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**A NEW SPECIES OF KARST-ASSOCIATED PITVIPER OF THE
Trimeresurus kanburiensis COMPLEX (SQUAMATA: VIPERIDAE)
 FROM EASTERN THAILAND**

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Abstract

We describe a new species of karst-dwelling pitviper from Sa Kaeo Province in eastern Thailand based on morphological and molecular (2,296 bp from *cyt b*, ND4, and 16S rRNA mitochondrial DNA genes) lines of evidence. Our phylogenetic analysis places the new species as a sister lineage of *Trimeresurus venustus* ($p = 2.7\%$ and 3.7% for *cyt b* and ND4 genes, respectively). It is also closely related to *T. cardamomensis* ($p = 2.1\%$ and 2.6% for *cyt b* and ND4 genes, respectively). To date, the new species is known from only two adult specimens, and its distribution seems to be restricted to a narrow limestone karst area in the province of Sa Kaeo in Thailand near the national border with Cambodia. Additional studies are required to understand its life history, distribution, and conservation status. The discovery of this new species brings the total number of known *Trimeresurus* to 51 species, 19 of which occur in Thailand, including five that are endemic to this country.

Keywords: limestone, morphology, molecular phylogeny, systematics, Sa Kaeo Province.

Introduction

The Asian pitviper genus *Trimeresurus* Lacépède, 1804 is a species-rich group of venomous snakes distributed across South and

Southeast Asia (Mirza *et al.* 2023; Vogel *et al.* 2022). The number of species within the genus has increased considerably in the recent past, largely due to increased sampling efforts and

integrative taxonomic revisions resolving some particularly problematic complexes of cryptic pitviper species in Southeast Asia (e.g., Vogel *et al.* 2023; Idiiatullina *et al.* 2023, 2024a–c). Currently, the genus *Trimeresurus* comprises 50 species after the recent description of *T. cyanolabris* Idiiatullina, Nguyen, Bragin *et al.*, 2024 (Uetz *et al.* 2025). This latter species belongs to the *T. kanburiensis* species complex of the subgenus *Trimeresurus*, distributed in Indochina and including limestone karst-specialized species and forest-dwelling species.

The rupicolous members of the *T. kanburiensis* complex are typically characterized by having a dark green or brown dorsum with a prominent pattern. According to Idiiatullina *et al.* (2024c), the rupicolous group of the complex currently includes six species, namely: *T. ciliaris* Idiiatullina, Pawangkhanant, Tawan *et al.*, 2023 (southern part of the Thai-Malay Peninsula), *T. honsonensis* (Grismer, Ngo & Grismer, 2008) (endemic to Hon Son Island, Vietnam), *T. kanburiensis* Smith, 1943 (endemic to Kanchanaburi Province, Thailand), *T. kraensis* Idiiatullina, Pawangkhanant, Suwannapoom *et al.*, 2024 (endemic to Chumphon Province, Thailand), *T. kuiburi* Sumontha, Suntrarachun, Pauwels *et al.*, 2021 (Prachuap Khiri Khan Province, Thailand), and *T. venustus* Vogel, 1991 (southern peninsular Thailand).

In contrast, forest-dwelling members of the *T. kanburiensis* complex (formerly referred to as the *T. macrops* complex) are typically characterized by having a uniform bright green unpatterned dorsum, and currently include four species, namely: *T. macrops* Kramer, 1977 (Thailand, Laos, and Cambodia), *T. cardamomensis* (Malhotra, Thorpe, Mrinalini & Stuart, 2011) (southwestern Cambodia, eastern Thailand, and the Phu Quoc Island of Vietnam), *T. cyanolabris* (southern and central Vietnam), and *T. rubeus* (Malhotra, Thorpe, Mrinalini & Stuart, 2011) (southern Vietnam and eastern Cambodia).

During recent fieldwork in the limestone karst area in the eastern part of Sa Kaeo Province, located in the southern part of eastern Thailand, we collected two specimens of pitviper of the genus *Trimeresurus* that were morphologically similar to other members of the *T. kanburiensis* species complex. A closer examination of the Sa Kaeo specimens revealed genetic and morphological differences that separate them from all other members of the genus. Therefore,

we here describe the Sa Kaeo population as a new species.

Material and methods

Sample collection. Fieldwork was carried out in Sa Kaeo Province, Thailand, in October 2024 by Parinya Pawangkhanant, Ton Smits, Ian Dugdale, and Andrew Pierce (Fig. 1, locality 1). Geographic coordinates and elevations were recorded using a Garmin GPSMAP 60CSx GPS receiver (USA) in datum WGS 84.



Figure 1. Distribution of the members of the *Trimeresurus kanburiensis* species complex in Indochina; numbers denote the type localities of each species: ¹*T. erythrochloris* sp. nov. (red): Thailand, Sa Kaeo Prov., Klong Hat Dist., Klong Kai Thuen Subdist., Tham Khao Siwa Cave; ²*T. kanburiensis* (orange): Thailand, Kanchanaburi Prov., Sai Yok Dist., Wat Tham, Phom Lo Khao Yai; ³*T. macrops* (neon green): Thailand, Bangkok; ⁴*T. cardamomensis* (yellow): Cambodia, Koh Kong Prov., Sre Ambel Dist., Cardamom Mountains; ⁵*T. rubeus* (ruby red): Cambodia, Mondolkiri Prov., O’Rang Dist., Seima BCA; ⁶*T. cyanolabris* (light blue): Vietnam, Ninh Thuan Prov., Ninh Hai Dist., Nui Chua NP; ⁷*T. honsonensis* (black): Vietnam, Kien Giang Prov., Hon Son Island; ⁸*T. kuiburi* (dark blue): Thailand, Prachuap Khiri Khan Prov., Kuiburi Dist., Wat Khao Daeng; ⁹*T. kraensis* (purple): Thailand, Chumphon Prov., Wat Tham Sanook; ¹⁰*T. venustus* (light pink): Thailand, Krabi Prov., Mueang Krabi Dist., Tiger Cave viewpoint; ¹¹*T. ciliaris* (dark green): Thailand, Trang Prov., Palian Dist., Tham Khao Ting.

Specimens were collected by means of snake hooks in the field, photographed in life, and euthanized using MS-222 solution within 24 hr of capture. Specimens were fixed in 4% buffered formalin for 24 h and later stored in 70% ethanol. Specimens were subsequently deposited in the herpetological collection of the Rabbit in the Moon Foundation (RIM, Ratchaburi, Thailand). Tissues for genetic analyses were taken from the liver or heart prior to specimen preservation and stored in 96% ethanol.

DNA isolation and sequencing. Total genomic DNA was extracted from ethanol-preserved muscle or liver tissue using standard phenol-chloroform extraction procedures (Sambrook *et al.* 1989), followed by isopropanol precipitation. We used polymerase chain reaction (PCR) to amplify three mitochondrial DNA (hereafter mtDNA) fragments: complete sequences of cytochrome *b* (*cyt b*), NADH dehydrogenase subunit 4 gene (ND4), and a fragment of 16S rRNA. Primers used for both PCR and sequencing of the *cyt b* gene included H14910 (forward, 5'-GACCTGTGATMTGAAAAACCA YCGTT-3'), THRSN2 (reverse, 5'-CTTTGGTT TACAAGAACAATGCTTTA-3') (from Dahn *et al.* 2018); for ND4: Trim-ND4F (forward, 5'-CA CCTATGACTACCAAAAGCTCATGTAGAGC -3'), Trim-ND4LEUR (reverse, 5'-CATTACTTT TACTTGGATTTGC ACCA-3') (from Salvi *et al.* 2013); and for 16S rRNA: 16S1LM (forward, 5'-CCGACTGTTGACCAAAAACAT-3'), 16SH 1 (reverse, 5'-TCCGGTCTGAACTCAGATCAC GTAGG-3') (from Green *et al.* 2010).

For *cyt b* sequences, we used the modified PCR protocol of Dahn *et al.* (2018) with the touchdown: (1) initial denaturation step at 94°C for 5 min; (2) 10 cycles of denaturation at 94°C for 1 min, annealing for 1 min with temperature decreasing from 50°C to 45°C (with a cool-down at 0.5°C per each cycle) and extension at 72°C for 1 min; (3) 24 cycles of denaturation at 94°C for 1 min, annealing at 45°C for 1 min, and extension at 72°C for 1 min; (4) final extension at 72°C for 10 min; and (5) cooling step at 4°C for storage. For ND4, we followed the protocol from Salvi *et al.* (2013): (1) an initial denaturation step at 92°C for 3 minutes, followed by 16 touchdown cycles with 30 seconds at 92°C; (2) an annealing temperature decreasing 0.5°C per cycle from 60°C to 52°C (30 seconds); and (3) an extension for 1 minute at 72°C. Then 20 more cycles similar to these, but with annealing temperatures stable at 52°C, followed. A final extension was carried out at 72°C for 15

minutes. For 16S rRNA, the PCR protocol followed Green *et al.* (2010): (1) initial denaturation step at 94°C for 5 min; (2) 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 1 min, and extension at 72°C for 1 min; (3) final extension at 72°C for 10 min; and (4) cooling step at 4°C for storage. All amplifications were run using an iCycler Thermal Cycler (Bio-Rad). PCR products were loaded onto 1% agarose gels in the presence of ethidium bromide and visualized by electrophoresis. The successful targeted PCR products were purified by the Diatom DNA PCR Clean-Up kit and outsourced to Evrogen® (Moscow, Russia) for sequencing; sequence data collection and visualization were performed on an ABI 3730xl Automated Sequencer (Applied Biosystems).

Molecular phylogenetic analysis. To reconstruct the mitochondrial genealogy of the genus *Trimeresurus*, we used the newly obtained *cyt b*, ND4, and 16S rRNA sequences for two specimens of *Trimeresurus* sp. from Sa Kaeo together with previously published sequences of all currently recognized members of the *T. kanburiensis* species complex (42 sequences of ten species in total), as well as representative sequences of 25 species of *Trimeresurus* covering all major lineages of the genus, and five sequences of other crotaline species of the genera *Peltopelor* and *Craspedocephalus* as the outgroups (for a discussion on the generic status of *Peltopelor* see Mirza *et al.* 2023); sequence of *Azemiops feae* Boulenger (Viperidae: Azemiopinae) was used to root the tree (summarized in Sup. Table 1).

We initially aligned the nucleotide sequences in MAFFT online (Katoh *et al.* 2019) with default parameters and subsequently checked them by eye in BioEdit 7.0.5.2 (Hall 1999) and adjusted them when required. The mean uncorrected genetic *p*-distances between sequences were calculated with MEGA 6.0 with the pairwise deletion option (Tamura *et al.* 2013) based on *cyt b* sequences of pitvipers of the subgenus *Trimeresurus*. The best-fit substitution models for the data set were selected for genes and codon positions using PartitionFinder 2.1.1 (Lanfear *et al.* 2012) with Akaike information criterion (AIC), which selected GTR+I+G for 16S, the first codon position of *cyt b*, and the first codon position of ND4; GTR+G for the third codon position of *cyt b*; GTR for the second codon position of ND4; HKY+I for the second codon position of *cyt b*; and HKY+I+G for the

third codon position of ND4. When the same model was proposed for different codon partitions of a given gene, they were treated as a single partition; this resulted in five partitions in total.

Phylogenetic trees were reconstructed for the concatenated mitochondrial DNA fragments (cyt *b*, ND4, and 16S rRNA) data set. We inferred the matrilineal genealogy of *Trimeresurus* using maximum likelihood (ML) and Bayesian inference (BI) approaches. We used the IQ-TREE online server (Nguyen *et al.* 2015) to generate the ML tree and assessed the confidence in tree topology by 1000 ultrafast-bootstrap replications (UFBS). We conducted BI in the terminal version of MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for 40 million generations and sampled every 40,000 generations. The run was checked to ensure the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v. 1.7 (Rambaut *et al.* 2018). We discarded the initial 1000 trees as burn-in. We assessed the confidence in tree topology by the posterior probability (PP) of the nodes (Huelsenbeck & Ronquist 2001). We *a priori* regard nodes with UFBS values of 95% or higher and PP values over 0.95 as strongly supported; UFBS values between 95% and 90% and PP values between 0.95 and 0.90 were regarded as well-supported, and lower values were regarded as a lack of node support (Minh *et al.* 2013).

Morphological description. Measurements and meristic counts describing external morphology followed Idiattullina *et al.* (2023, 2024a,c). 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: 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; SOL, supraocular length; SOW, supraocular width; DEL, distance lower eye margin-edge of the lip; DPN, distance between nostrils, taken with the caliper tips inserted into the nostrils; DETP, distance from the anterior edge of the eye to the posterior edge of the pit cavity; DEN, distance from anterior

margin of eye to the posterior margin of the nostril; WInN, width of internasals (means); L3SL, length of 3rd supralabial; H3SL, height of 3rd supralabial; H4SL, length of 4th supralabial.

Examined meristic characters include: CP, cloacal plate(s) (divided or single); ASR, anterior number of dorsal scale rows (at one HL behind the head); IL, number of infralabial scales; IOS, interorbital scales, counted along a row between the middle of supraocular scales; MSR, number of dorsal scale rows at midbody (at the level of the ventral plate corresponding to half of the SVL); PosOc, number of postocular scale(s); PSR, posterior number of dorsal scale rows (at one HL before the cloacal plate); PreV, number of preventrals (scales directly preceding the ventrals, unpaired, wider than long but not in contact on each side with the 1st dorsal scale row); SC, number of subcaudal scales, not including the terminal pointed scute; SL, number of supralabial scales; VEN, number of ventral scales (counted following Dowling 1951). Sex was determined by examination of the hemipenes that were forcedly everted by using water injection in the tail base prior to the preservation of the specimen.

Other abbreviations. BCA, Biodiversity Conservation Area; Dist., District; NP, National Park; Prov., Province; Subdist., Subdistrict.

Results

Sequence variation. A total of 2,296 (1,091 bp from cyt *b*, 690 bp from ND4, and 515 bp from 16S) aligned base pairs were obtained from the three mtDNA fragments, respectively. Protein-coding sequences were translated into amino acids to confirm that no pseudogenes had been amplified. The final alignment of the cyt *b* gene contained 1,091 nucleotides, of which 599 sites were conserved and 492 sites were variable, including 383 parsimony-informative sites. The transition-transversion bias (R) was estimated to 6.19; nucleotide frequencies were 30.09 % (A), 29.15 % (T), 30.15 % (C), and 10.60 % (G). The final alignment of the ND4 gene contained 690 nucleotides, of which 375 sites were conserved and 315 sites were variable, including 233 parsimony-informative sites. The transition-transversion bias (R) was estimated to 7.43; nucleotide frequencies were 32.78 % (A), 26.34 % (T), 29.71 % (C), and 11.14 % (G). The final alignment of the 16S rRNA gene contained 515 nucleotides, of which 401 sites were conserved and 113 sites were variable, including 74 parsimony-informative sites. The transition-

transversion bias (R) was estimated to 2.82; nucleotide frequencies were 35.95 % (A), 24.70 % (T), 21.43 % (C), and 17.93 % (G) (all data given for the ingroup only). We deposited the newly obtained sequences in GenBank under the accession numbers PQ658816–PQ658818 and PQ654051–PQ654052 (Sup. Table 1).

Phylogenetic relationships. The ML and BI analyses recovered trees with almost identical topologies; the nodes that were reconstructed differently mostly refer to deeper phylogenetic relationships inside the genus *Trimeresurus*, while in this study we only focus on the analysis of relationships within the *T. kanburiensis* species complex (Fig. 2). According to our matrilineal genealogy, the genus *Trimeresurus* is monophyletic (96/1.0; hereafter node support values are given for ML UFBS/BI PP, respectively), but the intrageneric relationships remain essentially not resolved; monophyly of all species-level groupings was strongly supported (100/1.0). The monophyly of the subgenera *Himalayophis*, *Popeia*, and *Parias* was supported in both analyses (97/0.95, 100/1.0, and 100/1.0, respectively), while the monophyly of *Viridovipera* received low values of node support (77/0.82). The monophyly of the subgenus *Trimeresurus* was not supported by both the ML and BI analyses (43/0.54); this subgenus included two strongly supported clades (100/1.0): the first one regrouping the species from the *T. albolabris* and *T. purpureomaculatus* complexes and the second one — the members of the *T. kanburiensis* species complex. Inside this latter clade, the relationships between species were generally well-resolved. *Trimeresurus ciliaris* was suggested as sister to all other members of the *T. kanburiensis* species complex, although with low values of node support (58/0.79). *Trimeresurus rubeus* and *T. cyanolabris* formed a well-supported clade (100/1.0) and comprised the sister lineage to the remaining species of the *T. kanburiensis* complex (98/1.0). Among the remaining species, *T. kanburiensis* formed the sister lineage to the remaining species of the complex (100/1.0), which were regrouped in two reciprocally monophyletic subclades. The first subclade (99/1.0) included *T. kuiburi*, *T. kraensis*, *T. macrops*, and *T. honsonensis*; the latter two species were strongly suggested as sister species (99/1.0). The second subclade (100/1.0) included *T. cardamomensis*, *T. venustus*, and the newly discovered population of *Trimeresurus* sp. from Sa Kaeo; the latter population was reconstructed

as a sister species of *T. venustus*, though with moderate values of node support (94/0.87).

Genetic distances. The uncorrected *p*-distances for the *cyt b* and ND4 gene fragments among the members of the *T. kanburiensis* complex examined here are presented in Table 1. Interspecific distances in the *cyt b* gene varied from *p* = 2.1% (between *T. cardamomensis* and *Trimeresurus* sp. from Sa Kaeo) to *p* = 9.3% (between *T. kraensis* and *T. ciliaris*). Interspecific distances in the ND4 gene varied from *p* = 2.0% (between *T. macrops* and *T. honsonensis*) to *p* = 10.9% (between *T. kraensis* and *T. ciliaris*). The newly discovered population from Sa Kaeo Province differs from its sister species *T. venustus* by a genetic distance of *p* = 2.7% in the *cyt b* gene and of *p* = 3.7% in the ND4 gene (Table 1).

Taxonomy

The results of our phylogenetic analysis were further corroborated by morphological examination, which uncovered stable differences between the newly discovered population of *Trimeresurus* sp. from Sa Kaeo Prov., Thailand, and other congeners. These results support our hypothesis that this recently discovered lineage of *Trimeresurus* represents an undescribed species, which we formally describe below. The new species is assigned to the subgenus *Trimeresurus* based on its phylogenetic position and the presence of partially fused first supralabial and nasal scales (Malhotra & Thorpe 2004 [as *Cryptelytrops*]; David *et al.* 2011).

Trimeresurus erythrochloris sp. nov.

[urn:lsid:zoobank.org:act:9054AFAB-EC8C-4054-8FEC-583729E2F2F9]

(Figs. 2–5; Table 2, Sup. Table 2)

Holotype. RIM-00078, an adult male from Tham Khao Siwa Cave (13.319°N, 102.332°E; alt. 250 m a.s.l.), Klong Kai Thuen Subdistrict, Klong Hat District, Sa Kaeo Province, Thailand collected by Parinya Pawangkhanant, Ton Smits, Ian Dugdale & Andrew Pierce on 7 Oct 2024.

Paratype (n=1). RIM-00079, an adult female with the same collection details as the holotype.

Diagnosis. The new species differs from other members of the subgenus *Trimeresurus* by the following combination of characters: dorsal scales in 23-21-15 rows, moderately keeled except the outermost rows, which are smooth; ventral scales 164–172; subcaudals 54–67, all paired; iris golden yellow in both sexes; body

dorsally grass green with irregular, serrated, reddish-brown transverse markings; suborbital stripe white and wide in male, absent in female; ventrolateral stripe distinct, present on the first few dorsal scale rows, white and red in male, white in female; throat, chin, and lower labials

light turquoise; ventral surfaces pale blue in male, pale green in female; tail dorsally light brick-red mottled with dark spots, ventrally with irregular white markings; hemipenis with well-developed pointed almost spine-like papillae at its base.



Trimeresurus (Trimeresurus) erythrochloris sp. nov.

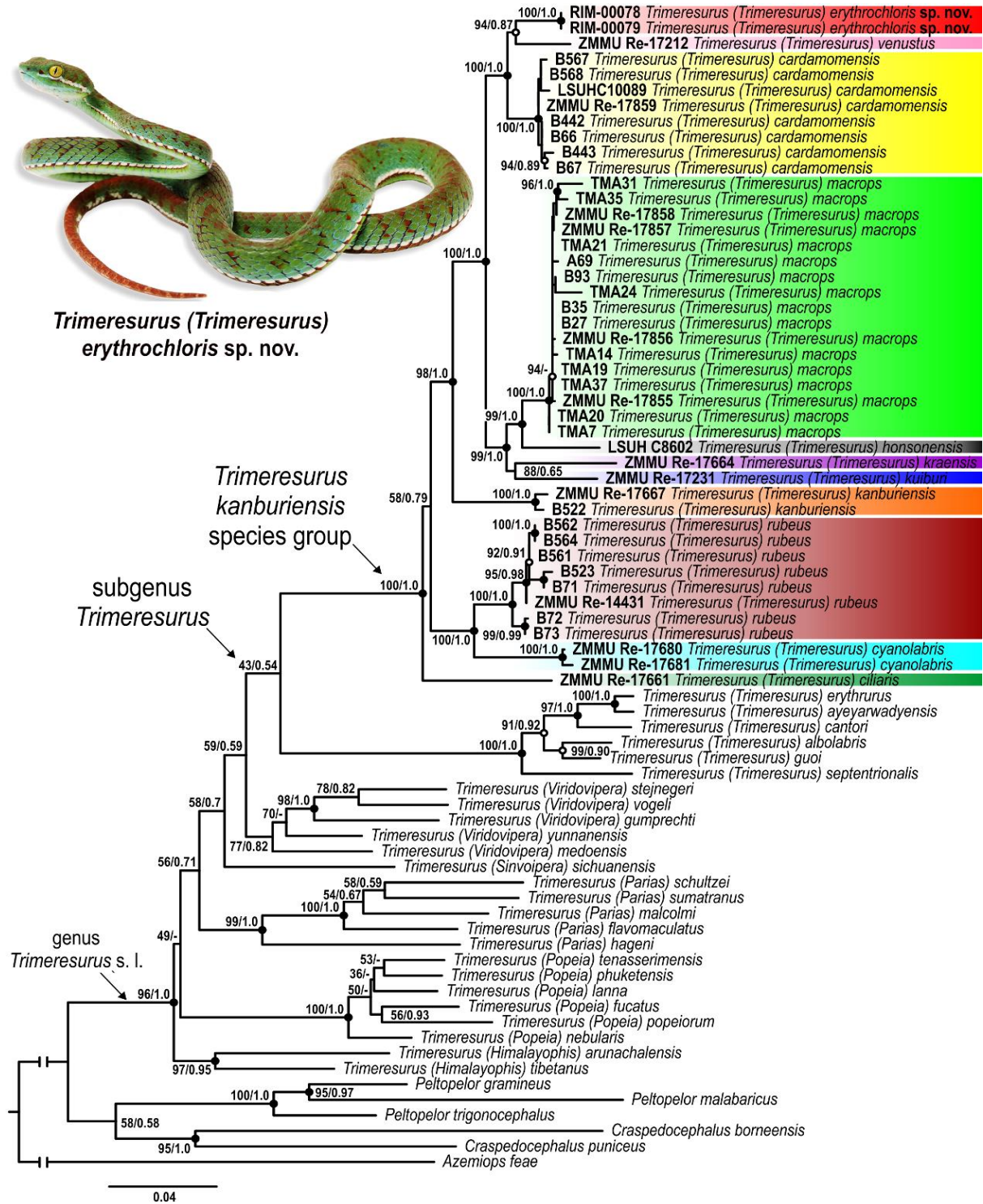


Figure 2. Maximum Likelihood (ML) phylogenetic tree of *Trimeresurus* derived from the analysis of 2,296 bp of cyt b, ND4, and 16S rRNA mitochondrial DNA gene sequences. Numbers at the nodes correspond to ML UFBS/BI PP support values, respectively. Colors of clades and locality numbers correspond to those on the map in Fig 1. © Photo: P. Pawangkhanant.

Table 1. Uncorrected *p*-distances (percentage) between the sequences of *cyt b* mtDNA gene (below the diagonal) and between the sequences of ND4 mtDNA gene (above the diagonal) of species of the subgenus *Trimeresurus* included in the phylogenetic analyses. Intraspecific genetic distances shown on the diagonal in bold are given in the *cyt b* / ND4 order, – = no data.

Species	1	2	3	4	5	6	7	8	9	10	11
1 <i>T. erythrochloris</i> sp. nov.	0/0	3.7	2.6	4.5	3.5	5.9	5.7	6.2	8.0	8.6	8.0
2 <i>T. venustus</i>	2.7	–	4.1	6.1	4.7	7.1	7.3	7.5	9.5	9.7	8.7
3 <i>T. cardamomensis</i>	2.1	3.2	–/0.2	4.9	2.8	6.6	6.5	6.7	8.0	8.6	9.1
4 <i>T. macrops</i>	3.8	4.7	4.4	0.2/0.1	2.0	5.8	4.3	7.2	7.5	8.3	8.2
5 <i>T. honsonensis</i>	4.5	5.8	4.7	3.3	–	5.6	4.7	6.0	6.9	7.7	8.0
6 <i>T. kraensis</i>	5.6	5.9	5.5	5.4	5.6	–	6.6	9.3	9.4	9.3	10.9
7 <i>T. kuiburi</i>	4.7	5.3	5.1	4.5	4.7	5.1	–	7.9	7.8	7.9	8.5
8 <i>T. kanburiensis</i>	5.1	7.2	5.3	6.5	6.7	7.5	7.5	–/0.4	7.4	6.9	7.2
9 <i>T. rubeus</i>	5.9	7.1	6.4	6.7	6.9	8.0	7.7	7.7	–/0.9	3.8	7.5
10 <i>T. cyanolabris</i>	7.1	8.0	6.9	8.1	8.0	8.5	8.7	7.9	6.4	0.3/0.2	7.6
11 <i>T. ciliaris</i>	7.2	8.8	7.4	7.8	7.9	9.3	8.7	9.2	8.0	8.0	–

Description of the holotype. Adult male, specimen in a good state of preservation. Body cylindrical, long, and thin (SVL 425 mm, TaL 110 mm, TL 535 mm; TaL/TL ratio 0.21). Head triangular in dorsal view, elongate, clearly distinct from the neck (HL 20.9 mm, HW 14.4 mm; HW/HL ratio 0.69). Snout elongated, flattened, and rounded in dorsal view, rather rectangular in lateral view, with a very distinct and sharp canthus rostralis; loreal region concave. Eyes large (ED 3.5 mm, DEL 5.3 mm; ED/EN ratio 0.66). Rostral barely visible in dorsal aspect, triangular. Pupil vertically elliptical, loreal pit present, located closer to eye than to nostril, triangular in shape. Nostril completely enclosed in nasal scale; nasal scale partially fused with first supralabial. Shield bordering the anterior edge of the loreal pit fused with second supralabial, forming a tall vertical scale. Subocular long, thin, crescent-like, separated from the 4th and 5th supralabials by one row of scales and separated from the 6th supralabial by 2/2 scales. Three preoculars on each side of the head; two upper preoculars located above the loreal pit, elongate, in contact with the single loreal, which separates them from the nasal; lower preocular forming the lower margin of the loreal pit, lower preocular in contact with third and second supralabials. A small scale between nasal and second supralabial; 2/2 postoculars; 10/10 supralabials, third the largest; 12/12 infralabials, those of the first pair in contact with each other behind the mental; the first three pairs of infralabials in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields

and the first preventral. One large pair of enlarged internasals, in contact; one large supraocular. Scales on snout and in the interorbital region smooth, irregular, subimbricate; temporal and occipital scales feebly keeled. Dorsal scales in 23–21–15 rows, moderately keeled, except the first row, on which scales are smooth. Two preventrals and 164 ventrals. Cloacal plate single; 67 subcaudals, all divided.

We failed to fully evert the hemipenial organs of the holotype. Partially everted hemipenis reaches the level of 6th–7th subcaudal without signs of bifurcation; it is likely that the organ is elongated and bifurcating as in the other members of the subgenus *Trimeresurus*. The sulcus spermaticus, shallow, is not divided on the everted part of the organ. The proximal half of the everted part of the hemipenis feebly calyculate; the distal half of the everted part of the organ covered with well-developed dense pointed almost spine-like papillae.

Coloration. In life (Based on Fig. 3), body dorsally bright grass green with 67 irregular serrated transverse reddish-brown markings, 1–2 scales wide in the middle of the dorsum, continuing to body flanks where they get thinner, ca. 1 scale wide, not reaching the ventrals. A prominent ventrolateral stripe, white dorsally, brick-red ventrally, running from the neck along the body to tail base, covering two lateral-most dorsal scale rows. Tail light brick-red, dorsally the red coloration extending as far as the vent level, laterally with faint reddish-brown markings; laterally and ventrally tail with distinct white markings, each approximately one scale in

width. Ventral surfaces of the body pale blue anteriorly, getting bluish-green posteriorly. Head dorsally grass green with indistinct brown spots; the lateral surface of the head with distinct white suborbital stripe, ca. 1.0–1.5 scales wide, starting from the lower preocular scale under the loreal pit, continuing under the eye posteriorly to the postocular and ventrolateral stripe; ventrally and dorsally the subocular / postocular stripe edged with a few dark-red blotches; supralabials, infralabials, chin, and throat regions light turquoise. Iris bright golden yellow.

Variation. The main meristic and morphometric characters of the type specimens of *T. erythrochloris* sp. nov. are summarized in Table 2; color variation of the name-bearing types is presented in Figs. 3 and 4. The paratype RIM-00078 (adult female) is larger than holotype (SVL 545 mm, TaL 105 mm, TL 650 mm, TaL/TL 0.16), VEN 172, SC 54; dorsal body coloration is bright grass green with indistinct reddish-brown transverse markings (Fig. 4A); suborbital and postocular stripe absent (Fig. 4C, 4D); ventrolateral stripe present, white, lacking red markings, with few brown spots ventrally; ventral surfaces pale green, getting brighter posteriorly (Fig. 4B).

Table 2. Morphological data of *Trimeresurus erythrochloris* sp. nov. holotype and paratype; M = male, F = female.

Collection number	RIM 00078	RIM 00079
Type status	Holotype	Paratype
Sex	M	F
SVL (mm)	425	545
TaL (mm)	110	105
HL (mm)	20.9	27.1
HW (mm)	14.4	19.3
HD (mm)	12.4	12.6
SnL (mm)	6.8	7.5
ED (mm)	3.5	3.3
Internasals	in contact	in contact
Fusion of Nasal & 1st SL	partially	partially
IOS	12	11
PosOc	2	2
SL	10-10	10-10
IL	12-12	12-12
ASR	23	23
MSR	21	21
PSR	15	15
VEN	164	172
SC	67	54
Suborbital stripe	present	absent
No. of bands on dorsum	67	58

Etymology. The species name “*erythrochloris*” is a Latinized adjective in the nominative singular, masculine gender, derived from the classical Greek adjective *eruthros* (ἐρυθρός), “*erythros*”, meaning “red”, and from the adjective *chloros* (χλωρός), “*chloris*”, meaning “green”. The species name is given in reference to the beautiful dorsal coloration of the new species, which consists of red bands on the green background. We suggest the following common names for the new species: “*Ngu Khiew Hang Mai Lai Yhak*” (งูเขียวหางไหม้ลายหยัก) (in Thai), “*Red-barred Green Pitviper*” (in English), and “*Krasno-zelenaya bambukovaya kufiya*” (Красно-зеленая бамбуковая куфия) (in Russian).

Comparison. The new species is phylogenetically placed within the subgenus *Trimeresurus* and is morphologically most similar to other green forest-dwelling pitviper species of the *T. kanburiensis* complex (including: *T. cardamomensis*, *T. cyanolabris*, *T. macrops*, and *T. rubeus*), and in lesser degree to the rupicolous species of the *T. kanburiensis* complex (including: *T. ciliaris*, *T. honsonensis*, *T. kraensis*, *T. kanburiensis*, *T. kuiburi*, and *T. venustus*); therefore, morphological comparison with these ten species appear to be the most pertinent. The main diagnostic characters separating *T. erythrochloris* sp. nov. from these ten species are given in Sup. Table 2.

Comparison with *T. kanburiensis* complex (forest-dwelling species). *Trimeresurus erythrochloris* sp. nov. differs from *T. macrops* by having: dorsal color and pattern (grass green with reddish-brown transverse markings vs. uniformly bluish-green, grass green or yellow-green lacking red markings); ventrolateral stripe color (red and white vs. green and white); and tail color and pattern (light brick-red mottled with brownish spots and distinct white markings vs. dull brick red with a clear margin on lateral side of tail).

The new species differs from *T. rubeus* by having: higher number of ventrals in females (VEN 172 vs. 158–163); lower number of subcaudals in males (SC 67 vs. 78–80); dorsal color and pattern (grass green with reddish-brown transverse markings vs. uniformly bluish green, grass green or yellow-green); and iris color (golden yellow vs. bright or deep reddish-orange).

The new species differs from *T. cardamomensis* by having: slightly higher

Plate 1

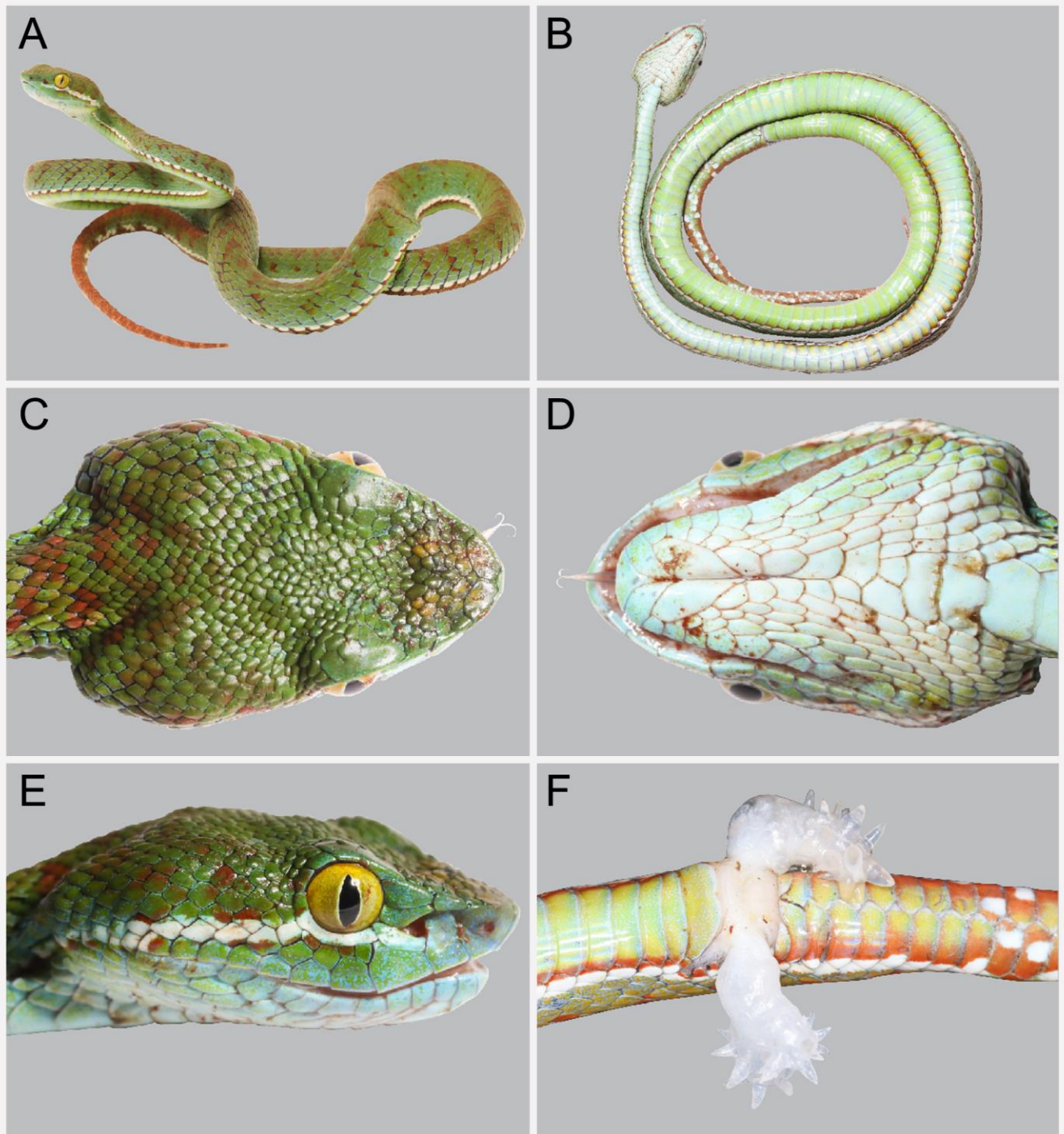


Figure 3. *Trimeresurus erythrochloris* sp. nov. adult male in life (RIM-00078, holotype): (A) Dorsolateral and (B) ventral views of body; (C) dorsal, (D) ventral, and (E) lateral (right) views of the head; and (F) left and right hemipenis; © Photo: P. Pawangkhanant

Plate 2

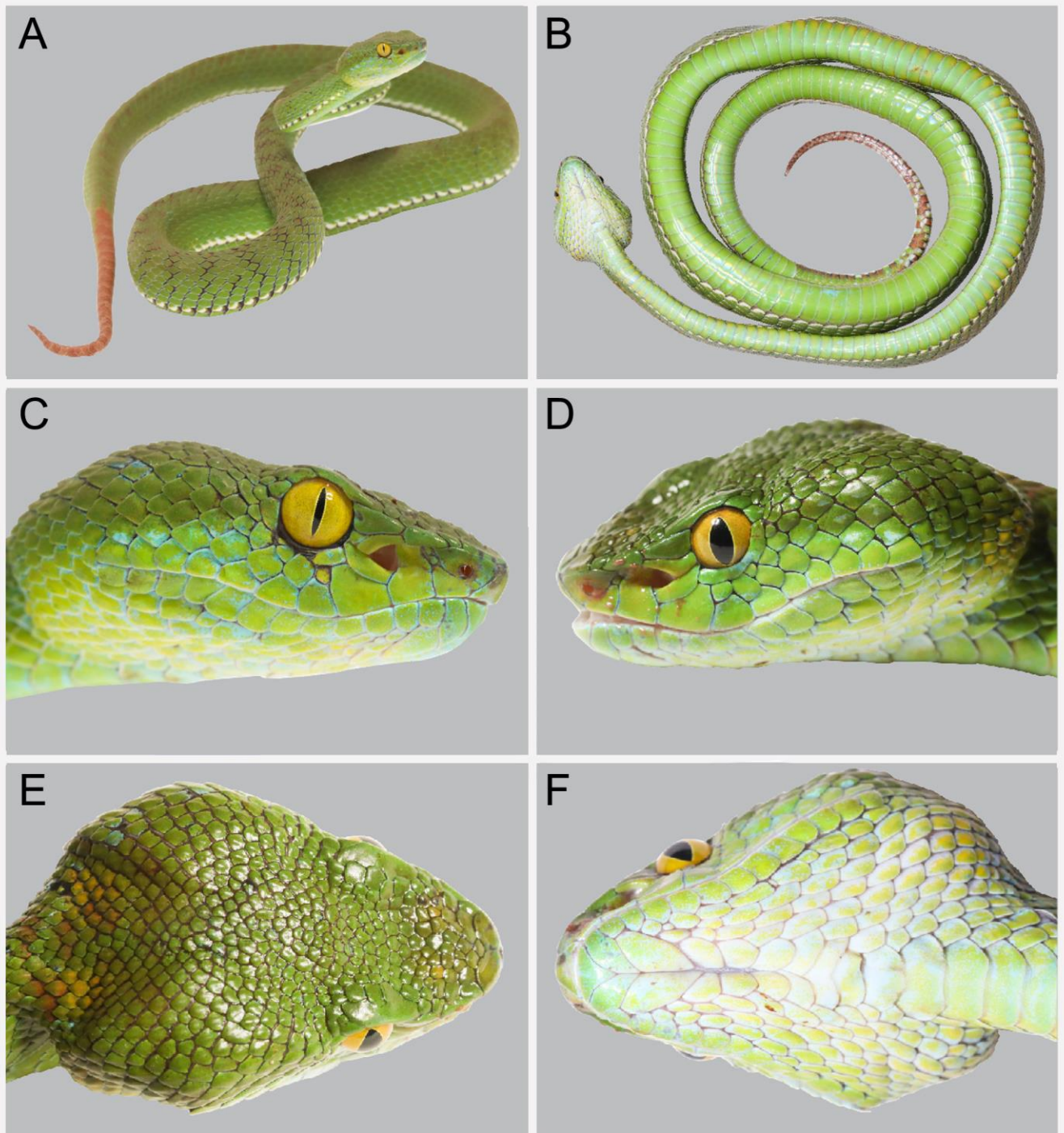


Figure 4. *Trimeresurus erythrochloris* sp. nov. adult female in life (RIM-00079, paratype) (A) Dorsolateral and (B) ventral views of body; (C) lateral (right), (D) lateral (left), (E) dorsal, and (F) ventral views of the head; © Photo: P. Pawangkhanant

TaL/TL ratio in males (0.21 vs. 0.17–0.20); slightly lower number of subcaudals in females (SC 54 vs. 58–63); dorsal color and pattern (grass green with reddish-brown transverse markings vs. uniformly bluish-green, grass green or yellow-green); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. dark brick red, reaching to ca. one-third (males) to half (females) distance to the vent on ventral surface).

The new species differs from *T. cyanolabris* by having: greater TaL/TL ratio in female (0.16 vs. 0.13–0.15); lower number of ventrals in male (VEN 164 vs. 166–175); lower number of subcaudals in male (SC 67 vs. 71–75); the presence of subocular streak in males (vs. absence); the presence of a distinct white and red ventrolateral body stripe (vs. indistinct or thin white stripe); and dorsal color and pattern (grass green with reddish-brown transverse markings vs. uniformly bluish green, grass green or yellow-green).

Comparison with *T. kanburiensis* complex (rupicolous species). The new species differs from *T. ciliaris* by having: higher TaL/TL ratio in both sexes (0.21 in male, 0.16 in female vs. 0.17 in males, 0.13 in female); higher number of ventrals in males (VEN 164 vs. 172–175); higher number of subcaudals in males (SC 67 vs. 59–63); higher number of midbody scale rows (MSR 21 vs. 17); dorsal color and pattern (grass green with reddish-brown transverse markings vs. emerald-green with reddish brown bands); the presence of subocular streak in males (vs. absence); the presence of ventrolateral body stripe (vs. absence); iris color (golden yellow vs. olive-green with faded brown horizontal stripe); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. dark brown mottled with rusty markings).

The new species differs from *T. honsonensis* by having: lower TaL/TL ratio in male (0.21 vs. 0.23); lower number of ventrals in both sexes (VEN 164 in male, 172 in female vs. 186 in male, 183–186 in females); dorsal color and pattern (grass green with reddish-brown transverse markings vs. straw-yellow with zig-zagged irregular dark-brown bands); the presence of subocular streak in males (vs. absence); the presence of ventrolateral body stripe (vs. absence); ventral coloration (pale blue or green vs. dull-white anteriorly becoming progressively darker posteriorly); iris color (golden yellow vs.

orange in the center and brown at periphery); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. orange with irregular dark bands).

The new species differs from *T. kanburiensis* by having: lower TaL/TL ratio in both sexes (0.21 in male, 0.16 in female vs. 0.17 in male, 0.14–0.15 in females); lower number of ventrals in male (VEN 164 vs. 172); higher number of subcaudals in male (SC 67 vs. 59); higher number of midbody scale rows (MSR 21 vs. 19); dorsal color and pattern (grass green with reddish-brown transverse markings vs. olive-gray with dark olive-brown bands); the presence of subocular streak in males (vs. absence); the presence of ventrolateral body stripe (vs. absence); ventral coloration (pale blue or green vs. creamy white); iris colour (golden yellow vs. brownish); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. brownish-gray with olive-brown blotches).

The new species differs from *T. kraensis* by having: higher TaL/TL ratio in males (0.21 in male, 0.16 in female vs. 0.17 in male, 0.14–0.15 in females); slightly higher number of subcaudals in male (SC 67 vs. 62); dorsal color and pattern (grass green with reddish-brown transverse markings vs. bottle green with transverse purple bands); the presence of subocular streak in males (vs. absence); ventral coloration (pale blue or green vs. pale creamish-green); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. brown with dark purplish-brown crossbars).

The new species differs from *T. kuiburi* by having higher TaL/TL ratio in both sexes (0.21 in male, 0.16 in female vs. 0.17–0.19 in males, 0.13–0.14 in females); slight higher number of subcaudals in males (SC 67 vs. 63–65); higher number of midbody scale rows (MSR 21 vs. 19); dorsal color and pattern (grass green with reddish-brown transverse markings vs. bottle green with purple bands); the presence of ventrolateral body stripe (vs. absence); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. red with few thin lighter bands).

The new species differs from its sister species *T. venustus* by having: lower TaL/TL ratio in both sexes (0.21 in male, 0.16 in female vs. 0.16–0.19 in males, 0.14–0.15 in females);

slightly lower number of ventrals in both sexes (VEN 164 in male, 172 in female vs. 166–175 in males, 173–181 in females); higher number of midbody scale rows (MSR 21 vs. 19); dorsal color and pattern (grass green with reddish-brown transverse markings vs. dark bottle green with purple bands); the presence of ventrolateral body stripe (vs. absence); iris colour (golden yellow vs. yellowish-brown); and tail color and pattern (light brick-red reaching the vent level mottled with brownish spots and distinct white markings vs. brown with dark purplish-brown crossbars).

Furthermore, among the other superficially similar species of the subgenus *Trimeresurus*, the new species can be readily distinguished from: *T. fasciatus* (Boulenger), *T. labialis* Fitzinger in Steindachner, *T. mutabilis* Stoliczka by dorsal coloration and pattern (grass green with reddish-brown transverse markings vs. reddish-brown or purple or dark olive-brown bands on olive-greyish background). *Trimeresurus erythrochloris* sp. nov. can be distinguished from *T. andersoni* Theobald, *T. ayeerwadyensis* Chan, Anuar, Sankar, Law, Law, Shivaram, Christian, Mulcahy & Malhotra, *T. cantori* (Blyth), *T. erythrurus* Cantor, and *T. purpureomaculatus* by lower number of midbody dorsal scale rows (MSR 21 vs. 23–25 in *T. andersoni* and *T. ayeerwadyensis*, 25–29 in *T. cantori*, 23 (rarely 24, 25) in *T. erythrurus*, 25 (rarely 27, 29) in *T. purpureomaculatus*). The new species can be further distinguished from: *T. caudornatus* Chen, Ding, Vogel & Shi, *T. davidi* Chandramouli, Campbell & Vogel, *T. guoi*, *T. insularis* Kramer, *T. salazar* Mirza, Bhosale, Phansalkar, Sawant, Gowande & Patel, *T. septentrionalis* Kramer, *T. uetzi* Vogel, Nguyen & David by having light turquoise throat, chin and lower labials (vs. creamy or white); by relatively larger size of the eye, and by the relatively wider supraoculars (see Vogel *et al.* 2023; Nguyen *et al.* 2024 for details).

Distribution and natural history. Currently, *T. erythrochloris* sp. nov. is known only from a narrow, isolated chain of limestone hills in Khlong Hat District, Sa Kaeo Province, Thailand (Fig. 1, locality 1). This limestone karst range runs along the national border of Thailand and Cambodia and continues partly into Chantaburi Province of Thailand, as well as across the border into the Phnom Preaek Mountain Range in the northwestern part of Battambang Province, Cambodia, where the occurrence of the new species in karst formations can be expected.

Trimeresurus erythrochloris sp. nov. was recorded at relatively low elevations (from ca. 200 to 300 m a.s.l.); the surrounding habitat consists of lowland mixed semi-deciduous monsoon tropical forests. The new species is semi-arboreal and nocturnal; both specimens were found between 20:00 and 01:00 hr after rain on a low bush close to the ground (Fig. 5). One juvenile female (not collected) was observed ambushing on the branch close to the karst area. Another individual was found moving on a limestone rock near a cave entrance, whilst several individuals (not collected) were found on small saplings and dead fallen branches in areas with no limestone rocks, up to 400 m away from the nearest rock outcrops. All individuals sat with their heads oriented downward, close to the forest floor, presumably waiting for terrestrial prey to pass (Fig. 5).

Other species of amphibians and reptiles in the same habitat at the type locality during the survey included *Ahaetulla prasina* (Boie), *Lycodon capucinus* (Boie), *Oligodon fasciolatus* (Günther), *Pareas margaritophorus* (Jan), *Psammodynastes pulverulentus* (Boie), *Naja* sp., *Cyrtodactylus khlonghatensis* Ampai, Rujirawan, Yodthongm Termprayoon, Stuart & Aowphol, *Gekko gekko* (Linnaeus), *Gehyra* sp., and *Cnemaspis* sp., *Cyclemys atripons* Iverson & McCord, *Kaloula pulchra* Gray, *Duttaphrynus melanostictus* (Schneider), and *Occidozyga martensii* Peters. Nothing is known about the diet, reproductive biology, or venom of the new species.



Figure 5. Habitat of *Trimeresurus erythrochloris* sp. nov. (in life) at the type locality in Klong Hat, Sa Kaeo, Thailand. © Photo: T. Smits.

Conservation status. Though *T. erythrochloris* sp. nov. appears to be locally common with up to 10 individuals observed during one night survey, it seems that the new species is quite elusive and is only active after heavy rains. Seemingly the quite narrow distribution of the new species makes it vulnerable to habitat degradation. Therefore, the main threat to the new species is habitat loss. As *T. erythrochloris* sp. nov. is a brightly colored species of pitviper, it can also be subjected to illegal pet trade. Further efforts are needed to accurately estimate the extent of the distribution of this new species and possible threatening factors. Therefore, at present, we tentatively suggest that *Trimeresurus erythrochloris* sp. nov. should be considered as Data Deficient (DD) following the IUCN's Red List categories (IUCN 2019).

Discussion

Our understanding of the diversity of the *T. kanburiensis* complex has significantly changed during the last several years. Before 2011, only four species were recognized, namely *T. macrops* sensu lato (which encompassed all forest-dwelling populations of the complex and was not placed in the *T. kanburiensis* complex at that time) and three rupicolous species: *T. kanburiensis*, *T. venustus*, and *T. honsonensis* (Poyarkov et al. 2023). Malhotra et al. (2011) revised *T. macrops* sensu lato and described two new forest-dwelling species: *T. rubeus* and *T. cardamomensis*. In the past three years, different teams of authors described three more limestone-dwelling species: *T. kuiburi*, *T. ciliaris*, and *T. kraensis* (Sumontha et al. 2021, Idiatullina et al. 2023, 2024a) and one new forest-dwelling species, *T. cyanolabris* (Idiatullina et al. 2024c). The discovery of *T. erythrochloris* sp. nov. brings the total number of the *T. kanburiensis* complex members to 11 and is quite remarkable from a biogeographic point of view. Apart from the presence of red markings on the dorsum, morphologically *T. erythrochloris* sp. nov. closely resembles *T. cardamomensis*, a forest-dwelling, uniformly green-colored species, which is widely distributed in the mountains of eastern Thailand and southwest Cambodia, in close proximity to the type locality of the new species (ca. 30 km direct distance, see Fig. 1). However, the putative sister species of *T. erythrochloris* sp. nov. is a karst-dwelling species, *T. venustus*, which occurs in the southern part of Peninsular Thailand on the

opposite side of the Gulf of Siam (see Fig. 1). A similar pattern of range disjunction was recently reported for geckoes of the *Cyrtodactylus intermedius* species group, most members of which inhabit southern Indochina and the offshore islands of the Gulf of Siam, and one limestone-adapted species was recently discovered in southern Peninsular Thailand (Grismer et al. 2023). This adds to a growing body of evidence that suggests a trans-Gulf of Siam phylogenetic connection across the submerged Sunda Shelf between the southern Thai-Malay Peninsula and southern Indochina (Grismer & Grismer 2017; Grismer et al. 2019, 2020, 2022, 2023; Chen et al. 2018; Sheridan & Stuart 2018; Nurngsomsri et al. 2019; Poyarkov et al. 2019, 2021, 2023, and the references therein).

The Kingdom of Thailand has a high degree of endemism and the highest diversity of *Trimeresurus* pitvipers in the world, with 18 species currently reliably recorded in the country, namely: *T. albolabris* (Gray, 1842), *T. cardamomensis*, *T. ciliaris*, *T. gumprechtii* David, Vogel, Pauwels & Vidal, 2002, *T. guoi* Chen, Shi, Vogel & Ding, 2021, *T. hageni* (Lidth De Jeude, 1886), *T. kanburiensis*, *T. kraensis*, *T. kuiburi*, *T. lanna* Idiatullina, Nguyen, Pawangkhanant et al., 2024, *T. macrops*, *T. phuketensis* Sumontha, Kunya, Pauwels et al., 2011, *T. purpureomaculatus* (Gray, 1832), *T. sabahi* Regenass & Kramer, 1981, *T. sumatranus* (Raffles, 1822), *T. tenasserimensis* Idiatullina, Nguyen, Pawangkhanant et al., 2024, *T. venustus*, and *T. vogeli* David, Vidal & Pauwels, 2001 (Poyarkov et al. 2023; Idiatullina et al. 2023, 2024a,b). Among them, there are four species currently considered endemic to Thailand namely: *T. kanburiensis*, *T. kraensis*, *T. kuiburi*, and *T. phuketensis*. It should be noted that the existing records of *T. nebularis* Vogel, David & Pauwels, 2004 from the southernmost peninsular Thailand are likely based on a misidentification with *T. sabahi* (see Poyarkov et al. 2023 for details). The discovery of *T. erythrochloris* sp. nov. brings the total number of *Trimeresurus* known to occur in Thailand to 19, and the number of endemic *Trimeresurus* species to five.

From the natural history perspective, *T. erythrochloris* sp. nov. is also quite peculiar as it demonstrates ecomorphology that is likely intermediate between the typical forest-dwelling and karst-adapted *Trimeresurus* species. Moreover, though the distribution of the new

species is restricted to karstic limestone areas, most specimens were observed while perching on saplings or bushes inside the forest, often quite far from the nearest limestone outcrops (Fig. 5). The recent papers by Mirza *et al.* (2023) and Idiiatullina *et al.* (2023, 2024a-c) based on the results of molecular phylogenetic analyses demonstrated that the karst-dwelling and forest-dwelling members of the *T. kanburiensis* complex are intermixed with each other and together form a distinct clade within the subgenus *Trimeresurus*. The systematic status of this clade will be discussed elsewhere in the frame of a revision of the whole genus *Trimeresurus* sensu lato, which currently includes six recognized subgenera (see Malhotra & Thorpe 2004; Mirza *et al.* 2023; Idiiatullina *et al.* 2023, 2024a-c). The non-monophyly of the formerly recognized forest-dwelling *T. macrops* complex with respect to the rupicolous species of the *T. kanburiensis* complex was for the first time demonstrated by Mrinalini *et al.* (2015) and later corroborated by the phylogenetic data of Idiiatullina *et al.* (2023, 2024a,c). Overall, our new data further underline the complicated evolutionary history of this group, which likely included numerous shifts between different morphotypes and habitat preferences in this radiation of pitvipers (see Sanders *et al.* 2004).

Fragmented karstic islands and archipelagos stretching across Indochina have served as foci for the independent evolution of highly diverse and endemic herpetofauna (e.g., Suwannapoom *et al.* 2018; Grismer *et al.* 2021; Poyarkov *et al.* 2021, 2023; Sithivong *et al.* 2023; Pawangkhanant *et al.* 2024). The description of *T. erythrochloris* sp. nov. continues to underscore the fact that limestone karstic habitats support an ever-increasing number of site-specific endemics that compose much of the herpetological diversity in Southeast Asia (e.g., Luu *et al.* 2016; Tolentino *et al.* 2020; Poyarkov *et al.* 2021, 2023). Unfortunately, karst habitats are some of the most imperiled ecosystems on the planet due to unregulated and unsustainable quarrying practices (Clements *et al.* 2006), and only 1% of these landscapes throughout Asia are afforded any form of legal protection (Grismer *et al.* 2023). Sadly, the immense financial returns from cement manufacturing render the challenge of karst conservation nearly insurmountable, and the continued exploitation of karstic habitats for limestone shows no signs of slowing down (Tolentino *et al.* 2020). Further investigations are required to elucidate the distribution, diet,

reproductive biology, population size, population trends, and conservation status of the new species.

Author contributions

P. Pawangkhanant: review & editing, writing original draft, visualization, validation, resources, investigation, conceptualization; S.S. Idiiatullina: review & editing, writing original draft, visualization, validation, software, resources, methodology, investigation, formal analysis, data curation, conceptualization; T. Smits: review & editing, visualization, validation, resources, investigation; I. Dugdale: review & editing, visualization, validation, resources, investigation; A. Pierce: review & editing, visualization, validation, resources, investigation; C. Suwannapoom: review & editing, validation, supervision, resources, project administration, funding acquisition; N.A. Poyarkov: review & editing, writing original draft, visualization, validation, supervision, software, resources, project administration, methodology, investigation, funding acquisition, formal analysis, data curation, conceptualization.

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Research permits

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 compliant 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).

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Supplemental data

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