. nov. is characterized by the following morphological characters: (1) dorsal scales in 17-17-15 rows, dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; (2) supralabials 8; (3) infralabials 10; (4) loreal entering orbit; (5) cloacal single; (6) ventral scales 241; (7) dorsal surface of body with 87 greyish yellow blotches; (8) ventral surface of body and tail uniformly grey cream.

Description of the holotype: Head elongate (HL 15.3 mm), moderately distinct from the neck, longer than wide (HW/HL ratio 0.71), depressed (HH/HL ratio 0.40), narrow anteriorly (IN/IO ratio 0.65); snout elongate (SnL/HL ratio 0.39); nostril lateral, oval shaped, located in the middle of the nasal; eye large (ED/HL ratio 0.17), pupils vertically elliptic; rostral triangular, much broader than high, hardly visible from above; nasal divided into two scales by a vertical ridge along posterior edge of nostril; two square internasals, as wide as long, bordered by two large, subpentagonal prefrontals posteriorly; frontal single, enlarged, pentagonal, narrowed posteriorly; parietals longer than wide, in contact with each other medially, with upper anterior and posterior temporals, paraparietal laterally and four nuchal scales posteriorly; loreal 1/1, elongate, entering orbit; supralabials 8/8, first and second in contact with nasal, third to fifth entering orbit, sixth largest; infralabials 10/10, first pair

in broad contact with each other, first to fifth in contact with first pair of chin shields; first and second pairs of chin shields elongate, of the same size and shape, separated by a medial groove, first pair larger than the second; preocular 1/1; postoculars 2/2, of the same size, bordering anterior temporals; anterior temporals 2/2, posterior temporals 3/3, upper ones smaller than lower ones.

Body elongate, SVL 415 mm; TaL >50 mm (tail tip lost); preventrals 2, ventrals 241; subcaudals 26 (tail tip lost), divided, weakly notched laterally; cloacal single; DSR 17-17-15; dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; the vertebral scales not enlarged.

Colouration in life: Head dark grey, without vertical light nuchal band; dorsal surface of body dark grey-yellow with 87 greyish yellow irregular dorsal blotches; first body blotch starting at ventral scale 13, a half vertebral scale covered by this blotch; two yellow stripes on each side, from behind the neck to vent, indistinct posteriorly; ventral scales grey cream; dorsal surface of tail with at least eleven greyish yellow tail blotches, ventral surface of tail grey cream.

Hemipenis: The left hemipenis is only in part everted but shows a spinose ornamentation.

Additional specimen: One specimen which was not collected but detected and photographed on 22 July 2016 by an arachnology team consisting of Peter Jaeger, Alope Sahu and Jonas Ewert, in Khammouane Province, in ca. 12.4 km distance from the type locality. The color pattern of this specimen resembles closely that of the holotype.

Comparisons: In our phylogenetic analysis, *Lycodon banksi* sp. nov. is nested in a clade containing *L. rufozonatus*, *L. semicarinatus* (Cope), '*L. flavozonatus*', *L. futsingensis* and *L. meridionalis*. The new species differs from the similar *L. meridionalis* by having loreal entering the orbit (*versus* separated from the orbit), dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows on the posterior body third feebly keeled (*versus* distinctly keeled), dorsal head pattern uniform dark grey (*versus* with yellow-black marbling in *L. meridionalis*), and ventral surface grey cream (*versus* yellow with dark spots posteriorly) (see Bourret, 1935; Orlov & Ryabov, 2004); from *L. rufozonatus* by having loreal entering the orbit (*versus* usually separated), a distinctly higher ventral scale count (241 *versus* 185-204), dorsal scales feebly keeled in the posterior body part (*versus* all smooth), dorsal head pattern uniform dark grey (*versus* dark brown with yellow borders), and body pattern blotched (*versus* banded) (Boulenger 1893); from *L. semicarinatus* by having loreal touching the orbit (*versus* separated), a higher ventral scale count

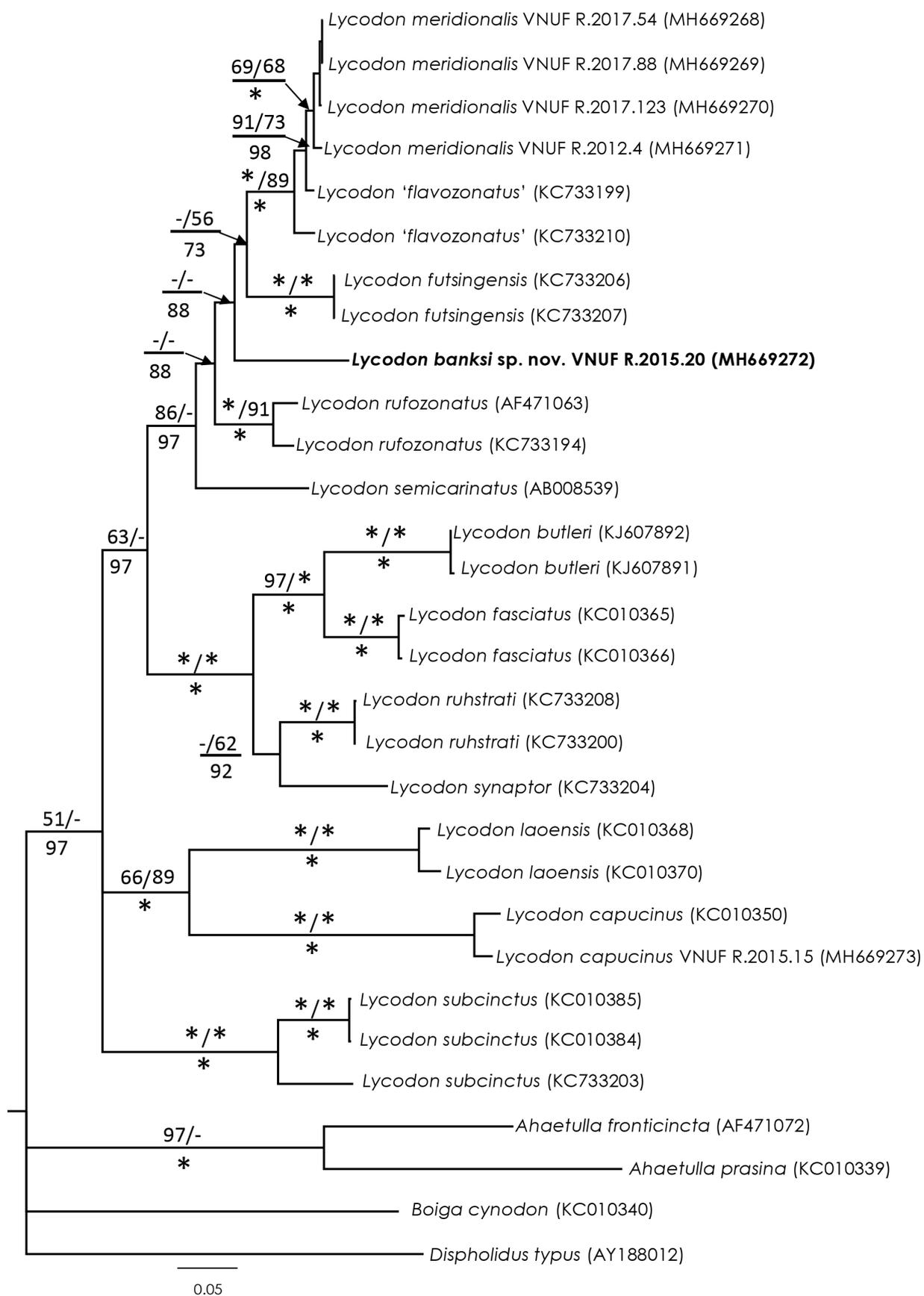


Fig. 1. Bayesian cladogram based on the partial cytochrome *b* gene. Numbers above and below branches are bootstrap values of MP/ML analyses (>50%) and Bayesian posterior probabilities, respectively. Asterisk denotes 100% value.

Table 3. Measurements (in mm) and morphological characters of the holotype of *Lycodon banksi* **sp. nov.** (measurements in mm; for other abbreviations see material and methods; * tail tip lost).

Character	<i>Lycodon banksi</i> sp. nov. VNUF R.2015.20
Sex	Male
SVL	415.0
TaL	50.0*
TL	465.0
HL	15.3
HW	10.8
HH	6.1
IO	6.3
EN	3.3
IN	4.1
ED	2.6
SnL	6.0
DSR	
ASR	17
MSR	17
PSR	15
Keeling	6 dorsal scale rows on the posterior body third feebly keeled
VEN	241
PrVEN	2
Ventral notched	Yes
Ventral keeled	No
SC	26*
divided	Yes
Cloacal	Single
Loreal	1/1
Loreal entering orbit	Yes
SL	8/8
entering orbit	3,4,5
largest SL	6/6
IL	10/10
IL in contact with 1st chin shield	1–5
PreOc	1/1
PostOc	2/2
Temporal scales	
anterior	2/2
posterior	3/3
Scales around paraparietal	5/7
Scales between parietals	4
Nuchal band	Absent
Body blotches	87 (yellow blotches)
Tail blotches	15*
Belly pattern	uniform grey cream
Ventral tail pattern	grey cream
First body blotch position (at VEN)	13
First blotch width (vertebral scales)	0.5



Fig. 2. Adult male holotype of *Lycodon banksi* sp. nov. (VNUF R.2015.20) in life. (A) dorsolateral view. (B) Head in dorsolateral view. (C) Head in dorsal view. Photos: V. Q. Luu.

(241 versus 211-234), dorsal scale rows keeled along posterior 1/3 (versus keeled along anterior half), belly pattern uniform grey cream (versus yellow), and body pattern blotched (versus banded) (Boulenger 1893); from *L. flavozonatus* by having loreal in contact with the orbit (versus separated), cloacal single (versus divided), six dorsal scale rows on the posterior third of the body feebly keeled (versus 10-12 keeled dorsal scale rows at midbody), dorsal head dark grey (versus black with light markings), and belly pattern uniform grey cream (versus yellow with large black spots); from *L. futsingensis* by having loreal entering the orbit (versus separated), a higher ventral scale count (241 versus 193-203 in males), dorsal scales feebly keeled in the posterior body part (versus all smooth), and body pattern blotched (versus banded) (Vogel *et al.*, 2012; Neang *et al.*, 2014) (Table 4).

The new species has a loreal entering the orbit and thus differs from the following species and subspecies of the *Lycodon ruhstrati* group which have the loreal separated

from the orbit: *L. cardamomensis* Daltry & Wüster, 2002, *L. davidi*, *L. multifasciatus* (Maki, 1931), *L. ophiophagus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009, *L. paucifasciatus* Rendahl in Smith, 1943, *L. ruhstrati ruhstrati* (Fischer, 1886), and *Lycodon ruhstrati abditus* (Vogel *et al.*, 2009). In addition, the new species differs from *L. cardamomensis* by having more ventral scales (241 versus 215), and in body pattern (87 blotches versus 12 bands); from *L. davidi* by having more ventral scales (241 versus 224), six dorsal scale rows on the posterior third of the body feebly keeled (versus dorsal scale rows at midbody slightly keeled, outermost rows entirely smooth throughout body), and belly pattern uniform grey cream (versus anterior third whitish-cream, posterior part heavily speckled with dark dots); from *L. multifasciatus* by having more ventral scales (241 versus maximum 237), and dorsal pattern blotched (versus banded); from *L. ophiophagus* by having more ventral scales (241 versus 211), and dorsal pattern (87 blotches versus 21-22 bands); from *L. paucifasciatus*



Fig. 3. Different head views of the adult male holotype of *Lycodon banksi* sp. nov. (VNUF R.2015.20). Photos V. Q. Luu.

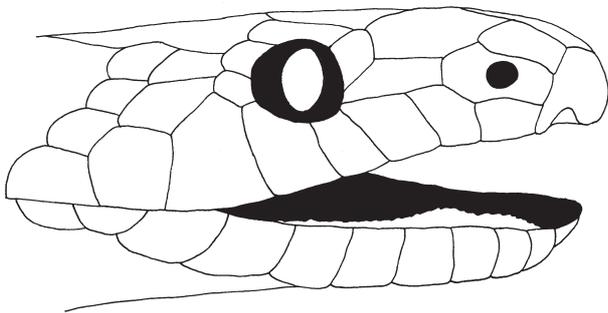


Fig. 4. Lateral head view of the adult male holotype of *Lycodon banksi* sp. nov. (VNUF R.2015.20). Drawing by T. Ziegler.

by having fewer dorsal scale rows at neck (17 *versus* 19), more ventral scale rows (241 *versus* 221-222), six dorsal scale rows on the posterior third of the body feebly keeled (*versus* two upper rows plus vertebral row distinctly keeled), and dorsal pattern blotched (*versus* banded) (Neang *et al.*, 2014); from *L. r. ruhstrati* and *Lycodon ruhstrati abditus* by having more ventral scales (241 *versus* 211-228; 241 *versus* 206-224, respectively), and dorsal pattern blotched (*versus* banded in the latter) (Vogel *et al.*, 2012); from *L. synaptor* by having much more ventral scale rows (241 *versus* 201-203), dorsal pattern with 87 blotches (*versus* 30-31 bands), and belly pattern uniform grey cream (*versus* banded) (Vogel & David 2010); from *L. zoosvictoriae* by having more

ventral scales (241 *versus* 213), dorsal pattern consisting of 87 blotches (*versus* 31), and having six dorsal scale rows on the posterior third of the body feebly keeled (*versus* all weakly keeled) (Neang *et al.*, 2014).

From the remaining species occurring in Laos, the new species can be distinguished as follows: from *L. capucinus* by having more ventrals (241 *versus* 182-211), fewer supralabials (8/8 *versus* 9-10), cloacal single (*versus* divided), dorsal blotches 87 (*versus* reticulated), and greyish yellow blotched body pattern (*versus* reticulated); from *L. fasciatus* by having more ventral scale rows (241 *versus* 182-225), dorsal pattern consisting of 87 blotches (*versus* 19-49 bands), and belly pattern uniform grey cream (*versus* white with dark blotches) (Neang *et al.*, 2014); from *L. laoensis* by having loreal in contact with the orbit (*versus* separated), more ventrals (241 *versus* 169-192), and dorsal scales feebly keeled in the posterior body part (*versus* all smooth) (Neang *et al.*, 2014); from *L. septentrionalis* by having more infralabials (10 *versus* 7-8), more ventral scales (241 *versus* 202-217), and dorsal pattern blotched (*versus* banded), as well as belly pattern uniform grey cream (*versus* white) (Neang *et al.*, 2014); from *L. subcinctus* by the presence of preocular scale (*versus* absent), having cloacal scale single (*versus* divided), dorsal pattern blotched (*versus* banded in anterior part), and more ventral scale rows (241 *versus* 129-230) (Neang *et al.*, 2014).

From the remaining species in the *fasciatus* group, the new species differs as follows: from *L. butleri* Boulenger by having more ventral scale rows (241 *versus* 220-227), dorsal pattern blotched (*versus* banded), and belly pattern



Fig. 5. Additional record of *Lycodon banksi* sp. nov. in life: (A–B) dorsolateral views. (C) Head in dorsal view. Photos A–C A. Sahu. (D) Dorsal view. Photo P. Jaeger.

uniform grey cream (*versus* banded & spotted) (Grismer *et al.*, 2014); from *L. cavernicolus* by having dorsal head uniformly dark grey (*versus* light brown), fewer supralabials (8 *versus* 9 or 10), more dorsal blotches (87 *versus* 36–45 bands), dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled (*versus* all keeled), and greyish yellow blotched pattern on the body (*versus* white bands); from *L. gongshan* by having six dorsal scale rows on the posterior third of the body feebly keeled (*versus* upper and vertebral dorsal rows keeled), more ventral scale rows (241 *versus* 210–216), and dorsal pattern with 87 blotches (*versus* 32–40 bands) (Vogel & Luo, 2011); from *L. liuchengchaoi* by having cloacal scale single (*versus* divided), dorsal pattern consisting of 87 irregular greyish yellow dorsal blotches (*versus* 40 well-defined yellow rings), and more ventral scales (241 *versus* 204) (Zhang *et al.*, 2011).

Distribution: *Lycodon banksi* sp. nov. is currently known only from the type locality in the Phou Hin Poun NPA, Khammouane Province, central Laos (Fig. 6).

Etymology: The name of the species is dedicated to our friend and colleague Chris Banks, International Coordinator, Philippine Crocodile National Recovery

Team, Zoos Victoria, Australia, for his outstanding contributions towards amphibian and reptile conservation, in particular of the Philippine Crocodile. We propose the following common names: Banks' Wolf Snake (English), Banks Wolfszahnatter (German).

Natural history: The holotype was found at 20:39 h, crawling on a limestone outcrop in the karst forest, approximately 0.3 m above the forest floor, at an elevation of 167 m a.s.l. The humidity at the time of collection was approximately 85% and the air temperature ranged from 23 to 26°C (Fig. 7). Another specimen was observed 12.4 km away from the type locality, active on the ground at 23:30 h, near a limestone cliff in the secondary forest.

DISCUSSION

In our phylogenetic analyses, *Lycodon banksi* is placed in a clade with other species previously considered to be members of the genus *Dinodon*. In addition, the specimen of *L. meridionalis* from Bac Kan Province, Vietnam was nested in the same clade with '*L. flavozonatus*' from Guangdong and Guangxi provinces in southern China. The genetic distance between the Vietnamese and Chinese

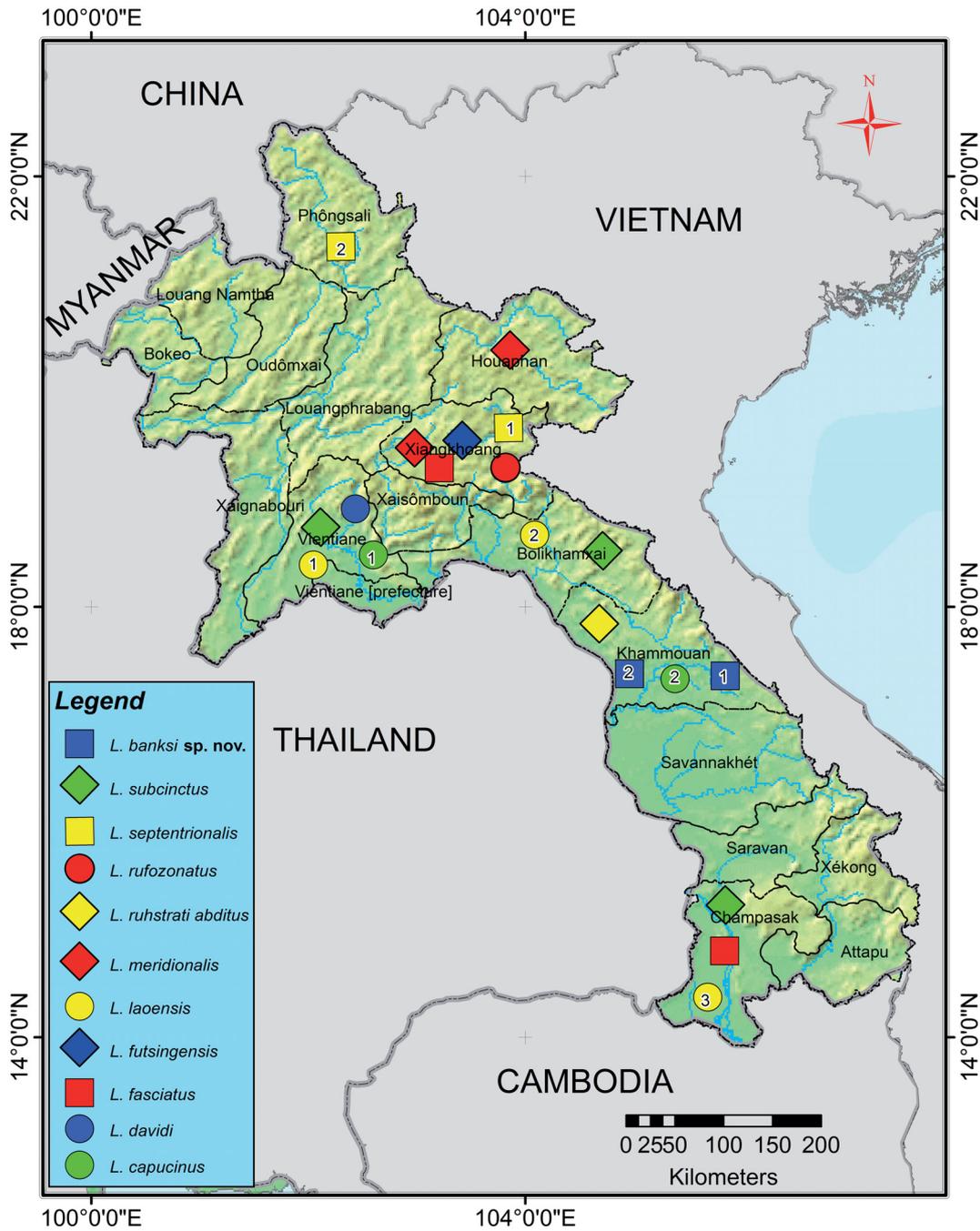


Fig. 6. Map showing the type locality of *Lycodon banksi* sp. nov. in Khammouane Province (black dots) and other records of the genus *Lycodon* occurring in Laos (after Deuve, 1970; Vogel *et al.*, 2012; Siler *et al.*, 2013; Luu *et al.*, 2013; Teynié *et al.*, 2014).

samples is approximately 1.4-2.4% (2.6% between two Chinese samples). Morphological features of the specimens from Bac Kan, Ninh Binh, and Thanh Hoa provinces were consistent with those in the descriptions of *L. meridionalis* by Bourret (1935) and Orlov & Ryabov (2004) in the following characters: snout-vent length in males reaching 1295 mm; dorsal head with yellow-black marble markings; transverse bands on body 86-115; ventral scales 234-245; cloacal plate single; belly pattern

uniform yellow with dark spots posteriorly (Table 4). Therefore, based on the molecular data, we herein initially assign two specimens ('*L. flavozonatus*' GP 1939, 2279) from China to *L. meridionalis*, although this placement needs to be confirmed by further morphological studies. Superficially, the new species is similar to *L. meridionalis* in dorsal pattern. However, they are clearly distinguishable in other morphological features, e.g., dorsal scalation, dorsal head, and belly patterns. Although the new species

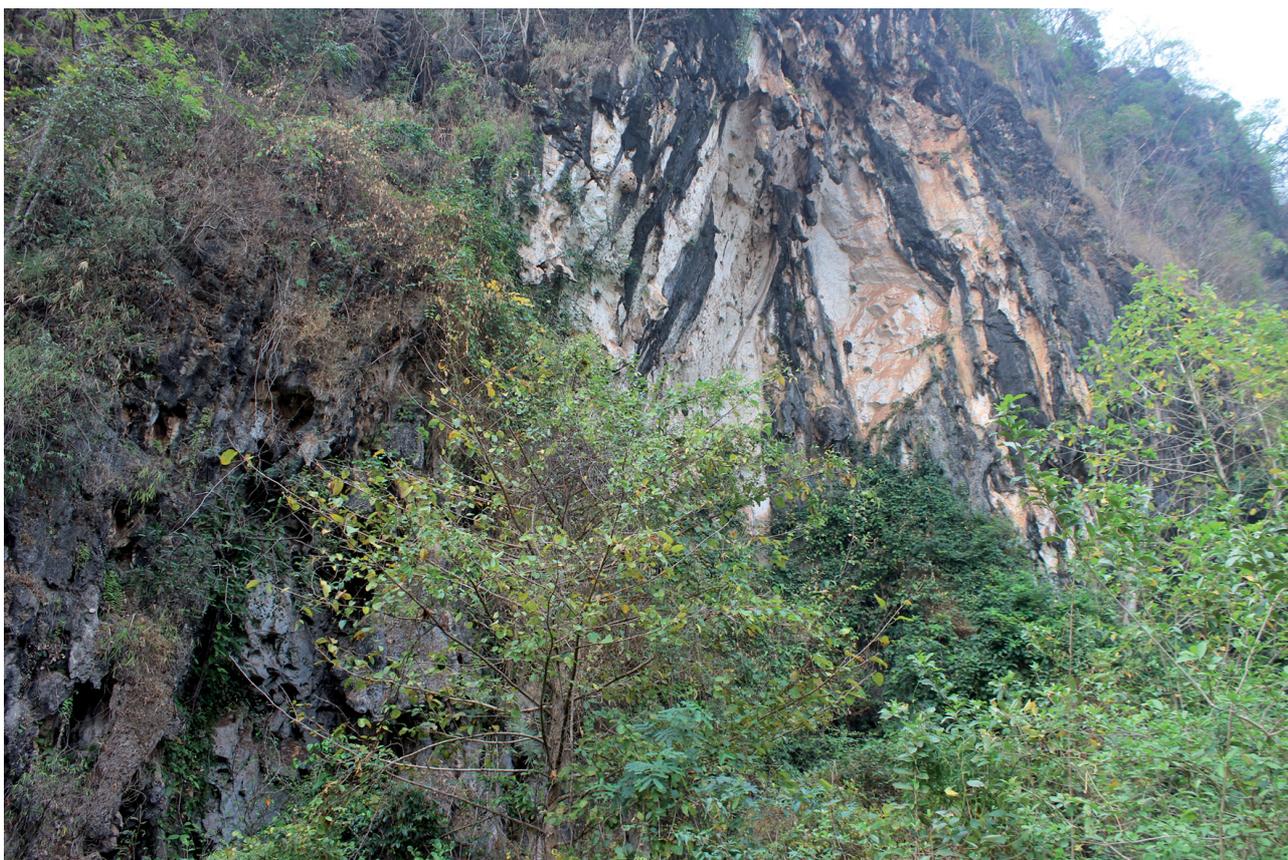


Fig. 7. Habitat of *Lycodon banksi* sp. nov. at the type locality. Photo V. Q. Luu.

has no clear sister species according to the phylogenetic analyses, it is most closely related to *L. meridionalis* in terms of genetic distance, but distinctly differing from the latter (ca. 9%).

The new species seems to be a nocturnal and terrestrial snake, and rare. It is a karst-dweller in the northern Truong Son Range, as are *L. davidi* and *L. ruhstrati abditus* (Vogel *et al.*, 2012; Luu *et al.*, 2013). *L. banksi* has a unique pattern of dark grey and yellow colouration on its dorsal surface, which offers a perfect camouflage among litter on the forest ground and on karst surface. Moreover, the species has indistinct banding on the dorsal surface in comparison with its congeners of the *L. ruhstrati* and *L. fasciatus* groups which are clearly banded.

The discovery of this new species increases the number of *Lycodon* species known from Laos to eleven. In the same area, we recently discovered two new bent-toed geckos (*Cyrtodactylus jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler, *C. soudthichaki* Luu, Calame, Nguyen, Bonkowski & Ziegler) and two new species of the genus *Gekko* (*G. thakhekensis* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler, *G. bonkowskii* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler) (Luu *et al.*, 2014a, b, 2015a, b). These recent discoveries together with the new *Lycodon* species provide strong evidence that the

northern Truong Son Range, and especially the extensive limestone karst formations in Khammouane Province, central Laos represent a hotspot of endemic biodiversity. The finding of this new *Lycodon* species with its unique colour pattern and morphology suggests that the species diversity within the genus *Lycodon* might be far greater than commonly assumed. Our study further underlines the need to combine detailed morphological and molecular data to delineate species complexes and better understand kinship. Unfortunately, it was not possible to obtain molecular data from all investigated reference species (e.g., *Lycodon fasciatus* MNHN 1928.69 from Xieng Khoang Province, northern Laos) due to formalin-fixed state and long-term storage. Therefore, further field studies are needed to accurately assess the diversity of *Lycodon* in the poorly studied karst forest systems of central Laos.

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Table 4. Diagnostic characters separating *Lycodon banksi* **sp. nov.** from closely related species and the remaining *Lycodon* species recorded from Laos (data obtained from Boulenger, 1893; Smith, 1943; Taylor, 1965; Deuve, 1970; Orlov & Ryabov, 2004; Vogel *et al.*, 2009, 2012; Siler *et al.*, 2013; Luu *et al.*, 2013; Teynié *et al.*, 2014; Neang *et al.*, 2014).

Characters	<i>Lycodon banksi</i> sp. nov.	<i>L. flavozonatus</i>	<i>L. futsingensis</i>	<i>L. meridionalis</i>	<i>L. rufozonatus</i>	<i>L. semicarinatus</i>
LoREAL scale touching the orbit	yes	no	no	no	no (rarely yes)	no
Head pattern	dark grey	black with light markings and yellow collar on the nape	grayish brown	yellow-black marble markings	dark brown with yellow borders	black
Ventral scales	241	202-225	193-208	234-246	185-204	211-234
Number of keeled dorsal scale rows	6 dorsal rows on the posterior body third feebly keeled	10-12	0	9 (distinctly keeled)	0	keeled in anterior half
Dorsal pattern	blotched	banded	banded	blotched	banded	banded
Belly pattern	uniform grey cream	yellow with large black spots	cream, speckled posteriorly	uniform yellow with dark spots posteriorly	not reported	yellowish
Blotch/band colour	greyish yellow	yellow	brownish-speckled white	yellow	dark brown	yellowish brown

Characters	<i>L. capucinus</i>	<i>L. davidi</i>	<i>L. fasciatus</i>	<i>L. laoensis</i>	<i>L. ruhstrati</i> <i>abditus</i>	<i>L. septentrionalis</i>	<i>L. subcinctus</i>
LoREAL scale touching the orbit	no	no	yes	no	no	yes	yes
Head pattern	dark	olive-brown	dark	dark	dark	light dark	largely white
Ventral scales	182-211	224	182-225	163-192	214-229	202-217	192-230
Number of keeled dorsal scale rows	weakly keeled	middorsal scale rows weakly keeled	weakly keeled	0	5 (middorsal scales keeled)	5-7 (middorsal scales weakly keeled)	10 (middorsal scales weakly keeled)
Dorsal pattern	reticulated	banded	banded	banded	banded	banded	banded
Belly pattern	dirty white	white with dark blotches	white with dark transverse blotches	white	cream	white	greyish
Blotch/band colour	mixed reticulate	pale tan brown	whitish grey	yellowish white	whitish	white	whitish

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Appendix: Comparative specimens examined

- Lycodon capucinus*. Laos: Bolikhamxay Province: Tad Leuk: VNUF R.2015.15 (field number: PKK06.15).
- Lycodon davidi*. Laos: Vientiane Province: Vang Vieng: IEBR A.2011.7 (field number: NQT 2010.39).
- Lycodon fasciatus*. Laos: Xieng Khoang Province: MNHN1928.69
- Lycodon fasciatus*. China: Yunnan Province: MNHN1919.148
- Lycodon fasciatus*. China: Tibet: MNHN1912.465
- Lycodon fasciatus*. China: Tibet: MNHN1912.466
- Lycodon fasciatus*. India: MNHN1912.47
- Lycodon futsingensis*. Laos: Khammouane Province: VFU A.2013.4
- Lycodon futsingensis*. Vietnam: Bac Giang Province: IEBR A.0822
- Lycodon futsingensis*. Vietnam: Ha Tinh Province: ZFMK 81474
- Lycodon futsingensis*. Vietnam: Lam Dong Province: IEBR A.0704
- Lycodon futsingensis*. Vietnam: Quang Binh Province: ZFMK 86453
- Lycodon meridionalis*. Vietnam: Bac Kan Province: Ba Be National Park: VNUF R.2012.4 (field number: BBR4). Ninh Binh Province: Trang An: VNUF R.2017.54 (field number: TA 17.54). VNUF R.2017.88 (field number: TA 17.88). VNUF R.2017.126 (field number: ND 17.126). Thanh Hoa Province: Nam Dong: VNUF R.2017.123 (field number: ND 17.123).
- Lycodon paucifasciatus*. Vietnam: Quang Binh Province: ZFMK 80662
- Lycodon paucifasciatus*. Vietnam: Quang Binh Province: ZFMK 86452
- Lycodon ruhstrati abditus*. Laos: Khammouane Province: VFU A.2013.5
- Lycodon ruhstrati abditus*. Vietnam: Quang Binh Province: ZFMK 86451