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A review of morphological variation in *Trimeresurus popeiorum* (Serpentes: Viperidae: Crotalinae), with the description of two new species

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ABSTRACT

Variation in morphological characters were investigated among 136 specimens (128 specimens examined by us and eight specimens described in the literature) from 44 populations of the whole range of the pitviper currently known as *Trimeresurus popeiorum* Smith, 1937. Univariate and mul-

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tivariate analyses of these morphological characters allowed us to recognize six clusters of populations that are morphologically diagnosable, and that are here considered to represent independent lineages. Five of these clusters are considered to be distinct species following the Biological Species Concept and the Phylogenetic Species Concept. Two of them are described as new. *Trimeresurus fucatus* spec. nov. includes populations from southern Thailand and most of West Malaysia. *Trimeresurus nebularis* spec. nov. is described for populations from Cameron Highlands of West Malaysia. A population from Toba Massif, northern Sumatra, is referred to this complex, but cannot be assigned to a species at the present time. *Trimeresurus popeiorum sabahi* is raised to specific status, *Trimeresurus sabahi* new comb., to accommodate the populations from Borneo, whereas *Trimeresurus barati* new comb. includes the populations from western Sumatra and the Mentawai Archipelago. Separate keys to the two sexes of the recognised species of the *T. popeiorum* complex are provided.

KEY WORDS: Thailand, West Malaysia, Sumatra, Borneo, Serpentes, Viperidae, *Trimeresurus*, *Trimeresurus popeiorum*, *Trimeresurus fucatus* spec. nov., *Trimeresurus nebularis* spec. nov., *Trimeresurus sabahi*, *Trimeresurus barati*

INTRODUCTION

Before the paper by Pope & Pope (1933), all green *Trimeresurus* species were gathered under the name *Trimeresurus gramineus* (Shaw, 1802). In a first step towards understanding the systematics of the genus, these authors split the nominal taxon *gramineus* into six species. The specific nomen *gramineus* was applied to a widespread species, ranging from northeastern India to western Indonesia. Indian populations were referred to a new species described as *Trimeresurus occidentalis*. Subsequently, Smith (1937) correctly showed that Pope & Pope (1933) misunderstood the type locality of *gramineus*, and showed that the type locality for *T. gramineus* was within the range of *T. occidentalis*. Therefore, *Trimeresurus occidentalis* Pope & Pope 1933 became a subjective junior synonym of *T. gramineus* (Shaw, 1802), leaving unnamed the distinct eastern taxon. Smith (1937) named it as *Trimeresurus popeiorum*. Unfortunately, he failed to designate a type specimen and a type locality for this new taxon. This interpretation was accepted by most subsequent authors except Hoge & Romano Hoge (1981) and Welch (1988). Another issue affecting the specific nomen is its spelling. Smith (1943) corrected the original spelling as *popeorum* on the basis that it was indeed a clerical error. This spelling was largely accepted, and was the subject of recent controversies. This problem will be addressed in another paper (David & Vogel, submitted). We consider that the correct spelling is indeed *popeiorum*. Eventually, Taylor & Elbel (1958), regarded as syntypes of *Trimeresurus popeiorum* Smith, 1937 all specimens referred by Pope & Pope (1933) to as *T. gramineus*, and designated the specimen BMNH 72.4.17.137 as the lectotype of the species. Consequently, the type locality was restricted to “Khasi Hills, Assam”, now in the State of Meghalaya, India.

Trimeresurus popeiorum was revised by Regenass & Kramer (1981) in a wider taxonomic investigation of the green Asian pitvipers. These authors described two new subspecies, *Trimeresurus popeiorum barati* and *T. popeiorum sabahi* to include populations of the islands of Sumatra and Borneo respectively, and conserved the nominotypical subspecies for all mainland populations. This interpretation was not subsequently modified. Vogel (1990) pointed out that a green *Trimeresurus* form from southern Thailand, that was often called *Trimeresurus erythrurus* in the pet trade, might represent a distinct taxon close to *T. popeiorum*. Several differences with *T. popeiorum*, as then defined, were noted, but no taxonomic decision was then taken. Within the framework of our study of members of the *Trimeresurus* complex, we examined a large series of specimens identified as *Trimeresurus popeiorum*. We here analyse this variation, which revealed several constant morphological differences between six clusters of populations that are considered to be taxonomically meaningful.

MATERIAL AND METHODS

The present paper is based on 128 preserved specimens examined by us from 44 localities from the whole range of *Trimeresurus popeiorum*, 8 specimens of unambiguous identification described in the literature (Taylor [1965] for two specimens of *Trimeresurus popeiorum* and Regenass & Kramer [1981], for insular taxa only), and 10 living specimens of the *Trimeresurus popeiorum* complex. Preserved specimens examined are listed under each relevant taxon. Living specimens used for this paper will be deposited in the collections of the MNHN and ZFMK upon their death.

Selection of morphological characters. We retained standard morphological characters used by Pope & Pope (1933), Regenass & Kramer (1981), along with other morphometric characters adapted from How et al. (1996). Measurements, except body and tail lengths, were taken with a slide-caliper to the nearest 0.1 mm; all measures on body were taken to the nearest millimetre. In order to minimize interobserver error, all measurements considered here were made by PD. Ventral scales were counted according to Dowling (1951). The terminal scute is excluded from the number of subcaudals. The numbers of dorsal scale rows are given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total number of ventrals) and at one head length before vent respectively. Values for symmetric head characters are given in left/right order. The real coloration of body and eyes were observed only on living animals or very freshly preserved specimens. The terminology used in the description of hemipenes follows Böhme (1988).

Morphometric and meristic characters retained for this study are listed in Table 1. Altogether, 66 morphological variables were considered, either standing on their own or derived from the raw characters listed above. Not all variables listed in this table proved to be useful to separate at least one taxon of the *Trimeresurus popeiorum* complex from the others, but all were investigated and used in combinations of characters and/or were used in univariate and multivariate analyses.

The colour of the eyes is problematic, as it proved to be of taxonomic value in our study, but usually cannot be observed in preserved specimens. According to our observations, the eye colour in adult animals is stable for each species and sex. There is however ontogenetic variation, as taxa with red eye colour in adults may have yellow eyes in very young animals. This phenomenon is also known in males of *Trimeresurus gumprechti*. The colour of the tail is diagnostic, too. Some populations have a sharp border between the reddish-brown and the green areas of the tail, so that the tail is totally green laterally, whereas most other populations have the tail mottled on its sides with green and rusty brown or even darkened with brown. If the tail coloration can hardly be described accurately in many preserved specimens, however the general pattern of the tail can be ascertained in most specimens. We thus here consider two kinds of pattern: "Uniform", for specimens which show the first pattern described above, or "Mottled", for the second case.

Selection of taxonomic units. A preliminary investigation showed morphological homogeneity between members of some of these populations, but constant differences with others. Following Wüster & Thorpe (1992) and the morphology of specimens according to their origin, we divided the investigated area into 12 operational taxonomic units (OTU). On the basis of geographic considerations, the populations were chosen as follows:

OTU 1 (2♂ 3♀): northeastern India (States of Sikkim, Arunachal Pradesh and Meghalaya, and other parts of northeastern India). OTU 2 (6♂ 3♀): Myanmar (all states and divisions except the south as defined in OTU 3). OTU 3 (2 ♂): southern Myanmar (central and southern Taninthayi Division). OTU 4 (12♂ 6♀): northern Thailand (here including Provinces of Chiangmai, Lampang, and Phitsanulok) and Laos. OTU 5 (2 ♂, alive, not included in calculations): western Thailand (here including only Tak Province). OTU 6 (25♂ 8♀): southern Thailand (Phetchaburi Province and all provinces further south). OTU 7 (3♂ 5♀): West Malaysia (Cameron Highlands). OTU 8 (13♂ 11♀): West Malaysia (all localities, except Cameron Highlands and Pulau Tioman). OTU 9 (1 ♂): West Malaysia (Pulau Tioman). OTU 10 (9♂ 5♀): Borneo Island. OTU 11 (13♂ 6♀): western and southern Sumatra Island. OTU 12 (2♂ 1♀): northern Sumatra Island.

Analyses of morphological data. Data were analysed in using both univariate and multivariate analyses. All ratios involving measures of any part of head were considered only in adult specimens in order to cope with ontogenetic variation. On the basis of mean values of TL observed in our sample, we arbitrarily fixed as 400 mm (TL) the lower limit to regard examined specimens as adult.

Univariate analyses. The analyses of external morphological data were based on comparisons of statistical values (mean value and standard deviations). A test of Mann-Whitney (U test; see Siegel, 1956) was applied as necessary.

Abbreviations are: n: number of specimens. x: mean value. s: standard deviation. P:

probability of occurrence of a value as extreme as or more extreme than the observed value. U: the statistic in the Mann-Whitney test.

Multivariate analyses. The main multivariate method used in this study is the Principal Component Analysis (PCA). All PCA analyses were run on the software Statistica 5.5 (Statsoft Inc., USA). These analyses were performed independently from an a priori classification of a total of 109 specimens. Both sexes were treated separately (68 males, 41 females), as our raw data showed strong sex-related differences in several morphological characters. Only adult specimens, as defined above, were considered for morphometric characters. PCA analyses were based on 18 log-transformed scalation variables selected among those listed in Table 1: NVEN, NSC, NASR, NMSR, NPSR, KDSR, TNSL, C3SL, C4SL, C45SL, NCep, CSupOC, KOcc, KTem, NInN, NSnSc, NHeSc and TNIL. Mean values of lateral variables were used. The variable SVL (reductant variable) was excluded. The first two canonical roots were used to generate graphs (see below).

TABLE 1. List of morphological characters and variables used in this study and their abbreviations.

Number	Abbreviation	Character
Morphometry		
1	SVL	Snout-vent length
2	TaL	Tail length
3	TL	Total length
4	HL	Head length
5	SnL	Snout length (from the tip of rostral to a line connecting the anterior eye margins)
6	HED	Eye diameter (horizontal)
7	VED	Eye diameter (vertical)
8	DEL	Distance lower eye margin–edge of the lip
9	DEN	Distance between the anterior eye margin and the nostril
10	DEP	Distance between the anterior eye margin and the loreal pit
11	WInN	Width of internasals (means)
12	LSupOc	Length of supraoculars
13	WSupOc	Width of supraoculars
14	L3SL	Length of 3rd supralabial
15	H3SL	Height of 3rd supralabial
16	H4SL	Length of 4th supralabial
17	TaL/TL	Ratio tail length/Total length
18	SnL/HL	Ratio snout length/head length
19	DEP/HL	Ratio distance eye–pit/head length
20	DEN/HL	Ratio distance eye–nostril/head length

......*continued on the next page*

TABLE 1 (continued)

Number	Abbreviation	Character
21	DEP/DEN	Ratio distance eye–pit/distance eye–nostril
22	WInN/WSupOc	Ratio width of internasals/width of supraoculars
23	L3SL/HL	Ratio length of 3rd supralabial/head length
24	VED/DEL	Ratio: vertical eye diameter/distance eye margin–edge of the lip
25	LSupOc/ WsupOc	Ratio of the length of supraocular/width of the supraoculars
Scalation		
26	DSR	Dorsal scale rows
27	MSR	Dorsal scale rows at midbody
28	VEN	Ventral plates
29	SC	Subcaudal plates
30	SL	Supralabial scales
31	HeSc	Head scales (scales on a longitudinal row between the internasals and the limit of the neck)
32	SnSc	Snout scales (scales on a line between the internasals and a line connecting the anterior margin of eye)
33	InN	Internasal scale(s)
34	Can	Canthal scales (scales between the internasal and the subocular)
35	Cep	Cephalic scales (scales on a line between the middle of supraoculars)
36	Tem	Temporal scales
37	IL	Infralabials
38	NVEN	Number of ventral plates
39	NSC	Number of subcaudal plates
40	NASR	Number of dorsal scale rows behind head
41	NMSR	Number of dorsal scale rows at midbody
42	NPSR	Number of dorsal scale rows before vent
43	KMSR	Keeling of dorsal scale rows at midbody
44	TNSL	Total number of supralabial scales
45	C3SL	Number of scales between 3rd supralabial and subocular
46	C4SL	Number of scales between 4th supralabial and subocular
47	C45SL	Number of scales between 4th and 5th supralabial and subocular
48	NCep	Number of cephalic scales on a line between the supraoculars
49	KOcc	Keeling of the occipital scales
50	KTem	Keeling of temporal scales
51	NInN	Number of scales separating the internasals
52	CSupOC	Number of scales directly in contact with supraocular

......continued on the next page

TABLE 1 (continued)

Number	Abbreviation	Character
53	NSnSc	Number of snout scales (defined as above)
54	NHeSc	Number of longitudinal head scales (defined as above)
55	TNIL	Total number of infralabial scales
Pattern		
56	DBB	Presence of darker bands on body
57	VSB	Presence of a line of white vertebral spots
58	POSTM	Presence of a postocular streak in males
59	POSTF	Presence of a postocular streak in females
60	CPOST	Coloration of the postocular streak
61	VELSM	Presence of a ventrolateral stripe in males
62	VELSF	Presence of a ventrolateral stripe in females
63	CVEL	Coloration of the ventrolateral stripe
64	COLEM	Colour of eyes in males
65	COLEF	Colour of eyes in females
66	TAP	Pattern of the tail.

The specimens were classified to predicted OTUs using Discriminant Canonical Analyses (DCA). Analyses were carried out for males and females independently for the same reasons as stated above. The analyses were performed on a total of 107 specimens (66 males, 41 females). The three specimens placed in OTU 12 were excluded from DCA analyses. These analyses were based on 18 log-transformed scalation variables selected among those listed in Table 1: NVEN, NSC, NASR, NMSR, NPSR, KDSR, TNSL, C3SL, C4SL, C45SL, NCep, CSupOC, KOcc, KTem, NInN, NSnSc, NHeSc and TNIL.

A MANCOVA test was used to determine significant morphometric variables. A total of 13 variables were used (HL, SnL, VED, DEL, DEN, DEP, WInN, LSupOc, WSupOC, L3SL, H3SL, H4SL), and SVL (covariable). Factors: Sex (Males / Females) and Clusters (I, II, III, IV and V). Specimens from OTU 12 were excluded. The MANCOVA test was conducted on a total sample of 106 specimens.

A MANOVA analysis was performed in using 18 log-transformed scalation variables (NVEN, NSC, NASR, NMSR, NPSR, KDSR, TNSL, C3SL, C4SL, C45SL, NCep, CSupOC, KOcc, KTem, NInN, NSnSc, NHeSc and TNIL) on a total of 106 specimens. Factors: Sex (Males / Females), Cluster (I, II, III, IV and V). Specimens from OTU 12 were also excluded.

Museum abbreviations. BMNH: The Natural History Museum, London, UK. CAS: California Academy of Sciences, San Francisco, USA. FMNH: Field Museum of Natural History, Chicago, USA. IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA. MNHN: Muséum National d'Histoire Naturelle, Paris, France. NHMB: Naturhistorisches Museum, Basel, Switzerland. NHMW: Naturhistorisches Museum Wien, Austria. NMBE: Naturhistorisches Museum Bern, Switzerland. PSGV: Gernot Vogels private collection, Heidelberg, Germany. QSMI: Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand. RMNH: Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands. SMF: Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany. ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. ZMH: Zoologisches Institut und Museum, Universität Hamburg, Hamburg, Germany. ZRC: Zoological Reference Collection, National University of Singapore, Singapore. ZSM: Zoologische Staatssammlung, München, Germany.

RESULTS

Multivariate analyses. The following multivariate analyses were performed: PCA (Principal Component Analysis), DCA (Discriminant Canonical Analysis) and a MANCOVA test. Score of each variable on the two first principal components (males and females separated), results of DCA analyses (males and females separated) with Eigenvalues and Cumulative variability, and results of MANCOVA and MANOVA tests appear in Tables 2–11 respectively. Graphs generated by these analyses are shown in Figs. 1–4 respectively.

Principal Component Analysis (PCA)

PCA in males (68 specimens) gave the following results indicated in Tables 2–3. The two first principal components explain a moderate total variability. All variables show positive loadings in 1st PC. Variables VEN and TNSL are the most positively loaded, in contrast to the lower load of NInN. In the second PC, most variables related to head scalation show negative loadings, especially NSnSc. With the only exception of NDSR, variables related to body scalation have positive loadings, KMSR being the most positively loaded one. Results of the PCA in males are plotted in Fig. 1. In this graph, plots of the two first PC show five groups: Cluster V, Cluster IV, Cluster I and Cluster II, and Cluster III, close to Clusters V and IV. Clusters I and II are differentiated but comparatively close. There is little overlap among these two clusters, at the exception of two specimens which are discussed below. The two male specimens of OTU 12 are placed either close to Cluster I or between Clusters IV and V. Clusters IV and V show very high influence of NinN and C4SL, average for NCep and low for NVEN and TNSL. Clusters I and II have higher values of NVEN and NHeSc, and lower influence of NInN and C4SL.

TABLE 2. Eigenvalues and Percentage of Cumulative variability in males.

PCA	Eigenvalue	Percentage of Cumulative variability
1st	4.731886	26.29
2nd	1.926896	36.99

TABLE 3. Scores of each variable on the two first principal components in males.

Variable	PC1	PC2
NVEN	0,826213	0,1870635
NSC	0,529266	0,1406145
NASR	0,543645	0,1907918
NMSR	0,618206	0,1427035
NDSR	0,315793	-0,0234553
KMSR	0,574077	0,4129249
TNSL	0,648355	0,1279692
C3SL	0,555731	-0,1408118
C4SL	0,094435	-0,3459907
C45SL	0,116134	-0,1260699
NCep	0,405939	-0,5093861
CSupOC	0,475728	-0,2973736
KOcc	0,610400	0,2088747
KTem	0,591761	0,3068280
NInN	0,073117	-0,5820242
NSnSc	0,322609	-0,6458032
NHeSc	0,631764	-0,4798492
TNIL	0,536713	-0,0274488

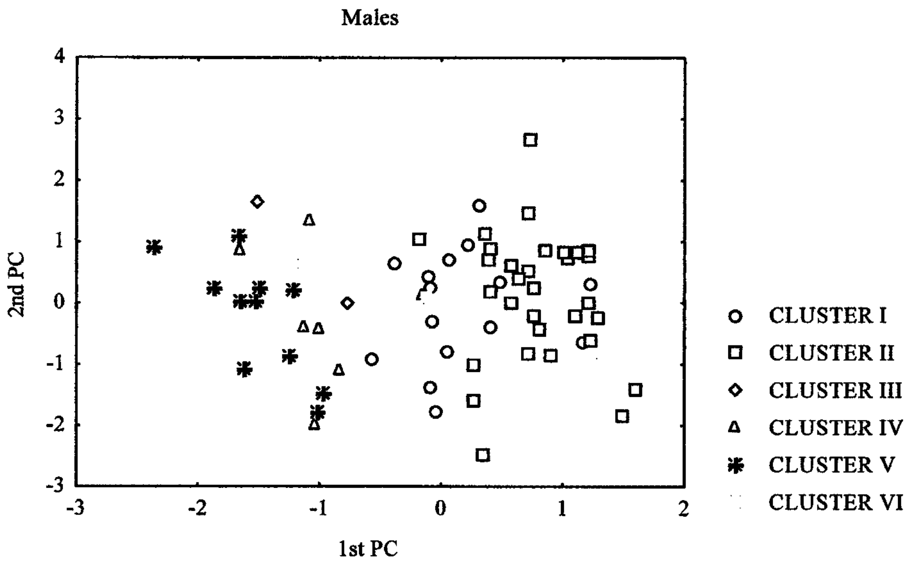

FIGURE 1. Plot of first two canonical variables of the Principal Component Analysis on males of the *Trimeresurus popeiorum* group.

PCA in females (41 specimens) gave the results presented in Tables 4–5 and Fig. 2. The first and second PC explain a moderate total variability, similar to males although comparatively slightly higher. The first principal component shows high positive loadings of HeSc, NCep, Kocc and TNIL, and inversely a lowest load of NDSR and NKSR. Hence, these variables polarize the specimens in these PC. The second principal component is strongly structured by variables related to cephalic scalation, NinN, NSnSc, TNIL and NCep, all with negative loads. In contrast, variables related to body scalation showing the highest positively loads are NMSR, NDSR and NVEN. As in males, the graph (Fig. 2) of the plots of the two first PC in females shows four groups: Cluster III, Cluster IV, Cluster V and Cluster I + II, with again a close proximity between Clusters I and II. The sole female specimen of OTU 12 is placed between Cluster V, Cluster IV and Cluster I + II. Clusters I and II show high influence of NCep and NVEN and low influence of NDSR and NInN. Cluster III shows high action of NDSR, NVEN and low influence of NHeSc, NCep and NinN. Cluster V is characterized by a high influence of NDSR and NVEN and low influences of NinN and Ncep; Cluster IV shows values intermediate between Clusters III and V.

TABLE 4. Eigenvalues and Percentage of Cumulative variability in females

PCA	Eigenvalue	Percentage of Cumulative variability
1st	4,995289	27,75
2nd	2,180380	39,86

TABLE 5. Scores of each variable on the two first principal components in females.

Variable	PC1	PC2
NVEN	0,745796	0,4959339
NSC	0,668053	0,1799324
NASR	0,499779	0,3166725
NMSR	0,371556	0,6626531
NDSR	-0,018360	0,4767301
KMSR	0,227735	0,1736255
TNSL	0,578710	-0,1797968
C3SL	0,390826	0,0955095
C4SL	0,257609	0,1442838
C45SL	0,443001	0,3092670
NCep	0,764373	-0,3515846
CSupOC	0,479522	-0,3108519
KOcc	0,614987	0,1657900
KTem	0,450537	0,1013386
NInN	0,233872	-0,5296241
NSnSc	0,510397	-0,4670201
NHeSc	0,797652	-0,1571126
TNIL	0,675002	-0,4074823

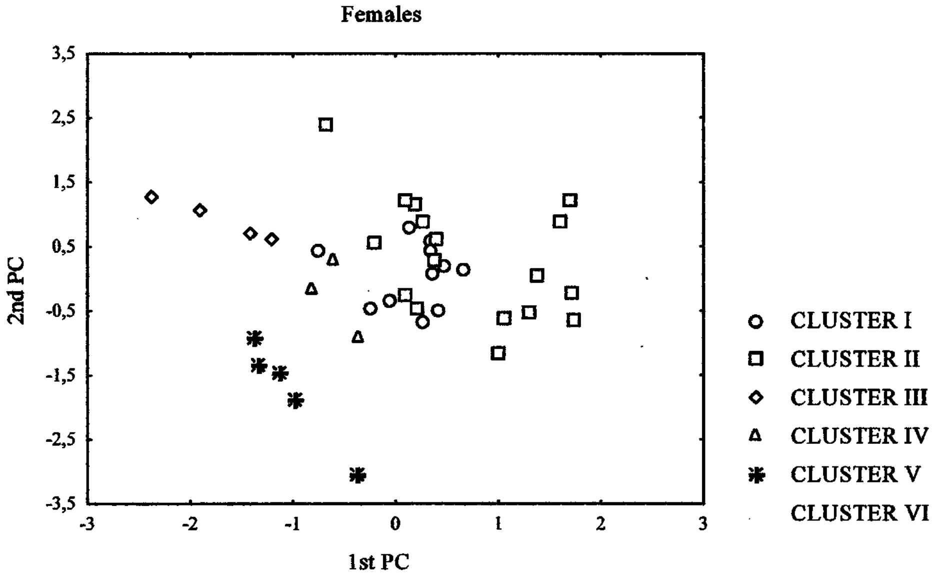

FIGURE 2. Plot of first two canonical variables of the Principal Component Analysis on females of the *Trimeresurus popeiorum* group.

The results of the PCA in males (Fig. 1) and in females (Fig. 2) show in both cases the occurrence of five clusters of plots, identified as Cluster I to V on the graph. According to the OTUs defined above, these clusters are generated by specimens according to the following scheme, without any mixing between OTUs at the exception of two specimens of OTU 4 appearing in Cluster II. These specimens are discussed below.

Cluster I: OTU 1 + OTU 2 + OTU 4 + OTU 5
Cluster II: OTU 3 + OTU 6 + OTU 8 + OTU 9 (plus 2 specimens of OTU 4)
Cluster III: OTU 7
Cluster IV: OTU 10
Cluster V: OTU 11

The two male specimens of the OTU 12 are placed either close to Cluster I or, for the second one, between Clusters IV and V. Due to the low amount of available material, these results make the interpretation of the graph difficult for these specimens. It suggests that, although originating from the same locality, they would belong to two different clusters. For the sake of convenience, we place in a sixth cluster the specimens of OTU 12, all three originating from the same locality.

Discriminant Canonical Analysis (DCA)

The DCA was performed on a final sample of 107 specimens. However, due to limited samples available in some clusters or missing information in specimens, a significative regression to obtain residuals could not be performed. Morphometric measurements were excluded, and DCA were done in using only log-transformed pholidotic variables. Results are presented in Tables 6–9. Graphs of the DCA for males (66 specimens) and females (41 specimens) appear on Figs. 3–4 respectively.

TABLE 6. DCA Analyses. Eigenvalues and Percentage of Cumulative variability in males

DCA	Eigenvalue	Percentage of Cumulative variability
1st	23,2251148	2,82303
2nd	0,8017624	0,89922

TABLE 7. DCA Analyses. Scores of each variable on the two first canonical roots in males.

Variable	1st Canonical root	2nd Canonical root
NVEN	-0,6812993	-0,4201907
NSC	0,1136673	-0,4063711
NASR	-0,3569256	-0,1654710
NMSR	-0,9766082	0,6432408
NDSR	-0,1693844	0,0983768
KMSR	0,2714834	-0,2673491
TNSL	-0,3887179	0,0825614
C3SL	0,2795490	0,0711077
C4SL	-0,0668861	0,0463007
C45SL	-0,2449031	-0,4005521
NCep	-0,4217636	-0,2022168
CSupOC	0,2384583	0,2723742
KOcc	-0,7434848	-0,0276876
KTem	-0,0747214	-0,0366586
NInN	0,2419945	-0,1247776
NSnSc	-0,1881291	-0,0345630
NHeSc	-0,5232323	-0,0692010
TNIL	-0,0366216	-0,6041005

TABLE 8. DCA Analyses. Eigenvalues and Percentage of Cumulative variability in females.

DCA	Eigenvalue	Percentage of Cumulative variability
1st	43,0357323	7,04148
2nd	0,81140083	0,94416

TABLE 9. DCA Analyses. Scores of each variable on the two first canonical roots in females.

Variable	1st Canonical root	2nd Canonical root
NVEN	-0,5443161	0,9684833
NSC	-0,3565063	0,1385541
NASR	0,2331533	-0,6794884
NMSR	-1,1877324	-0,4752084
NDSR	0,0809883	-0,1641757
KMSR	0,1206765	0,0134911
TNSL	-0,4437366	0,4046829
C3SL	0,3059078	0,1943754
C4SL	0,2486527	-0,4178887
C45SL	0,0735177	-0,3098882
NCep	0,1750976	0,9245650
CSupOC	-0,3421841	-0,1269829
KOcc	-0,3932099	0,2682046
KTem	0,1166298	-0,4352555
NInN	0,0207201	-0,3773321
NSnSc	0,1961537	-0,7490384
NHeSc	-0,7631642	0,5762838
TNIL	0,5850396	0,0601266

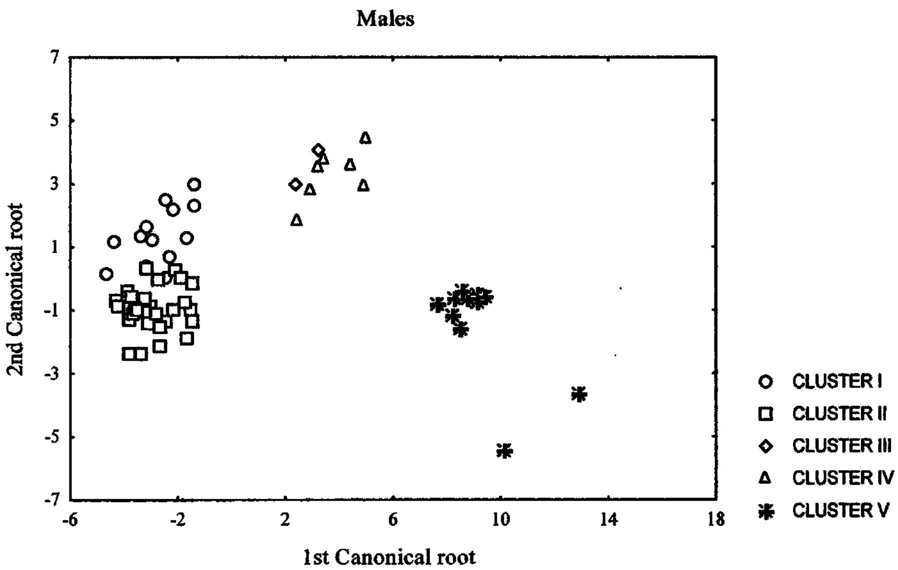

FIGURE 3. Plot of first two canonical variables of the Discriminant Canonical Analysis on males of the *Trimeresurus popeiorum* group.

A high variability is obtained from the first two canonical roots. According to the coefficients, the most discriminant variables in the first root are NInN, C3SL and KMSR (positive) and NVEN, KOcc and NMSR (negative). In the second root, NMSR (positive) and TNIL (negative) are the most important variables, but the importance of this root is secondary. On the graph of DCA in males (Fig. 3), Clusters III, IV and V are well differentiated but we again find some overlap between Clusters I and II. Results show a sharper separation between Cluster III and Cluster IV (less VEN and MSR) and a lower overlap between Cluster I and Cluster II (more VEN and MSR). Specimens of OTU 12 are placed among Cluster III and IV. There is no clear structure or significance of both canonical root, but its higher variability probe that they are powerfull separating the groups.

In females, a high percentage of variability is also contained in the two first canonical roots. The first canonical root shows a strong positive load of C3SL, C4SL and NASR and negative of NVEN, NHeSc and NMSR. In the second root, NVEN, NCep and NHeSc are the most positively influencing variables and NSnSc and NASR the most negative ones. Nevertheless, the graph (Fig. 4) shows similar results than in males, with Clusters III and IV well differentiated but with more overlap among Clusters I and II.

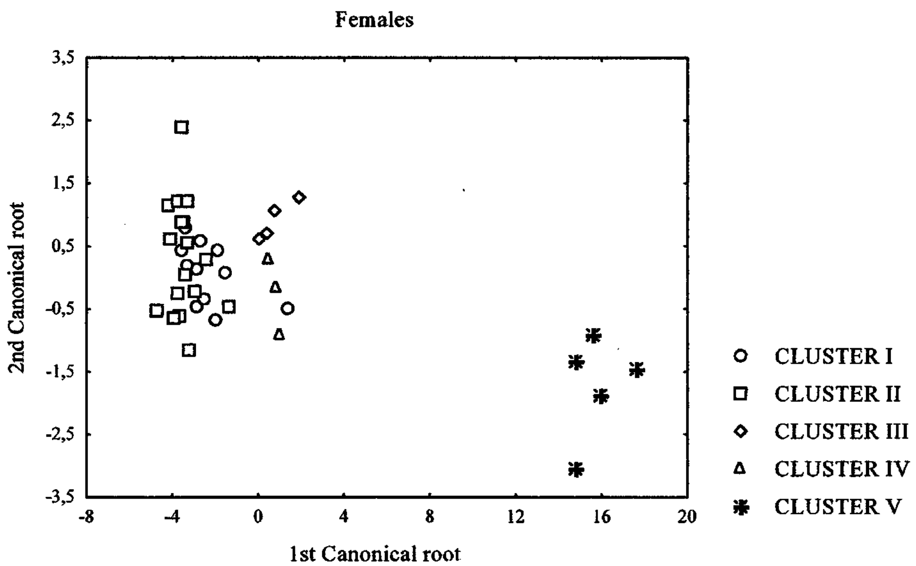

FIGURE 4. Plot of first two canonical variables of the Discriminant Canonical Analysis on females of the *Trimeresurus popeiorum* group.

MANCOVA and MANOVA Analyses

These analyses were performed on the sample of 106 specimens. Specimens with incomplete set of data were discarded. For the MANCOVA test, 13 morphometric variables were retained. The variable SVL was used as covariable. Results are presented in Tables 10–11.

Results of Table 10 show that there are both sexual differences and differences between the clusters, and there is a significant interaction between these factors. This significant interaction among both factors means that the pattern of sexual dimorphisms is different among considered OTUs. There are thus cluster-related differences but also differences in pattern of sexual dimorphism (Interaction significative). A significative comparison within each sex and between populations, at P<0.005, corrected for multiple correlated tests, was performed, but detailed results will not be presented here.

Table 10. Factor of sexual interaction in MANCOVA test (morphometric variables).

Factor	Lambda Wilks	*P*
OTU	0,23993249	0,000004
Sex	0,65017229	0,001819
Interaction	0,2111989	<0,00001

Interestingly, results of Table 11 show that there are both sexual differences and differences between the clusters, and there is no significant interaction between these factors. This absence of interaction among both factors means that the pattern of sexual dimorphisms is similar among considered OTUs.

TABLE 11. Factor of sexual interaction in MANOVA test (pholidotic variables).

Factor	Lambda Wilks	*P*
OTU	0,0049208	<0,00001
Sex	0,3691977	<0,00001
Interaction	0,3281512	0,222858

Univariate analyses. Results of such analyses and statistical calculations are presented below under each taxon account and are summarized in Tables 12 and 13 below. The analysis of morphological data lead to results identical with those of the multivariate analyses. However, univariate morphological analyses show much more clear differences between specimens of Cluster I and II than do multivariate analyses.

Taxonomic interpretation. Univariate and multivariate analyses distinguish six clusters of OTUs. These six clusters differ from each other by combinations of morphometric and meristic characters and patterns. Within each cluster, there is no indication of geographic or clinal variation. However, two male specimens from northern Thailand (BMNH 1937.2.1.25, from Chiang Mai Province and IRSNB 16545, from Lampang Province) are problematical. Although belonging to OTU 4, for which all other specimens are referable to Cluster I, they appear in the PCA analysis amidst specimens of Cluster II. We definitely retain them within Cluster I, as (1) both fully agree with all diagnostic morphological characters of Cluster I as defined here, and (2) a female (IRSNB 16546, from same locality than the male) also fully agrees with diagnostic characters defining Cluster I and appears within this cluster in the PCA. However, more fresh material from western and northern Thailand, with unambiguous colour and pattern, is needed to better understand variation of specimens of Clusters I and II in this region and their distributional limits.

TABLE 12. Comparison of main morphological characters in the *Trimeresurus popeiorum* group.

TAXON	TaL/TL		VEN		SC		MSR	Cep	SL	KOcc	NC3SL
	Males	Females	Males	Females	Males	Females					
popeiorum **(n = 32)**	0.181–0.211 (x = 0.195) (s = 0.009)	0.149–0.173 (x = 0.163) (s = 0.009)	151–166 (x = 161.0) (s = 4.0)	154–168 (x = 161.2) (s = 4.2)	59–75 (x = 68.1) (s = 4.2)	56–64 (x = 59.8) (s = 3.0)	(20) 21	10–14 (x = 11.5) (s = 1.0)	9–11 (x = 10.1 (s = 0.7)	♂: ++ ♀: 0/+	♂: 0–1 ♀: (0) 1
fucatus **(n = 60)**	0.201–0.241 (x = 0.218) (s = 0.011)	0.159–0.189 (x = 0.171) (s = 0.009)	156–171 (x = 164.0) (s = 3.5)	157–170 (x = 163.5) (s = 3.4)	69–84 (x = 75.9) (s = 3.5)	59–73 (x = 63.8) (s = 3.6)	(19) 21	10–14 (x = 11.3) (s = 1.2)	9–12 (x = 10.4) (s = 0.6)	♂: +/++ ♀: 0/+	♂: 0–1 ♀: (0) 1
nebularis **(n = 8)**	0.190–0.193 (x = 0.191) (s = 0.002)	0.165–0.172 (x = 0.168) (s = 0.003)	149–153 (x = 151.7) (s = 2.3)	147–153 (x = 150.4) (s = 2.3)	61–65 (x = 63.0) (s = 2.8)	50–60 (x = 55.2) (s = 3.8)	(20) 21	9 (10) (x = 9.1) (s = 0.4)	9–11 (x = 9.6) (s = 0.7)	♂: 0/+ ♀: 0 (+)	♂: 0 ♀: 0
sabahi **(n = 14)**	0.186–0.238 (x = 0.210) (s = 0.022)	0.173–0.178 (x = 0.176) (s = 0.003)	147–157 (x = 151.6) (s = 2.8)	148–156 (x = 152.2) (s = 3.0)	69–76 (x = 71.6) (s = 2.5)	59–65 (x = 62.2) (s = 2.7)	21	9–11 (x = 10.3) (s = 0.8)	8–10 (x = 9.4) (s = 0.6)	♂: 0 (+) ♀: 0	♂: 0–1 ♀: 1
barati **(n = 19)**	0.194–0.231 (x = 0.214) (s = 0.012)	0.164–0.176 (x = 0.172) (s = 0.005)	142–153 (x = 148.3) (s = 3.3)	146–158 (x = 149.8) (s = 4.3)	62–73 (x = 69.4) (s = 2.5)	55–59 (x = 57.2) (s = 1.6)	17–19	9–13 (x = 10.8) (s = 1.1)	9–11 (x = 9.6) (s = 0.6)	♂: 0/+ ♀: 0/+	♂: 0 (1) ♀: 0 (1)
cf. *sabahi* **(n = 3)**	0.215–0.230 (x = 0.223) (s = 0.010)	0.157	153–155 (x = 154.0) (s = 1.4)	153	73 (x = 73.0) (s = 0.0)	58	21	10–11 (x = 10.7) (s = 0.6)	9–10 (x = 9.7) (s = 0.5)	♂: 0 ♀: 0	♂: 0 (1) ♀: 0

Abbreviations. – See in Material and Methods, except: KOcc (keels of occipital scales): 0: smooth, +: weakly keeled, ++: strongly keeled.

Note. – This table includes data on two specimens of *Trimeresurus popeiorum* described by Taylor (1965), four specimens of *T. sabahi* and two of *T. barati* described by Regenass & Kramer (1981).

On the basis of our results, we regard the first five clusters as distinct species (see below in the discussion for the species concepts used in this study), and we propose the following taxonomic interpretation: Cluster I corresponds to *Trimeresurus popeiorum* sensu stricto. Cluster II and Cluster III correspond to two yet unnamed species which are described herein. Clusters IV and V, which were previously recognized as subspecies of *T. popeiorum* (sensu Regenass & Kramer, 1981), are raised to specific status. The status of the population included in Cluster VI (OTU 12), sharing characters with Cluster IV but for which we only have three specimens, cannot be ascertained at the present time; it is considered to be related to Cluster IV but is left *incertae sedis*. These clusters are treated below in this order.

TABLE 13. Comparison of pattern features in living specimens of the *Trimeresurus popeiorum* group.

TAXON	Vertebral spots	Eye colour		Postocular streak		Ventrolateral stripe		Tail
	Males	Males	Females	Males	Females	Males	Females	
popeiorum	Absent (rarely present)	Deep red	Deep red	Bicolor, wide	White, wide or absent	Bicolor, wide	White	Rusty red, mottled, no clear border between green and rusty red
fucatus	Present (rarely absent)	yellowish-green, gold or copper	Yellowish-green, gold or copper	White or bicolor (sometimes absent)	Absent	Bicolor	White	Mostly rusty brown, mottled with brown and white, or (W. Malaysia) laterally green, mottled with rusty brown, without sharp border
nebularis	Absent	Pale green	Pale green	Absent	Absent	White or blue	Absent	Laterally green, rusty or dark brown above, with a sharp border between the two areas
sabahi	Rarely present	Deep red or orange	Deep red or orange	Absent	Absent	Bicolor	White or yellow	Rusty red, mottled, without sharp border between the green and rusty brown areas
barati	Absent	Orange	Orange or yellow	Absent	Absent	White or bicolor	Absent	Laterally green, with a sharp border between green and rusty brown areas
cf. *sabahi*	Absent	?	?	Absent	Absent	White	Absent	Rusty red, mottled, without sharp border between the green and rusty brown areas

Trimeresurus popeiorum
(Fig. 5)

Trimeresurus popeiorum Smith, 1937: 730. — **Type locality**. Not given in the original description. Established as "Khasi Hills", State of Meghalaya, India. — **Lectotype**, by designation of Taylor & Elbel (1958: 1174). BMNH 72.4.17.137, adult male. Presented by T. C. Jerdon.

Material (30 specimens). — India. BMNH 72.4.17.137 (male), "Khasi Hills", State of Meghalaya. — BMNH 72.4.17.377 (male), BMNH 72.4.17.378 (female), Darjeeling, State of West Bengal. — BMNH 74.4.29.881 (female), "Himalayas". — BMNH 1946.1.19.20 (female), "Sikkim". — **Laos**. BMNH 62.7.28.1 (female), BMNH

62.7.28.4 (male), “Lao Mountains, Cochinchina”, now Louangphrabang Range, western Laos, probably between Pak Lai (Xaigna Bouri Province) and Luang Prabang (Louangphrabang Province) (on the basis of Mouhot [1864]). — FMNH 14430 (male), “Muong Yo, N. Laos”, now Ban Muangyo (21°31'N, 101°50'E), Phongsaly Province — MNHN 2004.0262 (male), Long Nai, Phongsaly Province. — **Myanmar**. BMNH 1924.5.20.38 (female), “Taok Plateau, Tenasserim”, now in the vicinity of Mt. Pya Taung, Taninthayi Division. — CAS 205847 (female), Bago Yoma, 18°52'59.8"N, 95°52'44.9"E, 420 m, Bago Division. — CAS 222195 (male), Kyaik–Hti–Yo Wildlife Sanctuary, tributary of Moe Baw Chaung, 17°29'48.5"N–97°04'49.6"E, Kyaik Htyo Township, Mon State. — NHMB 2596–2597 (males), “Karin Berge”, now Mts. Karen, Kayah State. — NHMW 23923:1 (male), NHMW 23923:2 (male), “Carin Geb.”, now Mts. Karen, Kayah State. — ZMB 11637 (male), “M. Carin”, now Mts. Karen, Kayah State. — ZMH R 06267 (female), “Mti. Carin, Burma, 900–1000 m”, now Mts. Karen, Kayah State. — **Thailand**. BMNH 1937.2.1.24 (female), BMNH 1937.2.1.25 (male). — “Pa Meang, N. of Chiangmai, N. Siam”, Chiang Mai Province. — BMNH 1937.2.1.26 (female), “N. of Chiangmai”, Chiang Mai Province. — FMNH 178655 (male), Doi Suthep, Chiang Mai Province. — FMNH 178656 (male), Mae Solat, 4000 ft, Chiang Mai Province. — FMNH 178658 (male), Doi Suthep, Fisheries Station, ca 3000 ft., Chiang Mai Province. — IRSNB 16545 (male), IRSNB 16546 (female), Djè Son National Park, Djè Son subdistrict, Muang Pan District, Lampang Province. — MNHN 1987.3836 (male), Doi Inthanon, Chiang Mai Province. — PSGV/S0062 (male), PSGV/S0063 (female), Doi Inthanon, Chiang Mai Province. — USNM 84757 (female), Doi Nangka, Chiang Mai Province.

Diagnosis. — A species of the genus *Trimeresurus*, characterized by (1) hemipenes long, reaching at least 25th SC, without spines; (2) 1st supralabial distinct from nasal; (3) 21 DSR at midbody (20 in 1 specimen); (4) overall green coloration in males and females, without darker crossbands on the scales (some kind of crossbands may be visible, resulting only from striping on the interstitial skin); (5) a conspicuous bicolor postocular streak in males, thin and white below, wide and bright red above, reversed from the scheme of the ventrolateral stripe (in about one half of the female specimens, the streak is white and thin, and is entirely missing in the other half); (6) eyes deep or fire red in both sexes in adult specimens (yellow in juveniles); (7) in males, a vivid, wide bicolor ventrolateral stripe, bright and deep red below, white above; in females, stripe white but well defined; (8) tail brown, mottled with green laterally, no obvious border between the red and green colours (similar to *Trimeresurus stejnegeri*); (9) VEN: 151–168, SC: 56–75; (10) tail long in males, with a ratio TaL/TL between 0.181 and 0.211, moderate in females, 0.149–0.173; (11) occipital scales distinctly keeled in males.

Description and variation. — The maximal confirmed total length known is 925 mm (SVL 758 mm, TaL 167 mm) for a male (BMNH 72.4.17.137, lectotype). The largest known female is 845 mm long (SVL 709 mm, TaL 136 mm; BMNH 62.7.28.1).

FIGURE 5. *Trimeresurus popeiorum*. Living male from Tak Province, Thailand. Photograph by Gernot Vogel.

Body slender in males, thick in females. Triangular head average, amounting (in adults above SVL 400 mm) for 4.7–5.6 % of SVL (x = 5.2 %) in males, 5.1–6.2 % of SVL (x = 5.6 %) in females, wide at its base, flattened in males, rather thick in females when seen from the side. Snout rather long, amounting (in adults) for 23.9–28.6 % (x = 26.7 %) of HL in males and 23.0–28.6 % (x = 26.4 %) of HL in females, or 1.7–2.2 (x = 2.0) times as long as diameter of eye, flattened, rounded when seen from above, oblically truncated when seen from the side, with a distinct *canthus rostralis*. Eye large, amounting for 0.9–1.2 (x = 1.0) times in males and 0.7–1.1 (x = 0.9) times in females of the distance eye–lip. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.149–0.211, with a strong sexual dimorphism (see below).

DSR: 21-23(25) – 21(20 in 1 specimen) – 15, more or less strongly keeled in males, weakly keeled in females, always smooth on the first DSR in both sexes.

VEN: 151–168 (plus 1–2 preventrals); SC: 56–75, all paired; anal shield entire.

Rostral visible from above, about 1.5 times broader than high, triangular; nasals sub-rectangular, undivided; one pair of enlarged, curved internasals, separated by 1 (in 26/30 specimens) or 2 (4/30) small scales; 4 or 5 canthal scales, slightly larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2–3 small postoculars; one entire supraocular on each side, long and rather narrow, 2.4–3.9 (x = 3.1) times as long as wide, 0.51–0.90 (x = 0.75) time as wide as the internasals, indented on their inner margins by the upper head scales; 5 or 6 (7 in 6/30 specimens) enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, smooth, juxtaposed, irregular in shape; 10–14 (x = 11.5, s = 1.0) cephalic scales on a line between supraoculars (10: 5/30 specimens; 11: 11/30; 12: 9/30; 13: 4/30; 14: 1/30), always smooth and flat; occipital scales larger than cephalic scales, in males moderately (in 4/18 specimens) or strongly (14/18) keeled, in females weakly keeled (8/12) or smooth (4/12); temporals small, in males either smooth (in 4/18 specimens) or distinctly keeled (14/18 specimens), smooth in all 12 examined females, subequal, in 2 or 3 rows; one thin, elongated, crescent-like subocular; 9–11 SL (9–9: 4/30 specimens; 9–10: 4/30; 10–10: 9/30; 10–11: 10/30; 11–11: 3/30); 1st SL always separated from nasal; 2nd SL forming the anterior border of loreal pit, separated from nasal by 1 or 2 scales; 3rd SL longest and highest, 1.0–1.4 times as long as high (x = 1.23), in contact with the subocular on both sides (15/30 specimens) or in contact on one side (3/30), or separated by 1 scale on both sides (12/30); 4th SL, as long as high, 0.6–0.9 (x = 0.75) time lower than 3rd SL, separated from subocular by 1 scale on each side in all examined specimens; 5th and posterior SL smaller than 4th one, 5th SL separated from subocular by 2 scale rows of similar size in all specimens; 10–15 IL (usually 12/12 [8/30], 12/13 [9/30] or 13/13 [4/30]; x = 12.3, s = 0.8), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7–9 rows of smooth gular scales; throat shields regularly arranged.

In life, the background colour is uniformly bright green, grass-green more or less deep, bluish-green or even turquoise blue (see Wall, 1909), sometimes with faint and irregular crossbands. A wide and conspicuous bicolor ventrolateral stripe, bright red, deep red or chocolate red below (rusty brown in alcohol) on lower half or slightly more of 1st DSR, white or whitish-yellow above and on the lower part of 2nd DSR, extends from the angle of the mouth through first 1/3–1/2 of the tail. In females, it is replaced by a conspicuous white or yellowish-white stripe on the first DSR.

The tail surface is basically the same colour as the dorsum, with the whole length of its sides and upper part irregularly mottled with reddish-brown or rusty brown, without a clear border between the red and green colours, entirely reddish-brown backwards.

The dorsal head surface and temporal regions are of the same colours as the dorsum, paler green on the supralabials. In males, a vivid bicolor reversed postocular streak, narrow and white below, wide and bright red, deep rusty-red or even brownish-red above (rusty brown in alcohol), is present at any age. The white part of the postocular streak and that of the ventrolateral stripe, respectively, may be either confluent, with red stripes present on its both sides for a short distance, or separated by a short gap on the posterior part of the head. In females, the postocular streak is either absent, or present, in about half of the specimens, as a white and thin line. In adults of both sexes, eyes are bright red, fire red or deep red.

The coloration of juveniles is similar to that of adults. The postocular streak and ventrolateral stripes of males are as conspicuous as in adults. Eyes are deep yellow.

Comparison with other species. — *Trimeresurus popeiorum* differs from all other pitvipers of the *Trimeresurus popeiorum* complex by the combination of the following characters: (1) tail rusty or reddish-brown mottled with green laterally, without obvious border between the colours; (2) eye colour deep red in both sexes in adult specimens; (3) conspicuous bicolor white/red postocular streak in males, a thin and white postocular stripe in some females; (4) vivid, wide red/white bicolor ventrolateral stripe in males, white and well defined in females; (5) a northern range: India, Myanmar (except Tanin-thayi State), northern and western Thailand, northern Laos.

Main differences between *Trimeresurus popeiorum* as here conceived and the other members of the *Trimeresurus popeiorum* complex are summarized in Tables 12–13, and are detailed under the accounts of each other species.

Sexual dimorphism. — It is significant in the relative length of the tail, in the number of subcaudals, and in the pattern:

(1) Strong difference in the ratio TaL/TL:

males: 0.181–0.211 (x = 0.195); females: 0.149–0.173 (x = 0.163)

(2) Differences in the number of subcaudals:

59–75 (x = 68.1) in males vs. 56–64 (x = 59.8) in females.

(3) Occipital and temporal scales more strongly keeled in males than in females.

(4) Pattern:

1. A bicolor postocular streak in males, absent or thin, white in females.

2. Red/white ventrolateral stripe in males, white in females.

In our sample of 30 preserved specimens, there is no noticeable difference of size between males and females.There is no difference in the numbers of ventral scales nor in other scalation characters, nor in eye colour.

Range. — India: known from the states of Sikkim, West Bengal (Darjeeling), Meghalaya (Khasi Hills) (Smith, 1943; Regenass & Kramer, 1981, Ahmed & Dasgupta, 1992; and examined specimens), and Arunachal Pradesh (Miao, Changlang District; A. Captain & S. Sengupta, unpublished). — Myanmar: known from Bago Division, northern Tanin-thayi Division, Kayah State and Chin State (Smith, 1943; Leviton et al., 2003; examined specimens), possibly Kayin State. — Laos: Phongsaly Province and Vientiane Province (examined specimens). — Thailand: known from the northern and western part of the country, in provinces of Chiang Mai, Chiang Rai, Lampang (Taylor, 1965; Cox, 1991; examined specimens) and Tak (examined specimens); possibly Loei Province (see below).

The specimen described by Taylor & Elbel (1958: 1171), from Mt. Phu Nam Lang, Dan Sai, Loei Province, has a ratio TaL/TL much lower and a number of ventral scales greater than in other specimens. Unfortunately, Taylor & Elbel (1958) did not describe its hemipenes. We did not examine this juvenile specimen, but in terms of morphology, it is closer to *Trimeresurus gumprechti* David, Vogel, Pauwels & Vidal, 2002, a species to which we tentatively refer it. Specimens from the RMNH cited in Regenass & Kramer (1981: 186, as ML 16714 and 16716A–B) are *Trimeresurus vogeli* David, Pauwels & Vidal, 2001.We did not examine RMNH 16715.

The occurrence of this species in Vietnam is unclear. The specimen cited in Campden-Main (1970) from South Vietnam, USNM 95094 (from Blao or Bao Loc, Lam Dong Province), was based on a juvenile male *Trimeresurus vogeli*, with typical spinose hemipenes. Recently, *T. popeiorum* was mentioned from Tam Dao Mountain Range, Vinh Phu Province, northern Vietnam (Orlov, 1997). We did not examine these specimens, but the published illustrations suggest that they belong to a taxon different from *Trimeresurus popeiorum* as here conceived.

Specimens from Cambodia referred to *Trimeresurus popeiorum* (for example BMNH 1928.6.29.12, from "Bokor, Kamchay Mts.") turned out to be *Trimeresurus vogeli*. David et al. (2001, 2002) showed that specimens cited from eastern Thailand (for example, by Inger & Colwell [1977]) were in fact also referrable to *Trimeresurus vogeli*. Lastly, we examined a specimen from extreme northern Laos collected only a few kilometers from the Lao–Chinese border, suggesting that *T. popeiorum* should be present in southeastern Yunnan Province.

Comments. — As surprising as it may be, and to our best knowledge, *Trimeresurus popeiorum* has been depicted alive in the literature only in Cox et al. (1998: 21, top right). Pictures of preserved specimens appeared in Regenass & Kramer (1981: 181: Fig. 4). The specimen depicted in Taylor & Elbel (1958: 1172: Fig. 36) and Taylor (1965: 1074: Fig. 125) might be in fact a specimen of *Trimeresurus gumprechti*, although the description of Taylor (1965) indeed refers to *T. popeiorum*. As noted in David et al. (2002), the similarities in the colour patterns of *Trimeresurus popeiorum* and *Trimeresurus gumprechti* are striking.

***Trimeresurus fucatus* spec. nov.**
(Figs. 6–13)

Lachesis gramineus (non *Coluber gramineus* Shaw, 1802): Boulenger (1896: 555–556, part.); Flower (1896: 896 [part.], 1899: 695, part.)

Trimeresurus gramineus: Boulenger (1912: 217, part.); Smith (1922: 267, 1930: 90, part.); Pope & Pope (1933: 7, part.); Hoge & Romano Hoge (1981: 257, part.)

Trimeresurus gramineus gramineus: Welch (1988: 137, part.)

Trimeresurus popeiorum (non *Trimeresurus popeiorum* Smith, 1937 as defined here): Smith (1937: 730, part.); Tweedie (1954: 117, 1957: 121, 1983: 139, all part.); Lim (1982: 20 [part.];

1990: 393, 394: Fig. 7; 1991: 23 [part.]); Lim et al. (1995: 361, part.); Cox et al. (1998: 21 [not figure at top left, depicting a *Trimeresurus albolabris*]); Manthey & Grossmann (1997: 409, part. [not on Fig. 316]); Gumprecht (2001: 29).

Trimeresurus popiorum: Maslin (1942: 23, part.)

Trimeresurus popeorum: Smith (1943: 518, part.); Grandison (1978: 94); Dring (1979: 236); Wüster (1992: 23, 24: Fig. 6); Jintakune & Chanhome (1995: 122, Figs. 178–184); McDiarmid et al. (1999: 340).

Trimeresurus popeorum popeorum: Regenass & Kramer (1981: 186, 181: Fig. 4, part.); Cox (1991: 384 [the specimen on Pl. 157 cannot be positively identified]); Golay et al. (1993: 103, part.); Orlov et al. (2002b: 353, part.).

Trimeresurus popeiorum popeiorum: David & Ineich (1999: 288, part.); Iskandar & Colijn (2001: 159, part.); Orlov et al. (2002a: 194, part.); Leong & Lim (2003: 134).

Trimeresurus popae: Tweedie (1941: 131, part.)

Trimeresurus popeorum ssp.: Vogel (1990).

Trimeresurus popeiorum ssp.: Chan-ard et al. (1999: 201 [all pictures]).

Trimeresurus cf. *popeiorum*: Lim & Lim (1999: 151, 152: Fig. 3); Grossmann & Tillack (2001: 28, 29: Figs. 17–18).

Trimeresurus sumatranus (non *Coluber sumatranus* Raffles, 1822): Nootpand (1971: 48).

Trimeresurus erythrurus (non *Trigonocephalus erythrurus* Cantor, 1839): Thumwipat & Nutphand (1982: 96, 138); Nutphand (2001: 300).

Holotype. — MNHN 1990.4283, adult male, from Province of Nakhon Si Thammarat, Thailand. Collector unknown.

FIGURE 6. *Trimeresurus fucatus*. Holotype (MNHN 1990.4283). Lateral view of the head, left side. Photograph by Roger Bour.

FIGURE 7. *Trimeresurus fucatus*. Holotype (MNHN 1990.4283). Lateral view of the head, right side. Photograph by Roger Bour.

FIGURE 8. *Trimeresurus fucatus*. Holotype (MNHN 1990.4283). Dorsal view of the head. Photograph by Roger Bour.

FIGURE 9. *Trimeresurus fucatus*. Holotype (MNHN 1990.4283). General view. Photograph by Roger Bour.

Paratypes (28 specimens). — BMNH 1974.4995–4996 (males), BMNH 1974.4997–4998 (females), east ridge camp (5°27’40"N–102°37’18"E), Gunung Lawit, State of Trengganu, West Malaysia, 790 m. – BMNH 1974.4999 (female), BMNH 1974.5000 (male), summit ridge (5°25’20"N–102°36’20"E), Gunung Lawit, State of Trengganu, West Malaysia, 1280 m. – BMNH 1988.879–884 (all males), Surat Thani Province, Thailand. – IRSNB 2588 (male), IRSNB 2589 (female), Ban Pak Song, about 12 km E of Ban Ratchakrut, Phato District, Chumphon Province, Thailand. – MNHN 1990.4280–4281 (females), MNHN 1990.4284, MNHN 1990.4287 (males), Thung Song, Nakhon Si Thammarat Province, Thailand. – QSMI 510–511, QSMI 519 (males), Krabi Province, Thailand. – QSMI 520 (male), Nakhon Si Thammarat Province, Thailand. – ZRC 2.2876 (male), Pinang Island, State of Pinang, West Malaysia. – ZFMK 82855 (male), Nakhon Si Thammarat Province, Thailand. – PSGV 274 (male), Thung Song, Nakhon Si Thammarat Province, Thailand. – ZRC 2.2881 (female), Gunung Padang, State of Trengganu. – ZRC 2.3493 (male), Pulau Tioman, State of Pahang, West Malaysia. – ZSM 4/2004, near Thung Song, Nakhon Si Thammarat Province, Thailand.

Non-type material (31 specimens). — Myanmar. BMNH 56.5.6.105 (male), “Mergui”, now Myeik, Taninthayi Division. — BMNH 1940.3.9.43 (male), “Kissaraing, Mergui”, now Kanmaw Kyun Island (or Kisseraing Island; 11°40'N, 98° 28'E), Taninthayi Division. — **Thailand**. BMNH 1988.889–891 (females), no locality. — BMNH 1988.895

(female), BMNH 1988.896–900, BMNH 1988.1051 (all males), Surat Thani Province. — BMNH 1988.878 (male), Trang Province. — MNHN 1991.296 (male), Thung Song, Nakhon Si Thammarat Province. — QSMI 0351, Krabi Province. — **Federation of Malaysia (West Malaysia)**. BMNH 60.3.19.1300A (female), BMNH 60.3.19.1300B (male), Pinang Island, State of Pinang. — BMNH 96.5.25.32 (female), BMNH 96.5.25.33–35 (males), "Wellesley", now Seberang Perai, mainland part of State of Pinang. — BMNH 1934.5.21.73, "River Yum, headwaters, R. Plus, East Perak, F.M.S., 2000 ft", now in State of Perak. — BMNH 1967.2289 (female), near Camp IV, Gunung Benom, State of Pahang, 3700 ft. — PSGV 592 (male), no locality (through the pet trade), West Malaysia. — USNM 141751 (female), State of Selangor. — ZRC 2.2880 (female), Maxwell Hills, State of Perak. — ZRC 2.2883 (female), Gunung Taha, State of Pahang. — ZRC 2.2877 (female), Pinang Island. — ZRC 2.2888–2890, Fraser's Hills, State of Pahang.

Diagnosis. — A species of the genus *Trimeresurus*, characterized by (1) hemipenes long, reaching at least 25th SC, without spines; (2) 1st supralabial distinct from nasal; (3) 21 MSR (20 in 1 specimen); (4) overall green coloration in males and females; (5) irregular rusty or reddish-brown dorsal crossbands in most males; (6) a vertebral row of white dots in males, especially those from southern Thailand and Pulau Tioman, conspicuous in life (often invisible in preserved specimens or in living old specimens), present also in females, especially in juvenile specimens from same areas; (7) in males, a postocular streak usually thin, irregular, either entirely white or white below with an irregular, dark red or rusty brown streak above, sometimes totally absent (this streak is often much subdued and invisible in preservative); this streak is absent in females, but some white spots may be present; (8) eyes yellowish-green, greenish-gold or yellow-copper in both sexes in adult specimens; (9) in males, a vivid, bicolor ventrolateral stripe, bright and deep orange or red below, white above; in females, a thin, white but well defined stripe; (10) a tail entirely rusty brown or reddish-brown in the northern part of the range, mottled in the southern part; (11) a long tail in males, with a ratio TaL/TL between 0.200 and more than 0.240; (12) a high number of SC in males (at least 69); (13) occipital and temporal scales distinctly keeled; (14) an elongated snout, oblically truncated.

Etymology. — The specific nomen is the Latin adjective *fucatus*, that could be translated by "with make-up". It was used in classical Latin language to describe the red and white hues harboured on their cheeks by actors of the ancient Latin theater, and was chosen here in allusion to the bicolor white and red postocular streak present in some males of this species.

Suggested English name: Siamese Peninsula pitviper.

Description of the holotype. — Body elongated, cylindrical; head triangular, wide at its base, thick, rather elongated, 1.7 times as long as wide, clearly distinct from the neck; snout long, accounting for 28.3 % of total HL, 2.3 times as long as diameter of eye, flattened, rounded when seen from above, strongly oblically truncated when seen from lateral side, with a very distinct *canthus rostralis*; eye large, with VED/DEL ratio 0.9; nostril–loreal pit distance/nostril–eye distance ratio 0.55 (mean value of both sides); tail long, slender and tapering, distinctly prehensile.

SVL: 550 mm; TaL: 154 mm; TL: 704 mm; HL: 28.90 mm; ratio TaL/TL: 0.219.

VEN: 166 (+ 2 preventrals); SC: 74, paired, plus one terminal scale; anal shield entire.

DSR: 21 – 21 – 15 scales, rhomboid, rather strongly keeled, first row smooth.

Rostral visible from above, about 1.6 times broader than high, triangular; nasals subrectangular, undivided, with nostril in their middle; one pair of enlarged, slightly curved internasals, 1.6 times as wide as deep, separated by one scale as wide as adjacent upper snout scales; 4/5 canthal scales bordering the *canthus rostralis* between the internasal and corresponding supraocular, slightly larger than adjacent snout scales; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 3/2 postoculars; 1 entire, long and relatively narrow supraocular on each side, about 2.5 times as long as wide, about 0.7 time as wide as the internasals; supraocular indented on their inner margin by the upper head scales; scales on upper snout surface smooth, juxtaposed, irregular in shape, enlarged, with 7 snout scales on a line between the scale separating the internasals and a line connecting the anterior margins of eyes; cephalic scales small, much irregular, juxtaposed, smooth and flat on upper head surface; 13 Cep in a line between supraoculars; occipital scales flat but strongly keeled; temporals small, subequal, in 2 or 3 rows, smooth; one thin, elongated, crescent-like subocular; 10/10 SL; 1st SL triangular, short, totally separated from the corresponding nasal; 2nd SL high, forming the anterior border of loreal pit, separated from nasal by 1/2 small scales; 3rd SL much larger than the other labials, pentagonal, high and long, 1.3 times as long as high, separated from the subocular by one scale; 4th SL high, as high as 3rd one, separated from the subocular by one scale; 5th and posterior SL smaller than 4th one, 5th SL separated from the subocular by one scale, others in contact with the first row of temporals; 12/11 infralabials, those of the first pair in contact with each other, the first three pairs in contact with the chin shields; 7/7 rows of smooth gular scales; chin shields regularly arranged.

In preservative, the dorsal and lateral body surfaces are uniformly very dark greyish-brown, with faint black crossbands and some indistinct white vertebral spots; the interstitial skin is grey; a well defined but thin bicolor ventrolateral stripe extending from the neck (not reaching the corner of the mouth) through the first third of the tail, with the lower part, brown, extending along the lower half of scales of the first and an upper part white on the upper half of the first row and a very small part in the lower half of scales of the second row of DSR; this stripe ends on the tail as broken bicolor spots. The tail is reddish-brown, paler than the body, heavily mottled with dark brown.

The dorsal head surface is uniformly very dark greyish-brown, barely paler on the supralabials; a faint postocular streak, reduced to white spots (see below for the condition in life), extends from eye to the corner of the mouth on the limit between the 1st and 2nd rows of temporals. The postocular streak is not connected with the upper white half of the ventrolateral stripe.

The chin and throat are brownish-grey, barely paler than upper head surface. Venter is dark bluish-black.

In life, the dorsal colour was deep grass green, with numerous white vertebral spots regularly spaced throughout the body every 2 to 4 vertebral scales and faint rusty-red crossbars on the 5 to 7 upper DSR; a well defined bicolor ventrolateral stripe, the anterior and lower parts of the 1st DSR coral red, the posterior and upper parts of this row and the lower part of 2nd DSR pure white, from neck to the first third of tail. Tail greyish-green, heavily mottled on its sides and above with large, irregular, rusty-brown blotches, then reddish-brown at its posterior part with darker blotches.

Head like the body, paler yellowish-green on the supralabials, a little bit darker on the temporals; a very faint and discontinuous white postocular streak runs along the limit between the first and second row of temporals from the rearmost upper part of subocular backwards up to the angle of the mouth; two or three very faint reddish-brown dots above the white streak. Eyes deep yellowish-copper.

Venter and chin green, paler than body, with posterior margins of ventral plates pale green.

Description of the paratypes. — A summary of morphological and meristic data of the paratypes is given in Table 14. In females, the postocular streak is absent, but sometimes faint spots are present and the ventrolateral stripe is only white.

TABLE 14. Morphological characters of the paratypes of *Trimeresurus fucatus.*

Collection number	Sex	SVL (mm)	TaL (mm)	TaL/ TL	PosOc streak	Lateral stripe	VEN	SC	SL	Cep	IL	C3SL / SubOc
BMNH 1974.4995	M	351	93	0,209	None	Red/white	161	80	10/9	12	11/12	0/0
BMNH 1974.4996	M	289	78	0,213	None	White (?)	163	76	10/10	13	13/13	1/1
BMNH 1974.5000	M	506	128	0,202	None	White (?)	163	76	10/11	13	13/12	1/1
BMNH 1988.879	M	582	181	0.237	None	Red/white	165	76	10/10	10	11/11	0/0
BMNH 1988.880	M	540	148	0.215	None	Red/white	163	72	10/11	11	12/12	1/1
BMNH 1988.881	M	520	156	0.231	None	Red/white	164	78	10/11	10	13/12	1/1
BMNH 1988.882	M	594	179	0.232	None	Red/white	166	80	11/11	9	12/12	0/0
BMNH 1988.883	M	598	174	0.225	None	Red/white	168	84	11/11	10	13/13	1/1
BMNH 1988.884	M	525	143	0.214	White	Red/white	165	75	11/10	10	12/13	1/1
IRSNB 2588	M	466	128	0.215	White/red	Red/white	166	74	10/10	10	13/13	1/0
MNHN 1990.4284	M	525	160	0.234	White/red	Red/white	164	80	10/10	11	13/13	1/1
MNHN 1990.4247	M	327	104	0.241	White	Red/white	165	82	10/10	11	12/13	1/1
ZFMK 82855	M	495	155	0.238	White/red	Red/white	161	77	10/9	9	12/12	1/1

......continued on the next page

TABLE 12 (continued)

Collection number	Sex	SVL (mm)	TaL (mm)	TaL/ TL	PosOc streak	Lateral stripe	VEN	SC	SL	Cep	IL	C3SL / SubOc
PSGV 274	M	652	182	0.218	None	Red/white	166	78	12/11	10	12/14	1/1
QSMI 510	M	441	123	0.218	White	Red/white	169	80	11/11	12	13/13	0/0
QSMI 511	M	415	108	0.207	None	Red/white	169	81	10/10	10	12/11	0/1
QSMI 519	M	504	133	0.209	None	Red/white	164	74	10/10	12	12/12	1/1
QSMI 520	M	590	173	0.227	None	Red/white	162	76	10/10	11	11/12	0/1
ZRC 2.2876	M	530	143	0.212	None	Red/white	158	69	10/11	12	13/14	0/0
ZRC 2.3493	M	583	160	0.215	None	Red/white	170	76	9/10	12	13/11	0/0
BMNH 1974.4997	F	340	67	0.165	None	White	161	64	11/11	13	13/14	0/0
BMNH 1974.4998	F	288	61	0.175	None	White	163	67	10/10	14	12/13	1/1
BMNH 1974.4999	F	418	82	0.164	None	White	164	66	10/10	14	13/13	1/1
IRSNB 2589	F	265	53	0.167	None	White	170	61	11/10	12	15/14	1/1
MNHN 1990.4280	F	288	65	0.184	None	White	162	69	10/10	11	12/12	0/0
MNHN 1990.4281	F	266	62	0.189	None	White	168	73	10/10	10	12/12	1/1
ZRC 2.2881	F	306	62	0.168	None	White	157	63	10/11	13	14/13	0/0
ZSM 4/2004	F	715	153	0.176	None	None	168	64	11/11	12	13/13	1/1

Description and variation. — The maximal confirmed total length known is 868 mm (SVL 715 mm, TaL 153 mm) for a female (ZSM 4/2004, a specimen kept in captivity for more than 10 years). The largest known male is 834 mm long (SVL 652 mm, TaL 182 mm; PSGV 274). In our sample of 60 specimens, there is no noticeable difference of size between males and females.

Body, compressed laterally, slender in males and somewhat thicker in females. Triangular head average, amounting (in adults above SVL 400 mm) for 4.6–5.9 % of SVL (x = 5.1 %) in males, 5.0–6.3 % of SVL (x = 5.7 %) in females, wide at its base, flattened in males, rather thick in females when seen from the side. Snout rather long, amounting for 25.7–34.5 % (x = 27.9 %) of HL in males and 25.3–33.6 % (x = 27.6 %) of HL in females, or 1.7–2.8 (x = 2.3) times as long as diameter of eye, flattened, rounded when seen from above, elongated and strongly oblically truncated when seen from the side, with a very distinct *canthus rostralis*. Eye large, amounting for 0.9–1.2 (x = 1.0) times in males and 0.7–1.1 (x = 0.9) time in females of the distance eye–lip. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.159–0.241, with a strong sexual dimorphism (see below).

DSR: 21-27–(19)21–15(17), distinctly and strongly keeled by a sharp but narrow keel in both sexes, always smooth on the 1st DSR.

We recorded 19 MSR in only 1/60 specimens, and 17 PSR in 2/60 specimens.

VEN: 156–171 (plus 1–2 preventrals); SC: 59–84, all paired; anal shield entire.

Head scalation as described for the holotype, with the following variation for major features: internasals either in contact (in 4/60 specimens) or usually separated by 1 (43/60 specimens) or 2 (13/60) small scales; 4–5 canthal scales, slightly larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; usually 2 (rarely 3) small postoculars; one entire supraocular on each side, long and rather narrow, 2.5–4.0 (x = 2.9) times as long as wide, 0.50–0.90 (x = 0.67) time as wide as the internasals, indented on their inner margins by the upper head scales; 4–7 (4 in 1/60 specimens) on a line between the internasals or the scale separating the internasals and a line connecting the anterior margins of the eyes; 9–14 (x = 11.3, s = 1.2) cephalic scales on a line between supraoculars (9: 3/60 specimens; 10: 15/60; 11: 16/60; 12: 17/60; 13: 7/60; 14: 2/60), smooth and flat; occipital scales larger than cephalic scales, in males distinctly (24/40 specimens) or strongly (16/40) keeled, in females weakly keeled (15/19) or smooth (4/19 females); temporals small, smooth (15/41 specimens) or keeled in males (in 26/41 specimens), smooth (in 13/19 females) or weakly keeled (6/19 females), subequal, in 2 or 3 rows; 9–12 SL (9–10: 5/60; 10–10: 22/60; 10–11: 21/60; 11–11: 10/60; 11–12: 2/60); 1st SL separated from nasal; 2nd SL forming the anterior border of loreal pit, separated from nasal by 1 or 2 scales; 3rd SL longest and highest, 0.9–1.5 times as long as high (x = 1.35), in contact with the subocular on both sides (21/60 specimens) or in contact on one side (9/60), or separated by 1 scale on both sides (30/60); 4th SL, as long as high, 0.6–0.9 (x = 0.75) time lower than 3rd SL, separated from subocular by 1 scale on each side (in 56/60 specimens) or by 1–2 scales (1/60), or in contact on both sides (2/60), or in contact on one side (1/60); 5th SL separated from subocular by 2 scale rows of similar size in all specimens; 10–15 IL (usually 12–12 or 12–13 or 13–13; x = 12.3, s = 1.4), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7–9 rows of smooth gular scales; throat shields irregularly arranged.

FIGURE 10. *Trimeresurus fucatus*. Living adult male from Thung Song, Nakhon Si Thammarat Province, Thailand. Photograph by Gernot Vogel.

FIGURE 11. *Trimeresurus fucatus*. Living juvenile male from Thung Song, Nakhon Si Thammarat Province, Thailand. Photograph by Gernot Vogel.

FIGURE 12. *Trimeresurus popeiorum* adult male (Tak Province, Thailand), bottom, and T. fucatus, adult male (Thung Song, Nakhon Si Thammarat Province, Thailand), top. Photograph by Gernot Vogel.

In life (Figs. 10–12), the background colour is more or less bright grass-green, deep green or emerald green, often with irregular dorsal rusty red or reddish-purple crossbands on the upper dorsal scale rows, usually more conspicuous in males than females. Small white vertebral spots usually present in males throughout the length of the body, but are often absent in females. In males, the bicolor ventrolateral stripe is well-defined, bright red, deep red or chocolate red below (rusty brown in alcohol), white or whitish-yellow above and runs from the angle of the mouth through first third to half of the tail. As the red part is restricted to the anterior and lower part of scales of the 1st DSR, the white component seems indented by the red and the stripe appears as a succession of red dots on a white background. In alcohol, the red part turns to dark greenish-brown and is often confused with the background colour and invisible. In females, it is replaced by a faint white, bluish-white or yellowish-white stripe on the middle of the first DSR.

In Thai populations, the tail is greyish-green, heavily mottled with large, irregular, rusty-brown blotches on its sides in its anterior part, becoming posteriorly nearly totally rusty brown mottled with darker hues and white. In populations from central West Malaysia, the tail is green laterally, rusty brown or dark brown above, with a sharp border between the green and brown areas.

The dorsal head surface and temporal regions are of the same colours as the dorsum, although paler green or yellowish-green supralabials. In males, a more or less distinct postocular streak, usually thin, irregular, either entirely white, or white below with an irregular, vivid red, dark red or rusty brown elongated blotch above (see Vogel, 1990 and Grossmann & Tillack, 2001: 29), often reduced to a few faint rusty brown spots. The postocular streak is sometimes totally absent. It is often much subdued and invisible in preservative; in our sample of 27 preserved males, the streak is absent (in preservative) in 16 specimens, white in 7/27 and bicolor in only 4/27, although it can be reduced to faint spots. Usually, the upper red part of the streak does not reach the lower component of the ventrolateral stripe. The postocular streak is absent in females, but some white spots may be present. In females, the postocular streak is absent, but faint white dots or even a thin line may be visible. In life, eyes are yellowish-green, greenish-gold or yellow-copper in both sexes in adult specimens; they are never bright red.

The coloration of juveniles is similar to that of adults, with dorsal crossbands and vertebral white spots much more contrasted. The postocular streak and ventrolateral stripes of males are visible.

There is some intraspecific variation in the pattern of this species. Specimens from southern Thailand have a more colourful body than those from West Malaysia (see Chanard et al. [1999: 201]), and have a clear sexual dimorphism. There is always a line of vertebral spots visible, and males are distinctly banded. In females, the crossbands are paler and nearly vanish when the animals grew old. Especially the new born specimens from southern Thailand are vividly coloured, with a clear difference between males and females, the males having a much contrasted pattern. Furthermore the population from southern Thailand has a nearly totally brown tail with very little green and often white spots, whereas the Malayan animals tend to have the lateral part of the tail green, but without a sharp limit with the brown part. We did not record a postocular streak in Malaysian specimens, whereas it was visible in more than a third of the Thai and Burmese specimens that we examined. The interstitial skin normally is either black or dark grey in Thai animals, whereas it is banded in grey and black in Malayan animals. In West Malaysia, the animals from Fraser’s Hills are slightly different from those of other populations. The most striking difference is the presence of only faint dorsal crossbands in males, but these differences in colouration are not correlated with differences in pholidosis compared with other specimens of *T. fucatus*.

Lastly, we examined one specimen from Pulau Tioman, an island off the east coast of the Malayan mainland. This animal has a colourful and sharp pattern compared to other specimens of *T. fucatus*. A colour photograph is shown in Lim & Lim (1999). We examined its pholidosis in detail, but, as pointed out by Lim & Lim (1999), there is no scalation difference with specimens from the mainland. Although the patterns of head and body of this specimen are clealy different from those of specimens of the mainland, our sample is too limited to allow us to take a decision. We refer the population from Pulau Tioman to *Trimeresurus fucatus*.

The northern populations occur in both lowlands and hilly areas (Grossmann & Tillack 2001), whereas populations from West Malaysia are more or less confined to higher elevations, although Lim et al. (1995) recorded one specimen from only 400 m asl. Specimens cited by Dring (1979) were collected at 790 and 1280 m. Specimen BMNH 1967.2289 (Gunung Benom, State of Pahang) was collected at 1130 m.

Comparison with other species. — Main characters separating *Trimeresurus fucatus* from other taxa of the group are given in Tables 12–13. *Trimeresurus fucatus* differs from its "northern" relative *Trimeresurus popeiorum* by (1) the presence of dorsal crossbands in males of most populations; (2) the colour of the tail (see the description) in the northern populations; (3) the colour of the eyes: green or greenish-gold or copper in *T. fucatus*, vs. deep red in *T. popeiorum*; (4) the postocular streak in males, in *T. fucatus* sometimes absent, or white, or white with a dark red upper part (see Vogel [1990]) vs. always wide and vividly bicolor in *T. popeiorum*; (5) the postocular streak in females, lacking in females of *T. fucatus*, faint but present in *T. popeiorum*; (6) a higher value of TaL/TL in males (0.201–0.241 [x = 0.218, s = 0.001] vs. in *T. popeiorum* 0.181–0.211 [x = 0.195, s = 0.009]; U = 4.5, P < 0.001); (7) a higher number of SC in males (69–84 [x = 75.9, s = 3.5] vs. 59–75 [x = 68.1, s = 4.2] in *T. popeiorum*; U = 58, P < 0.001); (8) a more elongated, flattened head and oblically truncated snout; (9) a slightly smaller size in *T. fucatus* compared to *T. popeiorum*. See also Fig. 12.

Trimeresurus fucatus differs from the Sundaic species of the complex (see below) by (1) the presence of dorsal crossbands in most males; (2) the presence of a conspicuous white ventrolateral stripe in females (also present in *Trimeresurus sabahi*); (3) the presence of dorsal white spots in many specimens of *T. fucatus*, although, according to Stuebing & Inger (1999), white dots are sometimes present in *Trimeresurus sabahi*; (4) higher numbers of ventral scales in males and in females; (5) occipital and temporal scales strongly keeled in *T. fucatus*, smooth or much more weakly keeled in Sundaic species.

Sexual dimorphism. — It is significant in the relative length of the tail, in the number of subcaudals, and in the pattern:

(1) Strong difference in the ratio TaL/TL:

males: 0.201–0.241 (x = 0.218); females: 0.159–0.189 (x = 0.171)

(2) Differences in the number of subcaudals:

69–84 (x = 75.9) in males vs. 59–73 (x = 63.8) in females

(3) Pattern:

1. Presence of white vertebral dots in males (in many populations), barely visible or absent in females
2. Often a postocular streak in males, always absent in females
3. Red/white ventrolateral stripe in males, white or absent in females

There is no difference in the numbers of ventral scales nor in other scalation characters, nor in eye colour.

Description of the hemipenes (Fig. 13). — From MNHN 1990.4283 (holotype): hemipenes are bilobed, long and slender, 26.1 mm long or reaching the 23rd SC, rounded at their extremity. The area near the *sulcus spermaticus* is strongly calyculate. The shallow *sulcus spermaticus* divides at the base of the organ.

FIGURE 13. *Trimeresurus fucatus*. Hemipenes (from MNHN 1990.4283, holotype). Photograph by Roger Bour.

Range. — Myanmar. Known only from southern Taninthayi Division (Tenasserim), in the vicinity of Myeik (Mergui) and on Kanmaw Kyun (Kisseraing) Island. — Thailand. Known from the provinces of Prachuap Khiri Khan (on the basis of a specimen depicted in Wüster [1992], see below), Chumphon, Phang–Nga (Grossmann & Tillack, 2001), Krabi, Nakhon Si Thammarat, Surat Thani, and Trang, and probably occurs in all provinces farther south. — Federation of Malaysia. West Malaysia. Recorded from the States of Perak, Kedah (Lim et al., 1995), Pinang, Trengganu, Selangor, and Pahang, but probably present throughout, except the Cameron Highlands as far as is known.

The northern limits of the current distribution is at about 12.5°N, at Myeik (Myanmar) and Ban Pala–U, a locality cited by Wüster (1992) that is situated near the border between Prachuap Khiri Khan and Phetchaburi provinces (Anonymous [2000]; also Pauwels et al. [2003]). This species might be searched for in other suitable localities of Phetchaburi Province (Thailand) and Taninthayi Division (Myanmar).

Trimeresurus nebularis spec. nov.
(Figs. 14–19)

Trimeresurus gramineus (non *Coluber gramineus* Shaw, 1802): Boulenger (1912: 217, part.); Smith (1930: 90, part.); Smedley (1932: 123); Hoge & Romano Hoge (1981: 257, part.)
Trimeresurus popeiorum (non *Trimeresurus popeiorum* Smith, 1937): Tweedie (1954: 117, 1957: 121, 1983: 139, all part.); Lim (1982: cover, 20 & 21: Fig. 22; 1990: 393, 394: Fig. 7; 1991: cover, 23: Fig. 25); Lim et al. (1995: 361, part.); Manthey & Grossmann (1997: 409: Fig. 316).
Trimeresurus popae: Tweedie (1940: 131, part.)
Trimeresurus popeiorum ssp.: Chan-ard et al. (1999: 199 [bottom], 200 [both pictures]).

Holotype. — USNM 142425, adult female, from Gunung Brinchang [now Gunung Batu Berinchang], Cameron Highlands, State of Pahang, West Malaysia. Collected by H. Baker, 17 October 1959.

FIGURE 14. *Trimeresurus nebularis*. Holotype (USNM 142425). Lateral view of the head, left side. Photograph by Roger Bour.

FIGURE 15. *Trimeresurus nebularis*. Holotype (USNM 142425). Lateral view of the head, right side. Photograph by Roger Bour.

FIGURE 16. *Trimeresurus nebularis*. Holotype (USNM 142425). Dorsal view of the head. Photograph by Roger Bour.

FIGURE 17. *Trimeresurus nebularis*. Holotype (USNM 142425). General view. Photograph by Roger Bour.

Paratypes (7 specimens). — All from West Malaysia, Federation of Malaysia: IRSNB 2627 (male), Cameron Highlands (4°29'N–101°23'E), State of Pahang. – MNHN 2004.0501, ZRC 2.2887 (males), PSGV 626, ZRC 2.2884–85 (females), Cameron Highlands, State of Pahang. – ZFMK 82856, Gunung Batu Berinchang, Cameron Highlands, State of Pahang.

Diagnosis. — A species of *Trimeresurus* characterized by (1) hemipenes long, without spines; (2) 1st supralabial distinct from nasal; (3) 21 DSR at midbody, moderately keeled; (4) overall bright green coloration with blue tones and blue upper lips in males and females, and yellowish green chin and throat; (5) large size, with a TL up to about 1000 mm in males and at leat 950 mm in females; (6) postocular streak absent in males and females; (7) ventrolateral stripes often missing, or white or pale blue; (9) upper lips bluish-green; (10) eye green in males and females; (11) tail dark rusty brown vertebrally, green laterally with a sharp border between the colours (similar to *Trimeresurus albolabris* or *T. macrops*); (12) a low number of scales between the supraoculars (9–10); (13) tail average in females, with a ratio TaL/TL 0.165–0.172; (14) VEN 147–153; SC: 50–65.

Etymology. — The specific nomen is the Latin adjective *nebularis*, meaning "from the clouds", in allusion to the cloudy montane rainforests, or cloud forests, inhabited by this species.

Suggested English name: Cameron Highlands pitviper.

Description of the holotype. — Body rather stout, cylindrical; head triangular, very wide at its base, thick, rather elongated, 1.5 times as long as wide, clearly distinct from the neck; snout long, accounting for 24.4 % of total HL, 3.0 times as long as diameter of eye, flattened, rounded when seen from above, rather quadrangular when seen from lateral side, with a distinct *canthus rostralis*; eye rather small, with an VED/DEL ratio 0.55; nostril–loreal pit distance/nostril–eye distance ratio 0.55 (mean value of both sides); tail rather short, tapering, distinctly prehensile.

SVL: 734 mm; TaL: 147 mm; TL: 881 mm; HL: 50.65 mm; ratio TaL/TL: 0.167.

VEN: 153 (+ 2 preventrals); SC: 53, paired, plus one terminal scale; anal shield entire.

DSR: 23–21–15 scales, rhomboid, weakly keeled, first row smooth.

Rostral visible from above, about 1.5 times broader than high, triangular; nasals subrectangular, undivided, with nostril in their middle; one pair of enlarged, slightly curved internasals, 1.7 times as wide as deep, separated by 1 scale as wide as adjacent upper snout scales; 4/3 canthal scales bordering the *canthus rostralis* between the internasal and corresponding supraocular, slightly larger than adjacent snout scales; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2/2 postoculars; 1 entire, long and relatively wide supraocular on each side, about 2.4 times as long as wide, about 0.8 time as wide as the internasals; supraocular not indented on their inner margin by the upper head scales; scales on upper snout surface smooth, juxtaposed, irregular in shape, enlarged, with 5 snout scales on a line between the scale separating the internasals and a line connecting the anterior margins of eyes; cephalic scales small, much irregular, juxtaposed, smooth and flat on upper head surface; 9 Cep in a line between supraoculars; occipital scales flat and smooth; temporals small, subequal, in 2 or 3 rows, smooth or weakly, obtusely keeled; one thin, elongated, crescent-like subocular; 9/9 SL; 1st SL triangular, short, totally separated from the corresponding nasal; 2nd SL high, forming the anterior border of loreal pit, separated from nasal by two large scales on each side; 3rd SL much larger than the other labials, pentagonal, high and long, 1.1 times as long as high, in contact with the subocular on both sides; 4th SL shorter and smaller, 0.8 as high as 3rd one, separated from the subocular by one scale; 5th and posterior SL smaller than 4th one, 5th SL separated from the subocular by 2 scales, others in contact with the first row of temporals; 11/11 infralabials, those of the first pair in contact with each other, the first three pairs in contact with the chin shields; 6/6 rows of smooth gular scales; chin shields regularly arranged.

In preservative, the dorsal and lateral body surfaces are uniformly dark bluish-green, slightly paler on the lower sides. The interstitial skin is grey. The centre of scales of the 1st DSR is somewhat paler, but without the formation of a ventrolateral stripe. The tail is green on its side and below, pale pinkish-brown above.

The dorsal head surface and temporal regions are uniformly green, not paler on the supralabials; no postocular streak. The chin, throat and venter are green, paler than upper head surface.

Description of the paratypes. — A summary of morphological and meristical data of the six paratypes is given in Table 15. All morphological characters and coloration and pattern of females agree with those of the holotype. The postocular streak is absent in the two available males. The ventrolateral stripe is only white.

Description and variation. — The maximal confirmed total length known is 1002 mm (SVL 809 mm, TaL 193 mm) for a male (MNHN 2004.0501). The longest female seen by us (ZFMK 82856, paratype) is 948 mm long (SVL 792 mm, TaL 156 mm).

Body moderately thick in males and females. Triangular head elongated, massive, 5.8 % of SVL in one male, 6.2–6.9 % (x = 6.5 %) in 5 females, wide at its base, thick and flattened in males, rather convex in females when seen from the side. Snout moderately long, amounting for about 24.5–28.0 % of HL in both sexes, or 1.9 (in 1 male), 2.1–2.9 times as long as diameter of eye, flattened, rounded when seen from above, rather quadrangular when seen from the side, with a distinct *canthus rostralis*. Eye small, with a diameter 0.6–1.0 time the distance between its lower margin to the lip margin. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.165–0.193, with a sexual dimorphism (see below).

DSR: 21-23(24)–(20)21–(13)15, moderately keeled at midbody, less keeled or nearly smooth ventrolaterally, smooth on the first outer row.

VEN: 147–153 (plus 1–2 preventrals); SC: 50–65, all paired; anal shield entire.

TABLE 15. Morphological characters of the paratypes of *Trimeresurus nebularis*.

Collection number	Sex	SVL (mm)	TaL (mm)	TaL / TL	PosOc streak	Lateral stripe	VEN	SC	SL	Cep	IL	C3SL / SubOc
IRSNB 2627	M	595	____	____	None	Blue	153	____	9/9	9	11/10	0/0
ZRC 2.2887	M	269	63	0.190	None	White	153	65	10/11	9	11/11	0/0
MNHN 2004.0501	M	809	193	0.193	None	None	149	61	9/11	10	12/12	0/0
ZFMK 82856	F	792	156	0.165	None	None	147	50	9/9	9	11/11	0/0
PSGV 626	F	302	62	0.170	None	White	150	56	10/9	9	10/12	0/0
ZRC 2.2884	F	702	156	0.172	None	None	150	60	10/10	9	12/11	0/0
ZRC 2.2885	F	465	94	0.168	None	None	152	57	10/10	9	12/13	0/0

Head scalation as described for the holotype, with the following variation for major features: internasals either in contact (in 1/8 specimens) or separated by 1 (6/8 specimens) or 2 (1/8 specimens) small scale; 5–6 canthal scales, slightly larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; 2–3 small postoculars; one entire supraocular on each side, long and rather narrow, 2.5–2.8 (x = 2.5) times as long as wide, 0.6–0.8 (x = 0.7) time as wide as the internasals, not indented on their inner margins by the upper head scales; 4–6 (6 in only 1 specimen) on a line between the internasals or the scale separating the internasals and a line connecting the anterior margins of the eyes; 9 or 10 cephalic scales on a line between supraoculars (9 in 7/8 specimens, 10 in 1/8 specimens), smooth and flat; occipital scales larger than cephalic scales, weakly keeled (in 3/8 specimens) or smooth (5/8); temporals small, smooth in all seen specimens, subequal, in 2 or 3 rows; 9–11 SL (9–9: 3/8; 9–10: 1/8; 10–10: 2/8; 9–11: 1/8; 10–11: 1/8); 1st SL separated from nasal; 2nd SL forming the anterior border of loreal pit, separated from nasal by 1 or 2 scales; 3rd SL longest and highest, 1.1–1.3 times as long as high (x = 1.20), in contact with the subocular on both sides in all examined specimens; 4th SL, as long as high, 0.7–0.9 (x = 0.80) time lower than 3rd SL, separated from subocular by 1 scale on each side (in 6/8 specimens), or in contact on both sides (1/9), or in contact on one side (1/9); 5th SL separated from subocular by 2 scale rows of similar size; 10–13 IL (11–11 in 4/8 specimens; x = 11.3, s = 0.6), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 6–7 rows of smooth gular scales; throat shields irregularly arranged.

In life (See Figs. 18–19, which show a female and a juvenile respectively; a male was depicted in Chan-ard et al. [1999: 200]), the background colour is uniformly emerald green, grass green, with some blue hue or blue-green. A ventrolateral stripe, white or pale blue in males (hardly visible in the male depicted in Chan-ard et al. [1999: 200]), absent or white and faint in females, extends from the angle of the mouth through first third to half of the tail on the 1st DSR. The interstitial skin is very dark grey. The tail surface is basically the same colour as the dorsum on its sides, dark reddish-brown above, with a clear border between the two areas.

FIGURE 18. *Trimeresurus nebularis*. Living adult female. Photograph by Gernot Vogel.

The dorsal head surface and temporal regions are uniformly green, paler bluish-green on the supralabials; no postocular streak in all examined specimens. The chin, throat and venter are green or greenish-yellow, paler than upper head surface, or sometimes bright yellow. In life, eyes are green or slightly yellowish-green in both sexes and in juveniles.

Comparison with other species. — *Trimeresurus nebularis* differs from all other pitvipers of the *Trimeresurus popeiorum* complex by the combination of the following characters: (1) tail with a sharp border between the green and the brown colour; (2) eye colour green at both sexes; (3) postocular streak absent in both sexes; (4) a larger size; (5) the lowest number of scales between the supraoculars; (6) the lowest number of subcaudals; (7) a low number of ventrals; (8) the lack of sexual dimorphism; (9) upper lips bluish-green; (10) ventrolateral stripes often pale blue.

Main characters separating *Trimeresurus nebularis* from other taxa of the group are given in Tables 12–13. *Trimeresurus nebularis* differs from *T. popeiorum* by (1) the colour of the eye (never red in *T. nebularis*); (2) the number of Cep between the supraoculars; (3) the presence of a postocular streak in males of *T. popeiorum*; (4) the presence of a ventrolateral streak in females of *T. popeiorum*; (5) a stronger keeling of the Occ and Tem in *T. popeiorum*; (6) a lower number of VEN in females (147–153 [x = 150.4, s = 2.3] vs. 154–168 [x = 161.6, s = 4.2] in *T. popeiorum*).

FIGURE 19. *Trimeresurus nebularis*. Living juvenile. Photograph by Gernot Vogel.

Trimeresurus nebularis differs from *Trimeresurus fucatus* by (1) the absence of dorsal crossbands in males; (2) a white or blue ventrolateral stripe in males, vs. a bicolor ventrolateral stripe in males of *T. fucatus*, and the absence of this stripe in females vs. a conspicuous white stripe in females of *T. fucatus*; (3) the absence of a postocular streak in males; (4) the pattern of the tail; (5) a lower number of ventral scales (149–153 [x = 151.7, s = 2.3] in males of *T. nebularis* vs. 156–171 [x = 164.0, s = 3.5] in males of *T. fucatus*; in females 147–153 [x = 150.4, s = 2.3] vs. 157–170 [x = 163.5, s = 3.4] in *T. fucatus*; (6) a lower number of subcaudal scales (61–65 [x = 63.0, s = 2.8] in males of *T. nebularis* vs. 69–84 [x = 75.9, s = 3.5] in males of *T. fucatus*; in females 50–60 [x = 55.2, s = 3.8] vs. 59–73 [x = 63.8, s = 3.6] in *T. fucatus*).

Trimeresurus nebularis differs from *Trimeresurus sabahi* by: (1) a larger size; (2) the colour of the eyes (green vs. bright red in *T. sabahi*); (3) the pattern of the tail; (4) the presence of ventrolateral stripes in both sexes of *T. sabahi*; (5) a lower number of SC in both sexes (in males 61–65 [x = 63.0, s = 2.8] vs. 69–76 [x = 71.6, s = 2.5] in *T. sabahi*; in females 50–60 [x = 55.2, s = 3.8] vs. in *T. sabahi* 59–65 [x = 62.2, s = 2.7]); (6) the contact of 3rd SL with the subocular, in contact in all examined specimens of *T. nebularis*, separated in 14/20 occurrences in *T. sabahi*; (7) by proportionnally wider supraocular scales in *T. nebularis* (ratio L–SpOc/W–SpOc: 2.4–2.8 ([x = 2.5, s = 0.1] in *T. nebularis*, vs. 2.8–3.3 [x = 3.0, s = 0.2] in *T. sabahi*).

Lastly, *Trimeresurus nebularis* differs from *T. barati* by: (1) a larger size; (2) the pattern of the tail; (3) the colour of eyes in both sexes; (4) the ventrolateral stripe in males (bicolor in *T. barati*); (4) the number of MSR (21 vs. usually 17–19 in *T. barati*); (5) a snout shorter in *T. nebularis* than in *T. barati* (ratio DEP/DEN: 0.52–0.57 [x = 0.53, s = 0.03] vs. in *T. barati* 0.56–0.62 [x = 0.59, s = 0.02]).

Sexual dimorphism. — The dimorphism is very weak in this species, contrary to other species of the group. It is especially noteworthy that there is no difference in sizes of males and females. There are no differences in the numbers of ventral scales nor in other scalation characters, as well as in coloration and pattern. The sexual dimorphism is significant only in the relative length of the tail (3 males: 0.190–0.193; 5 females: 0.165–0.172) and in the number of subcaudals (3 males: 61–65; 5 females: 50–60).

Range. — Federation of Malaysia. West Malaysia. *Trimeresurus nebularis* should currently be regarded as endemic to the Cameron Highlands, State of Pahang.

This species may occur in the adjacent mountain ranges, as the Fraser's Hills, but from this area we examined only specimens of *T. fucatus*. *Trimeresurus nebularis* is a montane taxon, inhabiting wet subtropical montane forest covering the higher parts of the Cameron Highlands. Some biological data appeared in Smedley (1932). Specimen ZFMK 82856 was collected on slopes of Gunung Batu Berinchang. It was crawling about 23.00 on a road among rainforest, in fog shortly after a rainshower at a temperature of 18 C.

Trimeresurus sabahi new comb.

(Fig. 20)

Trimeresurus popeorum sabahi Regenass & Kramer, 1981: 190, 191: Figs. 9–12. — **Type locality**. "Mount Kinabalu, Kulapis River, British North Borneo", an unidentified river on slopes of Gunung Kinabalu, State of Sabah. — **Holotype**. MCZ 43608, adult male. Collected by J. A. Griswold, 6.8.1937.

Chresonymy subsequent to the original description only:

Trimeresurus popeorum sabahi: Malkmus (1992: 137; 1994: 248); Golay et al. (1993: 103); Orlov et al. (2002b: 353).

Trimeresurus popeiorum sabahi: David & Vogel (1996: 165); David & Ineich (1999: 288); Malkmus et al. (2002: 377); Orlov et al. (2002a: 194).

Trimeresurus popeiorum: Manthey & Grossmann (1997: 409, part.)
Trimeresurus popeorum: Stuebing (1991: 357); McDiarmid et al. (1999: 340, part.); Stuebing & Inger (1999: 229).

Material (10 specimens). — BMNH 96.4.29.10 (male), "Saiap, Kina Balu", now Sayap, Gunung Kinabalu, State of Sabah. — FMNH 233155, FMNH 243942 (females), Sipitang District, State of Sabah. — FMNH 251048 (male), Tambunan District, State of Sabah. — MNHN 1889.220–221 (males), "Mont Kinabalu", State of Sabah. — RMNH 8241 (male), "Borneo, voet van de Simedoen" [foot of the Simedoen], now Mt. Semedoem (1118 m asl), a mountain feeding Sungei Landak, a tributary which falls into Kapoeas River at 00°01'S–109°21'E, at a short distance from Pontianak, State of Sarawak. — USNM 130253 (male), Bundu Tuhan, Mt. Kinabalu, State of Sabah. — USNM 134128 (female), Tenompak, Mt. Kinabalu, State of Sabah. — ZFMK 51767 (male), Headquarters, Mt. Kinabalu, 1500 m asl, State of Sabah.

Diagnosis. — A species of the genus *Trimeresurus*, endemic to Borneo Island, characterized by the following points: (1) hemipenes long, smooth, without spines; (2) 1st supralabial distinct from nasal; (3) 21 DSR at midbody, moderately keeled; (4) overall green coloration in males and females, without crossbands; (5) postocular streak absent in males and females; (6) a bicolor ventrolateral stripe present in males, red or rusty-red below, white above; in females, the stripe is white of yellow; (7) eyes bright or deep red or deep orange in males and females, orange, yellowish-copper or yellowish-green in juvenile specimens; (8) tail sides green, widely mottled with rusty brown, with a sharp border between the colours; (9) tail long in males and females, with a ratio TaL/TL of 0.186–0.238, and 0.173–0.178 respectively; (10) VEN: 147–157; SC: 59–76; (11) Occipital and temporal scales smooth or very weakly keeled.

Description and variation. — The maximal confirmed total length known is 810 mm (SVL 619 mm, TaL 191 mm) (male; FMNH 251048). The largest known female is 880 mm long (SVL 662 mm, TaL 138 mm; FMNH 233155). In our sample, there is no noticeable difference of size between males and females.

Body relatively slender in males and thick in females. Triangular head average, amounting (in adults) for 5.0–5.8 % of SVL (x = 5.4 %) in males, 5.8–6.3 % of SVL (x = 6.0 %) in females, wide at its base, flattened in males, rather thick in females when seen from the side. Snout rather long, amounting (in adults) for 23.9–27.9 % (x = 26.2 %) of HL in males and 24.3–26.5 % (x = 25.4 %) of HL in females, or 1.8–2.5 (x = 2.2) times as long as diameter of eye, flattened, rounded when seen from above, oblically truncated when seen from the side, with a distinct *canthus rostralis*. Eye rather small, amounting (in adults) for 0.75–0.85 (x = 0.80) time in males and 0.60–0.80 (x = 0.70) time in females of the distance eye–lip. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.173–0.238, with a strong sexual dimorphism (see below).

DSR: 21(23)–21–15, more or less strongly keeled in males, weakly keeled in females, always smooth on the first DSR in both sexes.

VEN: 147–157 (plus 1–2 preventrals); SC: 59–76, all paired; anal shield entire. These values include those cited by Regenass & Kramer (1981).

Rostral visible from above, about 1.5 times broader than high, triangular; nasals subrectangular, undivided; one pair of enlarged, curved internasals, separated by 1 (in 7/10 specimens) or 2 (3/10) small scales; 4–5 canthal scales, larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; 1 triangular loreal between upper preocular and nasal; 2 upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2–3 small postoculars; one entire supraocular on each side, long and narrow, 2.7–3.3 (x = 2.9) times as long as wide, 0.50–0.75 (x = 0.65) time as wide as the internasals, indented on their inner margins by the upper head scales; 5–7 (7 in 5/10 specimens) enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, smooth, juxtaposed, irregular in shape; 9–11 (x = 10.3, s = 0.8) cephalic scales on a line between supraoculars (9: 2/10 specimens; 10: 4/10; 11: 4/10), smooth and flat; occipital scales larger than cephalic scales, smooth in both sexes (very weakly keeled in 1 male); occipital small in all examined specimens; temporals small, smooth in both sexes, subequal, in 2 or 3 rows; one thin, elongated, crescent-like subocular; 8–10 SL (8–9: 1/10 specimens; 9–9: 3/10; 9–10: 2/10; 10–10: 4/10); 1^{st} SL separated from nasal; 2^{nd} SL forming the anterior border of loreal pit, separated from nasal by 1 or 2 scales; 3rd SL longer and higher than other ones, 1.1–1.7 times as long as high (x = 1.40), in contact with the subocular on both sides (4/10 specimens) or separated by 1 scale on both sides (6/10), including in the three examined females; 4^{th} SL about as long as high, 0.7 to 0.9 (x = 0.85) time lower than 3^{rd} SL, separated from subocular by 1 scale on each side in 6/10 specimens, in contact on both sides in others; 5^{th} and posterior SL smaller than 4^{th} one, 5^{th} SL separated from subocular by 1 scale row of similar size in all specimens; 11–13 IL (10 [4/20 occurrences], 11 [6/20]; 12 [9/20]; 13 [1/20]; x = 11.3, s = 1.5), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7–9 rows of smooth gular scales; throat shields regularly arranged.

In life, the background colour is uniformly bright green or grass-green. In males, a bicolor ventrolateral stripe, rusty red or deep red below (rusty brown in alcohol) on lower half of 1^{st} DSR, white or whitish-yellow above and on the lower part of 2^{nd} DSR, extends from the angle of the mouth through first third to half of the tail. In females, the ventrolateral stripe is white or rarely yellow (white in preservative). The tail surface is basically the same colour as the dorsum, with the whole length of its upper part irregularly mottled with reddish-brown or rusty brown, without a sharply defined border between the red and green colours, entirely reddish-brown backwards.

The dorsal head surface is of the same colour than the body. A postocular streak is absent in both sexes. Eyes are bright red or deep red-orange in males and females (see Fig. 20), yellowish-copper in juveniles.

FIGURE 20. *Trimeresurus sabahi*. Living adult female. Photograph by Björn Lardner.

Comparison with other species. — *Trimeresurus sabahi* differs from all other pitvipers of the *Trimeresurus popeiorum* complex mostly by the combination of the following characters:(1) the eye colour, red or orange-red in both males and females; (2) no postocular streak in males and females; (4) a bicolor ventrolateral stripe in males, red below/white above, only white or yellow in females; (5) a low ventral count in males and females; (6) occipital and temporal scales smooth or very weakly keeled.

Main characters separating *Trimeresurus sabahi* from other taxa of the group are given in Tables 12–13. *T. sabahi* differs from *T. popeiorum* by (1) a smaller size; (2) by the absence of postocular streaks in both sexes; (3) a lower number of Cep between the supraoculars (9–11 [x = 10.3, s = 0.8] vs. in *T. popeiorum* 10–14 [x = 11.5, s = 1.0]; U = 45.5; $P < 0.05$)]); (4) a lower number of VEN in females (148–156 vs. 154–168 in *T. popeiorum*); (5) occipital and temporal scales smooth, vs. distinctly or strongly keeled in *T. popeiorum*.

Trimeresurus sabahi differs from *T. fucatus* by (1) a smaller size; (2) the absence of dorsal crossbands in *T. sabahi*; (3) the colour of the eyes in males and females (red in *T.*

sabahi vs. yellowish-green or gold or copper in *T. fucatus*); (4) the absence of vertebral white spots in *T. sabahi*, although, according to Stuebing & Inger (1999), white dots are sometimes present; (5) the tail pattern; (6) a higher number of ventral scales in both sexes of *T. fucatus* (in males 156–171 [x = 164.0, s = 3.5] vs. 147–157 [x = 151.6, s = 2.8] in *T. sabahi*; U = 1.5; P < 0.001; in females 157–170 [x = 163.5, s = 3.4] vs. in *T. sabahi* 148–156 [x = 152.2, s = 3.0]); (7) by weakly keeled or smooth occipital and temporal scales in *T. sabahi*, strongly keeled in *T. fucatus*.

Range. — Federation of Malaysia. State of Sabah (Borneo Island): known from the vicinity of Mt. Kinabalu, Mt. Lumaku, Mendolong (Stuebing, 1991) and Crocker Range (I. Das, pers. comm., May 2004). — State of Sarawak (Borneo Island): Kuching, Mt. Dulit, Mt. Gading, Mt. Penrissen and Pangkalan Ampat (Stuebing, 1991) and Muruk Miau, a mountain just south of Long Pasia, near the Indonesia–Sarawak border (R. B. Stuebing, pers. comm., April 2004).

This species, known from the elevated parts of Borneo Island in the Malaysian states of Sabah and Sarawak, has not been definitely recorded from the Indonesian part of Borneo (Kalimantan) (Malkmus et al., 2002; R. B. Stuebing, pers. comm., April 2004).

Trimeresurus barati new comb.

Trimeresurus popeorum barati Regenass & Kramer, 1981: 189, Figs. 5–8 (on p. 188). **Type locality**. “Solok, Sumatra”, now Solok, Sumatera Barat Province, Sumatra Island, Indonesia. – **Holotype**. NHMB 2587, adult male. Collected by M. Müller, 1885.

Chresonymy subsequent to original description only:

Trimeresurus popeorum barati: Dring et al. (1990: 123, 124); Golay et al. (1993: 103); Orlov et al. (2002b: 353).

Trimeresurus popeiorum barati: David & Vogel (1996: 164); David & Ineich (1999: 288); Orlov et al. (2002a: 194).

Trimeresurus popeiorum: Manthey & Grossmann (1997: 409, part.)

Trimeresurus popeorum: McDiarmid et al. (1999: 340, part.)

Material (17 specimens). — Indonesia (Sumatra Island). BMNH 1915.12.2.42 (male), “Sungei Kumbang, Korinchi, Sumatra”, a stream on slopes of Mt. Kerinci, Sumatera Barat Province. — NHMB 2587 (male, holotype), Solok, Sumatera Barat Province. — SMF 21226 (male), Bungur, Riau Province. — NHMW 23910:1, NHMW 23910:3 (females), NHMW 23910:2 (male), “Pagay, Sumatra”, one of Pagai Islands, Mentawai Archipelago, Sumatera Barat Province. — NHMW 23917:1–23917:6, NHMW 23917:8–23917:9 (all males), NHMW 23917:7, NHMW 23917:10 (females), Padang, Sumatera Barat Province. — RMNH 17190A (female), Padang, Sumatera Barat Province.

Diagnosis. — A species of the genus *Trimeresurus*, endemic to Sumatra Island, characterized by the following points: (1) hemipenes long, smooth, without spines; (2) 1st supralabial distinct from nasal; (3) 19 MSR (rarely 17); (4) overall green coloration in males and females, without crossbands; (5) postocular streak absent in males and females; (6) in males a ventrolateral stripe, reddish-brown below / white above, absent in females; (7) tail green, rusty-red above, slightly mottled with green laterally but with a definite border between the red and green colours; (8) VEN: 142–158; SC: 55–73; (8) tail long in males, with a ratio TaL/TL of 0.194–0.231, and in females, 0.164–0.176.

Description and variation. — The maximal total length known is 729 mm (SVL 570 mm, TaL 159 mm) for a male (NHMW 23917:1). The largest known female is 720 mm long (SVL 596 mm, TaL 124 mm; NHMW 23910:1). In our sample of 17 specimens, there is no noticeable difference of size between males and females.

Body slender in males and thick in females. Triangular head elongated, amounting for 5.1–5.8 % of SVL (x = 5.5 %) in males, 5.4–6.4 % of SVL (x = 5.7 %) in females, wide at its base, flattened in males, rather thick in females when seen from the side. Snout rather long, amounting (in adults) for 23.7–29.0 % (x = 26.8 %) of HL in males and 25.7–28.2 % (x = 26.8 %) of HL in females, or 1.6–2.3 (x = 2.1) times as long as diameter of eye, flattened, rounded when seen from above, oblically truncated when seen from the side, with a distinct *canthus rostralis*. Eye large, amounting for 0.9–1.2 (x = 1.0) times in males and 0.8–0.9 (x = 0.8) times in females of the distance eye–lip. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.164–0.231, with a strong sexual dimorphism (see below).

DSR: 19-21–(17)19 – 13-15, more or less strongly keeled in both sexes, smooth on 1st DSR.

In our samples of 17 specimens, the number of MSR is as follows: 17 (2/17) and 19 (15/17).

VEN: 142–158 (plus 1–2 preventrals); SC: 55–73, all paired; anal shield entire.

These values include those cited by Regenass & Kramer (1981).

Rostral visible from above, about 1.5 times broader than high, triangular; nasals subrectangular, undivided; one pair of enlarged, curved internasals, usually separated by 1 (in 13/17 specimens) or 2 (3/17) small scales, in contact in 1/17 specimens; 4–5 canthal scales, larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2–3 small postoculars; one entire supraocular on each side, moderately elongated and narrow, 2.6–3.3 (x = 2.9) times as long as wide, 0.50–0.70 (x = 0.60) time as wide as the internasals, indented on their inner margins by the upper head scales; 5–7 (7 in 1/17 specimens) enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, smooth, juxtaposed, irregular in shape; 9–13 (x = 10.8, s = 1.1) cephalic scales on a line between supraoculars (9: 1/17 specimens; 10: 7/17; 11: 5/17; 12: 2/17; 13: 2/17), always smooth and flat; occipital scales larger than cephalic scales, in males either smooth or weakly keeled in 6 out of 12 specimens, in females nearly entirely smooth or with some faint traces of keeling; temporals small, smooth in all examined specimens, subequal, in 2 or 3 rows; one thin, elongated, crescent-like subocular; 9–11 SL (9–9: 4/17 specimens; 9–10: 5/17; 10–10: 6/17; 9–11: 1/17; 10–11: 1/17); 1^{st} SL separated from nasal; 2^{nd} SL forming the anterior border of loreal pit, separated from nasal by 2 scales; 3^{rd} SL longest and highest, 1.2–1.7 times as long as high (x = 1.4), usually in contact with the subocular on both sides (14/17 specimens), or in contact on one side (3/17); 4^{th} SL, as long as high, 0.8–1.2 (x = 0.9) as high as 3^{rd} SL, separated from subocular by 1 scale on each side in 16/17 examined specimens, in contact one side in 1/17; 5^{th} and posterior SL smaller than 4^{th} SL, 5^{th} SL separated from subocular by 1 scale row of similar size in all specimens; 10–14 IL (10–11 [1/17], 11–11 [2/17], 11–12 [5/17], 12–12 [5/17], 13–13 [2/17], and 13–14 [1/17]; x = 11.7, s = 0.85), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7–9 rows of smooth gular scales; throat shields regularly arranged.

In life, the background colour is uniformly bright green or grass-green. In males, a rather thin bicolor ventrolateral stripe, deep red or chocolate red below (rusty brown in alcohol) on lower half of 1^{st} DSR, white above, extends from the angle of the mouth through first third of the tail. In females, this stripe is absent.

The tail surface is basically the same colour as the dorsum, rusty-red above, slightly mottled with green laterally but with a definite border between the red and green colours, entirely reddish-brown backwards.

The dorsal head surface and temporal regions are of the same colours as the dorsum, paler green on the supralabials. In both males and females, the postocular streak is absent, except in specimen BMNH 1915.12.2.42, which has a faint bicolor postocular streak.

Comparison with other species. — *Trimeresurus barati* differs from all other pitvipers of the *Trimeresurus popeiorum* complex by the combination of the following characters: (1) the number of MSR, usually 19; (2) tail with a definite border between the red and green colours; (3) postocular streak absent in males and females; (4) a weak ventrolateral stripe, bicolor reddish-brown below and white above or only white in males, absent in females; (5) a smaller size; (6) a low number of VEN in males and females; (7) occipital and temporal scales smooth or weakly keeled; (8) the pattern of the tail.

Main characters separating *Trimeresurus barati* from other species of the group are given in Tables 12–13. From *T. popeiorum*, it differs by: (1) a smaller size; (2) the lack of postocular streak in males; (3) the lack of ventrolateral stripe in females; (4) the number of MSR; (5) a lower number of ventrals in females (146–158 vs. 154–168 in *T. popeiorum*); (6) occipital and temporal scales much more weakly keeled; (7) by the higher value for TaL/TL in males, although with a wide overlap in the ranges (see Table 12); (8) the pattern of the tail.

Trimeresurus barati differs from *Trimeresurus fucatus* by (1) a smaller size in *T. barati*; (2) the number of MSR (17–19 vs. 21 in *T. fucatus*); (3) the lack of dorsal crossbands in *T. barati*; (4) the lack of a ventrolateral stripe in females of *T. barati*; (6) the pattern of the tail; (7) by a higher number of VEN in both sexes of *T. fucatus* (males: 156–171

[x = 164.0, s = 3.5] vs. in *T. barati* 142–153 [x = 148.3, s = 3.3]; in females: 157–170 in *T. fucatus* [x = 163.5, s = 3.4] vs. in *T. barati* 146–158 [x = 149.8, s = 4.3]); (8) a higher number of SC in males and especially in females of *T. fucatus* (59–73 [x = 63.8, s = 3.6] vs. in *T. barati* 55–59 [x = 57.2, s = 1.6]); (9) occipital and temporal scales much more weakly keeled or smooth in *T. barati*; (10) the pattern of the tail.

Trimeresurus barati differs from *T. sabahi* by: (1) the number of MSR; (2) a smaller size; (3) the presence of a white or yellow ventrolateral stripe in females of *T. sabahi*, absent in *T. barati*; (4) the colour of the eyes, orange or yellow in *T. barati* vs. red or orange-red in *T. sabahi*; (5) a slightly lower ratio TaL/TL in females (0.164–0.176 [x = 0.172, s = 0.005] vs. 0.173–0.178 [x = 0.176, s = 0.003] in *T. sabahi*; U = 1; $P < 0.05$); (6) a lower number of SC in females (55–59 [x = 57.2, s = 1.5] vs. 59–65 [x = 62.2, s = 2.7] in *T. sabahi*); (7) by the contact of the 3rd SL with the SubOC, usually in contact in both sexes of *T. barati* (in 31/34 total occurrences [left + right sides], vs. in contact in only 8/20 occurrences in *T. sabahi* and separated by 1 scale in the three examined females; (8) the pattern of the tail.

Range. — Indonesia. Sumatra Island: known from the provinces of Sumatera Barat, Riau and Benkulu (unpublished). Mentawai Archipelago: Pagay Islands. According to Dring et al. (1990), perhaps also Sipora and Siberut Islands.

A list of localities appeared in David & Vogel (1996). In Sumatra, this species has mostly been recorded from mountainous areas of the island.

Trimeresurus* cf. *sabahi

Lachesis gramineus (non *Coluber gramineus* Shaw, 1802): Baumann (1913: 272).

Material (3 specimens). — Indonesia (Sumatra Island). NMBE 1018072–73 (males), NMBE 1018 074 (female), “Mts. Battak”, at present the Toba Massif, Sumatera Utara Province.

Taxonomic comments. — In Sumatra, two groups of populations may be easily distinguished by their morphology. Populations from western Sumatra (Padang Highlands, Mt. Kerinci) have 17–19 MSR, and are assigned here to *Trimeresurus barati*, a rather homogeneous taxon. Three specimens from Toba Massif, in Northern Sumatra, have 21 MSR, and differ from *Trimeresurus barati* by other morphological features (see below). These specimens, cited in Baumann (1913), were not examined by Regenass & Kramer (1981) and were not included in the account of *Trimeresurus popeiorum barati* in David & Vogel (1996). On the basis of several characters detailed below, we tentatively regard these specimens as related to the Bornean *Trimeresurus sabahi*. However, our limited material does not allow us to ascertain its relationships, inasmuch as the colour of the eyes and other features of the pattern of these animals are not known. Pending the collect of further specimens from this area of Sumatra, we refrain to conclude on their taxonomic position. This population with 21 MSR does not appear in the keys given below.

Diagnosis. — These specimens are referred to *Trimeresurus* cf. *sabahi* on the basis of (1) overall green coloration in males and females without darker crossbands; (2) the absence of a postocular streak in both males and female; (3) the absence of a ventrolateral stripe in the sole available female; (3) the long tail in males (TaL/TL 0.215–0.230); (4) the low number of VEN (153–155); (5) smooth occipital scales.

Description and variation. — The maximal confirmed total length known is 730 mm (SVL 562 mm, TaL 168 mm) for a male (NMBE 1018 072).

Morphology of head and body typical of *Trimeresurus sabahi*. Triangular head elongated, amounting for 5.1–5.5 % of SVL in males, 6.0 % of SVL in the female. Snout rather long, amounting for 23.7–25.6 of HL in males and 23.3 of HL in the female, or 1.8–2.2 times as long as diameter of eye. Eye large, amounting for 0.8–1.2 times in males the distance eye–lip. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.157–0.230, with a seemingly strong sexual dimorphism (see below).

DSR: 21-24–21–15, strongly keeled in males, weakly keeled in females, smooth on 1st DSR.

VEN: 153–155 (plus 2 preventrals); SC: 58–73, all paired; anal shield entire.

Main head scalation features include: internasals separated by 1 (in 2/3 specimens) or 2 scales; 4–5 canthal scales bordering the *canthus rostralis*; 2 small postoculars; one entire supraocular on each side, 2.3–3.4 times as long as wide, 0.6–0.8 time as wide as the internasals, indented on their inner margins by the upper head scales; 5 enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes; 10–11 Cep on a line between supraoculars; occipital and temporal scales smooth in 3 available specimens; 9–10 SL (9–9: 1 specimen; 10–10: 2 specimens); 1st SL separated from nasal; 2nd SL forming the anterior border of loreal pit, separated from nasal by 2 scales; 3rd SL longest and highest, 1.2–1.7 times as long as high, in contact with the subocular on both sides (1/3 specimens), or in contact on one side (1/3) or separated by 1 scale on both sides (1/3); 4th SL, as long as high, 0.8–1.3 as high as 3rd SL, separated from subocular by 1 scale on each side; 5th SL separated from subocular by 1 scale row of similar size in all specimens; 10–13 IL, those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7–8 rows of smooth gular scales.

In preservative, the background colour is uniformly dark green. In males, a thin white ventrolateral stripe (perhaps deep red or chocolate red below, white above in life? The faded pattern does not allow to ascertain the colour in life), extends from the neck. In the female, this stripe is absent.

The tail surface is basically the same colour as the dorsum, mottled with rusty-brown on its sides and below, entirely reddish-brown backwards.

The dorsal head surface and temporal regions are of the same colours as the dorsum, paler green on the supralabials. In both males and female, the postocular streak is absent.

Comparison with other species. — *Trimeresurus* cf. *sabahi* differs from *Trimeresurus sabahi* mostly by (1) a much lower ratio TaL/TL in females (0.157 vs. 0.173–0.178) and (2) a slightly shorter snout; most other characters are similar. It differs from *T. barati*, occurring also in Sumatra, by (1) the number of MSR (21 vs. 17–19); (2) a lower value of the ratio TaL/TL in females (0.157 vs. 0.164–0.176); (3) slightly lower values of the ratio DEP/DEN in males (0.51–0.53 vs. 0.55–0.62 in *T. barati*); and (4) the pattern of the tail, mottled in *T.* cf. *sabahi*. Lastly, *T.* cf. *sabahi* differs from *T. nebularis* by (1) differences in the ratio TaL/TL as noted in Table 12; (2) a seemingly higher number of SC in males (73 in two specimens vs. 61–65 in *T. nebularis*); (3) a higher number of Cep (10–11 vs. 9–10 in *T. nebularis*); (4) a wider and more conspicuous ventrolateral stripe than in males *T. nebularis*; (5) the pattern of the tail, mottled in *T.* cf. *sabahi*.

Range. — Indonesia. Sumatra Island: known from the province of Sumatera Uttara (Toba Massif).

DISCUSSION

Taxonomic rank of recognized taxa

In the last revision of the complex of *Trimeresurus popeiorum*, Regenass & Kramer (1981) recognized three subspecies. We have here presented a different interpretation. Two species concept are currently prevailing in herpetology, either the Biological Species Concept (BSC) (see, for example, Dubois, 1977; Frost & Hillis, 1990; Mayr & Ashlock, 1991; Mayden, 1997; Mayr, 2000) or the Phylogenetic Species Concept (PSC) (see Frost & Hillis, 1990; Mayden, 1997, Wheeler & Platnik, 2000). As pointed out by Cracraft (1997: 332), these two concepts provide a very different way to ascertain the status of populations. In this paper, we adopt the Phylogenetic Species Concept for allopatric populations and the Biological Species Concept for sympatric populations. The presence of four widely allopatric populations, three of them being insular, makes the BSC of little use as it is now impossible to ascertain whether these populations are genetically compatible, in being able to produce fertile offsprings in natural conditions and if gene flow would occur between them if they were in contact. In contrast, these six clusters are fully diagnosable by the combination of a low number of morphological characters and fall into the basic definition of the PSC.

Cluster I and Cluster II include specimens with a conservative morphology over the entire range of their distribution. Between these two clusters, there is both a discreet geographic border and a sharp difference in several characters of scalation and colouration (see respective species accounts), without, or at best, with a slight overlap in some characters between the clusters. Based on these characters, we regard these clusters as distinct species according to the PSC. There are also differences in characters that may be supposed to be sexually related, such as the presence of a postocular streak, that we previously regarded as significant to separate species within the genus *Trimeresurus* (see David et al., 2001, 2002). Furthermore, these populations are, for a large part, ecologically isolated (see below). The BSC would also lead to the recognition of two distinct species.

The situation is more complicated in the case of Clusters III–VI. The position of Cluster III (OTU 7) with respect to Cluster II is obvious, as OTU 7 occurs within the distributional limits of OTU 8 (belonging to Cluster II), without observed interbreeding. This agrees with the definition of distinct species according to the BSC, and makes Cluster III distinct from Cluster II. Specimens of both clusters show a homogeneous morphology, clearly distinct each from the other, and are biologically separated by different ecological requirements (see below). There are also differences in a character that may be supposed to be sexually related, the occurrence of ventrolateral stripes.

However, Clusters III to VI both show constant morphological differences of their own and are clearly diagnosable, and, at same time, show also several strong morphological similarities (low number of ventral scales, lack of postocular streak in both sexes, and so on) distinguishing them from other species in the *T. popeiorum* complex of clusters I and II, suggesting that they are more closely related to each other than to clusters I and II. According to the PSC, these allopatric clusters, fully diagnosable, deserve a specific status, a position that is here adopted (except for Cluster VI, for which we do not have enough specimens to conclude on its position). On the other hand, Clusters III, IV, V and VI occur in mountains of the Sunda Region and seem to have similar ecological requirements. These populations are now isolated and allopatric, Clusters IV–VI occurring on the islands of Borneo and Sumatra respectively. However, the palaebiogeography of the Sunda Region suggests that these now isolated populations are remnants of a former widespread equatorial species. During the Pleistocene period of the Quaternary (about 1.6M–17.000 years BP), the world climate was affected by alternating periods of cooling and heating, with associated dry and wet periods in the intertropical regions. Southeast Asia was hence repeatedly affected by several severe modifications of the climate (Voris, 2000; Inger & Voris, 2001; see also Pauwels et al., 2003, for a more complete discussion and references). The consequence of these climatic phenomenons led to a global lowering of sea levels and the emergence of a large landmass connecting Sumatra, Borneo and Java with mainland Southeast Asia, and to alternating warmer and cooler temperatures, with both a higher seasonality and a sharp decrease in the volume of rainfalls. The most likely effect of the increasing drier conditions during the Pleistocene was a wide scale reduction of the land covered with lowland rain forests in the Sunda Region, replaced by savannas and open woodlands (Inger & Voris, 2001), whereas higher parts of the Sundaland, namely the mountain ranges on the margin of this basin which now constitute the current ranges of West Malaysia (Cameron Highlands), Sumatra (Barisan Range) and Borneo (Mt. Kina Balu, Crocker Range, and so on) were not as much affected. These data suggest that current OTUs of the Sunda Region are remnants of a previously more widespread species, which found there suitable refuges within their current range. According to Voris (2000), these populations were completely isolated on several occasions, the last one only quite recently (up to about 17,000 years). Are they currently biologically differentiated or reproductively compatible? The strict application of the BSC is here impossible, except by inference, namely by comparison with other species in the *Trimeresurus* complex. Cluster V is both the most morphologically differentiated and isolated, and, on the basis of known variation in the genus *Trimeresurus*, deserves a specific status. Cluster III lacks all characters that we suppose to be sexually related, and is hence biologically isolated. By elimination, Cluster IV, different from the other Sundaic clusters, also deserves a specific status according to the BSC. We regard Cluster IV and Cluster V as distinct species, along with Cluster III, on the basis of both species concepts discussed here.

Generic allocation

Recently, Malhotra & Thorpe (2004) split the genus *Trimeresurus* auctorum into seven genera, primarily on the basis of molecular data and hemipenes morphology. *Trimeresurus popeiorum* was allocated to the new genus *Popeia* Malhotra & Thorpe, 2004. Pending further investigations on the status of these genera, we prefer to adopt a conservative generic taxonomy in retaining the taxon *popeiorum* and the related species considered in this paper in the genus *Trimeresurus*.

Keys

The five recognized species are separated each from the others by combinations of characters, which are summarized in the following keys:

Key to males

1 17 or 19 MSR, endemic to Sumatra and Mentawai Islands............ *Trimeresurus barati*
- 21 MSR 2
2 Postocular streak present.. 3
- Postocular streak absent 4
3 Eyes deep red, ratio Tal/TL 0.180.21, less than 76 SC, usually no crossbands on the body, only rarely with white vertebral dots ....*Trimeresurus popeiorum*
- Eyes greenish-yellow, gold or yellow copper, ratio TaL/TL 0.200.24, more than 69 SC, dark bands on the body, usually white vertebral dots present ...... *Trimeresurus fucatus*
4 Less than 66 SC, faint ventrolateral stripe; tail uniform, eyes green ....*Trimeresurus nebularis*
- More than 68 SC, conspicuous ventrolateral stripe; tail mottled; eyes not green 5
5 Vertebral white dots usually present, more than 155 VEN, eyes greenish-yellow, gold or yellowish-copper, not from Borneo .... *Trimeresurus fucatus*
- Normally without vertebral white dots, 157 VEN or less, eyes red, endemic to Borneo .... *Trimeresurus sabahi*

Key to females

1 17 or 19 MSR, endemic to Sumatra and Mentawai islands .... *Trimeresurus barati*
- 21 MSR 2
2 At least 154 VEN 3
- Less than 156 VEN 4
3 56–64 SC, eyes red, no white vertebral dots, often with a white postocular streak, tail at the basis laterally widely green ....*Trimeresurus popeiorum*
- 59–73 SC, eyes greenish-yellow, gold or yellowish-copper, often with white vertebral dots, no postocular streak, tail at the basis laterally with little or no green .... *Trimeresurus fucatus*
4 Less than 61 SC; tail with a sharp border between the green and rusty areas; no ventrolateral stripe; eye green; West Malaysia ....*Trimeresurus nebularis*
- More than 58 SC; tail mottled, without a sharp border between the green and rusty areas; a white or yellow ventrolateral stripe; eye red; endemic to Borneo Island .... *Trimeresurus sabahi*

Relationships

On the basis of morphological comparison, two groups can be defined within the complex. The first one includes *Trimeresurus popeiorum* and *Trimeresurus fucatus*. Both species are characterized by a high number of ventral scales, usually strongly keeled occipital and temporal scales, at least in males, and the presence of a postocular streak. *Trimeresurus fucatus* is differentiated by the combination of characters listed above, but also has different ecological requirements. *T. popeiorum* is a species largely infeodated to wet hill and montane areas, although it has been collected as low as 420 m asl in Myanmar. *Trimeresurus fucatus* has been collected in both lowland and hilly rainforests of Peninsular Thailand, but was recorded in hills and mountains in West Malaysia.

The second group is characterized by a low number of ventral scales, usually smooth occipital scales and smooth temporal scales, and the absence of a postocular streak in males. It includes three Sundaic species inhabiting highlands of West Malaysia, Borneo and Sumatra respectively. In this group, Trimeresurus nebularis is the most differentiated by its uniform pattern in both sexes and its bright green eyes. Trimeresurus sabahi and T. barati are rather similar in pattern, and differ mostly by the number of dorsal scales at midbody. Molecular analyses of these taxa are in preparation.

There are still numerous points that remain unresolved. Firstly, the distributions of *Trimeresurus popeiorum* towards the east (Laos, Northeast Thailand) and south (Myanmar, Northwest Thailand) of its range, and the distributional limits of *Trimeresurus fucatus* in Thailand and Myanmar remain to be ascertained. The status of specimens from northern Vietnam and central Sumatra needs to be investigated. The next step in this study of green pitvipers will be the investigations of relationships on the basis of molecular analyses. Recent mt-DNA based phylogenies (Giannasi et al., 2001) did not include representatives of all taxa recognized in this paper. Such results will be published elsewhere.

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