European Journal of Taxonomy 930: 20–52
https://doi.org/10.5852/ejt.2024.930.2489
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Idiiatullina S. *et al.*

Research article

urn:lsid:zoobank.org:pub:C9615291-8DBB-459E-A420-1AAA5DEF625A

Another new species of karst-associated pitviper (Serpentes, Viperidae: *Trimeresurus*) from the Isthmus of Kra, Peninsular Thailand

Sabira S. IDIIATULLINA[1], Parinya PAWANGKHANANT[2], Chatmongkon SUWANNAPOOM[3], Tanapong TAWAN[4], Lawan CHANHOME[5], Tan Van NGUYEN[6,*], Patrick DAVID[7,*], Gernot VOGEL[8,*] & Nikolay A. POYARKOV[9,*]

[1,9] Department of Vertebrate Zoology, Lomonosov Moscow State University, Leninskiye Gory, GSP–1, Moscow 119991, Russia.
[2,3] Rabbit in the Moon Foundation, Suanphueng, Ratchaburi 70180, Thailand.
[3] Division of Fishery, School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand.
[4,5] Queen Saovabha Memorial Institute, Thai Red Cross Society, Pathumwan, Bangkok 10330, Thailand.
[6] Institute for Research and Training in Medicine, Biology and Pharmacy, Duy Tan University, Da Nang, 550000, Vietnam.
[6] College of Medicine and Pharmacy, Duy Tan University, 120 Hoang Minh Thao, Lien Chieu, Da Nang, 550000, Vietnam.
[7] Institut de Systématique, Évolution et Biodiversité (ISYEB), Muséum national d'histoire naturelle, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, CNRS, CP 30, 57 rue Cuvier, F-75005 Paris, France.
[8] Society for South East Asian Herpetology, Im Sand-3, Heidelberg, Germany.
[9] Joint Vietnam-Russia Tropical Science and Technology Research Centre, 63 Nguyen Van Huyen Road, Nghia Do, Cau Giay, Hanoi, Vietnam.

[*] Corresponding authors: tan.sifasv@gmail.com; patrick.david@mnhn.fr; Gernot.Vogel@t-online.de; n.poyarkov@gmail.com
[1] Email: idsbr158@mail.ru
[2] Email: Peat_swamp@hotmail.com
[3] Email: chatmongkonup@gmail.com
[4] Email: jozzloricae@gmail.com
[5] Email: lchanhome@yahoo.com

[1] urn:lsid:zoobank.org:author:5C05BAFB-E2DF-4198-A7B2-B70CE869ED16
[2] urn:lsid:zoobank.org:author:0BD7F28B-AE6F-4040-9F0A-51D2EF23AEB2
[3] urn:lsid:zoobank.org:author:D24BAA45-C65C-48FD-9CB2-416DB3EE3389
[4] urn:lsid:zoobank.org:author:B6FD0FDD-2800-49E8-BEA7-3A0D674C4B88
[5] urn:lsid:zoobank.org:author:125AA37F-77C6-4705-ACD5-BE1C51B417F2
[6] urn:lsid:zoobank.org:author:94EABB6E-180C-424E-8E9C-60DB36125550

[7] urn:lsid:zoobank.org:author:92A7F3DA-471F-47E3-B061-C9E69266DF3B
[8] urn:lsid:zoobank.org:author:26C84E11-E43F-4076-B268-28C32E9FD2D0
[9] urn:lsid:zoobank.org:author:A7F79AB9-D9F0-49A0-BE9C-CCE8FFB4DFC3

Abstract. We describe a new species of karst-dwelling pitviper from Chumphon Province of Peninsular Thailand, in the Isthmus of Kra, based on morphological and molecular data (2427 bp from cyt *b*, ND4 and 16S rRNA mitochondrial DNA genes). Morphologically, *Trimeresurus kraensis* sp. nov. is distinguished from other congeners by the following combination of morphological characters: a dark/bottle-green dorsum with reddish-brown or purple crossbands; pale green venter lacking dark dots; stripes present on the lateral sides of the ventrals; internasals generally in contact; one large supraocular scale on each side of the head; iris pale copper; tail brown with dark purplish-brown crossbars; dorsal scales in 21–21–15 rows; ventral scales 167 in a single male, 169–171 in females; subcaudal scales 62 in a single male, 52–54 in females, all paired. White vertebral spots present in males, located on approximately every two or four dorsal scales; dark brown spots forming discontinuous pattern present on 1–3 lateral dorsal scale rows; males with reddish-brown postocular stripe with jagged edges. The new species differs from the morphologically similar species *Trimeresurus venustus* s. str. by a notable divergence in cytochrome *b* mitochondrial DNA gene sequences ($p = 5.9\%$).

Keywords. Crotalinae, *T. kanburiensis* complex, Peninsular Thailand, karst, taxonomy.

Idiiatullina S., Pawangkhanant P., Suwannapoom C., Tawan T., Chanhome L., Nguyen T.V., David P., Vogel G. & Poyarkov N.A. 2024. Another new species of karst-associated pitviper (Serpentes, Viperidae: *Trimeresurus*) from the Isthmus of Kra, Peninsular Thailand. *European Journal of Taxonomy* 930: 20–52.
https://doi.org/10.5852/ejt.2024.930.2489

Introduction

The genus *Trimeresurus* Lacépède, 1804 currently comprises 47 species of Asian pitvipers after the recent description of *Trimeresurus ciliaris* by Idiiatullina *et al.* (2023). This latter species belongs to the complex of species of *Trimeresurus kanburiensis* Smith, 1943, which currently includes four species from Southeast Asia, namely: *T. ciliaris* Idiiatullina, Pawangkhanant, Tawan, Worranuch, Dechochai, Suwannapoom, Nguyen, Chanhome & Poyarkov, 2023, *T. kanburiensis*, *T. kuiburi* Sumontha, Suntrarachun, Pauwels, Pawangkhanant, Chomngam, Iamwiriyakul & Chanhome, 2021, and *T. venustus* Vogel, 1991. Based on molecular phylogenies, the recent papers by Mirza *et al.* (2023) and Idiiatullina *et al.* (2023) demonstrated that the complex of *T. kanburiensis* forms a distinct clade in the subgenus *Trimeresurus* together with the complex of *Trimeresurus macrops*, which currently includes four species, namely: *T. cardamomensis* (Malhotra, Thorpe, Mrinalini & Stuart, 2011), *T. honsonensis* (Grismer, Ngo & Grismer, 2008), *T. macrops* Kramer, 1977 and *T. rubeus* (Malhotra, Thorpe, Mrinalini & Stuart, 2011). The systematic status of this clade will be discussed elsewhere in the frame of a revision of the whole complex of *Trimeresurus* s. lat., namely in including other subgenera recognized by Mirza *et al.* (2023) and Idiiatullina *et al.* (2023).

The subgenus *Trimeresurus* is distinguished from other members of the genus *Trimeresurus* by the combination of a long papillose or calyculate hemipenis and a (partially) fused first supralabial and nasal scales (Malhotra & Thorpe 2004a; Sumontha *et al.* 2021). Molecular data suggests the presence of numerous cryptic species which are very similar morphologically and are often hard to distinguish in the wild (Mrinalini *et al.* 2015; Vogel *et al.* 2023). Consequently, molecular methods have helped to resolve some particularly problematic taxonomic issues among such complexes of cryptic pitviper species, with new taxa being described every year such as in the *T. albolabris* complex (e.g., Mirza *et al.* 2020; Chen *et al.* 2020, 2021), *T. kanburiensis* complex (e.g., Sumontha *et al.* 2021; Idiiatullina *et al.* 2023), *T. popeiorum* complex (e.g., Mirza *et al.* 2023), and *T. stejnegeri* complex (e.g., Rathee *et al.* 2022).

In the frame of the revision of several complexes of species and the identification of cryptic species in the subgenus *Trimeresurus*, in the present study, we focus on the *Trimeresurus kanburiensis* species complex. This group comprises relatively small, brightly coloured and patterned, karst-dwelling pitvipers distributed across the limestone karst formations of western and southern Thailand, and northwestern Peninsular Malaysia. Following Idiiatullina *et al.* (2023), this complex currently includes the four species listed above, the ranges of which are as follows, from north to south (see Fig. 1):

- *T. kanburiensis*: western Thailand, endemic to Kanchanaburi Province;
- *T. kuiburi*: northern Peninsular Thailand, endemic to Prachuap Khiri Khan Province;
- *T. venustus*: southern part of Peninsular Thailand, namely in the Thai-Malay Peninsula, southern Thailand, in the provinces of Krabi, Nakhon Si Thammarat, Phang-Nga, Surat Thani, and Trang. This species was also reported from the Langkawi Island off extreme northwestern Peninsular Malaysia, in Kedah State, but its status is not resolved (see below);
- *T. ciliaris*: extreme southern part of the Thai-Malay Peninsula, from Trang and Satun provinces to the extreme northwestern Peninsular Malaysia, in Perlis State.

We refer to Fig. 1 for a map showing the distribution ranges of these four species, based on Chanhome *et al.* (2011), Grismer *et al.* (2006), Chan-ard *et al.* (2015), Sumontha *et al.* (2021), and Idiiatullina *et al.* (2023).

However, our investigation of the *Trimeresurus kanburiensis* species complex suggests that the status of two populations is problematical and has to be re-assessed. The first one inhabits the island of Langkawi, off the west coast of West Malaysia. This population was first reported by Grismer *et al.* (2006) and identified in Idiiatullina *et al.* (2023) as *Trimeresurus* cf. *venustus* 2; its status will not be addressed here.

The second problematical population was initially recorded as *Trimeresurus venustus* from Chumphon Province, in the central part of Peninsular Thailand, by Pauwels *et al.* (2013). It was further discussed by Sumontha *et al.* (2021), and identified in Idiiatullina *et al.* (2023) as *Trimeresurus* cf. *venustus* 1. These latter authors demonstrated that specimens of the population from Chumphon differ in colouration and pattern from the typical specimens of the south Thailand, namely *T. venustus* s. str., and pointed out that its taxonomic status required further investigation. During our recent field surveys in Chumphon Province, we collected four specimens of this population. Although they are superficially similar to *T. venustus* s. str. in overall morphological habitus and body colouration, they differ in a number of other taxonomically significant morphological characters. Furthermore, we demonstrate that they also distinctly differ by a notable divergence in mitochondrial DNA (hereafter mtDNA) gene sequences. Subsequent phylogenetic analyses of three mtDNA genes (cyt *b*, ND4, and 16S) by Idiiatullina *et al.* (2023), and the present paper confirm the placement of the population of *Trimeresurus* sp. from Chumphon within the *T. kanburiensis* species complex, but in which it forms a divergent lineage, sister to *T. kuiburi* and distantly related to *T. venustus* s. str., *T. ciliaris*, and *T. kanburiensis*. Consequently, based on our new data, we herein describe the *Trimeresurus* cf. *venustus* 1 population from Chumphon Province as a new species, and discuss the taxonomy and distribution of the *T. kanburiensis* species complex.

Material and methods

Sampling

Fieldwork was carried out in the area of Sanook Cave, Muang District, Chumphon Province, Peninsular Thailand, by P. Pawangkhanant, C. Suwannapoom, and N.A. Poyarkov in January 2022, and by P. Pawangkhanant and S. Idiiatullina in July 2023 (Fig. 1, locality 5). Geographic coordinates and altitude were obtained using a Garmin GPSMAP 60CSx GPS receiver (USA) and recorded in datum WGS 84. Specimens were collected in the field by means of snake hooks, photographed in life, and euthanized using a benzocaine solution within 24 h of capture. Specimens were fixated in 4% buffered formalin for 24 h

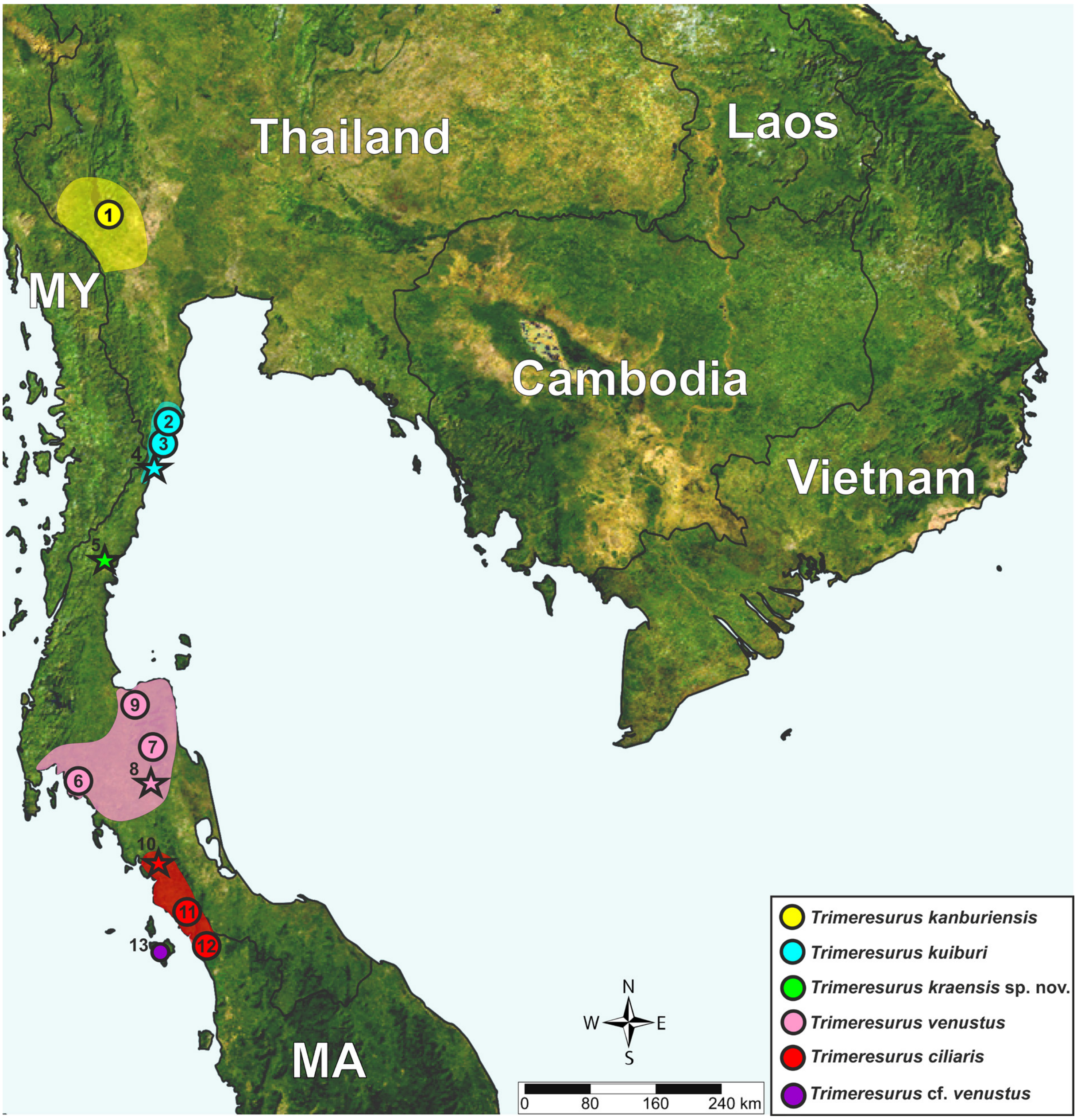

Fig. 1. Distribution of members of the *Trimeresurus kanburiensis* species complex in Thai-Malay Peninsula. Localities: Thailand: *T. kanburiensis* Smith, 1943 (yellow): 1 = Kanchanaburi Prov., Sai Yok Dist., Wat Tham, Phom Lo Khao Yai; *T. kuiburi* Sumontha *et al.*, 2021 (blue): 2 = Prachuap Khiri Khan Prov., Kuiburi Dist., Wat Khao Daeng; 3 = Prachuap Khiri Khan Prov., Kuiburi Dist., Khao Daeng Beach; 4 = Prachuap Khiri Khan Prov., Kuiburi Dist., Khao Daeng, near Ban Thung Noi; *Trimeresurus kraensis* sp. nov. (green): 5 = Chumphon Prov., Wat Tham Sanook; *T. venustus* Vogel, 1991 (pink): 6 = Krabi Prov., Mueang Krabi Dist., Tiger Cave viewpoint; 7 = Nakhon Si Thammarat Prov., Khao Luang; 8 = Nakhon Si Thammarat Prov., Thung Song; 9 = Surat Thani Prov.; *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023 (red): 10 = Trang Prov., Pa Lian Dist., Thum Khao Ting; 11 = Tha Le Ban NP., Khuan Don Dist., Satun Prov.; Malaysia: 12 = Perlis State National Park, Perlis State; *T.* cf. *venustus* (purple): 13 = Langkawi Island, Kedah State. Stars denote type localities (except for *T. kanburiensis* for which the type locality was not sampled). Abbreviations: MY = Myanmar; MA = Malaysia; Prov. = Province; Dist. = District.

and later stored in 70% ethanol. Specimens were subsequently deposited in the herpetological collection of the School of Agriculture and Natural Resources, University of Phayao (AUP, Phayao, Thailand), and the Zoological Museum of Moscow State University (ZMMU, Moscow, Russia). Tissues for genetic analyses were taken from liver or heart prior to preservation of specimens, and stored in 96% ethanol.

Specimen collection and animal use protocols were approved by the Institutional Ethical Committee of Animal Experimentation of the University of Phayao, Phayao, Thailand (certificate number UP-AE64-02-04-005, issued to Chatmongkon Suwannapoom) and were strictly complacent with the ethical conditions of the Thailand Animal Welfare Act. Field work, including collection of animals in the field, was authorized by the Institute of Animals for Scientific Purpose Development (IAD), Bangkok, Thailand (permit numbers U1-01205-2558 and UP-AE59-01-04-0022, issued to Chatmongkon Suwannapoom).

DNA isolation and sequencing

We extracted the total genomic DNA from ethanol-preserved muscle or liver tissues using standard phenol-chloroform extraction procedures (Sambrook *et al.* 1989), followed by isopropanol precipitation as described in Idiiatullina *et al.* (2023). We used the polymerase chain reaction (PCR) to amplify three mtDNA fragments: complete sequences of cytochrome *b* (cyt *b*) and NADH dehydrogenase subunit 4 (ND4) genes and a fragment of 16S rRNA gene. PCR conditions and primers used for both PCR and sequencing are described in detail in Idiiatullina *et al.* (2023).

All amplifications were run using a T100 Thermal Cycler (Bio-Rad). PCR products were loaded onto 1% agarose gels in the presence of ethidium bromide and visualized in electrophoresis. The successfully targeted PCR products were purified by Diatom DNA PCR Clean-Up kit and outsourced to Evrogen® (Moscow, Russia) for sequencing; sequence data collection and visualization was performed on an ABI 3730xl Automated Sequencer (Applied Biosystems).

Molecular phylogeny

The matrilineal genealogy of the genus *Trimeresurus* was assessed using the Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. The newly obtained cyt *b*, ND4, and 16S rRNA sequences were aligned together with all available sequences of *T. ciliaris*, *T. kanburiensis*, *T. kuiburi*, and *T. venustus* obtained from GenBank, as well as the sequences of 29 species of *Trimeresurus* representing all major lineages within the genus, and five species of the genus *Craspedocephalus* Kuhl & Hasselt, 1822. The sequence of *Azemiops feae* Boulenger, 1888 was used as an outgroup to root the tree. The data on voucher and locality information, and GenBank accession numbers is summarized in Table 1.

The nucleotide sequences were initially aligned using MAFFT ver. 6 online webserver (Katoh *et al.* 2019) with default parameters, and subsequently checked by eye in BioEdit ver. 7.0.5.2 (Hall 1999). The genetic divergence among the members of the subgenus *Trimeresurus* was assessed by calculating the mean uncorrected genetic *p*-distances between the cyt *b* sequences using MEGA ver. 6.0. (Tamura *et al.* 2013). The best-fit DNA evolution models for the data set were estimated for genes and codon positions in Partitionfinder ver. 2.1.1 (Lanfear *et al.* 2012) using Akaike information criterion (AIC). The optimal estimated models of DNA evolution included: GTR+I+G model for 16S rRNA and the second codon position of ND4, GTR+G model for the first codon position of cyt *b*, HKY+I+G model for the second codon position of cyt *b* and the first and the third codon positions of ND4, and HKY+I model for the third codon position of cyt *b*. When the same model was suggested for different codon partitions of a given gene, they were treated as a single partition, what resulted in four partitions in total.

Phylogenetic trees were estimated for the concatenated alignment including fragments of cyt *b*, ND4, and 16S rRNA gene sequences. The ML-tree was generated using IQ-TREE webserver (Nguyen *et al.* 2015); the confidence in tree topology was assessed by 1000 ultrafast-bootstrap replications (ML UFBS). The BI analysis was conducted in MrBayes ver. 3.1.2 (Huelsenbeck & Ronquist 2001). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated

Table 1 (continued on next two pages). Sequences and voucher specimens of the genus *Trimeresurus* Lacépède, 1804 and outgroup taxa used in this study.

No	Sample ID	GenBank number			Species	Country	Locality	References
		cyt *b*	ND4	16S				
1	ZMMU Re-17665	OR470569	OR470551	OR471628	*Trimeresurus kraensis* sp. nov.	Thailand	Chumphon, Wat Tham Sanook temple	Idiiatullina *et al.* 2023; this paper
2	ZMMU Re-17666	OR470568	OR470552	OR471629	*Trimeresurus kraensis* sp. nov.	Thailand	Chumphon, Wat Tham Sanook temple	Idiiatullina *et al.* 2023; this paper
3	ZMMU Re-17664	OR470567	OR470535	OR471627	*Trimeresurus kraensis* sp. nov.	Thailand	Chumphon, Wat Tham Sanook temple	Idiiatullina *et al.* 2023; this paper
4	ZMMU Re-17661	OR470557	OR470538	OR471621	*Trimeresurus ciliaris*	Thailand	Trang, Palian, Thum Khao Ting	Idiiatullina *et al.* 2023
5	AUP-02011	OR470558	OR470539	OR471623	*Trimeresurus ciliaris*	Thailand	Trang, Palian, Thum Khao Ting	Idiiatullina *et al.* 2023
6	ZMMU Re-17662	OR470559	OR470540	OR471624	*Trimeresurus ciliaris*	Thailand	Trang, Palian, Thum Khao Ting	Idiiatullina *et al.* 2023
7	ZMMU Re-17663	OR470560	OR470541	OR471622	*Trimeresurus ciliaris*	Thailand	Trang, Palian, Thum Khao Ting	Idiiatullina *et al.* 2023
8	ZMMU Re-17231	OR470575	OR470545	OR471625	*Trimeresurus kuiburi*	Thailand	Prachuap Khiri Khan, Kuiburi, Wat Khao Daeng	Idiiatullina *et al.* 2023
9	ZMMU Re-17095	OR470576	–	OR471626	*Trimeresurus kuiburi*	Thailand	Prachuap Khiri Khan, Kuiburi, Khao Daeng Beach	Idiiatullina *et al.* 2023
20	QSMI 1500	MW806923	–	MW699849	*Trimeresurus kuiburi*	Thailand	Prachuap Khiri Khan, Kui Buri, Khao Daeng	Sumontha *et al.* 2021
10	ZMMU Re-17212	OR470570	OR470547	OR471632	*Trimeresurus venustus*	Thailand	Krabi, Mueang Krabi, Tiger Cave viewpoint	Idiiatullina *et al.* 2023
11	ZMMU Re-17213	OR470565	OR470548	OR471633	*Trimeresurus venustus*	Thailand	Krabi, Mueang Krabi, Tiger Cave viewpoint	Idiiatullina *et al.* 2023
12	ZMMU Re-17214	OR470566	OR470549	OR471631	*Trimeresurus venustus*	Thailand	Krabi, Mueang Krabi, Tiger Cave viewpoint	Idiiatullina *et al.* 2023
13	QSMI TV07	OR470563	OR470537	OR471630	*Trimeresurus venustus*	Thailand	Krabi	Idiiatullina *et al.* 2023
14	A74	AY289224	AY289230	–	*Trimeresurus venustus*	Thailand	Nakhon Si Thammarat, Khao Luang	Malhotra & Thorpe 2004b
15	A75	AY289223	AY289229	–	*Trimeresurus venustus*	Thailand	Nakhon Si Thammarat, Khao Luang	Malhotra & Thorpe 2004b
16	A249	AY289234	AY289233	–	*Trimeresurus venustus*	Thailand	Nakhon Si Thammarat, Khao Luang	Malhotra & Thorpe 2004b
17	A237	AY289222	AY289228	–	*Trimeresurus venustus*	Thailand	Nakhon Si Thammarat, Thung Song	Malhotra & Thorpe 2004b
18	A241	AF171914	AY293930	AY352723	*Trimeresurus venustus*	Thailand	Nakhon Si Thammarat, Thung Song	Malhotra & Thorpe 2004b
19	B29	–	KR021049	–	*Trimeresurus venustus*	Thailand	Surat Thani	Mrinalini *et al.* 2015
21	ZMMU Re-17667	OR470579	OR470553	OR471634	*Trimeresurus kanburiensis*	Thailand	Kanchanaburi, Sai Yok, Khao Yai NP.	Idiiatullina *et al.* 2023
22	QSMI TA091164	OR470562	OR470536	OR471641	*Trimeresurus albolabris*	Thailand	Bangkok	Idiiatullina *et al.* 2023

Table 1 (continued). Sequences and voucher specimens of the genus *Trimeresurus* Lacépède, 1804 and outgroup taxa used in this study.

No	Sample ID	GenBank number			Species	Country	Locality	References
		cyt *b*	ND4	16S				
23	ZMMU NAP-03760	OR470577	OR470543	OR471635	*Trimeresurus cardamomensis*	Vietnam	Kien Giang, Phu Quoc	Idiiatullina *et al.* 2023
24	ZMMU NAP-06685	OR470572	OR470544	OR471638	*Trimeresurus fucatus*	Malaysia	Pahang, Raub, Fraser's Hil	Idiiatullina *et al.* 2023
25	ZMMU NAP-11772	OR470580	OR470554	OR471643	*Trimeresurus guoi*	Thailand	Nan, Doi Phu Kha Mt.	Idiiatullina *et al.* 2023
26	ZMMU ISS-074	OR470564	KX660619	KX660222	*Trimeresurus honsonensis*	Vietnam	Kien Giang, Hon Son Island,	Figueroa *et al.* 2016; Idiiatullina *et al.* 2023
27	ZMMU NAP-09445	OR470573	OR470546	OR471639	*Trimeresurus popeiorum*	Myanmar	Kachin, Indawgyi NP., Inn Gyin Taung Mt.	Idiiatullina *et al.* 2023
28	ZMMU Re-17668	OR470574	OR470550	OR471636	*Trimeresurus* cf. *popeiorum*	Thailand	Ratchaburi, Suan Phueng, Lamtarn Song	Idiiatullina *et al.* 2023
29	AUP-00061	OR470571	OR470534	OR471637	*Trimeresurus* cf. *popeiorum*	Thailand	Chiang Mai, Chom Thong, Doi Inthanon NP.	Idiiatullina *et al.* 2023
30	QSMI Tpur74	OR470556	AY352772	OR471642	*Trimeresurus* cf. *purpureo-maculatus*	Myanmar	Ayeyarwade, Mwe Hauk	Malhotra & Thorpe 2004a; Idiiatullina *et al.* 2023
31	ZMMU NAP-02776	OR470578	OR470542	OR471640	*Trimeresurus rubeus*	Vietnam	Lam Dong, Bao Loc	Idiiatullina *et al.* 2023
32	APF/SFRI-1871	MK720609	–	MK722155	*Trimeresurus arunachalensis*	India	Arunachal Pradesh	Captain *et al.* 2019
33	AM A85	AF171899	U41891	AY352741	*Trimeresurus cantori*	India	Nicobar	Malhotra & Thorpe 2004a; Kraus *et al.* 1996
34	CAS 243566	ON804490	ON804505	–	*Trimeresurus erythrurus*	Myanmar	Rangoon	Chan *et al.* 2022
35	AM B4	AY352764	AY352830	AY059551	*Trimeresurus flavomaculatus*	Philippines		Malhotra & Thorpe 2004a
36	AUP-01988	OR470561	OR470555	AF517181	*Trimeresurus gumprechti*	Thailand	Nan, Doi Phu Kha NP.	Creer *et al.* 2003; Idiiatullina *et al.* 2023
37	AM B33	AY059567	AY059585	AY059552	*Trimeresurus hageni*	Thailand	Songhkla	Malhotra & Thorpe 2004a
38	GP 1474	KP999371	AY352808	AF517176	*Trimeresurus macrops*	Laos	Khammouane	Malhotra & Thorpe 2004a; Zhu *et al.* 2016; Creer *et al.* 2003
39	AM B349	AY371832	–	AY371793	*Trimeresurus malcolmi*	Malaysia	Borneo, Sabah, Kinabalu	Sanders *et al.* 2004
40	B416	AY352765	AY352831	AY352735	*Trimeresurus* cf. *medoensis*	Myanmar	Kachin	Malhotra & Thorpe 2004a
41	LSUHC 10268	KX660506	KX660634	KX660236	*Trimeresurus nebularis*	Malaysia	Pahang	Figueroa *et al.* 2016
42	B467	MW806924	–	MW694483	*Trimeresurus phuketensis*	Thailand	Phuket	Sumontha *et al.* 2021
43	AM B210	AY352756	AY352819	AY352725	*Trimeresurus schultzei*	Philippines	Palawan	Malhotra & Thorpe 2004a
44	GP 07	HQ850448	HQ850449	HQ850446	*Trimeresurus sichuanensis*	China	Sichuan	Guo & Wang 2011
45	B367	AY371824	–	AY371792	*Trimeresurus sumatranus*	Indoneisa	Bengkulu Sumatra	Sanders *et al.* 2004

Table 1 (continued). Sequences and voucher specimens of the genus *Trimeresurus* Lacépède, 1804 and outgroup taxa used in this study.

No	Sample ID	GenBank number			Species	Country	Locality	References
		cyt *b*	ND4	16S				
46	ZMB 65641	AY352749	AY352810	AY352715	*Trimeresurus tibetanus*	Nepal	Helambu	Malhotra & Thorpe 2004a
47	AM B97	AY059574	AF517225	AF517183	*Trimeresurus vogeli*	Thailand	Nakhon Ratchasima	Malhotra & Thorpe 2004c; Creer *et al.* 2003
48	ROM 30791	AF171903	U41892	AY059562	*Trimeresurus* cf. *vogeli*	Vietnam	Gia Lai	Malhotra & Thorpe 2004a; Kraus *et al.* 1996
49	SCUM 035045	EF597522	EF597528	EU443812	*Trimeresurus* cf. *yunnanensis*	China	Sichuan, Hulli	Dawson *et al.* 2008
Outgroups								
50	B301	AY352754	AY352817	AY352722	*Craspedocephalus* (*Craspedocephalus*) *borneensis*	Malaysia	Borneo	Malhotra & Thorpe 2004a
51	B392	AY352757	AY352820	AF517177	*Craspedocephalus* (*Craspedocephalus*) *puniceus*	Indonesia	–	Creer *et al.* 2003
52	AM B261	AY352762	AY352828	AY352732	*Craspedocephalus* (*Peltopelor*) *gramineus*	India	–	Malhotra & Thorpe 2004a
53	A218	AY059569	AY352829	AY059564	*Craspedocephalus* (*Peltopelor*) *malabaricus*	India	Taminadu	Malhotra & Thorpe 2004a
54	RAP 0453	KC347479	AY059597	AY059565	*Craspedocephalus* (*Peltopelor*) *trigonocephalus*	Sri Lanka	–	Malhotra & Thorpe 2004a; Pyron *et al.* 2013
55	B499	AY352747	AY352808	AY352713	*Azemiops feae*	China	–	Malhotra & Thorpe 2004a

chains for one million generations and sampled every 1000 generations; the run was checked to ensure the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER ver. 1.7 (Rambaut *et al.* 2018). The initial 1000 trees were discarded as burn-in. The confidence in tree topology was assessed by calculating the posterior probability (BI PP) (Huelsenbeck & Ronquist 2001). We a priori regarded the tree nodes with ML UFBS values of 95% or higher and PP values over 0.95 as strongly supported; ML UFBS values between 95% and 90% and PP values between 0.95 and 0.90 were regarded as moderate support, while lower values were regarded as a lack of node support (Huelsenbeck & Hillis 1993).

Morphological differentiation

Morphological examination, including measurements and meristic counts, followed Idiiatullina *et al.* (2023). Paired meristic characters were given in the left/right order. The following measurements were taken with a Mitutoyo digital caliper to the nearest 0.1 mm. Abbreviations used were as follows:

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 margin)
SOL = supraocular length
SOW = supraocular width
SVL = snout-vent length
TaL = tail length
TL = total length
VED = vertical eye diameter

Meristic characters examined include:

ASR = anterior number of dorsal scale rows (at one HL behind the head)
CP = cloacal plate(s)
DSR = dorsal scale rows
IL = number of infralabial scales
InN sep = internasal scales in contact (1) or not (0)
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 the half of the total number of ventrals)
PosOc = number of postocular scale(s)
PreV = number of preventrals (scales directly preceding the ventrals, unpaired, wider than long but not in contact on each side with the 1^{st} dorsal scale row)
PSR = posterior number of dorsal scale rows (at one HL before anal plate)
SC = number of subcaudal scales, not including the terminal pointed scute
SL = number of supralabial scales
SRR = dorsal scale rows reduction (counted following Dowling 1951a)
VEN = number of ventral scales (counted following Dowling 1951b)

We also counted the number of maxillary teeth for each specimen. The sex was determined by examination of the hemipenes that were forcedly everted by water injection in the tail base prior to the preservation of the specimen. Morphological data for the additional examined specimens are presented in Appendix 1.

Museum and other acronyms:

AUP = Agriculture University of Phayao, Phayao, Thailand
NHMUK = The Natural History Museum, London, UK (formely BMNH)

PSUZC	=	Prince of Songkhla University Zoological Collection, Songkhla, Thailand
QSMI	=	Queen Saovabha Memorial Institute, Bangkok, Thailand
ZMB	=	Zoologisches Museum für Naturkunde der Humbolt-Universität zu Berlin, Berlin, Germany
ZMMU	=	Zoological Museum of Moscow State University, Moscow, Russia

Results

Sequence characteristics

The final alignment of the three examined mtDNA fragments comprised 2427 base pairs, including: 1104 bp of cyt *b*, 803 bp of ND4, and 520 bp of 16S rRNA genes. Protein-coding sequences were translated into amino acids in order to confirm that no pseudogenes have been amplified. The GenBank accession numbers of the obtained sequences and specimen information are summarized in Table 1.

Phylogenetic relationships

The ML and BI phylogenetic analyses recovered trees with essentially identical topologies; the only minor topological differences were associated with several nodes with low values of nodal support, which are not relevant to the analysis of the focal group (Fig. 2). Monophyly of the genus *Craspedocephalus* is not supported in our tree: it consists of two deeply-divergent mtDNA clades corresponding to the Southeast-Asian subgenus *Craspedocephalus* (95/1.0, hereafter node support values are given for ML UFBS/BI PP, respectively), and to the Indian and Sri-Lankan subgenus *Peltopelor* Günther, 1864 (100/1.0); however, this topology lacks significant nodal support (56/0.74; Fig. 2). The matrilineal genealogy strongly supported the monophyly of the genus *Trimeresurus* (100/1.0) with respect to its sister genus *Craspedocephalus*; however, the phylogenetic relationships among the main groups of *Trimeresurus* remained unresolved. The subgenus *Trimeresurus* was recovered as paraphyletic in our analysis with the *T. albolabris* species group (100/1.0; which included: *T. albolabris* Gray, 1842, *T. guoi* Chen, Shi, Vogel & Ding, 2021, *T. septentrionalis* Kramer, 1977, *T. cantori* (Blyth, 1846), *T. erythrurus* (Cantor, 1839), and *T. purpureomaculatus* (Gray, 1832)) which was suggested as a sister group to all other members of the genus, though with ambiguous topological support values (93/0.98; Fig. 2).

The remaining members of the subgenus *Trimeresurus* included the *T. macrops* species complex and the *T. kanburiensis* species complex, which formed a strongly supported monophyletic group (100/1.0) (Fig. 2). The genealogical relationships within this clade were generally sufficiently resolved and strongly suggested that *Trimeresurus* sp. from Chumphon Province belongs to one clade with *T. honsonensis*, *T. macrops*, and *T. kuiburi* (100/1.0; Clade 2 in Fig. 2). The matrilineal genealogy recovered *Trimeresurus* sp. from Chumphon as a monophyletic group (1.0/100), and suggested that it represents a sister species of *T. kuiburi*, though this topology was not supported in ML ananlysis and received only moderate support in BI analysis (66/0.95; Fig. 2). The phylogenetic position of *T. ciliaris* from southernmost Thailand and *T. rubeus* from Vietnam remained unresolved in our tree. *Trimeresurus kanburiensis* was strongly suggested as a sister species to the remaining members of the species complex with exception of *T. ciliaris* and *T. rubeus* (99/1.0; Fig. 2), while *T. cardamomensis* was recovered as a sister species of *T. venustus* s. str. with ambiguous support (92/1.0; Fig. 2)

Genetic distances

The uncorrected *p*-distances for the cyt *b* gene fragment among examined members of the subgenus *Trimeresurus* are presented in Table 2. Interspecific distances among the members of the subgenus *Trimeresurus* varied from $p = 3.0\%$ (between *T. venustus* s. str. and *T. honsonensis*) to $p = 15.1\%$ (between *T. kuiburi*, *T. erythrurus*, and *T. albolabris*). The *Trimeresurus* sp. lineage from Chumphon Province is highly divergent from other congeners in cyt *b* mtDNA gene sequences with genetic distance varying from $p = 4.1\%$ (with *T. honsonensis*) to $p = 14.0\%$ (with *T. erythrurus*).

In summary, our phylogenetic analyses demonstrated that *Trimeresurus* sp. from Chumphon Province clearly represents a highly divergent lineage of pitvipers, which is most closely related to *T. honsonensis*, *T. macrops*, and *T. kuriburi*, with more distant genealogical relationships to *T. venustus* s. str. and *T. cardamomensis* (Fig. 2).

Taxonomy

Sumontha *et al.* (2021) and Idiiatullina *et al.* (2023) suggested that the population of *Trimeresurus* sp. occurring in Chumphon Province, in the Isthmus of Kra, was distinct from *Trimeresurus venustus* s. str. Molecular analyses clearly demonstrate that this population forms a distinct clade in the phylogeny of the *Trimeresurus kanburiensis* species complex (Fig. 2), which is also significantly divergent from other members of the complex in cyt *b* mtDNA gene sequences (Table 2). Based on examination of our new material, morphological analyses also recovered a number of important diagnostic characters allowing us to distinguish the Chumphon population of *Trimeresurus* sp. from *T. venustus* s. str., with which it was previously confused, as well as from all other members of the genus *Trimeresurus* (summarized below in Table 3). Based on these results, we regard the population from Chumphon Province as a distinct species, which we formally describe below.

Taxonomic account

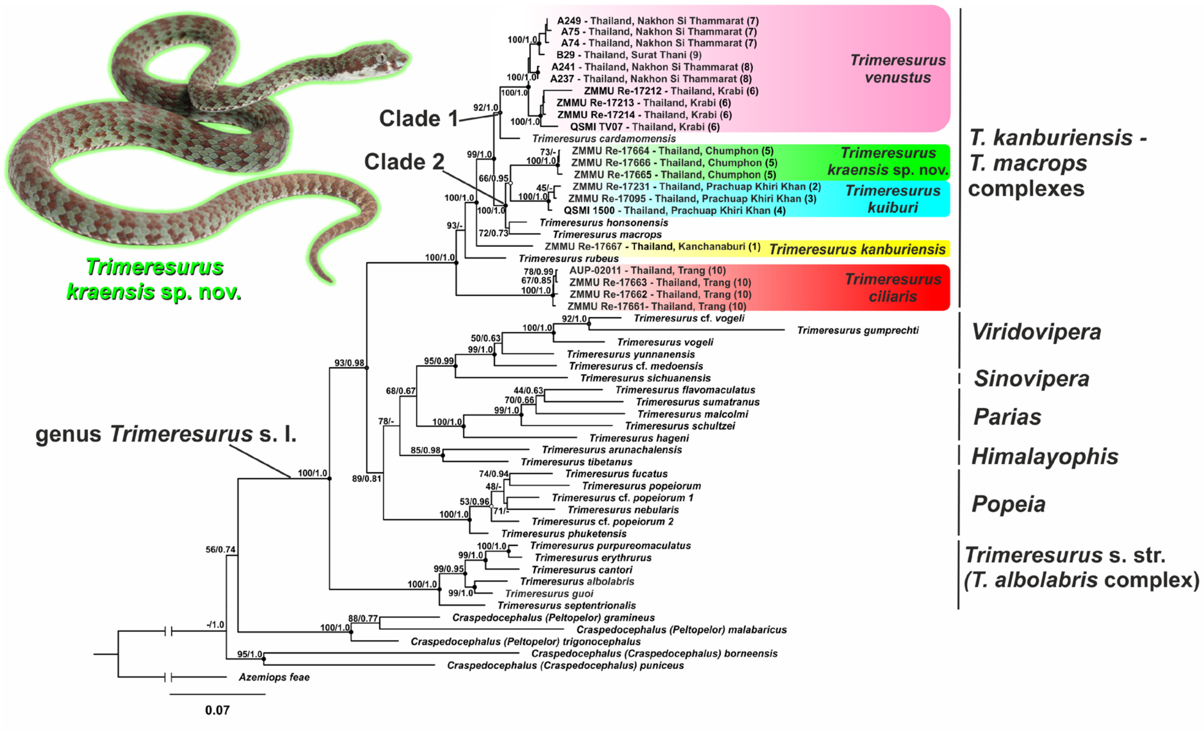

Fig. 2. Maximum Likelihood (ML) tree of the genus *Trimeresurus* Lacépède, 1804 derived from the analysis of 2427 bp of cyt *b*, ND4, and 16S rRNA mitochondrial DNA gene sequences. For voucher specimen information and GenBank accession numbers see Table 1. Numbers at tree nodes correspond to ML UFBS/BI PP support values, respectively. Colours of clades and locality numbers correspond to those on the map in Fig. 1. Photograph showing the new species *Trimeresurus kraensis* sp. nov. by P. Pawangkhanant.

Table 2. Uncorrected *p*-distances (percentage) between the sequences of cyt *b* mtDNA gene of species of the subgenus *Trimeresurus* Lacépède, 1804 included in the phylogenetic analyses; genetic differentiation of the new species *Trimeresurus kraensis* sp. nov. is shown in bold.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	*T. ciliaris*														
2	*T. venustus*	12.5													
3	*T. kraensis* sp. nov.	**12.2**	**5.9**												
4	*T. kuiburi*	12.1	9.5	**6.6**											
5	*T. kanburiensis*	8.0	6.8	**7.6**	7.2										
6	*T. honsonensis*	7.7	3.0	**4.1**	7.4	–									
7	*T. macrops*	10.9	5.6	**5.9**	5.3	6.0	4.8								
8	*T. cantori*	13.4	12.9	**13.0**	13.4	12.2	–	12.4							
9	*T. erythrurus*	17.0	17.4	**14.0**	15.1	13.3	13.7	13.9	5.2						
10	*T. septentrionalis*	14.1	17.9	**13.3**	14.9	13.2	4.8	13.1	7.6	8.1					
11	*T. purpureomaculatus*	14.0	18.2	**13.3**	14.0	12.8	5.6	12.6	5.0	1.7	8.1				
12	*T. albolabris*	17.3	14.0	**13.9**	15.1	13.6	13.3	14.1	7.0	6.4	8.0	7.2			
13	*T. cardamomensis*	7.7	9.3	**6.0**	5.6	4.8	–	4.9	10.8	13.5	13.2	12.9	12.4		
14	*T. guoi*	14.1	10.5	**10.8**	12.5	8.5	12.2	9.9	3.5	3.4	4.1	3.1	3.5	8.1	

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Serpentes Linnaeus, 1758
Family Viperidae Oppel, 1811
Subfamily Crotalinae Oppel, 1811
Genus *Trimeresurus* Lacépède, 1804

Trimeresurus kraensis sp. nov.
urn:lsid:zoobank.org:act:AF38FFC5-F4E0-48CE-A897-8C350982625F
Figs 2–4, 5C, 6A–B; Tables 3–4

Trimeresurus venustus (partim) – Pauwels *et al.* 2013: 280. — Sumontha *et al.* 2021: 320.
Trimeresurus cf. *venustus* – Sumontha *et al.* 2021: 321, fig. 9B.
Trimeresurus cf. *venustus* 1 – Idiiatullina *et al.* 2023: 699, 704.

Diagnosis

The new species is assigned to the subgenus *Trimeresurus* based on the following morphological attributes: a long papillose hemipenis and partially fused first supralabial and nasal scales (Malhotra & Thorpe 2004a; Idiiatullina *et al.* 2023). The new species *Trimeresurus kraensis* sp. nov. is distinguished from all other species of the subgenus *Trimeresurus* by the following combination of morphological characters: (1) a dark olive-green or bottle green dorsum; (2) dorsal pattern consisting of about 60 reddish-brown or purple blotches, transversally elongate but not reaching the lower part of the flanks, two or three series of dark brown spots forming a discontinuous pattern on the 1st to 3rd dorsal scale rows and white vertebral spots present in males, located approximately on every two or four dorsal scales; (3) venter creamish-green with some dark brown spots; (4) tips of the ventral plates both cream and dark brown, forming a discontinuous, alternating pale and dark, ventrolateral stripe; (5) males with a reddish-brown postocular stripe; (6) internasals generally in contact behind the posteror tip of the rostral; (7) single large supraocular scale; (8) iris pale copper, (9) tail brown with dark purplish-brown crossbars; (10) dorsal scales in 21–21–15 rows; (11) ventral scales 167 in a single male, 169–171 in females; (12) subcaudal scales 62 in a single male, 52–54 in females, all paired.

Etymology

The species name is the modern Latin adjective '*kraensis*' in the nominative singular, masculine gender, combining the noun 'Kra', from the name of the Kra Isthmus in Peninsular Thailand where the type locality of the species is located, and the Latin suffix '-*ensis*' (-*is*, -*e*), meaning 'from'. The species name therefore means, 'from Kra'. We suggest the following common names for the new species: **งูหางแฮ่มชุมพร** (Ngu Hang Ham Chumphorn) (in Thai), and Kra Isthmus Pitviper (English).

Type material

Holotype

THAILAND • ♀ adult; Chumphon Province, Muang District, Banna Subdistrict, Wat [= Temple] Tham Sanook and its cave Tham Sanook; 10.48089° N, 99.07323° E; 65 m a.s.l.; 27 Jul. 2022; P. Pawangkhanant, N.A. Poyarkov and C. Suwannapoom leg.; AUP-02036.

Paratypes

THAILAND • 1 ♂ adult; same collection data as for holotype; 27 Jul. 2022; ZMMU Re-17664 (field label NAP-11581) • 1 ♀ adult; same collection data as for holotype; 27 Jul. 2022; ZMMU Re-17666 (field label NAP-11582) • 1 ♀ subadult; same collection data as for holotype; 15 Jan. 2023; P. Pawangkhanant and S.S. Idiiatullina leg.; ZMMU Re-17665 (field label ISS-004).

Description (holotype)

Adult female specimen (Fig. 3) in good state of preservation; measurements of holotype presented in Table 4. Body cylindrical, long and thin (SVL 459 mm, TaL 83 mm, TL 542 mm, TaL/TL 0.153) (Fig. 3). Head triangular in dorsal view (Fig. 3E), elongate, clearly distinct from neck (HL 21.7 mm, HW 17.3 mm, HW/HL 0.80). Snout elongate, flattened, and rounded in dorsal view (Fig. 3E), rather rectangular in lateral view (Fig. 3D), with very distinct and sharp canthus rostralis (SnL/HL 0.31, SnL/ED 2.31). Rostral barely visible in dorsal aspect, triangular (Fig. 3E). One pair of enlarged internasals, in contact with each other behind posteror tip of rostral (Fig. 3E). Pupil vertically elliptical, loreal pit present, and triangular in shape (Fig. 3D). Nostril completely enclosed in entire nasal scale, nasal scale partially fused with first supralabial (Fig. 3D). Shield bordering anterior edge of loreal pit fused with second supralabial (Fig. 3D). One subocular long, thin, crescent-like, separated from 4th and 5th supralabials by one row of scales; single posterior subocular small (Fig. 3D). Three preoculars on each side of head; two upper preoculars located above loreal pit, elongated, in contact with single scale formed by fused second supralabial and loreal, which separates them from nasal; lower preoculars elongated, rectangular, forming lower margin of loreal pit, lower preocular in contact with third supralabial (Fig. 3D). Supralabials 12/12, fourth one largest (Fig. 3D); 12/12 infralabials, those of first pair in contact with each other behind mental (Fig. 3F); first three pairs of infralabials in contact with single pair of chin shields (Fig. 3F). Seven pairs of gulars aligned between chin shields and single preventral (Fig. 3F). One supraocular on each side, enlarged, slightly indented on its inner margin by upper head scales (Fig. 3E). Scales on snout and in interorbital region smooth, irregular, subimbricate; temporal and occipital scales moderately keeled (Fig. 3D–E). Dorsal scales in 21–21–15 rows. Dorsal scales all keeled, except first row, which is smooth. Single preventral + 171 ventrals. Cloacal plate single; 54 subcaudals, all divided.

Colouration of holotype in life (Fig. 3)

The background dorsal colour is bright olive-green above, slightly paler bluish-green on the lower part of each side; many dorsal scales heavily stippled with minute reddish-brown dots, especially on the lower part of the sides; a dorsal series of about 60 dorsal blotches, dark reddish-brown, transversally elongate, rather short, wider than long, not extending downwards on the flanks beyond the 5th dorsal scale row and not forming true crossbands; these dorsal blotches are much irregular in shape, often constricted in their middle or partially divided into two lateral blotches, united or alternating with one another along the vertebral row; white, elongate narrow spots or dashes aligned on the vertebral row, located approximately every two or four dorsal scales; one or two series of dark brown spots, about one-scale long, scattered on the 1st to 3rd dorsal scale rows, irregularly spaced, usually forming pair obliquely arranged; some scales of the 1st dorsal row cream as the tips of dorsals. The tail is coloured and patterned like the dorsum, with about 15 dorsal blotches, turning to dark brown on a pink background on the posterior quarter of the tail.

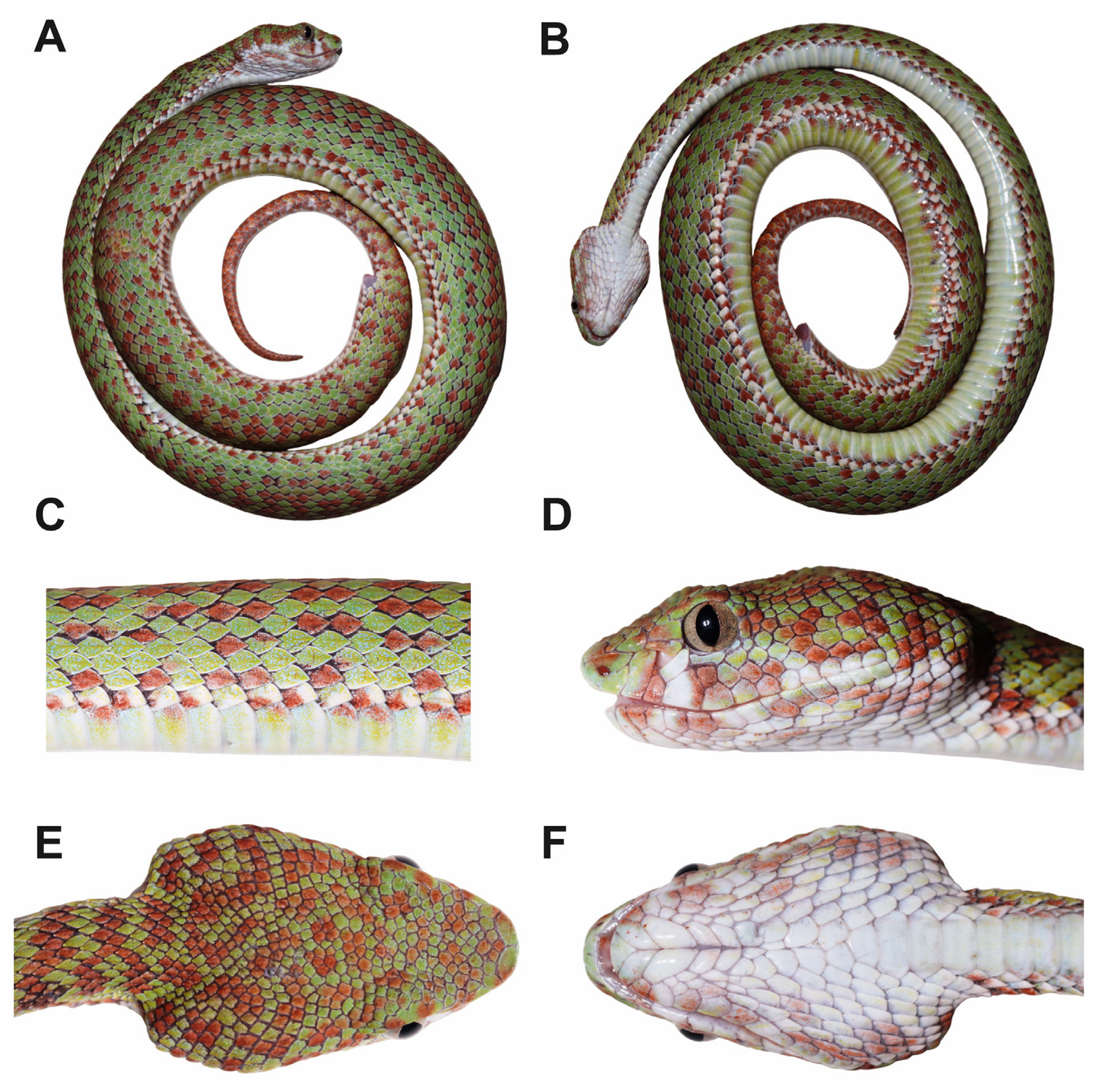

Fig. 3. The holotype of *Trimeresurus kraensis* sp. nov. in life (AUP-02036, adult female) from Wat Tham Sanook, Chumphon Province, Thailand. **A**. Dorsolateral view. **B**. Ventrolateral view. **C**. Close-up of dorsal scales. **D**. Left side of the head. **E**. Dorsal view of the head. **F**. Ventral view of the head. Photographs by P. Pawangkhanant.

The head is bright olive-green like the body above, largely covered with dark reddish-brown areas, of the same colour as the dorsal blotches, so extensively that the head appears reddish-brown above with narrow olive-green lines; rostral olive-green on its lower part, dark reddish-brown on its upper part; internasals and the canthal scales more extensively green than reddish-brown; side of the head pale green; paler than the upper head surface; nasal, loreal and preoculars with dark reddish-brown spots or blotches; supralabials dotted with pale blue; two broad vertical streaks, dark reddish brown covering the parts of the supralabials located below the loreal pit and the eye, respectively; a broad, dark reddish-brown postocular streak, edged above with a narrow area of bright olive-green, extends from the eye to the corner of the mouth. The infralabials, chin and throat are cream with dark brown spots, more numerous on the mental scale and the supralabials.

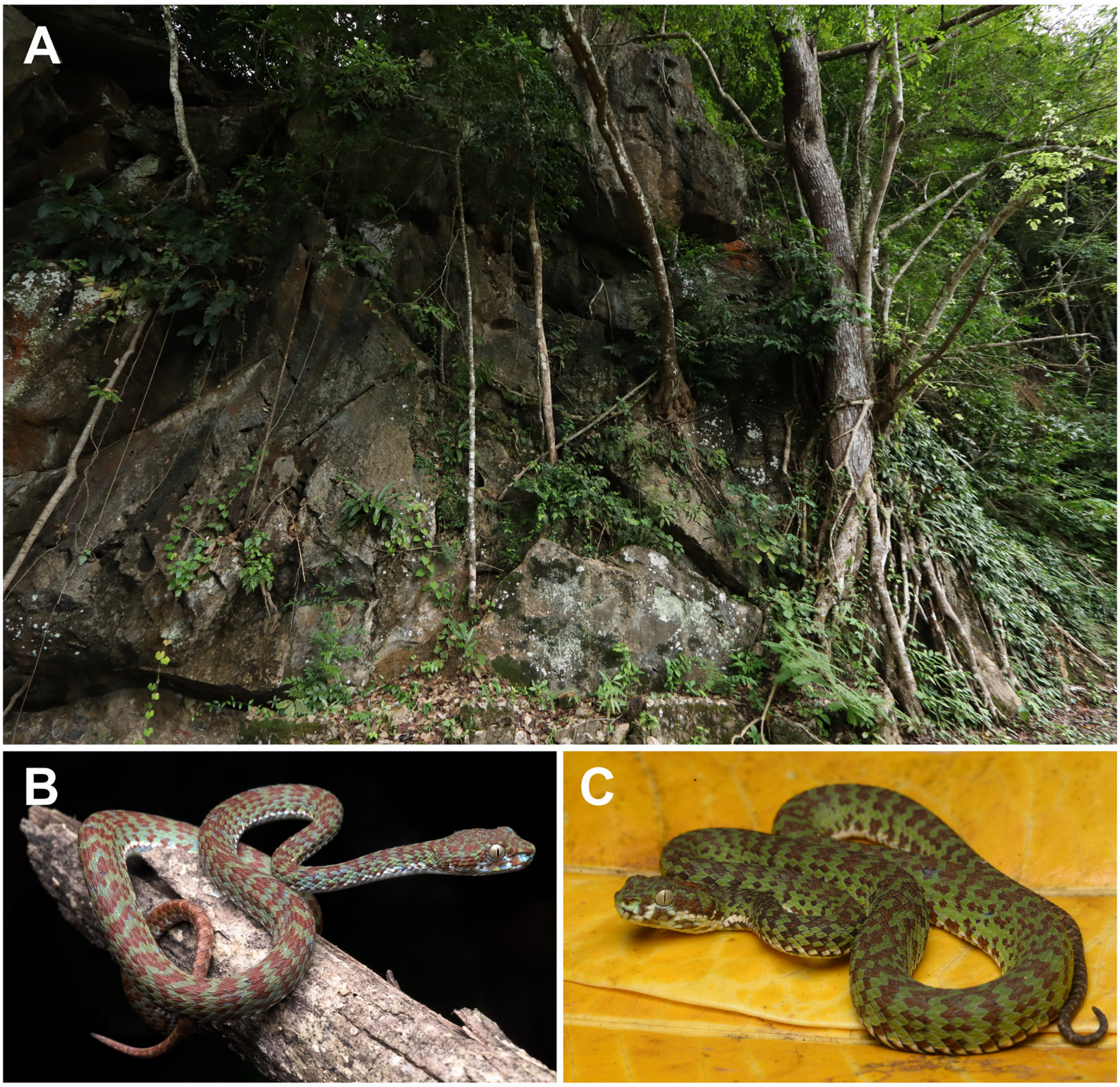

Fig. 4. Habitat of *Trimeresurus kraensis* sp. nov. **A**. Macrohabitat of the new species near the Wat Tham Sanook, Chumphon Province, Thailand. **B**. Photos in life in situ, adult male (uncollected). **C**. Subadult female (paratype, ZMMU Re-17665). Photographs by P. Pawangkhanant (A), Rupert Grassby-Lewis (B), and N.A. Poyarkov (C).

The venter is pale creamish-green, mostly uniform but with some scattered dark brown spots; tips and outer parts of most ventral plates both cream and dark brown, forming a discontinuous, pale and dark, ventrolateral stripe extending from the neck to the vent. The ventral surface of the tail is cream heavily blotched with dark brown, becoming entirely dark brown posteriorly.

Colouration of holotype in preservative

In preservative, the background dorsal colour fades to dark grey, but the pattern remains generally unchanged.

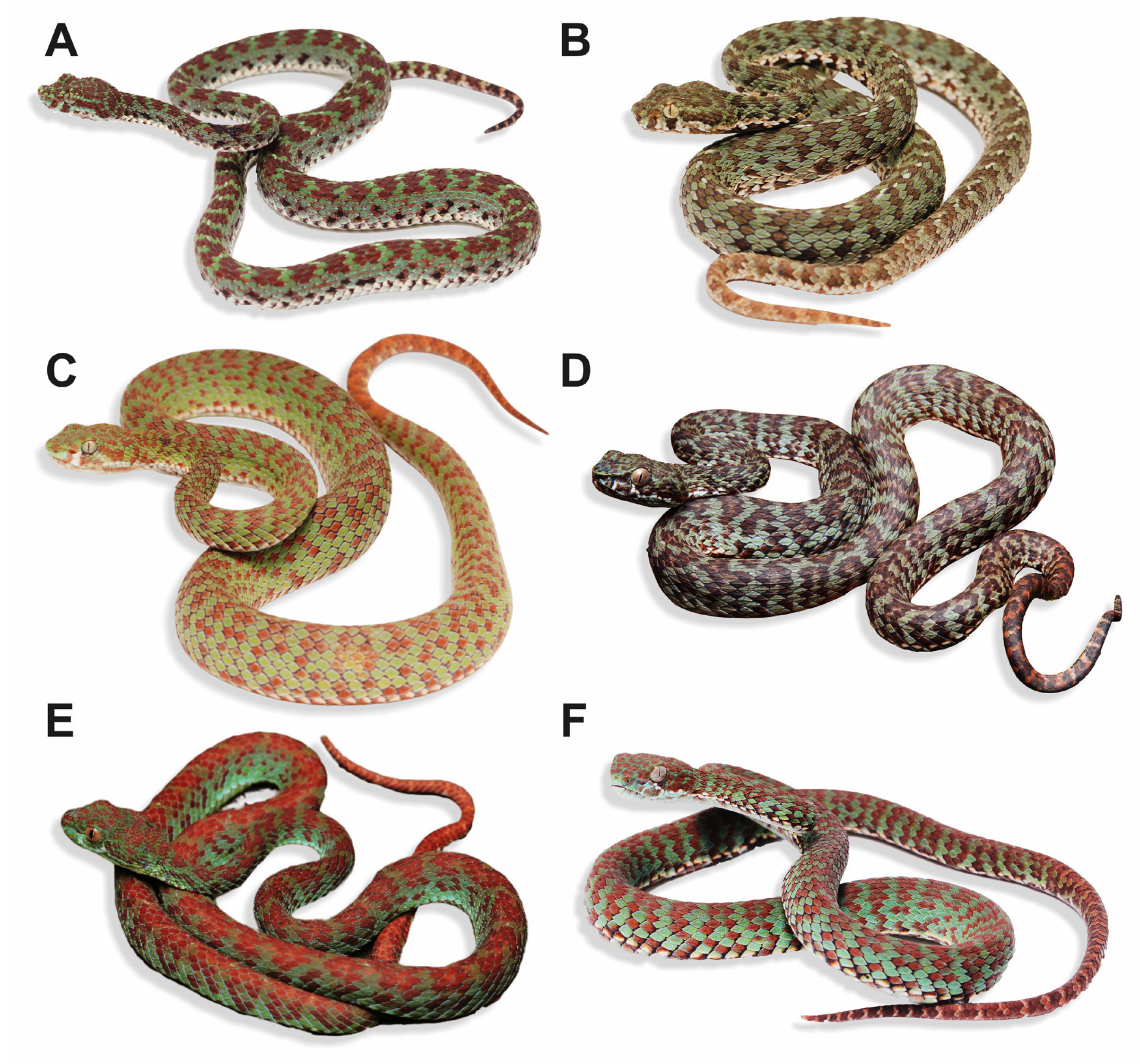

Fig. 5. Comparison of body colouration between members of the *Trimeresurus kanburiensis* species complex (males). **A**. *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023 from Trang Province, Thailand. **B**. *T. kanburiensis* Smith, 1943 from Kanchanaburi Province, Thailand. **C**. *Trimeresurus kraensis* sp. nov. from Chumphon Province, Thailand. **D**. *T.* cf. *venustus* Vogel, 1991 from Langkawi Island, Kedah State, Malaysia. **E**. *T. kuiburi* Sumontha *et al.*, 2021 from Prachuap Khiri Khan Province, Thailand. **F**. *T. venustus* from Krabi Province, Thailand. Photographs by P. Pawangkhanant (A–C, F), T. Chalton (D), and T. Woranuch (E).

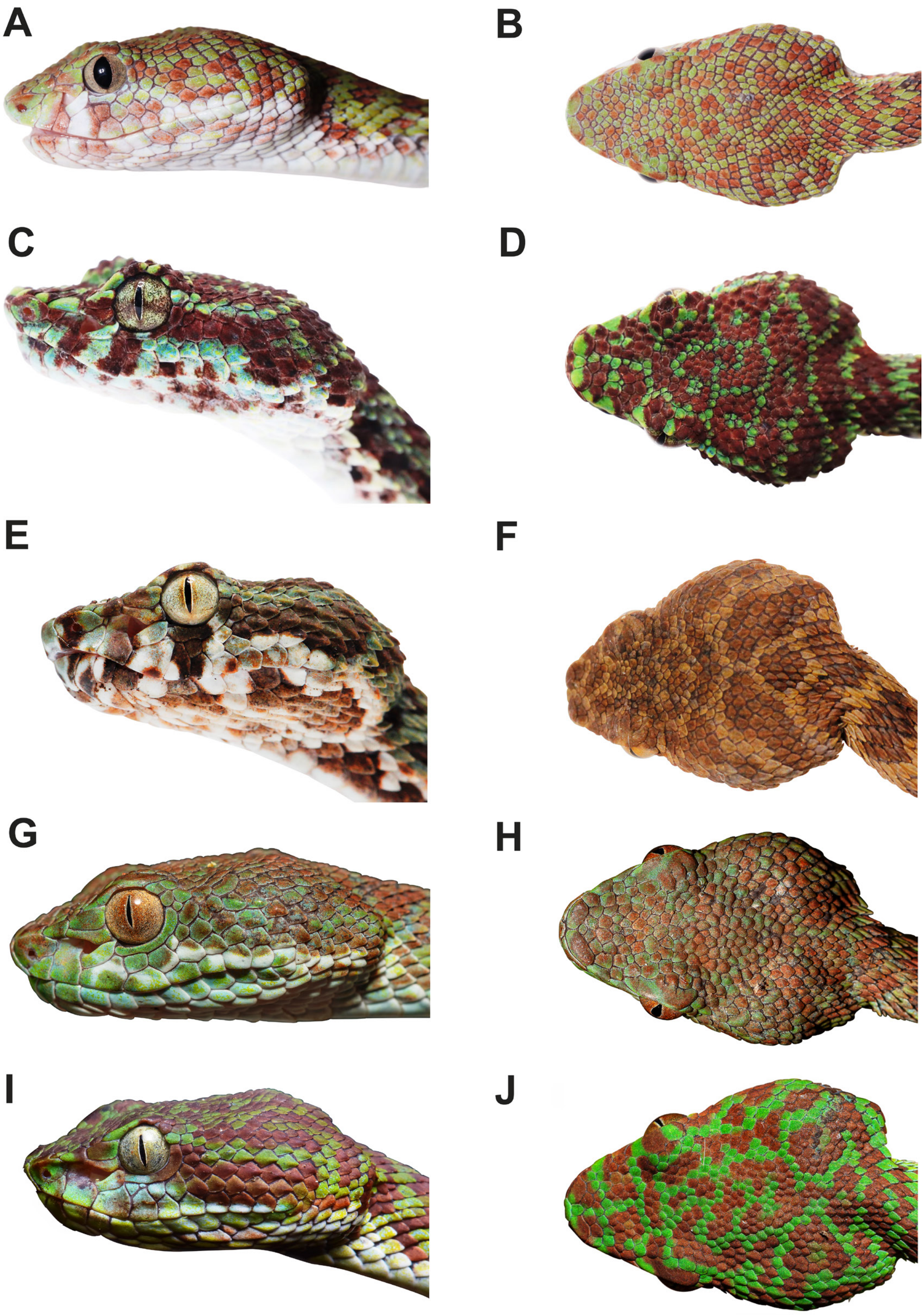

Fig. 6. Comparison of head colouration (left profile and dorsal view of the head) between members of the *Trimeresurus kanburiensis* species complex (males). **A–B**. *Trimeresurus kraensis* sp. nov. **C–D**. *T. ciliaris* Idiiatullina *et al.*, 2023. **E–F**. *T. kanburiensis* Smith, 1943. **G–H**. *T. kuiburi* Sumontha *et al.*, 2021. **I–J**. *T. venustus* Vogel, 1991. Photographs by P. Pawangkhanant (A–F), A. Kaosung (G–H, J) and M. Naiduangchan (I).

Table 3 (continued on next page). Comparison of morphological characters of *Trimeresurus kraensis* sp. nov. with *T. ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991. Diagnostic differences from the new species are marked in bold. For abbreviations see Material and methods section. n = number of specimens.

Character	*T. kraensis* sp. nov.	*T. ciliaris*	*T. kanburiensis*	*T. kuiburi*	*T. venustus*
TL (males, mm)	397 (n = 1)	**417–432 (avg. 425.5, n = 4)**	**500 (n = 1)**	**412–465 (avg. 435.7, n = 4)**	**383–580 (avg. 481.0, n = 12)**
TL (females, mm)	305–542 (avg. 388.0, n = 3)	384 (n = 1)	**426–667 (avg. 531.8, n = 5)**	372–522 (n = 2)	**476–530 (avg. 514.8, n = 4)**
TaL/TL (males)	0.174 (n = 1)	0.167–0.173 (avg. 0.169, n = 4)	0.176 (n = 1)	0.173–0.190 (n = 0.182, n = 4)	0.155–0.193 (avg. 0.180, n = 12)
TaL/TL (females)	0.138–0.153 (avg. 0.146, n = 3)	0.133 (n = 1)	0.124–0.142 (avg. 0.133, n = 5)	0.133–0.135 (n = 2)	0.137–0.151 (avg. 0.146, n = 4)
VEN (males)	167 (n = 1)	**172–175 (avg. 173, n = 4)**	**172 (n = 1)**	164–166 (avg. 165.5, n = 4)	166–175 (avg. 170.9, n = 14)
VEN (females)	169–171 (avg. 170.3, n = 3)	171 (n = 1)	170–178 (avg. 174.3, n = 4)	164–171 (n = 2)	**173–181 (avg. 177.3, n = 4)**
SC (males)	62	59–63 (n = 2)	59 (n = 1)	63–65 (avg. 64.5, n = 4)	60–75 (avg. 67.5, n = 13)
SC (females)	52–54 (avg. 53.0, n = 3)	52 (n = 1)	**46–51 (avg. 48.3, n = 4)**	51–53 (n = 2)	51–57 (avg. 54.3, n = 4)
VEN + SC(males)	229 (n = 1)	232–238 (avg. 234.0, n = 4)	227–231 (avg. 230, n = 4)	231 (n = 1)	**229–248 (avg. 238.7, n = 13)**
VEN + SC (females)	222–225 (avg. 223.3, n = 3)	223 (n = 1)	215–224 (n = 2)	219–229 (avg. 222.5, n = 4)	**224–236 (avg. 231.5, n = 4)**
ASR	21 (n = 4)	**17 (n = 5)**	**21–23 (avg. 22.2, n = 6)**	21–23 (avg. 21.3, n = 6)	**21–25 (avg. 22.5, n = 10)**
MSR	21 (n = 4)	**17 (n = 5)**	**19 (n = 6)**	**19 (n = 6)**	19–21 (avg. 20.8, n = 18)
PSR	15 (n = 4)	15 (n = 5)	15–16 (avg. 15.2, n = 6)	15 (n = 6)	15 (n = 18)
IOS	11–13	11–14	**7–9**	9–11	8–12
InN sep	0 (n = 4)	0–1 (n = 5)	**1–2 (avg. 1.33, n = 6)**	0 (n = 6)	**0–1 (avg. 0.538, n = 17)**
Suborbital stripe (males)	straight	**concave**	straight	**concave**	straight
Small scale between nasal and 2nd supralabial	absent	**present**	**present/absent**	absent	absent
Dorsum colour in life	red/purple bands on dark/ bottle green background	reddish brown bands on emerald-green background	dark olive-brown bands on olive-grayish background	red/purple bands on bottle green background	red/purple bands on dark/ bottle green background
White vertebral dots (in males)	present, every 2–4 scales	present, every 2–3 scales	present, every 3–5 scales	**present, every 5–6 scales**	**absent**
White vertebral dots (in females)	absent	**present, every 2–3 scales**	absent	absent	absent
Belly background colour in life	pale green	**creamy white**	**creamy white**	pale green	pale green

Table 3 (continued). Comparison of morphological characters of *Trimeresurus kraensis* sp. nov. with *T. ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991. Diagnostic differences from the new species are marked in bold. For abbreviations see Material and methods section. n = number of specimens.

Character	***T. kraensis*** **sp. nov.**	***T. ciliaris***	***T. kanburiensis***	***T. kuiburi***	***T. venustus***
Lateral dark stripe on ventrals	always present, discontinuous, reddish brown	**absent**	always present, discontinuous, olive-brown	**absent**	always present, continuous or discontinuous, red
Supraocular scale	one, large	**three or four, small**	one, large	one, large	one, large
Iris colour	slight copper	**olive-green with faded brown horizontal stripe**	brown, slightly golden	copper	yellowish-brown/gold
Tail colour	brown with dark purplish-brown crossbars	dark brown mottled with rusty	brownish-gray with olive-brown blotches	red with some thin lighter bands	brown with dark purplish-brown crossbars
Distribution	Thailand (Chumpon)	Thailand (Trang, Satun), Malaysia (Perils)	Thailand (Kanchanaburi)	Thailand (Prachuap Khiri Khan)	Thailand (Surat Thani, Phang-Nga, Trang, Nakhon Si Thammarat, Surat Thani, Krabi), Malaysia (Kedah?)
Sources	Sumontha *et al.* 2021; our data	Idiiatullina *et al.* 2023; our data	Smith 1943; David *et al.* 2004; our data	Sumontha *et al.* 2021; our data	Vogel, 1991; David *et al.* 2004; Malhotra & Thorpe 2004b; our data

Table 4. Morphological data on the type series of *Trimeresurus kraensis* sp. nov. For abbreviations see Material and methods section.

Specimen ID	AUP-02036	ZMMU Re-17664	ZMMU Re-17665	ZMMU Re-17666
Type status	Holotype	Paratype	Paratype	Paratype
Sex	F	M	F	F
SVL (mm)	459	328	270	263
TaL (mm)	83	69	47	42
TL (mm)	542	397	317	305
HL (mm)	21.7	16.2	15.8	14.8
HW (mm)	17.3	11.5	11	10.5
HD (mm)	10.4	7.4	8.1	6.7
SnL (mm)	6.7	4.4	4.3	4
ED (mm)	2.9	3.1	2.9	2.9
VED (mm)	2.4	2.2	2.1	2.1
SOL (mm)	3.5	2.9	3.5	2.9
SOW (mm)	1.3	1.1	1.2	1.1
Internasals in contact	yes	no	yes	yes
Contact nasal–1st SL	partially fused	partially fused	partially fused	partially fused
IOS	11	11	13	11
PosOc	2/2	2/2	2/2	2/2
SL	12/12	9/9	10/9	9/9
IL	12/12	11/10	12/13	11/11
ASR	21	21	21	21
MSR	21	21	21	21
PSR	15	15	15	15
SRR 21 to 19 (V)	112	112	111	108
SRR 19 to 17 (V)	122	122	121–122	117
SRR 17 to 15 (V)	131	131-132	131	125
PreV	1	2	2	1
VEN	171	167	169	171
CP	1	1	1	1
SC	54	62	53	52

Variation

The main meristic and morphometric characters of the type series of *Trimeresurus kraensis* sp. nov. are summarized in Table 4; photographs of paratype female ZMMU Re-17665 and an uncollected specimen are presented in Fig. 4C and Fig. 4B, respectively. The holotype AUP-02036 represents the longest known specimen and is 542 mm long. The longest known male is 397 mm long (SVL 328 mm, TaL 69 mm, ZMMU Re-17664). Ratio TaL/TL: 0.138–0.174 (male: 0.174, females: 0.138–0.153). Below, we will summarize the variation among the sexes in several main morphological characters.

Body scalation

21–21–15 DSR; 167–171 VEN (male: 167, females: 169–171); 52–62 SC (male: 62, females: 52–53); total number of VEN + SC: 222–229 (male: 229, females: 222–225).

Head scalation

The internasals in contact in all examined specimens but in the male paratype ZMMU Re-17664 they are separated by a small scale; SL: 9–12; IL: 10–13.

Main characters of colouration pattern

Reddish-brown dorsal blotches not forming true crossbands, not extending downwards below the 5th dorsal scale rows; postocular streak always present, dark reddish-brown, broad and conspicuous in both males and females; white ventrolateral stripe present in both sexes.

Distribution and natural history

Currently, *Trimeresurus kraensis* sp. nov. is known only from two small karst formations, namely the Sanook Cave (environs of Wat Tham Sanook Monastery; Fig. 4A) and Chang Phueak Cave (environs of Wat Tham Chang Phueak Monastery), both in Banna Subdistrict, Muang District, Chumphon Province, Thailand (approximate coordinates: 10.446216° N, 99.035114° E; 87 m a.s.l.; Sumontha *et al.* 2021; our data). The two localities are separated by a distance of 5.8 km from each other and are located on the opposite sides of a low limestone hilly area spanning from north-east to south-west for ca 22 km in the central part of the Chumphon Province of Thailand. It is highly likely that *Trimeresurus kraensis* sp. nov. can be found at additional localities along this karst area; nevertheless, the estimated distribution range of the new species seems to be restricted to this limestone landscape.

The new species appears to be a locally abundant species of snake. Adult individuals were recorded after dusk (18:30–22:00) while foraging on large karst rocks and walls (Fig. 4A). Young snakes were generally found while perching on small bushes growing among the limestone rocks; individuals in pre-shedding phase were also recorded while perching on bushes. *Trimeresurus kraensis* sp. nov. is quite aggressive when handled. Toxicological status of the new species remains unknown. Nothing is known about the diet of the new species in the wild either, but it is most likely a generalist predator, as captive individuals ate geckos, small frogs and mice, similar to *T. kuiburi* as described by Sumontha *et al.* (2021). Reproduction of the new species was not observed.

At the type locality (the Sanook Cave), the habitat of the new species represents tropical secondary forest with numerous lianas and bushes covering the limestone formations (Fig. 4A). The new species was found in syntopy with snake species *Ahaetulla prasina* Boie, 1827 and *Elaphe taeniura* Cope, 1861 (Colubridae Oppel, 1811), and *Trimeresurus* cf. *albolabris* Gray, 1842 (Viperidae), as well as with gecko species *Cyrtodactylus sanook* Pauwels, Sumontha, Latinne & Grismer, 2013, *C.* cf. *oldhami* (Theobald, 1876), *Gehyra lacerata* (Taylor, 1962), *Dixonius siamensis* (Boulenger, 1899), and *Gekko gecko* (Linnaeus, 1758) (Gekkonidae Oppel, 1811) (see Pauwels *et al.* 2013; our data). The syntopic species of amphibians included: *Microhyla tetrix* Poyarkov, Pawangkhanant, Gorin, Juthong & Suwannapoom, 2020, *M. butleri* Boulenger, 1900, *M. heymonsi* Vogt, 1911, *M. mukhlesuri* Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014, *Micryletta* cf. *erythropoda* (Tarkhnishvili, 1994), and *Glyphoglossus guttulatus* (Blyth, 1856) (Microhylidae Günther, 1858 (1843)); *Kurixalus* sp. (Rhacophoridae Hoffman, 1932 (1858)); *Occidozyga martensii* (Peters, 1867) and *Limnonectes hascheanus* (Stoliczka, 1870) (Dicroglossidae Anderson, 1871); and *Ingerophrynus parvus* (Boulenger, 1887) (Bufonidae Gray, 1825).

Comparisons

The new species is morphologically and phylogenetically placed within the subgenus *Trimeresurus* (Malhotra & Thorpe 2004a; David *et al.* 2011) and is morphologically overall most similar to other limestone-dwelling species of pitvipers belonging to the *T. kanburiensis* complex, including: *T. ciliaris*, *T. kanburiensis*, *T. kuiburi*, and *T. venustus* s. str.; therefore, the comparisons of the new species with these four congeners appear to be the most pertinent. The main diagnostic characters separating *Trimeresurus kraensis* sp. nov. from these four species are summarized in Table 3, additional morphological data are presented in Appendix 1. The comparison of body colouration and head scalation of these species is presented in Figs 5 and 6, respectively.

Trimeresurus kraensis sp. nov. differs from *T. ciliaris* by having lower total length in males (max TL 397 mm vs 432 mm); lower number of ventrals in males (VEN 167 vs 172–175 [avg. 173]); slightly lower number of ventrals plus subcaudals in males (VEN+SC 229 vs 232–238 [avg. 234.0]); higher number of anterior dorsal scale rows (ASR 21 vs 17); higher number of midbody scale rows (MSR 21 vs 17); postocular stripe straight (vs concave); small scale between nasal and 2nd supralabial absent (vs present); single large supraocular scale (vs three or four small supraocular scales); white vertebral dots absent in females (vs present, every 2–3 scales); ventral surface pale creamish-green (vs creamy white); pale and dark ventrolateral stripe always present, discontinuous, reddish-brown (vs absent); and iris pale copper (vs olive-green with faded brown horizontal stripe).

The new species differs from *T. kanburiensis* by having lower total length in both sexes (max TL 397 mm in male, 542 mm in female vs 500 mm in male, 667 mm in female, respectively); slightly lower number of ventrals in males (VEN 167 vs 172); slightly higher number of subcaudals in females (SC 52–54 [avg. 53.0] vs 46–51 [avg. 48.3]); slightly lower anterior number of dorsal scale rows (ASR 21 vs 21–23 [avg. 22.2]); higher number of midbody scale rows (MSR 21 vs 19); higher number of interorbital scales (IOS 11–13 vs 7–9); internasals generally in contact (vs always separated); ventral surface pale creamish-green (vs creamy white).

Trimeresurus kraensis sp. nov. further differs from *T. kuiburi* by having lower total length in males (max TL 397 mm vs 465 mm); higher number of midbody scale rows (MSR 21 vs 19); postocular streak straight (vs concave); white vertebral dots present on every 2–4 scales in males (vs every 5–6 scales); and pale and dark lateral stripe on ventrals always present, discontinuous, cream, and reddish-brown (vs absent).

Finally, *Trimeresurus kraensis* sp. nov. can be differentiated from *T. venustus* s. str. by having lower total length in both sexes (max TL 397 mm in male, 542 mm in female vs 580 mm in male, 530 mm in female, respectively); slightly higher number of ventrals in females (VEN 169–171 [avg. 170.3] vs 173–181 [avg. 177.3]); slightly lower number of ventrals plus subcaudals in both sexes (VEN+SC 229 in male, 222–225 [avg. 223.3] in females vs 229–248 [avg. 238.7] in males, 224–236 [avg. 231.5] in females); internasals always in contact (vs always separated); white vertebral dots present every 2–4 scales in males (vs absent); dorsal pattern consisting of transversally elongate blotches, not extending downwards beyond the 5th dorsal scale row (vs true crossbands, narrow and reaching the 1st dorsal scale row).

Among the other species of the subgenus *Trimeresurus*, the new species can be readily distinguished from *T. albolabris* Gray, 1842, *T. andersonii* Theobald, 1868, *T. cantori* (Blyth, 1846), *T. cardamomensis* (Malhotra, Thorpe, Mrinalini & Stuart, 2011), *T. caudornatus* Chen, Ding, Vogel & Shi, 2020, *T. davidi* Chandramouli, Campbell & Vogel, 2020, *T. erythrurus* (Cantor, 1839), *T. fasciatus* (Boulenger, 1896), *T. guoi* Chen, Shi, Vogel & Ding, 2021, *T. honsonensis* (Grismer, Ngo & Grismer, 2008), *T. insularis* Kramer, 1977, *T. labialis* (Fitzinger in Steindachner, 1867), *T. macrops* Kramer, 1977, *T. mutabilis* Stoliczka, 1870, *T. purpureomaculatus* (Gray, 1832), *T. rubeus* (Malhotra, Thorpe, Mrinalini & Stuart, 2011), *T. salazar* Mirza, Bhosale, Phansalkar, Sawant, Gowande & Patel, 2020, and *T. septentrionalis* Kramer, 1977 by dorsal colouration and pattern (reddish-brown or purple dorsal blotches on olive-green or bottle-green background in the new species vs uniform green or green colouration with no pattern or pattern consisting of small brownish spots or speckles in other species, or straw-yellow background with irregular, dark-brown transverse body bands in *T. honsonensis*). Moreover, by having 21 MSR, the new species can be further separated from *T. cantori* (27, 29 or 31 MSR), *T. erythrurus* (23 rarely 21, 25 MSR), and *T. purpureomaculatus* (25 rarely 27, 29 MSR) (see Gumprecht *et al.* 2004; Grismer *et al.* 2008; Malhotra *et al.* 2011; Chandramouli *et al.* 2020; Chen *et al.* 2020, 2021; Mirza *et al.* 2020; our data).

Discussion

Our phylogenetic data are congruent with the results of Idiiatullina *et al.* (2023) and suggest a similar set of genealogical relationships among the members of the *T. kanburiensis* species complex. Following the description of *Trimeresurus kraensis* sp. nov., the subgenus *Trimeresurus*, as defined by Mirza *et al.* (2023)

and Idiiatullina *et al.* (2023), currently includes 23 species namely, *Trimeresurus albolabris*, *T. andersonii*, *T. cantori*, *T. cardamomensis*, *T. ciliaris*, *T. caudornatus*, *T. davidi*, *T. erythrurus*, *T. fasciatus*, *T. guoi*, *T. honsonensis*, *T. insularis*, *T. kanburiensis*, *T. kraensis* sp. nov., *T. kuiburi*, *T. labialis*, *T. macrops*, *T. mutabilis*, *T. purpureomaculatus*, *T. rubeus*, *T. salazar*, *T. septentrionalis*, and *T. venustus* (Sumontha *et al.* 2021; Mirza *et al.* 2023; Poyarkov *et al.* 2023). Within this group, the members of the *T. kanburiensis* and *T. macrops* species complexes do not form reciprocally monophyletic clades but form a strongly supported monophylum with poorly resolved phylogenetic relationships within it. Comparable results were reported by an earlier genome-wide analysis by Mrinalini *et al.* (2015) and mtDNA-based genealogy by Idiiatullina *et al.* (2023). Overall, these results suggest a complicated evolutionary history in this group, with the shifts between the limestone-associated and the forest-associated lifestyles likely happened several times during the evolution of *Trimeresururs* pitvipers (see discussion in Sanders *et al.* 2006 and Idiiatullina *et al.* 2023).

In the present study, we report on a previously undescribed lineage of limestone-associated pitvipers of the subgenus *Trimeresurus*. According to our mtDNA-based phylogeny, the newly discovered species *Trimeresurus kraensis* sp. nov. forms a highly divergent lineage of pitvipers, which is suggested as a sister species of *T. kuiburi* in our phylogenetic tree (Fig. 2). Both species occur in the Thai-Malay Peninsula which suggests that the area around the Isthmus of Kra likely played an important role in the differentiation of the *T. kanburiensis* and *T. macrops* species complexes. The importance of the Isthmus of Kra as an area of herpetofaunal turnover was demonstrated in numerous recent publications; this narrow zone likely shaped radiation in many groups of reptiles (e.g., Chomdej *et al.* 2021; Grismer *et al.* 2020a, 2020b, 2022; Poyarkov *et al.* 2019, 2022, 2023) and amphibians (e.g., Chen *et al.* 2018; Gorin *et al.* 2020; Matsui *et al.* 2005; Pawangkhanant *et al.* 2018; Poyarkov *et al.* 2020, 2021; Suwannapoom *et al.* 2018, 2020, 2021, 2022) inhabiting Southeast Asia. Furthermore, the new species is also separated from its congeners by a significant divergence in cyt *b* gene sequences (with p = 4.1–14.0%), which is slightly higher than the genetic distances between many other recognized species of the subgenus *Trimeresurus* (Table 2). Therefore, the molecular and morphological evidence presented here confirm the status of *Trimeresurus kraensis* sp. nov. as a previously undescribed new species of pitvipers which warrants taxonomic recognition.

The Beautiful pitviper *Trimeresurus venustus* was described from southern Thailand in 1991. Subsequently, for a long time its relationships with the Kanburi pitviper *T. kanburiensis* remained controversial because very few specimens of *T. kanburiensis* were known at the time of its description (Vogel 1991). However, based on molecular and morphological evidence, Malhotra & Thorpe (2004b) and David *et al.* (2004) recognized *T. venustus* as a valid species, and formerly reported this species to be distributed in Southern Thailand and the Langkawi Island in northern West Malaysia (see Zimmerer 2004; Grismer *et al.* 2006; Chan-ard *et al.* 2015; Poyarkov *et al.* 2023). In the recent study of the *T. venustus* complex by Idiiatullina *et al.* (2023), a new species *T. ciliaris* was described from Trang and Satun provinces in southwestern part of Thailand, and from Perlis State of northern Peninsular Malaysia. At the same time, this work along with Sumontha *et al.* (2021) also underlined the need to study populations of *T.* cf. *venustus* from Chumphon Province, Thailand, which we herein describe as *Trimeresurus kraensis* sp. nov. The taxonomic status of the population of *T.* cf. *venustus* from Langkawi Island, Kedah State, West Malaysia, originally reported by Grismer *et al.* (2006), still remains controversial. In colouration, this population appears to be different from all presently recognized members of the *T. kanburiensis* species complex (see Fig. 5D). Therefore, based on the results of Vogel (1991), Malhotra & Thorpe (2004b), David *et al.* (2004), Idiiatullina *et al.* (2023), and our data, herein we propose to restrict the distribution of *T. venustus*, as now defined, to the central part of southern peninsular Thailand, in the provinces of Surat Thani, Phang-Nga, Trang, Nakhon Si Thammarat, Surat Thani, and Krabi. Meanwhile, the status of the insular population of *T.* cf. *venustus* from Pulau Langkawi, Malaysia, remains unclear and will be addressed elsewhere.

Trimeresurus kraensis sp. nov. is to date reliably recorded only from two small limestone caves in Chumphon Province, Thailand. This is a highly secretive snake which appears to be a strict forest-dweller, associated with limestone karst forests. Unfortunately, karst formations of Southeast Asia are being destroyed at an unprecedented rate by limestone quarrying, which constitutes the primary threat (see Grismer *et al.* 2021; Suwannapoom *et al.* 2018). These quarrying activities heavily affect the lowland evergreen or semi-evergreen tropical forests growing at the foot of karst formations. Given the available information, we suggest *Trimeresurus kraensis* sp. nov. to be considered Near Threatened (NT), following the IUCN's Red List categories (IUCN Standards and Petitions Committee 2019).

The description of *Trimeresurus kraensis* sp. nov. makes Thailand the country with the richest diversity of species of *Trimeresurus* in the world, with 17 species currently recorded, namely: *T. albolabris*, *T. cardamomensis*, *T. gumprechti* David, Vogel, Pauwels & Vidal, 2002, *T. guoi*, *T. hageni* (Lidth De Jeude, 1886), *T. kanburiensis*, *T. kraensis* sp. nov., *T. kuiburi*, *T. macrops*, *T.* cf. *nebularis* Vogel, David & Pauwels, 2004, *T. phuketensis* Sumontha, Kunya, Pauwels, Nitikul & Punnadee, 2011, *T.* cf. *popeiorum* Smith, 1937, *T. purpureomaculatus*, *T. sabahi* Regenass & Kramer, 1981, *T. sumatranus* (Raffles, 1822), *T. venustus*, and *T. vogeli* David, Vidal & Pauwels, 2001 (Poyarkov *et al.* 2023; this study). Despite the recent significant progress, our knowledge on molecular phylogeny, classification, distribution, and toxicology of pitvipers of the genus *Trimeresurus* in Thailand as well as Asia, is still far from being complete. Therefore, we call for more research, especially for integrative studies of taxonomically controversial species groups in Thailand, such as the members of the *T. albolabris*, *T. macrops*, *T. purpureomaculatu*s, and *T. popeiorum-sabahi* species complexes. Further multilocus studies are also required to achieve a better phylogenetic resolution of evolutionary relationships within the *T. kanburiensis* and *T. macrops* complexes of the genus *Trimeresurus*, this would likely yield a better understanding of shifts between different morphotypes and habitat preferences during the evolution of this radiation of pitvipers. Finally, the medical importance of *Trimeresurus* pitvipers further underscores the need for future studies on the diversity and evolutionary relationships of this genus of snakes.

Acknowledgements

We would like to thank the Laboratory Animal Research Center, University of Phayao and The Institute of Animal for Scientific Purposes Development (IAD), Thailand, for permission to do field work. We are deeply grateful to Thanawut Worranuch, Thiti Ruangsuwan, Mali Naiduangchan, Kanokwan Yimyoo, and Priwan Srisom (Thailand) for help during the field surveys. N.A. Poyarkov thanks the members of MSU HerpLab including Vladislav A. Gorin, Evgeniya N. Solovyeva, Andrey M. Bragin, Alexey V. Trofimets, Nikita S. Klyukin, and Dmitriy V. Akhipov for support and assistance. S. Idiiatullina is thankful to Sunutcha Suntrarachun, Nararat Laopichienpong, and Apinya Longya (QSMI) for helping in the lab during her work in Thailand. We express our gratitude to Andaman Kaosung, Tom Chalton, and Rupert Grassby-Lewis (Thailand) for sharing information and providing photographs and information of *Trimeresurus* spp. We thank two anonymous reviewers for helpful comments which allowed us to improve the previous version of the manuscript. This work was supported by the Russian Science Foundation to N.A. Poyarkov (Grant No. 22-14-00037, specimen collection and preservation, molecular and morphological analyses, data analysis), and in part by the Unit of Excellence 2023 on Biodiversity and Natural Resources Management, University of Phayao [FF66-UoE003] to C. Suwannapoom (AUP, data collection). Specimen collection and animal use protocols were approved by the Institutional Ethical Committee of Animal Experimentation of the University of Phayao, Phayao, Thailand (certificate number UP-AE64-02-04-005, issued to C. Suwannapoom) and were strictly complacent with the ethical conditions of the Thailand Animal Welfare Act. Field work, including collection of animals in the field, was authorized by the Institute of Animals for Scientific Purpose Development (IAD), Bangkok, Thailand (permit numbers U1-01205-2558 and UP-AE59-01-04-0022, issued to C. Suwannapoom).

References

Captain A., Deepak V., Pandit R., Bhatt B. & Athreya R. 2019. A new species of pitviper (Serpentes: Viperidae: *Trimeresurus* Lacepède, 1804) from west Kameng District, Arunachal Pradesh, India. *Russian Journal of Herpetology* 26: 111–122. https://doi.org/10.30906/1026-2296-2019-26-2-111-122

Chan K.O., Sind L.I., Thong L.I., Ananthanarayanan S., Rasu S., Aowphol A., Rujirawan A., Anuar S., Mulcahy D., Grismer J.L. & Grismer L.L. 2022. Phylogeography of mangrove pit vipers (Viperidae, *Trimeresurus erythrurus-purpureomaculatus* complex). *Zoologica Scripta* 51: 664–675. https://doi.org/10.1111/zsc.12562

Chan-ard T., Nabhitabhata J. & Parr J.W. 2015. *A Field Guide to the Reptiles of Thailand*. Oxford University Press, New York.

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 and Reptile Conservation* 14: 169–176.

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

Chen J.M., Poyarkov N.A., Suwannapoom C., Lathrop A., Wu Y.H., Zhou W.W., Yuan Z.Y., Jin J.Q., Chen H.M., Liu H.Q., Nguyen T.Q., Nguyen N.S., Duong T.V., Eto K., Nishikawa K., Matsui M., Orlov N.L., Stuart B.L., Brown R.M., Rowley J.J.L., Murphy R.W., Wang Y.Y. & Che J. 2018. Large-scale phylogenetic analyses provide insights into unrecognized diversity and historical biogeography of Asian leaf-litter frogs, genus *Leptolalax* (Anura: Megophryidae). *Molecular Phylogenetics and Evolution* 124: 162–171. https://doi.org/10.1016/j.ympev.2018.02.020

Chen Z., Yu J., Vogel G., Shi S., Song Z., Tang Y., Yang J., Ding L. & Chen C. 2020. 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

Chen Z., Shi S., Gao J., Vogel G., Song Z., Ding L. & Dai R. 2021. A new species of *Trimeresurus* Lacépède, 1804 (Squamata: Viperidae) from Southwestern China, Vietnam, Thailand and Myanmar. *Asian Herpetological Research* 12: 167–177. https://doi.org/10.16373/j.cnki.ahr.200084

Chomdej S., Pradit W., Suwannapoom C., Pawangkhanant P., Nganvongpanit K., Poyarkov N.A., Che J., Gao Y. & Gong S. 2021. Phylogenetic analyses of distantly related clades of bent-toed geckos (genus *Cyrtodactylus*) reveal an unprecedented amount of cryptic diversity in northern and western Thailand. *Scientific Reports* 11: 2328. https://doi.org/10.1038/s41598-020-70640-8

Creer S., Malhotra A. & Thorpe R.S. 2003. Assessing the phylogenetic utility of four mitochondrial genes and a nuclear intron in the Asian pit viper genus, *Trimeresurus*: separate, simultaneous, and conditional data combination analyses. *Molecular Biology and Evolution* 20: 1240–1251. https://doi.org/10.1093/molbev/msg136

David P., Vogel G., Sumontha M., Pauwels O.S.G. & Chanhome L. 2004. 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: 81–90.

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

Dawson K., Malhotra A., Thorpe R.S., Guo P., Mrinalini & Ziegler T. 2008. Mitochondrial DNA analysis reveals a new member of the Asian pitviper genus *Viridovipera* (Serpentes: Viperidae: Crotalinae). *Molecular Phylogenetics and Evolution* 49: 356–361. https:/doi.org/10.1016/j.ympev.2008.05.044

Dowling H.G. 1951a. A proposed method of expressing scale reductions in snakes. *Copeia* 1951: 131. https:/doi.org/10.2307/1437542

Dowling H.G. 1951b. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1: 97–99.

Figueroa A., McKelvy A.D., Grismer L.L., Bell C.D. & Lailvaux S.P. 2016. A species-level phylogeny of extant snakes with description of a new Colubrid subfamily and genus. *PLoS ONE* 11: e0161070. https:/doi.org/10.1371/journal.pone.0161070

Gorin V.A., Solovyeva E.N., Hasan M., Okamiya H., Karunarathna D.M.S.S., Pawangkhanant P., de Silva A., Juthong W., Milto K.D., Nguyen L.T., Suwannapoom C., Haas A., Bickford D.P., Das I. & Poyarkov N.A. 2020. A little frog leaps a long way: compounded colonizations of the Indian Subcontinent discovered in the tiny Oriental frog genus *Microhyla* (Amphibia: Microhylidae). *PeerJ* 8: e9411. https:/doi.org/10.7717/peerj.9411

Grismer L.L., Yushchenko P.V., Pawangkhanant P., Naiduangchan M., Nazarov R.A., Orlova V.F., Suwannapoom C., Poyarkov N.A. 2020a. A new species of *Hemiphyllodactylus* Bleeker (Squamata; Gekkonidae) from Peninsular Thailand that converges in morphology and color pattern on *Pseudogekko smaragdinus* (Taylor) from the Philippines. *Zootaxa* 4816 (2): 171–190. https:/doi.org/10.11646/zootaxa.4816.2.2

Grismer L.L., Yushchenko P.V., Pawangkhanant P., Nazarov R.A., Naiduangchan M., Suwannapoom C. & Poyarkov N.A. 2020b. A new species of *Cnemaspis* Strauch (Squamata: Gekkonidae) of the *C. siamensis* group from Tenasserim Mountains, Thailand. *Zootaxa* 4852 (5): 547–564. https:/doi.org/10.11646/zootaxa.4852.5.3

Grismer L.L., Youmans T.M., Wood P.L., 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* 30: 61–75.

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

Grismer L.L., Wood P.L., Poyarkov N.A., Le M.D., Karunarathna S., Chomdej S., Suwannapoom C., Qi S., Liu S., Che J., Quah E.S.H., Kraus F., Oliver P.M., Riyanto A., Pauwels O.S.G. & Grismer J.L. 2021. Karstic landscapes are foci of species diversity in the World's third-largest vertebrate genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata; Gekkonidae). *Diversity* 13 (183): 1–15. https:/doi.org/10.3390/d13050183

Grismer L.L., Poyarkov N.A., Quah E.S.H., Grismer J.L. & Wood P.L. 2022. The biogeography of bent-toed geckos, *Cyrtodactylus* (Squamata: Gekkonidae). *PeerJ* 10: e13153. http:/doi.org/10.7717/peerj.13153

Gumprecht A., Tillack F., Orlov N.L., Captain A. & Ryabov S. 2004. *Asian Pit Vipers*. GeitjeBooks Berlin, Berlin.

Guo P. & Wang Y.Z. 2011. A new genus and species of cryptic Asian green pitviper (Serpentes: Viperidae: Crotalinae) from southwest China. *Zootaxa* 2918 (1): 1–14. https:/doi.org/10.11646/zootaxa.2918.1.1

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic acids Symposium Series* 41: 95–98.

Huelsenbeck J.P. & Hillis D.M. 1993. Success of phylogenetic methods in the four-taxon case. *Systematic Biology* 42: 247–264. https:/doi.org/10.1093/sysbio/42.3.247

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

Idiiatullina S., Pawangkhanant P., Tawan T., Worranuch T., Dechochai B., Suwannapoom C., Nguyen T.V., Chanhome K. & Poyarkov N.A. 2023. Limestone jewel: a new colourful karst-dwelling pitviper (Serpentes, Viperidae: *Trimeresurus*) from the poorly explored borderlands of southern peninsular Thailand. *Vertebrate Zoology* 73: 697–716. https://doi.org/10.3897/vz.73.e109854

IUCN Standards and Petitions Committee. 2019. *Guidelines for Using the IUCN Red List Categories and Criteria. Version 14*. Prepared by the Standards and Petitions Committee.

Katoh K., Rozewicki J. & Yamada K.D. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20: 1160–1166. https:/doi.org/10.1093/bib/bbx108

Kraus F., Mink D.G. & Brown W.M. 1996. Crotaline intergeneric relationships based on mitochondrial DNA sequence. *Copeia* 763–773. https://doi.org/10.2307/1447637

Lanfear R., Calcott B., Ho S.Y.W. & Guindon S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701. https:/doi.org/10.1093/molbev/mss020

Malhotra A. & Thorpe R.S. 2004a. A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pitvipers (*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. 2004c. Maximizing information in systematic revisions: A combined molecular and morphological analysis of a cryptic green pitviper complex (*Trimeresurus stejnegeri*). *Biological Journal of the Linnean Society* 82: 219–235. https:/doi.org/10.1111/j.1095-8312.2004.00354.x

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

Matsui M., Khonsue W. & Nabhitabhata J. 2005. A new *Ansonia* from the Isthmus of Kra, Thailand (Amphibia, Anura, Bufonidae). *Zoological Science* 22: 809–814. https://doi.org/10.2108/zsj.22.809

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: 123–138. https:/doi.org/10.3897/zse.96.48431

Mirza Z.A., Lalremsanga H.T., Bhosale H., Gowande G., Patel H., Idiiatullina S. & Poyarkov N.A. 2023. Systematics of *Trimeresurus popeiorum* Smith, 1937 with a revised molecular phylogeny of Asian pitvipers of the genus *Trimeresurus* Lacépède, 1804 sensu lato. *Evolutionary Systematics* 7: 91–104. https://doi.org/10.3897/evolsyst.7.97026

Mrinalini, Thorpe R.S., Creer S., Lallias D., Dawnay L., Stuart B.L. & Malhotra A. 2015. Convergence of multiple markers and analysis methods defines the genetic distinctiveness of cryptic pitvipers. *Molecular Phylogenetics and Evolution* 92: 266–279. https:/doi.org/10.1016/j.ympev.2015.06.001

Nguyen L.T., Schmidt H.A., Von Haeseler A. & Minh B.Q. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. https:/doi.org/10.1093/molbev/msu300

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

Pawangkhanant P., Poyarkov N.A., Duong T.V., Naiduangchan M. & Suwannapoom C. 2018. A new species of *Leptobrachium* (Anura, Megophryidae) from western Thailand. *PeerJ* 6: e5584. https:/doi.org/10.7717/peerj.5584

Poyarkov N.A., Geissler P., Gorin V.A., Dunayev E.A., Hartmann T. & Suwannapoom C. 2019. Counting stripes: revision of the *Lipinia vittigera* complex (Reptilia, Squamata, Scincidae) with description of two new species from Indochina. *Zoological Research* 40 (5): 358–393. https:/doi.org/10.24272/j.issn.2095-8137.2019.052

Poyarkov N.A., Pawangkhanant P., Gorin V.A., Juthong W. & Suwannapoom C. 2020. A new species of miniaturized narrow-mouth frog of the genus *Microhyla* Tschudi, 1838 (Amphibia: Anura: Microhylidae) from northern Tenasserim, Thailand. *Journal of Natural History* 54 (23–24): 1525–1558. https:/doi.org/10.1080/00222933.2020.1804005

Poyarkov N.A., Nguyen T.V., Popov E.S., Geissler P., Pawangkhanant P., Neang T., Suwannapoom C. & Orlov N.L. 2021. Recent progress in taxonomic studies, biogeographic analysis and revised checklist of amphibians in Indochina. *Russian Journal of Herpetology* 28 (3A): 1–110. https:/doi.org/10.30906/1026-2296-2021-28-3A-1-110

Poyarkov N.A., Nguyen T.V., Pawangkhanant P., Yushchenko P.V., Brakels P., Nguyen L.H., Nguyen H.N., Suwannapoom C., Orlov N.L. & Vogel G. 2022. An integrative taxonomic revision of slug-eating snakes (Squamata: Pareidae: Pareineae) reveals unprecedented diversity in Indochina. *PeerJ* 10: e12713. https:/doi.org/10.7717/peerj.12713

Poyarkov N.A., Nguyen T.V., Popov E.S., Geissler P., Pawangkhanant P., Neang T., Suwannapoom C., Ananjeva N.B. & Orlov N.L. 2023. Recent progress in taxonomic studies, biogeographic analysis and revised checklist of Reptilians in Indochina. *Russian Journal of Herpetology* 30 (5): 255–476. https://doi.org/10.30906/1026-2296-2023-30-5-255-476

Pyron R.A., Kandambi H.K.D., Hendry C.R., Pushpamal V., Burbrink F.T. & Somaweera R. 2013. Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Molecular Phylogenetics and Evolution* 66: 969–978. https:/doi.org/10.1016/j.ympev.2012.12.004

Rambaut A., Drummond A.J., Xie D., Baele G. & Suchard M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. https:/doi.org/10.1093/sysbio/syy032

Rathee Y.S., Purkayastha J., Lalremsanga H.T., Dalal S., Biakzuala L., Muansanga L. & Mirza Z.A. 2022. A new cryptic species of green pit viper of the genus *Trimeresurus* Lacépède, 1804 (Serpentes, Viperidae) from northeast India. *PLoS ONE* 17: 1–17. https:/doi.org/10.1371/journal.pone.0268402

Sambrook J., Fritsch E.F. & Maniatis T. 1989. *Molecular Cloning: A Laboratory Manual. 2nd Ed.* Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Sanders K.L., Malhotra A. & Thorpe R.S. 2004. Ecological diversification in a group of Indomalayan pitvipers (*Trimeresurus*): convergence in taxonomically important traits has implications for species identification. *Journal of Evolutionary Biology* 17: 721–731. https:/doi.org/10.1111/j.1420-9101.2004.00735.x

Sanders K.L., Malhotra A. & Thorpe R.S. 2006. Evidence for a Müllerian mimetic radiation in Asian pitvipers. *Proceedings of the Royal Society B: Biological Sciences* 273 (1590): 1135–1141. https:/doi.org/10.1098/rspb.2005.3418

Sumontha M., Suntrarachun S., Pauwels O.S.G., Pawangkhanant P., Chomngam N., Iamwiriyakul P. & Chanhome L. 2021. A new karst-dwelling, colorful pitviper (Viperidae: *Trimeresurus*) from northern Peninsular Thailand. *Zootaxa* 4974 (2): 307–332. https://doi.org/10.11646/zootaxa.4974.2.4

Suwannapoom C., Sumontha M., Tunprasert J., Ruangsuwan T., Pawangkhanant P., Korost D.V. & Poyarkov N.A. 2018. A striking new genus and species of cave-dwelling frog (Amphibia: Anura: Microhylidae: Asterophryinae) from Thailand. *PeerJ* 6: e4422. https://doi.org/10.7717/peerj.4422

Suwannapoom C., Nguyen T.V., Pawangkhanant P., Gorin V.A., Chomdej S., Che J. & Poyarkov N.A. 2020. A new species of *Micryletta* (Amphibia: Microhylidae) from southern Thailand. *Zoological Research* 41 (5): 581–588. https://doi.org/10.24272/j.issn.2095-8137.2020.139

Suwannapoom C., Grismer L.L., Pawangkhanant P., Naiduangchan M., Yushchenko P.V., Arkhipov D.V., Wilkinson J.A. & Poyarkov N.A. 2021. Hidden tribe: a new species of Stream Toad of the genus *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from the poorly explored mountainous borderlands of western Thailand. *Vertebrate Zoology* 71: 763–779. https://doi.org/10.3897/vz.71.e73529

Suwannapoom C., Grismer L.L., Pawangkhanant P. & Poyarkov N.A. 2022. A new species of stream toad of the genus *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from Nakhon Si Thammarat Range in southern Thailand. *Zootaxa* 5168 (2): 119–136. https://doi.org/10.11646/zootaxa.5168.2.2

Tamura K., Stecher G., Peterson D., Filipski A & Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Vogel G. 1991. Eine neue *Trimeresurus*-Art aus Thailand, *Trimeresurus venustus* sp. nov. (Reptilia: Serpentes: Crotalidae). *Sauria* 13 (1): 23–28. [In German.]

Vogel G., Nguyen T.V. & David P. 2023. A new green pitviper of the complex of *Trimeresurus albolabris* complex (Reptilia, Serpentes, Viperidae) from central and southern Myanmar. *Zootaxa* 5357 (4): 515–554. https://doi.org/10.11646/zootaxa.5357.4.3

Zhu F., Liu Q., Che J., Zhang L., Chen X., Yan F., Murphy R., Guo C. & Guo P. 2016. Molecular phylogeography of white-lipped tree viper (*Trimeresurus*; Viperidae). *Zoologica Scripta* 45: 252–262. https://doi.org/10.1111/zsc.12156

Zimmerer J. 2004. *Nature Guide, Langkawi*. Sakti Mega Enterprise, Penang.

Manuscript received: 4 September 2023
Manuscript accepted: 14 December 2023
Published on: 27 March 2024
Topic editor: Magalie Castelin
Section editor: Aurélien Miralles
Desk editor: Radka Rosenbaumová

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.

Appendix 1 part 1 (continued on next page). Main measurements and meristic characters of the examined specimens of *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991 s. str. Remark: data for *T. kuiburi* from Sumontha *et al.* (2021). N/a = data not available. For abbreviations see Material and methods section.

No.	Species	Number	Status	Sex	Location	SVL (mm)	TaL (mm)	TL (mm)	TaL/TL
1	*Trimeresurus ciliaris*	ZMMU Re-17661	Holotype	M	Satun, Thailand	345	72	417	0.173
2	*Trimeresurus ciliaris*	AUP-02011	Paratype	M	Satun, Thailand	357	73	430	0.170
3	*Trimeresurus ciliaris*	ZMMU Re-17662	Paratype	M	Satun, Thailand	360	72	432	0.167
4	*Trimeresurus ciliaris*	ZMMU Re-17663	Paratype	M	Satun, Thailand	352	71	423	0.168
5	*Trimeresurus ciliaris*	QSMI 1538	Paratype	F	Satun, Thailand	333	51	384	0.133
1	*Trimeresurus kanburiensis*	NHMUK 1992.535		M	Sai Yok, Kanchanaburi, Thailand	412	88	500	0.176
2	*Trimeresurus kanburiensis*	NHMUK 1946.1.8.91	Holotype	F	Kanchanaburi, Thailand	366	60	426	0.141
3	*Trimeresurus kanburiensis*	NHMUK 1987.943		F	Sai Yok, Kanchanaburi, Thailand	572	95	667	0.142
4	*Trimeresurus kanburiensis*	NHMUK 1988.383		F	Kanchanaburi, Thailand	438	68	506	0.134
5	*Trimeresurus kanburiensis*	QSMI 508		F	Kanchanaburi, Thailand	386	55	441	0.125
6	*Trimeresurus kanburiensis*	QSMI 509		F	Kanchanaburi, Thailand	542	77	619	0.124
1	*Trimeresurus kuiburi*	QSMI 1500	Holotype	M	Prachuap Khiri Khan, Thailand	376.4	88.2	465	0.190
2	*Trimeresurus kuiburi*	AUP-02005	Paratype	M	Prachuap Khiri Khan, Thailand	372.9	81.1	454	0.179
3	*Trimeresurus kuiburi*	PSUZC-R 734	Paratype	M	Prachuap Khiri Khan, Thailand	340.8	71.1	412	0.173
4	*Trimeresurus kuiburi*	PSUZC-R 735	Paratype	M	Prachuap Khiri Khan, Thailand	334.4	77.7	412	0.189
5	*Trimeresurus kuiburi*	QSMI 1501	Paratype	F	Prachuap Khiri Khan, Thailand	451.2	70.6	521.8	0.135
6	*Trimeresurus kuiburi*	AUP-02006	Paratype	F	Prachuap Khiri Khan, Thailand	323.1	49.5	372.6	0.133
1	*Trimeresurus venustus*	ZMB 48045	Holotype	M	Nakhon Si Thammarat, Thailand	490	90	580	0.155
2	*Trimeresurus venustus*	NHMUK 1983.384	Paratype	M	Nakhon Si Thammarat, Thailand	380	85	465	0.183
3	*Trimeresurus venustus*	NHMUK 1983.385	Paratype	M	Nakhon Si Thammarat, Thailand	325	67	392	0.171
4	*Trimeresurus venustus*	NHMUK 1983.386	Paratype	M	Nakhon Si Thammarat, Thailand	320	63	383	0.164
5	*Trimeresurus venustus*	NHMUK 1987.945	Paratype	M	Nakhon Si Thammarat, Thailand	405	90	495	0.182
6	*Trimeresurus venustus*	NHMW 40573:1		M	Lan Sake, Nakhon Si Thammarat, Thailand	421	95	516	0.184
7	*Trimeresurus venustus*	NHMW 39596:1		M	Lan Sake, Nakhon Si Thammarat, Thailand	407	94	501	0.188
8	*Trimeresurus venustus*	QSMI 353		M	Thung Song, Nakhon Si Thammarat, Thailand	358	78	436	0.179
9	*Trimeresurus venustus*	QSMI 357		M	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	431	N/a	N/a	N/a
10	*Trimeresurus venustus*	QSMI 352		M	Thung Song, Nakhon Si Thammarat, Thailand	397	95	492	0.193
11	*Trimeresurus venustus*	QSMI 356		M	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	391	88	479	0.184
12	*Trimeresurus venustus*	QSMI 517		M	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	426	96	522	0.184
13	*Trimeresurus venustus*	QSMI 518		M	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	414	97	511	0.190

Appendix 1 part 1 (continued). Main measurements and meristic characters of the examined specimens of *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991 s. str. Remark: data for *T. kuiburi* from Sumontha *et al.* (2021). N/a = data not available. For abbreviations see Material and methods section.

No.	Species	Number	Status	Sex	Location	SVL (mm)	TaL (mm)	TL (mm)	TaL/TL
14	*Trimeresurus venustus*	ZSM 127.1990	Paratype	M	Nakhon Si Thammarat, Thailand	N/a	N/a	N/a	N/a
15	*Trimeresurus venustus*	NHMUK 1987.944	Paratype	F	Nakhon Si Thammarat, Thailand	455	72	527	0.137
16	*Trimeresurus venustus*	QSMI 354		F	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	450	76	526	0.144
17	*Trimeresurus venustus*	QSMI 355		F	Khao Klab, Thung Song, Nakhon Si Thammarat, Thailand	404	72	476	0.151
18	*Trimeresurus venustus*	ZMB 48046	Paratype	F	Thung Song, Nakhon Si Thammarat, Thailand	450	80	530	0.151

Appendix 1 part 2 (continued on next page). Main measurements and meristic characters of the examined specimens of *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991 s. str. Remark: data for *T. kuiburi* from Sumontha *et al.* (2021). N/a = data not available. For abbreviations see Material and methods section.

No.	Species	Number	Sex	VEN	SC	VEN + SC	ASR	MSR	PSR	InN sep	SL	IL	Sources
1	*Trimeresurus ciliaris*	ZMMU Re-17661	M	172	61	233	17	17	15	0	9/9	11/10	our data
2	*Trimeresurus ciliaris*	AUP-02011	M	173	59	232	17	17	15	0	9/8	10/10	our data
3	*Trimeresurus ciliaris*	ZMMU Re-17662	M	175	63	238	17	17	15	0	9/9	10/10	our data
4	*Trimeresurus ciliaris*	ZMMU Re-17663	M	172	61	233	17	17	15	0	9/9	11/10	our data
5	*Trimeresurus ciliaris*	QSMI 1538	F	171	52	223	17	17	15	0	9/9	10/11	our data
1	*Trimeresurus kanburiensis*	NHMUK 1992.535	M	172	59	231	22	19	15	2	10/11	11/11	our data
2	*Trimeresurus kanburiensis*	NHMUK 1946.1.8.91	F	157	41	198	23	19	15	1	10/10	11/12	our data
3	*Trimeresurus kanburiensis*	NHMUK 1987.943	F	178	51	229	23	19	15	1	10/11	12/13	our data
4	*Trimeresurus kanburiensis*	NHMUK 1988.383	F	170	49	219	23	19	15	1	10/10	12/12	our data
5	*Trimeresurus kanburiensis*	QSMI 508	F	175	46	221	21	19	16	2	9/9	11/11	our data
6	*Trimeresurus kanburiensis*	QSMI 509	F	174	47	221	21	19	15	1	10/9	11/12	our data
1	*Trimeresurus kuiburi*	QSMI 1500	M	166	65	231	21	19	15	0	11/10	13/12	Sumontha *et al.* 2021
2	*Trimeresurus kuiburi*	AUP-02005	M	164	63	227	21	19	15	0	10/10	11/11	Sumontha *et al.* 2021
3	*Trimeresurus kuiburi*	PSUZC-R 734	M	166	65	231	21	19	15	0	9/9	10/10	Sumontha *et al.* 2021
4	*Trimeresurus kuiburi*	PSUZC-R 735	M	166	65	231	21	19	15	0	10/11	10/10	Sumontha *et al.* 2021
5	*Trimeresurus kuiburi*	QSMI 1501	F	171	53	224	23	19	15	0	10/11	11/11	Sumontha *et al.* 2021
6	*Trimeresurus kuiburi*	AUP-02006	F	164	51	215	21	19	15	0	10/11	12/12	Sumontha *et al.* 2021
1	*Trimeresurus venustus*	ZMB 48045	M	170	60	230	N/a	21	15	0	10/10	10/10	our data
2	*Trimeresurus venustus*	NHMUK 1983.384	M	175	71	246	N/a	21	15	1	10/10	13/13	our data
3	*Trimeresurus venustus*	NHMUK 1983.385	M	171	66	237	N/a	21	15	1	10/10	12/12	our data
4	*Trimeresurus venustus*	NHMUK 1983.386	M	171	71	242	N/a	21	15	0	11/10	12/12	our data
5	*Trimeresurus venustus*	NHMUK 1987.945	M	174	67	241	N/a	21	15	0	10/9	11/12	our data
6	*Trimeresurus venustus*	NHMW 40573:1	M	171	65	236	23	19	15	1	9/9	11/12	our data
7	*Trimeresurus venustus*	NHMW 39596:1	M	166	63	229	21	19	15	1	11/9	11/10	our data
8	*Trimeresurus venustus*	QSMI 353	M	167	68	235	23	21	15	0	10/10	11/12	our data
9	*Trimeresurus venustus*	QSMI 357	M	166	N/a	N/a	21	21	15	0	9/10	12/12	our data
10	*Trimeresurus venustus*	QSMI 352	M	173	68	241	23	21	15	1	10/10	11/?	our data
11	*Trimeresurus venustus*	QSMI 356	M	173	70	243	23	21	15	0	10/10	12/12	our data
12	*Trimeresurus venustus*	QSMI 517	M	171	64	235	23	21	15	1	8/8	N/a	our data

Appendix 1 part 2 (continued). Main measurements and meristic characters of the examined specimens of *Trimeresurus ciliaris* Idiiatullina *et al.*, 2023, *T. kanburiensis* Smith, 1943, *T. kuiburi* Sumontha *et al.*, 2021, and *T. venustus* Vogel, 1991 s. str. Remark: data for *T. kuiburi* from Sumontha *et al.* (2021). N/a = data not available. For abbreviations see Material and methods section.

No.	Species	Number	Sex	VEN	SC	VEN + SC	ASR	MSR	PSR	InN sep	SL	IL	Sources
13	*Trimeresurus venustus*	QSMI 518	M	173	75	248	23	21	15	1	8/9	N/a	our data
14	*Trimeresurus venustus*	ZSM 127.1990	M	171	69	240	N/a	21	15	?	9/9	N/a	our data
15	*Trimeresurus venustus*	NHMUK 1987.944	F	181	54	235	N/a	21	15	0	11/10	11/11	our data
16	*Trimeresurus venustus*	QSMI 354	F	179	57	236	21	21	15	0	9/10	12/11	our data
17	*Trimeresurus venustus*	QSMI 355	F	173	51	224	25	21	15	1	10/10	12/13	our data
18	*Trimeresurus venustus*	ZMB 48046	F	176	55	231	N/a	21	15	1	10/10	12/12	our data