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Contribution to the knowledge of *Lycodon ruhstrati* (Fischer, 1886) in Vietnam – taxonomy and biology of a little-known species

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Abstract. Hitherto *Lycodon ruhstrati* has been known from China, Vietnam and Laos. The subspecies from the Japanese Ryukyu islands is here elevated to species status, *Lycodon multifasciatus*. In spite of distinct differences between populations from Taiwan and Vietnam versus those from China *L. ruhstrati* is – at present – regarded as monotypic. The colouration of Vietnamese juveniles is described for the first time. Differences among superficially similar species are worked out. *Lycodon cardamomensis* is a valid species closely related to *L. ruhstrati*. *Lycodon ruhstrati* was bred in captivity, but the juveniles failed to survive. The biology of this species is discussed in terms of literature data and our own observations.

Key words. Reptilia, *Lycodon ruhstrati*, biology, taxonomy, distribution, breeding, *Lycodon multifasciatus,* taxonomic status.

Introduction

Comprising 29 recognised species, the genus *Lycodon* Fitzinger, 1827, ranks amongst the most diverse snake genera of tropical Asia (EMBL Database, authors' unpubl. data). During the past twelve years alone, eight species have been newly described (Ota & Ross 1994, Gaulke 2002). Extensive systematic studies have yet to be carried out, and identification of the individual species proves rather difficult in some instances. Juveniles of many species share an identical colour pattern often consisting of a light ground colouration with dark rings (or vice versa). An identification key to the species can be found in Lanza (1999), but does not always produce accurate results (also see below). Genus *Dinodon* Duméril, 1853, is closely related to *Lycodon* and can be clearly distinguished only on the basis of the shape of the maxillary (Smith 1943, David & Vogel, own data).

In an attempt to curb the persistent misidentification of *Lycodon ruhstrati* and similar species we will outline their differences here.

Paradoxically, only a few contributions to the biology of the genus *Lycodon* exist (Wall 1911, Ziegler 2002). As far as we know, nothing at all has been published on the husbandry and breeding of these species other than brief statements in terrarium books (Obst et al. 1984, Mehrtens 1987, Trutnau 2002). Reasons may include the difficulty of identifying reliably the individual species, and difficulty keeping species alive in captivity. Therefore here we report for the first time on the successful captive husbandry and repeated oviposition of one species. We will furthermore provide a contribution to the systematics and variation of *L. ruhstrati* in Vietnam.

The species dealt with here has an eventful taxonomic history. It was first described as *Ophites ruhstrati* by Fischer in 1886, with the type locality of "South Formosa" (today southern Taiwan). Boulenger (1893) then synonymised this taxon with *Dinodon septentrionalis* (Günther, 1875), but distinguished it later as *Dinodon septentrionalis* var. *ruhstrati* in 1899. Stejneger (1907) then formalised it as *Dinodon septentrionalis ruhstrati*. In 1928, Pope described *Dinodon futsingensis* from Fukien, China and accepted *Dinodon ruhstrati* next to it as a valid species in 1929 but without providing differential data. Fol-

lowing a comparison with *Lycodon fasciatus* (Anderson, 1879), the same author was the first to use the combination *Lycodon ruhstrati ruhstrati*, with which he synonymised his taxon *D. futsingensis* (Pope 1935).

In 1931, Maki introduced *Dinodon septentrionale multifasciatum* on the basis of a single specimen from the island of Ishigakijima in the Ryukyu Archipelago, Japan. Toriba (1982) transferred this taxon to genus *Lycodon* and proposed the name *L. ruhstrati multifasciatus* for the Japanese population. This notion was subsequently followed by Ota (1988) after a more detailed comparison of Taiwanese specimens with those from the Ryukyus. It was unfortunate that this author had no specimens from the mainland available. His taxonomy was followed by later authors, such as Lanza (1999) and Ziegler (2002). According to Ota (1988) and Ziegler (2002), intraspecific variability had not yet been investigated sufficiently, the purpose of our present paper.

Daltry & Wüster (2002) recently described *Lycodon cardamomensis* from Cambodia, and *L. cardamomensis* has already been recorded from Thailand (Pauwels et al. 2005). The relationships between this species and *L. ruhstrati* will also be discussed here.

Lycodon ruhstrati was first recorded from Vietnam by Bourret in 1934 under the name of *Dinodon futsingensis*. Further specimens of this species surfaced in a series of papers by Bourret who alternately used the spellings *D. futsingensis* and *D. futsingense* (Bourret 1935a; 1935b; 1937; 1939a; 1939b; 1939c; 1939d). In his extensive treatise of the snakes of Indochina (1936), he referred to this species as *D. futsingense* and mentioned *D. septentrionale ruhstrati* only for Taiwan.

Both Nguyên & Hô (1996) and Szyndlar & Nguyên (1996) provided further locality records from museum specimens, and *L. ruhstrati* was recently recorded from Vietnam by Ziegler (2002). A number of authors included this species in various faunal lists, one example being Orlov et al. (2000). On the other hand, Vietnamese records have sometimes been overlooked as a result of the Babylonian confusion of names, for example by Zhao & Adler (1993) and Daltry & Wüster (2002).

Material and methods

A total of 13 preserved specimens of *L. ruhstrati* from Vietnam were available to us, in addition to a living pair under our care. A list of these specimens and those used for comparisons is given in Appendix 1. The description of colour traits is based on photographs published in recent literature (e.g., Karsen et al. 1998, Lue et al. 1999, Uchiyama et al. 2002, Ziegler 2002, Zhao 2003, Goris & Maeda 2004, Tu 2004).

Ventral counts begin with the first enlarged shield behind the gular scales. In order to provide data compatible with the existing literature, we did not employ the method suggested by Dowling (1951).

The following terminology and abbreviations have been used:

Sex (sexual identity); length, tL (total length); TL (tail length); R (ratio tail length / total length); Ve (ventrals); Sc (subcaudals, exclusive of the terminal scute); Do (dorsals); Supral. (supralabials); bands on body, resp. tail (number of bands on the body and the tail, respectively); statistics: *n* (number of specimens examined); *x* (mean value); BNHS: Bombay Natural History Society, India; IEBRH: National Centre of Scientific Research of Vietnam in Hanoi, Vietnam; MNHN: Muséum National d'Histoire Naturelle, Paris, France; PSGV: Private Collection Gernot Vogel, Heidelberg, Germany; RBINS: Royal Belgian Institute for Natural Sciences, Brussels, Belgium; SMF: Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; VPHCM: Pasteur Museum in Ho Chi Minh City, Vietnam; VST: Vien Sinh thai (Ecological Museum) (Ho Chi Minh City), Vietnam; ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZMB: Zoolo-

gisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; ZSM: Zoologische Staatssammlung, Munich, Germany.

Results and discussion

Distribution

Lycodon ruhstrati is known from Laos (Tranninh Plateau) and Vietnam (Deuve 1970, Bourret 1936), and occurs in southern China inclusive of Hong Kong and Taiwan, with records existing from the following provinces: Anhui, Fujian, Gansu, Guangdong, Guanxi, Guizhou, Jiangxi, Shaanxi, Sichuan, and Zhejiang (Zhao & Adler 1993).

Lycodon ruhstrati multifasciatus has been described from the Ryukyu Islands of Japan (Maki 1931) and subsequently recorded from the following islands: Iriomotejima, Ishigakijima (both in the Yaeyama Group), and Miyakojima (in the Miyako Group) (Toyama 1985, Toda 1987). The taxonomic identities of the individual populations will be discussed below.

Within Vietnam, all locality records are situated in the north. The following localities are known: Tam Dao (Vinh Phuc Province), Sa Pa (Lao Cai Province), Ngan Son (district of Bac Kan Province, east of Lake Ba Be, ca. 165 km northwest of Hanoi), Chin Xai (Ha Tinh Province, one of the three watersheds in the Ke Go Nature Reserve) (Bourret 1934, 1935a, 1939a, Ziegler 2002). Nguyên & Hô (1996) furthermore mentioned the following localities: Nui Yen Tu (Der Yen Tu, a mountain situated 14 km from Uong Bi in Quang Ninh Province) and Ngoc Lau (a settlement near Hoa Binh, Ha Son Binh Province) from specimens in the collections VST and VPH-MC. Szyndlar & Nguyen (1996) added Binh Khe (Quang Ninh Province) and Ngoc Lau (Ha Son Binh Province). Nguyen et al. (2005) gave only the following three localities: Cao Bang (Nguyen Binh Province), Tam Dao (Vinh Phuc Province), and Da Nang (Ba Na Province). The locality Tranninh mentioned by Bourret (1936) and not located by Ziegler (2000) lies in Laos, and not in Vietnam.

Deuve (1970: 129, as *D. futsingense*) and Ziegler (2002) included Myanmar in the distribution range of *L. ruhstrati,* but both failed to provide a source for this inclusion. Smith (1943) did not mention this species. Following the checklist by Dowling & Jenner (1988), *L. ruhstrati* is not known from Burma, (Myanmar), and is not included in the list of species expected to occur there. The latest checklist of the California Academy of Sciences on the Internet (http://www.calacademy.org/research/herpetology/myanmar/checklist_snakes.html as of 2006) confirms this absence, as foretold by Slowinski et al. (2001). It is likely that the inclusion of Myanmar by Deuve (l. c.) was based on a confusion of the literature data for *D. septentrionalis*, which Ziegler (l. c.) then republished. However, an occurrence of this species in Myanmar is entirely possible, and specimens of *L. ruhstrati* may in fact exist in scientific collections, concealed under names such as *L. fasciatus*, *D. futsingense,* or *D. septentrionalis*.

Lycodon ruhstrati has as yet not been recorded from Thailand. *Lycodon cardamomensis* has been found in the northeast of this country, and a closely related and very similar species lives in the south of Thailand (Pauwels et al. 2005).

Description

A number of authors have provided information on the appearance and pholidosis of *L. ruhstrati*. A large part of the relevant literature has been published in the Chinese language and is difficult to access, however. Table 1 summarizes data for populations from the Chinese mainland, while data for Vietnam in Table 2 originate from the various works by Bourret (see Introduction), Ziegler (2002), and the specimens examined by ourselves.

Fig. 1. *Lycodon multifasciatus*, Miyakojima, Ryukyu Islands. Photo: Hidetoshi Ota.

The species of this species complex share the following pholidotic traits:

In all taxa dealt with here, the number of dorsals around mid-body is 17. This is a number typical of the genus *Lycodon*. The vertebral row is not enlarged, and the anal scute is entire.

There are altogether 8 supralabials of which the 3rd through 5th usually touch the orbit. The 4th through 6th supralabial shields, or even the 3rd through 6th, may be in contact with the eye in exceptional specimens. One of the specimens examined (MNHN 2006.0438, formerly PSGV 651/1) has 7 supralabials of which the 3rd and 4th touch the orbit. It is apparent that the original 3rd and 4th shields are fused to form the 3rd shield in this specimen. This anomaly is present bilaterally.

There are only one preocular and one loreal. The loreal is exceptionally in contact with the eye. The preocular does not touch the frontal (this character state was not mentioned in the original description of *L. cardamomensis*, and the holotype had not yet been forwarded to London at the time of this manuscript). With the exception of the holotype of *L. cardamomensis*, all populations have 2 postoculars and 2 anterior temporals (rarely one). For more detailed descriptions, including dentition and genital morphology, see Pope (1935) and Zhang et al. (1984).

Information on the keeled state of the dorsals in this species varies. All 13 specimens from Vietnam examined had unkeeled dorsals. Ziegler (l. c.) and Bourret (1936) also described the dorsal scutellation as smooth. The single specimen examined from the Chinese mainland, (ZFMK 23363, Fujian), had unkeeled dorsals, as did the specimen available to Pope (1928, 1929, type of *D. futsingensis* from Fujian). Pope (1929, 3 specs. from Chungan Hsien, Fujian) and Mell (1922, one spec. from Guangdong) described a keeled character state for specimens from the Chinese mainland.

In the two syntypes of *Ophites ruhstrati*, the scales comprising the central rows were keeled (Fischer 1885). Both specimens were preserved in the Großherzogliches Museum zu Oldenburg, whose entire collection is apparently now lost (Hallermann pers. comm.). Maki (1931) studied 12 specimens from Taiwan, which had keeled scales. These findings suggest that specimens from Taiwan have keeled dorsals, those from Vietnam have unkeeled ones, and those from the Chinese mainland apparently show both character states.

Major differences exist in the ventral and subcaudal counts as well as with regard to the colour pattern, in particular where colours and numbers of bands are concerned. These data are summarised in Table 3. Colour and pattern are highly variable and moreover age-dependent. The tables show a remarkable range in this respect, which is emphasised by what Pope (1935) had to say about it: "It would be very difficult to give an accurate colour description of this species because the variation in pattern, especially posteriorly, is astounding." Colour and pattern of Vietnamese specimens are therefore best portrayed by means of illustrations (Figs. 3-6). A detailed description of the colour pattern can also be found in Ziegler (2002).

As is common throughout this genus, the colour pattern of young specimens dif-

fers from that of adult individuals. The juvenile colouration of *L. ruhstrati* from Vietnam has not yet been described completely and is therefore outlined in detail here.

Whereas adult specimens exhibit at most the remnants of a light nuchal band, 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 correspond 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. According to Karsen et al. (1998), each ventral is marked with a dark spot in juveniles, which is something we cannot confirm for Vietnamese juveniles. Following Pope (1935), young specimens from Taiwan exhibit a stronger tendency to continue the dark dorsal bands across the ventral surface than those from China. Such a trend is not at all recognizable in newly hatched animals from Vietnam. It would appear that this character state varies substantially between populations.

Fig. 2. *Lycodon ruhstrati*, Taiwan. Photo: Ming-Chung Tu.

The largest specimen on record is a female with a total length of 94 cm from Guizhou Province (Wu et al. 1985). In our view, this value is likely to be a measuring or typographic error, especially as this specimen at the same time has the lowest ratio between tail and body length of all known female specimens from China. The second largest female measures 81.7 cm tL (Pope 1935). The largest male has a length of 86.3 cm. This corresponds to the relative ratios found in the specimens analysed by ourselves. The males of this species are not only longer than the females, but they also exhibit a much sturdier build. Very little information exists with regard to sexual size dimorphism within the genus *Lycodon*. In the most widely distributed species, *L. capucinus*, the females grow larger than the males (How et al. 1996). This also applies to *L. subcinctus* (Kopstein 1941), but the situation may also be reversed in some species in the Philippines (Leviton 1965).

Differentiation from similar species

Distinguishing between the *L. ruhstrati* complex and morphologically similar species has been a problem leading to repeated misiden-

Tab. 1. Pholidosis of *Lycodon ruhstrati* from the Chinese mainland. [1] Mell's (1922) specimen, which Pope included in his table, was excluded here as a consequence of contradictory details in both descriptions; [2] the largest available specimens known to these authors; [3] values in brackets refer to the „unusual" specimen in Wu et al.; [4] printing error, max. 95 according to text; n.d.: no data; t.i.: tail incomplete.

Author	Locality	Number of specimens/Sex	Total length	TL	R	Ve	Sc	Bands on body	Bands on tail
Chen 1991	Anhui	2,0	616/863	141/182	0.23/0.21	214/215	90/96	n.d.	n.d.
Chen 1991	Anhui	0,2	491/748	106/155	0.22/0.21	220-221	93/95	n.d.	n.d.
Wu et al. 1985	Guizhou	1,0	590	140	0.24	216	100	39	23
Wu et al. 1985	Guizhou	0,1	940	178	0.19	223	94	38	16
Wu et al. 1985	Guizhou	1,0	784	179	0.23	217	93	35	16
Wu et al. 1985	Guizhou	1,0	647	137	0.21	220	90	35	18
Wu et al. 1985	Guizhou	0,1	448	98	0.22	220	95	36	18
Boulenger 1896	Lushan	1,0	n.d.	n.d.	n.d.	211	88	n.d.	n.d.
Pope 1935[1]	Futsing Hsien	0,1	227	47	0.21	197	79	22	12
Pope 1935	Futsing Hsien	0,1	227	47	0.21	204	77	25	12
Pope 1935	Chungan Hsien	0,1	817	180	0.22	221	92	35	14
Pope 1935	Chungan Hsien	0,1	672	147	0.22	227	94	36	17
Pope 1935	Chungan Hsien	1,0	729	158	0.22	223	92	33	15
Pope 1935	Mt. Omei	1,0	n.d.	n.d.	n.d.	220	t.i.	33	15
Pope 1935	Huangchiakou	1,0	n.d.	n.d.	n.d.	219	90	35	14
Zhao et al. 1998	Fujian	4,0	n.d.	n.d.	n.d.	200-224	76-97	21-40	13-19
Zhao et al. 1998	Fujian	0,5	n.d.	n.d.	n.d.	197-227	75-94	20-22	11-14
Zhao et al. 1998	Fujian	1,0	n.d.	n.d.	n.d.	200	95	46	17
Zhao et al. 1998	Fujian	0,1	n.d.	n.d.	n.d.	227	94	n.d.	n.d.
Zhao et al. 1998	Fujian	0,1	n.d.	n.d.	n.d.	197	76	n.d.	n.d.
Zhao et al. 1998	Sichuan	1,0	n.d.	n.d.	n.d.	216	95	35	14
Zhao et al. 1998	Anhui	1,0	n.d.	n.d.	n.d.	215	95	45	19
Zhao et al. 1998	Zhejiang	1,0	n.d.	n.d.	n.d.	230	95	n.d.	n.d.
Zhao et al. 1998	Zhejiang	0,1	n.d.	n.d.	n.d.	227	110[4]	32	16
Zhao et al. 1998	Zhejiang	0,1	n.d.	n.d.	n.d.	211	92	45	20
Zhao et al. 1998	China	male	877[2]	202[2]	0.23	n.d.	n.d.	n.d.	n.d.
Zhao et al. 1998	China	female	817[2]	180[2]	0.22	n.d.	n.d.	n.d.	n.d.
ZFMK 23363	China, Fujian		745	t.i.	n.d.	227	n.d.	43	20
ZMB 65454	Laung Tao Shan, China	1,0	320	84	0.21	213	95	32	16
Total males			877	202	0.21-0.24	200-230	76-100	21-46	13-23
Total females[3]			817 (940)	180	(0.19) 0.21-0.22	197-227	75-95	20-45	11-20

tifications in the past. Here we attempt to differentiate this species unequivocally from the four species *Lycodon fasciatus*, *Dinodon orientale*, *D. semicarinatum* and *D. septentrionale*.

L. fasciatus differs from *L. ruhstrati* in that the loreal almost always touches the eye; the light bands encircle the body completely, including the belly; the ventrals are more distinctly angular; the dorsals are apparently al-

Tab. 2. Pholidotic data for *Lycodon ruhstrati* found in Vietnam. [1] obviously 3 and 4 fused on either side; [2] Bourret gives a value of 0.27, which is obviously a printing or calculation error; t.i.: tail icomplete; n.d.: no data.

Source	Locality	Sex	Total length	TL	R	Ve	Sc	Do	Supral	Touching the eye	Bands on body	Bands on tail
Bourret 1934	Tam Dao	?	225	47	0.21	197	79	17	8		25	12
Bourret 1934	Tam Dao	?	395	85	0.22	197	87	17	8	3.4.5 or 4.5.6.	25	13
Bourret 1934	Tam Dao	?	698	153	0.20	199	81	17	8		23	13
Bourret 1934	Tam Dao	?	903	172	0.19	217	75	17	8		24	13
Bourret 1935a	Sa Pa	?	470	90	0.19	229	89	17	8	n.d.	26	11
Bourret 1935b	Tam Dao	?	595	120	0.20	199	73	17	8	n.d.	31	16
Bourret 1935b	Tam Dao	?	642	142	0.22[2]	195	76	17	8	n.d.	34	12
Bourret 1935b	Tam Dao	?	215	45	0.21	194	79	17	8	n.d.	31	16
Bourret 1937	Sa Pa	?	493	102	0.21	229	80	17	8/9	n.d.	22	15
Bourret 1939a	Ngan-Son	?	736	136	0.18	204	65	17	8	n.d.	36	14
Bourret 1939a	Sa Pa	?	292	60	0.20	216	87	17	8	n.d.	32	16
Bourret 1939b	Tam Dao	?	292	60	0.20	208	78	17	8	n.d.	?	?
Bourret 1939b	Sa Pa	?	408	83	0.20	221	86	17	8	n.d.	?	?
Ziegler 2002	Chin Xai	0,1	482	99	0.21	206	80	17	8	3.4.5.	24	11
MNHN 1938.130	Ngan-Son	1,0	663	187	0.22	203	84	17	8	3.4.5/4.5	26	13
MNHN 1935.99	Tam Dao	0,1	500	140	0.22	195	76	17	8	3.4.5	33	16
MNHN 1935.100	Tam Dao	1,0	167	46	0.22	193	82	17	8	3.4.5	30	
MNHN 2006.0436 (formerly PSGV 495l)	Tam Dao	0,1	612	147	0.24	207	100	17	8	3.4.5.	29	19
MNHN 2006.0437 (formerly PSGV 495s)	Tam Dao	0,1	212	42	0.20	204	72	17	8	3.4.5.	31	13
PSGV 651 (0017S)	Tam Dao	1,0	569+	t.i.	t.i.	200	t.i.	17	7[1]	3.4.	25	t.i.
PSGV 651 (0098S) MNHN	Tam Dao	1,0	659	144	0.22	200	83	17	8	3.4.5.	36	14
live 1,0	Tam Dao	1,0	810	180	0.22	194	80	17	8	3.4.5.	27	14
live 0,1	Tam Dao	0,1	540+	t.i.	t.i.	203	t.i.	17	8	3.4.5.	31	t.i.
PSGV 676 (1)	Tam Dao	1,0	221	51	0.23	198	84	17	8	3.4.5	31	17
PSGV 676 (2)	Tam Dao	1,0	213	45	0.21	193	76	17	8	3.4.5	29	14
RBINS 17282 (formerly PSGV 676 (3))	Tam Dao	0,1	651+	t.i.	t.i.	209	t.i.	17	8	3.4.5	31	t.i.
RBINS 17281 (formerly PSGV 590)	Tam Dao	1,0	222	39	0.18	199	67	17	8	3.4.5	28	14
Total			903	180	(0.18) 0.19-0.24	193-229	65-89 (100)	17	8(9)	3.4.5. (3.4.; 4.5.6.)	22-36	11-19

ways keeled (Lanza 1999, Slowinski et al. 2001); the bands are usually lighter in colour (Wall 1911).

Maki (1931) distinguished *D. septentrionale* from *L. ruhstrati* as follows: ground colour black above and on the sides; bands narrow and whitish, forming complete rings around the tail (in *L. ruhstrati*, the light bands are much narrower than the dark interspaces anteriorly and much wider posteriorly); ventral side dark brown (in *L. ruhstrati*, it is light at least in the anterior portion).

Dinodon semicarinatum differs from *L. ruhstrati* as follows: keeling of the central dorsal rows obligatory; the rostral is much larger and clearly visible from above (Maki 1931); its form is similar to that found in the species of the genus *Oligodon* Fitzinger, 1826; the ground colour is reddish (Ryabov et al. 2003) to chocolate brown (Maki 1931).

Dinodon orientale has two anal scutes and no preocular shield (Maki 1931) and is therefore readily distinguished.

Lycodon cardamomensis differs in having a smaller number of bands.

The three species of *Dinodon* furthermore differ in terms of their genus-specific dentition. The posterior group of maxillary teeth comprises two teeth in the genus *Lycodon*, whereas there are three in the genus *Dinodon*. According to Smith (1943), the maxillary bone is more angular in *Lycodon* than in *Dinodon*. The maxillary teeth of a *L. ruhstrati* from Vietnam are illustrated in Fig. 7.

Comparisons of populations of the *Lycodon ruhstrati* complex

a) *L. ruhstrati* in Vietnam

The pholidotic data for *L. ruhstrati* in Vietnam are listed in Table 2. Owing to the unfortunate fact that the sexual identities of most of the specimens studied by Bourret are unknown, we have opted for not differentiating the sexes in our comparison of variations. The maximum length is 90.3 cm. Ventral counts range from 193 to 229 (n = 24, x = 204.96), subcaudal counts from 65 to 89 (n = 20), but specimen PSGV 495 has 100 subcaudals and thus differs substantially from this population. It also has a very long tail (see Rooijen & Vogel in print). This produces a total range of 65-100 subcaudals (n = 21, x = 80.05). All specimens examined by us had unkeeled dorsal scales.

b) Comparison of the Vietnamese population with Chinese mainland populations

A comparison of the relevant values of the individual populations is given in Table 3.

Chinese populations are noteworthy for their usually having lower subcaudal counts than those from Vietnam. The number of body bands is also lower on average. Both values show broad overlaps, however. As has been discussed already above, the dorsals of Vietnamese specimens are unkeeled, while there appear to be both specimens with keeled and unkeeled dorsals on the Chinese mainland.

No major differences are notable with regard to maximum sizes.

Fig. 3. *Lycodon ruhstrati*, Tam Dao, Vietnam. Photo: G Vogel.

Fig. 4. *Lycodon ruhstrati*, adult male, Tam Dao, Vietnam. Photo: G. Vogel.

The present results do not justify a taxonomic separation of the southern populations even though more detailed studies might prove this to be appropriate. It is also entirely possible that this name is currently applied to two Chinese species.

c) Comparison of mainland populations with specimens from Taiwan

The Taiwanese populations differ distinctly from the populations on the mainland (Table 3). Their ventral counts are mostly higher than those of the mainland populations, but fall within the range of variation (211-233 vs. 197-230). The higher subcaudal counts are more conspicuous (94-116 vs. 75-100) in that the overlap is narrower. Only one of the seventeen Vietnamese specimens falls into the range of the Taiwanese population (i.e., the exceptional specimen mentioned above), but several of the Chinese mainland specimens do. Specimens from Taiwan usually have significantly more bands on the body and also on the tail. Broad overlaps exist also in this regard, however. As has been discussed above, the dorsals of specimens from Taiwan are keeled, whereas most known, or rather examined, animals from the mainland have unkeeled dorsals.

This is worthy of note in so far as obligatory keeling of the dorsals has been used as a key character for individual species that can lead to misidentification (e.g., Lanza 1999). Keeled dorsals are furthermore a character state that suggests a certain type of ecology. In Taiwan, *L. ruhstrati* appears to live predominantly in the lowlands (Kuntz 1963, Lue 1999), whereas on the mainland, it appears to be more of a highland form (Orlov 2000, Zhao 2003). Because we are currently unable to examine a larger number of specimens, we will refrain from differentiating the two forms taxonomically at this point of time. However, like Ota (1988), we are convinced that such a separation would be sensible. If the population from Taiwan was to be recognized at subspecific level, the name *Lycodon ruhstrati futsingensis* would be available for the mainland population. It should be noted, though, that the generic name *Dinodon* is neuter, whereas *Lycodon* is masculine (Toriba & Hikida 1999).

From a zoogeographical perspective, the Taiwanese population of *L. ruhstrati* nestles in "Group C" *sensu* Ota (1991), as the closest relative is native to the mainland opposite. "Group A" is ruled out by the fact that the populations on the Ryukyu Islands are obviously more distantly related, as far as can be told from the external characteristics studied here (see below).

d) Comparison of the populations from Cambodia and northeast Thailand with those on the Chinese mainland

In 2002, Daltry & Wüster described a new species of the genus *Lycodon* from the Cardamom Mountains of Cambodia. According to these authors, *L. cardamomensis* is most similar in its pholidosis to *L. ruhstrati*, but differs from it by having 3 postoculars (*L. ruhstrati*: 2) and a lower number of bands on body and tail. Following these authors, there are counts of 12 body bands in *L. cardamomensis* versus 22 or more in *L. ruhstrati*, and 6 tail bands versus 11 or more. The southern distribution border of *L. ruhstrati* is furthermore given as south China, and the resultant distribution gap is viewed as an additional pointer for its specific distinctiveness. However, as has been demonstrated above, the distribution range of *L. ruhstrati* actually extends much farther south into Laos, Vietnam, and possibly even Thailand. Owing to this species having been recorded under a variety of names by various authors, these locality records were obviously simply overlooked by said authors. *Lycodon cardamomensis* has meanwhile also been recorded from Thailand (Pauwels et al. 2005).

Following Tables 1 and 2, the difference in the numbers of bands around the body is diminished by the fact that specimens of

Tab. 3. Pholidosis of individual populations of the *Lycodon ruhstrati* complex (no separation of sexes). [1] according to Ota (1988); [2] according to Tab. 2; [3] according to Tab. 1 and information in the text; [4] Pauwels et al. (2005); [5] according to Maki (1931); [6] according to Mori (1984); [7] according to Uchiyama et al. (2002); [8] Tu 2004.

Pholidosis	*Lycodon ruhstrati* Taiwan[1]	*L. ruhstrati*, Vietnam[2]	*L. ruhstrati*, China [3]	*L. caramomensis*[4]	*L. multifasciatus*[1]
Postoculars	2	2	2	2/3	2
Ve	211-233	194-229	197-230	215-223	229-237
Sc	94-116	65-100	75-100	86-93	106-119
Bands on body	34-45	22-36	20-46	12	54-80
Bands on tail	16-28	11-19	11-23	6	26-42
Ground colour	dark	dark	dark	dark	light
Maximum length	1030[5] and 1100[8]	903	940	896	700[6] and 800[7]

L. ruhstrati with only 20 instead of 22 bands have meanwhile become known (Zhao et al. 1998). The specific status of *L. cardamomensis* appears justified nonetheless. Even though the number of postoculars in *L. cardamomensis* has been found to be variable and cannot therefore be regarded as of diagnostic value, the number of dorsal bands is distinctly different and an overlap or clinal variation appears unlikely.

e) Comparison of specimens from the Ryukyu Islands with mainland populations

The Ryukyu population was studied in detail by Ota (1988). It differs substantially from both the mainland population and the population on Taiwan. The number of rings around the body of 54 to 80 lies clearly above the values for mainland and Taiwanese populations. Looking at the animals, it becomes apparent that their colour pattern is very different from that of the other populations. Their background colour is light and not dark like in the other forms (comp. Goris & Maeda 2004). The dark rings are very narrow in the posterior portion of the body and do not compare with the width of the dark markings in the other populations. Moreover, there are distinct differences in the ventral count, which Ota (1988) specified as 229-237. This means that these snakes have distinctly more ventrals than those from the mainland (194-230). The overlap is merely one ventral scale, and that after an analysis of more than 54 mainland specimens and of the relevant literature and further available sources. The overlap is wider in a comparison with Taiwanese specimens, however. Moreover, the subcaudal count is higher, and so is the number of rings on the tail (see Table 3). These differences are more substantial than those distinguishing *L. cardamomensis* from *L. ruhstrati*. If the specific status of *L. cardamomensis* is to be accepted, *L. multifasciatus* must also be granted specific recognition as a consequence.

According to the evolutionary species concept, much smaller differences would be sufficient to regard this form as a separate species. The same conclusion would impose itself even from a viewpoint of the biological species concept. *Lycodon multifasciatus* is therefore here elevated to species rank.

The biogeography of the Ryukyu Islands has been discussed, for example, by Grismer et al. (1994) and Hikida et al. (1989). Most of the terrestrial reptiles living there have their closest relatives either on 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 the is-

lands. *Lycodon multifasciatus* must therefore be placed in "Group D" sensu Toyama (Hikida et al. 1989). This group comprises endemic species with a distributional centre on the Miyako and Yaeyama Island Groups that immigrated some 1.5 million years ago.

Following Ota (1991), the fauna of Taiwan is much more closely related to that of the Chinese mainland than that of the Ryukyu Islands. Elevating *L. multifasciatus* to species level therefore also makes sense from this perspective.

A comparison of traits of both pholidosis and colour pattern of all populations reveals higher ventral, subcaudal, and band counts on body and tail in northern specimens. The population from the Ryukyu Islands has the highest number of ventrals and subcaudals, as well as the most bands on body and tail. It is followed by the population in Taiwan, then by the Chinese specimens, even though these cannot be regarded as a separate population. Last come the animals from Vietnam. *Lycodon cardamomensis* from Cambodia and Thailand also fits into this trend if one considers the number of rings, but not the ventral and subcaudal counts. This could be interpreted as a case of clinal variation at least in the mainland populations of *Lycodon ruhstrati*. Splitting them into formal subspecies is therefore not called for. This does not apply to the allopatric populations of Taiwan or the Ryukyu Islands.

Taxonomy

It follows that the following names are to be regarded as valid:
Lycodon ruhstrati (Fischer, 1886) from China, Vietnam, Laos and Taiwan; *Lycodon multifasciatus* (Maki, 1936) from Ryukyu Islands, Japan; *Lycodon cardamomensis* Daltry & Wüster, 2002 from Cambodia and Thailand.

The material available to us is insufficient to comprehensively evaluate the complex taxonomically. The name *L. ruhstrati* might still comprise several taxa, as is suggested by differences in size and the presence or absence of keeled dorsals in Chinese specimens.

Biology

Pope (1929) provided the following details on three *L. ruhstrati* that were collected in Fujian: All three animals were found at night in the beds of mountain streams. They were discovered between July 9 and September 4. The stomach of one specimen contained a small skink, that of another a lizard of the genus *Takydromus*. A gravid female contained four well-developed eggs of which one measured 33 × 8 mm. Embryos were not yet recognizable. One animal tried to strike when molested, and was very agile and swift in its movements.

Karsen et al. (1998) made the following statements on the biology of this species in Hong Kong: It lives in forested mountain and hilly country up to altitudes of 760 m. It is nocturnal and a skilled climber. When threatened, it will discharge a pungent-smelling liquid from its anal glands. It feeds almost exclusively on lizards, which are killed by means of constriction and swallowed head first. The species is very rare in some parts of Hong Kong.

Lue et al. (1999) reported about the biology of this species in Taiwan. Here, it inhabits mountain and farm country. The species is predominantly active at night and can scale trees with ease. It feeds on lizards or insects, and it reproduces by laying eggs. *Lycodon ruhstrati* is usually found on Taiwan at altitudes below 500 m, but specimens have also occasionally been observed at altitudes of up to 1500 m.

According to Kuntz (1963), this species is found in forested hilly country and shrubs near rice paddies on Taiwan.

Orlov et al. (2000) found *L. ruhstrati* in Tam Dao, Vietnam, in bushes and various forest types at altitudes of 500-1500 m.

Tab. 4. Oviposition data for *Lycodon ruhstrati* from Tam Dao, Vietnam.

Date of finding clutch	Incubation period	Number of eggs	Number of hatchlings	Annotations
18.6.1998	50 days	4	2	1 infertile, 1 perished during incubation
26.5.1999	–	5	0	discovered too late and lost to fungus
13.5.2000	46 days	7	6	1 egg spoiled
12.7.2000	not recorded	5	3	2 infertile
21.7.2000	not recorded	4	0	spoiled by malfunction of incubator
19.7.2001	43-45 days	4	4	

The specimen collected by Ziegler (2002) in Vietnam was encountered in a forested area at an altitude of 160 m in early August. It was found at night on a slope some 30 m from a more substantial forest stream on the leaf litter between the mossy roots of a large tree. The gastro-intestinal tract of this specimen contained the remains of a skink.

Zhao & Yang (1997) reported about a specimen that was found in the mountain chain of Hengduan Shan in Sichuan at 1400 m altitude.

Generally, *L. ruhstrati* lives in Sichuan at altitudes between 800 and 1850 m a.s.l. (Zhao 2003).

Captive husbandry and biological observations

We received four adult specimens from Tam Dao (Vinh Phuc Province) on 1.6.1998. These comprised two males and two females. The animals were placed in a terrarium measuring 60 × 30 × 30 cm. The enclosure did not receive any external heating. Peat served as bottom substrate. The terrarium was furthermore furnished with a water bowl of about 15 cm in diameter, a climbing branch, and shelters in the shape of two flower pots with holes in the top and on the side, and a piece of cork bark. Temperatures corresponded to that of the surrounding room, resulting in extremes of up to 30 °-C in summer and 18 °C in winter. Illumination was provided by fluorescent tubes mounted in the room. The photoperiod was about 12 hours of daylight during the warmer months (April through October), and ca. 9 hours during the rest of the year. No overwintering was purposely carried out. Warm water was used for misting several times per week.

These husbandry conditions saw the animals thrive. Occasional problems with shedding initially were remedied by keeping some spots of the bottom substrate damp at all times. This did not keep the snakes from sometimes soaking in their water bowl for days prior to a moult. They usually spent the days beneath the piece of bark or in the flower pots. Both types of shelters were used without any predilection being apparent. The animals were often seen lying together. They were often found buried in the bottom substrate during the winter months in particular. They largely ceased to feed during this time. *Lycodon ruhstrati* presented itself as nocturnal and crepuscular during the warmer months, and was often seen climbing in the branchwork, which was also where the snakes would sometimes rest during the day. Activity was most intense at temperatures between 25 and 28°C. The animals were never particularly shy. Some specimens sometimes attempted to strike when handled, while others would not. The level of aggressiveness was higher at higher temperatures and during the activity periods, as expected. Manipulations, such as performing scale counts, caused the animals to empty their stink glands and disseminate a smell reminiscent of that produced by our native grass snake *Natrix natrix*.

Feeding in the terrarium was easy right from the start. The snakes would readily and

regularly take live baby mice or also those that had been dead for some time. They would also consume strips of beef or beef heart that had been placed in some water to prevent them from drying up over night. Egg yolk was offered but shunned. Non-viable neonates of *Protobothrops mucrosquamatus* did not raise much interest and were left alone after brief examination by means of tongue-flicking. The animals were extremely jealous over food. On several occasions a feeder animal was grasped by two snakes. It must therefore be ensured that feeding does not escalate into one specimen swallowing another that has attached itself to the same feeder animal.

Reproduction

According to Karsen et al. (1998), no information at all is available on this subject. Pope (1929) found a gravid female that contained four well-developed eggs, of which one measured 33 × 18 mm. Ziegler (2002) found a specimen in early August that contained light-coloured, small eggs of 1.5 + 1.1 cm; no number of eggs was given.

Goris & Maeda (2004) reported about a *L. multifasciatus* from the Ryukyu Islands that laid six eggs in the month of May. We recorded instances of mating on the following dates and times: 6.9.1999 (20.00 – 22.00 h); 3.2.2000 (about 20.00 – 22.00 h); 7.2.2000 (about 14.30 h); 23.2.2000 (about 14.30 h); 25.9.2000 (about 12.00 h); 24.10.2002 (about 14.30 through 18.30 h). On 14.4.2002, copulation commenced around the onset of dark and continued until noon of 15.4.2002. It appears that mating, at least in captivity, takes place both during spring and autumn. This might, of course, only be applicable to the population from which our animals originated. Oviposition events are summarized in Table 4.

Measurements were taken of several eggs: all four eggs of the first clutch measured 31 × 12 mm. The following measurements were recorded from the second clutch, laid on 26.5.99: 36 × 11, 26 × 11, 26 × 11, 27 × 11, 32 × 11 mm. The clutch of 21.7. contained eggs with the following measurements: 25 × 10, 26 × 10, 28 × 10, 27 × 10 mm. All clutches were found together with the mother animal in the peat substrate beneath the water bowl or other items of the decoration. Newly hatched babies measured approximately 15 cm. They shed for the first time some ten days after hatching.

Fig. 5. *Lycodon ruhstrati*, hatchings, Tam Dao, Vietnam. Photo: N. Brachtel.

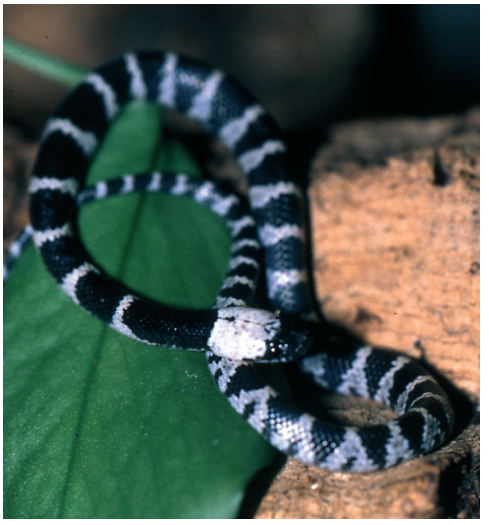

Fig. 6. *Lycodon ruhstrati*, hatchling, Tam Dao, Vietnam. Photo: N. Brachtel.

Raising the juveniles proved very difficult. Even though it was not particularly difficult to force-feed these small, delicate snakes with very finely cut strips of beef heart (they

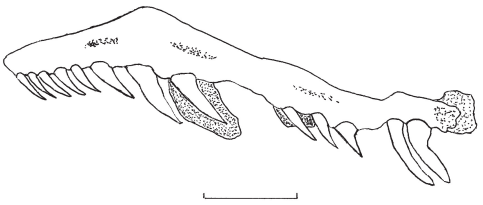

Fig. 7. *Lycodon ruhstrati*, Maxilla, Tam Dao, Vietnam. Drawing: P. David.

would even readily swallow when the meat was pushed in just slightly with a pair of forceps), there were fatalities for no apparent reason, possibly as a result of sheer stress during feeding. As much as the captive husbandry of the adults was easy due to their not being particularly choosy with regard to feeding on meat or pink mice, the more complicated it proved to encourage hatchlings to start feeding on their own. All attempts with offers of very fine strips of various types of meat in shallow bowls failed. Small earthworms and mealworms were also rejected. Specimens kept in the Serpentarium of Tula did not even feed on *Lacerta agilis* that had been bred explicitly for this purpose (S. Ryabov pers. comm.). Small geckos and frogs of appropriate sizes were unavailable.

The hatchlings also proved very sensitive in other aspects. Once unearthed from the bottom substrate into which they had retreated and placed on top, they would sometimes coil up and lie on their back, slowly twitching the tail. This would continue for several minutes before they righted themselves and disappeared into the substrate once more. We would interpret this observation as stress rather than instinctive defence behaviour. We therefore stopped all measuring and other manipulations of the tiny babies.

Efforts by the junior author to raise healthy hatchlings were unfortunately also fraught with a string of mishaps. Several hatchlings escaped through ventilation slits of the incubator (a simple incubator after Golder [1996]) and from miniature plastic terraria whose lids had openings that provided unexpected escape routes. More juveniles perished for reasons that were not exactly identifiable, but it is likely that stress caused by force-feeding played a major role.

In summary it can be stated that successful propagation was mainly hampered by problems with feeding. Since the natural diet of these baby snakes is unknown, experimenting with various potential foods, for example, various species of lizards and frogs, remains the only option in the quest of finding a suitable feeder animal.

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Appendix
Material used

*Lycodon fasciatus***:**
BNHS 1220, Shillong, Assam, India; BNHS 1223, Maymyo, Myanmar; BNHS 1224, Maymyo, Myanmar; BNHS 1228, Thandung Hills, Myanmar; BNHS 1230, Gyabari, Darjeeling, India; MNHN 1928.69, "Xieng-Khouang, Haut Laos", Xiengkhuang Province, Laos; MNHN 1919.148, Yunnan, China; MNHN 1912.465-466, Tibet; ZMB 65453 Talifu, W-Yunnan, China; ZSM 75/1938 Kuantum (Fukien), China.

Lycodon ruhstrati:
MNHN 1928.67-68, "Xieng-Khouang, Haut Laos", Xiengkhuang Province, Laos; MNHN 1935.99-100, Tam Dao, Vietnam; MNHN 1938.130, Ngan-Son, Vietnam; MNHN 2006.0436 (formerly PSGV 495 l), Tam Dao, Vietnam; MNHN 2006.0437 (formerly PSGV 495 s), Tam Dao, Vietnam; MNHN 2006.0438 (formerly PSGV 651/1); Tam Dao, Vietnam; PSGV 651/2; Tam Dao, Vietnam; RBINS 17281 (formerly PSGV 590), 1 juvenile; Tam Dao, Vietnam; RBINS 17282 (formerly PSGV 676 (3)), Tam Dao, Vietnam; PSGV 676(1)/(2), 2 juveniles;

Tam Dao, Vietnam; ZFMK 23363, Fujian: Kuatun, China; ZMB 65454 Laung Tao Shan, China.

Dinodon septentrionale:
MNHN 1893.411, Mts. Karin, Myanmar, 900-1000 m; MNHN 1933.11, holotype of *Dinodon septentrionalis chapaensis*, Sa Pa, Vietnam.

Dinodon semicarinatus:
MNHN 1969.10 Kagoshima Province, Japan.

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