A new karst-dwelling, colorful pitviper (Viperidae: Trimeresurus) from northern Peninsular Thailand

Article *in* Zootaxa · May 2021

DOI: 10.11646/zootaxa.4974.2.4

Zootaxa 4974 (2): 307–332
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4974.2.4
http://zoobank.org/urn:lsid:zoobank.org:pub:CC82F4EC-2C10-43E9-8408-246186C78DBD

A new karst-dwelling, colorful pitviper (Viperidae: *Trimeresurus*) from northern Peninsular Thailand

MONTRI SUMONTHA[1,*], SUNUTCHA SUNTRARACHUN[2,3], OLIVIER S. G. PAUWELS[5,*], PARINYA PAWANGKHANANT[6], NIRUT CHOMNGAM[7], PRAPANTH IAMWIRIYAKUL[8] & LAWAN CHANHOME[2,4]
[1]*Ranong Marine Fisheries Station, 157 Saphanpla Rd., Paknam, Muang, Ranong 85000, Thailand.*
montri.sumontha@gmail.com; https://orcid.org/0000-0003-4829-7731
[2]*Queen Saovabha Memorial Institute, Thai Red Cross Society, Pathumwan, Bangkok 10330, Thailand.*
[3] *https://orcid.org/0000-0001-8358-8230*
[4] *https://orcid.org/0000-0003-2425-5000*
[5]*Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium.*
opauwels@naturalsciences.be, osgpauwels@yahoo.fr; https://orcid.org/0000-0002-3265-5496
[6]*University of Phayao, Phayao, Thailand. peat_swamp@hotmail.com; https://orcid.org/0000-0002-0947-5729*
[7]*54 M. 2 Tha Pha, Ban Pong, Ratchaburi 70110, Thailand. https://orcid.org/0000-0002-7140-9044*
[8]*59 Soi Onnut 19 Suanluang, Bangkok 10250, Thailand. https://orcid.org/0000-0001-7286-3604*
[*]*Corresponding authors*

Abstract

We describe a colorful and distinctively patterned, karst-dwelling pitviper, *Trimeresurus kuiburi* **sp. nov.**, from the isolated, coastal massif of Khao Sam Roi Yot in Kui Buri District, Prachuap Khiri Khan Province, in northern Peninsular Thailand. The new species, member of the '*Cryptelytrops* group' *sensu* Malhotra & Thorpe (2004) and morphologically and genetically allied to *Trimeresurus kanburiensis* and *T. venustus*, differs from all pitviper taxa by a combination of red/purple bands on a green dorsum; a white concave suborbital stripe in males (straight and less visible in females); white, spaced vertebral dots in males (absent in females); pale green belly lacking dark dots or stripe on the lateral sides of the ventrals; partially fused first supralabial and nasal scale; 19 dorsal scale rows at midbody; 164–171 ventrals; 63–65 subcaudals in males, 51–53 in females; maximal known SVL of 451 mm; and long, papillose hemipenes.

Key words: Thai-Malay Peninsula, Gulf of Thailand, *Trimeresurus kuiburi* sp. nov., taxonomy, limestone

Introduction

During field surveys on the coastal limestone massif of Khao Sam Roi Yot which led to the discovery of the endemic geckos *Cyrtodactylus samroiyot* Pauwels & Sumontha and *Dixonius kaweesaki* Sumontha, Chomngam, Phanamphon, Pawangkhanant, Viriyapanon, Thanaprayotsak & Pauwels, we encountered a strikingly colored pitviper unknown to us that we listed as *Trimeresurus* sp. among the squamates found in the immediate surroundings (Sumontha *et al*. 2017a). In order to assess the identity of this pitviper we secured and examined a series of male and female individuals from a limestone hill just south of Khao Sam Roi Yot National Park. Confirming our first impression based on its habitus, this pitviper turned out to be a member of the '*Cryptelytrops*' group *sensu* Malhotra & Thorpe (2004a) diagnosed by the combination of a long papillose or calyculate hemipenis and a (partially) fused first supralabial and nasal scale. Although on a nomenclatural point of view the genus *Cryptelytrops* Cope was shown to be synonym with *Trimeresurus s.s*. by David *et al*. (2011), the phylogenetic grouping under *Cryptelytrops* as conceived by Malhotra & Thorpe (2004a) remains valid and practical, and we compared the Khao Sam Roi Yot population to all its members.

Only two species of the *Trimeresurus s.s*. (*Cryptelytrops*) group showing a banded dorsal pattern comparable to that of the population of Khao Sam Roi Yot occur in Thailand: *Trimeresurus kanburiensis* Smith, 1943 and *T. venustus* Vogel, 1991. Their nomenclatural history has been the subject of a long saga of conflictual publications.

Described on the base of a single female from Kanchanaburi Province in western Thailand, *Trimeresurus kanburiensis* remained an enigmatic pitviper until a few more individuals were discovered in the late 1980's and published by Warrell *et al.* in 1992. *Trimeresurus venustus*, a relatively similar-looking species, was described from Nakhon Si Thammarat Province in southern Peninsular Thailand. The main diagnostic characters to separate *Trimeresurus venustus* from *T. kanburiensis* were the following '21 scale rows at mid-body rather than 19; narrower, less indented and divided, supraoculars; slighter body and a distinctive brownish-red banded colour pattern' (as summarized by Malhotra & Thorpe 2004b). After a period during which the two species were regarded as synonyms by a number of authors (e.g., McDiarmid *et al*. 1999), in 2004 two studies (David *et al*. 2004b; Malhotra & Thorpe 2004b) independently confirmed the distinctiveness of *Trimeresurus kanburiensis* and *T. venustus* and hence the validity of the latter as a separate species. David *et al*. (2004b) listed a series of 14 differences in pattern, scalation and morphometrics separating these two species. Both studies mentioned the existence of a few specimens of *Trimeresurus venustus* with 19 MSR while the latter species was previously said to constantly have 21 MSR, rendering the MSR number a less reliable diagnostic character to distinguish the two species. David *et al*. (2004b) indeed examined two males with 19 MSR (PSGV 600 & PSGV 662) from the same locality 'Ampoe Lan Saka', thus Lan Saka District in central Nakhon Si Thammarat Province.

Malhotra & Thorpe (2004b) included three individuals with 19 MSR from 'near Khao Luang massif, near Nakhon Si Thammarat' and another one from Surat Thani in a phylogenetic analysis; as well as two individuals with 21 MSR, both from Thung Song, the type-locality of *Trimeresurus venustus* in southern Nakhon Si Thammarat Province. Their molecular results were based on three mitochondrial DNA fragments (cytochrome oxidase *c*, NADH dehydrogenase 4 and 12S rDNA). According to the phylogenetic tree obtained by Bayesian inference, the four specimens collected in Khao Luang, Nakhon Si Thammarat Province, and Surat Thani, Surat Thani Province, form a separate evolutionary lineage, distinct from the lineage formed by the two typical specimens collected in Thung Song. These two lineages form two distinct clades supported by maximal values of posterior probability (1) and of parsimony (100). These results only are not sufficient to prove the existence of two distinct species because these two clades could as well represent two geographically-separated populations of a single species, but they do certainly not contradict the possible existence of two species. Whether the typical, southern populations of *Trimeresurus venustus* with 21 MSR in southern Nakhon Si Thammarat Province are conspecific with the northern populations with 19 MSR in central and northern Nakhon Si Thammarat Province and farther north in Surat Thani Province consequently still has to be clarified. Since 2004 most authors have accepted that *Trimeresurus kanburiensis* and *T. venustus* are well distinct, and they were no longer confused, with few exceptions such as, accidentally, by Vogel himself, ironically (Pauwels 2008).

Their scalation, pattern, color and morphometric characteristics show that the pitvipers inhabiting Khao Sam Roi Yot are unambiguously distinct from *Trimeresurus kanburiensis*, *T. venustus* and all other congeneric taxa, and represent a new species, described here.

Material and methods

Morphological analysis. Voucher specimens were fixed in 90% ethanol and subsequently transferred into 70% ethanol for permanent storage. Hemipenes were forcedly everted just before preservation by injection of ethanol with a syringe at the base of the tail. Measurements and meristic counts followed Sumontha *et al*. (2020). Paired meristic characters are given left/right.

The following measurements were taken with a digital caliper to the nearest 0.1 mm: ED, horizontal eye diameter; HD, maximum head depth; HL, head length (from the tip of rostral to the posterior end of the jaw); HW, maximum head width; SnL, snout length (from the tip of rostral to the anterior eye margins); SOL, supraocular length; SOW, supraocular width; SVL, snout-vent length; TaL, tail length; TL, total length.

Meristic characters abbreviations: A, anal plate(s); ASR, anterior number of dorsal scale rows (at one HL behind head); IL, number of infralabial scales; IOS, interorbital scales, counted along a row between the middle of supraocular scales; MSR, number of dorsal scale rows at midbody (at the level of the ventral plate corresponding to half of the total number of ventrals); PosOc, (number of) postocular scale(s); PSR, posterior number of dorsal scale rows (at one HL before anal plate); PreV, number of preventrals (directly preceding the ventrals, unpaired, wider than long but not in contact on each side with the 1st dorsal scale row); SC, number of subcaudal scales, not including the terminal, pointed scute; SL, number of supralabial scales; SRR, dorsal scale rows reduction (according to the method of Dowling 1951b); V, (number of) ventral scales (counted according to the method of Dowling 1951a).

Museum and other acronyms: AUP: Agriculture University of Phayao, Phayao; MNHN: Muséum national d’Histoire naturelle, Paris; MS: Montri Sumontha’s field number series; PSGV: Gernot Vogel’s private collection, Heidelberg; PSUZC: Prince of Songkhla University Zoological Collection, Songkhla; QSMI: Queen Saovabha Memorial Institute, Thai Red Cross, Bangkok; RBINS: Royal Belgian Institute of Natural Sciences, Brussels. Other abbreviations: Prov.: Province.

Molecular analysis. Shedded skins of the samples were washed with sterile distilled water, dried in air and cut into small pieces. DNA extraction was performed using Genomic DNA extraction mini kit (Tissue) (RBC Bioscience, Taipei), according to the manufacturer’s instructions. Oligonucleotide primers for cytochrome b and 16S ribosomal RNA were designed using nucleotide sequences in GenBank (Table 1). DNA was amplified using the Polymerase Chain Reaction (PCR) in 50 µl reactions containing 10 x buffer, 100mM of each dNTP, 25 mM $MgCl_2$, 50 pmol/µl of forward and reverse primers, Taq DNA polymerase and 10 µl of DNA template. The PCR was performed using a thermocycle (MWG Biotech, USA) at 94°C for 3 minutes, followed by 40 cyclers of 94°C, 56°C, and 72°C for one minute each, and a final extension of 72°C for 7 minutes. PCR products were electrophoresed on a 1.5% agarose gel containing ethidium bromide in 1xTAE buffer along with appropriate molecular size markers. The gel fragment containing the amplified product was excised and extracted using Gel/PCR DNA fragments extraction kit (RBC Bioscience, Taipei). DNA sequencing was carried out using the amplification primers by 1st BASE sequencing (Malaysia-http://www.base-asia.com).

TABLE 1. Oligonucleotide primers used for PCR and sequencing in this study.

Gene	Primers	Nucleotides (5’ 3’)	References
Cytochrome *b*	Cytb-F	5’ GCCTGAAAAACCACCGTTGT 3’	Sumontha *et al*. (2020)
	Cytb-R	5’ CCGTCTTTGGTTTACAAGAAC 3’	
16S rRNA	1216-F	5’ AAAGGAATCTAAGTTCCACT 3’	Sumontha *et al*. (2020)
	1616-R	5’ CGGTCTGAACTCAGATCACGT 3’	

The two sequences generated in this study have been submitted to NCBI GenBank. We assembled a dataset of cytochrome b and 16S ribosomal RNA for 42 species for comparison and phylogenetic analysis, including 34 of the 50 known *Trimeresurus* species (Table 2) and other viperids from GenBank. Sequences of a pareid species (*Pareas hamptoni*) was used as an outgroup to root the tree.

The sequences were aligned using default parameters and the cytochrome b alignment was checked to confirm the absence of unexpected stop codons that might indicate amplification of pseudogenes in MEGA Ver 7 (Kumar *et al*. 2016). All unalignable sites and gap-containing sites were carefully removed from these data sets. The level of sequence divergence within and between species was estimated using the uncorrected pairwise distance (p-distance) model in MEGA Ver 7. The best-fit model of DNA substitution was determined for the concatenated data sets using the program Kakusan 4 and the optimal model for nucleotide evolution was set to GTR+I+G (Tanabe 2011). Phylogenetic relationships of *Trimeresurus kuiburi* **sp. nov**. samples and related *Trimeresurus* species based on the cytochrome *b*, and 16S rRNA genes using Bayesian Inference (BI) analysis implemented under the program MrBayes Version 3.2.6 (Huelsenbeck & Ronquist 2001). The Markov chain Monte Carlo process was used to run four chains simultaneously for 1,000,000 generations. After the log-likelihood value plateaued, a sampling procedure was performed every 100 generations to obtain 10,000 trees, and then a majority-rule consensus tree with average branch lengths was provided. All sample points prior to reaching convergence were discarded as burn-in and the Bayesian posterior probability in the sampled tree population was obtained in percentage terms.

Systematics

Trimeresurus kuiburi sp. nov.

(Figures 1–6)

Trimeresurus sp.—Sumontha *et al*. 2017a: 561.

Holotype. QSMI 1500 (field number MS 703); adult male collected by Montri Sumontha, Nirut Chomngam, Parinya Phawangkhanant and Prapanth Iamwiriyakul on 27 November 2016 near Ban Thung Noi (ca. 12.084500 N, 99.948556 E), Khao Daeng Sub-district, Kui Buri District, Prachuap Khiri Khan Province, Peninsular Thailand.

Paratypes (5). AUP-02005 (field number MS 701), PSUZC-R 734 (MS 704) and PSUZC-R 735 (MS 731), adult males collected on 9 August 2015, 20 June 2014 and 3 October 2020, respectively (all preserved with everted hemipenes). QSMI 1501 (MS 702) and AUP-02006 (MS 732), adult females collected on 20 June 2014 and 26 June 2020, respectively. Same locality and collectors as the holotype.

Diagnosis. *Trimeresurus kuiburi* **sp. nov.** can be distinguished from all other congeneric species by the combination of its red/purple bands on a green dorsum; white concave suborbital stripe in males; white, spaced vertebral dots in males; pale green belly lacking dark dots or stripe on the lateral sides of the ventrals; partially fused 1^{st} supralabial and nasal scale; 19 dorsal scale rows at midbody; 164–171 ventrals; 63–65 subcaudals in males, 51–53 in females; maximal known SVL of 451 mm; and long, papillose hemipenes.

Description of holotype. Adult male (Figures 1–2). Body cylindrical, long and thin; SVL 376.4 mm; tail length 88.2 mm; total length 464.6 mm. Pupil vertically elliptical. Loreal pit present. Head triangular in dorsal view, elongate, clearly distinct from the neck; head length 18.0 mm; head width 13.4 mm; HW/HL 0.74; distance between nostrils 3.7 mm. Snout elongate, 34% of HL, 1.78 times as long as horizontal diameter of eye, obliquely truncated when seen from lateral side, flattened and rounded when seen from above, with a distinct *canthus rostralis*. Distance between eye and nostril 4.4 mm on both sides. Rostral slightly visible from above, triangular; rostral width 2.9 mm, rostral height 2.0 mm. Nostril completely enclosed in nasal scale; nasal scale partially fused with first supralabial. Shield bordering anterior edge of pit fused with second supralabial, lacking any small scales between it and nasal. Long, thin, crescent-like subocular scale, in contact with third supralabial, separated from the 4^{th} and 5^{th} supralabials by one row of scales, separated from the 6^{th} supralabial by 1/2 scales. Two upper preoculars above the loreal pit, elongated, and in contact with the single loreal which separates the upper preoculars from the nasal; lower preocular forming the lower margin of the loreal pit; 1/1 postocular. Eleven/ten supralabials, 3^{rd} supralabial largest; 13/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Six pairs of gulars aligned between the chin shields and the preventral. One pair of enlarged internasals, in contact above the rostral. Length of the single, unfragmented supraocular 4.1/4.1 mm; width of supraocular 1.3/1.3 mm; ratio SOL/SOW 3.15. Supraoculars slightly indented on their inner margin by the upper head scales. At least nine scales between the supraoculars. Scales on snout and in the interorbital region smooth, irregular, subimbricate; temporal and occipital scales moderately keeled. Dorsal scales in 21-19-15 rows. Scale row reduction from 21 to 19 rows resulted from the fusion of the 4^{th} and 5^{th} rows above ventrals 30/31; reduction from 19 to 17 from the fusion of the 4^{th} and 5^{th} rows above ventral 108; and reduction to 15 rows by fusion of the 5^{th} and 6^{th} rows above ventral 121 on the left side, and of the 4^{th} and 5^{th} rows above ventral 122 on the right side. Dorsal scales all moderately keeled, except the first row which is unkeeled. One preventral + 166 ventrals. Anal scale single; 65 subcaudals, all divided. Hemipenes long, papillose (holotype preserved with everted hemipenes). Tail distinctly prehensile.

Coloration in life. Dorsal surface of head dark green with many scales also partly or entirely dark red, especially on the snout, and the interorbital, temporal and occipital regions. A contrasting white stripe begins under the loreal pit, forms a concave curve under the eye, then continues straight from the 7^{th} to the last supralabial where it stops. Black vertical pupil; iris copper. The background color of the dorsum is dark green, similar to that of the head, with about 62 irregular, dark red crossbands. These red bands are about two dorsal scales long mediodorsally, but narrower on the lower flanks where they are about one dorsal scale long. At the level of the vertebral row, the red bands are generally separated by one dorsal scale. The vertebral row exhibits an interrupted line of white dots, spaced by five or six dorsal scales. Each scale of the lowest dorsal scale row shows a horizontally elongate white spot, forming a continuous white line from the neck to the end of the tail. Most of the scales of the first row also exhibit a smaller red dot, forming a dotted red line. Above the white stripe of the first dorsal scale row, the tail is red, except some thin lighter bands. The infralabials are green and white; the underside of the head is mostly white. The belly is uniformly pale green, of a lighter tone than the background color of the dorsum.

In preservative the background dorsal color turned to brownish, with poorly contrasted darker marks on the head and bands on the dorsum; the belly color became greenish grey. The suborbital concave white stripe remained contrasted, as well as the white stripe on the first dorsal scale row.

TABLE 2. Dataset of 16S rRNA and Cytb DNA sequences with GenBank accession numbers for 43 snake species, among them 34 currently recognized *Trimeresurus* species (including *T. kuiburi* **sp**. **nov**.), other viperids, and a pareid outgroup.

Taxa	16S rRNA	Cytb
1. *Calloselasma rhodostoma*	AY352718.1	AY223562.1
2. *Daboia russelii*	AY352712.1	AF471076.1
3. *Ovophis monticola*	AY059561.1	HQ325127.1
4. *Pareas hamptoni*	KX694656.1	KJ642150.1
5. *Protobothrops mangshanensis*	AY352726.1	HM567537.1
6. *Protobothrops mucrosquamatus*	AY294271.1	KT220318.1
7. *Protobothrops sieversorum*	AY352721.1	KT220320.1
8. *Trimeresurus albolabris*	AY059560.1	AY352770.1
9. *Trimeresurus arunachalensis*	*MK722155*	MK720609
10. *Trimeresurus borneensis*	AY352722.1	AY352754.1
11. *Trimeresurus buniana*	KX660234.1	KX660503.1
12. *Trimeresurus cantori*	AY352741.1	AF171899.1
13. *Trimeresurus erythrurus*	AY352739.1	AF171900.1
14. *Trimeresurus flavomaculatus*	AY059551.1	AY352764.1
15. *Trimeresurus fucatus*	KX660235.1	KX660505.1
16. *Trimeresurus gracilis*	AY352728.1	AF171913.1
17. *Trimeresurus gramineus*	AY352732.1	AY352762.1
18. *Trimeresurus gumprechti*	AY352736.1	AY059566.1
19. *Trimeresurus hageni*	AY059552.1	AY059567.1
20. *Trimeresurus insularis*	AY059550.1	AY059568.1
21. *Trimeresurus kanburiensis*	AY352737.1	AY289225.1
22. *Trimeresurus macrops*	AF517176.1	KP999371.1
23. *Trimeresurus malabaricus*	AY059564.1	AY059569.1
24. *Trimeresurus malcolmi*	AY371793.1	AY371832.1
25. *Trimeresurus medoensis*	AY352735.1	AY352765.1
26. *Trimeresurus nebularis*	KX660236.1	KX660506.1
27. *Trimeresurus popeiorum*	AY059558.1	AY059571.1
28. *Trimeresurus puniceus*	AF517177.1	AY352757.1
29. *Trimeresurus purpureomaculatus*	AY352746.1	AY352772.1
30. *Trimeresurus schultzei*	AY352725.1	AY352756.1
31. *Trimeresurus septentrionalis*	AY059559.1	AY352755.1
32. *Trimeresurus sichuanensis*	HQ850446.1	HQ850448.1
33. *Trimeresurus stejnegeri*	AY059562.1	AF171903.1
34. *Trimeresurus sumatranus*	AY371792.1	AY371824.1
35. *Trimeresurus tibetanus*	AY352715.1	AY352749.1
36. *Trimeresurus trigonocephalus*	AY059565.1	KC347479.1
37. *Trimeresurus venustus*	AY352723.1	AF171914.1
38. *Trimeresurus vogeli*	AF517183.1	AY059574.1
39. *Trimeresurus yunnanensis*	EU443812.1	EF597522.1
40. *Tropidolaemus wagleri*	AF517180.1	GQ428472.1
41. *Trimeresurus phuketensis*	MW694483	MW806924
42. *Trimeresurus kuiburi* sp. nov.	MW699849	MW806923

Variation. The main meristic, morphometric and chromatical characters of the type-series of *Trimeresurus kuiburi* **sp. nov.** are presented in Table 3. All paratypes and other specimens show a nasal scale partially fused with the first supralabial, similarly to the holotype (Figures 1, 2A, 5A & 5B, 6A & 6B). Scale row reduction from 21 to 19 rows and from 19 to 17 rows generally result from the fusion of the 4th and 5th dorsal rows, less frequently from the fusion of the 5th and 6th rows. All individuals, similarly to the holotype, show a pale green belly and lack a dark stripe or a dark dot on the lateral tips of the ventrals. *Trimeresurus kuiburi* **sp. nov.** shows a strong sexual dimorphism in the number of subcaudals (63–65 in males vs. 51–53 in females). All males exhibit a concave white suborbital stripe (Figures 1, 2A, 5A & 5B), while in females this stripe is straight, and less contrasted or sometimes not visible (Figures 1, 6A & 6B). The spaced white vertebral dots are present in all males, and absent in all females; they are regularly spaced by 5 to 6 vertebral scales. The number of dark bands on dorsum varies from 59 to 68 among the preserved types, without apparent sexual dimorphism; the highest number we observed was 70 in an adult female that we caught and released at the type-locality. All paratypes lost most of their dorsal pattern once in preservative; such a drastic color fading was also observed after a short time in preservative for *Trimeresurus kanburiensis* and *T. venustus* (Malhotra & Thorpe 2004b).

TABLE 3. Meristic, morphometric (in mm) and chromatical data for the type series of *Trimeresurus kuiburi* **sp. nov.** Paired meristic characters are given left/right.

	Holotype, QSMI 1500 (MS 703)	Paratype, AUP-02005 (MS 701)	Paratype, PSUZC-R 734 (MS 704)	Paratype, PSUZC-R 735 (MS 731)	Paratype, QSMI 1501 (MS 702)	Paratype, AUP-02006 (MS 732)
Sex	Male	Male	Male	Male	Female	Female
SVL	376.4	372.9	340.8	334.4	451.2	323.1
TaL	88.2	81.1	71.1	77.7	70.6	49.5
HL	18.0	17.2	16.8	15.4	20.7	15.9
HW	13.4	12.1	10.7	10.5	15.0	11.8
HD	7.2	7.3	6.7	7.0	8.9	6.4
SnL	6.2	5.6	5.2	4.6	6.6	4.7
ED	3.5	3.4	3.2	2.9	3.4	2.3
SOL	4.1/4.1	3.9/4.6	3.3/3.4	3.9/3.6	4.4/4.4	3.7/3.9
SOW	1.3/1.3	1.7/1.9	1.6/1.4	1.6/1.4	1.6/1.3	1.6/1.7
Internasals in contact	Yes	Yes	Yes	Yes	Yes	Yes
Contact nasal-1st SL	Partially fused	Partially fused	Partially fused	Partially fused	Partially fused	Partially fused
IOS	9	9	9	11	10	10
PosOc	1/1	2/2	2/2	2/2	2/1	2/2
SL	11/10	10/10	9/9	10/11	10/11	10/11
IL	13/12	11/11	10/10	10/10	11/11	12/12
ASR	21	21	21	21	23	21
MSR	19	19	19	19	19	19
PSR	15	15	15	15	15	15
SRR 21 to 19 (V)	30/31	19/16	37/38	23/25	28/30	47/44
SRR 19 to 17 (V)	108/108	103/103	111/111	111/109	114/114	109/108
SRR 17 to 15 (V)	121/122	113/113	128/124	127/124	125/126	124/124
PreV + V	1 + 166	2 + 164	1 + 166	2 + 166	1 + 171	2 + 164
A	1	1	1	1	1	1
SC	65	63	65	65	53	51
Suborbital white stripe	Concave, contrasted	Concave, contrasted	Concave, contrasted	Concave, contrasted	Straight, poorly visible	Straight, poorly visible
Number of red bands on dorsum	62	61	60	68	68	59
White vertebral dots	Present, every 5 or 6 scales	Present, every 5 or 6 scales	Present, every 5 or 6 scales	Present, every 5 or 6 scales	Absent	Absent

FIGURE 1. Live adult male holotype of *Trimeresurus kuiburi* **sp. nov.** (right) with a conspecific, non-preserved adult female from the same locality. Photograph by M. Sumontha.

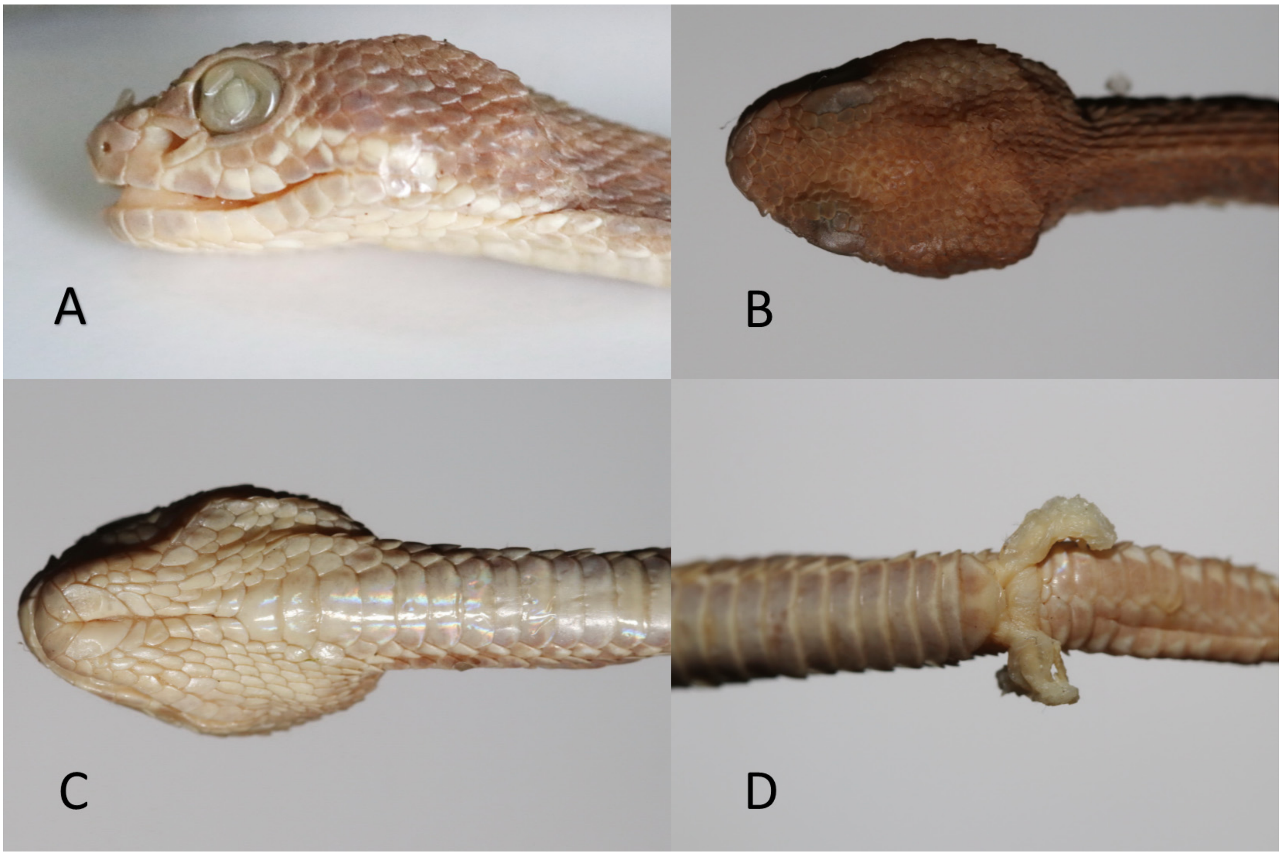

FIGURE 2. Preserved holotype of *Trimeresurus kuiburi* **sp. nov. A.** Left profile of the head. **B.** Dorsal view of the head. **C.** Ventral view of the head. **D.** Posterior part of the venter and cloacal area. Figures not to scale. Note the drastic fading of colors after preservation. Photograph by M. Sumontha.

FIGURE 3. A. Dorsal view of a preserved male paratype (AUP-02005) of *Trimeresurus kuiburi* **sp. nov.** Note the near total loss of dorsal pattern after preservation. **B.** Dorsal view of a preserved female paratype (QSMI 1501) of *Trimeresurus kuiburi* **sp. nov.** Note the eggs and the near total loss of dorsal pattern after preservation. Photographs by M. Sumontha.

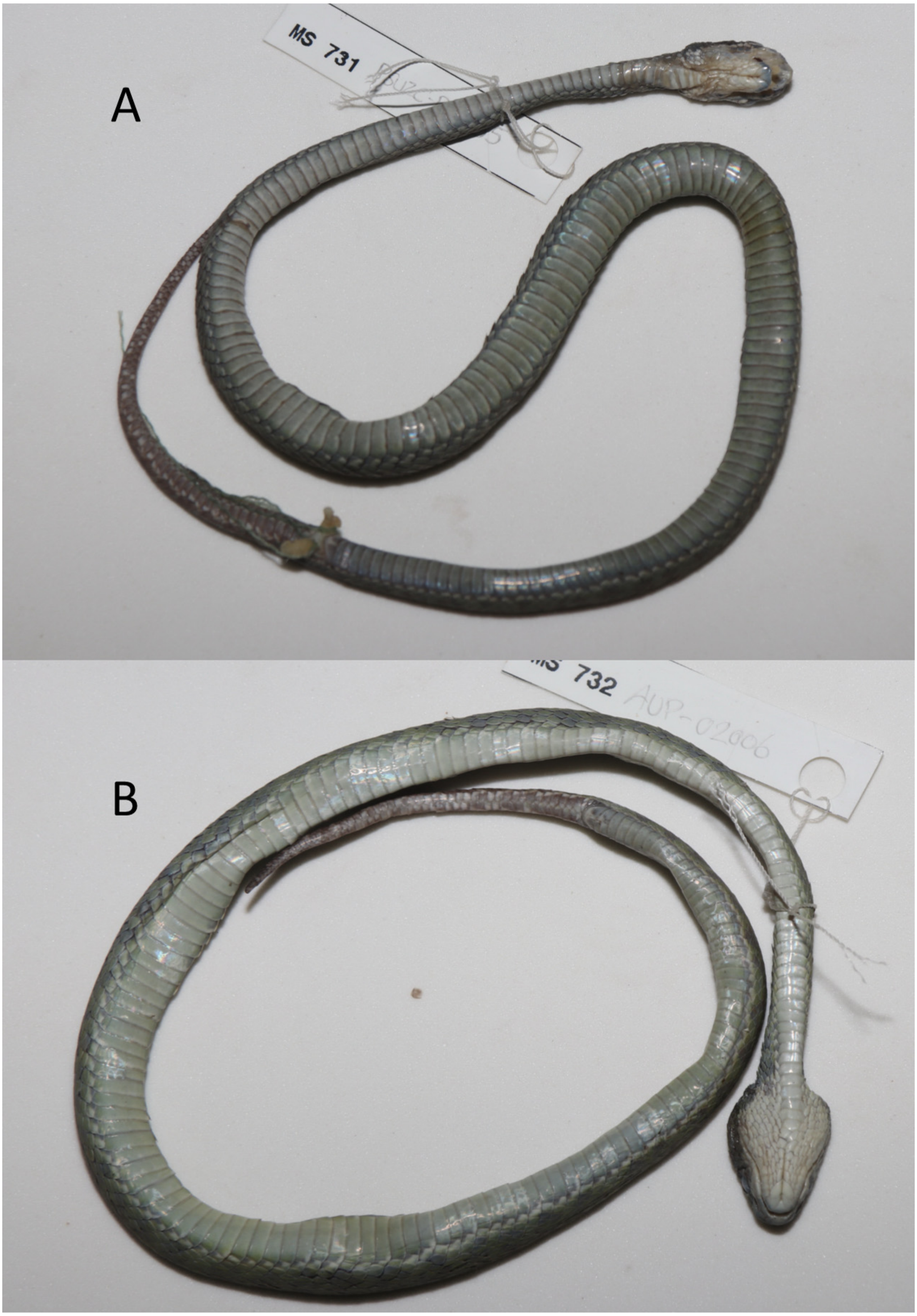

FIGURE 4. A. Ventral view of a freshly preserved male paratype (PSUZC-R 735) of *Trimeresurus kuiburi* **sp. nov. B.** Ventral view of a freshly preserved female paratype (AUP-02006) of *Trimeresurus kuiburi* **sp. nov.** Note the total absence of dots or stripes on the lateral sides of the ventrals in both specimens. Photographs by M. Sumontha.

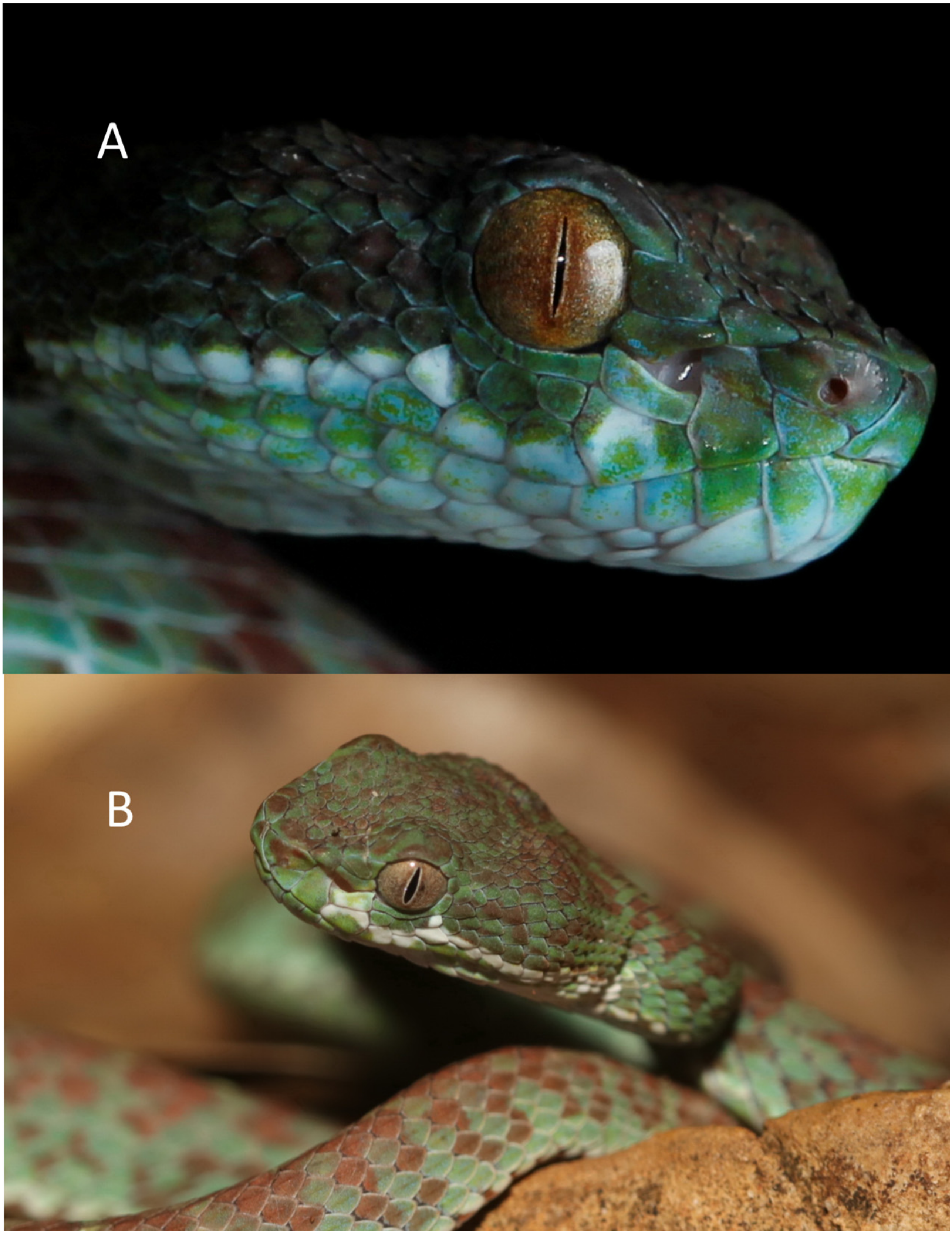

FIGURE 5. A. Head of an adult male *Trimeresurus kuiburi* **sp. nov.** from the type-locality; individual not collected. Photograph by P. Pawangkhanant. **B.** Male *Trimeresurus kuiburi* **sp. nov.** from Khao Sam Roi Yot National Park; individual not collected. Photograph by M. Sumontha.

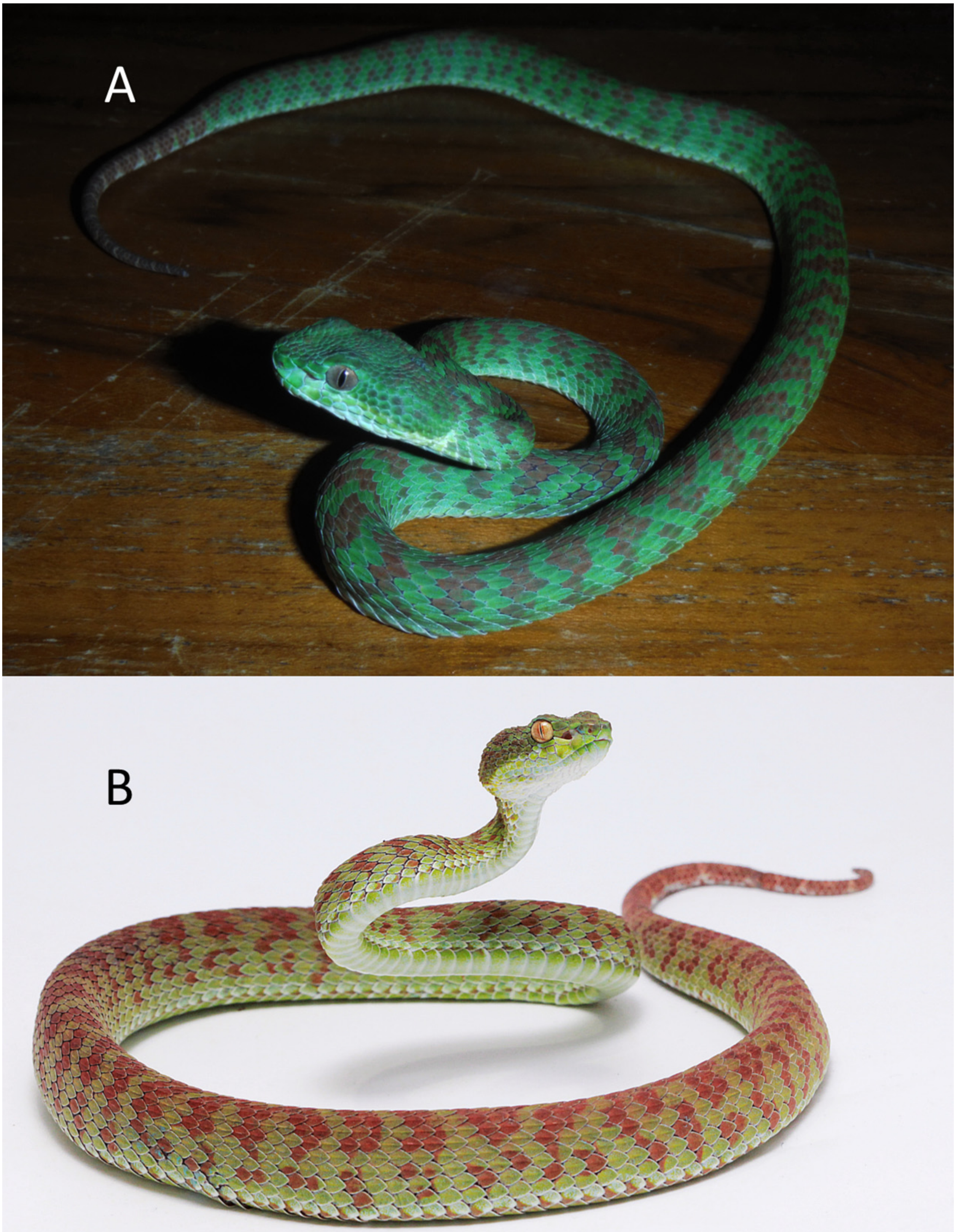

FIGURE 6. A. Female *Trimeresurus kuiburi* **sp. nov.** from the type-locality; individual not collected. Photograph by M. Sumontha. **B.** Adult female *Trimeresurus kuiburi* **sp. nov.** from Khao Sam Roi Yot National Park; individual not collected. Photograph by P. Pawangkhanant.

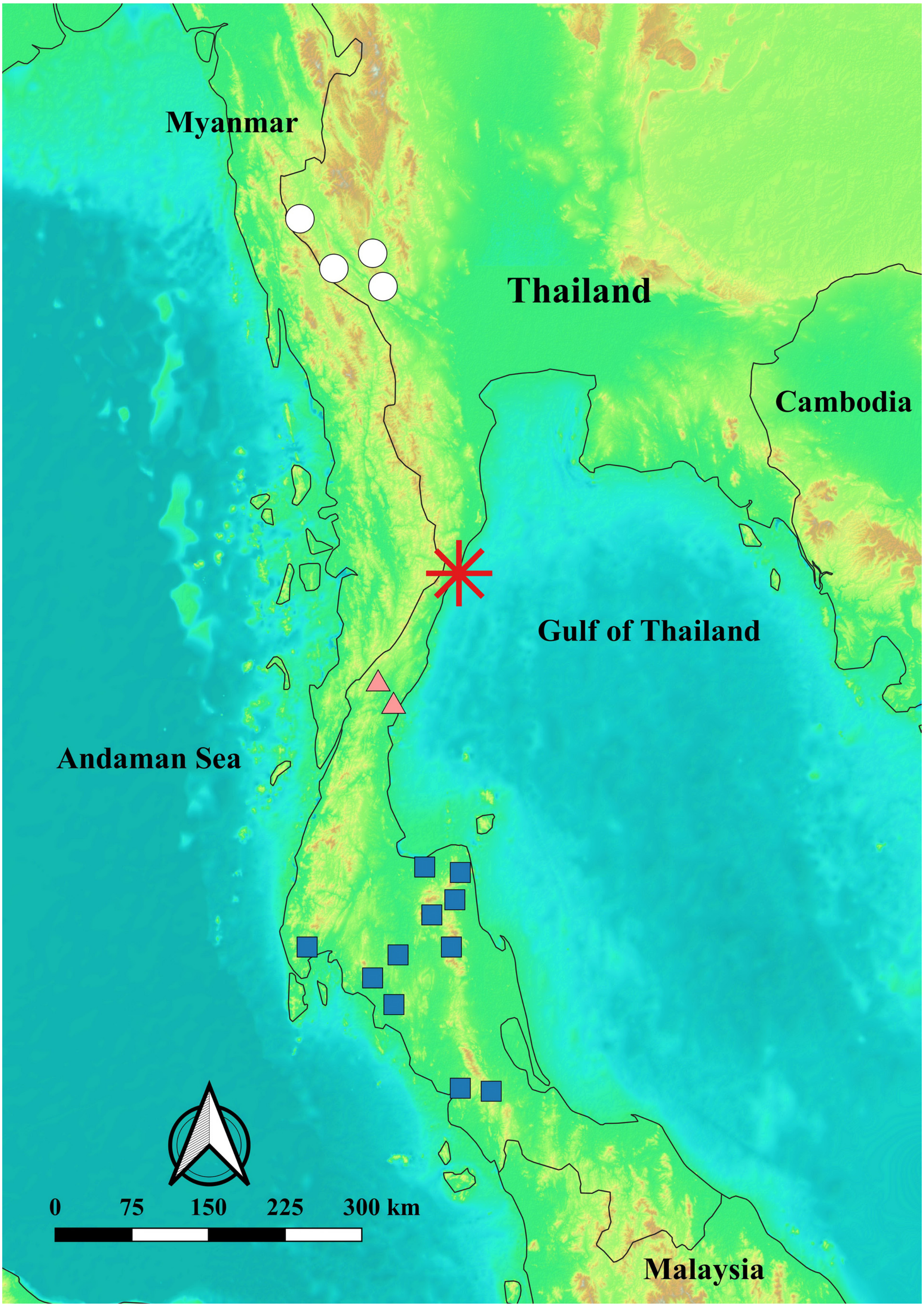

FIGURE 7. Distribution of *Trimeresurus kanburiensis* (white circles), *T. kuiburi* **sp. nov.** (red asterisk), *T.* cf. *venustus* (pink triangles) and *T. venustus* (blue squares) in Thailand. Map by A. Aksornneam. New localities in Krabi and Phang-Nga provinces are based on our Figures 12 & 13.

FIGURE 8. Microbiotope of *Trimeresurus kuiburi* **sp. nov.** within Khao Sam Roi Yot National Park. Photograph by P. Pawangkhanant. Adult individuals forage on the boulders, while young ones are mostly found on the bushes.

Distribution and natural history. The type-locality of *Trimeresurus kuiburi* **sp. nov.** (Figure 7) is situated along the border with the southern tip of Khao Sam Roi Yot National Park where we also observed the new species. It is locally an abundant snake. Adults are found foraging at night on karst boulders (Figure 8). Young individuals are generally found on small bushes growing among the boulders. Several individuals in pre-shedding phase were found perched high on taller bushes.

This pitviper is not aggressive if gently approached or handled. Nothing is known about its diet in the wild, except that one adult individual regurgitated a *Cyrtodactylus samroiyot* just after capture. *Trimeresurus kuiburi* **sp. nov.** is probably a generalist predator, as captive individuals ate geckos (*Hemidactylus murrayi* Gleadow, *H. frenatus* Duméril & Bibron and *H. platyurus* (Schneider)), frogs (*Fejervarya limnocharis* (Gravenhorst) and *Polypedates leucomystax* (Gravenhorst)) and mice. Mating was observed in captivity in the morning of 4 October 2020, after a rain shower. The preserved female QSMI 1501 contains nine eggs.

We found the following squamates in direct proximity to the new pitviper species: *Calotes versicolor* (Daudin) (Agamidae), *Cnemaspis lineogularis* Wood, Grismer, Aowphol, Aguilar, Cato, Grismer, Murdoch & Sites, *Cyrtodactylus samroiyot*, *Dixonius kaweesaki* and *D. siamensis* (Boulenger), *Gekko gecko* (Linnaeus), *Gehyra fehlmanni* (Taylor), *Hemidactylus frenatus* and *H. platyurus* (Gekkonidae), *Ahaetulla* sp., *Dendrelaphis subocularis* (Boulenger), *Lycodon capucinus* (Boie) and *Lycodon davisonii* (Blanford) (Colubridae), *Calliophis* cf. *maculiceps* (Günther) (Elapidae) and *Indotyphlops braminus* (Daudin) (Typhlopidae).

Etymology. The specific epithet is a noun in apposition, invariable, in reference to the administrative district Kui Buri in which the type-locality lies. We suggest the following common names: งูหางแห้มกุย (*Ngu Hang Ham Kui*, Thai), Kui Buri Pitviper (English), *Trimérésure de Kui Buri* (French), and *Kui Buri Bambusotter* (German).

Comparison to other species. The possession of a long papillose hemipenis and a partially fused first supralabial and nasal scale makes of *Trimeresurus kuiburi* **sp. nov.** a member of the *Trimeresurus* group *sensu stricto* (*Cryptelytrops* group *sensu* Malhotra & Thorpe 2004a), which currently includes the following 20 species: *Trimeresurus albolabris* (Gray), *T. andersonii* Theobald, *T. cantori* (Blyth), *T. cardamomensis* Malhotra, Thorpe, Mrinalini & Stuart, *T. caudornatus* Chen, Ding, Vogel & Shi, *T. davidi* Chandramouli, Campbell & Vogel, *T. erythrurus* (Cantor), *T. fasciatus* (Boulenger), *T. guoi* Chen, Shi, Vogel & Ding, *T. honsonensis* (Grismer, Ngo & Grismer), *T. insularis* Kramer, *T. kanburiensis* Smith, *T. labialis* Fitzinger *in* Steindachner, *T. macrops* Kramer, *T. mutabilis* Stoliczka, *T. purpureomaculatus* (Gray), *T. rubeus* Malhotra, Thorpe, Mrinalini & Stuart, *T. salazar* Mirza, Bhosale, Phansalkar, Sawant, Gowande & Patel, *T. septentrionalis* Kramer and *T. venustus* Vogel (David & Vogel 2015; Chandramouli *et al*. 2020; Chen *et al*. 2020a–b; Mirza *et al*. 2020).

Among these species, *Trimeresurus kuiburi* **sp. nov.** is readily distinguished from the widespread *Trimeresurus albolabris*, the Andaman and Nicobar Islands endemic *T. andersonii*, the Nicobar Archipelago endemics *T. cantori*, *T. davidi*, *T. labialis* and *T. mutabilis*, the Cardamom Mounts endemic *T. cardamomensis*, the Chinese *T. caudornatus*, the Indo-Burmese *T. erythrurus*, the Indonesian Tanahdjampea Island endemic *T. fasciatus*, the widespread *T. guoi*, the Vietnamese Hon Son Island endemic *T. honsonensis*, the Indonesian *T. insularis*, the Southeast Asian *T. macrops*, the southern Vietnamese-Cambodian *T. rubeus*, the Indian *T. salazar* and the Himalayan *T. septentrionalis* by its dorsal pattern made of purple-red bands on a green background (David & Vogel 2000; David *et al*. 2003; Grismer *et al*. 2008; Malhotra *et al*. 2011; Vogel *et al*. 2014; Chandramouli *et al*. 2020; Chen *et al*. 2020 a–b; Mirza *et al*. 2020). Its 19 MSR further separate it from *Trimeresurus andersonii* (21 MSR), *T. cantori* (27, 29 or 31), *T. cardamomensis* (21), *T. caudornatus* (21), *T. davidi* (21 or 23), *T. erythrurus* (23 or 25), *T. fasciatus* (21), *T. guoi* (21), *T. honsonensis* (21), *T. insularis* (21), *T. labialis* (21 or 23), *T. macrops* (21), *T. mutabilis* (21), *T. purpureomaculatus* (23–29), *T. rubeus* (21), *T. septentrionalis* (21) and most specimens of *T. venustus* (21, rarely 19).

Compared to all members of the *Cryptelytrops* group, *Trimeresurus kuiburi* **sp. nov.** is superficially similar only to *T. kanburiensis* and *T. venustus*, two geographically-restricted endemics of western Thailand and the Thai-Malay Peninsula, respectively.

The northernmost published record of *Trimeresurus venustus* was mentioned by Pauwels *et al.* (2013; Figure 9B) who listed the reptile taxa co-occurring at the type-locality of *Cyrtodactylus sanook* in Muang District, Chumphon Province. At that time we were not aware of the existence of the Kui Buri population and we did not morphologically examine in detail what we believed to be not more than a northern range extension of *Trimeresurus venustus*. The males of the Chumphon population, contrary to *Trimeresurus kuiburi* **sp. nov.**, do not show a concave but a straight suborbital stripe, and they show a white vertebral dot every 2 to 4 vertebral scales, while male *T. kuiburi* **sp. nov.** show a dot every 5 or 6 scales, and typical male *T. venustus* do not show white dots (Figure 9A).

In any case, *Trimeresurus kuiburi* **sp. nov.** is distinct from *Trimeresurus venustus sensu auctorum*. A striking pattern difference is the concave shape of the suborbital white stripe in male *Trimeresurus kuiburi* **sp. nov**. It is straight and bordering the orbit in males of the northern and southern populations of *T. venustus* (less contrasted or sometimes not visible in females), as can be clearly seen in photographs published in the original description of *T. venustus* showing specimens from Thung Song, as well as in Manthey & Grossmann (1997: 411, one individual from 'Süd-Thailand'), Chan-ard *et al*. (1999: 197–198, an individual from Tai Rom Yen National Park in Surat Thani Prov., and another from Surat Thani Province without locality details, identified as *T. kanburiensis*), Gumprecht & Ryabov (2002: 37, a female from Kanchanadit, Surat Thani Prov., as *T. kanburiensis*), Vogel (2006: 122–123, five individuals from 'South Thailand'), Figures 10–11, and in the museum material we examined (see Appendix).

Many other photographs and some drawings of *Trimeresurus venustus s.l.* were published without any locality information, but none of them showed a convex suborbital stripe, and as far as we know, none of them was illustrating individuals from Prachuap Khiri Khan Province. This includes among others the individuals illustrated by Thumwipat & Nutphand (1982: 140, identified as *T. purpureomaculatus*), Kundert (1984: Fig. 106, as *T. sumatranus*), Lim & Lee (1989: 107 top, as *T. purpureomaculatus*), Nabhitabhata (1989: 176, implicitly as *T. kanburiensis*), Cox (1991: 398, as *T. kanburiensis*), Jintakune & Chanhome (1995: 129, as *T. kanburiensis*), Cox *et al*. (1998: 22, as *T. kanburiensis*), Jintakune (2000: 151, as *T. kanburiensis*), Nutphand (2001: 298–299, as *T. purpureomaculatus*; see David *et al*. 2004a), Chan-ard (2002: 127, as *T. kanburiensis*), Sanders *et al*. (2006: Supplementary material: Fig. 2b), Anonymous (2010: 3, as *T. kanburiensis*), Chanhome *et al*. (2011: 326), O'Shea (2013: 18), Chan-ard *et al*. (2015: 287; individuals from Surat Thani or Nakhon Si Thammarat), Suteparuk & Vasaruchapong (2016: Fig. 2), Visser (2015: Figs 610, 612–613, 615–622), Oliveri *et al*. (2016: Fig. 7A-D) and Fuchs *et al*. (2019). The latter publication described the medical consequences of the bite by a F2 captive individual of unknown geographic origin; it is stated that this species (*T. venustus*) has 21-21-15 DSR, but these numbers actually come from the internet (http://www.toxinology.com/) and were not verified on the individual in question (J. Fuchs, pers. comm. to OSGP, Oct. 2020).

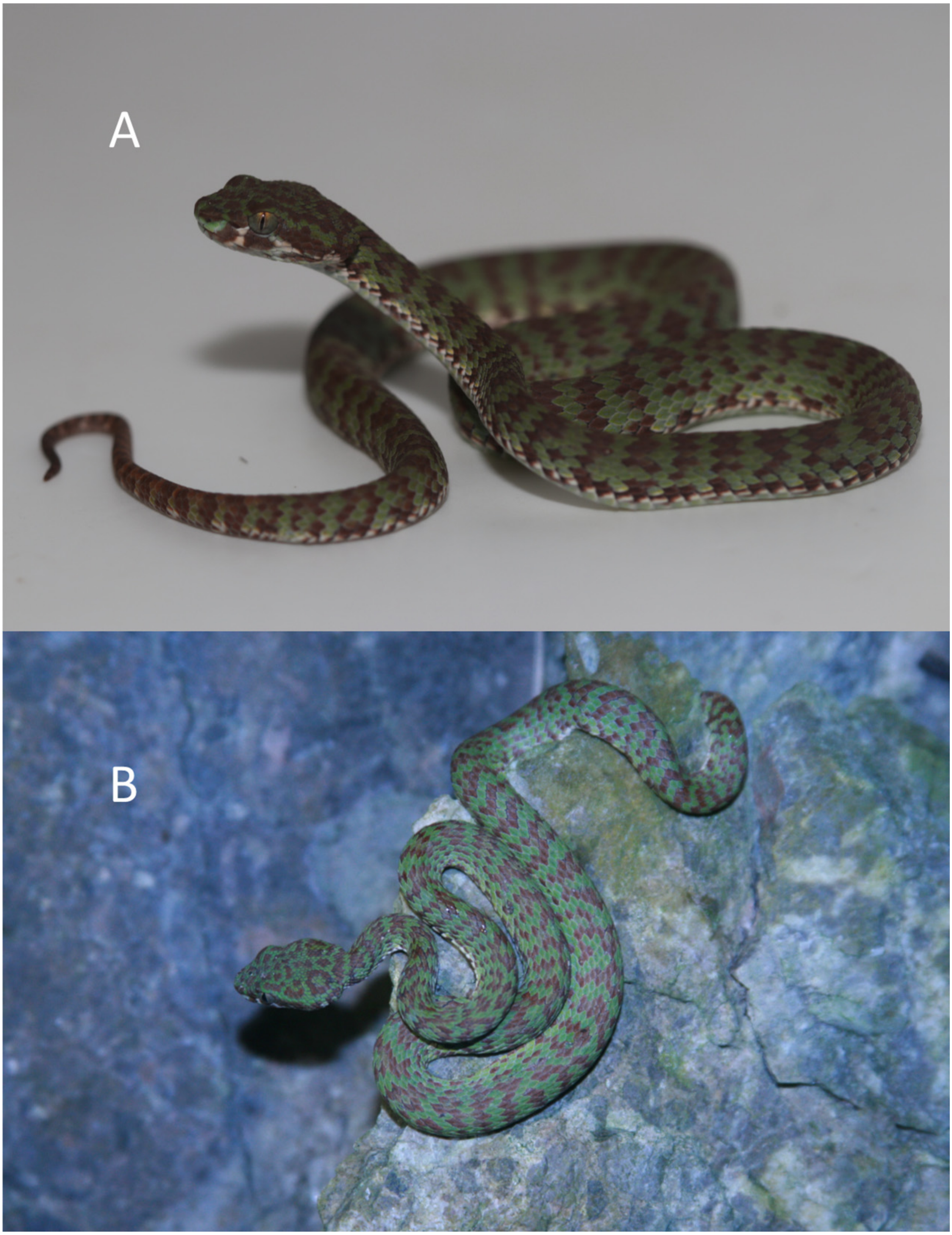

FIGURE 9. A. Adult male *Trimeresurus* cf. *venustus* from Tham Chang Phueak (ca. 10°26'48.9"N, 99°02'00.7"E), Muang District, Chumphon Province, showing a straight suborbital stripe. B. Adult female *Trimeresurus* cf. *venustus* from Tham Sanook (= Sanook Cave, ca. 10°28'53.2"N, 99°04'29.3"E), Muang District, Chumphon Province. Photographs by M. Sumontha.

TABLE 4. Main diagnostic characters of *Trimeresurus kuiburi* **sp. nov.**, *T. kanburiensis* and *T. venustus s.l*. Bolding indicates diagnostic differences from the new species.

	T. kanburiensis	*T. kuiburi* **sp. nov.**	*T. venustus s.l.*
Max. known SVL (mm)	**582**	451	486
Ratio TaL/TL females	0.124–0.139	0.133–0.135	**0.137–0.148**
Ratio SOL/SOW	**1.69–2.19**	2.06–3.38	2.33–3.21
IOS	**7–9**	9–11	8–12
Internasals in contact	**0%**	100%	45%
MSR	19	19	**21** (19)
SRR 21 to 19 (V)	18–28	16–47	106–111*
V males	170–178	164–166	166–181
V females		164–171	
SC males	**59**	63–65	63–72
SC females	**41–51**	51–53	50–66
Suborbital stripe (males)	**Straight**	Concave	**Straight**
Dorsum color in life	**dark olive-brown bands on olive-grayish background**	red/purple bands on bottle green background	red/purple bands on bottle green background
White vertebral dots (males)	**Present, every 3-5 scales**	Present, every 5-6 scales	**Absent (or present every 2–4 scales in Chumphon population)**
Belly background color in life	**creamy white**	pale green	pale green
Lateral dark stripe on ventrals	**Always present, discontinuous, olive-brown**	Always absent	**Always present, continuous or discontinuous, red**

*for the specimens with 21 MSR; for the two specimens with 19 MSR for which the SRR was noted it happened at V 22 and 84 (specimens PSGV 600 & PSGV 662; see David *et al*. 2004).

FIGURE 10. Adult male *Trimeresurus venustus* from Wat Tham Suea (= Tiger Cave Temple, ca. 8°07’32.6”N, 98°55’23.4”E), Muang District, Krabi Province, showing a straight suborbital stripe. Photograph by M. Sumontha.

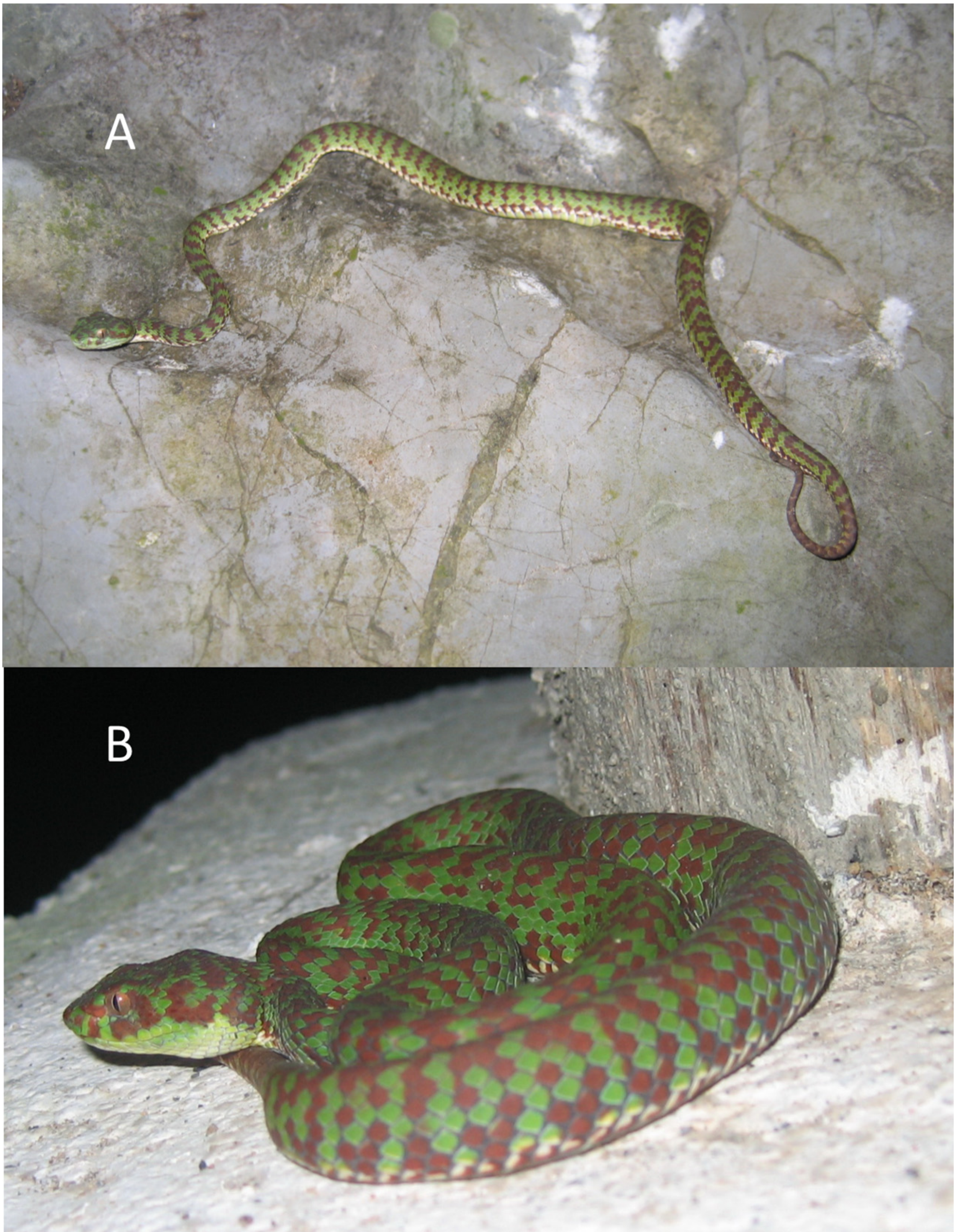

FIGURE 11. A. Adult male *Trimeresurus venustus* from Khao Phanom Wang (ca. 9°05'35.3"N, 99°36'30.9"E), Kanchanadit District, Surat Thani Province, showing a straight suborbital stripe. **B.** Adult female *Trimeresurus venustus* from Khao Phanom Wang, Kanchanadit District, Surat Thani Province. Photographs by M. Sumontha.

FIGURE 12. Adult female *Trimeresurus venustus* eating an adult *Polypedates leucomystax* (Gravenhorst) (Anura: Rhacophoridae), photographed *in situ* in Khao Phra—Bang Khram Wildlife Sanctuary, Khlong Thom District, Krabi Province. Photograph by P. Pawangkhanant.

FIGURE 13. Adult female *Trimeresurus venustus* on Khao Chang, Muang District, Phang-Nga Province. Photograph by P. Pawangkhanant.

Besides the differences in the suborbital stripe in males (concave vs. straight) and the lower number of midbody scale rows (19 vs. 21, exceptionally 19), *Trimeresurus kuiburi* **sp. nov.** differs from *T. venustus* by the absence (vs. presence) in both sexes of red dots on the lateral sides of the ventrals, the presence of white vertebral dots every 5 or 6 in males (vs. absence), a shorter tail in females (0.133–0.135 vs. 0.137–0.148), and the lower number of ventrals in males (164–166 vs. 166–181) (see Table 4). While the internasals are always in contact in *Trimeresurus kuiburi* **sp. nov.**, they are in contact in only 45% of cases in *T. venustus* (David *et al*. 2004b).

Trimeresurus kuiburi **sp. nov.** differs from *T. kanburiensis* by its smaller maximal SVL (451 vs. 582 mm), internasals always in contact (vs. always separated), generally wider supraocular, higher IOS (9–11 vs. 7–9), lower number of ventrals in males (164–166 vs. 170–178), more subcaudals in males (63–65 vs. 59), more subcaudals in females (51–53 vs. 41–51), distinct dorsal color (red/purple bands on bottle green background vs. dark olive-brown bands on grayish-olive background), concave (vs. straight) suborbital stripe in males, and pale green vs. creamy white belly (see Table 4). White vertebral dots in males are more spaced in *Trimeresurus kuiburi* **sp. nov.** than in *T. kanburiensis* (5 or 6 vs. 3–5 scales apart).

Geographically, *Trimeresurus kuiburi* **sp. nov.** is well separated from both *T. kanburiensis* and *T. venustus*. *Trimeresurus kanburiensis* is restricted to the area of Sai Yok in Kanchanaburi Province, a part of the Tenasserim Range showing a high endemism in squamates (Sumontha *et al*. 2017b), located about 300 km N-NW of the type-locality of *T. kuiburi* **sp. nov**. *Trimeresurus venustus* is separated from *T. kuiburi* **sp. nov.** by a gap of at least 180 km (population of Chumphon Province, whose status is not yet established, but similar to *T. venustus* in pattern; see Figures 9A & 9B) or at least 350 km (other *venustus*-like populations).

The analysis of cytochrome *b* revealed that mean interspecific *p*-distances between *Trimeresurus kuiburi* **sp. nov.** and related *Trimeresurus* species ranged from 4.57% to 18.10%, with the minimum of 4.57% ± 0.91% being to *T. macrops* and the maximum of 18.10% ± 1.68% being to *P. mucrosquamatus* (Table 5). Moreover, 16S rRNA gene was analyzed and showed the interspecific *p*-distances between *T. kuiburi* sp. nov. and related *Trimeresurus* species ranged from 1.23% to 8.15%, with the minimum of 1.23% ± 0.54% being to *T. macrops* and the maximum of 8.15% ± 1.34% being to *T. wagleri* (Table 6). Bayesian phylogenetic inference yielded a well-supported sister relationship between *T. kuiburi* sp. nov. and *T. macrops*. These two species are nested within the *Trimeresurus* clade (Figure 14). Therefore, the molecular results concur with the assignment of our specimens to a new species of *Trimeresurus s.s*.

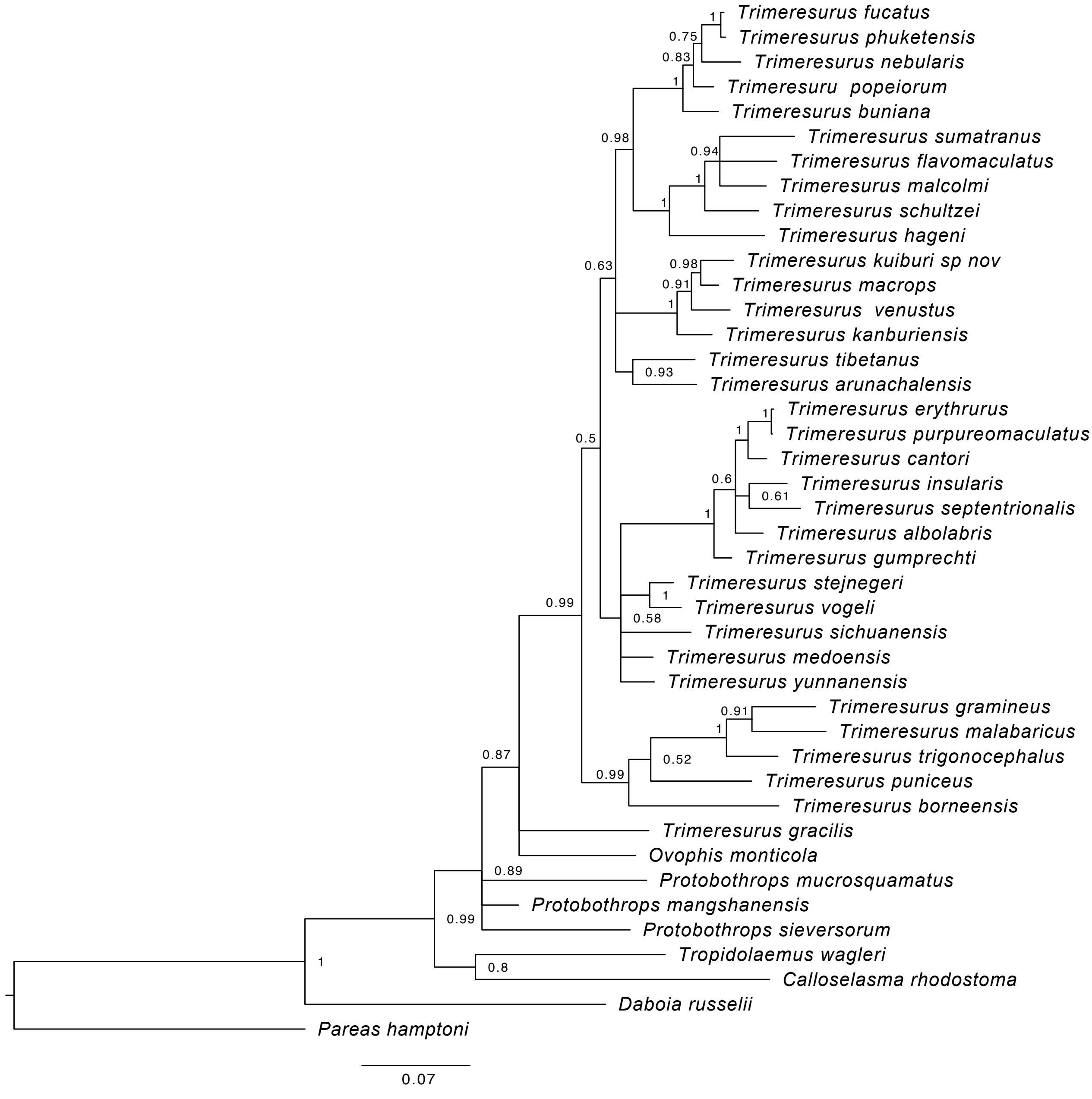

FIGURE 14. Bayesian inference tree showing inferred phylogenetic relationships of *Trimeresurus kuiburi* **sp**. **nov**. with *Trimeresurus* spp. and other viperids. Numbers at internal branches represent Bayesian posterior probability.

TABLE 5. Interspecific, uncorrected (*P*) sequence divergences (%) between *Trimeresurus kuiburi* **sp. nov.** and related *Trimeresurus* species using cytochrome b gene.

Taxa	Divergences (%)	Standard Error (SE)
Trimeresurus venustus	5.14	0.94
Trimeresurus kanburiensis	7.44	1.16
Trimeresurus fucatus	12.57	1.47
Trimeresurus phuketensis	12.38	1.47
Protobothrops mucrosquamatus	18.10	1.68
Protobothrops mangshanensis	13.90	1.53
Protobothrops sieversorum	16.38	1.70
Trimeresurus albolabris	13.00	1.45
Trimeresurus erythrurus	*13.33*	*1.46*
Trimeresurus gracilis	16.38	1.61
Trimeresurus gramineus	16.00	1.56
Trimeresurus gumprechti	13.14	1.45
Trimeresurus hageni	13.90	1.51
Trimeresurus macrops	4.57	0.91
Trimeresurus malabaricus	14.15	1.53
Trimeresurus popeiorum	11.24	1.39
Trimeresurus purpureomaculatus	13.14	1.45
Trimeresurus sichuanensis	12.38	1.45
Trimeresurus stejnegeri	10.67	1.37
Trimeresurus sumatranus	13.14	1.44
Trimeresurus tibetanus	12.00	1.40
Trimeresurus vogeli	10.67	1.38
Trimeresurus arunachalensis	11.09	1.36
Trimeresurus borneensis	16.19	1.60
Trimeresurus buniana	11.62	1.37
Trimeresurus cantori	13.14	1.44
Trimeresurus flavomaculatus	13.71	1.49
Trimeresurus insularis	11.83	1.40
Trimeresurus malcolmi	10.11	1.32
Trimeresurus medoensis	9.52	1.26
Trimeresurus nebularis	11.81	1.45
Trimeresurus puniceus	12.38	1.43
Trimeresurus schultzei	12.57	1.42
Trimeresurus septentrionalis	13.74	1.53
Trimeresurus Trigonocephalus	14.29	1.53
Trimeresurus yunnanensis	9.71	1.30
Tropidolaemus wagleri	16.76	1.64
Ovophis monticola	14.86	1.55
Pareas hamptoni	23.24	1.84
Calloselasma rhodostoma	20.00	1.77
Daboia russelii	18.97	1.76

TABLE 6. Interspecific, uncorrected (*P*) sequence divergences (%) between *Trimeresurus kuiburi* **sp. nov.** and related *Trimeresurus* species using 16S rRNA gene.

Taxa	Divergences (%)	Standard Error (SE)
Trimeresurus venustus	2.95	0.84
Trimeresurus kanburiensis	1.97	0.69
Trimeresurus fucatus	4.18	1.00
Trimeresurus phuketensis	4.42	1.02
Protobothrops mucrosquamatus	4.68	1.01
Protobothrops mangshanensis	4.93	1.08
Protobothrops sieversorum	5.93	1.11
Trimeresurus albolabris	5.22	1.08
Trimeresurus erythrurus	*5.42*	*1.10*
Trimeresurus gracilis	6.39	1.19
Trimeresurus gramineus	6.40	1.20
Trimeresurus gumprechti	3.69	0.92
Trimeresurus hageni	5.91	1.14
Trimeresurus macrops	1.23	0.54
Trimeresurus malabaricus	5.93	1.15
Trimeresurus popeiorum	4.19	1.01
Trimeresurus purpureomaculatus	5.17	1.07
Trimeresurus sichuanensis	3.69	0.90
Trimeresurus stejnegeri	3.94	0.99
Trimeresurus sumatranus	4.91	1.05
Trimeresurus tibetanus	3.69	0.93
Trimeresurus vogeli	4.68	1.02
Trimeresurus arunachalensis	4.42	1.00
Trimeresurus borneensis	5.17	1.07
Trimeresurus buniana	4.67	1.07
Trimeresurus cantori	4.93	1.05
Trimeresurus flavomaculatus	3.44	0.89
Trimeresurus insularis	4.94	1.03
Trimeresurus malcolmi	3.70	0.91
Trimeresurus medoensis	3.69	0.92
Trimeresurus nebularis	4.42	1.05
Trimeresurus puniceus	5.42	1.11
Trimeresurus schultzei	4.91	1.04
Trimeresurus septentrionalis	5.19	1.06
Trimeresurus Trigonocephalus	4.94	1.08
Trimeresurus yunnanensis	3.93	0.94
Tropidolaemus wagleri	8.15	1.34
Ovophis monticola	7.18	1.28
Pareas hamptoni	13.09	1.67
Calloselasma rhodostoma	8.87	1.38
Daboia russelii	10.89	1.49

Discussion

Three other squamate species are believed to be endemic to the small coastal massif of Khao Sam Roi Yot: *Cnemaspis lineogularis*, *Cyrtodactylus samroiyot* and *Dixonius kaweesaki* (Pauwels & Sumontha 2014; Sumontha *et al*. 2017a; Wood *et al*. 2017). Similarly to *Trimeresurus kuiburi* **sp. nov.**, all three are specialized karst-dwellers. The geographical isolation of the massif of Khao Sam Roi Yot (Surakiatchai *et al*. 2018) makes it unlikely to find the new pitviper further west, in the Tenasserim Range. Our extensive surveys of the hills and mountains of Phetchaburi and Prachuap Khiri Khan provinces during the last two decades have led to the discoveries of several new species (see the most recent descriptions by Pauwels *et al*. 2017, 2020; Sumontha *et al*. 2017a; and the literature cited therein), but did not reveal any pitviper similar to *Trimeresurus kuiburi* **sp. nov**. Khao Sam Roi Yot massif can be regarded as a habitat-island, and our present discovery of a micro-endemic species reinforces the already high proportion of island and habitat-island endemics in the *Cryptelytrops* group, as noted by Grismer *et al*. (2008).

The largest part of the distribution of *Trimeresurus kuiburi* **sp. nov.** is covered by Khao Sam Roi Yot National Park. However, the new pitviper species described here is as colorful as *Trimeresurus venustus*, which has been exported in large numbers for the pet trade in Europe, etc. and even South America (see among others Magalhães & São Pedro 2012; Visser 2015; Fuchs *et al*. 2019). Due to its attractiveness and the proximity to Bangkok of its type-locality, shared with other colorful reptile endemics, there is a substantial risk that *Trimeresurus kuiburi* **sp. nov.** becomes hunted for the pet trade, and we strongly recommend the Thai authorities to legally protect it. The conservation of Khao Sam Roi Yot National Park's wildlife has been a long battle (Parr *et al*. 1993; Sawasdee *et al*. 2012) and is still threatened, and we hope that the discovery of a fourth endemic squamate will reinforce the pride of Kui Buri inhabitants in their unique biodiversity heritage.

Cox *et al*. (2012: 757) listed *Trimeresurus venustus* from Phuket Island. One of us (OSGP) asked M. J. Cox on what basis this record was made, and he informed us (pers. comm., July 2016) that it was 'based on a personal communication by M. Sumontha or G. Vogel'. The latter colleague informed OSGP (pers. comm., July 2016) that he had not informed M. J. Cox of the presence of this species on Phuket as he did not know himself any record of that species on this island. We do not have any evidence of the presence of *Trimeresurus venustus* on Phuket Island and regard this record as dubious, and possibly based on a confusion with *Trimeresurus* (*Popeia*) *phuketensis* which also presents a striking dorsal pattern of alternate red and green bands (Sumontha *et al*. 2011).

Apart from the dubious Phuket Island record, several southern populations of snakes morphologically related to *Trimeresurus venustus*, all bottle green with red dorsal bands, but lacking the suborbital concave stripe which is typical of *Trimeresurus kuiburi* **sp. nov.**, are patchily distributed in various isolated massifs in the Thai-Malay Peninsula, including a population in Perlis State Park (referred to as *Cryptelytrops* cf. *venustus* by Chan *et al*. 2011) and an insular population on Pulau Langkawi (Grismer *et al*. 2006, 2008; Visser 2015: Fig. 609; Quah & Shahrul 2018). They are known only through photographs or isolated individuals, but were never morphologically assessed or compared in detail. Additional material would be necessary to determine how many taxa are possibly involved among these southern populations (from Chumphon Province southwards) besides true *Trimeresurus venustus*.

Acknowledgements

We are grateful to Ivan Ineich (MNHN, Paris) for making available the collections under his care, and to M. Jack Cox (Altoona), Joan Fuchs (Associated Institute of the University of Zurich), Gontran Sonet (RBINS, Brussels) and Gernot Vogel (Heidelberg) for useful information or literature. We thank Rushen Bilgin, Amonpong Khlaipet, Ton Smits, Chutiton Viriyapanon and Kanokwan Yimyoo for their help in the field work, Nararat Laopichienpong (Department of Genetics, Faculty of Science, Kasetsart University) for her suggestions on the bioinformatics analysis, and Akkachai Aksornneam for preparing the map. Patrick David (MNHN, Paris), V. Deepak (Natural History Museum, London) and an anonymous reviewer provided constructive comments on an earlier version of this manuscript.

References

Anonymous (2010) Venomous snakes of Thailand and the Red Cross Snake Farm & Institute in Bangkok. *ACT Herpetological Association Newsletter*, August–September, 2–3.

Chan, K.O., Grismer, L.L., Shahrul, A., Quah, E., Grismer, J.L., Wood, P.L.Jr., Muin, M.A. & Norhayati, A. (2011) A new species of *Chiromantis* Peters 1854 (Anura: Rhacophoridae) from Perlis State Park in extreme northern Peninsular Malaysia with additional herpetofaunal records for the park. *Russian Journal of Herpetology*, 18 (4), 253–259.

Chan-ard, T. (2002) *Kheeowphetchakhat* [Green killers]. *Advanced Thailand Geographic*, 7 (51), 114–132. [in Thai]

Chan-ard, T., Grossmann, W., Gumprecht, A. & Schulz, K.-D. (1999) *Amphibians and reptiles of Peninsular Malaysia and Thailand. An illustrated checklist. Amphibien und Reptilien der Halbinsel Malaysia und Thailands. Eine illustrierte Checkliste*. Bushmaster Publications, Wuerselen, 240 pp.

Chan-ard, T., Parr, J.W.K. & Nabhitabhata, J. (2015) *A field guide to the reptiles of Thailand*. Oxford University Press, New York, xxix + 314 pp.

Chandramouli, S.R., Campbell, P.D. & Vogel, G. (2020) A new species of green pit viper of the genus *Trimeresurus* Lacépède, 1804 (Reptilia: Serpentes: Viperidae) from the Nicobar Archipelago, Indian Ocean. *Amphibian & Reptile Conservation*, 14 (3), Taxonomy Section, e264, 169–176.

Chanhome, L., Cox, M.J., Vasaruchapong, T., Chaiyabutr, N. & Sitprija, V. (2011) Characterization of venomous snakes of Thailand. *Asian Biomedicine*, 5 (3), 311–328.

Chen, Z., Shi, S., Gao, J., Vogel, G., Song, Z., Ding, L. & Dai, R. (2020a) A new species of *Trimeresurus* Lacépède, 1804 (Squamata: Viperidae) from Southwestern China, Vietnam, Thailand and Myanmar. *Asian Herpetological Research*, 11 (4), 1–11.
https://doi.org/ 10.16373/j.cnki.ahr.200084

Chen, Z., Yu, J., Vogel, G., Shi, S., Song, Z., Tang, Y., Yang, J., Ding, L. & Chen, C. (2020b) A new pit viper of the genus *Trimeresurus* (Lacépède, 1804) (Squamata: Viperidae) from Southwest China. *Zootaxa*, 4768 (1), 112–128.
https://doi.org/10.11646/zootaxa.4768.1.7

Cox, M.J. (1991) *The snakes of Thailand and their husbandry*. Krieger Publishing Company, Malabar, xxxviii + 526 pp.

Cox, M.J., Hoover, M.F., Chanhome, L. & Thirakhupt, K. (2012) *The snakes of Thailand*. Chulalongkorn University Museum of Zoology, Bangkok, xx + 845 pp.

Cox, M.J., van Dijk, P.P., Nabhitabhata, J. & Thirakhupt, K. (1998) *A photographic guide to snakes and other reptiles of Thailand and Southeast Asia*. Asia Books, Bangkok, 144 pp.

David, P., Cox, M.J., Pauwels, O.S.G., Chanhome, L. & Thirakhupt, K. (2004a) When a book review is not sufficient to say all: an in-depth analysis of a recent book on the snakes of Thailand, with an updated checklist of the snakes of the Kingdom. *The Natural History Journal of Chulalongkorn University*, 4 (1), 47–80.

David, P. & Vogel, G. (2000) On the occurrence of *Trimeresurus albolabris* (Gray 1842) on Sumatra Island, Indonesia. *Senckenbergiana biologica*, 80 (1/2), 225–232.

David, P. & Vogel, G. (2015) An updated list of Asian pitvipers and a selection of recent publications. *In*: Visser, D. (Ed.), *Asian Pitvipers. Breeding experience & wildlife*. Edition Chimaira, Frankfurt am Main, pp. 545–565.

David, P., Vogel, G. & Dubois, A. (2011) On the need to follow rigorously the rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: the case of the nominal genus *Trimeresurus* Lacépède, 1804 (Reptilia: Squamata: Viperidae). *Zootaxa*, 2992 (1), 1–51.
https://doi.org/10.11646/zootaxa.2992.1.1

David, P., Vogel, G., Sumontha, M., Pauwels, O.S.G. & Chanhome, L. (2004b) Expanded description of the poorly known pitviper *Trimeresurus kanburiensis* Smith, 1943, with confirmation of the validity of *Trimeresurus venustus* Vogel, 1991 (Reptilia: Serpentes: Crotalidae). *Russian Journal of Herpetology*, 11 (2), 81–90.

David, P., Vogel, G. & Vidal, N. (2003) On *Trimeresurus fasciatus* (Boulenger, 1896) (Serpentes: Crotalidae), with a discussion on its relationships based on morphological and molecular data. *The Raffles Bulletin of Zoology*, 51 (1), 149–157.

Dowling, H.G. (1951a) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Dowling, H.G. (1951b) A proposed method of expressing scale reductions in snakes. *Copeia*, 2, 131–134.
https://doi.org/10.2307/1437542

Fuchs, J., Bessire, K. & Weiler, S. (2019) A confirmed bite by a Beautiful Pit Viper (*Trimeresurus venustus*) resulting in local symptoms. *Toxicon*, 163, 44–47.
https://doi.org/10.1016/j.toxicon.2019.03.019

Grismer, L.L., Ngo, V.T. & Grismer, J.L. (2008) A new species of insular pitviper of the genus *Cryptelytrops* (Squamata: Viperidae) from southern Vietnam. *Zootaxa*, 1715 (1), 57–68.
https://doi.org/10.11646/zootaxa.1715.1.4

Grismer, L.L., Youmans, T.M., Wood, P.L. Jr., Ponce, A., Wright, S.B., Jones, B.S., Johnson, R., Sanders, K.L., Gower, D.J., Yaakob, N.S. & Lim, K.K.P. (2006) Checklist of the herpetofauna of Pulau Langkawi, Malaysia, with comments on taxonomy. *Hamadryad*, 1 & 2, 61–74.

Gumprecht, A. & Ryabov, S. (2002) Die Gattung *Trimeresurus* Lacépède, 1804 - Zu Kenntnisstand der Forschung. *Draco*, 12 (3), 31–44.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
https://doi.org/10.1093/bioinformatics/17.8.754

Jintakune, P. (2000) *Ngoophit nai Prathet Thai* [*Venomous snakes of Thailand*]. Samnakphimmatichon, Bangkok, 176 pp. [in Thai]

Jintakune, P. & Chanhome, L. (1995) *Ngoophit nai Prathet Thai* [*Venomous snakes of Thailand*]. Queen Saovabha Memorial Institute, Thai Red Cross, Bangkok, 175 pp. [in Thai]

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33 (7), 1870–1874. https://doi.org/10.1093/molbev/msw054

Kundert, F. (1984) *De mysterieuze wereld van de slangen*. Van Holema & Warendorf, Weesp, 39 pp., 132 pls.

Lim, F.L.K. & Lee, M.T.-M. (1989) *Fascinating snakes of Southeast Asia - an introduction*. Tropical Press Sdn. Bhd., Kuala Lumpur, xvii + 124 pp.

Magalhães, A.L.B. & São Pedro, V.A. (2012) Illegal trade on non-native amphibians and reptiles in southeast Brazil: the status of e-commerce. *Phyllomedusa*, 11 (2), 155–160. https://doi.org/10.11606/issn.2316-9079.v11i2p155-160

Malhotra, A. & Thorpe, R.S. (2004a) A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pit vipers *Trimeresurus* and *Ovophis*. *Molecular Phylogenetics and Evolution*, 32, 83–100. https://doi.org/10.1016/j.ympev.2004.02.008

Malhotra, A. & Thorpe, R.S. (2004b) Reassessment of the validity and diagnosis of the pitviper *Trimeresurus venustus* Vogel, 1991. *Herpetological Journal*, 14, 21–33.

Malhotra, A., Thorpe, R.S., Mrinalini & Stuart, B.L. (2011) Two new species of pitviper of the genus *Cryptelytrops* Cope 1860 (Squamata: Viperidae: Crotalinae) from Southeast Asia. *Zootaxa*, 2757, 1–23. https://doi.org/10.11646/zootaxa.2757.1.1

Manthey, U. & Grossmann, W. (1997) *Amphibien & Reptilien Südostasiens*. Natur und Tier - Verlag, Münster, 512 pp.

McDiarmid, R.W., Campbell, J.A. & Touré, T.A. (1999) *Snake species of the World; a taxonomic and geographic reference. Vol. 1*. The Herpetologists' League, Washington, 511 pp.

Mirza, Z.A., Bhosale, H.S., Phansalkar, P.U., Sawant, M., Gowande, G.G. & Patel, H. (2020) A new species of green pit vipers of the genus *Trimeresurus* Lacépède, 1804 (Reptilia, Serpentes, Viperidae) from western Arunachal Pradesh, India. *Zoosystematics and Evolution*, 96 (1), 123–138. https://doi.org/10.3897/zse.96.48431

Nabhitabhata, J. (1989) Species diversity of Thai herpetofauna. *In*: *Biodiversity in Thailand. Biological Science Seminar 7*. Chiang Mai University & Science Society of Thailand, Bangkok, pp. 169–204. [in Thai, English summary]

Nutphand, W. (2001) *Patterns of the snakes in Thailand*. Amarin Printing and Publishing Public Co. Ltd., Bangkok, 319 pp. [in Thai]

Oliveri, M., Čermáková, E. & Knotek, Z. (2016) The viper fangs: clinical anatomy, principles of physical examination and therapy (a review). *Acta Veterinaria Brno*, 85, 247–250. https://doi.org/10.2754/avb201685030247

O'Shea, M. (2013) The trouble with Trims! *The Herptile*, 38 (1), 18–23.

Parr, J.W.K., Mahannop, N. & Charoensiri, V. (1993) Khao Sam Roi Yot—one of the World's most threatened parks. *Oryx*, 27 (4), 245–249. https://doi.org/10.1017/S0030605300028167

Pauwels, O.S.G. (2008) Book review. Venomous snakes of Asia. Giftschlangen Asiens. *Hamadryad*, 33, 130–132.

Pauwels, O.S.G., Chomngam, N., Larsen, H. & Sumontha, M. (2020) A new limestone-dwelling leaf-toed gecko (Gekkonidae: *Dixonius*) from coastal hills in Cha-am, peninsular Thailand. *Zootaxa*, 4845 (1), 97–108. https://doi.org/10.11646/zootaxa.4845.1.7

Pauwels, O.S.G., Larsen, H., Suthanthangjai, W., David, P. & Sumontha, M. (2017) A new kukri snake (Colubridae: *Oligodon*) from Hua Hin District, and the first record of *O. deuvei* from Thailand. *Zootaxa*, 4291 (3), 531–548. https://doi.org/10.11646/zootaxa.4291.3.6

Pauwels, O.S.G. & Sumontha, M. (2014) *Cyrtodactylus samroiyot*, a new limestone-dwelling Bent-toed Gecko (Squamata: Gekkonidae) from Prachuap Khiri Khan Province, peninsular Thailand. *Zootaxa*, 3755 (6), 573–583. https://doi.org/10.11646/zootaxa.3755.6.4

Pauwels, O.S.G., Sumontha, M., Latinne, A. & Grismer, L.L. (2013) *Cyrtodactylus sanook* (Squamata: Gekkonidae), a new cave-dwelling gecko from Chumphon Province, southern Thailand. *Zootaxa*, 3635 (3), 275–285. https://doi.org/10.11646/zootaxa.3635.3.7

Quah, E.S.H. & Shahrul, A.M.S. (2018) Herpetofauna of the northern corridor: a review of recent herpetological discoveries around the Malaysian-Thai border regions. *Journal of Wildlife and Parks*, 33, 15–29.

Sanders, K.L., Malhotra, A. & Thorpe, R.S. (2006) Evidence for a Müllerian mimetic radiation in Asian pitvipers. *Proceedings of the Royal Society*, B, 273, 1135–1141. https://doi.org/10.1098/rspb.2005.3418

Sawasdee, C., Phongkhieo, N.T. & Nieamsup, T. (2012) Bird conservation behavior of local people within the communities surrounding Khao Sam Roi Yot National Park. *Kasetsart Journal of Social Sciences*, 33 (3), 419–428. [in Thai, English summary]

Sumontha, M., Chomngam, N., Phanamphon, E., Pawangkhanant, P., Viriyapanon, C., Thanaprayotsak, W. & Pauwels, O.S.G. (2017a) A new limestone-dwelling leaf-toed gecko (Gekkonidae: *Dixonius*) from Khao Sam Roi Yot massif, peninsular Thailand. *Zootaxa*, 4247 (5), 556–568.

https://doi.org/10.11646/zootaxa.4247.5.2
Sumontha, M., Kunya, K., Dangsri, S. & Pauwels, O.S.G. (2017b) *Oligodon saiyok*, a new limestone-dwelling kukri snake (Serpentes: Colubridae) from Kanchanaburi Province, western Thailand. *Zootaxa*, 4294 (3), 316–328. https://doi.org/10.11646/zootaxa.4294.3.2
Sumontha, M., Kunya, K., Pauwels, O.S.G., Nitikul, A. & Punnadee, S. (2011) *Trimeresurus* (*Popeia*) *phuketensis*, a new pitviper (Squamata: Viperidae) from Phuket Island, southwestern Thailand. *Russian Journal of Herpetology*, 18 (3), 185–194.
Sumontha, M., Vasararuchapong, T., Chomngam, N., Suntrarachun, S., Pawangkhanant, P., Sompan, W., Smits, T., Kunya, K. & Chanhome, L. (2020) *Protobothrops kelomohy* sp. nov. (Squamata: Viperidae), the second known species of Lance-headed Pit Viper from Thailand. *Tropical Natural History*, 20 (1), 43–59.
Surakiatchai, P., Choowong, M., Charusiri, P., Charoentitirat, T., Chawchai, S., Pailoplee, S., Chabangborn, A., Phantuwongraj, S., Chutakositkanon, V., Kongsen, S., Nimnate, P. & Bissen, R. (2018) Paleogeographic reconstruction and history of the sea level change at Sam Roi Yot National Park, Gulf of Thailand. *Tropical Natural History*, 18 (2), 112–134.
Suteparuk, S. & Vasaruchapong, T. (2016) A report of a confirmed case of Beautiful pit viper (Trimeresurus venustus) bite. *15th Asia Pacific Association of Medical Toxicology International Scientific Conference*, Tan Tock Seng Hospital, Singapore, 17–20 November 2016, poster.
Tanabe, A.S. (2011) Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. *Molecular Ecology Resources*, 11 (5), 914–921. https://doi.org/10.1111/j.1755-0998.2011.03021.x
Thumwipat, B. & Nutphand, W. (1982) *Treatment of patients bitten by venomous snakes and venomous snakes of Thailand*. Thai Zoological Center, Bangkok, viii + 162 pp. [in Thai]
Visser, D. (2015) *Asian Pitvipers. Breeding experience & wildlife*. Edition Chimaira, Frankfurt am Main, 576 pp.
Vogel, G. (1991) Eine neue *Trimeresurus*-Art aus Thailand, *Trimeresurus venustus* sp. nov. (Reptilia: Serpentes: Crotalidae). *Sauria*, 13 (1), 23–28.
Vogel, G. (2006) *Venomous snakes of Asia. Giftschlangen Asiens*. Terralog 14, Edition Chimaira, Frankfurt am Main, 148 pp.
Vogel, G., David, P. & Chandramouli, S.R. (2014) On the systematics of *Trimeresurus labialis* Fitzinger *in* Steindachner, 1867, a pitviper from the Nicobar Islands (India), with revalidation of *Trimeresurus mutabilis* Stoliczka, 1870 (Squamata, Viperidae, Crotalinae). *Zootaxa*, 3786 (5), 557–573. https://doi.org/10.11646/zootaxa.3786.5.4
Vogel, G., David, P. & Pauwels, O.S.G. (2004) A review of morphological variation in *Trimeresurus popeiorum* (Serpentes: Viperidae: Crotalinae), with the description of two new species. *Zootaxa*, 727 (1), 1–63. https://doi.org/10.11646/zootaxa.727.1.1
Warrell, D.A., Looareesuwan, S., Stimson, A.F. & Hutton, R.A. (1992) Rediscovery and redefinition of Malcolm Smith's *Trimeresurus kanburiensis* in Thailand, with a report of envenoming. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 86, 95–99. https://doi.org/10.1016/0035-9203(92)90461-K
Wood, P.L.Jr., Grismer, L.L., Aowphol, A., Aguilar, C.A., Cota, M., Grismer, M.S., Murdoch, M.L. & Sites, J.W. (2017) Three new karst-dwelling *Cnemaspis* Strauch, 1887 (Squamata; Gekkoniade [*sic*]) from Peninsular Thailand and the phylogenetic placement of *C. punctatonuchalis* and *C. vandeventeri*. *PeerJ*, 5, e2884. https://doi.org/10.7717/peerj.2884

APPENDIX. Comparative material examined (members of the '*Cryptelytrops* group').

Trimeresurus albolabris: MNHN 1937.29A, 'environs de Bien-Hoa, Viêt Nam'; MNHN 1998.0569–70 & RBINS 15139, 'Ban Salakern, Ban Lat District, Phetchaburi Prov., Thailand'; MNHN 1988.2105, no locality; QSMI 669–715 & QSMI 719–729 & QSMI 756–757, 'Thailand'; QSMI 716–718 'Krabi Prov., Thailand'; QSMI 730, 'Kaeng Krachan Dam, Kaeng Krachan District, Phetchaburi Prov., Thailand'; RBINS 441ε, 'Cochinchine' (= southern Vietnam); RBINS 1168, 'Indes Néerlandaises' (= Indonesia); RBINS 15035, no locality (pet trade); RBINS 16544, 'near Nang Rong waterfall, Nakhon Nayok Prov., Thailand'; RBINS 16993, 'Ban Lat District, Phetchaburi Prov., Thailand'.
Trimeresurus cardamomensis: RBINS 16543, 'Khao Soi Dao Tai, Chantaburi Prov., Thailand'.
Trimeresurus insularis: RBINS 441ß, 'Tjandikoesoema, W. Bali' (= Candikesuma, Bali, Indonesia).
Trimeresurus kanburiensis: QSMI 508–509, 'Thailand'.
Trimeresurus macrops: MNHN 1970.585, 'Kirirom, Cambodge'; QSMI 731–754, 'Thailand'; QSMI 755, 'Ang Thong Prov., Thailand'; RBINS 15188–15191, 'Na Haeo, Dan Sai District, Loei Prov., Thailand'; RBINS 18559, '13.02 N - 105.926 E, Kratie Prov., Cambodia'.
Trimeresurus purpureomaculatus: MNHN 1999.7693, 'Klong Kian, Takua Thung District, Phang-Nga Prov., Thailand'; RB INS 15142, 'Ban Khoun Dan, Ao Phang-Nga, Muang District, Phang-Nga Prov., Thailand'; RBINS 16994, 'Phrakayang Cave, Lamliang Subdistrict, Kraburi District, Ranong Prov., Thailand'.
Trimeresurus venustus: QSMI 352–353, 'Thung Song, Nakhon Si Thammarat Prov., Thailand'; QSMI 354–356 & QSMI 517–518, 'Khao Klab, Thung Song, Nakhon Si Thammarat Prov., Thailand'; QSMI 357, 'Khao Klab, limestone, 2170 m, Thung Song, Nakhon Si Thammarat Prov., Thailand'; QSMI 383–384 & QSMI 512–513, 'Thailand'.