HERPETOLOGICAL JOURNAL, Vol. 14, pp. 65-77 (2004)

A MORPHOMETRIC ANALYSIS OF *TRIMERESURUS VOGELI* (DAVID, VIDAL AND PAUWELS, 2001), WITH NEW DATA ON DIAGNOSTIC CHARACTERISTICS, DISTRIBUTION AND NATURAL HISTORY

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Morphological similarity has created considerable taxonomic uncertainty among the Asian green pitvipers. A new species of green pitviper, *Trimeresurus vogeli*, was recently described from Thailand. *T. vogeli* represents a distinct phylogenetic clade within the *Trimeresurus stejnegeri* group and is morphologically different from other clades of the *T. stejnegeri* group in several respects. However, the only obvious consistent difference between *T. vogeli* and other clades of *T. stejnegeri* is its lack of a red tail. Here, we perform a morphometric analysis to compare *T. vogeli* to other species with which it may be confused. Our data on *T. vogeli* differs in many respects to those presented in the species description, including characters considered diagnostic. In the past, *T. vogeli* has frequently been mistakenly identified as *Trimeresurus popeiorum*, from which it can be distinguished by the hemipenis structure in males. The tail colour characteristic is not reliable in distinguishing *T. vogeli* from all populations of *T. popeiorum*, and we review the morphological differences between these and *T. vogeli* females. We report a range extension to Cambodia, Laos and Vietnam, and provide habitat data for the species. The range of *T. vogeli* does not overlap with that of *T. popeiorum* or other members of the *T. stejnegeri* group.

Key words: green pitviper, SE Asia, taxonomy, Viperidae

INTRODUCTION

The green pitvipers or bamboo vipers form a distinctive part of the Asian venomous snake fauna, because of their striking appearance and because they are often the most common venomous snakes in their range. However, their morphological similarity has created substantial taxonomic uncertainty, which has not been satisfactorily resolved despite almost a century of effort (Stejneger, 1927; Pope & Pope, 1933; Regenass & Kramer, 1981). Recently, molecular work has promised to resolve certain particularly vexing taxonomic issues. Malhotra & Thorpe (2000) presented a phylogeny of 21 species based on cytochrome *b* sequences, and evaluated the taxonomic value of certain morphological characteristics against it. They defined four species groups within *Trimeresurus sensu stricto* (*s.s.*), which are diagnosed by a combination of the condition of the first upper labial and nasal scale (fused or separate) and the hemipenial structure. *T. stejnegeri* formed a distinct species group under these criteria. While monophyletic, not enough sequences were included to fully evaluate the presence of cryptic species, as was possible for the *T. albolabris* species group in Malhotra & Thorpe (2000). Recently, increased access to remote and politically restricted areas has yielded a significant number of new specimens of green pitvipers for analysis. This has provided the opportunity to make a significant advance in the systematics of the green pitvipers in general, and *T. stejnegeri* in particular.

We have extensively reanalysed the relationships among populations of *T. stejnegeri*, based on phylogenetic analysis of DNA sequences (mitochondrial cytochrome *b* gene) and multivariate morphometrics (external and internal characters), from existing museum and newly collected material from across the known range of *T. stejnegeri* (Malhotra & Thorpe, in press). *T. stejnegeri sensu lato* (*s.l.*) was found to consist of at least three reciprocally monophyletic and morphologically distinct clades. The first occurs in Vietnam (north of latitude 20° N) and China and corresponds to the nominate form of *T. stejnegeri* (Schmidt, 1925), referred to here as *T. stejnegeri s.s*. A proposed subspecies of *T. stejnegeri*, *T. s. chenbihui* (Zhao, 1995) was indistinguishable from the nominate form. The second clade occurs in north-eastern Thailand, the Annamite Mountains on the border of Laos and Vietnam, and in southern Yunnan province, China. The north-eastern Thailand population has been recently described as *T. gumprechti* (David *et al*., 2002). The third clade occurs in Thailand, Cambodia, Laos and Vietnam. David *et al*. (2001) have recently described the population from Thailand as *T. vogeli*. In this paper, we present the results of a morphometric analysis of the three clades of *T. stejnegeri s.l.* Our data for this species are inconsistent

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with the published description in a number of points (e.g. in 12 out of 14 characters that are stated to separate the new species from other populations of the *T. stejnegeri* complex). Consequently, we evaluate and supplement the data on *T. vogeli* presented by David *et al*. (2001), and extend its known range.

T. stejnegeri group species can be separated from all other species groups (*sensu* Malhotra & Thorpe [2000]) by the structure of the hemipenis. The long, thin hemipenes of the *albolabris* group and the *popeiorum* group are easily distinguished from the short, stout hemipenes of *T. stejnegeri* (at least in adults) by an external examination of the shape of the tail (in *T. stejnegeri*, there is an abrupt reduction in tail thickness between subcaudals 20 and 25, whereas the tail tapers gradually to the tip in the *T. albolabris* and *T. popeiorum* group). Eversion of the hemipenis is necessary to distinguish the similarly short, stout hemipenes of the "Indian subcontinent" group (Malhotra & Thorpe, 2000), which however, differ considerably in the number, shape and distribution of the spines. Nevertheless, this character is not relevant for females, and there is no consistent, easily applied character that is capable of distinguishing female *T. vogeli* from females of the *T. popeiorum* group. Contrary to David *et al*. (2001), *T. vogeli* is not the only species of green pitviper which lacks obvious red coloration on the tail, this condition also being found in populations of *T. popeiorum* from southern Thailand and Sumatra, and *T. gramineus* from India. These species also may have 21 scale rows at mid-body (the Sumatran population of *T. popeiorum* does not invariably have 19 scale rows at mid-body as stated in Regenass & Kramer [1981]). All female *T. gramineus* seen by the senior author have some degree of dark cross-banding and a dark post-ocular streak, which is never seen in females of the *T. stejnegeri* group (although Smith [1943] states that this may be absent in *T. gramineus*). Thus, the females of *T. vogeli* may most easily be confused with *T. popeiorum*. We therefore also consider features that serve to distinguish females of *T. vogeli* and populations of *T. popeiorum* from southern Thailand and Sumatra.

MATERIALS AND METHODS

In 1999–2000, specimens were collected in Laos and Cambodia (BLS) and preserved in 10% buffered formalin after liver samples were fixed in 95% ethanol for later genetic analyses. These are deposited in the Field Museum, Chicago (FMNH), and specimens were transferred to 70% ethanol upon arrival, several months after preservation. A further specimen was found in the Dongraek Mountains of Thailand in 1999 by the senior author. A blood sample was taken from the caudal vein and preserved in buffer (5% EDTA, 100 mM Tris, 3% SDS), for later genetic analysis. Morphometric measurements and macro photographs were taken while the specimen was anaesthetized, and it was subsequently released. We also examined material in the holdings of a number of museums. Data were also obtained from specimens collected in the field in Thailand and Vietnam (AM and RST) and trade sources. All specimens used are listed in Appendix 2.

Phylogenetic analysis of cytochrome *b* sequences identified the presence of three distinct, reciprocally monophyletic clades (these data will be published separately). A multivariate analysis of morphological data (canonical variate analysis) was performed using only those populations represented in the phylogenetic analysis, grouped into clades. Specimens from populations not represented by DNA sequences were then mapped onto the resulting axes in order to establish their affinities. Specimens that were not clearly assignable to one of the three clades using this procedure were excluded from subsequent analysis. Canonical variate analysis (CVA) was then carried out to identify characters that distinguish the clades morphologically. Sexes were treated separately as considerable sexual dimorphism is present. A list of characters used can be found in Appendix 1. Sample sizes are given in Table 1. Certain characters (particularly colour-pattern characters) showed a degree of heteroscedascity, which may perturb the analysis. Its presence should be detectable in the results, as the heteroscedastic characters would dominate the axes. The presence of potential perturbation due to heteroscedascity was also checked by carrying out a principal component analysis (PCA). This has much less discriminatory power, but is less affected by departures from the assumptions of the model of homoscedascity (Thorpe, 1983). Since PCA does not take between-character correlations into account, all size-related characters were first adjusted to a common size using the pooled within-group slope, with either snout-vent length (SVL) or head length (LHEAD) as the covariate. If the same characters were found to be important in discrimination between groups using both methods, then CVA results were used in preference.

Adding internal characters improved the resolution of the clades. However, internal characters are not particularly useful for identification in many situations and also substantially reduce the sample size, as internal data were not available for many specimens. Therefore, two sets of analyses were carried out, the first including external characters only and the second including all characters. In order to find the characters most useful at distinguishing *T. vogeli*, a discriminant function analysis was also carried out between *T. vogeli* and each clade separately. This process was repeated to compare females of *T. vogeli* with *T. popeiorum* populations from southern Thailand and Sumatra. However, because of the smaller sample size (Table 1), it was necessary to screen the characters beforehand by one-way analysis of variance (ANOVA) or covariance (ANCOVA), as appropriate, so that non-significant characters could be removed from the analysis.

The 33 specimens used to describe *T. vogeli* were all from Nakhon Ratchasima Province in Thailand (David

TABLE 1. Sample sizes in the multivariate analyses. *Ts*1, *T. stejnegeri* (*s.s.*); *Tg* , *T. gumprechti*; *Tv*, *T. vogeli;* *Tp*1, *T. popeiorum* (southern Thailand); *Tp*2, *T. popeiorum* (Sumatra).

Analysis	*Ts*1		*Tg*		*Tv*		*Tp*1	*Tp*2
	M	F	M	F	M	F	F	F
All characters	18	23	7	10	14	14	-	-
External characters	41	34	10	15	25	23	4	7

et al., 2001). David *et al*. (2001) suggested that the species occupies a wider range. It is therefore likely to show a wider range of character variation than provided in the description, and we evaluate the distinguishing characters described in David *et al*. (2001), using ANOVA and ANCOVA. The assumption of homogeneity of variance was checked using Levene's test, and the Brown-Forsythe variant of the ANOVA, which relaxes this assumption, was used where it was violated (Brown & Forsythe, 1974). Where a significant result was found, post-hoc tests were used to examine which groups the difference lay between. Since this involves multiple tests (in this case, *t*-tests), the critical probabilities for rejection of the null hypothesis of no difference were adjusted using a Bonferroni correction (Grafen & Hails, 2002). All analyses were carried out using the BMDP software package.

RESULTS

MULTIVARIATE MORPHOMETRICS

PCA and CVA results were similar, with no apparent perturbation from heteroscedascity in the CVA. The CVA successfully discriminated between the three groups with 100% success. Inclusion of internal characters substantially improved the discrimination of the groups, particularly for females (Fig. 1), as was also found to be the case in distinguishing subspecies of the ringed snake, *Natrix natrix*, by Thorpe (1979, 1989). Table 2 lists characters that contribute to the discrimination of *T. vogeli,* their mean value, and range. The difference in any single character is subtle, with largely overlapping ranges (Table 2).

T. vogeli is distinguished from *T. stejnegeri s.s.* in both sexes by a relatively larger head (LHEAD, WHEAD), narrower internasal scales (WINTNAS), and more sublabial scales (SUBLAB). In males of *T. vogeli*, the scale reductions from 19 to 17 rows (VS19TO17) and 21 to 19 rows (VS21TO19) occur closer to the head, the scale reduction from 8 to 6 rows on the tail (SC8TO6) occurs closer the vent, and a postocular streak is less common (OCTSRIPE) than in *T. stejneger*i (Table 2A)**.** The right testis (RTANT, RTPOST) of male *T. vogeli* is more proximal in position, as is the anterior edge of the liver (LVANT) and posterior edge of the left testis (LTPOST), than in *T. stejnegeri*. In females, the reduction from 17 to 15 rows (VS17TO15) most clearly distinguishes the two species (Table 2B), again occurring closer to the head in *T. vogeli* (Table 2B), as does the liver (LVANT, LVPOST) and the anterior edge of the right kidney (RKANT). *T. vogeli* females also tend to have more scales between the supraocular scales (BTWSUPOC1 and 2), more ventral scales (VSC), more pterygoid teeth (PTERY), and fewer subcaudals (SCS) than *T. stejnegeri* females.

Male *T. vogeli* can be distinguished from *T. gumprechti* by the position of the scale reductions from 17 to 15 (VS17TO15) and 19 to 17 (VS19TO17) rows (Table 2C), which occur closer to the head in *T. vogeli*. Male *T. vogeli* also have more subcaudal scales, less keeled temporal scales (KTEMP), and narrower internasal scales (WINTNAS), than male *T. gumprechti*. Again, the relative position of the testes (RTANT, RTPOST, LTANT, LTPOST) allows *T. vogeli* males to be distinguished from *T. gumprechti* males, this time occurring closer to the vent in *T. vogel*i (Table 2C). Female *T. vogeli* can chiefly be distinguished by the fact that they have a longer head (LHEAD), smaller eye (DEYE), narrower internasal scales (WINTNAS), and a

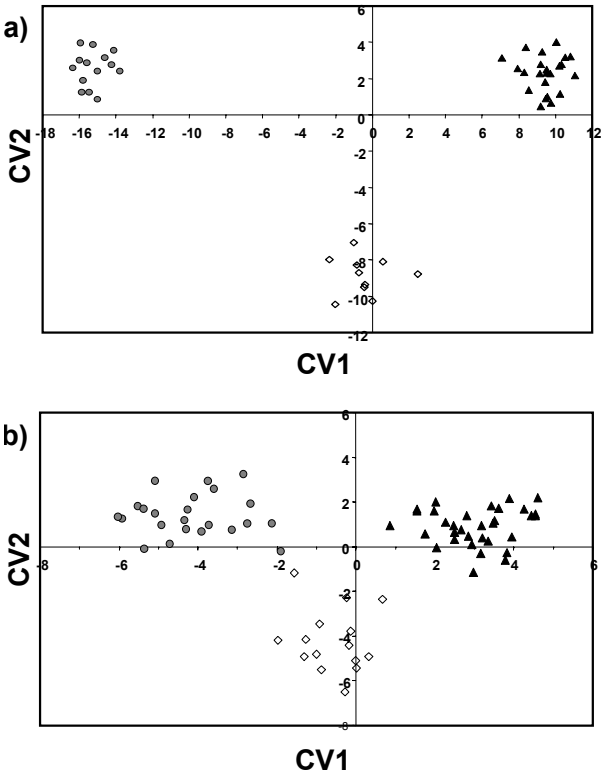

FIG. 1. Plot of first two canonical variates for females only, showing the increase in resolution gained by using internal as well as external characters. The difference is not as dramatic for males. (a) external and internal characters; (b) external characters only. Grey circles: *T. vogeli*; open diamonds: *T. gumprechti*; black triangles *T. stejnegeri* (*s.s.*).

TABLE 2. Mean values and range (in parentheses) of morphological characters important in multivariate discrimination between *T. vogeli* and other *stejnegeri* group clades (see text). To maximize sample size, the results of the analysis of external characters are used in preference. However, internal characters that are important in the discrimination when all characters are used are also listed. Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to the grand mean size of SVL and LHEAD (54.15 cm, 30.53 mm for females; 54.38, 27.59 for males respectively). A, *T. vogeli* and *T. stejnegeri (s.s.)* males; B, *T. vogeli* and *T. stejnegeri (s.s.)* females; C, *T. vogeli* and *T. gumprechti* males; D, *T. vogeli* and *T. gumprechti* females. Characters are listed in order of magnitude of their contribution to the discriminant function, and their abbreviations are explained in Appendix 1.

A. Males	*T. vogeli*	*T. stejnegeri (s.s.)*
LHEAD	29.1 (25.8–40.3)	27.0 (24.2–30.6)
WHEAD	13.5 (12.1–17.3)	2.7 (10.3–14.9)
VS19TO17	65.1 (51.2–69.6)	68.7 (61.7–77.4)
SC10TO8	6.3 (3.1–10.7)	7.9 (3.0–15.9)
WINTNAS	2.0 (1.4–2.6)	2.2 (1.7–2.6)
SUBLAB	12.4 (11–14)	11.8 (10–13)
OCSTRIPE	0.16 (0–1)	1.1 (0–2)
INTNAS	1.6 (1–4)	1.8 (1–4)
VS21TO19	60.1 (9.6–65.8)	64.1 (53.1–73.6)
SC8TO6	14.6 (7.0–27.4)	19.2 (7.5–29.7)
RTPOST	73.1 (70–79)	75.0 (72.6–78.1)
RTANT	70.4 (66.5–76.5)	71.6 (67.9–75.6)
LKPOST	93.1 (91.3–94.3)	94.4 (93.1–98.8)
LVANT	40.1 (38.1–42.1)	41.2 (38.9–45.8)
LTPOST	77.7 (75.3–80.1)	79.5 (77.4–87.7)

B. Females	*T. vogeli*	*T. stejnegeri (s.s.)*
VS17TO15	70.1 (66.8–73.2)	76.1 (70.5–93.2)
LHEAD	32.9 (26.8–56.6)	28.8 (13.6–33.0)
BTWSUPOC1	11 (9–13)	10.7 (8–14)
DEYE	3.9 (2.7–5.5)	4.1 (3. –5.3)
DV17TO15	4.6 (3–7)	3.9 (3-5)
SUBLAB	13.2 (11–14)	12.5 (11–1 5)
KTEMP	0.02 (0–0.5)	0.3 (0–0.5)
WINTNAS	1.9 (1.5–2.4)	2.1 (1.4 –2.7)
BTWSUPOC2	16.5 (14–19)	15.7 (12–20)
DV10TO8	3.0 (1–4)	3.4 (1–4)
VS25TO23	7.4 (55–12.9)	8.2 (5.7–13.9)
VSC	165.5 (157–173.5)	161.6 (152–171)
LVANT	38.3 (35.9–40.6)	39.5 (37.0–42.9)
LVPOST	56.4 (53.2–61.1)	58.3 (55.4–63.6)
PTERY	13.5 (12-16)	13.0 (11-15)
RKANT	78.3 (74.3–82.1)	79.7 (75.9–83.8)

C. Males	*T. vogeli*	*T. gumprechti*
SC10TO8	6.3 (3.1–10.7)	8.6 (5.5–12.7)
VS17TO15	69.2 (62.0–78.4)	73.8 (69.8–77.7)
DV23TO21	4.3 (3–5)	4.2 (3–5)
VS19TO17	65.1 (51.2–69.6)	67.0 (64.7–69.9)
SCS	66.7 (61–72)	64.8 (59–74)
SC8TO6	14.6 (7.0–27.4)	18.7 (14.2–21.2)
KTEMP	0.2 (0–0.5)	0.3 (0–0.5)
WINTNAS	2.0 (1.4–2.6)	2.2 (1.8–3.1)
DV12TO10	2.5 (1–5)	2 (1–5)
RTPOST	73.1 (70.0–79.0)	71.6 (70.2–73.4)
RTANT	70.4 (66.5–76.5)	68.5 (66.7–70.4)
LTPOST	77.7 (75.3–80.1)	76.2 (72.0–78.2)
LTANT	75.1 (72.4–77.0)	73.4 (70.1–75.2)

D. Females	*T. vogeli*	*T. gumprechti*
LHEAD	32.9 (26.8–56.6)	31.8 (29.2–36.0)
DEYE	3.9 (2.7–5.5)	4.1 (3.3–5.1)
VS23TO21	9.1 (5.3–12.6)	12.1 (7.9–17.2)
WINTNAS	1.9 (1.5–2.4)	2.0 (1.5–2.6)
DV27TO25	5.6 (4–10)	7.1 (4–13)
VS27TO25	5.7 (4.1–9.2)	6.9 (4.4–9.3)
STRIPE	2.0 (2–2)	1.5 (0–2)
SC8TO6	11.2 (6.5–15.3)	15.9 (12.1–22.1)
VENTEDGE	8.9 (7–10)	8.3 (8–10)
PREOC	3 (2–3)	2.4 (2–4)
INTNAS	2.0 (1–3)	1.3 (1–2)
VS17TO15	70.1 (66.8–73.2)	77.0 (69.0–87.2)
HTANT	34.8 (32.4–37.7)	33.6 (30.3–36.8)

much more pronounced lateral stripe (STRIPE) than female *T. gumprechti.* The scale reduction from 23 to 21 rows (VS23TO21) also occurs closer to the head in female *T. vogeli* than in female *T. gumprechti* (Table 2D), as does the scale reduction from 27 to 25 rows (VS27TO25) and the reduction from 17 to 15 rows (VS17TO15). Female *T. vogeli* have a larger number of scales between the internasals (INTNAS) and between the last sublabial and ventral scales (VENTEDGE) than female *T. gumprechti*. There is not much difference between females of these clades in position of internal organs, although the anterior edge of the heart (HTANT) tends to be more distal in *T. vogeli*.

Table 3 gives similar data for *T. vogeli* compared to *T. popeiorum* (females only), although only external characters were used because of very limited internal data for *T. popeiorum*. The most useful character distinguishing between *T. vogeli* and *T. popeiorum* from southern Thailand and Sumatra is the extent of the lateral stripe (STRIPE), which is much more prominent in *T. vogeli*. In southern Thailand *T. popeiorum* in particular, the lateral stripe is almost non-existent, being barely present on the first scale row (SCR1) and rarely encroaching upon the second scale row (SCRSTR). The pit is also closer to the eye (PIT2EYE) and there are more scales bordering the supraoculars (BORSUPOC) in *T. vogeli* than in either of the *T. popeiorum* populations. The internasal scales (WINTNAS) are much wider, the scale reduction from 17 to 15 rows on the body (DV17TO15) is more likely to involve lower scale rows, and the scale reduction from 6 to 4 rows on the tail (SC6TO4) occurs closer to the vent in

TABLE 3. Mean values and range of morphological characters important in multivariate discrimination between females of *T. vogeli* and populations of *T. popeiorum* with which it might be confused (see text). Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to the grand mean size of SVL (50.91 cm) and LHEAD (30.55 mm). A, *T. vogeli* and *T. popeiorum* from Sumatra; B, *T. vogeli* and *T. popeiorum*, southern Thailand. Characters are listed in order of magnitude of their contribution to the discriminant function, and their abbreviations are explained in Appendix 1.

Character	Taxa	
A.	*T. vogeli*	*T. popeiorum* (Sumatra)
SUBLAB	13.2 (11–14)	11.9 (10–13)
PIT2EYE	1.5 (1.1–1.8)	1.6 (1.3–1.8)
WINTNAS	1.9 (1.6–2.4)	2.5 (2.3–2.9)
STRIPE	2.0 (2–2)	0.3 (0–1)
SC6TO4	26.8 (16.4–42.5)	21.6 (15.5–32.0)
POSTOC	2.6 (2–4)	2.1 (2–3)
BORSUPOC	7.7 (6.5–9)	6.6 (6–8)
DV17TO15	4.6 (3–7)	3.8 (3–5)
VSC	165.5 (157–175.5)	147.9 (144–152)
DV10TO8	3.0 (1–4)	2.4 (1–3)
NASPIT	1.5 (0–2.5)	0.6 (0–2)
B.	*T. vogeli*	*T. popeiorum* (south Thailand)
EYE2NOS	6.5 (6.1–7.0)	6.9 (6.7–7.1)
PIT2EYE	1.5 (1.1–1.8)	1.8 (1.7–1.9)
STRIPE	2.0 (2–2)	0.25 (0–1)
KHEADSC	0.03 (0–0.5)	0.25 (0–0.5)
SCRSTR	1.1 (1–2)	0.25 (0–1)
BORSUPOC	7.7 (–9)	6.9 (6–8)
BTWSUPOC1	11.0 (9-13)	10.3 (10–11)
SCR1	0.31 (0.1–0.7)	0.03 (0–0.1)
VS19TO17	66.1 (63.8–69.1)	67.6 (66.0–69.9)
ROST	0.36 (0.23–0.50)	0.28 (0.22–0.34)

Sumatran *T. popeiorum* than *T. vogeli*. Sumatran *T. popeiorum* also tend to have fewer postocular scales (POSTOC) and ventral scales (VSC), and fewer small scales between the nasal scale and the scute forming the anterior border of the pit (NASPIT). Southern Thailand *T. popeiorum* tend to have a greater distance between the eye and the nostril (EYE2NOS), more keeled scales on the rear of the head (KHEADSC), fewer scales between supraoculars (BWTSUPOC1), a more distal scale reduction from 19 to 17 rows (VS19TO17), and a more pointed apex to the rostral scale (ROST) than *T. vogeli*.

Evaluation of Diagnostic Characters Presented in the Species Description.

David *et al*. (2001) presented a combination of six characters that distinguish *T. vogeli* from all other green pitvipers (listed as 1–6 below), four characters that distinguish *T. vogeli* from particular species of green pitvipers (of which two are discussed in 7–8 below), and 14 characters that separate *T. vogeli* from other populations of the *T. stejnegeri* complex (9–22 below). Our findings are inconsistent with many of these characters; this is expanded upon below. Phrases in italics are taken directly from David *et al*. (2001).

1. *Short, spinose hemipenis*. In contradiction to David *et al*. (2001), this description is insufficient to distinguish *T. vogeli* from many other *Trimeresurus* species. For example, *T. gramineus* also has a short spinose hemipenis, and the shape, number and distribution of spines is also important to distinguish *T. vogeli* from this species (as described above).

2. *First supralabial is separated from the nasal*. This will only distinguish *T.vogeli* from members of the *T. albolabris* group.

3. *Ventrolateral stripe nearly always white, whitish blue, or whitish yellow when present, very seldom red in females*. While the red stripe may be narrow, it was never absent altogether in the males examined, and it may, rarely, be present in females. Females always have a lateral stripe, and although not many live individuals have been seen, it was always yellow in those examined.

4. *White vertebral spots are always present in males, always absent in females*. White vertebral spots or flecks were not always present in males of *T. vogeli* examined. This may be an artefact of preservation. However, in a series from Dongraek, Thailand, which were all preserved at around the same time and are in a similar state of preservation and not excessively darkened, six out of nine males lacked vertebral spots. On the other hand, they were always found to be present in males from Dong Hua Sao National Biodiversity Conservation Area (NBCA), Laos. White vertebral spots are also present in males of *T. popeiorum* from southern Thailand, and juvenile male *T. gumprechti*. The difference in the mean number of spots between the *T. stejnegeri* group clades was found to be significantly different in an ANOVA (P=0.001), but this difference was largely due to the difference between *T. vogeli* (mean=14.9, range=0–58), and *T. stejnegeri* (s.s.) (mean=1.1, range=0–17), with the difference between *T. vogeli* and *T. gumprechti* not being significant. This character was also not important in the multivariate discrimination of *T. vogeli* from other clades of *T. stejnegeri*.

5. *Less than 174 ventrals*. This is confirmed, but does not serve to distinguish *T. vogeli* from many species. *T. popeiorum* from southern Thailand, for example, also have a similar number of ventral scales (range in females, n=4, is 166–173).

6. *No more than about 25% of its tail is rusty red*. This character is not reliable in specimens that have darkened in preservative. In live specimens that we have examined, the tail tip varies from grey to dark brown mottled, almost appearing banded. However, *T.*

gramineus, and some populations of *T. popeiorum*, also share this condition.

Thus a combination of these six characters will not distinguish female *T. vogeli* from *T. popeiorum* from southern Thailand, and possibly also from Sumatra. The next two characters were used by David *et al*. (2001) to distinguish *T. vogeli* from *T. popeiorum*.

7. *Thicker head*. Head depth was not measured in our study so cannot be evaluated.

8. *Lower number of subcaudals*. There is no significant difference between the mean number of subcaudals in *T. vogeli* females and southern Thailand and Sumatran populations of *T. popeiorum* ($P<0.05$).

Thus at least one of the cited characters does not serve to diagnose female *T. vogeli*. The following 14 characters are those stated by David *et al.* (2001) to separate *T. vogeli* from other *T. stejnegeri* populations.

9. *A greater maximal size, especially in female specimens*. The maximum sizes we have recorded for the species (720 mm, 990 mm SVL for males and females respectively) are in accord with data in David *et al*. (2001). However, this is not significantly different ($P>0.25$) from the maximum sizes recorded for *T. gumprechti* in north-eastern Thailand (745 mm, 876 mm SVL for males and females, respectively), contradicting the statement in David *et al*. (2001) that they are distinctly smaller than *T. vogeli*. This statement was also contradicted later by David *et al*. (2002), who gave large size as a diagnostic characteristic of *T. gumprechti*.

10. *Males of* T. vogeli *are dark green with faint black fasciatures, and females are bright grass green, whereas both males and females of other populations are bright, grass or deep green*. The difference between male and female dorsal coloration is not very obvious in close-up photographs of the Dong Hua Sao NBCA population, where both males and females are dark-green in colour. In a captive-born pair acquired from the trade, which DNA analysis indicates most likely come from the Dongraek Mountains of Thailand, the male and female are very different in dorsal coloration, with the male being blue-green and the female grass-green. The fasciatures mentioned are not obvious in the male specimens from Laos.

11. *The white or yellow ventrolateral stripes are only rarely bordered below by a red line in subadult and adult males of* T. vogeli. In later discussion, it is also stated by David *et al*. (2001) that juvenile male *T. vogeli* are more likely to possess a red stripe, implying that they lose it as they grow. This is unusual, but not unknown: in most *Trimeresurus* that possess a red stripe, it is present throughout life. However, as stated above, the rarity of the red stripe in *T. vogeli* is not supported by our data. Although in some preserved specimens which have darkened considerably, the stripe may be difficult to distinguish, in others it is perfectly clear as a darker region bordering the white stripe, clearly distinct from the lighter general dorsal hue. In two extensive and well preserved series of this species in the Field Museum, Chicago, from Sakaerat Experimental Station in Thailand (where many of the paratypes of the species originated), and Dong Hua Sao NBCA in Laos, 100% of males had this red stripe (n = 9 and 4 respectively). Unusually, one female from Sakaerat also possessed a red lateral stripe. As stated by David *et al.* (2001), in several populations of *T. stejnegeri (s.s)*, females also have a red stripe (notably in parts of China and north Vietnam), but this is clearly a rare condition in *T. vogeli* (one out of 23 specimens examined).

12. *A white or yellowish streak is present, although thin and faint in males, but always absent in females*. Postocular stripes were seen in two out of nine males examined from the Dongraek region and two out of eleven males examined in the central Vietnam population. It was absent altogether in the four males examined from Laos. Thus, it would seem that the occurrence of a postocular streak in male *T. vogeli* is at best a rare condition. Conversely, it is always present in male *T. gumprechti* and frequently present in *T. stejnegeri s.s.* (the difference between clades is highly significant, $P=0.0001$). This character is especially useful for distinguishing male *T. vogeli* from *T. gumprechti*, as the presence of the streak in *T. gumprechti* can easily be discerned in preserved specimens even if the constituent colour(s) cannot. A postocular stripe is never present in female *T. vogeli*, but the difference between clades in the presence of a postocular streak is not significant ($P=0.13$). The postocular stripe is also consistently absent in both sexes in other populations, such as *T. stejnegeri s.s.* from northern Vietnam.

13. *In* T. vogeli *the eye is yellow or yellowish green, and never red... whereas in T. stejnegeri the eye is red, orange or amber in males and females*. This statement overlooks sexual dimorphism in eye colour in *T. stejnegeri s.l.* In most populations, females have yellow eyes, as indeed is stated in Table 3 of David *et al*. (2001). Moreover, ontogenetic variation is present in males (senior author, pers. obs.). In Taiwan and north-east Thailand, where an extensive series of live animals has been examined, males are born with yellow eyes, and the degree of red pigmentation increases with age until they are bright or brick red in colour in large males. Thus, the discriminatory power of this character is weak for females and subadult males.

14. *The coloration of the tail is rather different from other green pitvipers of the mainland*. This is true for all *T. stejnegeri* populations, but not for all species of the mainland as indicated above. Here, the authors state that the rusty coloration may extend up to 50% of the tail on the upper side, rather than the maximum of 25% stated in point 6. We did not measure the extent of coloration on the tail, except in the three live specimens examined (where it is in accord with the lower figure). However, if the rusty coloration does extend to 50% of the tail, it would further decrease the contrast between *T. vogeli* and southern Thailand *T. popeiorum*.

15. T. vogeli *has a lower value for the ratio tail length: total length, especially in females*. The use of ratios is inappropriate where the relationships between

the component measurements is allometric (Thorpe, 1983), as they will be biased if the total length of the populations being compared is different, such being the case here. A better procedure would be to adjust tail length by regression (SVL rather than total length was used as a covariate) and then compare the groups. The difference between *T. vogeli* and other *T. stejnegeri* group populations is then not significant in females (P>0.5). However, in both sexes the assumption of equal within-group slopes is violated, due to a significantly lower slope in *T. vogeli*. This suggests that, although tail size of small individuals of *T. vogeli* may not be very different, the tail will grow less in this species than the others, and thus the tail may be considerably shorter in large animals: this makes the statistical significance of this difference impossible to assess between animals of different sizes.

16. T. vogeli *has a higher number of ventral scales than in all populations of* T. stejnegeri, *except for those from Hainan island*. The difference between clades is significant for both males and females (P=0.01) but this is mainly due to the difference between *T. vogeli* and *T. stejnegeri (s.s.)* (including Hainan island). *T. vogeli* and *T. gumprechti* are not significantly different in ventral scale number. This result did not differ when Hainan specimens were excluded from *T. stejnegeri s.s*., although the significance of the difference with *T. vogeli* increased (P = 0.003 in both sexes). However, VSC did not contribute to the multivariate discriminant analysis of male *T. vogeli* and *T. stejnegeri s.s.* (Table 2).

17. *There is a lower number of subcaudal scales in* T. vogeli… *although this character is barely significant*. In our data, there is a significant difference in the number of subcaudals between clades of *T. stejnegeri* (P=0.03, 0.0001 for males and females respectively). However, the difference is mainly between *T. vogeli* (mean=66.7, 60.9 in males and females respectively) and *T. gumprechti* (mean=64.8, 58.1 in males and females respectively), so this character is less useful in distinguishing *T. vogeli* and *T. stejnegeri s.s*. This character contributes to the discriminant analysis of *T. vogeli* and *T. gumprechti* males only (Table 2).

18. *In* T. vogeli, *the number of cephalic scales in males is slightly higher than in males of* T. stejnegeri, *except for specimens from Hainan island*. The definition of this character appears to be similar to BTWSUPOC1. However, we found no significant differences between clades for this character, whether Hainan island specimens were included or excluded (P=0.385, 0.300 respectively) from *T. stejnegeri s.s.* However, this character did contribute to the discriminant analysis of females of the two species (with Hainan island included in *T. stejnegeri s.s.*).

19. *The total number of supralabials is higher in* T. vogeli *than in* T. stejnegeri, *except for Hainan island specimens*. Although this character was measured in this study as the average of right and left sides rather than the total number, this character was only found to differ significantly between clades in females (P=0.12, 0.02 in males and females respectively). Again, this was solely due to the difference between *T. vogeli* (mean=10.7, range=10–12) and *T. stejnegeri s.s*. (mean=10.1, range= 9–14), and will not serve to distinguish *T. vogeli* from *T. gumprechti*. This character also did not contribute to the discriminant analysis of *T. vogeli* and *T. stejnegeri s.s.*

20. *The third supralabials are much less frequently in contact with the subocular in males of* T. vogeli. This character was only found to differ significantly between clades in females (P=0.94, 0.01 for males and females respectively). However, post-hoc tests showed that the difference was mainly between *T. stejnegeri s.s.* and *T. gumprechti. T. vogeli* was not significantly different from *T. gumprechti* (P>0.1), and only just signficantly different from *T. stejngeri s.s.* (P=0.04). .

21. *The fourth supralabials are more frequently separated by at least two scales* (from the subocular) *in males of* T. vogeli. This character was not found to differ significantly between clades in our study (P=0.08, 0.64 for males, females).

22. *The microdermatoglyphic pattern is different*. The patterns of *T. vogeli* from Thailand are described as being identical to those of *T. popeiorum* (locality not specified), while being different from that of Chinese *T. stejnegeri.* We cannot add to this observation. However, the systematic value of these patterns has been questioned, as the relationships inferred from these patterns is often in conflict with those inferred from genetic data (Estos, 1981; Beyerlein, 1998). Thus the diagnostic value of this character needs to be further investigated in additional populations of *T. vogeli* and other species of the *T. stejnegeri* group.

A few additional points are cited as being characteristic of *T. vogeli* in other parts of David *et al*. (2001), which are not covered in the list above.

23. *Twenty-one scale rows at mid-body, strongly keeled*. Twenty-one scale rows at mid-body is characteristic of many species of green pitviper, including most of the *T. stejnegeri* group. Strong keeling of the scales at mid-body is only significantly different between female *T. vogeli* and *T. stejnegeri s.s.* (P<0.003), with no significant difference between *T. vogeli* and *T. gumprechti* (P >0.9). However, it is *T. stejnegeri s.s.* that is the more heavily keeled and this character does not contribute to the multivariate discrimination of the two clades.

24. *An elongated snout covered with rather small scales*. We did not measure this character directly and so cannot evaluate it statistically.

25. *Internasals always separated by 1 or 2 (rarely 3) scales*. The maximum number of internasals recorded is four. The mean is significantly different between clades in both sexes (P=0.05, 0.0004 in males and females respectively), but this is mainly due to a significantly higher mean in *T. vogeli* (mean=1.6, 2.0, range=1–4, 1–3 in males and females respectively) than in *T. gumprechti* (mean=1.2, 1.3, range=0–2, 1–2 in males and females respectively). This is reflected in INTNAS and/or WINTNAS being important in discriminating both sexes of *T. gumprechti* (Table 2).

26. *Large, irregular supraoculars, as wide as internasals*. The ratio of the length to the width of the supraoculars is given as 2.4–2.8. Our data (2.1–4.2) shows upper limit of the range is much higher. There is no significant difference between clades in either sex (P=1.0, 0.15 in males and females respectively).

DISCUSSION

The lack of agreement of our data with the distinguishing characteristics presented in the species description may be due to the limited geographic sampling of *T. vogeli* in David *et al*. (2001). We therefore present a detailed description of variation in the specimens of *T. vogeli* examined for this study from Thailand, Laos, Vietnam and Cambodia.

REDESCRIPTION OF VARIATION WITHIN *T. VOGELI*

Colour in preservative. The lateral stripe is always well developed in males and was seen, unusually, in one female from Sakaerat, Thailand. A white stripe is present on the upper half of the first scale row, extending onto the second row, and a darker (originally red) stripe is present on the lower half of the first scale row. Specimens from Dong Hua Sao NBCA, examined shortly after preservation when the background colour was bright blue, had very clear red stripes. Although they have since darkened to uniform steely grey blue, the red pigmentation on the first scale row is still visible. The ventral surface is lighter than the dorsal, and the tail is entirely uniform in colour, although traces of the lateral stripe continue onto the subcaudal scales to about the tenth pair. Upper lip coloration is not distinct from the rest of the head. About 30 small light vertebral flecks are present in males of all sizes. Postocular stripes are only occasionally present in males as indistinct pale streaks.

Colour in life. This description is based on photographs of male and female specimens from Dong Hua Sao NBCA, Laos, and a female from Khao Yai National Park, Thailand. Dorsal surface is dark to grass green, contrasting with the ventral surface, which is yellowish green. The lateral stripe, on the first two scale rows of the body, is red below and white above. The upper lip is slightly more yellow than the rest of the dorsal surface of the head, although this is not discernible in preserved specimens. The bright blue interstitial skin may be very obvious towards the posterior of the body. The last 20 or so subcaudals are darker (but not red), although there are occasional rows of lighter scales interspersed with this to give a banded appearance. The pale vertebral flecks, although small, are very obvious towards the posterior of the body. Eye colour is light orange. In females, the red and white lateral stripe is replaced by a narrow yellow stripe, and the contrast between dorsal and ventral colour is less marked. Eye colour appears to be the same in both sexes.

MORPHOMETRIC AND MERISTIC CHARACTERS.

Females have relatively shorter tails than males, fewer subcaudals (ranging in females from 52–70, compared to 61–72 in males), relatively larger heads, and reach an overall larger size (maximum recorded 99.0 cm SVL compared to 70.0 cm for males). The number of ventral scales varies between 157 and 173 in both sexes. Body scales range from having no keeling to fairly strong keeling, while temporal and rear head scales are never strongly keeled, and often unkeeled. The ratio of the upper and lower edges of the rostral scale varies between 0.2 and 0.5 (note that this character is not noticeably allometric as it is not correlated with any linear measurement on the head or body). Supralabials vary from 8–12 and sublabials from 10–14. The minimum number of scales between supraoculars varies from 9–13 and there are 13–18 scales between the posterior edges of the supraoculars. The number of scales between the nasals and shield bordering the anterior of the pit varies from 0–3, and there may be 1–4 internasal scales. There may be 0–1 scales between the third supralabial and the subocular, and 1–2 scales between the fourth and fifth supralabials and the subocular scale. Some of these scalation patterns are illustrated in Fig. 2.

DISTRIBUTION

Based on the presence of verifiable records, *T. vogeli* is presently known from the western Dongraek Mountains (Khao Yai National Park), the western edge of the Khorat Plateau (Sakaerat Experimental Station), and small isolated south-eastern mountains (Khao Sai Dao Wildlife Sanctuary) in Thailand, the Cardamom Mountains in Cambodia (Bokor National Park), the Bolovens Plateau (Dong Hua Sao NBCA) in Laos, and the Kontum Plateau of central Vietnam (Fig. 3). David *et al*. (2001) mention literature records which apparently refer to this species from Trat and Prachin Buri provinces in south-eastern Thailand, and Krabi Province in southern Thailand (Jintakune & Chanhome, 1995). A male from Krabi (pictured in Figs. 185 and 186 in Jintakune & Chanhome [1995], while a female from Trat is depicted in Figs. 187 and 188, not as stated in David *et al*. [2001]) has been examined by the senior author, and is confirmed as a member of the *T. stejnegeri* group. However, the specimen was obtained from a dealer and must be regarded as a provisional record until further specimens of known provenance are obtained.

NATURAL HISTORY

T. vogeli occupies hill areas from about 200 m (Sakaerat, Thailand) upwards to at least 1200 m (Dong Hua Sao NBCA, Laos) throughout the southern end of the Indochinese peninsula. It is primarily found in evergreen forest, occasionally in sparsely vegetated grasslands on high elevation plateaus (e.g. at Bokor National Park in the Cardamom Mountains and on the Bolovens Plateau in Laos) and semi-evergreen or dry evergreen forest at lower elevations (e.g. at the Sakaerat Experimental Station, Nakhon Ratchasima Province, Thailand). *T. vogeli* is often found near water, and most specimens were found within a couple of metres of the ground (Table 4). Frogs were the most frequent food

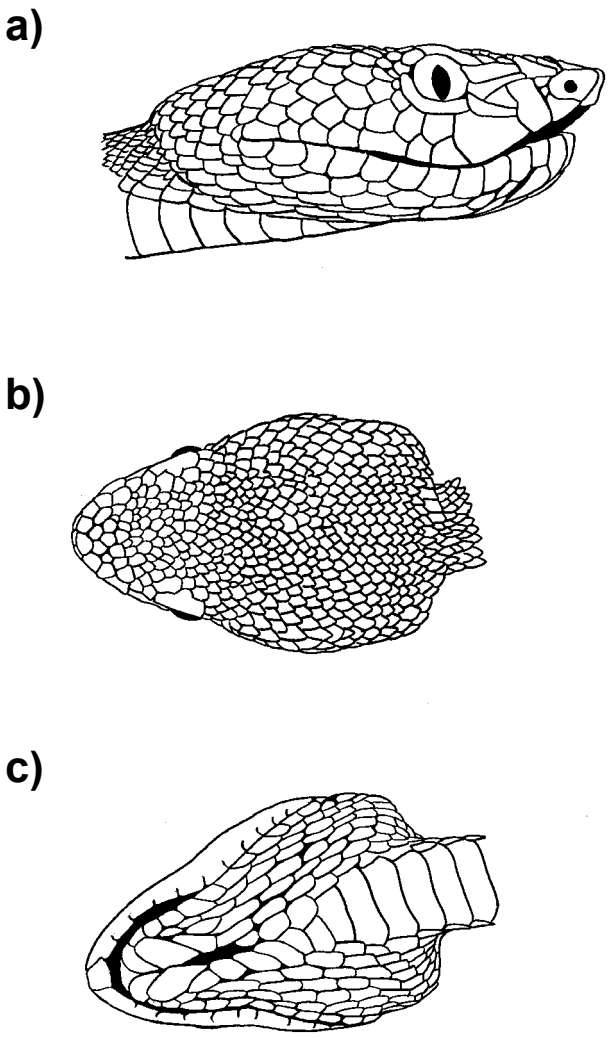

FIG. 2. Line drawing of the scalation on the head of a male specimen of *Trimeresurus vogeli* (FMNH 258946) from the Dong Hua Sao NBCA, Laos. a) lateral, b) dorsal, c) ventral.

items identified in the guts of the specimens examined (ROM 30782, 30785, 30786, FMNH 252076, 252099, 256419, 258946, RNHM 16716:1), followed by mammalian prey (FMNH 180258, 180273, 258944, ROM 34561). A skink was found in one adult female specimen (BMNH 2000.71) and insect remains in one juvenile specimen (FMNH 180277).

COMPARISONS

T. vogeli is presently known to share its geographic range with only two other green pitvipers, *T. albolabris* and *T. macrops*, both of which belong to the *T. albolabris* group (*sensu* Malhotra & Thorpe, 2000) and can be distinguished from the *T. vogeli* group by the partial to complete fusion of the first upper labial scale and nasal scale.

Trimeresurus vogeli is most similar to other members of *T. stejnegeri s.l.*, but can be distinguished from them by the lack of red on the tail. The extreme tip of the tail may be grey or brown, sometimes with a few bands, but

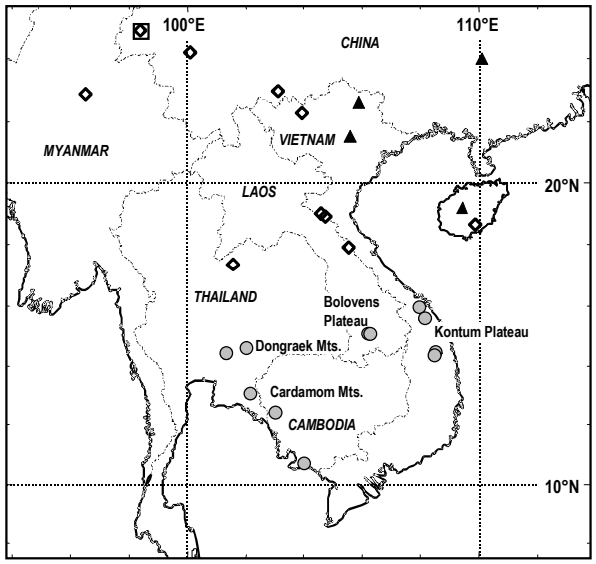

FIG. 3. Map of South-east Asia, showing the known distribution of *T. vogeli*. The occurrence of other members of the *T. stejnegeri* group in close proximity is also shown. Grey circles: *T. vogeli*; open diamonds: *T. gumprechti*; black triangles: *T. stejnegeri* (*s.s.*); black square: type locality of *T. yunnanensis*.

this is confined to the extreme distal portion of the tail. However, this character is not easy to distinguish in preserved specimens. *T. vogeli* is also morphologically distinguishable from other *T. stejnegeri* group species using multivariate analysis of characters. The values of the characters that contribute most to distinguishing the new species from both clades of *T. stejnegeri* are given in Table 2. *T. vogeli* can also be differentiated from all other species of the *T. stejnegeri* group by fixed molecular differences (14 fixed differences in a 737 bp stretch of the mitochondrial cytochrome *b* gene in the dataset used in Malhotra & Thorpe (in press) and available from GenBank, accession numbers AF277677-81, AF277709-11, AY059573, AY059575-6 for *T. stejnege*ri and *T. gumprechti* and AY059574, AY059577-81, AF171898 for *T. vogeli*. *T. vogeli* is also distinguished from all other green *Trimeresurus species*, except for *T. gramineus* and *T. popeiorum* from southern Thailand and Sumatra, by the lack of red on the tail. Male *T. vogeli* can be distinguished from *T. gramineus* and *T. popeiorum* by the presence of a hemipenis bearing 10-20 stout spines of varying size, largest near the base, with the tips being calyculate (identical to the hemipenis of *T. stejnegeri*, illustrated in Mao, Yin & Guo [1984]). Female *T. vogeli* can be distinguished from female *T. popeiorum* from populations which have similar tail coloration by the characteristics listed in Table 3. Diagnosis of this species will be more problematic for preserved specimens in which tail coloration cannot be reliably discerned, and which lack locality details. The characters given in Tables 2 and 3 can be used in combination to assist a diagnosis, but no single character will achieve this unequivocally.

TABLE 4. Natural history data for *T. vogeli*.

Museum number	Elevation (m)	Vegetation type	Distance from ground (m)	Proximity to water
FMNH 252070	700–750	bamboo thicket	-	River bank
FMNH 252076	700–750	wet evergreen	-	Near waterfall
FMNH 252097	700–750	wet evergreen	-	Near waterfall
FMNH 252099	700–750	wet evergreen	-	Near waterfall
FMNH 258940	1000	wet evergreen	0.5	Overhanging stream
FMNH 258941	1000	wet evergreen	1	3 m from stream
FMNH 258942	1000	wet evergreen	0.5	3 m from stream
FMNH 258943	1000	wet evergreen	1.5	Overhanging stream
FMNH 258944	1200	pine/grassland	0.5	None
FMNH 258945	1200	wet evergreen	1	3 m from large river
FMNH 258946	1200	wet evergreen	1	2 m from large river
FMNH 258952	1000	wet evergreen	0.4	8 m from stream
FMNH 258953	1000	wet evergreen	1.5	None
FMNH 259187	800–900	hill evergreen	2	5 m from stream
FMNH 259188	1000	heath forest	1.5	2 m from small pond
FMNH 180242	~ 200	dry evergreen	0.8	None
FMNH 180243	~ 200	dry evergreen	0	None
FMNH 180244	~ 200	dry evergreen	0.25	None
FMNH 180247	~ 200	dry evergreen	0	None
FMNH 180256	~ 200	dry evergreen	0.5	1 m from stream
FMNH 180257	~ 200	dry evergreen	0	None
FMNH 180258	~ 200	dry evergreen	2.5	None
FMNH 180259	~ 200	dry evergreen	1.5	None
FMNH 180260	~ 200	gallery	0	1 m from stream
FMNH 180261	~ 200	dry evergreen	1.2	None
FMNH 180263	~ 200	dry evergreen	0	None
FMNH 180265	~ 200	dry evergreen	0	None
FMNH 180269	~ 200	dry evergreen	0.3	3.5 m from stream
FMNH 180272	~ 200	dry evergreen	2.75	10 m from stream
FMNH 180273	~ 200	dry evergreen	2.5	None
FMNH 180274	~ 200	dry evergreen	0.6	None
FMNH 180277	~ 200	dry evergreen	< 1	None

Note added in proof. Since this paper was accepted changes to the taxonomy of the species discussed within have been made. The new generic names can be found in Malhotra & Thorpe (2004).

ACKNOWLEDGEMENTS

AM and RST are grateful to the following for field assistance or tissue samples: Jenny Daltry (Flora and Fauna International), Wen-hao Chou (National Museum of Natural Science, Taiwan), Tanya Chan-ard, Jarujin Nabhitabhata (National Science Museum of Thailand), Lawan Chanhome (Queen Savoabha Memorial Institute, Thailand), Kumthorn Thirakhupt and Peter Paul van Dijk (Chulalongkorn University, Thailand), Cheelaprabha Rangsiyanon (Chiang Mai University), Steve Paglia, Merel J. Cox, Jonathan Murray, Bob Murphy (Royal Ontario Museum, Canada), and Trinh Xuan Kiem (Cho-Ray Hospital, Vietnam). We acknowledge the National Science Council of Thailand, the National Science Council of Taiwan, Perhelitan, Malaysia, and the Ministry of Health, Vietnam for permission to carry out fieldwork. This study was funded (AM/RST) by the Leverhulme Trust (F174/I and F174/0), the Wellcome Trust (057257/Z/99/Z and 060384/Z/00/Z), and the Darwin Initiative (162/6/65), with additional support for fieldwork from the Royal Society, the Percy Sladen Trust, the Bonhote Trust, and the Carnegie Trust. The opportunity for BLS to work in Laos was made possible by the Wildlife Conservation Society/Division of Forest Resource Conservation Cooperative Program, and in Cambodia by the Wildlife Conservation Society / Ministry of Agriculture, Forestry and Fisheries / Ministry of Environment Cooperative Program. The Ministry of Agriculture and Forestry (Vientiane, Laos) and Ministry of Agriculture, Forestry and Fisheries (Phnom Penh, Cambodia) permitted export of specimens to the Field Museum. Fieldwork by BLS was supported by National Geographic Society Grant No.

6247-98 to Harold Heatwole. Harold Heatwole, Bee Thaovanseng, An Dara and Hout Piseth are thanked for fieldwork assistance, and Michael Hedemark, Arlyne Johnson, Troy Hansel, Suon Phalla, and Colin Poole are thanked for logistical support.

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Accepted: 25.6.03

APPENDIX 1

MORPHOLOGICAL CHARACTERS USED IN THE CANONICAL VARIATE ANALYSIS (CVA), AND THEIR ABBREVIATIONS.

(A) Scalation

VSC: the number of ventral scales (VS), not including anal scale, recorded by the Dowling (1951) method (i.e. the first VS is that which contacts the first dorsal scale row on both sides).
SCS: the number of pairs of subcaudal scales. Any unpaired scales are treated as a pair.
SUPLAB: the average number of supralabials on the left and right hand side.
SUBLAB: the average number of sublabials on the left and right hand side.
POSTOC: number of postocular scales.
PREOC: number of preocular scales.
BORSUPOC: the number of scales bordering the supraocular scales (average of right and left), not counting pre- or post-oculars.
BTWSUPOC1: the minimum number of scales between the supraoculars.
BTWSUPOC2: the number of scales between the posterior edge of the supraoculars.
INTNAS: the number of scales separating the internasal scales.
LAB3: minimum number of scales separating 3rd supralabial and subocular.
ROST: the ratio of the anterior margin of the rostral scale to the posterior margin.
KTEMP: the keeling of the temporal scales.
KHEADSC: the keeling of the scales on the back of the head.
VENTEDGE: the number of scales between the edge of the mouth and the ventral scales, starting at and including the last sublabial.

(B) Scale Reduction Formula

Recorded as a series of characters, each refering to a specific reduction. Each position will have two characters, the dorso-ventral (DV) position of the reduction (the lowest of the two merging scale rows), and the ventral scale (VS) position (counted from the head), which is the ventral scale to which the scale reduction traces diagonally. Before analysis, the VS position was transformed into the percentage of the total number of ventral scales (%VS), to control for variation.

VS31TO29: ventral scale position of the reduction from 31 to 29 scale rows.
DV31TO29: dorso-ventral position of reduction from 31 to 29 scale rows.
VS29TO27: ventral scale position of the reduction from 29 to 27 scale rows.
DV29TO27: dorsoventral position of reduction from 29 to 27 scale rows.
VS27TO25: ventral scale position of the reduction from 27 to 25 scale rows.
DV27TO25: dorsoventral position of reduction from 27 to 25 scale rows.
VS25TO23: ventral scale position of the reduction from 25 to 23 scale rows.
DV25TO23: dorsoventral position of reduction from 25 to 23 scale rows.
VS23TO21: ventral scale position of the reduction from 23 to 21 scale rows.
DV23TO21: dorsoventral position of reduction from 23 to 21 scale rows.
VS21TO19: ventral scale position of the reduction from 21 to 19 scale rows.
DV21TO19: dorsoventral position of reduction from 21 to 19 scale rows.
VS19TO17: ventral scale position of the reduction from 19 to 17 scale rows.
DV19TO17: dorsoventral position of reduction from 19 to 17 scale rows.
VS17TO15: ventral position of the reduction from 17 to 15 scale rows.
DV17TO15: dorsoventral position of reduction from 17 to 15 scale rows.
SC12TO10: subcaudal scale position of the reduction from 12 to 10 scale rows.
DV12TO10: dorsoventral position of reduction from 12 to 10 scale rows.
SC10TO8: subcaudal scale position of the reduction from 10 to 8 scale rows.
DV10TO8: dorsoventral position of reduction from 10 to 8 scale rows.
SC8TO6: subcaudal scale position of the reduction from 8 to 6 scale rows.
SC6TO4: subcaudal scale position of the reduction from 6 to 4 scale rows.

(C) Body Dimensions

All measurements are made on the right side of the head only unless this was damaged, in which case they were done on the left.

SVL: distance between the tip of the snout and the cloaca.
TAIL: distance between the anterior edge of the first subcaudal scale and the tip of the tail.
WHEAD: width of the head measured between the outer edges of the supraoculars.
LHEAD: length of the head measured between the tip of the snout to the posterior edge of the lower jawbone.
DEYE: diameter of the eye measured between the edges of the scales surrounding it.
EYE2NOS: distance between the eye and the nostril, measured between the suture between the second and third preocular (from the bottom) and the inner edge of the nostril.
NOS2PIT: distance between the pit and the nostril, measured between the outer edges.
WSUPOC: the width of the supraoculars measured in mm, at the widest part.
LSUPOC: the length of the supraoculars measured in mm.

WINTNAS: the width of the internasals (in mm).

(D) Internal Characters

VS positions are transformed to % VS before analysis (see scale reductions).

PTERY: the number of pterygoid teeth.

DENT: the number of dentary teeth.

HTANT: VS position of the thyroid gland.

LVANT: VS position of the anterior tip of the liver.

RKANT: VS position of the anterior tip of the right kidney.

RKPOST: VS position of the posterior tip of the right kidney.

LKANT: VS position of the anterior tip of the left kidney.

LKPOST: VS position of the posterior tip of the left kidney.

RETRACT: SC position of the insertion of the hemipenis retractor muscle (males only).

(E) Colour Pattern

STRIPE: presence of a lateral stripe (0, absent; 1, indistinct; 2, distinct).

SCRSTR: number of scale rows involved in stripe.

OCSTRIPE: presence of postocular stripe (0, absent; 1, indistinct; 2, distinct).

SCROC: number of scale rows involved in postocular stripe.

DORSPOT: the number of spots on the dorsal surface.

SPOTSIZE: the mean number of scales covered by the three largest dorsal spots.

SCR1: the proportion of the first scale row covered by the light area.

APPENDIX 2

SPECIMENS EXAMINED

Specimens not used in the canonical variate analysis (CVA) are indicated in italics. Abbreviations are as follows: American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Field Museum, Chicago (FMNH); Museum of Comparative Zoology, Harvard (MCZ); National Museum of Natural Science, Taiwan (NMNS); Naturhistorisches Museum Wien (NMW); Phu Luang Wildlife Research Station, Thailand (PLWRS); Royal Ontario Museum, Toronto (ROM); Shanghai Natural History Museum (SNHM); United States National Museum of Natural History, Smithsonian Institute; Washington (USNM); the author's personal collection (AM and RTV).

T. STEJNEGERI (S.S.)

Northern China: SNHM 729159, MCZ 163259, AMNH 33222-9, BMNH 99.4.24.61, BMNH 54.2.10.18, FMNH 25196-204, FMNH 170642, USNM 73140, NMNS 3651: 12347, 12349, 12351, 12354, NMW 23913:1, CAS 71957, USNM 64022-23;

Taiwan: FMNH 96807-11, FMNH 96816, FMNH 120772-5, NMNS 01882-7, NMNS 01889, NMNS 01334:1-3, NMNS 01549, NMNS 01584, NMNS 01434, NMNS 01479, NMNS 01722, NMNS 01841, NMNS 01845;

Southern China: SNHM 720068, SNHM 112-3;

Northern Vietnam: NMW 23913:3, ROM 35312-15, ROM 35318, ROM 35320-22, ROM 31066, ROM 31068, ROM 31072, AM99.15, AM99.17-18;

Hainan, China: SNHM 500128-9, SNHM 720065, SNHM 720069-72;

T. GUMPRECHTI

Annamite Mountains (Laos and Vietnam): FMNH 255579-80, FMNH 256419;

North-eastern Thailand: PLWRS 3-5, PLWRS 920503, AM94.1, AM94.3-18, AM94.20;

T. VOGELI

Central Vietnam: NMW 23913:2 (locality listed as Annam, Tonkin; both names refer to parts of what is now Vietnam, and is referred to this species on the basis of morphological analysis), ROM 30781, 30782, 30785, 30786, 30788, 30791, 25403 (Tram Lap District, Gia Lai Province, Vietnam, 14° 26' N, 108 33' E), ROM 34559-61, 34565 (Krong Pa District, Gia Lai Province, Vietnam, 14° 20' N, 108° 28' E), FMNH 252076, 252097, 252099 (Buon Luoi, 20 km north-west of Kannack, Ankhe District, Gia Lai Province, Vietnam, 14° 20' N, 108° 36'E), USNM 163967 (0.1 mile south, 1 mile west of Mt Sontra, Quang Nam, Vietnam), FMNH 1153 (Bana, Vietnam, 15° 59' N, 107° 59' E);

Bolovens Plateau, Laos: FMNH 258940-6, *FMNH 258952-53* (from the Dong Hua Sao National Biodiversity Conservation Area (NBCA), Pakxong District, Champasak Province, Laos, 15 03' 55" N, 106 13' 03" E);

Cardamom Mountains, Cambodia and south-eastern Thailand: BMNH 2000.71 (Tumpor Mt, Mt Samkos Wildlife Sanctuary, Pursat Province, Cambodia, 12° 26' N, 103° 02' E), RNHM 16716:1-2 (Khao Soi Dao Wildlife Sanctuary, Chantaburi Province, Thailand); *FMNH 259187-88* (Bokor National Park, Kampot Province, Kampot District, south-eastern Cardamom Mountains, Cambodia, 10° 38' 33" N, 104° 1' 33" E);

Dongraek Mountains and edge of Khorat Plateau, Thailand: RTV9-10 (trade), AM99.5, FMNH 180272 (Khao Yai National Park, Nakhon Ratchasima Province), FMNH 180242-44, 180247, 180256-61, 180263-65, 180269, 180273-74, 180277 (Sakaerat Experimental Station, Amphoe Pak Thong Chai, Nakhon Ratchasima Province, 14° 36' N, 102° 2' E).