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A revision of *Lycodon ruhstrati* (Fischer 1886) auctorum (Squamata Colubridae), with the description of a new species from Thailand and a new subspecies from the Asian mainland

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The Asian colubrid species related to *Lycodon ruhstrati* (Fischer 1886) are revised on the basis of their morphology, pattern and colouration, in combination with DNA analyses. *Lycodon ruhstrati* auctorum is revealed to be a species complex. We restrict this specific nomen to populations of Taiwan. The mainland populations thus far gathered under this name form two taxa. For the first one, with dorsal scales entirely smooth, the name *Lycodon futsingensis* (Pope 1928) is available. The second taxon is described here as *Lycodon ruhstrati abditus* n. subsp. This subspecies is genetically close to the nominate form restricted here to Taiwan but differs by some morphological characters. In addition to the differences in ventral and subcaudal scale counts, and maxillary teeth formula, *Lycodon ruhstrati abditus* n. subsp. has keeled vertebral scales whereas in *L. futsingensis* all dorsal scales are unkeeled. Another new

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taxon is described here as *Lycodon ophiophagus* n. sp. to accommodate an isolated population on the Thai Peninsula. It is distinguishable by its ventral and subcaudal scale counts, the long posterior maxillary teeth, the colouration and by having keeled dorsal scale rows. *Lycodon paucifasciatus* is a valid species, redefined on the basis of new material from central Vietnam. *Lycodon multifasciatus*, until recently regarded as a subspecies of *Lycodon ruhstrati*, is also considered to be a valid species.

KEY WORDS: Reptilia, Serpentes, *Lycodon r. ruhstrati*, *Lycodon ruhstrati abditus* n. subsp., *L. futsingensis*, *L. multifasciatus* new comb., *Lycodon ophiophagus* n. sp., *L. paucifasciatus*, morphology, systematics.

INTRODUCTION

The genus *Lycodon* Boie 1826 includes aglyphous colubrid snakes (Colubridae Colubrinae; see VIDAL et al. 2007) mainly characterized by (1) a strongly arched upper maxillary bone that is distinctly bent inwards anteriorly, with 3-6 anterior fang-like teeth increasing in size and separated by a toothless interspace from seven to 15 posterior teeth, the last 2-3 of which larger than the others; (2) a vertically elliptical pupil; (3) smooth or feebly keeled dorsal scales; and (4) 15-19 dorsal scale rows at midbody (SMITH 1943, LANZA 1999).

Lycodon is one of the largest genera of Asiatic snakes, currently containing 30 species (MUKHERJEE & BHUPATHY 2007, VOGEL & BRACHTEL 2008) that occur from central Asia and eastern Iran to southern China, the Indo-Australian Archipelago, Japan (Ryukyu Islands) and the Philippines (LANZA 1999). In the last 15 years, nine new species were described in this genus (OTA & ROSS 1994, SLOWINSKI et al. 2001, GAULKE 2002, MUKHERJEE & BHUPATHY 2007); furthermore several species are about to be described. Nevertheless, there has been no revision of this genus or even parts of it in the whole

history of herpetology. LANZA (1999) provided a key for the genus, but due to new knowledge and newly discovered species, this key is, at least in part, outdated. As in other large genera of Asian snakes (e.g., WÜSTER et al. 1997, DAVID et al. 2006, VOGEL & DAVID 2006, VOGEL & ROOIJEN 2007), some of the species (as understood at the moment) form species complexes, making the definitions inadequate and the delimitation of new forms very difficult. This leads to a large underestimation of the Asian snake diversity.

The recent findings of specimens from Thailand and Vietnam, which superficially seemed to be close to *Lycodon ruhstrati* (Fischer 1886), showed constant morphological differences, which led us to conduct the revision of this previously wide-ranging species. Indeed, *Lycodon ruhstrati* has a confusing history. It was described in 1886 as *Ophites ruhstrati* by JOHANN GUSTAV FISCHER, a German teacher and herpetologist, on the basis of two specimens originating from the south of Formosa (now Taiwan) and deposited in the Museum of Oldenburg. This species was synonymized with *Dinodon septentrionalis* (Günther 1875) by BOULENGER (1893) then recognized as a subspecies, *Dinodon septentrionalis* var. *ruhstrati* by BOULENGER (1899). It was accepted as *Dinodon septentrionalis ruhstrati* by STEJNEGER (1907). POPE (1928) briefly described *Dinodon futsingensis* Pope 1928 from Fukien (now Fujian) Province, China. The description was extended in POPE (1929). In this latter paper, *Lycodon ruhstrati* was also listed but differences between these two forms were not discussed. POPE (1935) synonymized *Dinodon futsingensis* with *L. ruhstrati* and hence transferred the taxon *futsingensis* into the genus *Lycodon* due to similarities with *Lycodon fasciatus* (Anderson 1879). MAKI (1931) described *Dinodon septentrionale multifasciatum* Maki 1931 on the basis of a single specimen from Ishigakijima Island, in the Ryukyu Archipelago, Japan. TORIBA (1982) transferred this subspecies into the genus *Lycodon* and introduced the name *Lycodon ruhstrati multifasciatus* for the Japanese populations. OTA (1988) discussed these taxa and followed TORIBA (1982), pointing out differences between the Taiwanese populations and those of the mainland. Eventually, VOGEL & BRACHTEL (2008) raised the subspecies from the Ryukyu Islands to the species status: *Lycodon multifasciatus*. We confirm this position and discuss this species only briefly, insofar as the differences between this taxon and the other forms treated here are important.

Another similar species described from Vietnam, *Lycodon paucifasciatus* (Rendahl 1943) is also discussed here, because it is obviously closely related to *Lycodon ruhstrati*. The status of this rare species known from only a few specimens had not been discussed before.

The recently described *Lycodon cardamomensis* (DALTRY & WÜSTER 2002) is not discussed, despite the fact that it seems to be a member of the same species complex, because a discussion of this species was provided elsewhere (PAUWELS et al. 2005, VOGEL & BRACHTEL 2008).

MATERIAL AND METHODS

This revision is based on a total of 46 preserved specimens examined for their external morphological characters and on several photographed specimens. Due to

the small number of available specimens of *Lycodon ruhstrati abditus* n. subsp., we also included 15 specimens described in the literature under different names but which were clearly assignable to this taxon. The data of the types of *Lycodon futsingensis* were taken from POPE (1928, 1929) and from the examination of the type specimens as well as additional specimens. Altogether, data on the pholidosis and pattern of 61 specimens were recorded. Lastly, 40 specimens of the *Lycodon fasciatus* species complex and of several members of the genus *Dinodon* were used for comparison. They are listed in Appendix 1.

In total, 54 morphological characters were recorded for each specimen. The 49 characters retained in this study and their abbreviations are listed in Table 1.

Table 1.

List of morphological characters used in this study and their abbreviations.

Number	Abbreviation	Characters
Morphometry		
1	SVL	Snout-vent length (mm)
2	TaL	Tail length (mm)
3	TL	Total length (mm)
4	Rel TL	Relative tail length TaL/TL
Anatomy		
5	TEETH	Number of maxillary teeth (on one side)
Scalation		
6	DSR	Dorsal scale rows
7	ASR	Dorsal scale rows at neck (at 10th VEN)
8	MSR	Dorsal scale rows at midbody
9	PSR	Dorsal scale rows before vent
10	Keel	Number of keeled dorsal rows
11	VEN	Ventral plates
12	VEN not	Ventrals notched or not
13	VEN keel	Ventrals keeled
14	SC	Subcaudal plates
15		
16	ANA	Anal plate: 1: single - 2: divided
17	Lor-l	Number of loreal scale (0 or 1) at left
18	Lor-r	Number of loreal scale (0 or 1) at right
19	SL-l	Number of supralabials at left
20	SL-r	Number of supralabials at right
21	SL/Eye-l	Number of the SL entering orbit at left
22	SL/Eye-r	Number of the SL entering orbit at right
23	Larg SL-l	Largest SL left
24	Larg SLrl	Largest SL right
25	IL-l	Number of infralabials at left
26	IL-r	Number of infralabials at right

(continued)

Table 1. (*continued*)

Number	Abbreviation	Characters
27	IL-tot	Total number of infralabials
28	IL/1st child	Number of IL in contact with anterior chin shield
29	PreOc-l	Number of preoculars at left
30	PreOc-r	Number of preoculars at right
31	PostOc-l	Number of postoculars at left
32	PostOc-r	Number of postoculars at right
33	ATem-l	Number of anterior temporals at left
34	ATem-r	Number of anterior temporals at right
35	PTem-l	Number of posterior temporals at left
36	PTem-r	Number of posterior temporals at right
37	ParaR	Temporal row containing the paraparietal
38	Paras	Plates around the paraparietal, see INGER & MARX (1965)
39	Parab	Scales between the paraparietals
Pattern		
40	BODCOL	Body colour 1: grey; 2: brown or ochre
41	Bands	Number of bands on body
42	Tail bands	Number of bands on tail
43	Tail venter	Colouration of tail venter
44	Bellycol	Colouration of belly
45	Bellyspeck	Speckling of belly
46	First band	That Ve before the first band starts, counted left side
47	Base	Number of Ve covered at the base of the first band
48	Broad vert	Numbers of vertebrals covered by the first band
49	Edged	Dorsal bands with light margins

Measurements, except body and tail lengths, were taken with a slide-caliper to the nearest 0.1 mm; all body measurements were made to the nearest millimeter. The number of ventral scales was counted according to DOWLING (1951). Half ventrals were not counted except when they were present on both sides (divided ventrals). The terminal scute is not included in the number of subcaudals. The dorsal scale row counts were taken at one head length behind the head, at midbody (i.e., at the level of the ventral plate corresponding to half the total number of ventrals), and at one head length before the vent. For sublabials, only those shields that were fully covered by a supralabial were counted. Values for paired head characters are given in left/right order.

The white or light bands on the body and tail were counted on one side. Indistinguishable or incomplete bands were counted as 1, bands that were fused were counted as 2. The collar in the neck was not counted and bands covering the anal shield were added to the bands on the body. Sometimes the bands formed a "Y", in which case the number of bands on one side was higher than on the other. The band covering the tail tip was not counted.

The analyses of morphological data were based on comparisons of statistical values (mean value and standard deviation). The Mann-Whitney *U* test (SIEGEL 1956) was applied when necessary, although all results are not presented here. Abbreviations are: *n*: number of specimens. – $\bar{x}$: mean value. – *s*: standard deviation.

DNA analysis

Molecular data were collected to support our morphological results, i.e. the genetic distances of related species of the genus *Lycodon*. We compared fragments of the mitochondrial 16S ribosomal RNA gene of five specimens of *Lycodon* (*L. futsingensis*, *L. paucifasciatus*, *Lycodon ruhstrati abditus* n. subsp., GenBank accession numbers: EU999209-EU999213) morphologically examined in this study as well as additional samples of two *L. fasciatus* (GenBank accession numbers: EU999214-EU999215) from Vietnam and nine *L. r. ruhstrati* (GenBank accession numbers: EU999200-EU999208) from Taiwan. Genomic DNA was extracted from tissue samples of adult specimens using a standard protocol for Salt extraction or a modified Chelex 100 extraction protocol (WALSH et al. 1991) and amplified by Primers 16Sar-L (light chain; 5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16Sbr-H (heavy chain; 5' - CCG GTC TGA ACT CAG ATC ACG T - 3') from PALUMBI et al. (1991). PCR products were purified with a Qiaquick purification kit (Qiagen) and sequenced with an automatic capillary sequencer (ABI 377). Resulting mitochondrial 16S rRNA fragments of up to 489 nucleotides were manually checked and edited with BioEdit version 7.0.9.0 (HALL 1999). We used the pairwise alignment option (optimal GLOBAL alignment) of BioEdit to compute the uncorrected pairwise distances and calculated the percentage distances for the sequences as shown in detail in Table 2.

Museum abbreviations

AMNH: American Museum of Natural History, New York, USA. BMNH: The Natural History Museum, London, UK. CAS: California Academy of Sciences, San Francisco, USA. FMNH: Field Museum of Natural History, Chicago, USA. IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam. IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. MNHN: Muséum National d'Histoire Naturelle, Paris, France. NMW: Naturhistorisches Museum Wien, Austria. NRM: Naturhistoriska Riksmuseet, Stockholm, Sweden. PSGV: Gernot Vogel's private collection, Heidelberg, Germany. QSMI: Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand. REP: Landesmuseum für Natur und Mensch, Oldenburg, Germany. USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA. ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. ZMB: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany. ZSM: Zoologische Staatssammlung, München, Germany.

RESULTS

On the basis of morphological analyses, we could identify a major level of separation, namely between taxa entirely smooth dorsally and those with at least the upper dorsal rows keeled. Specimens from the mainland with keeled and unkeeled dorsal scales also show different ventral and subcaudal scale counts without any overlap in the values (see below in the respective specific accounts and in the discussion).

As entirely smooth specimens previously identified as *Lycodon ruhstrati* auctorum constitute a homogeneous sample, distinct both morphologically and genetically from other populations, we regard it as a distinct species for

which the combination *Dinodon futsingensis* Pope 1928 is available. Unfortunately both syntypes of *Dinodon futsingensis* are juveniles, which typically for this genus show a different juvenile pattern. Still, the pholidosis fits very well with the other specimens we could examine.

To assess the relationships of the keeled and unkeeled populations from the Asian mainland and from Taiwan, we genetically compared several specimens.

Molecular analyses clearly separated taxa of the mainland (unkeeled and keeled), namely *L. fasciatus*, *L. futsingensis* and *L. paucifasciatus*. The analyses showed a maximum intraspecific sequence divergence of about 0.4% for *L. fasciatus* (EU999214-215), *L. futsingensis* (EU999210-211) and *L. paucifasciatus* (EU999212-213) and clearly separated each taxon by a minimum interspecific sequence divergence of 2.8%. These three taxa are thus recognized as distinct species. The situation is more complex among populations with keeled dorsal scales referred to *L. ruhstrati*. The comparison of the keeled taxa showed only very small differences (0.6-0.8%) between the populations of the mainland (*Lycodon ruhstrati abditus* n. subsp., EU999209) and Taiwan (*L. r. ruhstrati*), and there was also small differences within the Taiwanese population itself. Three (*L. r. ruhstrati* 1, EU999200-202) of the nine samples showed a genetic distance of 0.6% from the remaining samples (*L. r. ruhstrati* 2). These low distances suggest not only the existence of more than one taxon on Taiwan (pending further research on more material) but also imply a close relationship to the mainland taxon (*Lycodon ruhstrati*

Table 2.

Uncorrected pairwise distances (lower left) and percentage distances (upper right) calculated for sequences of the mitochondrial 16s ribosomal RNA data set. Due to a sequence congruence of 100% only one sequence of each Taiwanese population was used as representative.

	Species	1	2	3	4	5	6	7	8	9
1	*L. ruhstrati ruhstrati* 1 Taiwan	—	0.614	0.614	4.490	4.,684	5.714	5.714	2.245	2.245
2	*L. ruhstrati ruhstrati* 2 Taiwan	0.994	—	0.818	4.694	4.888	5.918	5.918	2.045	2.045
3	*Lycodon ruhstrati abditus* n. subsp. ZFMK 86451	0.994	0.992	—	4.286	4.481	5.510	5.510	1.636	1.636
4	*L. futsingensis* Live specimen	0.955	0.953	0.957	—	0.408	2.857	2.857	4.073	4.073
5	*L. futsingensis* ZFMK 86453	0.953	0.951	0.955	0.996	—	3.259	3.259	4.472	4.472
6	*L. paucifasciatus* ZFMK 86452	0.943	0.941	0.945	0.971	0.967	—	0.000	4.490	4.490
7	*L. paucifasciatus* ZFMK 80662	0.943	0.941	0.945	0.971	0.967	1.000	—	4.490	4.490
8	*L. fasciatus* ZFMK 86448	0.978	0.980	0.984	0.959	0.955	0.955	0.955	—	0.000
9	*L. fasciatus* ZFMK 86450	0.978	0.980	0.984	0.959	0.955	0.955	0.955	1.000	—

abditus n. subsp.) whose closest relative among the mainland taxa is *L. fasciatus* with a sequence divergence of 1.6%.

The PCR results are widely congruent with those obtained from inspection of pholidosis and colouration.

Besides *Lycodon futsingensis*, the other mainland form is similar to *Lycodon ruhstrati* from Taiwan. There is a difference in the number of subcaudal scales with no overlap in males, whereas two of the eight females of the mainland form fall within the range of the Taiwanese specimens. The tail is shorter in this form but with a large overlap. On the basis of these results, we restrict the combination *Lycodon ruhstrati* sensu stricto to Taiwan Island. Due to the low genetic distance between the population from the mainland and the Taiwanese specimens, but the presence of morphological differences expressed in the results of the PCR, we regard the mainland taxon as a subspecies described below as *Lycodon ruhstrati abditus* n. subsp. We retain the combination *Lycodon ruhstrati ruhstrati* for the population (or, possibly, one of the populations) of Taiwan (see below under the account of *Lycodon ruhstrati*).

Recently collected specimens in Thailand showed differences in ventral and subcaudal scale counts as well as in colouration and dentition, and are referred to as a new species, described below as *Lycodon ophiophagus* n. sp. There is no doubt about the species status of *Lycodon paucifasciatus* (Rendahl 1943). However, we expand the definition of this species on the basis of two recently collected specimens. *Lycodon multifasciatus* (Maki 1931) and *Lycodon cardamomensis* (Daltry & Wüster 2002) are accepted as valid species on the basis of noteworthy differences in pholidosis and colouration (see species diagnoses).

Lycodon ruhstrati (Fischer 1886)

Ophites ruhstrati Fischer 1886: 16, Taf. II, fig. 6. – Type locality. "Süd-Formosa" (now southern Taiwan). Syntypes. REP 918-19. – Collected by Mr Ernst Ruhstrat, date unknown.

Ophites albofuscus (non *Ophites albofuscus* Duméril, Bibron & Duméril 1854): Günther 1868.

Dinodon septentrionalis (non *Ophites septentrionalis* Günther 1875): Boulenger 1896.

Dinodon septentrionale: Kuntz 1963.

Dinodon septentrionale ruhstrati: Stejneger 1907; Maki 1931 (part.), Maki 1933 (pl. XLVI); Bourret 1936.

Lycodon ruhstrati: Pope 1935 (part.); Tu 2004; Vogel & Brachtel 2008 (part.).

Lycodon ruhstrati ruhstrati: Ota 1988 (part.); Lue et al. 1999; Norval et al. 2007a, 2007b; Norval & Mao 2008a, 2008b.

Ophites ruhstrati: Zhao & Adler 1993 (part.).

Taxonomic comments. According to the molecular results, three distinct, although poorly genetically differentiated lineages can be defined, two of which occur in Taiwan and the third on the Asian mainland, where it is known from China and North Vietnam. It is unclear to us weather two taxa

or a single taxon with some genetic variation exist in Taiwan, so we will not address the morphological variation in Taiwan here in, due to insufficient material. A similar situation was met in *Trimeresurus stejnegeri* (CREER et al. 2001). However, the nominal taxon *ruhstrati* should be used only for the population(s) of Taiwan. The third lineage includes only specimens from the mainland. As we recorded morphological differences, we consider the mainland specimens to warrant recognition at the subspecific level. This new subspecies is described below.

The syntypes of *Ophites ruhstrati* were recently rediscovered (FUHRMANN & KUCHARZEWSKI 2008). A redescription of these specimens is in preparation (F. TILLACK pers. comm.).

Diagnosis. A species of the genus *Lycodon*, is characterized by: (1) a loreal not entering the orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) upper dorsal rows distinctly keeled; and (4) a banded body and tail.

Distribution. This species is known from Taiwan, People's Republic of China and northern Vietnam. The precise distribution is described in detail under each subspecies (Fig. 21).

As explained above, two subspecies are recognized, as follows:

Lycodon ruhstrati ruhstrati (Fischer 1886) (Figs 1-2)

Ophites ruhstrati FISCHER 1886: 16, Taf. II, fig. 6. – Type locality. "Süd-Formosa" (now Southern Taiwan). Syntypes. REP 918-19. – Collected by Mr Ernst Ruhstrat, date unknown.

Material (17 specimens). Taiwan. NMW 22794:1-16, 18, "Suishario", now Shui-she-liao, Taiwan. Coll. Sauter.

Diagnosis. A species of the genus *Lycodon*, characterized by: (1) a loreal not entering orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) upper dorsal rows distinctly keeled; (4) 212-228 ventrals in males and 217-224 in females; (5) 105-114 Sc in males and 97-108 in females; (6) a relative tail length of 0.220-0.248 in males and 0.211-0.239 in females; (7) 33-46 bands on body; (8) the first band starting at Ven 8-16.

Description and variation (based on MAKI [1931], OTA [1988], and 17 examined specimens).

Morphology. Body elongate, laterally compressed. Head distinct from neck, flattened. Snout elongate, projecting anteriorly beyond lower jaw. Pupil vertically elliptic.

The maximal known total length is 1055 mm for a male (NMW 22794:4, SVL 810 mm, TaL 245 mm). The largest female specimen examined by us is 876 mm long (NMW 22794:2; SVL 672 mm, TaL 204 mm).

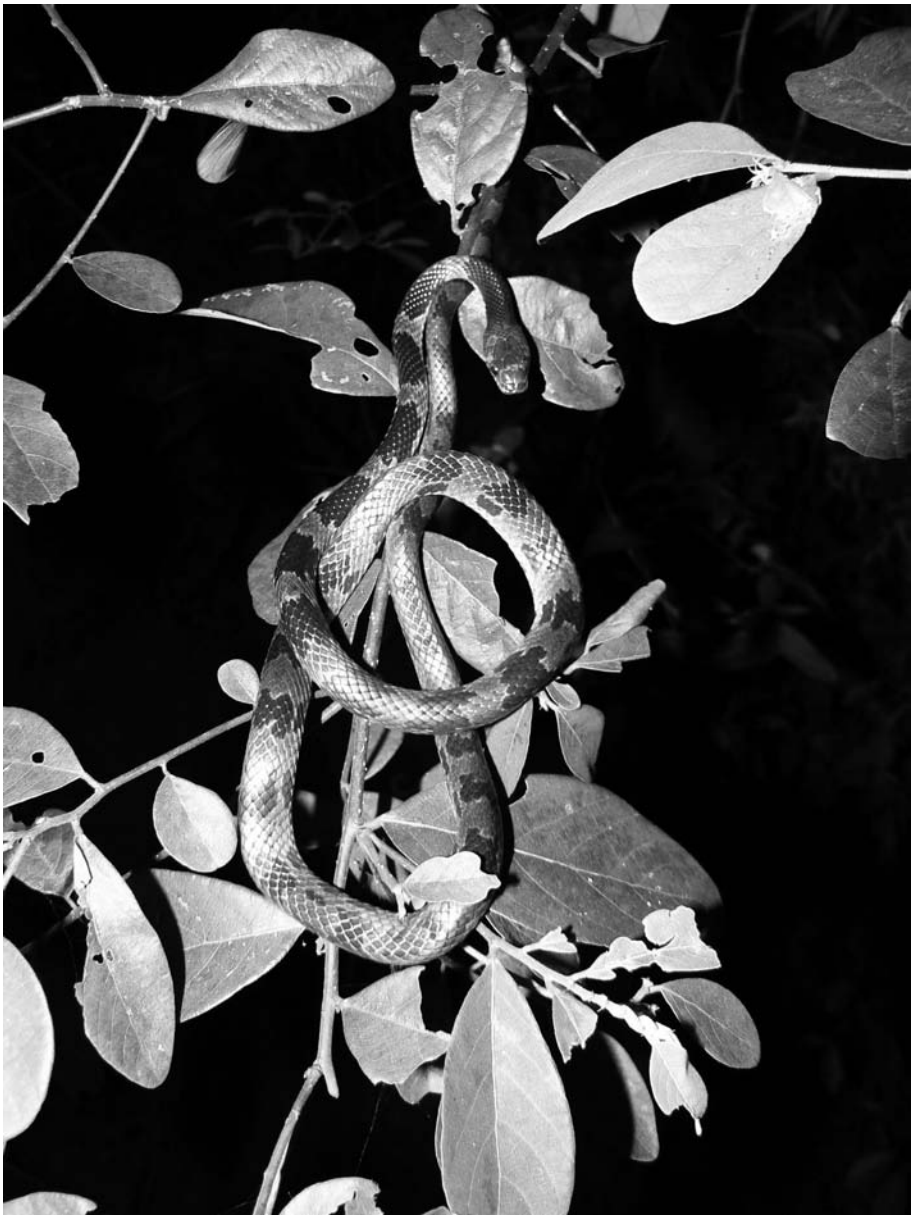


Fig. 1. — *Lycodon ruhstrati ruhstrati* from Taiwan in life. Photograph by Gerrut Norval.

Maki (1931) mentioned one female from NMW with a total length of 1030 mm; this is probably due to an erroneous sex identification. We examined the specimens in NMW and no such large specimen could be found.

Fig. 2. — *Lycodon ruhstrati ruhstrati* from Taiwan in life. Photograph by Gerrut Norval.

The second largest female mentioned by MAKI had a total length of 880 mm. According to our specimens, males are considerably larger than females, as is the case in *L. futsingensis* and *L. ruhstrati abditus*.

Ratio TaL/TL: 0.210-0.248 (n = 17), with strong sexual dimorphism (see below).

Dentition. Upper maxillary tooth formula – 10 maxillary teeth, arranged as follows: 4 small teeth, progressively increasing in size posteriorly followed by 1 strongly enlarged tooth, a gap, 2 larger enlarged teeth, a wide gap, longer than the size of the largest adjacent teeth, and 3 smaller posterior teeth.

Body scalation. DSR: 17-17-15 rows, all (in 1/17 specimens) or usually the 3-6 upper rows plus the vertebral row narrowly but distinctly keeled.

VEN: 212-233 (plus 1-2 preventrals), distinctly angulate laterally; SC: 97-116, all paired; anal plate entire.

Head scalation. Rostral large, barely visible from above; internasals broader than long, not touching loreal or preocular; frontal hexagonal, parietals longer than broad; nasal divided; one loreal not entering the eye, longer than wide; eight supralabials, 3rd to 5th entering eye, 6th the largest (5th, 7th); 10 (nine) infralabials, anteriormost in contact on the midline, first to 5th (4th) bordering anterior chin shields, 2-3 pairs of gular scales between the chin shields and the preventral; one preocular, in contact with loreal; two (one) postoculars, in contact with anterior temporals; two (one) anterior temporals, three (two) posterior temporals, one enlarged paraparietal shield.

Colouration and pattern. Above pale brownish grey to chocolate brown with 33-46 brownish-grey rings on body and 14-28 rings on the tail. The rings wider at their base, the first one starting at ventral scale 8-16 is 5-7 ventrals wide at its base and vertebrally 2-2.5 (0 in one specimen) dorsal scales wide; the rings are speckled with dots of the background colour, the speckling getting stronger posteriorly; rings become wider posteriorly; some rings form a Y, splitting into two parts on the opposite side; some bands with light margins; on some parts there is a lateral series of brownish black spots, partly on the ventrals, alternating with the dorsal bands.

Head as dorsal background colour, sometimes with the remnants of a ring at the level of the parietals; anterior part of the head irregularly light mottled.

Belly light grey, anterior more or less uniform, getting more and more speckled posteriorly; venter of the tail dark with tendencies of light bands, or just dark with light speckles.

Juvenile colouration with very discrete bands and a light collar at the posterior part of the head, the dark crossbands on the tail form complete light rings.

Hemipenis. The hemipenis is single, simple (not forked), short and reaches ca Sc 09. The entire organ is densely covered with numerous spines, except for the sulcus spermaticus, which is nude, well developed throughout and has very prominent sulcus lips. At the base, the spines are uniform and very small, while the spines at the proximal third of the organ are much larger and wider, decreasing progressively to become short on the distal half, and are not arranged in clearly discernable spine lines. No basal hooks, calyces, or flounces were observed.

Sexual dimorphism. It is clearly expressed in the total size and the number of subcaudals and only slightly expressed in the number of ventrals and the relative tail length:

(1) Total length: Males seem to be much larger than females. The largest male known has a length of 1055 mm, the largest female measures 880 mm, but see remarks above.

(2) Difference in the number of subcaudals, males: 105-114 (x = 107.8, s = 3.4); females: 97-108 (x = 103.1, s = 3.8) in our sample. Males: 99-113 (x = 105.4, s = 5.6); females: 97-116 (x = 103.6, s = 6.5) according to OTA (1988).

(3) Difference in the number of ventrals, males: 212-228 (x = 219.0, s = 5.2); females: 217-228 (x = 220.8, s = 3.1) in our sample. Males: 216-228 (x = 220.2, s = 4.6); females: 216-233 (x = 221.5, s = 5.5) according to OTA (1988).

Note: the counts given by OTA (1988) are most probably somewhat higher, as he obviously did not use the Dowling method, which results in values lower by 1-2 ventrals.

(4) Relative tail length, males: 0.220-0.248 (x = 0.230, s = 0.009); females: 0.210-0.239 (x = 0.227, s = 0.009) in our sample.

Distribution. This subspecies is endemic to Taiwan, and has been recorded from sea level to medium elevations, in lowlands and hills (Fig. 21). A list of the exact localities is provided in Appendix 2.

Biology. According to LUE et al. (1999) *L. ruhstrati ruhstrati* inhabits cultivated areas and foothill forests. It is active mostly at night and can climb trees well. It feeds on lizards and insects, and is oviparous as all known members of the genus. *L. ruhstrati ruhstrati* is distributed throughout the island. It usually occurs below 500 m above sea level, but may occasionally reach elevations up to 1500 m. According to KUNTZ (1963) this species is found in low mountainous wooded areas, as well as in shrubs adjacent to rice paddies and gardens, while LEE (2005) reported this species up to 1427 m (mean 1127 m) above sea level, in natural forests, plantation forests, secondary forests and agricultural areas.

VOGEL & BRACHTEL (2008) summarize the biology of *Lycodon ruhstrati*, but this publication is mainly based on *L. futsingensis* as we now define it (see below).

The agamid, *Japalura swinhonis* (NORVAL & MAO 2008b), and the scincid, *Sphenomorphus indicus* (J.J. MAO unpubl. data), have been recorded as prey of *L. ruhstrati ruhstrati* in Taiwan, and recently the introduced anoline lizard *Anolis sagrei* (Duméril & Bibron 1837; a chresonym for *Norops sagrei*), was also found to form part of the diet of adults, as well as neonates, of this species (NORVAL et al. 2007a). On average the prey/predator weight-ratio was 21.35% (G. NORVAL unpubl. data), which is normal for Colubrids (GREENE 1997). One specimen was observed, hunting an adult sleeping *Anolis sagrei* at a height of about 140 cm above the ground (NORVAL & MAO 2008a). The snake had a weight (post-regurgitation) of 11.4 g and a SVL of 347 mm with a TaL of 109 mm. Seven specimens have been found on vegetation, up to ca 2 m above the ground, proving this species to be semiarboreal. One female with a TL of 706 mm laid 10 eggs on 26th August 2002 (NORVAL et

al. 2007b). A relative clutch mass of 1.012 was measured, which is unusually high. The eggs were 35.22 ± 1.93 (32.44-37.96) mm in length and 10.08 ± 0.47 (9.44-10.94) mm in width with a mass of 2.5 ± 0.35 (2.1-3.0) g. Eight of the eggs hatched after 49 days at a temperature of ca 29 °C. A road-killed female (TL 779 mm) was found on the18th of February 2006 and contained eight oviductal eggs. These clutch sizes are larger than those reported for *Lycodon futsingensis* (4-7 eggs under captive conditions [VOGEL & BRACHTEL 2008]) or *Lycodon ruhstrati abditus* (four eggs: POPE 1929). The neonates shed twice within the first month without having been fed (NORVAL et al. 2007b). The only reported parasites for *L. ruhstrati ruhstrati* are the pentastomids *Raillietiella orientalis* (NORVAL et al. 2009a), and *Kiricephalus pattoni* (NORVAL et al. 2009b), while the only observed natural predator is the elapid *Bungarus multicinctus multicinctus* (MAO et al. in prep.). Some references state that the colouration of the *L. r. ruhstrati* is a form of Batesian mimicry, i.e. it resembles the colouration of the many-banded krait (*Bungarus m. multicinctus*) (LUE et al. 1999). Although the colouration of *L. r. ruhstrati* does resemble that of *B. m. multicinctus*, especially in neonates, the defensive behaviour of *L. r. ruhstrati*, which includes a triple-looped neck display, bluff-striking, struggling (thrashing) and biting, is very dissimilar from that of *B. m. multicinctus* (NORVAL & MAO 2006).

Lycodon ruhstrati abditus n. subsp. (Figs 3-6)

Dinodon septentrionalis (non *Ophites septentrionalis* Günther 1875): MELL 1922; BOULENGER 1896.
Dinodon ruhstrati: POPE 1929.
Lycodon ruhstrati: POPE 1935 (part.); WU et al. 1985; CHEN 1991; ZHAO & YANG 1997; ZHAO et al. 1998 (part.); ZHAO 2002; ZHAO 2006 (part.).
Dinodon futsingense (non *Dinodon futsingensis* Pope 1928) DEUVE 1970 (part.).
Lycodon ruhstrati ruhstrati: OTA 1988 (part.); LANZA 1999 (part.).
Ophites ruhstrati: ZHAO & ADLER 1993 (part.).

*Holotype***.** ZFMK 86451 (GenBank: EU999209), adult female, from U Bo region, Phong Nha – Ke Bang NP, Quang Binh Province, Vietnam. Collected by Thomas Ziegler, 20 June 2006 (mentioned as *Lycodon* cf. *ruhstrati* in ZIEGLER et al. 2007).

Paratypes (3 specimens). ZFMK 23363 (adult male), "Kuatun", now Guadun, Chong'an County, Fujian Province, People's Republic of China. – ZMB 65454 (adult male), "Laung Tao Shan", now Longtou Shan, Guangdong Province, People's Republic of China. – MNHN 2006.0436 (former PSGV 495 l), (adult female), Tam Dao, Vinh Phù Province, Vietnam; collected by G. Vogel.

Comments. All specimens examined by us belong to the type series. Several specimens described in the literature are referable to this subspecies. Specimens AMNH 34584-6, USNM 80939, and USNM 73842 cited by POPE (1935) can be assigned to this subspecies on the basis of their ventral and subcaudal scale counts. A specimen cited by MELL (1922) (as *Dinodon septentrionalis*) and one by BOULENGER (1896) (as *Dinodon septentrionalis*) are identified as *Lycodon*

ruhstrati abditus n. subsp. according to the keeling of their vertebral and upper dorsal rows. Lastly, five specimens from Guizhou Province recorded by WU et al. (1985) and four specimens from Anhui Province described by CHEN (1991) also belong to this subspecies on the basis of the keeling of the dorsal scales, shown in the drawings, and of the ventral and subcaudal scale counts.

Diagnosis. A subspecies of *Lycodon ruhstrati*, characterized by: (1) a loreal not entering orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) three to five upper dorsal scale (including vertebral) rows distinctly keeled; (4) 214-224 ventrals in males and 220-229 in females; (5) 90-100 Sc in males and 92-103 in females; (6) a relative tail length of 0.208-0.237 in males and 0.207-0.236 in females; (7) 19-43 bands on body; (8) the first band starting at Ve 12-17; and (9) 6-7 + 3-4 + 2 much enlarged upper maxillary teeth, each group of teeth separated by a wide gap.

This new subspecies differs from the nominate subspecies by (1) a lower ratio of TaL/TL in males, 0.208-0.237 (x = 0.218, s = 0.009) vs 0.220-0.248 (x = 0.230, s = 0.009) in *L. ruhstrati ruhstrati*, (2) a lower number of SC, 90-100 (x = 93.5, s = 3.2) in males and 92-103 (x = 96.0, s = 4.1) in females vs 105-114 (x = 107.8, s = 3.4) and 97-106 (x = 103.1, s = 3.8) respectively in the nominate subspecies, and (3) a lower number of bands on the body, 29-43 (x = 34.6, s = 3.6) vs 33-46 (x = 38.6, s = 3.6) in the nominate subspecies.

Etymology. The subspecific nomen of this subspecies is the Latin adjective *abditus* (*-a*, *-um*), meaning "hidden", in allusion to the long confusion of this species with *Lycodon ruhstrati ruhstrati*.

Fig. 3. — Dorsal view of preserved holotype of *Lycodon ruhstrati abditus* n. subsp. (ZFMK 86451) from Phong Nha-Ke Bang NP, Quang Binh Province, Vietnam. Photograph by Thomas Ziegler.

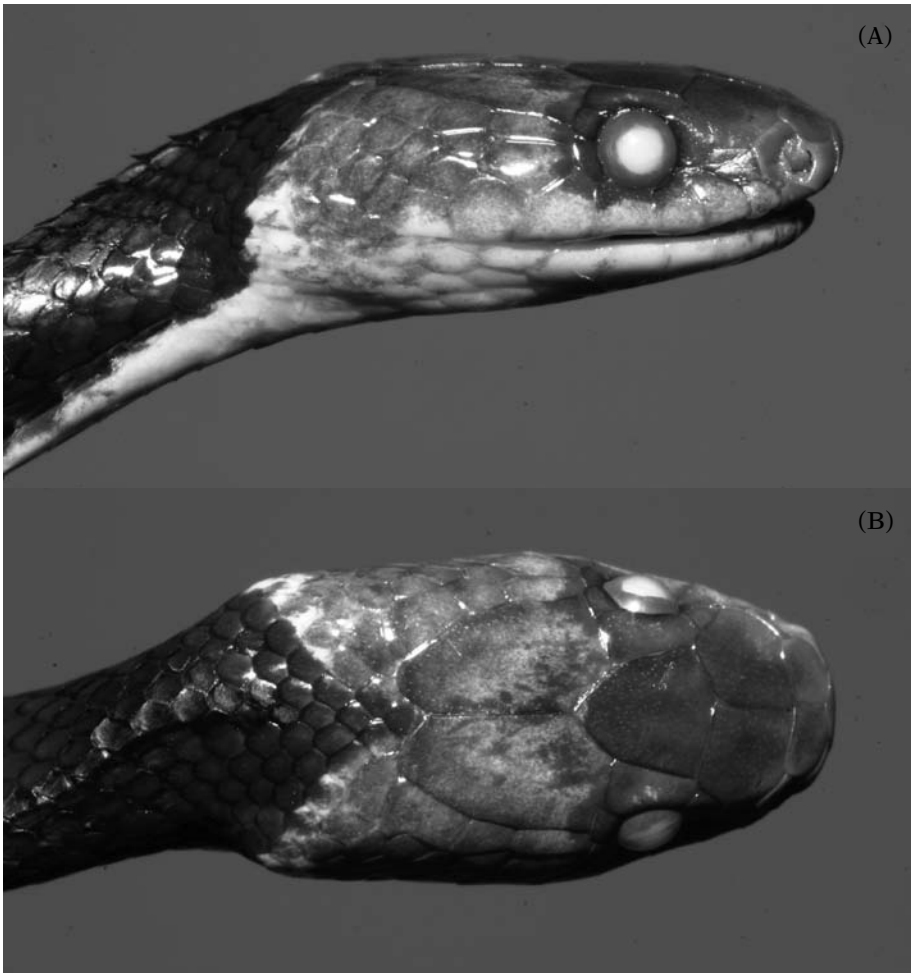


Fig. 4. — Lateral (a) and dorsal view (b) of the head of the preserved holotype of *Lycodon ruhstrati abditus* n. subsp. (ZFMK 86451) from Phong Nha-Ke Bang NP, Quang Binh Province, Vietnam. Photograph by Thomas Ziegler.

Description of the holotype (Figs 3-4). Body elongate, laterally compressed; ventral scales slightly keeled laterally; neck forming a natural angle with the head; head subrectangular, elongate, moderately distinct from the neck, strongly depressed, snout projecting over the lower jaw, long, strongly flattened, amounting to 28.7% of HL, or 2.0 times as long as diameter of eye; upper maxillary distinctly arched and bent inwards; eye rather small, with a vertical pupil; tail thin and tapering.

SVL: 460 mm; TaL: 140 mm; TL: 600 mm; HL: 15.55 mm; ratio TaL/TL: 0.233.

Dentition. Upper maxillary tooth formula: 12 maxillary teeth, as follows: four small teeth, progressively increasing in size posteriorly followed without diastema by two strongly enlarged teeth, a first wide gap, longer than the size of the largest adjacent tooth, four small teeth, a wide gap, longer than the size of the largest adjacent teeth, and two strongly enlarged posterior teeth.

Body scalation. DSR: 17-17-15 rows; scales elongate, smooth on rows 1-6, narrowly but distinctly keeled on rows 7-8 and vertebral row.

VEN: 229 (plus two preventrals), slightly angulated; SC: 103, all paired; anal plate single.

Head scalation. Rostral rather low, trapezoidal, well visible from above, not separating the internasals; nasals large, "butterfly-shaped", elongate, about 2.5 times as long as high, vertically divided into two parts of same length but with the posterior part larger and higher than the anterior one; nostril crescentic, piercing in the middle of the nasal, just in front of the division; internasals large, pentagonal, wide, in broad contact, much shorter and smaller than prefrontals; prefrontals subrectangular, wider than long; frontal short, wide, ogive-like, 1.1 times longer than wide; a supraocular on each side, distinctly longer than wide, about as wide as prefrontals; two large subtriangular parietals, much longer than the frontal, in broad contact; 1/1 loreal scales, small, elongate, pentagonal, narrowing posteriorly, 1.6 times longer than high, in broad contact with the nasal, not entering orbit

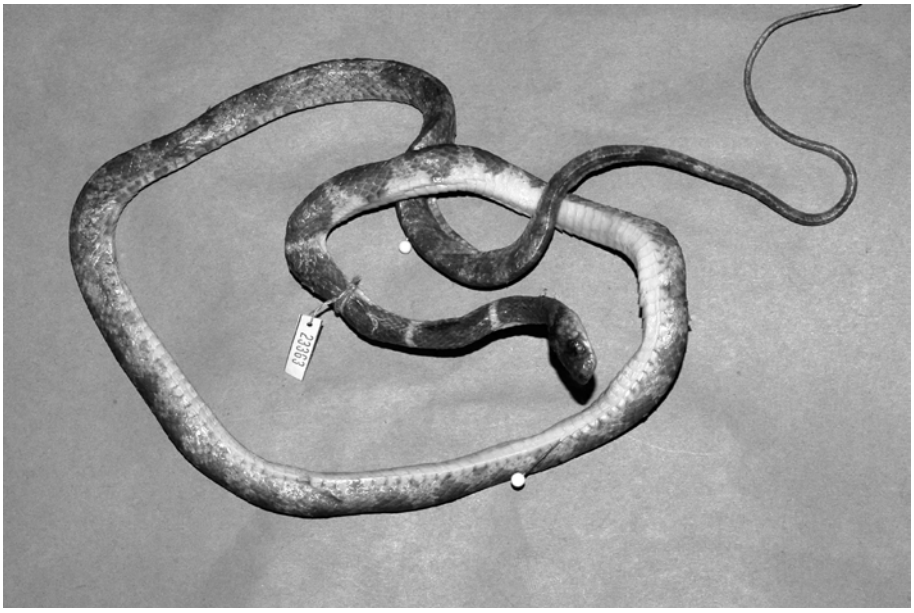


Fig. 5. — Paratype of *Lycodon ruhstrati abditus* n. subsp. (ZFMK 23363) from Guadun, Chong'an County, Fujian Province, People's Republic of China: general view of body. Photograph by Gernot Vogel.

from which it is separated by the top of SL 3 and the bottom of the preocular; 8/8 supralabials, 1st SL small, 1st and 2nd in contact with the nasal, 2nd and 3rd in contact with the loreal, 3rd SL high and strongly curved backwards, 3rd, 4th and 5th entering orbit, 6th and 7th largest; 1/1 preocular, high but narrow, placed above the 3rd SL and in contact with the upper posterior part of the loreal; 2/2 small postoculars, the upper one largest; 2+3/2+3 temporals, the lower anterior one much larger than the upper one, posterior temporals smaller; 10/10 infralabials, first pair in contact, IL 1-5 in contact with anterior chin shields, 5th IL the largest.

Colouration and pattern in alcohol. The upper surface is blackish-brown, with most dorsal scales narrowly edged with black; 19 more or less wide, cream crossbands (not ring-like or crossing the venter) which expand laterally at the bottom of the sides between the nape and the vent on the body; the first two crossbands are nearly entirely pure cream, the following ones are progressively increasingly speckled with dark brown in their centre then over nearly the whole of their surface after midbody so as to produce irregularly brownish-grey crossbands edged with cream with an irregular dark brown vertical central bar; the crossbands, trapezoidal and not constricted in their middle, are more or less equal in length, narrower on the vertebral row, about 4-5 dorsal scales long on the anterior part of the body and 3-4 scales long behind, than on the ventrolateral line, about 6-7 dorsal scales long anteriorly and 5-6 scales long posteriorly; the first crossband is at 17th dorsal scale from the nuchal collar (measured at mid-height of the side); 16 scales between 1st and 2nd crossbands, 14 scales between 2nd and 3rd ones; only the first three crossbands are separated from each other by a

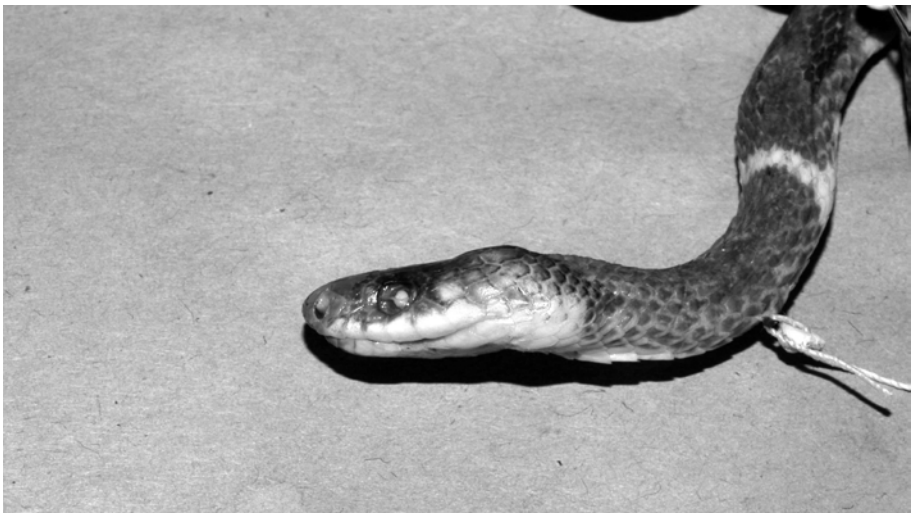


Fig. 6. — Paratype of *Lycodon ruhstrati abditus* n. subsp. (ZFMK 23363) from Guadun, Chong'an County, Fujian Province, People's Republic of China: lateral view of the head. Photograph by Gernot Vogel.

very large gap of about 14-17 dorsal scales; others are separated by a gap at mid-height of the body of about 7-8 scales and 5-6 scales above.

The tail is as the body above, with 10 entire rings of a cream-coloured background largely covered with dark brown and edged with cream; these rings cover the under surface of the tail.

The head is dark greyish-brown, distinctly lighter than the dorsal crossbands; supralabials and temporal region slightly and irregularly lighter than the upper head surface; lower parts of the supralabials creamish-brown; a faint, irregular and incomplete creamish-brown collar on the neck, not complete in the occipital region or on the venter, strongly speckled with dark brown above; some lighter dots on the parietals; chin and throat are cream, irregularly speckled with grey-brown near the mental groove; edges of infralabials also grey-brown; posterior part of the throat speckled with dark brown laterally; the nuchal collar does not extend downwards below the level of the last infralabials and scales behind the corner of the mouth.

The venter is creamish-yellow, progressively but not extensively speckled with dark greyish-brown on the posterior edges of ventral scales. The tail is dark greyish-brown interrupted by the lower dirty cream parts of the caudal rings.

Description and variation. The main characters of the specimens of the type series appear in Tables 3-4. Characters of other specimens which were identifiable by us without ambiguity are derived from POPE (1929, 1935), HUANG (1990) and CHEN (1991).

Obviously ZHAO et al. (1998) and ZHAO (2006) mixed specimens with upper dorsal scale rows keeled (*Lycodon ruhstrati abditus* n. subsp.) and dorsal scale entirely smooth (*Lycodon futsingensis*, see below).

Morphology. All specimens are elongate and laterally compressed; head forming a natural angle with the neck; tail long, very thin posteriorly. All other morphological characters agree well with those described for the holotype and are not repeated here.

Dentition. Maxillary tooth formula: 6-7 anterior teeth, the last two much enlarged + a wide gap + 3-4 small teeth + a wide gap + two much enlarged teeth.

Body scalation. DSR: 17-17-15 rows, smooth on DSR 1-3 to 1-6, distinctly keeled on rows 4-8 to 7-8 plus the vertebral row.

VEN: 197-229; SC: 90-103, without sexual dimorphism.

Ratio TaL/TL: 0.207-0.237, also without clear sexual dimorphism.

Head scalation. As for the holotype, with: rostral not or barely separating the nasals; nasals about 1.6-1.8 times as long as high; internasals in broad contact, much shorter than prefrontals in all specimens; prefrontals subrectangular, distinctly wider than long; frontal short and wide, ogive-like, 1.0-1.1 times longer than wide; 1/1 small, elongate, subrectangular loreal scale, about 1.5-1.6 times longer than high; 8/8 supralabials in paratypes and in a total of 18/19 specimens examined or described in the literature, 7/7 SL in one specimen cited by CHEN (1991); SL 3-5 entering orbit in all specimens, SL 3-4 in the same specimen of CHEN (1991); SL 6 or 6-7 the largest; 1/1 preocular and 2/2 postoculars in all known specimens; 2/2 anterior temporals in 18 specimens, 1/1 ATem in specimen AMNH 34585 (POPE

Table 3.

Main morphological data of the paratypes of *Lycodon ruhstrati abditus* n. subsp.

Number	Sex	Colour belly	Number of rings	First band starting	SVL (mm)	TaL (mm)	Ratio TaL/TL
ZFMK 23363	M	Speckled	43+18	12	761	964	0.211
ZMB 65454	M	Partly speckled	31+16	17	320	84	0.208
MNHN 2006.0436	F	Speckled	30+19	16	466	144	0.236

Table 4.

Main meristical data of the paratypes of *Lycodon ruhstrati abditus* n. subsp.

Number	Sex	VEN	SC	DSR	Keeled	Loreals	ATe
ZFMK 23363	M	224	91	17-17-15	Yes	Not entering orbit	2
ZMB 65454	M	214	95	17-17-15	Yes	Not entering orbit	2
MNHN 2006.0436	F	223	102	17-17-15	Yes	Not entering orbit	2

1935), 2/2 (in 6/14 specimens) or 3/3 (in 8/14) posterior temporals; 9/9 (in 2/13 specimens), 9/10 (1/13), 10/10 (9/13) or 11/11 (1/13) infralabials, IL 1-5 in contact with anterior chin shields in all specimens for which these data are available.

Colouration and pattern. The background colouration of the paratypes and other specimens vary from chestnut brown to blackish-brown, with cream or light beige-brown crossbands. According to our data and specimens unambiguously identifiable from the literature, the number of crossbands of the body ranges from 18 to 43, and the number of rings around the tail varies from eight to 23.

The pattern of paratypes and other specimens is similar to that of the holotype, but with much narrower dark brown areas between the first light crossbands and narrower anterior crossbands. The variation in these two characters explains the much higher number of crossbands of the body of the paratypes (30-43 vs only 19 in the holotype). However, their pattern does not differ from that of the holotype in other characters.

The pattern of the head is similar to that of the holotype, with a nuchal collar (cream or beige) much more distinct in smaller specimens.

The venter is usually cream, more or less speckled with dark brown. In most specimens the posterior half of the venter is heavily speckled.

Hemipenis. This description is based on examined specimens ZFMK 23363 and ZMB 65454 and on the data provided by Pope (1935; specimen AMNH 34586).

The organ is single, not forked, short and reaches Sc 10. It is densely covered with numerous spines throughout, with the exception of the base, which is smooth but folded. Spines are much larger and wider on the proximal third of the organ, decreasing progressively to become short on the dis-

tal half. The sulcus lips are very prominent and well developed throughout, densely covered with short spines on their outer side.

Distribution. People's Republic of China. This subspecies is definitely known from the following provinces: Fujian (Chong'an County; POPE 1935; examined specimen, paratype); Anhui (CHEN 1991); Zhejiang (HUANG 1990); Guangdong (Longtou Shan; examined specimen, paratype); Guizhou (Lungtou Mts; WU et al. 1985); Yunnan (Hengduan Mts; ZHAO & YANG 1997); Sichuan (Huangjiagou; Omei Shan; ZHAO 2002, 2006); and Gansu (FENG 1991). – Vietnam. Recorded from the provinces of Vinh Phù (Tam Dao; examined specimen, paratype) and Quang Binh (Phong Nha-Ke Bang National Park; holotype).

As it has often been confused with other species, its range is probably much wider, both in China (probably present in Guangxi Province) and in northern Vietnam (Fig. 21).

Biology. The female holotype was discovered during the dry season in primary forest. It was crawling at night on the forest floor near a steep cascade at an altitude of about 520 m above sea level (see ZIEGLER et al. 2007, mentioned therein as *Lycodon* cf. *ruhstrati*). Two stomachs of specimens from China contained remains of a small skink and of one *Takydromus* sp. A gravid female from China contained four developed eggs, one of which measured 33 × 8 mm. Three specimens were caught by torch-light at night in the beds of high mountain streams. Teasing caused one specimen to strike, it was very active and quick in its movements (POPE 1929). ZHAO & YANG (1997) found a specimen in Sichuan at a height of 1400 m. According to ZHAO (2002) it is found in Sichuan at heights between 800 and 1850 m above sea level.

Lycodon futsingensis (Pope 1928) (Figs 7-10)

Dinodon futsingensis POPE 1928: 5, fig. 11. – Type locality. "Futsing Hsien, Fukien Province", now Fuqing Xian [County], 25°44'N, 119°22'E, Fujian Province, People's Republic of China. – Holotype. AMNH 34106, collected by C.H. Pope, August-October, 1925. – Paratype. AMNH R34105, same data as the holotype.
Dinodon futsingensis: POPE 1929 (expanded description).
Dinodon septentrionale ruhstrati: MAKI 1931 (part.)
Dinodon futsingensis: BOURRET 1934, 1935a?, 1935b.
Dinodon futsingense: Bourret 1936, 1937, 1939a, 1939b, 1939c, 1939d, DEUVE 1970 (part.).
Lycodon ruhstrati: POPE 1935 (part.); SZYNDLAR & NGUYEN 1996; ZHAO et al. 1998 (part.); ORLOV et al. 2000 (part.); ZIEGLER 2002: 241 fig. 371; NGUYÊN et al. 2005 (part.); ZHAO 2006 (part.).
Lycodon ruhstrati ruhstrati: OTA 1988 (part.); LANZA 1999 (part.).
Ophites ruhstrati: ZHAO & ADLER 1993 (part.).

Material (19 specimens). – Vietnam. Bac Giang Province. IEBR A.0822, Yen Tu, Luc Nam. Cao Bang Province. MNHN 1938.130, Ngan-Son. Ha Tinh Province. ZFMK 81474, Ha Tinh (mentioned as *L. ruhstrati* in ZIEGLER 2002). Lam Dong Province. IEBR A. 0704, Cat Loc. Quang Binh Province. ZFMK 86453 (GenBank: EU999211), Phong Nha-Ke Bang National Park (mentioned as *Lycodon* sp. in ZIEGLER et al. 2007).

Thua Thien – Hue Province. IEBR A.0821, A Roang, A Luoi. Vinh Phuc Province. IEBR A.0705, IEBR A.0760, IEBR A.0761, IRSNB 17281 (formerly PSGV 590), IRSNB 17282 (formerly PSGV 676 (3)), MNHN 1935.0099-0100, MNHN 2006.0437 (former PSGV 495), MNHN 2006.0438-39 (formerly PSGV 651/1-2), PSGV 676-1/2, PSGV 760, ZFMK 59232, Tam Dao.

Taxonomic comments. This species was briefly but formally described by POPE (1928). The description was expanded by POPE (1929), although it was on the basis of the same specimens. The genus *Dinodon* is neuter in contrast to *Lycodon* (TORIBA & HIKIDA 1999). So the correct emendations would be *Dinodon futsingense* or *Lycodon futsingensis*.

There has been a great deal of confusion in the literature between this species and the mainland form of *Lycodon ruhstrati* described here as *Lycodon ruhstrati abditus* n. subsp. ZHAO et al. (1998) and ZHAO (2006) clearly wrote that specimens of *Lycodon ruhstrati* may have keeled or smooth dorsal scales. These references obviously gather under the same name *Lycodon ruhstrati*

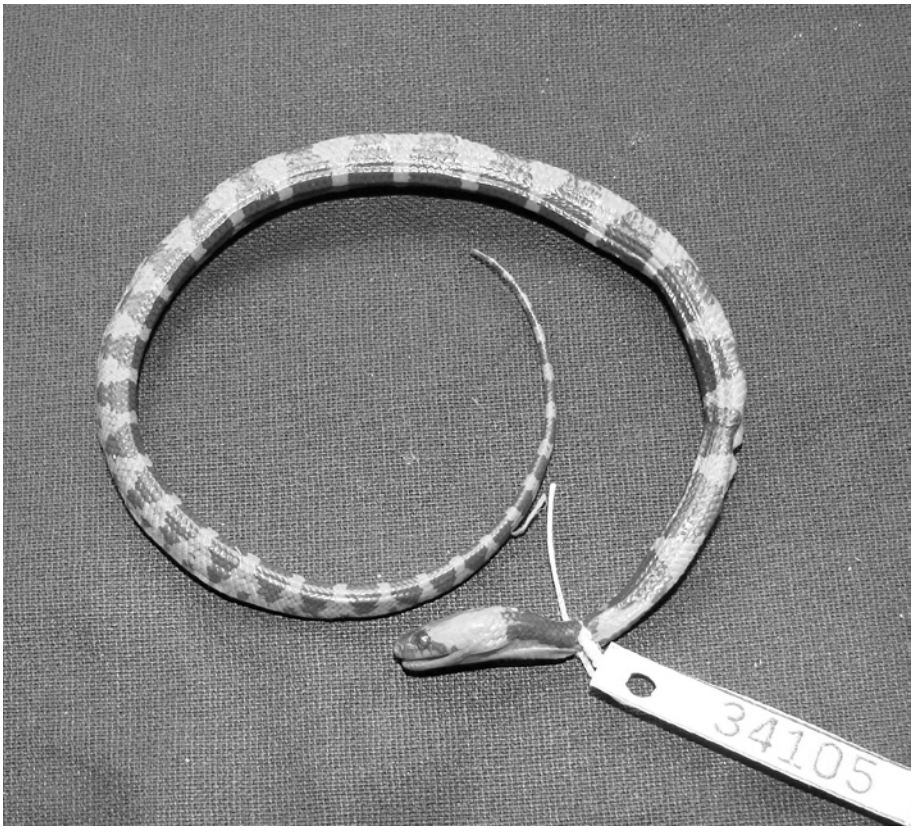


Fig. 7. — Paratype of *Lycodon futsingensis* (AMNH R34105) from Fuqing Xian, Fujian Province, People's Republic of China. Photograph by Patrick David.

abditus n. subsp. and *L. futsingensis*. Lastly, the specimen mentioned by BOURRET (1935a) might also be referable to *Lycodon ruhstrati abditus* n. subsp.

Diagnosis. A species of the genus *Lycodon*, characterized by: (1) a loreal not entering orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) the upper dorsal and vertebral scale rows entirely smooth; (4) 193-204 ventrals in males and 198-208 in females; (5) 72-87 SC in males and 78-85 in females; (6) a relative tail length ratio of 0.194-0.229 in males and 0.194-0.216 in females; (7) 19-33 light bands on a dark body; (8) the first band starting at Ve 13-21; and (9) upper maxillary teeth: 7-8 + 3-4 + 2-3.

This species can be recognized by the combination of unkeeled dorsal scale rows and low ventral and subcaudal counts.

Detailed comparisons with other species of *Lycodon* appear below in the Discussion.

Etymology. This species was named according to the name of the type locality, Futsing Hsien, now spelt as Fuxing Qian in Pinyin.

Description and variation (based on POPE [1928, 1929, 1935], and 19 examined specimens)

Morphology. Body subcylindrical, rounded on dorsum, flattened on venter. Head distinct from neck, flattened; snout elongate, projecting anteriorly beyond lower jaw. Pupil vertically elliptic.

The maximal known total length is 850 mm for a male (MNHN 1938.130; SVL 663 mm, TaL 187 mm). The largest female specimen examined by us is 773 mm long (AMNH R153709; SVL 605 mm, TaL 168 mm).

Ratio TaL/TL: 0.203-0.229 (n = 21), with no obvious sexual dimorphism (see below). One male juvenile specimen had a ratio of 0.194.

Fig. 8. — Paratype of *Lycodon futsingensis* (AMNH R34105) from Fuqing Xian, Fujian Province, People's Republic of China. Photograph by Patrick David.

Dentition. Upper maxillary tooth formula: 7-8 anterior teeth, the last two much enlarged + a wide gap + 3-4 short teeth + a small gap, shorter than posterior teeth + 2-3 much enlarged teeth.

Body scalation. DSR: 17-17 (rarely16)-15 (one specimen with 13) rows; all smooth.

VEN: 193-208 (plus 0-3 preventrals), distinctly angulate laterally; SC: 72-85, all paired; anal plate entire.

Head scalation. Rostral large, barely visible from above; internasals broader than long, not touching loreal or preocular; frontal hexagonal, parietals longer than broad; nasal divided; one loreal not entering the eye, longer than wide; eight (seven in one specimen) supralabials, 3rd to 5th (4th to 5th, 2nd to 4th or 4th to 6th) entering eye, 7th the largest (5th, 6th, 8th); 10 (9, 11) infralabials, anteriormost in contact on the midline, first to 5th (4th, 6th) bordering anterior chin shields, 1-3 pairs of gular scales between the chin shields and the preventral; one preocular, in contact with loreal; two (three) postoculars, in contact with anterior temporals; two (one) anterior temporals, three (two) posterior temporals, one enlarged paraparietal shield.

Colouration and pattern. Above pale brownish-grey to chocolate brown with 19-33 brownish rings on body and 9-18 rings on the tail. The rings wider at their base, the first one starting at ventral scale 13-23 is 5-8.5 ven-

Fig. 9. — *Lycodon futsingensis* from Tam Dao, Vietnam in life. Photograph by Gernot Vogel.

trals wide at its base and vertebrally 0-3 dorsal scales wide; the rings are speckled with dots of the background colour, the speckling getting stronger posteriorly; rings become wider posteriorly; some rings form a Y, splitting into two parts on the opposite side; some bands with light margins.

Head as dorsal background colour, sometimes with the remnants of a ring; anterior part of the head sometimes irregularly light mottled.

Belly cream, anterior more or less uniform, getting more and more speckled posteriorly, sometimes being uniform cream; venter of the tail dark with tendencies of light bands; or just dark with light speckles.

The juvenile colouration is taken from VOGEL & BRACHTEL (2008) verbatim: Juveniles have a distinctly formed band that crosses over the head and nape of the neck. It begins on the supralabials, where even the first supralabial exhibits some indistinct white speckling. The band extends in an oblique manner from the second supralabial through the loreal and the anterior portion of the preocular. The supraoculars are white only in their posterior portions whereas the largest parts of these shields are dark. A large portion of the posterior part of the frontal is also white. All in all, the frontal shows an individual extent of light and dark portions. The eyes are darkly framed. Individual white patches break up the otherwise dark portions of the head, and dark interruptions are included in the light parts. The extent and distribution of these markings varies with the individual. The first light band is followed by a wide dark zone that is wider than those between other body bands. The dorsal and lateral elements of the pattern otherwise corre-

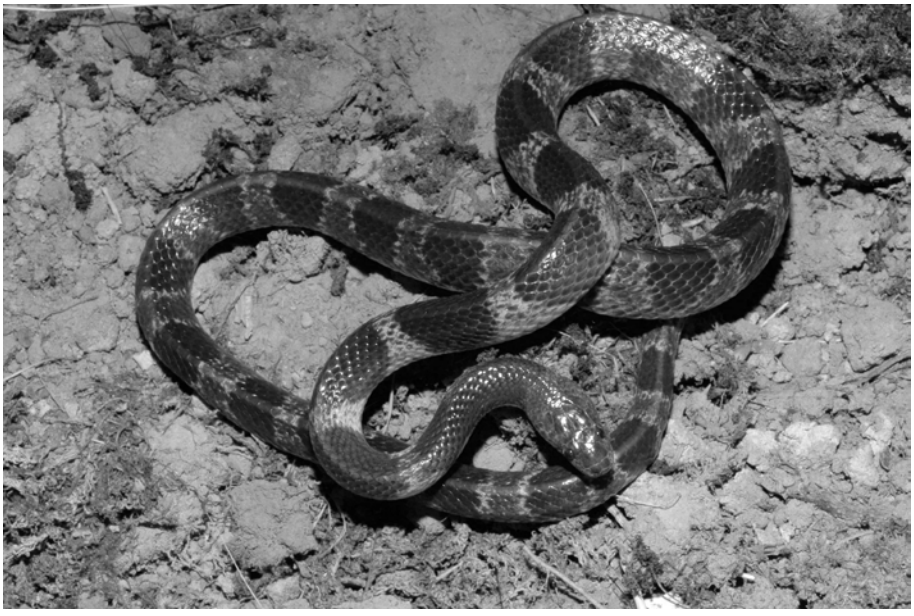


Fig. 10. — *Lycodon futsingensis* from Tam Dao, Vietnam in life. Photograph by Gernot Vogel.

spond to those found in adults. The ventral side of the head is whitish with the exception of the anterior sublabials. The anterior sublabials are speckled with dark. The anterior portion of the belly is also white, partly with dark ventrolateral spots that are continuations of the dorsal banded pattern. These are complemented to an increasing extent by a speckling on the ventrals, which may begin already after the first third of the body length and increases in density posteriorly. The underside of the tail is dark with a few light spots.

Hemipenis. This description is based on examined specimens IEBR A.0760, IEBR A.0761 and ZFMK 59232.

The organ is single, not forked, short, and massive. It reaches SC 7-9. It is densely covered with numerous spines on the two distal thirds, smooth and folded on its base and the first third. Proximal spines are much larger and wider than distal spines, decreasing progressively to become short but very dense on the distal half. The sulcus lips are very prominent and well developed throughout, densely covered with short spines on their outer side.

Sexual dimorphism. It is clearly visible in the total size and number of ventrals and little visible in the number of subcaudals:

(1) Total length: Males seem to be much larger than females. The largest male known has a length of 850 mm, the largest female of 773 mm. In a pair from Tam Dao kept in captivity for several years, the male was much larger than the female.

(2) Difference in the number of ventrals: males: 193-203 (x = 198.1, s = 3.2); females: 198-208 (x = 201.5, s = 4.4).

(3) Slight difference in the number of subcaudals, males: 75-85 (x = 79.1, s = 3.6); females: 78-85 (x = 80.6, s = 2.9) in our sample.

(4) relative tail length, males: 0.203-0.229 (x = 0.214, s = 0.010); females: 0.205-0.217 (x = 0.2157, s = 0.008).

Distribution. People's Republic of China. This species is currently definitely known only from the following provinces: Fujian (Fuqing Xian County, Type locality) and Hong Kong SAR (KARSEN et al. 1998: 118; depicted a specimen with smooth scales). – Vietnam. We examined specimens from the provinces of Vinh Phù (Tam Dao; examined specimen), Bắc Kạn (Ngan-Son), Lào Cai, Hà Tĩnh and Quang Binh (Phong Nha-Ke Bang National Park). Many literature records cannot with certainty be assigned to *L. futsingensis* or *Lycodon ruhstrati abditus* n. subsp. Thus the exact distribution, especially in China, remains unclear (Fig. 21).

Biology. There are few data on the biology of this species in the wild. One animal was found in a forest in August at an elevation of ca 160 m a.s.l. It was crawling on a slope close to a forest creek in the leaf litter between mossy roots of a large tree. Remains of a skink were found in its stomach (ZIEGLER 2002). ZIEGLER et al. (2007) reported on a specimen, therein listed as *Lycodon* sp., found at night on 30 July at the end of the dry season. This female was discovered at an altitude of about 450 m above sea level crawling on pebbles near a steep primary forest stream cascade. At that same site within Phong Nha-Ke Bang National Park, the holotype of *Lycodon ruhstrati abditus* n. subsp. was collected, thus proving the syntopic coexistence of *L. ruhstrati* and *L. futsingensis*.

VOGEL & BRACHTEL (2008) observed in captivity four specimens from Tam Dao (Vinh Phù Province, Vietnam). During daytime, these snakes remained hidden under pieces of bark, often together. In winter, they were often found buried in the substrate. Feeding was strongly reduced during that time. The animals were often found climbing and sometimes resting above the ground. Main activity was recorded at temperatures between 25 and 28 °C. These specimens were not shy; some of them were biting while being handled, others not. If roughly handled (e.g. for taking scale counts), they released the contents of their anal glands. The smell was similar to that of the Eurasian natricid species *Natrix natrix*.

VOGEL & BRACHTEL (2008) described in detail the reproductive behaviour in captivity. In summary, mating was observed during the day and night in captivity. One copulation lasted from dawn to noon on the next day. A total of six clutches, each containing 4-7 eggs were laid. The size of the eggs varied from 25-36 mm in length and from 10-12 mm in width. The neonates had a length of about 15 cm and shed about 10 days after hatching.

Lycodon ophiophagus n. sp. (Figs 11-16)

Holotype. QSMI 0596 (adult female; tail dissected), from Lamru Waterfall, Khao Lak-Lamru National Park, Phang-Nga Province, southern Thailand. Collected by Montri Sumontha on 30 December 2002.

Paratype. IRSNB 2611 (Fig. 14), juvenile male (dissected; hemipenes in situ), from a forest stream near Klong Hat Som Paen (ca 9°57'N, 98°41'E), Muang District, Ranong Province, southern Thailand. Collected by Montri Sumontha on 16 February 2004.

Additional specimens. A third specimen (adult male; Fig. 16) was collected on November 10th, 2004, at night at the same locality as the paratype, but was still alive at Nakhon Ratchasima Zoo (Khorat) at the time of the present description. Its colour and pattern are similar to the types, with 20 white bands on the body and 13 on the tail. Lastly, a fourth adult specimen was observed in May 2000 by M. Sumontha in Phatoh District, Chumphon Province. This specimen was not collected, but it was photographed and clearly identified as *L. ophiophagus*.

Diagnosis. A species of the genus *Lycodon*, characterized by: (1) a loreal not touching the orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) upper and vertebral dorsal row smooth; (4) about 212 ventrals in males and about 211 in females; (5) about 90 Sc in males and about 87 in females; (6) relative tail length of about 0.201 in males and about 0.228 in females; (7) 20-21 white bands on a dark body; (8) the first band starting at VEN 25-28; (9) maxillary teeth: 6-7 teeth (posterior ones much enlarged) + a wide gap + 2-3 small teeth + a small gap + three enlarged teeth.

This species can be recognized by its ventral scale count (lower than in *L. ruhstrati ruhstrati*, *Lycodon ruhstrati abditus* n. subsp., *L. paucifasciatus*, *L. multifasciatus* but higher than in *L. futsingensis*), its subcaudal scale count (lower than in *L. ruhstrati ruhstrati*, *Lycodon ruhstrati abditus*

n. subsp., *L. multifasciatus*, but higher than in *L. futsingensis*), by the first band, which starts more posteriorly than in the other species, and by the posterior teeth which are larger than in the other species treated here.

Detailed comparisons with other species of *Lycodon* appear below in the Discussion.

Etymology. The specific name is derived from the classical Greek *Ophis*, a snake, and *Phagein*, to eat, by allusion to the known diet of this species (see below).

We suggest the following common names: *Ngoo plongchanuan kin ngoo* (Thai), Snake-eater Wolf Snake (English), *Lycodon ophiophage* (French), *Schlangenfressende Wolfszahnnatter* (German), *Slangenetende Wolfslang* (Dutch).

Description of the holotype. *Habitus*. Body elongate, head flattened, well distinct from the neck. Eye moderate, with a vertically elliptic pupil.

SVL 702 mm; TaL 207 mm; TL 909 mm; ratio TaL/TL: 0.228.

Dentition (Fig. 15). Maxilla strongly arched, with an angulous apex, distinctly bent inwards anteriorly. A total of 13 maxillary teeth, with the following formula: four small anterior teeth, the last one enlarged + three strongly enlarged teeth, thick and not much curved + a wide gap, lon-

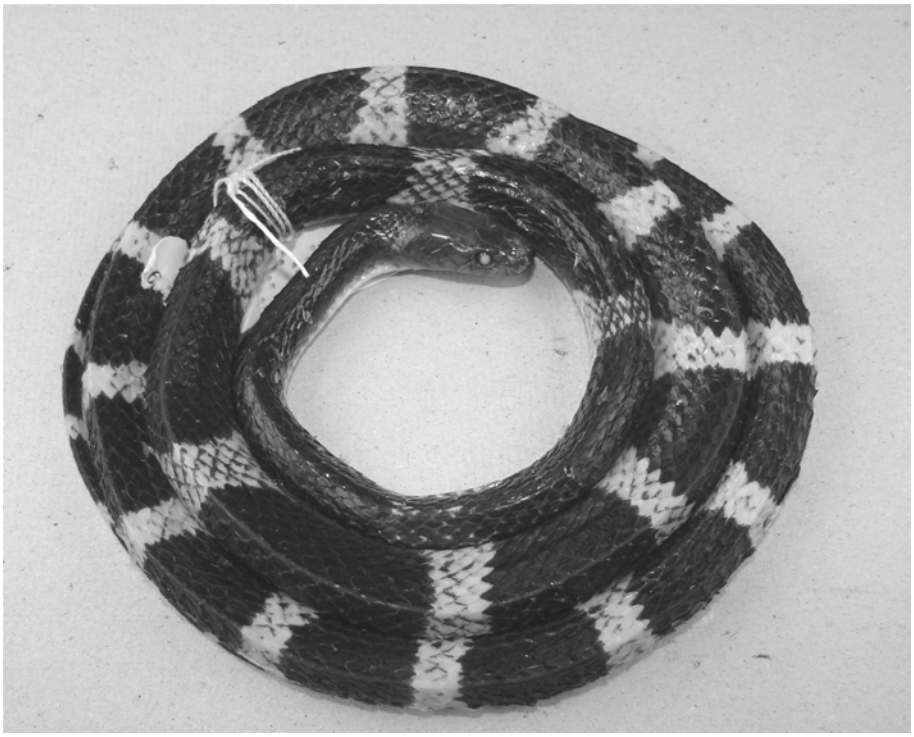


Fig. 11. — Holotype of *Lycodon ophiophagus* n. sp. (QSMI 0596): adult female from Lamru Waterfall, Khao Lak-Lamru National Park, Phang-Nga Province, southern Thailand, in general view. Photograph by Patrick David.

ger than the larger teeth + three small teeth + a small gap + three strongly enlarged, thick posterior teeth, also rather straight, the last one smaller than the two others.

Body scalation. 212 VEN (+ one preventral), 90 SC. Anal single.

Dorsal scales in 17-17-15 rows. Dorsal scales entirely smooth throughout body. Vertebral row not enlarged. No apical pit detected. Scale row formula (recount system):

$$17 \quad \frac{3{+}4 \rightarrow 3\ (143)}{3{+}4 \rightarrow 3\ (145)} \quad 15$$

Head scalation. A triangular, rather low rostral, well visible from above; nasal completely divided by the nostril; two trapezoidal internasals, widely in contact with each other and with prefrontals; two large prefrontals, much larger than internasals; one ogive-shaped frontal, about 1.15 times longer than wide and about 0.6 time as long as parietals; 1/1 preocular; 2/2 postoculars (the upper distinctly larger); 1/1 loreal, pentagonal, elongated and proportionally small, in contact with the 2nd and 3rd supralabials, preocular, prefrontal and the post-nasal; loreal not entering orbit; 8/8 supralabials, of which the 2nd widely borders the posterior edge of the postnasals, the 3rd to 5th reach the eye; 7th SL largest; 1/1 supraocular; 2+3 temporals on each side; 10/10 infralabials, the five anterior in contact with the first pair of sub-

Fig. 12. — Holotype of *Lycodon ophiophagus* n. sp. (QSMI 0596): adult female, from Lamru Waterfall, Khao Lak-Lamru National Park, Phang-Nga Province, southern Thailand, left side of head. Photograph by Patrick David.

linguals; anterior and posterior pair of sublinguals of about same length, but anterior pair wider.

Colouration in preservative. Above brownish-black, with 21 white crossbands on the back, 14 on the tail; these crossbands, about two dorsal scales long, widen at their ventrolateral limit (about 3-4 dorsal scales); on the anterior part of body, several scales of the crossbands are edged anteriorly with dark brown, producing irregular nets. The first crossband, beginning at the level of VEN 28, is nearly reduced to a few light blotches and is almost indistinct, whereas the second crossband begins at VEN 43; posterior crossbands become progressively more contrasted and closer to each other, separated by only 7-8, then 5-6 dorsal scales; crossbands of the tail are pure white. The head is nearly uniformly dark brown, slightly paler on the supralabials; no nuchal collar visible. The venter is pure whitish-cream on the anterior part of body, then marked with numerous dark brown blotches irregularly spread out over the background colour. Under surface of tail mostly dark brown.

Variation. The paratype (IRSNB 2611) agrees in most respects with the description of the holotype, except in the following points:

SVL 319 mm; TaL 80 mm; TL 399 mm; ratio TaL/TL: 0.201.

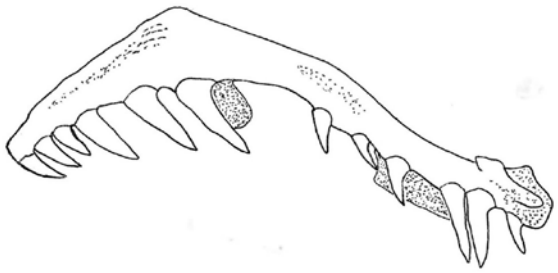
Preventral 1 + 211 slightly keeled VEN, 87 divided, slightly keeled, SC. One apical pit per dorsal scale (very difficult to detect). Scale row reduction from 17 to 15 occurs at the level of V 146 and 150 respectively. Loreal scale not as reduced as in holotype, but of same shape and bordered with same scales.

Fig. 13. — Holotype of *Lycodon ophiophagus* n. sp. (QSMI 0596): adult female, from Lamru Waterfall, Khao Lak-Lamru National Park, Phang-Nga Province, southern Thailand, dorsal view of head. Photograph by Patrick David.

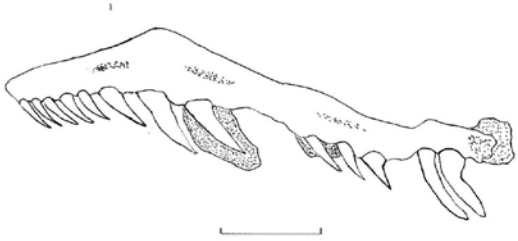
Fig. 14. — Paratype of *Lycodon ophiophagus* n. sp. (IRSNB 2611) in life from a forest stream near Klong Hat Som Paen, Ranong Province, southern Thailand: juvenile male. Photograph by Montri Sumontha.

The maxillary bone is identical to the holotype, but with a total of only 12 maxillary teeth. The tooth formula is 4 + 3 enlarged teeth + a wide gap + two small teeth + a small gap + three strongly enlarged posterior teeth.

The colouration is more complex than in the adult holotype. Above, the specimen is nearly black, with 20 strongly distinct, pure white crossbands on the back, the first one at the level of VEN 25, and 13 on the tail; these crossbands are also about 2-3 dorsal scales long and widen at their ventrolateral limit; crossbands of the tail are also pure white. The head is dark brown, variegated with whitish-brown on its anterior part, about up to a line connecting the posterior margin of eyes, followed by a strongly contrasted creamish-white posterior part, extending on the nape and neck up to about the 7th neck scale; this white colour produces a strongly visible nuchal collar. Anterior supralabials dark brown, the three next ones brown



Lycodon ophiophagus



Lycodon ruhstrati

Fig. 15. — Maxillae of *Lycodon ophiophagus* n. sp. (QSMI 0596, Holotype, from Khao Lak-Lamru National Park, Phang-Nga Province, southern Thailand), top, and *Lycodon futsingensis* (MNHN 2006.0438, from Tam Dao, Vinh Phu Province, Vietnam), bottom. Drawing by Patrick David.

in their upper half, dirty cream on their lower half, the last three supralabials being creamish-white with a few dark brown dots. The venter is entirely pure whitish-cream. Under surface of tail with dark brown transverse bands at the level of lateral crossbars, producing rings around the tail.

A third specimen (adult male; Fig. 16) was collected on November 10th, 2004, at night at the same locality as the paratype, but was still alive at Nakhon Ratchasima Zoo (Khorat) at the time of the present description. Its colour and pattern are similar to the types, with 20 white bands on the body and 13 on the tail. Lastly, a fourth adult specimen was observed in May 2000 by M. Sumontha in Phatoh District, Chumphon Province. This specimen was not collected, but it was photographed and clearly identified as *L. ophiophagus*.

Hemipenis. The sole available male specimen is a juvenile that does not allow us to provide a complete description. In situ, the organ is single, not forked, short and reaches SC 10. It seems to be densely covered with numerous spines throughout.

Distribution. Thailand. *Lycodon ophiophagus* is presently known from the provinces of Chumphon (Phatoh District), Ranong (Muang District), and Phang-Nga (Khao Lak-Lamru National Park), just south of the Isthmus of Kra (Fig. 21).

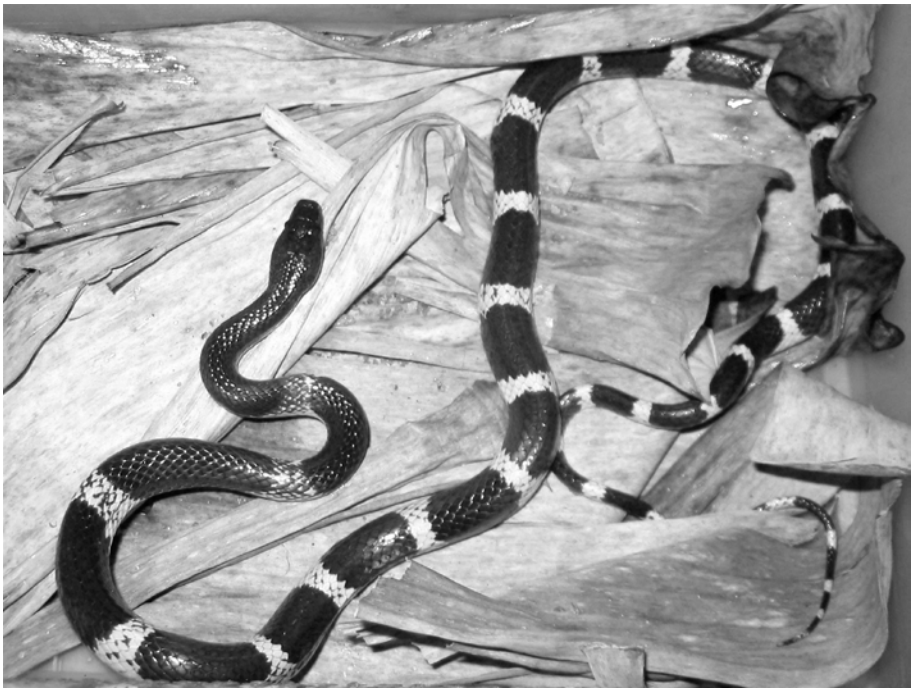


Fig. 16. — Adult male of *Lycodon ophiophagus* n. sp. in life, from the bank of a forest stream near Klong Hat Som Paen (ca 9°57'N, 98°41'E), Muang District, Ranong Province, southern Thailand. Photograph by Montri Sumontha.

Phatoh (also known as Pha To) is about 25 km southeast of Muang District of Ranong and 142 airline kilometres north of Khao Lak-Lamru NP. As a consequence, the known range of the species spans no more than ca 155 airline kilometers from north to south. The species should be searched for in primary or dense secondary forests, especially along streams, in Surat Thani and Krabi provinces, where it most probably also occurs, and in additional localities in Ranong and Phang-Nga. However, the lack of discovery of this new species during intensive field surveys in potentially suitable biotopes in Phang-Nga Province by PAUWELS et al. (2000a, 2000b, 2002) and GROSSMANN & TILLACK (2000, 2001a, 2001b) seems to indicate that the species is uncommon.

Biology. All available specimens were observed or collected while actively crawling at night in dense wet forest along streams. The holotype laid seven eggs, which proved to be unfertile. *L. ophiophagus* is prompt to bite if molested.

All three specimens were kept in captivity. Adults showed a strong dietary preference for colubrid snakes, consuming freshly killed or live *Chrysopelea ornata ornatissima* Werner 1925, *Coelognathus radiatus* (Boie 1827), *Dendrelaphis p. pictus* (Gmelin 1789), *Enhydris enhydris* (Schneider 1799), *Ptyas korros* (Schlegel 1837) and *Rhabdophis s. subminiatus* (Schlegel 1837). Captive specimens also accepted live cichlid fish (*Oreochromis niloticus niloticus* (Linnaeus 1758)), ranid frogs (*Fejervarya limnocharis* (Gravenhorst 1829), *Hoplobatrachus rugulosus* (Wiegmann 1835), *Ingerana tasanae* Smith, 1921 and *Limnonectes hascheanus* (Stoliczka 1870)) and skinks (*Eutropis macularia* (Blyth 1853), *Riopa bowringii* (Günther 1864) and *Sphenomorphus maculatus mitanensis* (Annandale 1905)). The juvenile *L. ophiophagus* fed readily on house geckos such as *Hemidactylus platyurus* (Schneider 1792) and *Hemidactylus frenatus* Duméril & Bibron 1836.

Comments. Morphologically this species is "nested" between *Lycodon futsingensis* and *Lycodon ruhstrati abditus* n. subsp. regarding the ventral and the subcaudal counts.

The localities where the species was found are of special herpetological importance. The herpetofauna of Khao Lak-Lamru National Park was investigated by GROSSMANN & TILLACK (2000, 2001a, 2001b) who demonstrated its high diversity, including several near-endemic species. The stream near Klong Hat Som Paen is the northernmost known locality for the rhacophorid frog *Nyctixalus pictus* (Peters 1871) (PAUWELS et al. 2004) and the colubrid *Ahaetulla fasciolata* (Fischer 1885) (PAUWELS & SUMONTHA 2007), and harbours several rare species such as *Tropidophorus robinsoni* Smith, 1919 (M. SUMONTHA & O.S.G. PAUWELS unpubl. observations).

The last snake additions made to the Thai herpetofauna were *Lycodon cardamomensis* by PAUWELS et al. (2005), *Opisthotropis maculosa* STUART & CHUAYNKERN (2007) and *Amphiesma leucomystax* David, Bain, Nguyen, Orlov, Vogel, Vu & Ziegler 2007, which were the 188th, 189th and 190th snake species recorded from Thailand respectively. *Lycodon ophiophagus* is thus the 191th snake species known from the country, which is now known to be inhabited by eight species of the genus *Lycodon*. More faunal surveys should be conducted in the forests of the western "backbone" of the country, this more or less continuous range connecting the southernmost offshoots of the

Himalaya of northwestern Thailand with the hills of Peninsular Thailand and West Malaysia. This region still largely covered with forests, has been shown to be of great biogeographical interest (PAUWELS et al. 2003).

Lycodon paucifasciatus (Rendahl 1943) (Figs 17-18)

Lycodon paucifasciatus Rendahl in SMITH 1943: 267. – Type locality. "Thua Lun, Annam, 50 km south of Hué", now Thua Luu, Thua Thien – Hué Province, Central Vietnam. – Holotype. NRM 3095, adult, sex not determined. Collected by B. Björkegren, July 1938-April 1939.

Material (2 specimens). – Vietnam. Quang Binh Province. ZFMK 80662 (GenBank: EU999213), ZFMK 86452 (GenBank: EU999121), Phong Nha-Ke Bang National Park.

Comments. In ZIEGLER et al. (2004: 34), ZFMK numbers of *Lycodon* cf. *paucifasciatus* and *Dinodon* cf. *rufozonatum* were interchanged. In addition, in that same publication, fig. 44 depicts *Lycodon paucifasciatus*, but it was interchanged in the pdf file of that paper with fig. 43.

Diagnosis. A species of the genus *Lycodon*, characterized by: (1) loreal not entering orbit; (2) 19 dorsal scale rows on the forepart of the body and 17 or 19 rows at midbody; (3) upper dorsal scale row or two upper rows plus vertebral row distinctly keeled; (4) 14-25 bands on body; (5) first band starting at Ven 10-15; (6) upper maxillary teeth: 6 + 3-4 + 2.

This species can mostly be recognized by the higher number of dorsal rows on the first third of the body, namely 19 vs 17 in other species treated here, and by the lower number of dorsal bands.

Etymology. This specific name is based on the Latin adjectives *paucus*, meaning "few" or "little", and "*fasciatus*", banded, due to the low number of dorsal bands of the holotype.

Description and variation (based on RENDAHL in SMITH [1943] and on two examined specimens).

Morphology. Body subcylindrical, slightly laterally compressed, rounded on dorsum, flattened on venter. Head elongate, distinct from neck, flattened; snout elongate, projecting anteriorly beyond lower jaw. Pupil vertically elliptic.

The maximal known total length is 763 mm (sex not given; Rendahl in SMITH [1943]). The male specimen examined by us (ZFMK 80662) is 673 mm long (SVL 536 mm, TaL 137 mm). The female specimen of our sample (ZFMK 86452) has a SVL of 640 mm (tail incomplete).

Ratio TaL/TL: 0.204 in the sole male specimen with a complete tail.

Dentition. Upper maxillary tooth formula: 6 anterior teeth, the last two much enlarged + a wide gap + 3-4 short teeth + a small gap, shorter than posterior teeth + two much enlarged teeth.

Body scalation. DSR: 19 – 17-19 – 15 rows, with, at midbody, either the upper dorsal scale row plus vertebral row or the two upper rows plus vertebral row distinctly keeled.

VEN: 219-222 (plus one preventral), distinctly angulate laterally; SC: 90-92, all paired; anal plate entire.

Head scalation. Rostral large, well visible from above; nasal divided with nostril piercing between the two parts of the scale; internasals rather small, about 3 times shorter than prefrontals, broader than long, not touching the loreal or preocular; prefrontals large and subrectangular; frontal rather small, hexagonal, longer than broad; parietals large, longer than broad; one small loreal, longer than wide, not entering orbit from which it is separated by the preocular and the top of 3rd SL eye; one preocular, large and high; two postoculars; eight supralabials in all known specimens, 3rd to 5th entering orbit, 6th the largest but 5th to 8th all much enlarged; 2 + 3 temporals in all specimens; one enlarged paraparietal shield; 10 infralabials, anteriormost in contact on the midline, first five in contact with anterior chin shields, 2-3 pairs of gular scales between the chin shields and the preventral.

Colouration and pattern. Above blackish-brown, dark brown or chocolate brown, with 14-25 very irregular beige or dirty cream crossbands on the body and 8-11 bands on the tail; all these light bands are speckled with the dark brown hues of the dorsal background, the speckling getting stronger on the posterior part of the body. The light crossbands are triangular and more or less wider at their base (3-5 DSR wide) than on the vertebral area (two DSR wide), and often enlarged also in their middle; some are more or less dissected or forming a Y, splitting into two parts on the opposite side. First light band starts at VEN 10-15 and is 9-11 ventrals wide at its base

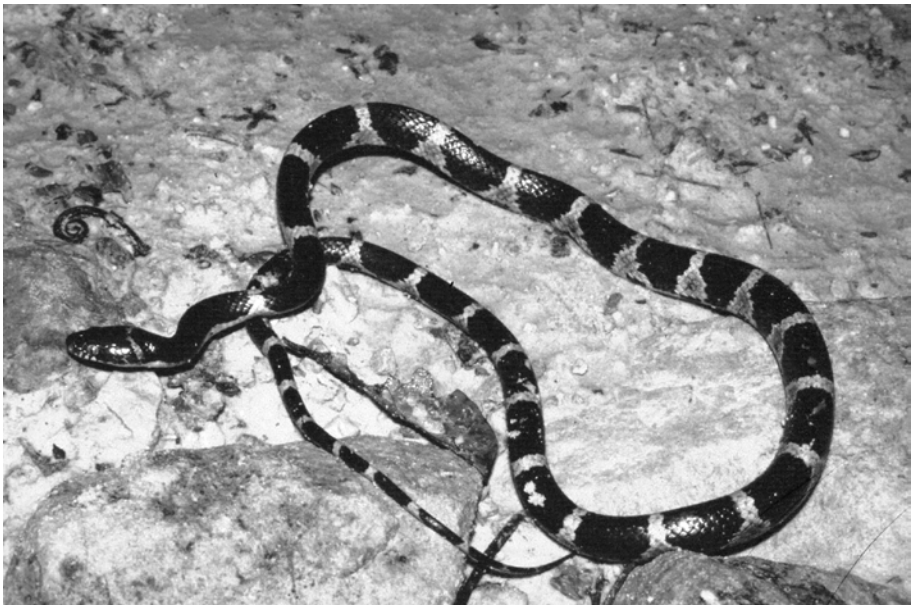


Fig. 17. — *Lycodon paucifasciatus* (ZFMK 80662) from Phong Nha, Vietnam in life. Photograph by Thomas Ziegler.

and vertebrally 2-2.5 dorsal scales wide; an irregular, elongated dark brown or dark brownish-grey blotch on the bottom of each crossband on the 1st DSR and the outer part of the corresponding ventrals; in specimen ZFMK 86452, some blotches extend on the whole length of the bottom of the crossband, forming a broken dark brown ventrolateral stripe. Crossbands of the tail are similar to that of the dorsum but the ventrolateral blotch is lacking in ZFMK 86452 (this specimen has a less contrasted and well-defined pattern than in ZFMK 80662).

Head as dorsal background, uniform except for a cream, inverted V-like nuchal marking, its apex in contact with the parietals; this marking is nearly absent in ZFMK 86452. Sides of the snout more or less irregularly mottled with cream. Supralabials cream, more or less strongly edged with dark brown anteriorly; infralabials more or less heavily speckled with dark greyish-brown; throat and chin uniformly light cream.

Venter cream or light beige-brown, uniform on the anterior quarter or third of the body, then getting progressively more intensely speckled with dark brown posteriorly; posterior part of the venter entirely obscured with dark brown; tail either entirely dark brown below or with irregular blotches corresponding to light crossbands; however, these bands do not form true rings.

Hemipenis. This description is based on examined specimen ZFMK 80662.

Fig. 18. — *Lycodon paucifasciatus* (ZFMK 86452) from Phong Nha, Vietnam in life. Photograph by Ralf Hendrix.

The organ is single, not forked, short, and massive. It reaches SC 7-9. It is densely covered with numerous spines on the distal 2/3, smooth and folded on its base and the first third. Proximal spines are much larger and wider than distal spines, decreasing progressively to become short but very dense on the distal half. The sulcus lips are very prominent and well developed throughout, densely covered with short spines on their outer side.

Sexual dimorphism. It is unknown. There is no difference in the number of ventrals in the male and the female of our sample; the tail of the latter specimen is incomplete.

Distribution. Vietnam. This species is currently known only from central Vietnam. It has been recorded from the following provinces: Thua Thien-Hué (Thua Luu; holotype) and Quang Binh (Phong Nha-Ke Bang National Park; examined specimens and ORLOV et al. 2003).

Biology. Specimen ZFMK 80662 was collected at night on the ground in a forest clearing (ZIEGLER et al. 2004). ZFMK 86452 was found in the area of Cha Noi in the northern part of the Phong Nha-Ke Bang National Park. At about 10 PM, it was crawling through the roots of a fallen tree, lying at the edge of a small creek. The temperature was 24 °C and the relative humidity was 85%. Nothing else is known about the biology of this rare or at least rarely collected species.

Lycodon multifasciatus (Maki 1931) (Figs 19-20)

Dinodon septentrionale multifasciatum MAKI 1931: 127, figs 83A-E (plate XLVII in MAKI 1933). – Type locality. "Ishigaki-Oshima, Loo Choo Islands", now Ishigaki-jima, Yaeyama Islands, Ryukyu Archipelago, Japan. – Holotype. Specimen Nr. a (adult female), College of Science, Kyoto Imperial University. Collected by S. Nishiishigaki, April 1929.

Lycodon ruhstrati multifasciatus: MORI 1984; TOYAMA 1985; TODA 1987; OTA 1988; LANZA 1999; UCHIYAMA et al. 2002; GORIS & MAEDA 2004; HOSO 2007.

Lycodon multifasciatus: VOGEL & BRACHTEL (2008).

Taxonomic comment. This taxon was recently elevated to species status (VOGEL & BRACHTEL 2008). It is not discussed in detail here. The main characteristics can be seen in Table 5. It is possible that there are two species combined under this name, as can be seen on Figs 19-20.

Etymology. This specific name is based on the Latin adjectives *multus*, meaning "many" or "numerous", and *"fasciatus"*, banded, due to the high number of dorsal bands in this taxon.

Diagnosis. A species of the genus *Lycodon*, characterized by: (1) a loreal not touching the orbit; (2) 17 dorsal scale rows at the forepart of the body and at midbody; (3) upper dorsal and vertebral rows keeled; (4) 232-237 ventrals in males and 229-235 in females; (5) 115-119 Sc in males and 106-117 in females; (6) relative tail length about 0.25 (MORI 1984) in males and about 0.244 (type) in females; (7) 54-80 dark bands on a light body; (8) the first band starting at about Ve 7.

This species can be recognized by its pattern, which rather looks like dark rings on a light background rather than the dark background with light

Fig. 19. — *Lycodon multifasciatus* from Miyakojima, southern Ryukyus, Japan in life. Photograph by Hidetoshi Ota.

Fig. 20. — *Lycodon multifasciatus* from Iriomotejima, southern Ryukyus, Japan in life. Photograph by Takehiko Sato.

rings in other species. It also differs by the number of rings on body (54-80 vs less than 46 in all other species). It has keeled dorsal rows and a higher number of ventral scales than all other species of this complex (229-237, all other species have 228 scales or less). Maxillary teeth are unknown.

Detailed comparisons with other species of *Lycodon* appear below in the Discussion.

Distribution. Japan. Ryukyu Islands (Fig. 21): Yaeyama group (Iriomotejima and Ishigakijima) and Miyako group (Miyakojima), according to TOYAMA (1985) and TODA (1987).

Fig. 21. — Map showing the distribution of *Lycodon r. ruhstrati* (yellow), *Lycodon ruhstrati abditus* subspec. nov. (black dots), *Lycodon futsingensis* (red dots), *Lycodon ophiophagus* n. sp. (blue dots), and *Lycodon multifasciatus* (black arrows). The known distribution of *L. paucifasciatus* in Vietnam corresponds to the southernmost black dot and the second red dot from below.

Key to the *Lycodon ruhstrati* group including *L. fasciatus* sensu lato

1	Loreal entering orbit ..... *L. fasciatus*-group	
—	Loreal not entering orbit	**2**
2	12-13 bands on body, 6 bands on tail ..... *L. cardamomensis*	
—	More than 13 bands on body, more than 9 bands on tail.....	**3**
3	19 dorsal scale rows on the forepart of the body, 14-25 dorsal bands on body..... *L. paucifasciatus*	
—	17 dorsal rows on the forepart of the body, more than 18 dorsal bands on body.....	**4**
4	At least 2 upper dorsal scale rows keeled	**5**
—	All dorsal scale rows smooth	**7**
5	229 or more ventrals, more than 53 bands on body..... *L. multifasciatus*	
—	Less than 229 ventrals, less than 47 bands on body.....	**6**
6	Ratio TaL/TL in males 0.220-0.248; subcaudals 105-114 in males; first light band starting at Ven 8-16; endemic to Taiwan ..... *L. ruhstrati ruhstrati*	

— Ratio TaL/TL in males 0.208-0.237; subcaudals 90-100 in males; first light band starting at Ven 12-17; present on Asian mainland .... *Lycodon ruhstrati abditus* n. subsp.

7 More than 86 Sc, more than 210 Ve, first band starting at Ve 25-28 ....*Lycodon ophiophagus* n. sp.

— Less than 88 Sc, less than 210 Ve, first band starting at Ve 13-21 ....*L. futsingensis*

Table 5.

Main morphological and colouration characters in species of the *Lycodon ruhstrati* group.

Characters	*Lycodon*					
	ruhstrati ruhstrati	*ruhstrati abditus* n. ssp.	*futsingensis*	*ophiophagus* n. ssp.	*paucifasciatus*	*multifasciatus*[1,2]
TL max (mm)	1055 N=17	964 N=19	850 N=22	909 N=2	<800 N=2	700
TaL / TL ♂	0.220-0.248 N=6	0.208-0.237 N=11	0.194-0.229 N=15	0.201 N=1	0.204 N=1	0.250
TaL / TL ♀	0.211-0.239 N=11	0.207-0.236 N=8	0.194-0.216 N=5	0.228 N=1	---	0.244
ASR	17	17	17	17	19	17
MSR	17	17	17 (16)	17	19/17	17
keeled	+	+	–	–	+	+
VEN ♂	212-228 N=6	214-224[3] N=10	193-204 N=15	212 N=1	221 N=1	232-237 N=3
VEN ♀	217-224 N=11	220-229[2] N=8	198-208 N=5	211 N=1	222 N=1	229-235 N=6
SC ♂	105-114 N=6	90-100 N=11	72-87 N=15	90 N=1	92 N=1	115-119 N=3
SC ♀	97-108 N=9	92-103 N=8	78-85 N=5	87 N=1	---	106-117 N=6
Lo touching eye	0	0	0	0	0	0
Bands body	33-46 N=17	19-43 N=15	19-33 N=20	20-21 N=2	14-25 N=3	54-80 N=10
Bands tail	14-22 N=17	10-23 N=15	9-18 N=19	13-14 N=2	8-11 N=3	26-42 N=10
First band starting at Ve	8-16 n=17	12-17 n=4	13-21 n=19	25-28 n=2	10-15 n=2	About 7[4]
Belly banded (adults)	–	–	–	–	–	–
Upper Maxillary teeth	Unknown	6–7 + 3–4 + 2	7–8 + 3–4 + 2–3	6–7 + 2–3 + 3	6 + 3–4 + 2	Unknown

Abbreviations: see Table 1. Conditions or values of rare occurrence are placed within brackets. Notes. 1: from Ota (1988); 2: from Mori (1984); 3: literature values were not taken according to the Dowling (1951) system, the difference is normally 1-2 plates, rarely 0 or 3.4 no literature records, taken from pictures.

DISCUSSION

The subsequently listed *Lycodon* species are known from China, Laos and Vietnam: *Lycodon subcinctus* Boie 1827, *Lycodon laoensis* Günther 1864, *Lycodon fasciatus* (Anderson 1879), and *Lycodon capucinus* Boie 1827. *Lycodon subcinctus* differs from the species discussed here by the absence of a preocular scale. In *Lycodon fasciatus* the loreal is touching the orbit, while in *Lycodon capucinus* and *L. laoensis*, the anal shield is divided, and *Lycodon subcinctus, L. laoensis* and *L. capucinus* differ completely in the colouration. An updated key to the species of that genus in Thailand and West-Malaysia can be found in PAUWELS et al. (2005).

The biogeography of the Ryukyu Islands, the area of distribution of *L. multifasciatus*, has been discussed, for example, by GRISMER et al. (1994) and HIKIDA et al. (1989). Most of the terrestrial reptiles living in this locality have their closest relatives either in Taiwan or in the Chinese province of Fujian. The reason for this is that two land bridges used to exist at different times, the second of which formed during the early Pleistocene. This was probably when the ancestor of *L. ruhstrati* and *L. multifasciatus* dispersed and reached these islands. *Lycodon multifasciatus* should therefore be placed in "Group D" sensu TOYAMA (HIKIDA et al. 1989). This group includes endemic species that immigrated some 1.5 million years ago, with a distributional centre on the Miyako and Yaeyama Island Groups.

The fauna of Taiwan is much more closely related to that of the Chinese mainland than to that of the Ryukyu Islands (OTA 1991). *L. ruhstrati ruhstrati* from Taiwan belongs to "Group C" sensu OTA (1991), as the closest relative is native to the opposite mainland.

Due to the fact that no phylogenetic studiesfor the genus *Lycodon*, have been conducted, a zoogeographical hypothesis for most other taxa is not possible at present.

Surprisingly *L. ruhstrati* is genetically much closer to specimens of *L. fasciatus* from Vietnam than to *L. futsingensis*. As *L. fasciatus*, as currently defined, is also a composite of species (G. VOGEL & P. DAVID in prep.) there is little possibility at this stage for a meaningful discussion on the relationships between the *L. ruhstrati* and *Lycodon fasciatus* groups.

The nearest relative of *L. futsingensis* seems to be *L. paucifasciatus*. As there was no DNA of *L. ophiophagus* available for study, the position of this species cannot be resolved. There is a large distribution gap between this species and the other taxa of this complex. The nearest relative of *L. ophiophagus* might also be *L. butleri*. Several species are known from a few specimens only, so the whole variation is unknown, which makes a discussion of the relationship between them highly speculative.

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APPENDIX 1
Additional comparative material.

Lycodon fasciatus:

India. Shillong, Assam, BMNH 92.1.25.1; BMNH 1908.6.23.6; BMNH 1908.6.23.8; BMNH 1907.12.16.28-29; BMNH 94.10.4.2; Shillong, Assam, BNHS 1220; Gyabari, Darjeeling, BNHS 1230.

Laos. Xieng-Khouang, Laos, MNHN 1928.69.

Myanmar. Maymyo, Burma, BMNH 1925.12.22.15-16; Mogok, Burma, BMNH 1900.9.20.5-7; "Burma", BMNH 1908.6.23.9-11; Toungyi, Shan State, Myanmar, BMNH 91.11.26.31; Bhamo, Burma, BMNH 1925.4.2.28; Kachin Hills, Burma, BMNH 1925.9.17.10-11; South Shan State, BMNH 1908.6.23.14; Burma-Siam Border, BMNH 1937.2.1.12; Rangoon, Burma, BMNH 1940.3.3.3; Maymyo, Burma, BNHS 1223-24; Thandung Hills, BNHS 1228.

People's Republic of China. Western China CAS 55147; Yunnan, China, MNHN 1919.148; "Yunnan Fu" (holotype of *Dinodon yunnanensis*), NMW 23417; Kuantun China, ZSM 75/1938 ; Kunming, Yunnan, BMNH 1930.11.16.4.

Thailand. Nakhon Ratchasima, Thailand, FMNH 180140, FMNH 180144-46, Chiang Mai, Thailand, FMNH 178369.

Vietnam. Phong Nha, Vietnam, ZFMK 86448-50 (GenBank: EU999214-215); ZFMK 80665; Ziegler unreg.

Dinodon septentrionale:

Laos. "Xieng-Khouang, Haut Laos", Xiengkhuang Province, Laos, MNHN 1928.0067-68

APPENDIX 2
Localities for *Lycodon ruhstrati ruhstrati* in Taiwan.

County/City	District	Township	Locality	Source
Keelung City				2, 10
Taipei County		Shihding		5
		Pingsi		5

(*continued*)

Appendix 2 (*continued*)

County/City	District	Township	Locality	Source
		Pinglin		4, 10
		Pinglin	Wuguliao	12
		Pinglin	Jioucyonggen	12
		Pinglin	Bihu	12
		Sindian	Sindian	?
		Sindian	Yinhedong	2, 4
		Wulai	Wulai (Urai)	2, 4
		Wulai	Tonghou	?
		Wulai	Fushan	5
		Sansia		5, 10
Taipei City	Wunshan		Jhihnan Temple	2
	Beitou		Yangmingshan	2
	Beitou		Datunshan	2
Taoyuan County		Fusing	Baling	?
		Fusing	Ronghua	?
		Gueishan		2
Hsinchu County (Shinchiku)				4
		Wufong	Tuchang	13
		Wufong	Guanwu	13
Miaoli County		Jhuolan		?
		Taian	Syuejian	13
		Zaociao		?
		Nanjhuang	Nanjhuang	5
Taichung County	Fongyuan City			2
		Dongshih		3
		Heping		3
Changhua County				14
Nantou Couty		Shueili		1
		Shueili	Minhe	2
		Sinyi	Heshe	2

(*continued*)

Appendix 2 (*continued*)

County/City	District	Township	Locality	Source
		Renai	Lushan	2
		Renai	Aowanda	5
		Caotun		1
		Jhongliao		1
		Mingjian		1
		Yuchih		1
		Lugu	Sitou	2
		Puli		1
		Jiji		7
		Gousing		1
Yunlin County	Douliou City		Hushan	5
Chiayi County		Dapu	Chiayi farm	1
		Alishan	Alishan	1, 4
		Alishan	Tanayiku	11
		Meishan		5
		Shueishang	Santzepu	8
		Dalin	Nanhua University	9
Chiayi City	Chiayi City		Lan Reservoir	9
			Renyi Reservoir	9
Tainan County				6
Kaohsiung County		Maolin	Shanping	2
		Sanmin	Nanzihsian River	15
		Liouguei		2
	Fongshan City	Cishan		2
Pingtung County		Majia	Liangshan	5
		Taiwu		2
			N. Mt. Dawu (Peitawu shan)	2
		Hengchun	Kenting	2
		Manjhou	Nanrenshan	2
Yilan County		Yuanshan	Dajioushi	16

(*continued*)

Appendix 2 (*continued*)

County/City	District	Township	Locality	Source
			Shuanglianpi	5
		Datong	Cilan	5
			Minchih	5
			Taipingshan	5
		Suao	Wushihbi	5
		Nanao	Mt. Nanao	5
		Sansing		5
Hualien County		Shoufong		2

1 – Lin (1996); 2 – Lue et al. (1989); 3 – Hong (1999); 4 – Maki (1931); 5 – Mao (unpubl. data); 6 – Chu (2000); 7 – Chu (unpubl. data); 8 – Norval et al. (2007b); 9 – Norval (unpubl. data); 10 – Chen (2006); 11 – Chu et al. (1998); 12 – Chang et al. (2003); 13 – Shang (2007); 14 – Lin (1997); 15 – Mou et al. (1998); 16 – Mao et al. (2008); and ? – unconfirmed reports from personal communications.