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A redescription and range extension of *Trimeresurus caudornatus* Chen, Ding, Vogel & Shi, 2020 (Serpentes: Viperidae)

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Abstract

The pitviper species *Trimeresurus caudornatus* was recently described based on only two specimens from Nabang Town, Yingjiang County, Yunnan Province, China. Here, we provide additional data on this species based on a re-examination of 19 preserved specimens, 16 specimens reported in earlier literature sources, and additional photo-documented records from northern Myanmar (Burma) and adjacent China. All new specimens were previously identified as *Trimeresurus albolabris* sensu lato or *Trimeresurus septentrionalis* sensu lato. Molecular analyses based on mitochondrial DNA supported the morphological findings in establishing conspecificity with *T. caudornatus*. The newly identified specimens have a pairwise distance of only 0.4–2.6% from those of the type series of *T. caudornatus* (based on the cytochrome *b* gene). Based on these findings, we confirm the presence of *T. caudornatus* from Myanmar and update its diagnostic characters and distribution. We suggest the species should be considered as Least Concern (LC) following the IUCN's Red List categories. Further studies reassessing the populations of the *Trimeresurus albolabris* complex are required.

Key words: morphology, Myanmar, new record, phylogeny, taxonomy, *Trimeresurus albolabris*, *T. salazar*

Introduction

Asian pit vipers of the genus *Trimeresurus* Lacépède, 1804 represent one of the most widespread and diverse radiations of medically significant venomous snakes, with 53 species currently recognized (Mirza *et al*. 2023; Chan *et al*. 2023; Idiiatullina *et al*. 2023, 2024a-c). Members of *Trimeresurus* have a broad distribution, extending from northeast India and Nepal in the west, to China and the Lesser Sunda Islands in the east and south-east (Gumprecht *et al*. 2004; Vogel, 2006; Poyarkov *et al*. 2023; Uetz *et al*. 2024). The taxonomic diversity of the genus *Trimeresurus* remains both underestimated and controversial, in part because many taxa are morphologically similar to one another.

The systematics of the *Trimeresurus albolabris* species complex is especially intricate (Vogel *et al*. 2023). This complex of species is widely distributed across the Indo-Himalayan region of India and Nepal, the southern-half of

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China, and the majority of Southeast Asia. Members of this complex are characterized by the combination of a long papillose or calyculate hemipenis, a first supralabial partially or totally fused with nasal scale, uniform green dorsal colouration, a lateral stripe present on the first few dorsal scale rows in one or both sexes, relatively small eyes, supraoculars narrower than the internasals, and an elongate oval-shaped head in lateral profile (Regenass & Kramer, 1981; Malhotra & Thorpe, 2004; Malhotra *et al*. 2011; Vogel *et al*. 2022, 2023). Throughout the past two decades, several pit vipers related to *T. albolabris* have been elevated to species rank or described as new species (Zhu *et al*. 2016; Chen *et al*. 2020, 2021; Mirza *et al*. 2020, 2023). However, the exact distributional limits between many of these species are poorly understood.

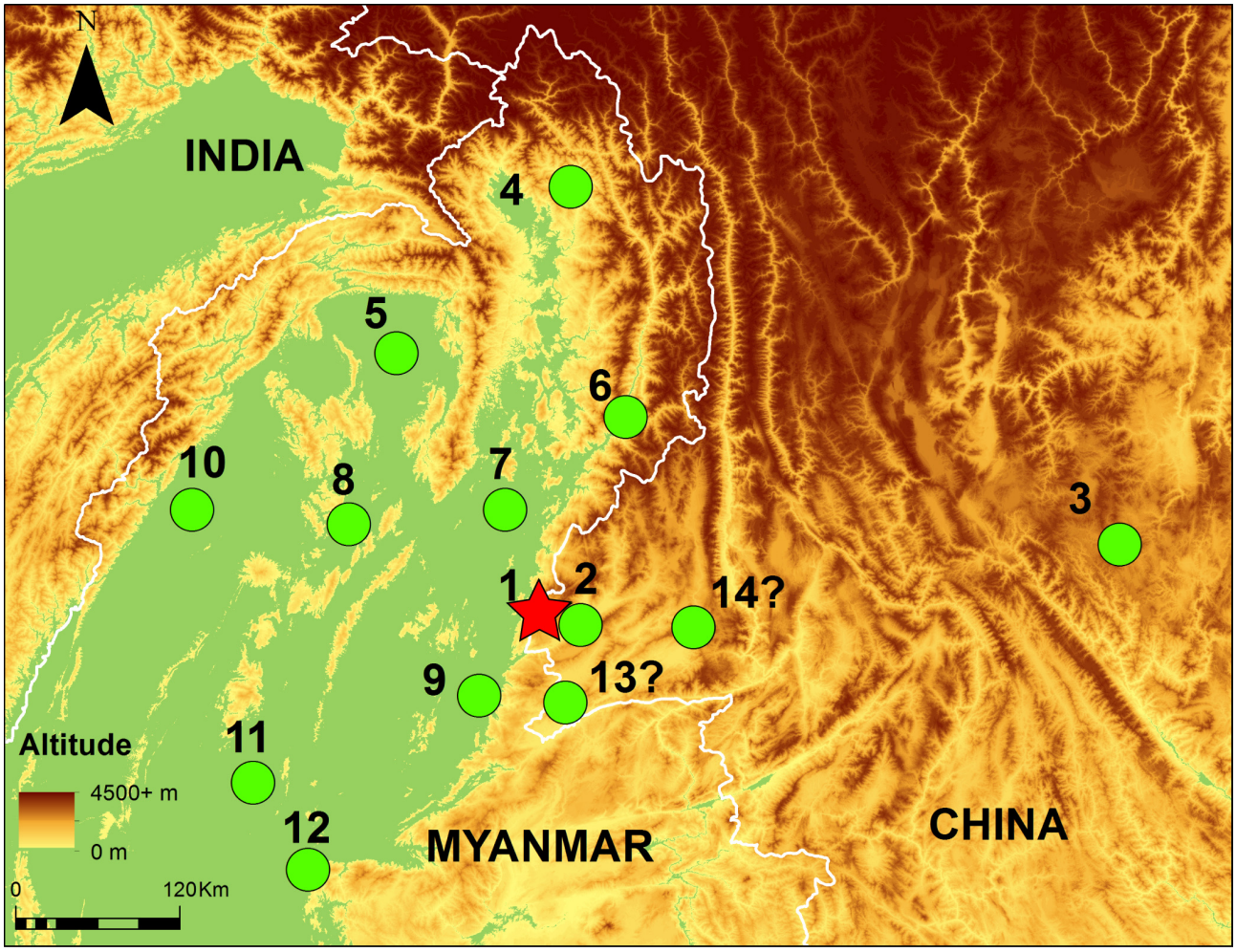

FIGURE 1. Map showing distributions of *Trimeresurus caudornatus* (red star: type locality). Notes: numbers indicate the different localities where this species has been recorded (see Appendix Table S8 for details of localities).

The Ornamental-tailed Pitviper, *Trimeresurus caudornatus* Chen, Ding, Vogel & Shi, 2020 belongs to the *Trimeresurus albolabris* species complex based on morphological and genetic data (Chen *et al*. 2020). This species was described based on one male and one female specimen, both originating from Nabang Town in Yingjiang County, Yunnan Province, China (Chen *et al*. 2020; see Fig. 1). The species is characterized by having a dark green dorsum with a lighter green lip; an absence of postocular streaks; a faint green yellow ventrolateral stripe present on the first row of dorsal scales; a golden yellow iris; and orange-red midventral stripe along the underside of the tail. Recent molecular phylogenies have demonstrated that populations previously identified as *Trimeresurus albolabris* Gray, 1842 and *T. septentrionalis* Kramer, 1977 from northern Myanmar (i.e., Mandalay Region and Kachin State) cluster within the same lineage as the holotype of *T. caudornatus* (Mallik *et al*. 2021; Vogel *et al*. 2022; Mirza *et al*. 2023). These results suggest that *T. caudornatus* has a more expansive distribution than currently recognized. However, most of these molecular studies were unaware that some of their genetic samples corresponded with *T. caudornatus* at the time of their publication, or did not provide morphological data associated with the specimens they sampled. Vogel *et al*. (2023) included preliminary morphological and distributional data suggesting that northern Myanmar

populations of *T. albolabris* and *T. septentrionalis* belonged to *T. caudornatus* but did not provide a detailed description of their material, as the scope of their paper was the description of neighboring species *Trimeresurus uetzi* Vogel, Nguyen & David. As a consequence, the morphological diagnosis of *T. caudornatus* has remained limited to the holotype and paratype, and the status of several populations of *Trimeresurus* from northern Myanmar has remained unresolved until now. To address this issue, we re-examined specimens previously identified as *T. albolabris* or *T. septentrionalis* from northern Myanmar (Sagaing and Mandalay regions, and Kachin State) deposited in five natural history collections, including all of the specimens that were included in Vogel *et al*. (2023). We also refer to data of 16 specimens of *T.* "*albolabris*" from northwest Yunnan Province that were reported in the literature by Zhao *et al*. (1998). Our results confirm that the specimens from Myanmar, as well as Longchuan and Tengchong counties, Yunnan Province, China, should be re-identified as *T. caudornatus*. We herein confirm the occurrence of *T. caudornatus* in Myanmar, update the distribution of this species and revise its diagnostic characters.

Material and Methods

Material examined. We examined 19 specimens that were previously registered as *Trimeresurus albolabris* or *T. septentrionalis* from northern Myanmar (see Table 1), and three digital images (DTU 651 from Yingjiang County, Dehong City, Yunnan Province, China; DTU 652 from Chuxiong City, Yunnan Province, China and DTU 653 from Mandalay City, Mandalay Region, Myanmar) of genuine specimens of *T. caudornatus*. Morphological comparisons were based on literature data from Kramer (1977), Chen *et al*. (2020, 2021); Mirza *et al*. (2020), Rathee *et al*. (2021), Vogel *et al*. (2023), Biakzuala *et al*. (2024), and 339 preserved specimens of other members of the *Trimeresurus albolabris* species complex (see Appendix Table S1 and Appendix II of Vogel *et al.* 2023 for a list of specimens examined for this study).

Morphological analyses: Altogether, 45 morphological characters (see Appendix Table S2) were considered, either as raw variables or derived from the raw characters listed above. Measurements were taken with a slide-caliper to the nearest 0.1 mm, except body and tail lengths, which were measured to the nearest of 1 mm with a measuring tape. Ventral scale numbers were counted according to Dowling (1951). Half ventrals were counted as a single scale. The enlarged shield(s) anterior to the first ventral were regarded as preventral(s). We regard the first subcaudal scale as the first scale on the underside of the tail posterior to the vent that meets an opposite scale and did not include the unpaired terminal scute (tail tip) in subcaudal counts. The dorsal scale rows were counted at one head length behind the head, at midbody approximately one-half the body length of each specimen, and at one head length before the vent. Values for paired head characters were recorded on both sides of the head and are reported in left / right order. The eye diameter (ED) was measured horizontally (the greatest diameter of the orbit); the distance from the eye to the nostril (EN) was measured from the anterior margin of the eye to the posterior margin of the nostril; the distance from the eye to the lip (SL) was measured from the ventral margin of the middle of the eye to the ventral margin of the upper labial below it; the head width (HW) was measured at the widest part of the head on posterior side. The sex was determined by dissection of the ventral tail base in preserved specimens and with a probe in live individuals.

To determine whether *Trimeresurus caudornatus* and other species related to *T. albolabris* and *T. septentrionalis* (including type specimens of the three species, in total 142 adult males specimens and 197 adult females specimens) exhibit significant morphological differences, we ran univariate statistical analyses on four scale counts (VEN, SC, VEN+SC, SL, and IL) and one body measurement ratio (TaL/TL). Since most of these variables represent meristic data, no size-correction on the morphological data was conducted for statistical analyses and both juvenile and adult specimens were included in all analyses. Males (N = 142) and females (N = 197) were analyzed separately in each analysis owing to the presence of sexual dimorphism present within many members of *Trimeresurus* (Zhu *et al.* 2022). We first subjected each character (separated by male and female specimen series) to Shapiro–Wilks Tests and Levene's Tests to determine if each data exhibits normality and homoscedasticity, respectively. Since most of the characters exhibited both non-normal and non-homoscedastic distributions, we employed pairwise Mann–Whitney U Tests (the non-parametric alternative to Student's *t*–tests) to determine whether scale counts and measurements exhibited statistically significant differences between species. In all cases, we considered characters to be significantly different if corresponding *p*–values were less than or equal to 0.05.

Molecular phylogeny. We synthesized previously published sequences of *Trimeresurus albolabris* complex members from GenBank to estimate the phylogenetic relationships of the genus *Trimeresurus* and genetically identical samples referrable to *T. caudornatus*. We focused on sequences for the mitochondrial DNA gene cytochrome *b* (cyt

b) as it is phylogenetically informative for most viperids and has the largest availability of any gene for *Trimeresurus*. We updated the taxonomic identities of the gene sequences to current taxonomy (Vogel *et al*. 2023; this work), regardless of what it had been originally submitted as. We aligned the cyt *b* sequences of 40 species of *Trimeresurus* species representing all major groups within the genus, ten species of the genus *Craspedocephalus* Kuhl & Hasselt; we used the sequence of *Azemiops feae* Boulenger and *Protobothrops elegans* (Gray) to root the tree (GenBank accession numbers, voucher specimens, locality, and source information are summarized in Appendix Table S3).

We initially aligned nucleotide sequences in MAFFT v.6 (Katoh *et al*. 2019) with default parameters, subsequently checked them by eye in BioEdit 7.0.5.2 (Hall, 1999) and slightly adjusted sequences for translation whenever required. Uncorrected pairwise genetic distances (p-distances) between sequences were calculated with MEGA 6.0. (Tamura *et al*. 2013) based on the cyt *b* sequences of all *Trimeresurus* subgenus samples, and missing data or gaps were affected by the pairwise deletion option. When the same model was proposed for different codon partitions of a given gene, they were treated as a single partition.

Phylogenetic trees were inferred using Bayesian inference (BI) and maximum likelihood (ML) approaches. We used the IQ-TREE webserver (Trifinopoulos *et al*. 2016) to generate the ML-tree and evaluate the confidence in tree topology by 1000 ultrafast-bootstrap replications (UFBS). The best-fit substitution models for the dataset were selected for gene and codon positions in ModelFinder using the Akaike information criterion (AIC) in IQ-TREE. We conducted BI in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) using the same partition scheme inferred for the ML analysis. Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyzes were run with one cold chain and three heated 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 v. 1.7 (Rambaut *et al*. 2018). We discarded the initial 1000 trees as burn-in. For BI-analysis we assessed the confidence in tree topology by the posterior probability (PP) (Huelsenbeck & Ronquist 2001). We *a priori* considered tree 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 as moderately supported, and any values lower than these were considered as lacking node support (Huelsenbeck & Hillis 1993).

Abbreviations. *Morphology and morphometry*. DSR: dorsal scale rows; IL: infralabials; SC: number of subcaudals excluding terminal scute; SL: number of supralabials; SVL: snout ventral length from snout to last ventral scale; TaL: tail length from anal to tail tip; TL: total length from the tip of the snout to the end of the tail; TL/TaL: ratio of total length to tail length; VEN: number of ventrals. *Other abbreviations*. Mt.: mount; NP: National Park; WS: Wildlife Sanctuary.

Institutions and museums acronyms. CAS: California Academy of Sciences, San Francisco, USA; CESS: Centre for Ecological Sciences, Bangalore, India; KIZ: Kunming Institute of Zoology, Chinese Academy of Sciences, Yunnan, China; MHNG: Muséum d'Histoire Naturelle de la Ville de Genève, Genève, Switzerland; MNHN: Muséum national d'Histoire naturelle, Paris, France; MSNG: Museo Civico di Storia Naturale "Giacomo Doria" Genova, Liguria, Italy; NHMUK (formerly BMNH): The Natural History Museum, London, UK; NHMW (formerly NMW) = Naturhistorisches Museum Wien, Vienna, Austria; QSMI: Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand; RMNH: Nationaal Natuurhistorisch Museum (Naturalis), Leyden, The Netherlands; SMF: Natur-Museum und Forschungs Institut Senckenberg, Frankfurt-am-Main, Germany; SYS: Sun Yat-Sen University, Guangdong, China; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMB: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; ZMH: Zoologisches Museum Hamburg, Universität Hamburg, Hamburg, Hamburg, Germany; ZMNH: Zhejiang Museum of Natural History, Zhejiang, China; ZSI: Zoological Survey of India, Kolkata [Calcutta], West Bengal, India

Results

Phylogenetic relationships

The ML and BI analyses recovered trees with similar topologies, but minor discrepancies associated in deeper and shallower nodes were observed (Fig. 2). With respect to the position of *T. caudornatus*, our phylogenetic results mostly conform to those of Zhu *et al*. (2016), Chen *et al*. (2020), Mirza *et al*. (2023), and Vogel *et al*. (2022), who focused on relationships among *Trimeresurus albolabris* and *T. septentrionalis*, to which *T. caudornatus* belongs. The reconstructed phylogenetic relationship indicates that four species: *T. caudornatus*, *T. salazar* Mirza, Bhosale,

FIGURE 2. Maximum Likelihood (ML) tree of *Trimeresurus* derived from the analysis of cyt *b* mitochondrial DNA gene sequences. For voucher specimen information and GenBank accession numbers see Appendix Table S3. Numbers at tree nodes correspond to ML UFBS/BI PP support values, respectively.

Phansalkar, Sawant, Gowande & Patel, *T. septentrionalis*, and *T. uetzi* Vogel, Nguyen & David are nested within a single monophyletic clade (Fig. 2); however, the nodes connecting each species in this clade received poor support in the ML analysis (UF BS = 55) and exhibited different phylogenetic positions in the BI genealogy. Despite

the low branch support of the clade containing all four species, the internal nodes of each species within that clade were all strongly supported, including *T. caudornatus* (100/1.0). The uncorrected *p*-distances of the cyt *b* gene fragment among members of the *Trimeresurus albolabris* and *T. septentrionalis* species groups are presented in see Appendix Table S4. Three sequences of *Trimeresurus* spp. (KP999351 **[**CAS 216144], KP999351 **[**CAS 216173**]**, and ON804486 [CAS 235956], respectively) reported from Sagaing Region and Kachin State, Myanmar, respectively, were approximately 0.4–2.6% divergent from the type series of *Trimeresurus caudornatus* from Nabang Town, Yingjiang County, Yunnan Province, China. These intraspecific distances are consistent with other species related to *T. albolabris* and *T. septentrionalis* **(**Appendix Table S4), with the geographically adjacent species *T. uetzi* having intraspecific distances ranging from 0.0–3.6% and *T. albolabris* having a much wider span of intraspecific divergences (0.1–4.3%). Genetic distances between *T. caudornatus* and related species were consistent with other pairwise distances between other related *Trimeresurus*. Specifically, *T. caudornatus* was 5.3–7.3% divergent from *T. salazar*, 5.9–6.9% divergent from *T. septentrionalis*, and 5.8–7.0% divergent from *T. uetzi*. These results strongly suggest that the northern Myanmar populations of *Trimeresurus* are genetically conspecific with *T. caudornatus*.

Morphological analysis

With the exception of relative tail length (TaL/TotalL), statistically significant differences were found between all *Trimeresurus* in the remaining four morphological characters we examined (see Suppl. material 1: table S5 for more details). However, most of these differences were subtle, and overlaps between scale counts are present. Both male and female *Trimeresurus caudornatus* had a statistically higher number of ventrals ($p < 0.0001$ in males; $p = 0.0163$ in females) relative to *T. albolabris*. Male *T. caudornatus* have a slightly lower number of subcaudals than *T. septentrionalis* ($p = 0.0289$). Female *T. caudornatus* also have a statistically lower number of ventrals ($p = 0.0039$**)** and subcaudals ($p = 0.0077$) than female *T. septentrionalis*, and a slightly higher number of subcaudals ($p = 0.0020$) and infralabials ($p = 0.047$) than female *Trimeresurus uetzi*. We also examined the morphology of other *Trimeresurus* specimens previously registered as *T. albolabris* or *T. septentrionalis* from Myanmar, including specimen CAS 216144 (see Fig. 3 E–F), which was sequenced for genetic data, and found that they were all morphologically referrable to *T. caudornatus*. The Burmese specimens of *Trimeresurus* share the presence of a distinct midventral stripe on the underside of the tail and have a faint ventrolateral stripe on the first scale row of the dorsal surface, all of which match the type series from Yunnan Province (Chen *et al.* 2020). Moreover, live photographs of specimens from Myanmar lack a distinct postorbital streak and have a golden yellow iris, characters that are not found in other closely related species such as *T. salazar* and *T. uetzi*. These results support our hypothesis that previous records of *T. albolabris* (restricted to southern China, Vietnam, Laos, Cambodia, Thailand, and Indonesia) and *T. septentrionalis* (restricted to western and central Himalayan regions of Nepal and northern India) in northern Myanmar (Sagaing, Mandalay, and Kachin) and northwestern Yunnan (Longchuan and Tengchong counties), China, should be referred to as *T. caudornatus*. In conjunction with our genetic results, we extend the distribution of *Trimeresurus caudornatus* to Myanmar and provide an expanded diagnosis and description below.

Taxonomic account

Trimeresurus caudornatus

(Table 1; Figs. 3–5)

Trimeresurus caudornatus Chen, Ding, Vogel & Shi *in* Chen *et al.* (2020: 116, Fig. 2A-B, 3A-D & 4A-D). **Holotype**: ZMNH AR1238, adult male, collected by L. Ding and Z. Chen on 17 September 2018. **Type locality**: Nabang Town, Yingjiang County, Dehong City, Yunnan Province, China (24.6973°N, 97.5805°E; elevation 389 m asl.).

Chresonymy

Trimeresurus gramineus (*non Coluber gramineus* Shaw, 1802)—Wall (1925: 821; 1926: 566, both in part).

Trimeresurus albolabris (*non Trimesurus albolabris* Gray, 1842)—Smith (1943: 523, in part); Zhao *et al*. (1998: 448, in part); Orlov *et al*. (2002: 189, in part); Leviton *et al.* (2003: 444, in part, 462); David *et al.* (2003: 157, in part), Gumprecht *et al.* (2004: 30, in part); Wogan & Win (2005: 72, in part); Vogel (2006: 83, in part); Stuart *et al*. (2012: 1 & 3, in part); Yang & Rao (2008: 336, in part); Wallach *et al.* (2014: 726, in part); Zhu *et al*. (2022: 32, in part); Uetz *et al*. (2024, page "*Trimeresurus albolabris*", in part);

Cryptelytrops albolabris—David *et al.* (2001, 221, in part), Leviton *et al.* (2008: 71, in part).

Trimeresurus albolabris albolabris—David & Vogel (1998: 87, in part), Regenass & Kramer (1981: 168 & 169, in part); David & Tong (1997: 26, in part).

Trimeresurus *septentrionalis* (*non Trimeresurus septentrionalis* Kramer, 1977)—Orlov *et al*. (2002: 352; in part); Zhu *et al*. (2016: 253, 256, 258 & 259, in part).

Trimeresurus caudornatus—Chen *et al*. (2021: 167, 172, 175 & Tables S1–S2); Mallik *et al*. (2021: 580); Vogel *et al*. (2022: 344, 347, 358, 363, 365); Vogel *et al*. (2023).

Specimens examined (n=19, all from Myanmar): ***Sagaing Region***: CAS 244953 (adult male) from Homalinn, Khandi District, USNM 537444 (adult male) and USNM 524076 (adult female) from Chatthin W.S., Kanbalur Township. ***Mandalay Region***: CAS 216144 (subadult female) from Shwe U Daung, Pyin Oo Lwin District. ***Kachin State***: CAS 230260, CAS 232425 (two subadut females), CAS 241264 (subadult male), CAS 245234 (subadult female) from Indawgyi Lake, Myitkyina District; CAS 221549 (subadult male), CAS 224646 (adult male) and CAS 230233 (adult female) from Putao District; MNHN RA-1893.0415, MSNG 30533-B (two adult males) & MNHN RA-1893.0416, MSNG 2180, MSNG 30533-A (three adult females) from Bhamo District; NHMUK 1974.907 (adult male) from Sumprabum District; MSNG 30814 (sub adult female) from Teinzo, Bhamo District; NHMUK 1974.906 (adult female) from N'Changyang District (remark: for more information details of CAS specimens see Appendix Table S6).

Additional material (n=3). DTU 651 (Digital images) photo taken by Spark T on 29 August 2023 in Pingyuan Town, Yingjiang County, Dehong City, Yunnan Province, China. DTU 652 (Digital images) photo taken by Fan Gao on 14 May 2021 in Chuxiong City, Yunnan Province, China. DTU 653 (Digital images) photo taken by Kyaw Zin Htet on 13 Jun 2023 in Mandalay City, Mandalay Region, Myanmar.

Referred material (n=16; all from Yunnan Province, China, based on specimens cited by Zhao *et al*. 1998). ***Longchuan County***: KIZ 74I0024 (adult male), KIZ 74I0032-33 (two subadult males), KIZ 74I0045-46 (two adult males), KIZ 74I0006, KIZ 74I0010, KIZ 74I0018, KIZ 74I0027-28 (five adult females), KIZ 74I0012 (subadult female). ***Tengchong County***: KIZ 741I0358 (adult female).

Revised diagnosis. A species of *Trimeresurus* inhabiting Yunnan Province (China) and Northern Myanmar showing the following combination of characters: head and body generally dark green, upper labials light green; postocular stripes absent in both sexes; ventrolateral stripe faint green-yellow, present on the first row of DSR in both sexes; iris golden yellow in both sexes; dorsal surface of the tail mostly dark red, lateral and ventral surfaces green; an orange-red medial stripe present across the underside of the tail; DSR 21(rarely 22 or 23)–21–15; VEN 158–167 in males, 158–174 in females; SC 53–74 in males, 52–68 in females; ratio TaL/TL 0.17–0.22 in males, 0.14–0.18 in females; Cep 10–12; first upper labial partially fused to the nasal; hemipenes elongated, bilobed at the level of the 6th subcaudal, tips reaching SC 37–38, small spines present posterior to the bifurcation, *sulcus spermaticus* shallow, visible, divides at the base of the organ (based on Zhao *et al*. 1998; Chen *et al*. 2020, and our material).

Comparisons. *Trimeresurus caudornatus* is morphologically similar to *Trimeresurus salazar*, a species described from Pakke Tiger Reserve, East Kameng District, Arunachal Pradesh State, India, which is widely distributed across central and northeastern India, eastern Nepal, Bhutan, and Bangladesh (Mirza *et al*. 2020; Vogel *et al*. 2022). *Trimeresurus caudornatus* differs from *T. salazar* by having a dark green dorsum (vs. usually green-yellow, more so in females); ventrolateral stripes faint, green-yellow and poorly contrasting dorsal ground color (vs. stripes distinct, brick red ventrally plus white dorsally, and conspicuous); presence of an irregular, red-orange stripe on the midventral surface of the tail (vs. absent); iris golden yellow (vs. copper) and tip of the hemipenes reaching SC 37–38 (vs. 12–13).

Trimeresurus caudornatus differs from *Trimeresurus albolabris* s. str. (restricted to southeastern China, Vietnam [throughout except the northwest], Laos [central and southern], Cambodia [throughout], and Thailand [eastern and central]) by having faint ventrolateral stripes that are greenish-yellow and poorly contrasted (vs. distinct, white, conspicuous); postocular streak absent in males (vs. present); iris golden yellow (vs. copper); tip of hemipenes reaching SC 37–38 (vs. 15–18) and small scales absent in front of the pit (vs. usually present).

Trimeresurus caudornatus differs from *T. erythrurus* (Cantor), a species present in Myanmar, India, Bangladesh, possibly in Bhutan, by having: ventrolateral body stripes faint, greenish-yellow, poorly contrasted (vs. distinct, white, conspicuous); postocular stripe absent in males (vs. present); iris golden yellow (vs. copper); temporal scales and dorsal body scales feebly keeled (vs. strongly keeled); lower number of mid-body scale rows (21 vs. 23 [rarely 21, 24, 25]).

TABLE 1. Main measurements and meristic characters of *Trimeresurus caudornatus* from China and Myanmar.

No.	Previous identification	New identification	Locality	Voucher number	Sex	Status	SVL (mm)	TaL (mm)
1	*T. albolabris*	*T. caudornatus*	Yingjiang, Yunnan, China	ZMNH AR1238	M	Holotype	573	122
2	*T. septentrionalis*	*T. caudornatus*	Indawgyi Lake, Myitkyina, Kachin, Myanmar	CAS 241264	M		436	110
3	*T. albolabris*	*T. caudornatus*	Putao, Kachin, Myanmar	CAS 221549	SM		333	72
4	*T. albolabris*	*T. caudornatus*	Putao, Kachin, Myanmar	CAS 224646	M		601	168
5	*T. albolabris*	*T. caudornatus*	Homalinn, Khandi, Sagaing, Myanmar	CAS 244953	M		507	141
6	*T. albolabris*	*T. caudornatus*	Bhamo, Kachin, Myanmar	MNHN 1893.0415	M		546	143
7	*T. albolabris*	*T. caudornatus*	Bhamo, Kachin, Myanmar	MSNG 30533-B	M		463	116
8	*T. albolabris*	*T. caudornatus*	Sumprabum, Kachin, Myanmar	NHMUK 1974.907	M		523	141
9	*T. albolabris*	*T. caudornatus*	Chatthin WS, Kanbalur, Sagaing, Myanmar	USNM 537444	M		425	114
10	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0024	M		420	108
11	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0032	SM		378	95
12	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0033	SM		363	85
13	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0045	M		425	120
14	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0046	M		465	130
15	*T. caudornatus*	*T. caudornatus*	Yingjiang, Yunnan, China	ZMNH AR1239	F	Paratype	425	77
16	*T. yunnanensis*	*T. caudornatus*	Hukaung WS, Myitkyina, Kachin, Myanmar	CAS 230260	SF		283	55
17	*T. albolabris*	*T. caudornatus*	Ta Ruing, Ta Nai, Myitkyina, Kachin, Myanmar	CAS 232425	SF		297	59
18	*T. septentrionalis*	*T. caudornatus*	Shwe U Daung, Pyin Oo Lwin, Mandalay, Myanmar	CAS 216144	SF		322	55
19	*T. albolabris*	*T. caudornatus*	Chipwe, Myitkyina, Kachin, Myanmar	CAS 245234	SF		279	50
20	*T. albolabris*	*T. caudornatus*	Madanbaw, Putao, Kachin, Myanmar	CAS 230233	F		534	98
21	*T. albolabris*	*T. caudornatus*	Bhamo, Kachin, Myanmar	MSNG 30533-A	F		702	74+
22	*T. albolabris*	*T. caudornatus*	Bhamo, Kachin, Myanmar	MSNG 2180	F		660	136
23	*T. albolabris*	*T. caudornatus*	Teizo, Kachin, Myanmar	MSNG 30814	SF		332	58
24	*T. albolabris*	*T. caudornatus*	Bhamo, Kachin, Myanmar	MNHN 1893.0416	F		625	130
25	*T. albolabris*	*T. caudornatus*	N'Changyang, Kachin, Myanmar	NHMUK 1974.906	F		679	133
26	*T. albolabris*	*T. caudornatus*	Chatthin WS, Kanbalur, Sagaing, Myanmar	USNM 524076	SF		329	58
27	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0006	F		538	95
28	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0010	F		470	75
29	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0012	SF		310	69
30	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0018	F		568	106
31	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0027	F		474	83
32	*T. albolabris*	*T. caudornatus*	Longchuan, Yunnan, China	KIZ 74I0028	F		540	105
33	*T. albolabris*	*T. caudornatus*	Tengchong, Yunnan, China	KIZ 741I0358	F		442	93
34	*T. albolabris*	*T.* cf. *caudornatus*	Jingdong, Yunnan, China	KIZ 75II0358	M		600	142
35	*T. albolabris*	*T.* cf. *caudornatus*	Yongde, Yunnan, China	KIZ 79I501	M		400	99
36	*T. albolabris*	*T.* cf. *caudornatus*	Kunming, Yunnan, China	KIZ 740005	F		?	?
37	*T. albolabris*	*T.* cf. *caudornatus*	Yongde, Yunnan, China	KIZ 79I207	F		500	92

.....continued on the next page

TABLE 1. (Continue)

No.	New identification	Voucher number	Sex	DSR	VEN	SC	SL	IL	Source
1	*T. caudornatus*	ZMNH AR1238	M	21– 21– 15	163	72	10/10	13/12	Chen *et al*. (2020)
2	*T. caudornatus*	CAS 241264	M	21– 21– 15	162	66	10/10	12/11	This study
3	*T. caudornatus*	CAS 221549	SM	21– 21– 15	162	66	10/10	14/13	This study
4	*T. caudornatus*	CAS 224646	M	21– 21– 15	161	71	10/11	12/13	This study
5	*T. caudornatus*	CAS 244953	M	21– 21– 15	164	71	10/10	13/13	This study
6	*T. caudornatus*	MNHN 1893.0415	M	21– 21– 15	161	62	10/10	12/12	This study
7	*T. caudornatus*	MSNG 30533-B	M	23– 19– 15	165	69	11/10	11/12	This study
8	*T. caudornatus*	NHMUK 1974.907	M	23– 21– 17	158	67	12/11	12/11	This study
9	*T. caudornatus*	USNM 537444	M	23– 21– 15	166	53	11/11	13/14	This study
10	*T. caudornatus*	KIZ 74I0024	M	21– 21– 15	158	69	10/10	12/12	Zhao *et al*. (1998)
11	*T. caudornatus*	KIZ 74I0032	SM	19– 21– 15	160	69	11/10	13/13	Zhao *et al*. (1998)
12	*T. caudornatus*	KIZ 74I0033	SM	23– 21– 17	167	74	11/10	14/13	Zhao *et al*. (1998)
13	*T. caudornatus*	KIZ 74I0045	M	21– 21– 15	163	73	11/11	13/14	Zhao *et al*. (1998)
14	*T. caudornatus*	KIZ 74I0046	M	21– 21– 15	164	71	10/10	12/13	Zhao *et al*. (1998)
15	*T. caudornatus*	ZMNH AR1239	F	21– 21– 15	161	52	10/11	13/14	Chen *et al*. (2020)
16	*T. caudornatus*	CAS 230260	SF	19– 21– 15	158	61	11/11	13/12	This study
17	*T. caudornatus*	CAS 232425	SF	21– 21– 15	159	60	11/10	12/12	This study
18	*T. caudornatus*	CAS 216144	SF	21– 21– 15	169	55	10/9	13/13	This study
19	*T. caudornatus*	CAS 245234	SF	21– 21– 15	158	57	10/10	13/13	This study
20	*T. caudornatus*	CAS 230233	F	21– 21– 15	164.00	57.00	11/11	12/13	This study
21	*T. caudornatus*	MSNG 30533-A	F	23– 21– 17	173	?	11/10	11/12	This study
22	*T. caudornatus*	MSNG 2180	F	23– 21– 15	174	68	11/11	13/14	This study
23	*T. caudornatus*	MSNG 30814	SF	23– 21– 15	162	60	?	?	This study
24	*T. caudornatus*	MNHN 1893.0416	F	21– 21– 15	165	66	10/10	13/13	This study
25	*T. caudornatus*	NHMUK 1974.906	F	21– 21– 15	160	55	11/11	13/13	This study
26	*T. caudornatus*	USNM 524076	SF	21– 21– 15	160	53	11/11	12/12	This study
27	*T. caudornatus*	KIZ 74I0006	F	21– 21– 15	160	53	12/10	13/14	Zhao *et al*. (1998)
28	*T. caudornatus*	KIZ 74I0010	F	21– 21– 15	159	54	13/13	15/16	Zhao *et al*. (1998)
29	*T. caudornatus*	KIZ 74I0012	SF	21– 21– 15	161	57	11/11	13/14	Zhao *et al*. (1998)
30	*T. caudornatus*	KIZ 74I0018	F	21– 21– 15	168	55	10/10	13/12	Zhao *et al*. (1998)
31	*T. caudornatus*	KIZ 74I0027	F	21– 21– 15	161	?	11/12	12/13	Zhao *et al*. (1998)
32	*T. caudornatus*	KIZ 74I0028	F	21– 21– 15	164	61	11/11	12/12	Zhao *et al*. (1998)
33	*T. caudornatus*	KIZ 741I0358	F	21– 21– 15	159	52	11/11	13/13	Zhao *et al*. (1998)
34	*T.* cf. *caudornatus*	KIZ 75II0358	M	21– 21– 15	163	67	10/10	12/14	Zhao *et al*. (1998)
35	*T.* cf. *caudornatus*	KIZ 79I501	M	22– 21– 15	161	69	10/9	13/13	Zhao *et al*. (1998)
36	*T.* cf. *caudornatus*	KIZ 740005	F	21– 21– 15	155	54	10/11	14/15	Zhao *et al*. (1998)
37	*T.* cf. *caudornatus*	KIZ 79I207	F	22– 21– 15	162	57	10/11	13/14	Zhao *et al*. (1998)

Trimeresurus caudornatus differs from *T. guoi* Chen, Shi, Vogel & Ding by having a golden yellow eye color (vs. always firebrick-red); tip of hemipenes reaching SC 37–38 (vs. 23–32).

Trimeresurus caudornatus differs from *T. septentrionalis*, a species now restricted to Nepal and north-western India, by having a lower number of subcaudals in males (53–74, 68.07 ± 5.38 vs. 71–80, 76.67 ± 3.50) and females (52–68, 57.41 ± 4.69 vs. 56–66, 63.07±2.53), and tip of hemipenes reaching SC 37–38 (vs. 5–7).

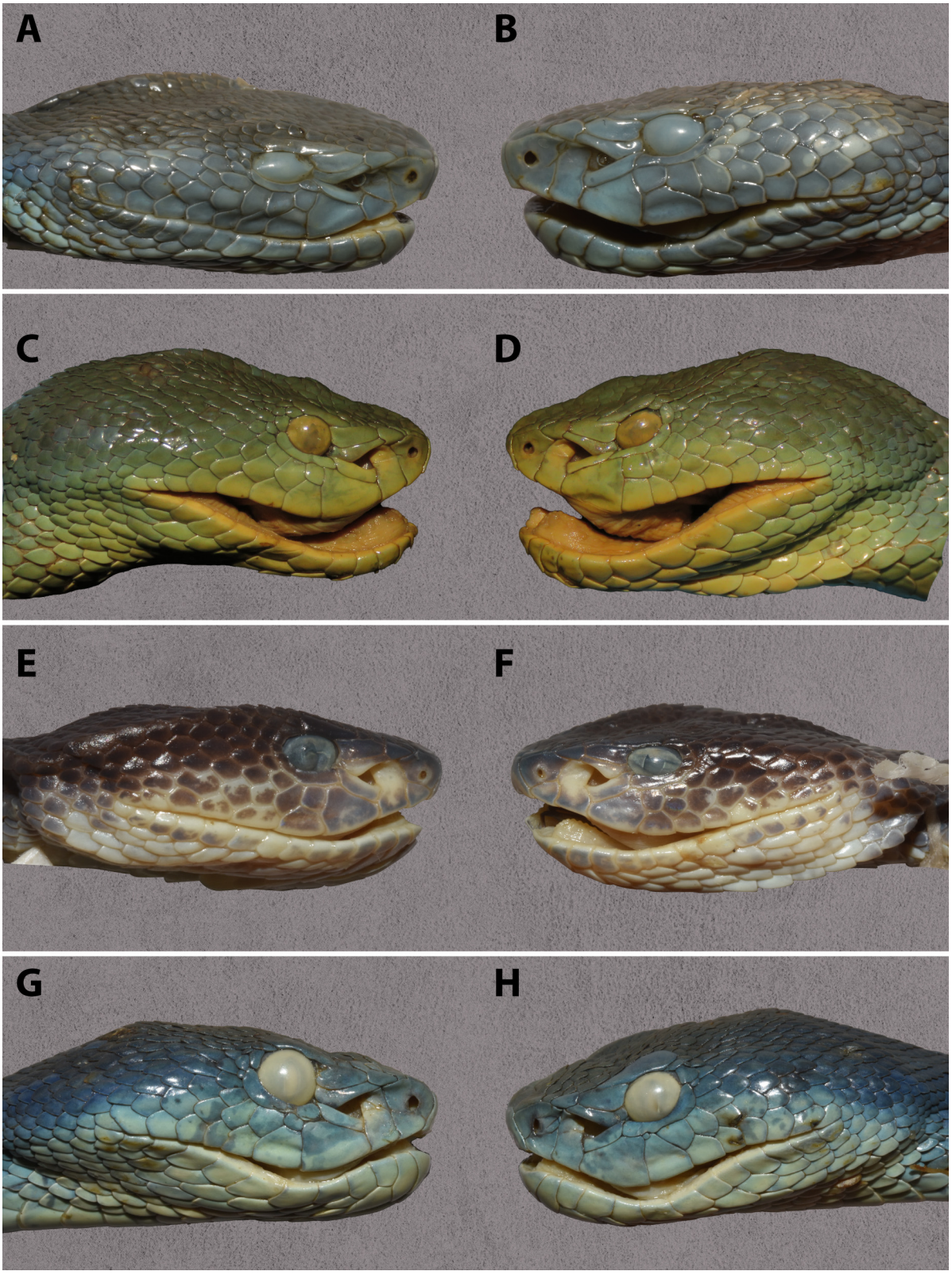

FIGURE 3. The head of preserved *Trimeresurus caudornatus* from Myanmar in lateral right and lateral left views: (A–B) specimen CAS 224646, adult male, and (C–D) specimen MSNG 30533-B, adult male, from Myitkyina and Bhamo, Kachin, respectively; (E–F) specimen CAS 216144, subadult female, from Pyin Oo Lwin, Mandalay; (G–H) specimen NHMUK 1974.907, adult female, from Sumprabum, Kachin. Photos by G. Vogel (A, B, E–H) and J. Lee (C–D).

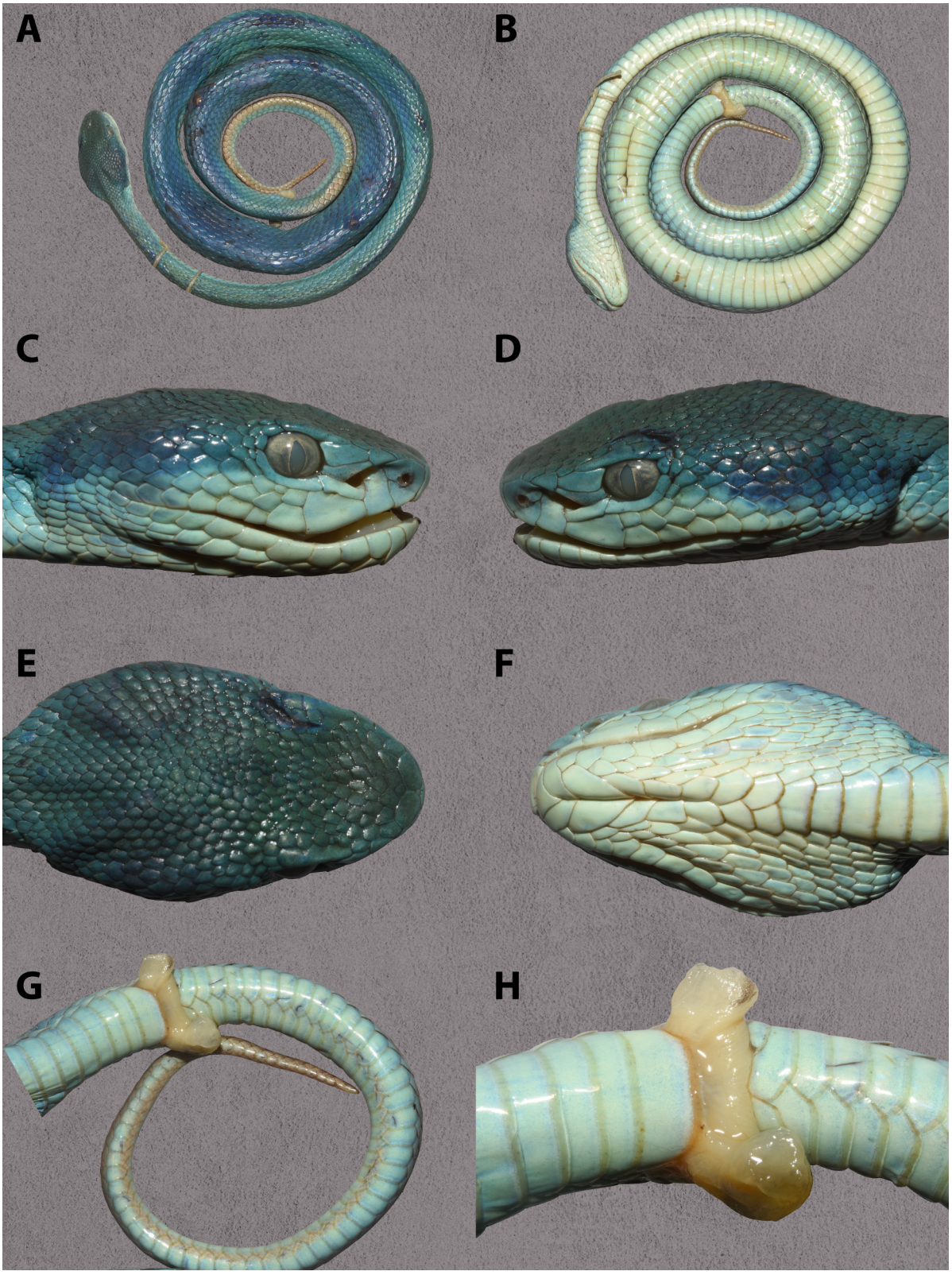

FIGURE 4. *Trimeresurus caudornatus* in preservative: specimen CAS 241264 (subadult male) from Myitkyina, Kachin, Myanmar. (A–B) Dorsolateral and ventral views of body, respectively; (C–F) head in lateral right, lateral left, dorsal, and ventral aspects, respectively; (G–H): Ventral view of the tail with the everted hemipenes. Photos by G. Vogel.

Trimeresurus caudornatus differs from *T. uetzi*, a species recently described from central and southern Myanmar, also present in Northeast India, by having the tip of the hemipenes reaching the 37th–38th SC (vs. 6th–8th SC); postocular stripe absent in males (vs. present); ventrolateral body stripe faint, greenish-yellow, poorly contrasted

(vs. present, white, conspicuous); in life, iris golden yellow in male (vs. copper in male); and the presence of an irregular, red-orange stripe in the middle of the ventral surface (vs. no median stripe on the lower surface of the tail) (see Appendix Table S7).

Description based on examined specimens from Myanmar (n=19).

Morphology. Body moderately elongate, slender [the longest known specimen is 776+ mm long, (SVL 702 mm, TaL 74+ mm, female; MSNG 30533-A, incomplete tail); the longest known male is 769 mm long (SVL 601 mm, TaL 168 mm; CAS 224646); tail typically cylindrical in cross section, fairly short, prehensile, tapering (TaL/TL 0.17–0.22 in males (n=9) and 0.15–0.17 in females (n=8)). Head triangular and elongate, flattened, clearly distinct from neck. Snout moderate, overall flattened from top and side view, rounded from top view, truncate when seen from lateral side, canthus rostralis distinct, eye moderate.

Body scalation. DSR 21 (rarely 23)–21 (rarely 19)–15 scales, rhomboid, moderately keeled except for the first row which is smooth; VEN 158–166 in males (n=9), 158–174 in females (n=9); SC 53–71 in males (n=9), 55–66 in females (n=8), paired; single cloacal plate.

Head scalation. Rostral subtriangular, slightly visible when viewed from above; nasal large, sub-rectangular, undivided, half-separated from the first upper labial by a suture behind the nostril; one pair of enlarged internasals, in good contact with each other, slightly broader than long; second and third supralabial and three preoculars encompass the loreal pit; the lower preocular forms the lower margin of the loreal pit; one elongate and narrow supraocular; cephalic scales small, irregular, subimbricate, smooth; occipital scales smooth; temporals feebly keeled and subequal; subocular crescent shaped; 9–13 supralabials; SL1 not fused with nasal scale, 2nd much higher than 1st, 3rd SL largest, longest of all, about twice as long as 2nd SL, longer than high, in contact with the subocular, 4th SL distinctly shorter, more than 2/3 time as high as 3rd one, 5th and other posterior SL slightly smaller than 4th; both 4th and 5th SL separated from the subocular by one scale row, others in contact with the first lowest row of temporals; 11–16 infralabials, the first pair in contact with each other; the first three pairs in contact with anterior chin shields; six pairs of chin shields, each pair in contact medially; separated from infralabials by 1–6 scale rows.

Coloration in life (Fig. 5): Dorsal body dark green. Lateral body green above and gradually pale green yellow below. Ventral body greenish yellow, paler in anterior part, light green in posterior part. Dorsal part of the tail dark red, about 2 dorsal scale rows wide and not mottled. Lateral and ventral part of the tail green. Ventrally, a thin orange red stripe extends across the posterior third of the tail. Tail tip uniformly red. Iris golden yellow (based on DTU 651–653 from Yunnan Province, China as well as Mandalay Region, Myanmar, all unknown sex).

Coloration in preservative (see Figs. 3–4): Dorsal body black gray or light blue without ventrolateral body stripes. Ventral body uniformly cream. The head dorsally back gray or light blue; without postocular streak, but a clear boundary below the eyes, olive above and grass green below. The chin and throat are white (based on CAS 241264 [male] and CAS 216144 [female], respectively).

Distribution (Fig. 1). *Trimeresurus caudornatus* was previously known only from Nabang Town, Yingjiang County, Yunnan Province, China (Chen *et al*. 2020). We here add a second and third Chinese locality from Yunnan Province: Tongbiguan Township, Yingjiang County, Longchuan, Tengchong countys and Chuxiong City (see the Discussion). The new location in Chuxiong City is ca. 390 airline kilometers east of the type locality. We also present several records of this species from Myanmar. *T. caudornatus* is currently known from the Mandalay and Sagaing regions, and from Kachin State. Given its geographic proximity, it likely occurs in Shan State as well. Detailed localities within each first-level regions of Myanmar are presented in Appendix Table S8.

Natural history notes. Prior to this study, the biological data of *Trimeresurus caudornatus* were very limited; it was only reported from an altitude of 389 m a.s.l. at the type locality (Chen *et al*. 2020). According to metadata associated with specimens deposited in the California Academy of Sciences collections (accessible at https://researcharchive.calacademy.org/research/herpetology/catalog/Index.asp), specimens of *T. caudornatus* were collected between 16h09 to 22h30 local time on trees, shrubs, or branches. The air temperature when specimens were observed varied from 24.7ºC to 30ºC and the relative humidity from 69–92%. This species seems to be distributed at low and medium elevations ranging from 169 to 560 m a.s.l. The stomach of CAS 221549 contained a skink *Sphenomorphus indicus* (Gray). An adult male specimen CAS 224646 was inactive ca. 25 cm below ground level inside a termite mound located near a trail in an agricultural area next to a subtropical evergreen forest (see Wogan & Win 2005).

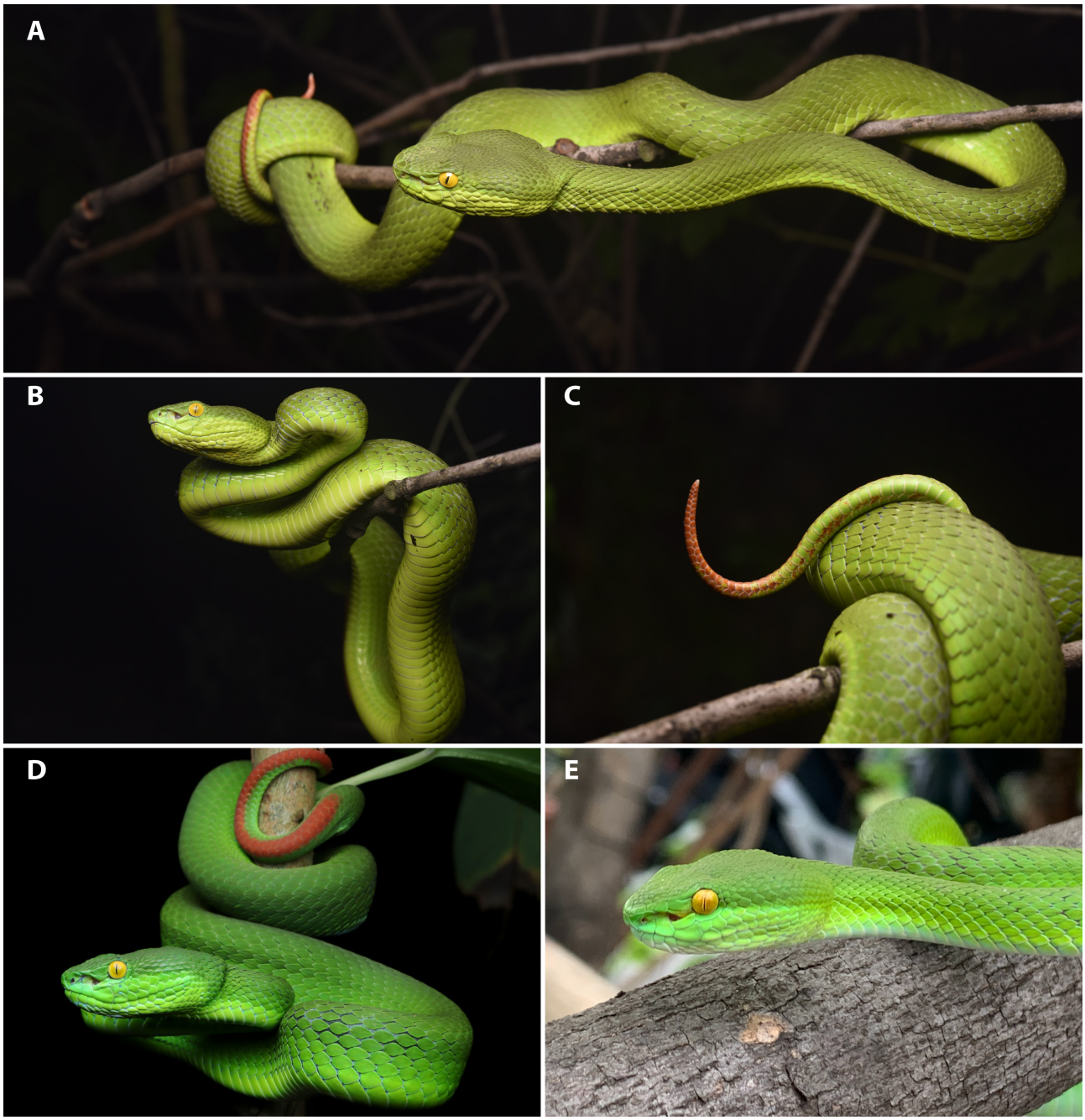

FIGURE 5. Adult *Trimeresurus caudornatus* alive (all uncollected and sex unknown). (A–C) from Chuxiong, Yunnan, China (digital image DTU 652); (D) from Pingyuan, Yingjiang, Dehong, Yunnan, China (digital image DTU 651); (E) from Mandalay, Mandalay, Myanmar (digital image DTU 653). Photos by: Fan Gao (A–C), Spark Thomas (D), and Kyaw Zin Htet (E).

Conservation status. *Trimeresurus caudornatus* is reliably known from 14 localities, including one national park and three wildlife sanctuaries in northern Myanmar. Outside of these protected regions, we predict habitat loss, habitat degradiation and killing/persecution by humans may act as conservation threats for this species. The actual extent of distribution, population trends, reproductive behavior, ecology, toxicology of this species remain poorly known. For now, based on its much more extensive distribution covering multiple protected areas in two countries, we suggest *Trimeresurus caudornatus* be considered as Least Concern (LC) following the criteria provided in the IUCN's Red List categories (IUCN 2024).

Discussion

In this study, we re-examined specimens that were previously assigned to *Trimeresurus albolabris* sensu lato or *Trimeresurus septentrionalis* sensu lato from northern Myanmar (Kachin State, Mandalay and Sagaing regions) and found that all of them should be assigned to the recently described *Trimeresurus caudornatus*. These also include records of *T. albolabris* and *T. septentrionalis* reported from northern Myanmar by Wall (1925; 1926), Smith (1943), Regenass & Kramer (1981), David & Tong (1997), Orlov *et al*. (2002), Leviton *et al*. (2003, 2008), Gumprecht *et al*. (2004), Vogel (2006), and Zhu *et al*. (2016). Presently *T. albolabris* s. str., should be restricted to southeastern China and adjacent Indochina (Laos (centre and south), Cambodia (throughout), Vietnam (throughout except the northwest), and Thailand (eastern and central) whereas *T. septentrionalis* s. str. should be restricted to the western Himalayan regions of Nepal and India (Vogel *et al*. 2022, 2023). As previously mentioned, historical records of *Trimeresurus* from central Myanmar and adjacent parts of northeastern India (Mizoram State) were recently described/re-classified as *T. uetzi* (David *et al*. 2023; Biakzuala *et al*. 2024). Morphologically, the presence of a red or orange midventral stripe on the underside of the tail and the lack of conspicuous white ventrolateral and postocular striping appear to be consistent across *Trimeresurus caudornatus* in both sexes. These two traits remain the easiest methods of identification for this species, especially relative to its geographically proximate congeners *Trimeresurus salazar* and *T. uetzi*. Some female *Trimeresurus uetzi* also have inconspicuous ventrolateral and postocular striping, but the absence of the red midventral stripe in that species should act to distinguish it from *T. caudornatus* if the former characters overlap.

Previous accounts (Zhao *et al*. 1998; Yang & Rao 2008; Zhu *et al*. 2022) reported that the species *Trimeresurus albolabris* is widely distributed in the northwestern region of Yunnan Province, China such as Longchuan County in Dehong City, Tuantian Town in Tengchong City. However, according to the morphological data of specimens from these two localities (Table 1), they belong to *Trimeresurus caudornatus*, rather than *T. albolabris*. Other populations in northwestern Yunnan Province with similar morphological characteristics as *T. caudornatus* (such as those reported from Yongde and Shuangjiang counties in Lincang City, Jingdong County in Puer City, and Kunming City, see Table 1) should also be re-examined for verification, and molecular data. These specimens, which were mentioned by Zhao *et al.* (1998), are included in the referred material of *T. caudornatus*, but are not included in our redescription until further confirmation. In addition, Li *et al*. (2020) followed by Wu *et al*. (2023), recorded *Trimeresurus albolabris* from Tongbiguan Township, Yingjiang County, Yunnan Province, China based on specimen SYS r001228 (or CHS 661) under Genbank numbers MK194130 (16S) and MK064805 (COI) as a lineage distinct from *Trimeresurus albolabris* s. str. and *T. guoi*. As these specimens were sequenced for separate mitochondrial genes, we did not include them in our genetic analyses. Nevertheless, the location of the specimen (Tongbiguan, Yingjiang County) is very close to the type locality of *Trimeresurus caudornatus* (approximately 28 km). We suspect that SYS r001228 is referrable to *Trimeresurus caudornatus*, but a re-examination of the specimen is required to verify this.

In addition, our molecular results support the existence of two clades that were originally identified as *Trimeresurus albolabris*: the first from Peninsular Thailand, and the second from Mengzi City, Yunnan Province, China. Both clades were recovered separately from the respective clades of *T. albolabris* sensu stricto and topotypic *T. guoi*. The first clade of *Trimeresurus albolabris* (from Peninsular Thailand) was also recovered in a more comprehensive phylogeny by Zhu *et al*. (2016), there labeled as Clade B, sister to their remaining samples of *T. albolabris* (Clade A in their study all correspond to samples of *T. guoi*). In contrast, samples of the second clade (from Mengzi City, Yunnan Province, China) were published a year earlier (Guo *et al*. 2015) and were not included in Zhu *et al*. (2016); however, their geographic location is certainly within the range of *Trimeresurus guoi*. Based on the position of each clade in our phylogeny, we tentatively identify these populations as *Trimeresurus* cf. *albolabris* and *Trimeresurus* cf. *guoi*, respectively. Both clades exhibit moderate genetic distances that are somewhat higher than the intraspecific distances of species such as *Trimeresurus albolabris* (see Appendix Table S4) and may represent cryptic species. However, the phylogenetic positions of both clades could be due to poor genetic coverage, as our molecular dataset only included a single genetic marker and do not replicate the topological results of Zhu *et al*. (2016), which place samples of *Trimeresurus guoi* sister to the clade containing *T.* cf. *albolabris* in this study. We await a more comprehensive genetic and morphological assessment of the Thai and southern Yunnan populations of *Trimeresurus* before making any further taxonomic decisions.

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Appendix Table S1. Comparative materials examined of *Trimeresurus albolabris* and *T. septentrionalis* species groups.

No.	Species	Collection number	Country	Locality	Sex	Status
1	*T. albolabris*	NHMUK 1946.1.19.85	China	Hong Kong	M	Lectotype
2	*T. albolabris*	MNHG 1400.69	China	Guangdong	M	
3	*T. albolabris*	NHMW 23927	China	Koksingas Port	M	
4	*T. albolabris*	NHMW 23926.5	China	Hong Kong	M	
5	*T. albolabris*	ZMB 66283	China	Guangdong	M	
6	*T. albolabris*	ZMB 52600	China	Nam Fung Wan, Hong Kong	M	
7	*T. albolabris*	NHMW 23905.2	China	Tingan, Hainan	M	
8	*T. albolabris*	NHMW 23905.8	China	Wuzhi Mt., Hainam	M	
9	*T. albolabris*	ZFMK 86454	Vietnam	Phong Nha Ke Bang, Quang Binh	M	
10	*T. albolabris*	ZFMK 101038	Vietnam	Bach Long Vy, Hai Phong	M	
11	*T. albolabris*	NHMUK 1946.1.23.73	China	Hong Kong	F	Paralectotype
12	*T. albolabris*	MNHG 1464.88	China	Guangdong	F	
13	*T. albolabris*	NHMW 23905.3	China	Tingan, Hainan	F	
14	*T. albolabris*	NHMW 23905.4	China	Tingan, Hainan	F	
15	*T. albolabris*	NHMW 23905.5a	China	Tingan, Hainan	F	
16	*T. albolabris*	NHMW 23905.6	China	Tingan, Hainan	F	
17	*T. albolabris*	NHMW 23905.5b	China	Tingan, Hainan	F	
18	*T. albolabris*	NHMW 23905.7	China	Tingan, Hainan	F	
19	*T. albolabris*	NHMW 23905.9	China	Tingan, Hainan	F	
20	*T. albolabris*	SMF 21224	China	Hainan	F	
21	*T. albolabris*	SMF 21222	China	Hainan	F	
22	*T. albolabris*	NHMW 23926.4	China	Hong Kong	F	
23	*T. albolabris*	ZMB 66282	China	Guangdong	F	
24	*T. albolabris*	ZMB 27669	China	Guangdong	F	
25	*T. albolabris*	MNHN 1999.9030	China	Guangdong	F	
26	*T. albolabris*	MNHN 1999.9031	China	Guangdong	F	
27	*T. albolabris*	DTU 602	Vietnam	Bac Huong Hoa, Quang Tri	F	
28	*T. albolabris*	S 0093-1	China	Guangdong	F	
29	*T. albolabris*	S 0093-2	China	Guangdong	F	
30	*T. albolabris*	S 0093-3	China	Guangdong	F	
31	*T. albolabris*	MNHN 1904.0404	Vietnam	Bao Lac, Cao Bang	F	
32	*T. albolabris*	MNHN 1904.0405	Vietnam	Bao Lac, Cao Bang	F	
33	*T. caudornatus*	MNHN 1893.0415	Myanmar	Bhamo, Kachin	M	
34	*T. caudornatus*	CAS 232425	Myanmar	Myitkyina, Kachin	SM	
35	*T. caudornatus*	CAS 241264	Myanmar	Indawgyi Lake, Myitkyina, Kachin	M	
36	*T. caudornatus*	CAS 221549	Myanmar	Putao, Kachin	SM	
37	*T. caudornatus*	CAS 224646	Myanmar	Putao, Kachin	M	
38	*T. caudornatus*	CAS 244953	Myanmar	Homalinn, Khandi, Sagaing	M	
39	*T. caudornatus*	MSNG 30533-B	Myanmar	Bhamo, Kachin	M	
40	*T. caudornatus*	NHMUK 1974.907	Myanmar	Sumprabum, Kachin	M	
41	*T. caudornatus*	USNM 537444	Myanmar	Chatthin WS, Sagaing	M	
42	*T. caudornatus*	USNM 524076	Myanmar	Chatthin WS, Sagaing	F	
43	*T. caudornatus*	CAS 216144	Myanmar	Shwe U Daung, Pyin Oo Lwin, Mandalay	F	
44	*T. caudornatus*	CAS 245234	Myanmar	Myitkyina, Kachin	F	
45	*T. caudornatus*	CAS 230233	Myanmar	Madanbaw, Putao, Kachin	F	

.....continued on the next page

Appendix Table S1. (Continued)

No.	Species	Collection number	Country	Locality	Sex	Status
46	*T. caudornatus*	MNHN 1893.0416	Myanmar	Bhamo, Kachin	F	
47	*T. caudornatus*	MSNG 30533-A	Myanmar	Bhamo, Kachin	F	
48	*T. caudornatus*	MSNG 2180	Myanmar	Bhamo, Kachin	F	
49	*T. caudornatus*	MSNG 30814	Myanmar	Teizo, Kachin	F	
50	*T. caudornatus*	NHMUK 1974.906	Myanmar	N'Changyang, Kachin	F	
51	*T. caudornatus*	CAS 230260	Myanmar	Hukaung WS, Myitkyina, Kachin	F	
52	*T. davidi*	Not collected	India	Chuckchucka, Nicobar	M	
53	*T. davidi*	NHMUK 1936.7.7.47	India	Nicobar	M	
54	*T. davidi*	NHMUK 1936.7.7.48	India	Andaman	M	
55	*T. davidi*	NHMUK 1936.7.7.46	India	Nicobar	M	
56	*T. davidi*	BNHS3304	India	Chuckchucka, Nicobar	F	
57	*T. davidi*	NHMUK 1936.7.7.40	India	Chuckchucka, Nicobar	F	
58	*T. davidi*	NHMUK 1936.7.7.41	India	Chuckchucka, Nicobar	F	
59	*T. davidi*	NHMUK 1936.7.7.42	India	Chuckchucka, Nicobar	F	
60	*T. davidi*	Not collected	India	Chuckchucka, Nicobar	F	
61	*T. davidi*	Not collected	India	Chuckchucka, Nicobar	F	
62	*T. davidi*	DOSMB 05104	India	Chuckchucka, Nicobar	F	
63	*T. davidi*	NHMW 23925:1	India	Nicobar	F	
64	*T. davidi*	NHMW 23925:2	India	Nicobar	F	
65	*T. guoi*	MNHN 1935.0464	Vietnam	Sapa, Lao Cai	M	
66	*T. guoi*	MNHN 1935.0464	Vietnam	Sapa, Lao Cai	M	
67	*T. guoi*	PSUaa 0046	Thailand	Chiang Mai	M	
68	*T. guoi*	PSUaa 0046	Thailand	Chiang Mai	M	
69	*T. guoi*	ZFMK 70442	Thailand	Phu Luang, Loei	M	
70	*T. guoi*	ZFMK 74282	Thailand	Samoeng, Chiang Mai	M	
71	*T. guoi*	ZFMK 74283	Thailand	Samoeng, Chiang Mai	M	
72	*T. guoi*	NHMW 23926.6	Thailand	Phu Kin Mt, Chiang Rai	M	
73	*T. guoi*	NHMW 23926.9	Thailand	Phu Kin Mt, Chiang Rai	M	
74	*T. guoi*	NHMW 23926.7	Thailand	Phu Kin Mt, Chiang Rai	M	
75	*T. guoi*	NHMW 23926.8	Thailand	Phu Kin Mt, Chiang Rai	M	
76	*T. guoi*	NHMW 23903.3	Myanmar	Mt Caren (Karen Hills), Shan	M	
77	*T. guoi*	NHMW 23920.1	Myanmar	Mawlamyine, Mon	M	
78	*T. guoi*	CAS 222595	Myanmar	Mudon, Mawlamyine, Mon	M	
79	*T. guoi*	MNHN 1935.0465	Vietnam	Lao Cai	F	
80	*T. guoi*	MNHN 1935.0466	Vietnam	Lao Cai	F	
81	*T. guoi*	QSMI 0761	Thailand	Chiang Mai	F	
82	*T. guoi*	NHMW 23930.1	Thailand	Phu Kin Mt, Chiang Rai	F	
83	*T. guoi*	NHMW 23930.2	Thailand	Phu Kin Mt, Chiang Rai	F	
84	*T. guoi*	NHMW 23926.10	Thailand	Phu Kin Mt, Chiang Rai	F	
85	*T. guoi*	ZFMK 70443	Thailand	Phu Luang, Loei	F	
86	*T. guoi*	ZMH R06267	Myanmar	Mt Caren (Karen Hills), Shan	F	
87	*T. guoi*	MNHN 1935.0465	Vietnam	Lao Cai	F	
88	*T. guoi*	MNHN 1935.0466	Vietnam	Lao Cai	F	
89	*T. guoi*	QSMI 0761	Thailand	Chiang Mai	F	

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Appendix Table S1. (Continued)

No.	Species	Collection number	Country	Locality	Sex	Status
90	*T. insularis*	ZMH R06938	Indonesia	Java	M	
91	*T. insularis*	NHMW 23928	Indonesia	Sumba	M	
92	*T. insularis*	NHMW 23929	Indonesia	Sumbawa	M	
93	*T. insularis*	SMF 21229	Indonesia	Sumbawa	M	
94	*T. insularis*	SMF76353	Indonesia	Florès	M	
95	*T. insularis*	MNHN 4056	Indonesia	Timor	M	
96	*T. insularis*	MNHN 4057	Indonesia	Timor	M	Lectotype
97	*T. insularis*	NHMW 39581	Indonesia	Bali	F	
98	*T. insularis*	NHMW 23924	Indonesia	Kisser Isl	F	
99	*T. insularis*	SMF 73324	Indonesia	Bali, near Tangu	F	
100	*T. insularis*	SMF 48734	Indonesia	Bali	F	
101	*T. insularis*	SMF 23374	Indonesia	Sumbawa, Batoe Doelang	F	
102	*T. insularis*	SMF 21220	Indonesia	Timor	F	
103	*T. insularis*	SMF76352	Indonesia	Florès	F	
104	*T. insularis*	MNHN 2002.0402	Indonesia	Wetar	F	
105	*T. insularis*	SMF 106707	Indonesia	Flores Korabewa	F	
106	*T. insularis*	SMF 106708	Indonesia	Flores Korabewa	F	
107	*T. insularis*	SMF 106706	Indonesia	Flores Korabewa	F	
108	*T. insularis*	SMF 106705	Indonesia	Flores Korabewa	F	
109	*T. salazar*	NHMUK 72.4.17.379	India	Darjeeling, West Bengal	M	
110	*T. salazar*	NHMUK 1908.6.23.99	India	Dibrugarh, Assam	F	
111	*T. salazar*	NHMUK 1937.3.1.14	India	Central Prov	F	
112	*T. septentrionalis*	MHNG 1404.31	Nepal	Pokhara	M	Holotype
113	*T. septentrionalis*	MHNG 1400.24	Nepal	Pokhara	M	Paratype
114	*T. septentrionalis*	MHNG 1400.31	Nepal	Pokhara	M	Paratype
115	*T. septentrionalis*	MHNG 1400.47	Nepal	Pokhara	M	Paratype
116	*T. septentrionalis*	SH 762	Nepal	No specific	M	
117	*T. septentrionalis*	MHNG 1400.29	Nepal	Pokhara	M	Paratype
118	*T. septentrionalis*	CAS 135750	Nepal	Pokhara	F	Paratype
119	*T. septentrionalis*	MNHG 1400.18	Nepal	Pokhara	F	Paratype
120	*T. septentrionalis*	MHNG 1400.35	Nepal	Pokhara	F	Paratype
121	*T. septentrionalis*	MHNG 1400.34	Nepal	Pokhara	F	Paratype
122	*T. septentrionalis*	MHNG 1400.26	Nepal	Pokhara	F	Paratype
123	*T. septentrionalis*	MHNG 1400.32	Nepal	Pokhara	F	Paratype
124	*T. septentrionalis*	MHNG 1400.38	Nepal	Pokhara	F	Paratype
125	*T. septentrionalis*	MHNG 1400.45	Nepal	Pokhara	F	Paratype
126	*T. septentrionalis*	MHNG 1400.39	Nepal	Pokhara	F	Paratype
127	*T. septentrionalis*	MHNG 1400.36	Nepal	Pokhara	F	Paratype
128	*T. septentrionalis*	MHNG 1400.25	Nepal	Pokhara	F	Paratype
129	*T. septentrionalis*	MHNG 1400.37	Nepal	Pokhara	F	Paratype
131	*T. septentrionalis*	MHNG 1400.30	Nepal	Pokhara	F	Paratype
130	*T. septentrionalis*	SH 688	Nepal	No specific	F	
131	*T. septentrionalis*	SH 1166	Nepal	No specific	F	
132	*T. septentrionalis*	SH 761	Nepal	No specific	F	

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Appendix Table S1. (Continued)

No.	Species	Collection number	Country	Locality	Sex	Status
133	*T. uetzi*	CAS 232480	Myanmar	Pyin Mana, Naypyidaw	M	Paratype
134	*T. uetzi*	CAS 204846	Myanmar	Mandalay, Mandalay	M	
135	*T. uetzi*	CAS 204847	Myanmar	Mandalay, Mandalay	M	
136	*T. uetzi*	CAS 246991	Myanmar	Myingchan, Kandaw, Mandalay	M	
137	*T. uetzi*	CAS 215907	Myanmar	Taung Aoe, Magway	M	
138	*T. uetzi*	CAS 210665	Myanmar	Kyaukpadaung, Mandalay	M	
139	*T. uetzi*	CAS 242723	Myanmar	Yangon-Pyay, Bago	M	
140	*T. uetzi*	CAS 220124	Myanmar	Mindat, Chin	M	
141	*T. uetzi*	CAS 243055	Myanmar	Gangaw, Pakhokku, Magway	M	Paratype
142	*T. uetzi*	CAS 243159	Myanmar	Gangaw, Pakhokku, Magway	M	
143	*T. uetzi*	CAS 243024	Myanmar	Gangaw, Pakhokku, Magway	M	Holotype
144	*T. uetzi*	CAS 215400	Myanmar	Pyaro, Yin Ma Bin, Sagaing	F	
145	*T. uetzi*	CAS 213722	Myanmar	Le Kaing, Pwint Byu, Min Bu, Magway	F	
146	*T. uetzi*	CAS 215343	Myanmar	Ma Bin, Sagaing	F	
147	*T. uetzi*	CAS 214110	Myanmar	Popa Mt. Mandalay	F	
148	*T. uetzi*	CAS 210691	Myanmar	Kyaukpadaung, Mandalay	F	
149	*T. uetzi*	CAS 235954	Myanmar	Nyaungshwe, Taunggyi, Shan	F	Paratype
150	*T. uetzi*	CAS 214110	Myanmar	Popa Mt. Mandalay	F	
151	*T. uetzi*	CAS 210691	Myanmar	Kyaukpadaung, Mandalay	F	Paratype
152	*T. uetzi*	CAS 210690	Myanmar	Kyaukpadaung, Mandalay	F	
153	*T. uetzi*	CAS 246953	Myanmar	Yesagyo, Pakhokku, Magway	F	
154	*T. uetzi*	CAS 242985	Myanmar	Gangaw, Pakhokku, Magway	F	
155	*T. uetzi*	CAS 234852	Myanmar	Mindat, Chin	F	Paratype
156	*T. uetzi*	CAS 215540	Myanmar	Mon Ywa, Sagaing	F	Paratype
157	*T. uetzi*	CAS 215472	Myanmar	Mon Ywa, Sagaing	F	Paratype
158	*T. uetzi*	CAS 210109	Myanmar	Alaungdaw Kathapa, Sagaing	F	Paratype
159	*T. uetzi*	CAS 235958	Myanmar	Phalum, Chin	F	

Appendix Table S2. List of morphological variables recorded from each specimen studied.

Number	Abbreviation	Meaning	Code
1	Sex	Sex	**1**: male; **2**: female; **3**: unsexed
2	SVL	Snout-vent length	value
3	TaL	Tail-length	value
4	TL	Total length	value
5	TaL/TL	ratio tail length / TL	value
7	Ven	Number of ventrals	value
9	Sc	Number of subcaudals	value
11	ASR	Number of scale-rows on neck	value
12	MSR	Number of scale-rows at midbody	value
13	DSR	Number of scale rows before vent	value
14	KSR	Keeling of dorsal scales at midbody in males	**0**: smooth; **1**: weakly keeled; **2** distinctly keeled
16	SL-l	Number of supralabials at left	value
17	SL-r	Number of supralabials at right	value
18	Σ SL	Total number of supralabials	value
19	C3SL/SubOc-l	Number of scales between 3rd SL and subocular (left)	value
20	C3SL/SubOc-r	Number of scales between 3rd SL and subocular (right)	value
19	C4SL/SubOc-l	Number of scales between 4th SL and subocular (left)	value
20	C4SL/SubOc-r	Number of scales between 4th SL and subocular (right)	value
27	C45SL/SubOc-l	Number of scales between 4th and 5th SL and subocular (left)	value
28	C45SL/SubOc-r	Number of scales between 4th and 5th SL and subocular (right)	value
31	CEP	Number of cephalic scales	value
32	SC/SpOc-l	Number of scales surrounding the supraocular at left	value
33	SC/SpOc-r	Number of scales surrounding the supraocular at right	value
34	Σ SC/SpOc	Total number of scales surrounding both supraoculars	value
35	K-Occ	Keeling of occipital scales in males	**0**: smooth; **1**: weakly keeled; **2**: distinctly keeled
37	K-Tem	Keeling of temporal scales in males	**0**: smooth; **1**: weakly keeled; **2**: distinctly keeled
39	IN-sep	Number of scale(s) between the internasals	value
40	Sn-SC	Number of scales on the snout	value
41	He-SC	Number of scales on upper head	value
42	IL-l	Number of infralabials at left	value
43	IL-r	Number of infralabials at right	value
44	Σ IL	Total number of infralabials	value
45	HL	Head length	value
46	HL/SVL	Ratio head length / snout-vent length in males	value
48	SnL	Snout length	value
49	SnL/HL	Ratio snout length / head length in males	value
51	ED	Eye diameter (vertical)	value
52	DEL	Distance eye-lip	value
53	SnL/ED	Ratio snout length / eye diameter in males	value
55	ED/DEL	Ratio eye diameter / distance eye-lip in males	value
57	D E-nostril	Distance eye-nostril	value
58	D E-pit	Distance eye-pit	value

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Appendix Table S2. (Continued)

Number	Abbreviation	Meaning	Code
59	D E-nostril/HL	Ratio distance eye-nostril / head length in males	value
61	D E-pit/HL	Ratio distance eye-pit / head length in males	value
63	D E-pit/D E-nostril	Ratio distance eye-pit / distance eye-nostril in males	value
65	W-In	Width of internasal	value
66	L-SpOc	Length of supraocular(s)	value
67	W-SpOc	Width of supraocular(s)	value
68	L-SpOc/W-SpOc	Ratio length of SupOc / Width of SupOc	value
69	W-In/W-SpOc	Ratio width of internasals / Width of SupOc	value
70	W-SpOc/W-In	Ratio width of SupOc / Width of internasals	value
71	L-3SL	Length of 3rd supralabial	value
72	H-3SL	Height of 3rd supralabial	value
73	L-3SL/H-3SL	Ratio length of 3rd supralabial / height of 3rd supralabial	value
74	L-3SL/HL	Ratio length of 3rd SL / head length in males	value
76	H-4SL	Height of 4th supralabial	value
77	H-4SL/H-3SL	Ratio height of 4th supralabial / heigth of 3rd supralabial	value
78	BoCol	Body color	**1**: green
79	DorBan	Presence of dark dorsal bands	**0**: absent; **1**: present
80	DorDots	Presence of white vertebral dots	**0**: absent; **1**: present
81	EyeCol	Eye color	**1**: red; **2**: yellow, gold or greenish yellow; **3**: green; **4**: orange
82	POcStr	Postocular streak	**0**: absent; **1**: present
83	COLPOcStr	Postocular streak	**0**: absent; **1**: white; **2**: red above, white below
84	VLSTRIPE	Ventrolateral stripe	**0**: absent; **1**: present
85	COLVLSTRIPE	Ventrolateral stripe	**0**: absent; **1**: cream or bluish-white; **2**: white above, red below
86	TAILPAT	Tail pattern (dorsal surface)	**1**: blotched, no sharp limit with green; **2**: uniform, sharp limit with green

Appendix Table S3. Sequences and voucher specimens of the genus *Trimeresurus* and outgroup taxa used in this study.

No.	Taxon	Collection ID	Locality	Cytb	Source
	Subgenus *Trimeresurus*				
1	*T. albolabris*	AM A157	Hong Kong, China	AF171884	Malhotra & Thorpe (2000)
2	*T. albolabris*	AM B6	Cilacap, Java, Indonesia	AF517186	Creer *et al*. (2003)
3	*T. albolabris*	AM B22	Nonthaburi, Thailand	AF517189	Creer *et al*. (2003)
4	*T. albolabris*	AM B117	Ho Chi Minh, Vietnam	AF517190	Creer *et al*. (2003)
5	*T. albolabris*	ROM 30854	Tam Dao, Vinh Phuc, Vietnam	AY352769	Malhotra & Thorpe (2004)
6	*T. albolabris*	ROM 34544	Gia Lai, Vietnam	AY352770	Malhotra & Thorpe (2004)
7	*T. albolabris*	GP 1087	Cenxi, Guangxi, China	KP999364	Zhu *et al*. (2016)
8	*T. albolabris*	GP 1472	Sekong, Laos	KP999370	Zhu *et al*. (2016)
9	*T. albolabris*	GP 2534	Fujian, China	KP999403	Zhu *et al*. (2016)
10	*T. albolabris*	GP 5	Hainan, China	KP999410	Zhu *et al*. (2016)
11	*T. albolabris*	GP 977	Guangxi, China	KP999420	Zhu *et al*. (2016)
12	*T. albolabris*	ROM 27475	Kon Tum, Vietnam	KP999428	Zhu *et al*. (2016)
13	*T. albolabris*	ROM 34545	Gia Lai, Vietnam	KP999432	Zhu *et al*. (2016)
14	*T. albolabris*	ROM 35300	Hai Duong, Vietnam	KP999435	Zhu *et al*. (2016)
15	*T. albolabris*	ROM 35323	Cao Bang, Vietnam	KP999438	Zhu *et al*. (2016)
16	*T. albolabris*	SYS r001526	Guangdong, China	MK201514	Li *et al*. (2020)
17	*T. albolabris*	GV 2019111704	Tam Dao, Vinh Phuc, Vietnam	MN746390	Chen *et al*. (2021)
18	*T.* cf. *albolabris*	AM B47	Phetburi, Thailand	AF517187	Creer *et al*. (2003)
19	*T.* cf. *albolabris*	AM B 20	Nakhon Si Thammarat, Thailand	GQ428474	Malhotra *et al*. (2010)
20	*T. andersoni*	AM A77	Andam, India	AF171922	Malhotra & Thorpe (2000)
21	*T. cantori*	AM A85	Nicobar, India	AF171889	Malhotra & Thorpe (2000)
22	*T. caudornatus*	CAS 216144	Mandalay, Myanmar	KP999351	Zhu *et al*. (2016)
23	*T. caudornatus*	CAS 216173	Mandalay, Myanmar	KP999352	Zhu *et al*. (2016)
24	*T. caudornatus*	ZMNH AR1238	Yingjiang, Yunnan, China	MK575036	Chen *et al*. (2020)
25	*T. caudornatus*	ZMNH AR1239	Yingjiang, Yunnan, China	MK575037	Chen *et al*. (2020)
26	*T. caudornatus*	CAS 235956	Indawgyi, Kachin, Myanmar	ON804486	Chan *et al* (2022)
27	*T. erythrurus*	CAS 239745	Rakhine, Myanmar	KP999357	Zhu *et al*. (2016)
28	*T. fasciatus*	AM B212	Tanadjampea, Indonesia	GQ428475	Malhotra *et al*. (2010)
29	*T. guoi*	AM A165	Loei, Thailand	AF517185	Creer *et al*. (2003)
30	*T. guoi*	AM A229	Pha Yao, Thailand	AY059566	Malhotra & Thorpe (2004)
31	*T. guoi*	CAS 222595	Mon, Myanmar	KP999354	Zhu *et al*. (2016)
32	*T. guoi*	KIZ 05191	Mengla, Yunnan, China	KP999424	Zhu *et al*. (2016)
33	*T. guoi*	ROM 39389	Lao Cai, Vietnam	KP999440	Zhu *et al*. (2016)
34	*T. guoi*	YNJC0012	Yunnan, China	MN746393	Chen *et al*. (2020)
35	*T. guoi*	JCR 2019062401	Jiangcheng, Yunnan, China	MN746395	Chen *et al*. (2020)
36	*T. guoi*	DL 20190906	Simao, Yunnan, China	MN746396	Chen *et al*. (2020)
37	*T.* cf. *guoi*	GP 3565	Mengzi, Yunnan, China	KT216372	Guo *et al*. (2015)
38	*T.* cf. *guoi*	GP 3566	Mengzi, Yunnan, China	KT216374	Guo *et al*. (2015)
39	*T.* cf. *guoi*	GP 3567	Mengzi, Yunnan, China	KT216375	Guo *et al*. (2015)
40	*T. insularis*	AM B7	Timor, Indonesia	AY059568	Malhotra & Thorpe (2004)
41	*T. purpureomaculatus*	AM B139	Perak, Malaysia	AY352771	Malhotra & Thorpe (2004)
42	*T. ayeyarwadyensis*	CAS 212246	Ayeyarwade, Myanmar	AY352772	Malhotra & Thorpe (2004)
43	*T. salazar*	AM A100	Mahattari, Nepal	AF171909	Malhotra & Thorpe (2000)
44	*T. salazar*	CESS 331	Meghalaya, India	MT762236	Mallik *et al*. (2021)

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Appendix Table S3. (Continued)

No.	Taxon	Collection ID	Locality	Cytb	Source
45	*T. septentrionalis*	CESS 388	Foothills of Himalayas, India	MT762239	Mallik *et al*. (2021)
46	*T. septentrionalis*	V 39	Mussoorie, Uttarakhand, India	MG995825	Vaishnavi *et al*. unpublished
47	*T. septentrionalis*	AM B487	Kathmandu, Nepal	AY352755	Malhotra & Thorpe (2004)
48	*T. uetzi*	CAS 215472	Sagaing, Myanmar	KP999348	Malhotra & Thorpe (2004)
49	*T. uetzi*	CAS 215540	Sagaing, Myanmar	KP999349	Zhu *et al*. (2016)
50	*T. uetzi*	CAS 215604	Sagaing, Myanmar	KP999350	Zhu *et al*. (2016)
51	*T. uetzi*	CAS 220124	Chin, Myanmar	KP999353	Zhu *et al*. (2016)
52	*T. uetzi*	CAS 232480	Mandalay, Myanmar	KP999355	Zhu *et al*. (2016)
53	*T. uetzi*	CAS 234852	Chin, Myanmar	KP999356	Zhu *et al*. (2016)
54	*T. uetzi*	CAS 243051	Magway, Myanmar	KP999360	Zhu *et al*. (2016)
55	*T. uetzi*	CAS 243086	Magway, Myanmar	KP999361	Zhu *et al*. (2016)
56	*T. uetzi*	CAS 243144	Magway, Myanmar	KP999362	Zhu *et al*. (2016)
57	*T. uetzi*	CAS 210301	Alaungdaw, Kathapa, Sagaing, Myanmar	ON804499	Zhu *et al*. (2016)
58	*T. uetzi*	CAS 243175	Gangaw, Magway, Myanmar	ON804500	Zhu *et al*. (2016)
	Out group				
59	*Trimeresurus (Viridovipera) gumprechti*	KIZ 047083	Jingdong, Yunnan, China	KT216398	Guo *et al*. (2015)
60	*Trimeresurus (Viridovipera) stejnegeri*	GP 475	Qimen, Anhui, China	KX019099	Guo *et al*. (2015)
61	*Trimeresurus (Viridovipera) truongsonensis*	VNUH 190606 = AM B659	Phong Nha-Ke Bang, Quang Binh, Vietnam	EU443815	Dawson *et al*. (2008)
62	*Trimeresurus (Viridovipera) yunnanensis*	SCUM 035114 =GP 38	Huili, Sichuan, China	EF597523	Dawson *et al*. (2008)
63	*Trimeresurus (Viridovipera) sichuanensis*	GP 07	Hejiang, Sichuan, China	HQ850447	Guo & Wang (2011)
64	*Trimeresurus (Viridovipera) mayaae*	BNHS-365	Ri-Bhoi, Meghalaya, India	OM966860	Rathee *et al*. (2022)
65	*Trimeresurus (Viridovipera) medoensis*	KIZ YPX46123	Tibet, China	MW133479	Che *et al*. unpublished
66	*Trimeresurus (Viridovipera) vogeli*	AM B97	Nakhon Si Ratchasima, Thailand	AY059574	Malhotra & Thorpe (2004)
67	*Trimeresurus (Trimeresurus) kuiburi*	N.a	Kui Buri, Prachuap Khiri Khan, Thailand	MW806923	Sumontha *et al*. (2021)
68	*Trimeresurus (Trimeresurus) venustus*	AM A241	Nakhon Si Thammarat, Thailand	AF171914	Malhotra & Thorpe (2000)
69	*Trimeresurus (Trimeresurus) kanburiensis*	AM B522	Kanchanaburi, Thailand	AY289225	Malhotra & Thorpe (2000)
70	*Trimeresurus (Trimeresurus) macrops*	AM B27	Bangkok, Thailand	AF517184	Creer *et al*. (2003)
71	*Trimeresurus (Himalayophis) arunachalensis*	APF/SFRI–1871	Arunachal Pradesh, India	MK720609	Captain *et al*. (2019)
72	*Trimeresurus (Himalayophis) tibetanus*	ZMB 65641 = AM B258	Helambu, Nepal	AY352749	Malhotra & Thorpe (2004)
73	*Trimeresurus (Popeia) sabahi barati*	MZB-OPHI5197	Jambi, Sumatra, Indonesia	KP899264	Wostl *et al*. (2016)

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Appendix Table S3. (Continued)

No.	Taxon	Collection ID	Locality	Cytb	Source
74	*Trimeresurus (Popeia) sabahi fucatus*	A203	Thung Song, Nakhon Si Thammarat, Thailand	AY371796	Sanders *et al*. (2006)
75	*Trimeresurus (Popeia) sabahi buniana*	LSUHC 6118	Pulau Tioman, Pahang, Malaysia	KX660502	Figueroa *et al*. (2016)
76	*Trimeresurus (Popeia) sabahi sabahi*	B344	Mt Kinabalu, Sabah, Malaysia	AY371815	Sanders *et al*. (2006)
77	*Trimeresurus (Popeia) sabahi toba*	MZB-OPHI5342	Sumatra Utara, Indonesia	KP899266	Wostl *et al*. (2016)
78	*Trimeresurus (Popeia) popeiorum*	DL 2017070101	Yingjiang, Yunnan, China	MH779875	Chen *et al*. (2019)
79	*Trimeresurus (Popeia) tenasserimensis*	USNM 587988	Lenya, Tanintharyi, Myanmar	MF476867	Mulcahy *et al*. (2017)
80	*Trimeresurus (Popeia) lanna*	GP 3328	Mengla, Yunnan, China	KT216361	Guo *et al*. (2015)
81	*Trimeresurus (Popeia) phuketensis*	LSUHC 7566	Thailand	KX660505	Figueroa *et al*. (2016)
82	*Trimeresurus (Popeia) nebularis*	LSUHC 10268	Cameron Highlands, Pahang, Malaysia	KX660506	Figueroa *et al*. (2016)
83	*Trimeresurus (Parias) flavomaculatus*	AM B4	Mindanao, Philippines	AY352764	Figueroa *et al*. (2016)
84	*Trimeresurus (Parias) mcgregori*	AM B289	Batan, Philippines	AY371831	Sanders *et al*. (2004)
85	*Trimeresurus (Parias) malcolmi*	AM B349	Mt. Kinabalu, Sabah, Borneo, Malaysia	AY371832	Sanders *et al*. (2004)
86	*Trimeresurus (Parias) sumatranus*	B367	Bengkulu, Sumatra, Indonesia	AY371824	Sanders *et al*. (2004)
87	*Trimeresurus (Parias) schultzei*	AM B210	Palawan, Philippines	AY352756	Malhotra & Thorpe (2004)
88	*Trimeresurus (Parias) hageni*	AM B33	Songhkla, Thailand	AY059567	Malhotra & Thorpe (2004)
89	*Craspedocephalus gramineus*	CESS 056	Amboli, Maharashtra, India	MT762212	Mallik *et al*. (2021)
90	*Craspedocephalus occidentalis*	CESS 040	Karnataka, India	MT762208	Mallik *et al*. (2021)
91	*Craspedocephalus trigonocephalus*	RAP0453	Sri Lanka	KC347479	Pyron *et al*. (2013)
92	*Craspedocephalus strigatus*	CESS142	Kerala, India	MT762220	Mallik *et al*. (2021)
93	*Craspedocephalus malabaricus*	CESS273	Karnataka, India	MT762234	Mallik *et al*. (2021)
94	*Craspedocephalus travancoricus*	CESS074	Kerala, India	MT762213	Mallik *et al*. (2021)
95	*Craspedocephalus peltopelor*	CESS108	Kerala, India	MT762218	Mallik *et al*. (2021)
96	*Craspedocephalus borneensis*	B301	East, Malaysia	AY352754	Malhotra & Thorpe (2004)
97	*Craspedocephalus wiroti*	No number	Thailand	DQ646788	David *et al*. (2006)
98	*Craspedocephalus puniceus*	B 392	Indonesia	AY352757	Malhotra & Thorpe (2004)
99	*Azemiops feae*	AM B499	China	AY352747	Malhotra & Thorpe (2004)
100	*Protobothrops elegans*	UMMZ 199970	Japan	AY223575	Parkinson *et al*. (2002)

Appendix Table S4. Uncorrected *p*-distances (percentage) between the sequences of cyt *b* mtDNA gene of species of the complex of *Trimeresurus albolabris* and *T. septentrionalis* species groups distributed in Indo-Burma area included in the phylogenetic analyses of this study.

No.	Species	1	2	3	4	5	6	7	8	9
1	***T. caudornatus***	**0.0–2.6%**								
2	***T. albolabris***	6.7–9.6%	**0.1–4.3%**							
3	***T.* cf. *albolabris***	5.8–7.3%	3.4–6.2%	**1.40%**						
4	***T.* cf. *guoi***	5.9–6.5%	2.6–3.2	2.5–4.7%	**0**					
5	***T. guoi***	5.6–7.2%	3.6–6.0%	2.8–4.2%	2.3–3.3%	**0.0–1.8%**				
6	***T. salazar***	5.3–7.3%	7.5–10.2%	7.3–8.5%	7.1–7.8%	6.9–8.5%	**1.20%**			
7	***T. septentrionalis***	5.9–6.9%	7.0–8.7%	6.2–7.4%	6.0–6.8%	5.9–7.4%	5.9–6.9%	**0.4–1.6%**		
8	***T. uetzi***	5.8–7.0%	6.9–9.9%	6.1–6.9%	6.1–7,3%	6.5–8.2%	5.9–7.6%	6.4–6.9%	**0.0–3.6%**	
9	***T. insularis***	7.3–8.4%	7.8–10.1%	8.0–8.2%	7.60%	6.5–7.2%	8.0–8.6%	7.2–8.0%	8.3–9.0%	**0**

Appendix Table S5. Statistically significant differences between *Trimeresurus caudornatus* and the remaining members of *Trimeresurus* in the *T. albolabris* and *T. septentrionalis* species groups based on Mann–Whitney U Tests. See Appendix Table S2 for acronyms of morphological characters. Data left of the gray line represent male specimens, whereas data right of the gray line represent female specimens. Data with an asterisk (*) represent test results with p-values less than 0.01.

Taxon	*albolabris*	*caudornatus*	*guoi*	*salazar*	*septentrionalis*	*uetzi*
albolabris	–	VEN, VEN+SC	–	–	VEN*, SC*, VEN+SC*	VEN*, SC*, SL*, IL
caudornatus	VEN*, VEN+SC	–	–	–	VEN*, SC*, VEN+SC*	SC*, IL
guoi	VEN*		–	–	SC*, VEN+SC*	VEN, SC
salazar	VEN*		VEN	–	–	–
septentrionalis	VEN*, SC*, VEN+SC*	SC	SC*, VEN+SC	–	–	VEN*, VEN+SC*
uetzi	VEN*			–	SC	–

Appendix Table S6. Detailed infomation on *Trimeresurus caudornatus* specimens from Myanmar preserved at CAS (see: https://researcharchive.calacademy.org/research/herpetology/catalog/Index.asp or http://portal.vertnet.org/search?q=Trimeresurus+CAS+Myanmar)

Collection number	Verified by molecular	Verified by morphology	Previous ID	Proposed ID	Field number	Sex	Date collected	Elevation
CAS 216144	yes	yes	*T. septentrionalis*	*T. caudornatus*	JBS-5776	adult female	4/10/2000	No data
CAS 216173	no	yes	*T. septentrionalis*	*T. caudornatus*	JBS-5847	adult male	12/10/2000	No data
CAS 216173	yes	no	*T. albolabris*	*T. caudornatus*	JBS-5847	adult male	12/10/2000	No data
CAS 221549	no	yes	*T. septentrionalis*	*T. caudornatus*	JBS-10322	adult male	17/9/2001	No data
CAS 224646	no	yes	*T. septentrionalis*	*T. caudornatus*	JBS-12289	adult male	13/4/2002	560 m
CAS 230260	no	yes	*T. yunnanensis*	*T. caudornatus*	JBS-13002	adult female	13/6/2002	No data
CAS 232425	no	yes	*T. septentrionalis*	*T. caudornatus*	JBS-16900	adult female	2/4/2003	234 m
CAS 235956	yes	yes	*T. erythrurus*	*T. caudornatus*	JBS-17204	adult female	7/5/2003	169 m
CAS 241264	no	yes	*Trimeresurus* sp.	*T. caudornatus*	MHS-25907	adult male	19/7/2008	215 m
CAS 244953	no	yes	*T. septentrionalis*	*T. caudornatus*	JBS-15459	adult male	1/11/2002	155 m
CAS 245234	no	yes	*T. septentrionalis*	*T. caudornatus*	MHS-28046	subadult female	7/7/2009	304 m

Appendix Table S6. (Continue)

Collection number	Collecter (CAS team)	Biology	Location
CAS 216144	H. Win & T. Thin	1940 hrs. Air temp. 76.5 F. Relative humidity 92%. In tree.	Myanmar: Mandalay Region: Pyin Oo Lwin District: Tha Bake Kyin Township, Shwe U Daung Wildlife Sanctuary, N 22 52 28.4, E 96 05 25.2
CAS 216173	H. Win, T. Thin & S.L. Oo	2040 hrs. Air temp. 84.2 F. Relative humidity 69%. In shrub.	Myanmar: Mandalay Region: Pyin Oo Lwin District: Tha Bake Kyin Township, Shwe U Daung Wildlife Sanctuary, Kyauk Kyi Village, N 22 58 37.4, E 96 05 54.3
CAS 216173	H. Win, T. Thin and S.L. Oo	2040 hrs. Air temp. 84.2 F. Relative humidity 69%. In shrub.	Myanmar: Mandalay Division: Pyin Oo Lwin District: Tha Bake Kyin Township, Shwe U Daung Wildlife Sanctuary, Kyauk Kyi Village, N 22 58 37.4, E 96 05 54.3
CAS 221549	K.S. Lwin & H. Tun	Stomach contained a *Sphenomorphus indicus* (in separate vial), swallowed tail first.	Myanmar: Kachin State: Putao Dist.: Putao Township: Ahtonga Village, 27 15 41.8 N, 97 48 10.0 E
CAS 224646	H. Win, Y.N.T. Na, H. Ram & S. Di	1609 hrs. In termite mound, 10 inches deep.	Myanmar: Kachin State: Putao District: Nagmung Township: Nagmung Town, 27 30 36.5 N, 97 49 50.4 E, 1840 ft
CAS 230260	H. Win, K.S. Lwin, A.K. Shein & H. Tun	No data	Myanmar: Kachin State: Tanai Township, Ma Kaw Village; along the Lero Road, in Hukaung Valley Sanctuary, N 26 27 00.0 E 96 41 35.5
CAS 232425	H. Win, K.S. Lwin & A.K. Shein	Under log.	Myanmar: Kachin State: Ta Nai Township, Ta Ruing Village, N 26 35 24.6, E 96 29 19.3, 770 ft
CAS 235956	G.O.U. Wogan, J.A. Wilkinson, J.V. Vindum, H. Win, T. Thin, K.S. Lwin, A.K. Shein & W. Aung	2206 hrs. Air temp. 79 F, 78% relative humidity. In bush, 1 m above ground.	Myanmar: Kachin State: Mohnyin Township, Lone Ton Village, Indawgyi Wildlife Sanctuary, 25 05 54.2 N, 96 17 20.1 E, 557 ft
CAS 241264	K.T. Kyaw, M. Win, Y.M. Win & S.L. Oo	2230 hrs. Air temp. 84.0 F, 89% relative humidity.	Myanmar: Kachin State: Mohnyin Township, Indawgyi Wildlife Sanctuary, NW of Nyang Bin village, 25 16 09.8 N, 96 20 32.7 E, 707 ft
CAS 244953	T. Thin, K.S. Lwin & H. Tun	1948 hrs. Air temp. 75.2 F. 85% relative humidity. On boat beside river.	Myanmar: Sagaing Region: Homalin Township, North of Swekawngaw, 25 22 19.6 N, 95 21 44.9 E, 510 ft
CAS 245234	M. Hlaing, S.L. Oo, Z.H. Aung, Y.M. Win & K.S. Lwin	2105 hrs. Air temp. 86.0 F, 75% relative humidity.	Myanmar: Kachin State: Myitkyina District, Chipwe Township: East side of Chipwe Town, 25 52 54.2 N, 98 07 55.2 E, 998 ft

Appendix Table S7. Comparison of morphological characteristics of *Trimeresurus caudornatus* with those of the *Trimeresurus albolabris* and *T. septentrionalis* species groups distributed in Indo-Burma area.

Species	Body pattern	Ventral color	Ventrolateral body stripes	Postocular stripe in males	1 or 2 small scales in front of the pit	Temporal scales	Dorsal body scales	Iris color	MSR	TaL/TL (Males)	TaL/TL (Females)
caudornatus	verdant green	yellow green	absent	absent	absent	hardly keeled	feebly keeled	golden yellow	21 (22 or 23)	0.18–0.22 (0.20±0.02, n=14)	0.14–0.18 (0.16±0.01, n=19)
albolabris	multicolor (verdant green, yellowish-green, cream)	yellow	present	present	usually present	hardly keeled	moderately keeled	copper	21 (19)	0.19–0.21 (0.20±0.01, n=55)	0.14–0.17 (0.15±0.01, n=81)
guoi	yellow green	yellow green	absent	absent	absent	hardly keeled	moderately keeled	Firebrick-red	21	0.14–0.22 (0.19±0.22, n=23)	0.15–0.20 (0.16±0.01, n=18)
salazar	Yellowish- green	yellowish green	present	present	absent	hardly keeled	moderately keeled	copper	21 (19)	0.15–0.20 (0.18±0.02, n=6)	0.14–0.15 (0.15±0.01, n=3)
septentrionalis	verdant green	yellow green	absent or present	absent	absent	hardly keeled	feebly keeled	green gold or copper	21	0.19–0.23 (0.21±0.02, n=6)	0.15–0.17 (0.16±0.01, n=14)
uetzi	verdant green or yellowish green	yellowish green	present	present	absent	hardly keeled	moderately keeled	copper or green gold	21	0.16–0.22 (0.20±0.02, n=10)	0.14–0.16 (0.15±0.01, n=11)

Appendix Table S7. (Continue)

Species	VEN (Males)	VEN (Females)	SC (Males)	SC (Females)	VEN+SC (Males)	VEN+SC (Females)	Hemipenes	Distribution	Sources
caudornatus	158–167 (162.43±2.71, n=14)	158–174 (162.89±4.86, n=19)	53–74 (68.07±5.38, n=14)	52–68 (57.41±4.69, n=17)	219–241 (230.50±5.96, n=14)	211–242 (219.82±7.88, n=17)	reaching SC 37–38	China, Myanmar	Zhao *et al*. (1998); Chen *et al*. (2020); our data
albolabris	146–162 (154.93±4.67, n=70)	151–172 (158.80±4.78, n=112)	40–75 (63.08±8.44, n=67)	49–64 (53.54±3.71, n=104)	210–232 (218.00±11.04, n=64)	200–232 (211.58±7.34, n=104)	reaching SC 15–18	China, Vietnam, Laos, Cambodia, Thailand, Indonesia	Vogel *et al*. (2023); our data
guoi	154–167 (159.95±4.19, n=27)	155–167 (161.07±3.73, n=18)	52–75 (66.37±5.25, n=25)	53–69 (58.64±4.68, n=18)	210–242 (226.00±7.67, n=25)	210–228 (219.71±5.98, n=18)	reaching SC 23–32	China, Vietnam, Laos, Thailand, Myanmar	Chen *et al*. (2021); our data
salazar	163–170 (166.40±2.88, n=6)	167–171 (169.33±2.08, n=3)	62–73 (68.80±4.21, n=6)	56–59 (58.00±1.73, n=3)	225–241 (235.20±6.22, n=6)	223–230 (227.33±3.79, n=3)	reaching SC 12–13	India, Nepal, Bhutan, Bangladesh?	Mirza *et al*. (2020); Rathee *et al*. (2021); our data
septentrionalis	164–170 (165.00±4.56, n=6)	162–173 (168.94±2.59, n=16)	71–80 (76.67±3.50, n=6)	56–66 (63.07±2.53, n=14)	238–250 (241.67±7.76, n=6)	224–237 (231.79±3.68, n=14)	reaching SC 5–7	Nepal, India	Kramer (1977); our data
uetzi	154–172 (163.27±5.61, n=11)	157–171 (164.14±3.84, n=16)	60–71 (66.90±3.35, n=10)	50–55 (52.08±1.62, n=14)	216–240 (230.4±7.88, n=10)	209–223 (216.08±3.99, n=14)	reaching SC 6–8 (n=2)	Myanmar, India	Vogel *et al*. (2023); Biakzuala *et al*. (2024)

Appendix Table S8. Literature used for the revised distribution of *Trimeresurus caudornatus*. Remark: ?: requested verification

Nr on the map	Verified by morphology	Verified by molecular	Locality	Sources
1	no	no	Nabang, Yingjiang, Dehong, Yunnan, China (type locality)	Chen *et al*. (2020)
2	no	yes	Tongbiguan, Yingjiang, Dehong, Yunnan, China	Li *et al*. (2020)
3	yes	no	Chuxiong Yi, Yunnan, China	Vogel *et al*. (2023); our data
4	yes	no	Putao, Kachin, Myanmar	Vogel *et al*. (2023); our data
5	yes	no	Hukaung WS, Myitkyina , Kachin, Myanmar	our data
6	yes	no	Chipwe, Myitkyina, Kachin, Myanmar	our data
7	yes	no	Htingnan, Kachin, Myanmar	Smith (1940); our data
8	yes	yes	Indawgyi Lake, Myitkyina, Kachin, Myanmar	Vogel *et al*. (2023); our data
9	yes	no	Bhamo, Kachin, Myanmar	our data
10	yes	no	Homalinn, Khandi, Sagaing, Myanmar	Vogel *et al*. (2023); our data
11	no	yes	Chatthin WS., Sagaing, Myanmar	our data
12	yes	yes	Shwe U Daung, Pyin Oo Lwin, Mandalay, Myanmar	Vogel *et al*. (2023); our data
13?	no	yes	Longchuan, Dehong, Yunnan, China	Zhao *et al*. (1998); Zhang & Rao (2008); Zhu *et al*. (2022)
14?	no	yes	Tuantian, Tengchong, Baoshan, Yunnan, China	Zhao *et al*. (1998); Zhang & Rao (2008); Zhu *et al*. (2022)