



An integrative taxonomic revision of the *Trimeresurus popeiorum* group of pitvipers (Reptilia: Serpentes: Viperidae) with descriptions of two new species from the Indo-Burma Biodiversity Hotspot

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Abstract

Despite recent progress in our understanding of diversity within the genus *Trimeresurus* Lacépède, 1804, the subgenus *Popeia* Malhotra & Thorpe, 2004, distributed across most parts of East and Southeast Asia, remains taxonomically challenging. We applied an integrative taxonomic approach including analyses of morphological data and four mitochondrial genes (12S and 16S rRNA, cytochrome *b*, and NADH dehydrogenase subunit 4), along with examination of available type material, to address longstanding taxonomic questions in one clade within *Popeia*, the *T. popeiorum* group, and reveal a high level of hidden diversity of these snakes in the Indo-Burma Biodiversity Hotspot. We confirm that *T. popeiorum* Smith, 1937 sensu stricto is restricted to Northeast India, eastern Nepal, southern Bhutan, southeastern Bangladesh, western Yunnan Province (China), and northern and southwestern Myanmar. We further confirm that the recently described species *T. yingjiangensis* Chen et al., 2019 is a junior synonym of *T. popeiorum*. In addition, we discovered that the combination *Trimeresurus* [sic] *elegans* Gray, 1853 is a valid senior synonym of *T. popeiorum* and threatens the stability of the latter taxon. Therefore, in order to protect the nomen *popeiorum* and in accordance with Article 23.9 of the International Code of Zoological Nomenclature, we regard the taxon *Trimeresurus elegans* as a nomen oblitum and render *Trimeresurus popeiorum* a nomen protectum. Examination of a larger series of specimens allows us to describe two new cryptic species of *Trimeresurus* from the Indo-Burma Region. This study brings the total number of species in the subgenus *Popeia* to six and also suggests that the subspecific taxonomy of the *T. sabahi* complex requires further investigation. We urge adequate actions regarding the conservation of the newly discovered species and recommend further studies on their toxicology.

Keywords

Asia, Biodiversity, Crotalinae, ICZN, Indochina, molecular phylogeny, morphology, mtDNA, nomen protectum, nomenclature, *Popeia*, systematics

Introduction

The genus *Trimeresurus* Lacépède, 1804 has long included most pitvipers of eastern and southeastern Asia (e.g., Maslin 1942). Other authors split the genus and erected or revalidated genera, including *Ovophis* Burger, 1981, *Protobothrops* Hoge & Romano-Hoge, 1983, and *Tropidolaemus* Wagler, 1830 (Hoge and Romano-Hoge 1981; Gloyd and Conant 1990). Malhotra and Thorpe (2000) and Tu et al. (2000) established the first phylogenies of what the former authors called the “*Trimeresurus* group” and documented that *Trimeresurus* included several divergent clades. Based on a combination of morphological characters, most notably head scales and hemipenes, as well as their molecular analysis, Malhotra and Thorpe (2004) split *Trimeresurus* into seven genera: *Trimeresurus*, *Cryptelytrops* Cope, 1860, *Himalayophis* Malhotra & Thorpe, 2004, *Parias* Gray, 1849, *Peltopelor* Günther, 1864, *Popeia* Malhotra & Thorpe, 2004, and *Viridovipera* Malhotra & Thorpe, 2004. Subsequently, Guo and Wang (2011) described the genus *Sinovipera* for *S. sichuanensis* Guo & Wang, 2011, which was subsequently synonymized with *Viridovipera* by Alencar et al. (2016). Malhotra and Thorpe (2004)’s new genus-level taxonomy was adopted by several authors (e.g., Gumprecht et al. 2004).

David et al. (2011) discussed the taxonomic status of the genera defined by Malhotra and Thorpe (2004). They showed that Malhotra and Thorpe (2004) and all authors before them had made an error when identifying the type species of *Trimeresurus* Lacépède, 1804. It was neither *Coluber viridis* Bechstein, 1802 nor *Vipera viridis* Daudin, 1803 (both objective junior synonyms of *Coluber gramineus* Shaw, 1802), but the nomen oblitum *Trimeresurus viridis* Lacépède, 1804, a subjective senior synonym of *T. insularis* Kramer, 1977. Given this realization, the nomen *Trimeresurus* should be applied to a large complex of species related to *T. albolabris* Gray, 1842, which had been placed into *Cryptelytrops* by Malhotra and Thorpe (2004). Thus *Cryptelytrops* became a junior synonym of *Trimeresurus* sensu stricto (hereafter, s. str.), with the consequence that the Indian species placed into *Trimeresurus* sensu Malhotra and Thorpe (non *Trimeresurus* Lacépède, 1804) had to be placed into their own distinct genus, for which the nomen *Craspedocephalus* Kuhl & van Hasselt, 1822 was available. David et al. (2011) also discussed the taxonomic ranks of these taxa (genus vs. subgenus) and concluded that recognizing them as subgenera would maximise information within the family Viperidae. Furthermore, it was noted that these “genera” were hardly diagnosable on a morphological basis. David et al. (2011) also considered recognizing

genera that could not be diagnosed reliably using external features, such as the shape and ornamentation of the hemipenes shared between several clades, to be unhelpful to practising taxonomists (as well as for amateur herpetologists, herpetoculturists, and medical practitioners), especially when the use of molecular facilities is impractical. Consequently, following the point of view adopted by Wallach et al. (2009), David et al. (2011) recognized the distinct taxonomic status of the clades recovered by Malhotra and Thorpe (2004) but accepted the following subgenera of *Trimeresurus*: *Trimeresurus*, *Craspedocephalus*, *Parias*, *Peltopelor*, *Himalayophis*, *Popeia*, and *Viridovipera*.

The proposal by David et al. (2011) to preserve taxonomic information by using subgenera was subsequently not adopted by several authors, including Wallach et al. (2014) and Boundy (2020), who followed Malhotra and Thorpe (2004) and continued to recognize the taxa of the “*Trimeresurus* group” at the level of genus. After Mallik et al. (2021) recognized *Craspedocephalus* as a distinct genus and placed *Peltopelor* into its synonymy, Mirza et al. (2023) accepted the validity of both *Craspedocephalus* and *Peltopelor* as genera; however, further discussion of this taxonomy is beyond the scope of this paper. The departing point of our discussion is that *Trimeresurus* currently comprises five subgenera: *Trimeresurus*, *Popeia*, *Viridovipera* (including the previously recognized *Sinovipera*), *Parias*, and *Himalayophis*.

Of particular interest to us is the subgenus *Popeia* (type species *T. popeiorum*, by original designation), which was originally defined by Malhotra and Thorpe (2004) as a genus for the *T. popeiorum* group. This subgenus is distinguished by two major morphological characters: a long, slender, and calyculate hemipenis, and a distinct suture separating the first supralabial scale and the nasal scale. However, the phylogeny of Malhotra and Thorpe (2004: 93, their fig. 3) showed that a long, calyculate hemipenial morphology was not only found in members of *Popeia*, but was also observed in several species of the former subgenus *Cryptelytrops* (now the subgenus *Trimeresurus*). Subsequent studies, including those of Idiatullina et al. (2021) and Mirza et al. (2023), have confirmed the monophyly of *Popeia*. However, the species-level taxonomy of this group remains contentious, with past studies recognizing one to as many as ten species, depending on the investigating authors. As we begin our discussion of this group, *Popeia* comprises the following four species and five subspecies: *T. popeiorum* Smith, 1937; *T. nebularis* Vogel et al., 2004; *T. phuketensis* Sumontha et al., 2011; and *T. sabahi* Regenass & Kramer, 1981, with the

subspecies *T. s. sabahi* Regenass & Kramer, 1981, *T. s. barati* Regenass & Kramer, 1981, *T. s. buniana* Grismer et al., 2006; *T. s. fucatus* Vogel et al., 2004, and *T. s. toba* David et al., 2009. Hereafter, we refer to the latter clade as the *T. sabahi* complex.

Trimeresurus popeiorum Smith, 1937, as currently defined (see Vogel et al. 2004; Sanders et al. 2006; Wostl et al. 2016), is a common venomous snake distributed across parts of Northeast India, China, Bhutan, Nepal, Bangladesh, Myanmar, Laos, and Thailand. The species has been widely confused with other Asian green pitvipers in the literature, and its taxonomic status has been controversial since the work of Pope and Pope (1933). Before their revision, all green pitvipers were gathered under the name *T. gramineus* (Shaw, 1802) or its chresonyms in the genus *Lachesis* Daudin, 1803. Pope and Pope (1933) split *gramineus* into five species, with the nomen *gramineus* applied to green pitvipers ranging discontinuously from Northeast India into western Indonesia, whereas populations of green pitvipers in Peninsular India were referred to *T. occidentalis* Pope & Pope, 1933 (now *Craspedocephalus occidentalis*). Smith (1937) briefly addressed the taxonomy of *T. gramineus* (as defined by Pope and Pope 1933), and showed that these authors had misunderstood the type locality of *Coluber gramineus* Shaw, 1802, a species described based on a specimen depicted in Russell (1796: 13, his plate 9) from “Vizagapatam”, now Visakhapatnam, Andhra Pradesh State, India. Due to this mistake, Pope and Pope (1933) misapplied the name *gramineus* to snakes with long, slender, and smooth hemipenes ranging from Northeast India to west Indonesia (now in the *T. albolabris* species complex) instead of to populations with thick, spinose hemipenes inhabiting southern India, for which these authors described *T. occidentalis*. As the actual type locality of *T. gramineus* was within the range of *T. occidentalis*, Smith (1937) considered *T. occidentalis* to be a subjective junior synonym of *T. gramineus* and, therefore, named the Northeast Indian and Indonesian populations *T. popeiorum*. We purposely use the word “named” rather than “described”, as Smith clearly stated that he was proposing a new name for populations already defined by Pope and Pope (1933). Nevertheless, Smith’s taxonomic decision amounts to a Code-compliant description (ICZN 1999). The validity of *T. popeiorum* for the “eastern” pitviper species was accepted by most subsequent authors with the exception of Hoge and Romano-Hoge (1981) and Welch (1988), who still recognized *T. occidentalis*. Mallik et al. (2021) resurrected *T. occidentalis* for populations in southwestern Peninsular India and proposed to transfer this species and *T. gramineus* into the genus *Craspedocephalus*. However, Mirza et al. (2023) placed these species along with other taxa from Peninsular India and Sri Lanka into the genus *Peltopelor*.

Unfortunately, Smith (1937) failed to designate a type specimen and a type locality for *T. popeiorum*, which led Taylor and Elbel (1958) to consider all *T. gramineus* specimens referred by Pope and Pope (1933) as syntypes of *T. popeiorum*. From these specimens, they designated an adult male specimen from the British Museum of Nat-

ural History (NHMUK 72.4.17.137) as the lectotype of the species. Consequently, the type locality was restricted to “Khasi Hills, Assam”, now in Meghalaya State, India.

The taxonomy of what we call the *T. popeiorum* group within the subgenus *Popeia* was first addressed by Regenass and Kramer (1981) in a large systematic study of Asian green pitvipers. These authors described two new subspecies, *T. p. barati* and *T. p. sabahi* to accommodate populations from the islands of Sumatra and Borneo, respectively, and they conserved the nominate subspecies, *T. p. popeiorum*, for all mainland populations. This interpretation was subsequently modified in the revision of Vogel et al. (2004). These authors split *T. popeiorum*, as then defined, into five species, elevating some subspecies to full species level: *T. fucatus* from southern Peninsular Thailand and Myanmar, *T. nebularis* from the highlands of Peninsular Malaysia, *T. barati* from southern Sumatra, *T. sabahi* from Borneo, and *T. popeiorum* for all remaining mainland populations. During the same year, Sanders et al. (2004) described *Popeia inornata*, another new species in this group, currently considered a junior synonym of *T. nebularis* (see Sanders et al. 2006). Thus, *T. popeiorum* was redefined as the taxon for populations in Northeast India, Myanmar, China, northern and western Thailand, and northern Laos. Literature records of this species from Cambodia and Vietnam refer to unrelated taxa, namely species of the subgenus *Viridovipera*, including *T. gumprechtii* David et al., 2002, *T. stejnegeri* Schmidt, 1925, and *T. vogeli* David et al., 2001 (Poyarkov et al. 2023).

The *T. popeiorum* group was further revised by Sanders et al. (2006), who recognized only three major clades within it. Meanwhile, Grismer et al. (2006) described *P. buniana* from Pulau Tioman, Pahang State, West Malaysia, a taxon currently considered a subspecies of *T. sabahi* (Mulcahy et al. 2017). Another species in this group, *Trimeresurus (Popeia) phuketensis* was described by Sumontha et al. (2011) from Phuket Island, Thailand. David et al. (2009) and Wostl et al. (2016) addressed the systematics of *Trimeresurus* populations inhabiting Sundaland, with the former describing another new species, *T. toba*, based on a series of specimens collected from northern Sumatra. Wostl et al. (2016) essentially supported the taxonomy proposed by Sanders et al. (2006) and refuted the conclusions of David et al. (2009), recognizing *T. sabahi* as the taxon to encompass all populations inhabiting southern Peninsular Thailand, West Malaysia, Sumatra, and Borneo, and accepting *T. nebularis* as a distinct species from the West Malaysian highlands.

On the Asian mainland, Guo et al. (2015) reviewed the green pitviper species of Yunnan Province, China, and were the first authors to report *T. popeiorum* from that country. Moreover, Mulcahy et al. (2017) addressed the status of populations referred to as *T. popeiorum* from beyond the Indo-Burma Region (including Thailand, Vietnam, Laos, Cambodia, and Myanmar) and demonstrated the existence of two distinct Operational Taxonomic Units (hereafter, OTUs) in this area: a northern clade comprising populations inhabiting northern and eastern Myanmar, northern Thailand, northern Laos, and south-

ern China, which the authors identified as ‘true’ *T. popeiorum*, and a southern clade, yet unnamed, for populations in the Tanintharyi Region of southern Myanmar and adjacent western and southwestern Thailand. Mulcahy et al. (2017) also addressed the systematics of other *T. popeiorum* group taxa inhabiting Sundaland, where they recognized a single species, *T. sabahi*, and relegated the five taxa formerly recognized by Vogel and David (2004) to the level of subspecies (see also Wüster 2021). Although Mulcahy et al. (2017) designated two major OTUs within the ‘*T. popeiorum*’ populations of mainland Asia (namely, the northern clade, referred to as *T. popeiorum* s. str., and a southern clade, labelled as *Trimeresurus* sp. nov.), these authors refrained from formally describing the putative new species and called for further integrative taxonomic studies of the whole group. The last species described in the subgenus *Popeia* was *T. yingjiangensis*, named by Chen et al. (2019) from western Yunnan, China. At the same time, Chen et al. (2019) assigned the populations of *Popeia* from the southernmost part of Yunnan Province to *T. popeiorum*, but did not provide a detailed justification for this taxonomy.

Recently, Mirza et al. (2023) pointed out that the taxonomy of the *T. popeiorum* group still remained unresolved. Based on the inclusion of molecular data from the type locality of *T. popeiorum* as well as from other parts of Northeast India, these authors recognized six presumably species-level OTUs in the group, of which the first three included the taxa attached to populations present in southern Peninsular Thailand, West Malaysia, and Indonesia, and the other three were found in the Indo-Burma Region; these last three are the focus of this study. Among these three OTUs of interest, which all appear to be recognizable using species-level taxonomy, Mirza et al. (2023) restricted *T. popeiorum* to Northeast India, Bangladesh, northern Myanmar, and the westernmost part of Yunnan, and also demonstrated that *T. yingjiangensis* was a junior synonym of *T. popeiorum* due to overlapping morphological characters, molecular data, and range. However, Mirza et al. (2023) also refrained from making any taxonomic decisions regarding the two remaining OTUs from Indo-Burma, which likely represent undescribed species. The taxonomic history of the subgenus *Popeia* is summarized in Table S1.

In the analysis we present below, we used both molecular and morphological data to analyze variation in populations from the whole range of the *T. popeiorum* group. Pitvipers of the genus *Trimeresurus* cause a large percentage of the snakebites reported in Southeast Asia and therefore have a high medical relevance (Patikorn et al. 2022). Studies on the taxonomy and distribution of these snakes are therefore important for a better understanding of their toxicology and toxinology. While our analyses of populations in mainland Southeast Asia confirm the earlier molecular results of Mulcahy et al. (2017) and Mirza et al. (2023), our increased sampling effort allow us to address the taxonomy of populations not considered by previous researchers. These results lead us to recognize three distinct species in the Indo-Burma Region, of which two represent new species and are described below.

Material and Methods

Sampling

Fieldwork was carried out in Tak Province, Thailand, by G. Vogel in 2006 and 2007; in Chiang Mai Province, Thailand, by P. Pawangkhanant, N. A. Poyarkov, and C. Suwannapoom in August 2017 and July 2018; in Ratchaburi Province, Thailand, by P. Pawangkhanant, N. A. Poyarkov, and C. Suwannapoom in June and July 2019; in Kachin and Sagaing States of Myanmar, by N. A. Poyarkov and P. Pawangkhanant in July 2018 and July 2019; in Arunachal Pradesh State, India, by Z.A. Mirza in July 2019; and in Mizoram State, India, by G. Vogel in 2013, 2015, 2017, and 2023 (Fig. 1). GPS coordinates and elevations were recorded using a Garmin GPSMAP 60CSx GPS receiver using the WGS 84 datum. Specimens were collected in the field using snake hooks, photographed in life, and euthanized using an intracardial injection of MS-222 within 24 h after capture. Specimens were fixed in 4% buffered formalin for 24 h, stored in 70% ethanol, and deposited in the herpetological collections of the School of Agriculture and Natural Resources, University of Phayao (AUP, Phayao, Thailand), the Vietnam National Museum of Nature (VNMN, Hanoi, Vietnam), and the Zoological Museum of Moscow State University (ZMMU, Moscow, Russia). Tissues for genetic analyses were taken from the liver or heart prior to preservation of specimens and stored in 96% ethanol. Additional tissue samples were obtained from herpetological collections of the National Centre for Biological Sciences (NCBS, Karnataka, India); Chengdu Institute of Biology (CIB, Chengdu, China); Joint Vietnam - Russia Tropical Science and Technology Research Centre (VRTC, Hanoi, Vietnam); Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig (ZFMK, Bonn, Germany); and Queen Saovabha Memorial Institute, Thai Red Cross Society (QSMI, Bangkok, Thailand).

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

Species delimitation

The General Lineage Concept (GLC: de Queiroz 2007) adopted herein proposes that a species constitutes a population of organisms evolving independently from other such populations owing to a lack of gene flow. By “independently,” it is meant that new mutations arising in one

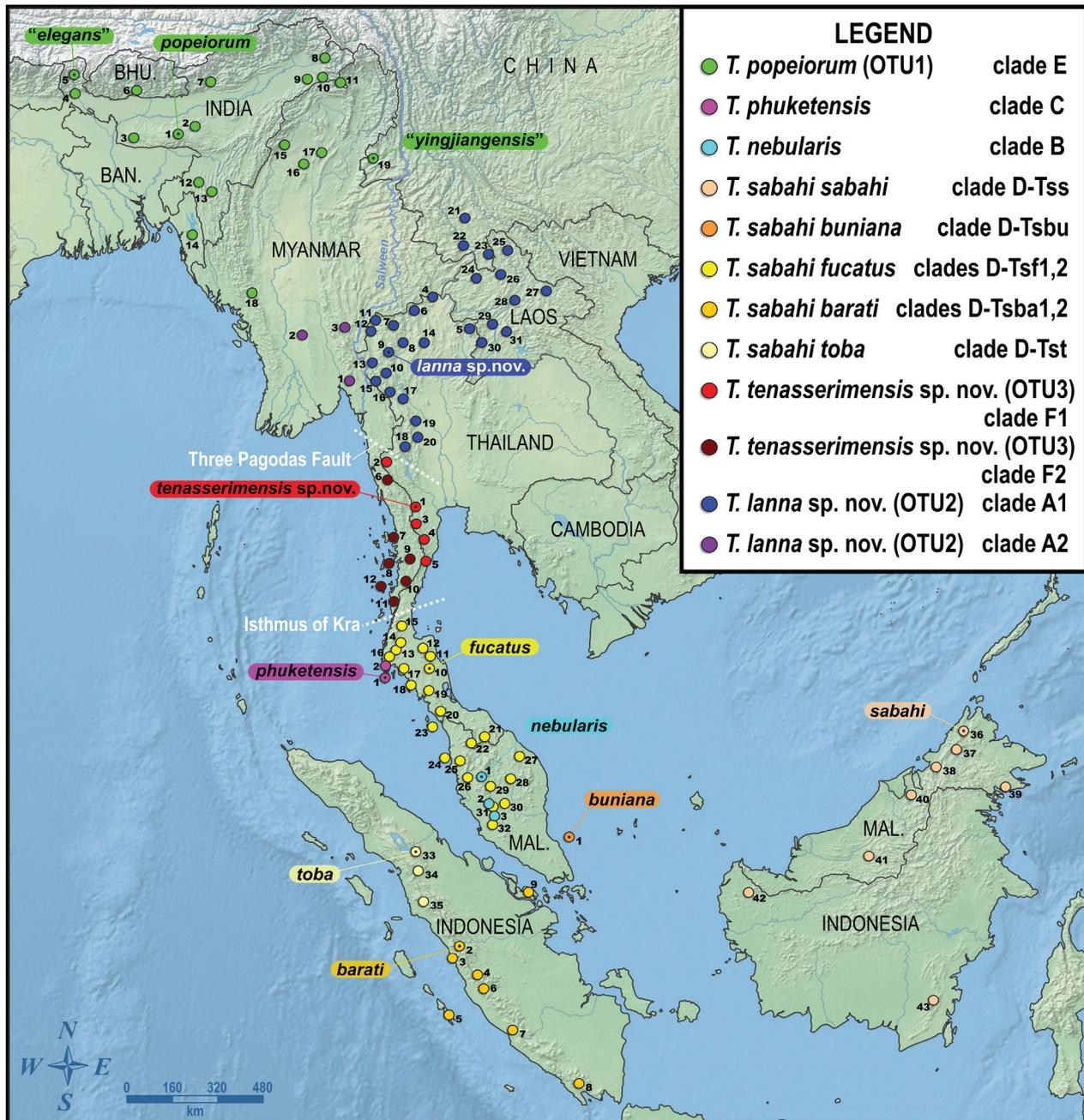


Figure 1. Distribution of the species and subspecies of the subgenus *Popeia*. Base map created using simplemappr.net. A dot in the center of a colored circle denotes type locality. Colors of circles and locality numbers correspond to those in Figures 2–3 and Appendix II; for locality information see Appendix VIII. Type localities of the included taxa are shown in colored clouds; taxon names that are not valid nomina of recognized taxa are shown in quotes.

species cannot spread readily into another species (Barclough et al. 2003; de Queiroz 2007). Under the GLC implemented here, molecular phylogenies were used to recover monophyletic mitochondrial lineages of populations, represented by individual snakes, in order to develop initial species-level hypotheses – the grouping stage of Hillis (2019). We assign OTUs to the geographically-circumscribed populations corresponding to the independent clades of the mtDNA-based, matrilineal genealogy. Discrete color pattern data and morphological data were then used to search for unique characters and patterns consistent with previous OTU designations or species-level hypotheses – the construction of boundaries representing

the hypothesis-testing step of Hillis (2019) – thus providing independent morphological diagnoses to complement the molecular analyses. In this way, species delimitation (phylogeny) and diagnostic characters (taxonomy) are not conflated (Frost and Hillis 1990; Frost and Kluge 1994; Hillis 2019; Dufresnes et al. 2023; Grismer et al. 2023).

DNA isolation and sequencing

Total genomic DNA was extracted from ethanol-preserved muscle or liver tissues using standard phenol-chloroform extraction procedures (Sambrook et al. 1989) followed by

isopropanol precipitation. We used the polymerase chain reaction (PCR) to amplify four regions of mitochondrial DNA (hereafter mtDNA): complete sequences of cytochrome *b* (*cyt b*) and NADH dehydrogenase subunit 4 gene (ND4), and partial fragments of 12S rRNA (12S) and 16S rRNA (16S). Primers used for both PCR and sequencing are summarized in Appendix I.

For *cyt b* sequences we used a modification of the PCR protocol by Dahn et al. (2018) with touchdown: (1) initial denaturation 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 50–45°C (with cool-down set at 0.5°C per 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 at 4°C for storage. For ND4, we followed the protocol of Salvi et al. (2013): (1) initial denaturation at 92°C for 3 min, followed by 16 touchdown cycles of 30 s at 92°C; (2) annealing temperature decreasing at 0.5°C per cycle from 60–52°C (30 s), and extension for 1 min at 72°C. Then 20 more cycles similar to the latter but with annealing temperatures stable at 52°C. A final extension was carried out at 72°C for 15 min. For 16S and 12S fragments, we used the PCR protocol of 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 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 using electrophoresis. The successfully amplified PCR products were purified using a 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 phylogeny

To estimate the phylogenetic relationships of the genus *Trimeresurus*, we used the newly obtained *cyt b*, ND4, 12S, and 16S sequences together with previously published sequences of 95 representatives of the subgenus *Popeia*, as well as representative sequences of 26 species of other *Trimeresurus* subgenera and sequences of five species of the sister genus *Craspedocephalus* as recognized by Mallik et al. (2021); we used the sequence of *Azemiope fuae* to root the tree (see Appendix II).

We initially aligned the nucleotide sequences in MAFFT online (Katoh et al. 2019) with default parameters and subsequently checked them by eye in BioEdit v7.0.5.2 (Hall 1999) and adjusted when required. The mean uncorrected genetic p distances between sequences were calculated with MEGA v6.0. (Tamura et al. 2013) based on *cyt b* sequences of pitvipers in the subgenus *Popeia*. The best-fit substitution models for the data set were selected for genes and codon positions using Partition-

finder v2.1.1 (Lanfear et al. 2012) using the Akaike Information Criterion (AIC), which selected GTR+I+G for 16S and the second codon position of ND4, GTR+G for the first codon position of *cyt b*, HKY+I+G for the second codon position of *cyt b* and the first and the third codon positions of ND4, and HKY+I for the third codon position of *cyt b*. When the same model was proposed for different codon partitions of a given gene, they were treated as a single partition; this resulted in four partitions in total.

Phylogenetic trees were estimated for the combined mitochondrial DNA fragments (*cyt b*, ND4, 12S, and 16S). We inferred the matrilineal genealogy of *Trimeresurus* using Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. We used IQ-TREE (Nguyen et al. 2015) to generate the ML tree and assessed confidence in tree topology with 1000 bootstrap pseudoreplicates via the ultrafast bootstrap (UFBS) approximation algorithm (Hoang et al. 2018). We calculated BI in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001). Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) analyses 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 > 200 by exploring the likelihood plots using TRACER v1.7 (Rambaut et al. 2018). We discarded the initial 1000 trees as burn-in. We assessed the confidence in tree topology using posterior probability (BIPP) (Huelsenbeck and Ronquist 2001). We a priori considered tree nodes with ML UFBS $\geq 95\%$ and BIPP ≥ 0.95 as strongly supported, ML UFBS values of 90–95% and BIPP values of 0.95–0.90 as tendencies, and lower values as lacking node support (Huelsenbeck and Hillis 1993; Minh et al. 2013).

Morphological analysis

For this study, a total of 159 preserved specimens of taxa in the subgenus *Popeia* were examined for their morphological characters (Appendix III). Altogether, 45 morphological characters, including the structure of the hemipenes, were examined (see Appendix IV). Not all of these characters were useful to distinguish between the subject species, but all of them were compared because they may be used for further studies on taxonomy and geographical variation in this group of snakes.

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. The number of ventral scales was counted according to Dowling (1951); half-ventral plates were counted as one plate. The enlarged wide (i.e., notably wider than long) plate(s) anterior to the first ventral were regarded as pre-ventral(s); other plates anterior to the first ventral were regarded as gulars. The first scale under the tail meeting its opposite was considered the first subcaudal scale, and the unpaired terminal scute was not included in the number of subcaudals. The number of dorsal scale rows was counted at one head length behind the head, at midbody, and at one head length before the vent. Infralabials were

defined as those shields that were completely below a supralabial and bordering the mouth gap. Values for paired head characters were recorded on both sides of the head and were reported in a left/right order. Eye size was measured horizontally (ED, the greatest diameter; see below and in Appendix IV for abbreviations); the eye–nostril distance (EN) was measured from the anterior margin of the eye to the posterior margin of the nostril; the distance from eye to the lip (DEL) was measured from the ventral margin of the middle of the eye to the ventral margin of the upper labial below it; the head length (HL) was measured from snout tip to the angle of the jaw; the head width (HW) was measured at the widest part of the head on posterior side. Sex was determined by dissection of the ventral tail base in preserved specimens and with a probe in live individuals.

For comparison with other taxa, we relied on data previously published for the subgenus *Popeia*, including Pope and Pope (1933), Smith (1937, 1943), Regenass and Kramer (1981), Vogel et al. (2004), Gumprecht et al. (2004), Sanders et al. (2004), Grismer et al. (2006), David et al. (2009), Guo et al. (2015), Wostl et al. (2016), Mulcahy et al. (2017), Chen et al. (2019), Liu et al. (2022), and Mirza et al. (2023).

Abbreviations. Morphology and morphometry: **ASR:** number of dorsal scale rows on the neck; **CEP:** number of cephalic scales between the supraoculars; **CLP:** condition of the cloacal plate; **DSR:** number of dorsal scale rows before vent; **ED:** eye diameter; **G:** pairs of gular scales; **HL:** head length; **IL:** infralabials; **IN:** internasals; **MSR:** number of dorsal scale rows at midbody; **PV:** pre-ventrals; **SbS:** number of scales between supraoculars; **SC:** number of subcaudals excluding terminal scute; **SC/SpOc:** number of scales surrounding the supraocular; **SL:** number of supralabials; **SN:** snout length; **SO:** number of supraoculars; **SVL:** snout–vent length, from tip of snout to last posterior edge of the last ventral scale; **TaL:** tail length, from posterior edge of the cloacal plate to the tip of the tail; **TL:** total length, SVL + TaL; **TaL/TL:** ratio of tail length to total length; **VEN:** number of ventrals.

Other abbreviations. **asl.:** above sea level; **Mt:** Mountain; **NP:** National Park; **WS:** Wildlife Sanctuary; **Is:** Island.

Museum acronyms. **AUP:** School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand; **BNHS:** Bombay Natural History Society, Mumbai, India; **CAS:** California Academy of Sciences, San Francisco, California, USA; **CESS:** Centre for Ecological Sciences Bangalore, India; **CIB:** Chengdu Institute of Biology, Chengdu, China; **IRSNB:** Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MHNG:** Muséum d'Histoire Naturelle, Ville de Genève, Switzerland; **MNHN:** Muséum national d'Histoire naturelle, Paris, France; **NHMUK** (formerly **BMNH**): The Natural History Museum, London, UK; **NCBS NRC:** National Research Collections of

the National Centre for Biological Sciences, Bangalore, India; **NHMW** (formerly **NMW**): Natural History Museum Vienna, Vienna, Austria; **NMBE:** Naturhistorisches Museum Bern, Switzerland; **PSGV:** private collection of Gernot Vogel, Heidelberg, Germany; **QSMI:** Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand; **RMNH:** Naturalis Biodiversity Center, Leiden, Netherlands; **SMF:** Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; **VNMN:** Vietnam National Museum of Nature, Hanoi, Vietnam; **ZFMK:** Leibniz Institute for the Analysis of Biodiversity Change, Museum Alexander Koenig, Bonn, Germany; **ZMH:** Leibniz Institute for the Analysis of Biodiversity Change, Museum der Natur, Hamburg, Germany; **ZRC:** Zoological Reference Collection, National University of Singapore, Singapore; **ZSM:** Zoologische Staatssammlung, München, Germany; **ZMB:** Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; **ZMMU:** Zoological Museum of Moscow State University, Moscow, Russia.

All statistical analyses were conducted in STATISTICA v8.0 (StatSoft Inc.). Univariate analyses were ran separately on males and females to reduce the effects of sexual dimorphism. Multivariate analyses were run on the male dataset because we lacked sufficient sample sizes for females. We used Shapiro-Wilks Tests and Levene's Tests to test for normality and heteroscedasticity, respectively. We used Mann-Whitney U Tests and Student's T Tests to compare quantitative differences between species. Tests for sexual dimorphism within species were performed using Mann-Whitney U Tests. For all univariate statistics, differences between characters were determined to be statistically significant when p-values were ≤ 0.05 . After univariate analyses, we log-transformed the dataset and conducted a Principal Components Analysis (PCA) on the remaining residuals to determine whether there was visible structure in the morphological variation observed between species. We ran Mann-Whitney U Tests on PCA 1 and PCA 2 factors using the same procedures described above to determine if the PCA centroids of the two taxa were also significantly different. All data used in the PCA were scaled to standard deviation prior to analysis to help eliminate the effects of covariance and ensure the data were normally distributed. The following morphological characters were used for univariate and multivariate statistical analyses (abbreviations in parentheses): ASR, CEP, DSR, ED/HL, HL/SVL, IL, MSR, Sc, SC/SpOc, SL, SnL/HL, TaL/TL, VEN, and VEN+SC.

Results

Sequence characteristics

A total of 2205 aligned base pairs (1150 from cyt *b*, 853 from ND4, and 1352 from the 12S and 16S rRNA fragments) were obtained. Protein-coding sequenc-

es were translated into amino acids to confirm that no pseudogenes had been amplified. We deposited the newly obtained sequences in GenBank under accession numbers OR470534–38; OR470543–46; OR470550–57; OR470561–64; OR470571–80; OR471621–25; OR471630–43; OR999082–99; PP032774–811 (see Appendix II). Sequence characteristics, including the estimated transition / transversion bias, nucleotide frequencies, and suggested models of DNA evolution for each genetic marker are summarized in Appendix V.

Phylogenetic relationships

ML and BI analyses recovered trees with very similar topologies and nodes that were reconstructed differently were not important to the analysis (Fig. 2). Our mtDNA-genealogy confirmed the monophyly of the genus *Trimeresurus* (100/1.0; hereafter node support values are given for ML UFBS/BIPP, respectively) with respect to its sister genus *Craspedocephalus*. However, the genealogical relationships within *Trimeresurus* remained insufficiently resolved. The monophyly of the subgenus *Popeia* was strongly supported (100/1.0). It consists of six major clades with essentially unresolved phylogenetic relationships among them (Fig. 2, clades A–F).

Within the subgenus *Popeia*, the populations currently assigned to '*T. popeiorum*' comprise three OTUs and are recovered as paraphyletic. Populations from the northern part of the group's range in Northeast India, northern Myanmar (Kachin and Sagaing States), and the westernmost part of Yunnan Province form Clade E (100/1.0), which corresponds to OTU1 (*T. popeiorum* s. str.; Fig. 2). This clade also includes the topotypic specimens of *T. yingjiangensis* (Fig. 1, Locality 19). The specimen from Northeast India forms a matriline sister to all other lineages of this clade.

Populations from eastern Myanmar, northern Thailand, Laos, and southernmost China form OTU2, corresponding to Clade A (99/1.0, Fig. 2) with strong geographic substructuring. Clade A consists of two highly divergent subclades: Subclade A1 is composed of all examined populations from the southernmost part of Yunnan, western Laos, and northern Thailand (100/1.0). Subclade A2 is moderately supported (98/0.84) and includes three specimens from eastern Myanmar, with the specimen from Bago (Fig. 1, Locality 2) forming a matriline highly divergent from the two specimens from Mon Division (Fig. 1, Locality 1).

OTU3 includes populations from the southern part of the group's range in the Tenasserim Mountains of northern Peninsular Thailand and southeastern Myanmar, and forms a distinct clade (Clade F; 99/1.0) with sister relationships to all other members of the subgenus *Popeia* (69/0.91; not significantly supported). The populations of OTU3 from the eastern slopes of the Tenasserim Mountains in Thailand and from the western slopes in Myanmar (see Fig. 1) form two reciprocally monophyletic groups (identified as F1 and F2 in Fig.

2), with node support values of 99/1.0 and 82/1.0, respectively.

The phylogenetic positions of *T. nebularis* (Clade B, 100/1.0), *T. phuketensis* (Clade C, 100/1.0), and *T. sabahi* (Clade D, 100/1.0) remain essentially unresolved, but with each species forming a distinct and well-supported clade (Fig. 2). Specimen B467 (as listed by Malhotra et al. 2004) from Phang Nga Province, Thailand, is grouped in one clade with two specimens of *T. phuketensis* from Phuket Island. This confirms the occurrence of *T. phuketensis* in mainland Peninsular Thailand. Finally, the *T. sabahi* complex forms a distinct clade but the phylogenetic relationships among the included populations and subspecies remain unresolved. Of the currently five recognized subspecies of *T. sabahi* the monophyly of only three is supported in our analysis (Fig. 2): *T. s. sabahi* from Sabah State, Borneo, Malaysia (100/1.0), *T. s. buniana* from Pulau Tioman in Pahang State, Malaysia (100/1.0), and *T. s. toba* from northern Sumatra, Indonesia (100/1.0). *Trimeresurus s. barati* from the remaining parts of Sumatra is not monophyletic and includes two subclades, one from Jambi Province in central Sumatra (99/1.0) and one from Lampung and Bengkulu Provinces in southern Sumatra (100/1.0). The subspecies *T. s. fucatus* from the southern Thai-Malay Peninsula is also not monophyletic with respect to other subspecies of *T. sabahi*, and consists of several matriline from Pahang and Perak States in West Malaysia and Nakhon Sri Thammarat Province of Thailand, with unresolved phylogenetic relationships among them (Fig. 2).

Genetic distances

The uncorrected p distances for the *cyt b* gene fragment among the examined members of the subgenus *Popeia* are presented in Appendix VI. Intraspecific distances among *Popeia* species varied from 3.4% (between Clade C of *T. phuketensis* and Subclade A1 of OTU2 from northern Indochina) to 8.4% (between Clade E of OTU1 [*T. popeiorum* s. str.] and Clade B of *T. nebularis*). Genetic differentiation between the three main OTUs presently assigned to '*T. popeiorum*' was significant and varied from 3.7–4.8% (between Clade A1 of OTU2 and Clade F of OTU3) to 7.6% (between Clade E of OTU1 and Subclade A1 of OTU2). The inter-group genetic differentiation varied from identity (in *T. s. sabahi*, *T. s. buniana*, and *T. s. toba*) to 2.1% (between Subclades F1 and F2 of OTU3) and 2.3% (between specimens in Subclade A2 of OTU2).

Morphological differentiation

Five characters (VEN, SC, VEN+SC, CEP, ASR) exhibited normal distributions in all datasets. Univariate analysis revealed statistically significant differences between the members of the *T. popeiorum* group, including the three OTUs presently assigned to '*T. popeiorum*', including OTU1 (= *T. popeiorum* s. str.),

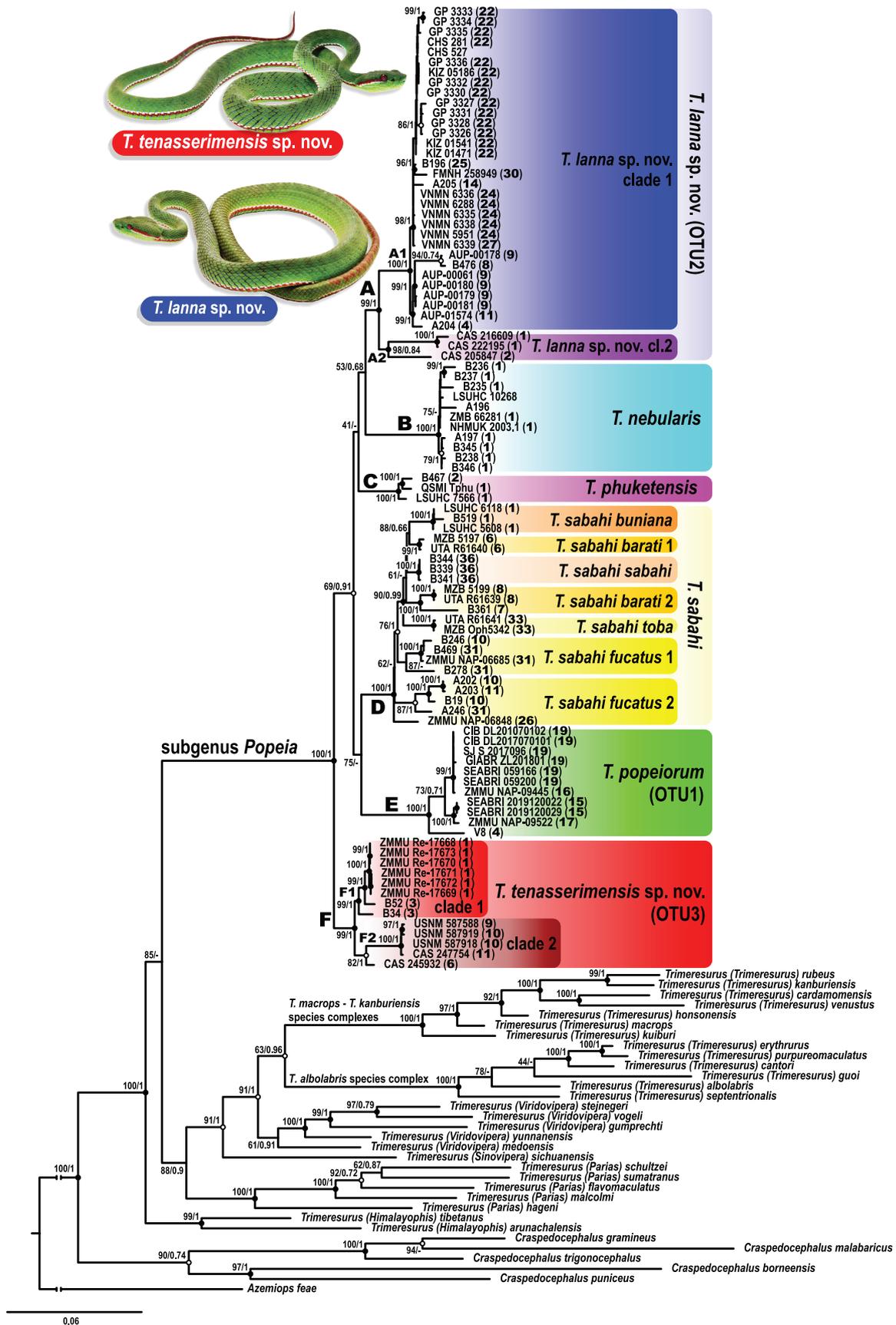


Figure 2. Maximum Likelihood (ML) phylogenetic tree of *Trimeresurus* from the analysis of 12S rRNA, 16S rRNA, ND4, and cyt *b* mitochondrial DNA gene sequences. Part 1 (subgenus *Popeia*). For voucher specimen information and GenBank accession numbers see Appendix II. Numbers at tree nodes correspond to ML UFBS / BIPP support values, respectively; an en-dash denotes no support. Colors of clades and locality numbers given in brackets after specimen ID correspond to those in Figure 1 and Figure 3. Bold letters A–F on the branches correspond to the main mtDNA clades revealed by our analysis (see Results). Photos showing two new species described herein by N.A. Poyarkov and P. Pawangkhanant.

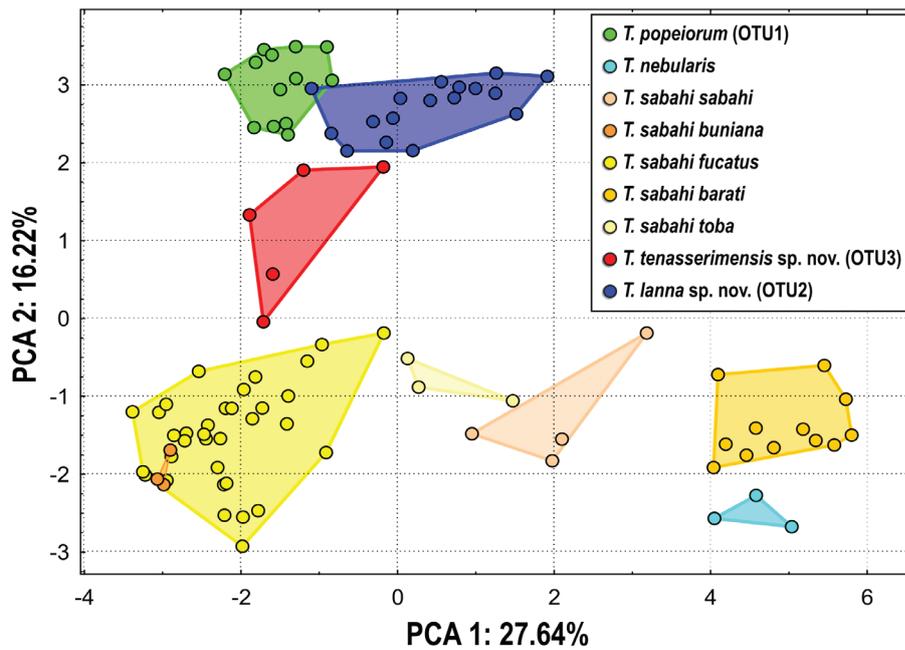


Figure 3. Principal Component Analysis (PCA) plot comprised of morphological data from males of *Trimeresurus popeiorum* species group members.

OTU2, and OTU3. Resulting p-values from univariate morphological analyses comparing OTU1 with OTU2 from northern Indochina and OTU3 from the Tenasserim Range are summarized in Table S2. Univariate analyses for both male, female, and combined datasets showed significant differentiation in the number of body scales (except SL), in relative tail and snout lengths, and relative eye-nostril distance between three OTUs of the complex (Table S2).

PCA plots revealed that the taxa of the *T. popeiorum* group are generally well-separated in morphospace, with members of the *T. sabahi* complex clearly distinct from OTU1–3 of the *T. popeiorum* group from Indo-Burma (Fig. 3). All subspecies of *T. sabahi* were clearly separated from each other with the exception of *T. s. buniana*, which fully overlapped with *T. s. fucatus* in our analysis (Fig. 3). The three OTUs of the Indo-Burmese members of the *T. popeiorum* group are modestly separated in morphospace, although considerable overlap exists between OTU1 (*T. popeiorum* s. str.) and OTU2 (Fig. 3). PCA1 accounted for 27.64% of the total variance and loaded most heavily for ventrals and cumulative number of ventrals and subcaudals (VEN+SC and VEN). PCA2 accounted for 16.22% of the total variance and loaded most heavily for relative tail length and number of cephalic scales between the supraoculars (TaL/TL and CEP). More details on the PCA results can be found in Appendix VII.

In summary, the combined univariate and multivariate analyses show that the three OTUs of the *T. popeiorum* group from the Indo-Burma Biodiversity Hotspot, corresponding to clades A, F and E of our mtDNA-based genealogy (Fig. 2), differ from other members of the subgenus *Popeia* as well as from each other in a number of statistically significant differences in scalation and coloration characters and in relative head and body proportions.

Systematics

Results from our molecular phylogenetic analysis are generally consistent with those of Mirza et al. (2023). Herein, they are further corroborated by the morphological data, which uncovered significant morphological differentiation among the three OTUs of mainland *Popeia* and other members of the subgenus. In our analysis, we do not treat the *Trimeresurus sabahi* complex, as defined by Wostl et al. (2016) and Mulcahy et al. (2017), which is widespread in the Sundaland Region.

Based on our morphological and molecular analyses, we recognize the three OTUs from Indo-Burma, which have so far collectively been identified as '*Trimeresurus popeiorum*', as three distinct species:

(1) OTU1 (mtDNA Clade E) encompasses populations from Northeast India, Kachin State and the Sagaing Region in Myanmar, as well as the western Yunnan population (formerly known as *T. yingjiangensis*). According to the type locality of *T. popeiorum*, this clade corresponds to *T. popeiorum* s. str. as defined by Vogel et al. (2004).

(2) OTU2 (mtDNA Clade A) contains populations inhabiting southwestern China, northern and western Thailand, northern Laos, and southeastern Myanmar. As first indicated by Mirza et al. (2023), this clade undoubtedly corresponds to a distinct, cryptic species that we describe below. Furthermore, as shown in our matrilineal genealogy (Fig. 2), three populations from Mon State and Bago Region, west of the Salween (or Thanlwin) River in southern Myanmar, are genetically quite different from the populations of Thailand, Laos and China; we do not yet recognize this differentiation as taxonomically significant and retain them as distinct subclades A1 and A2.

(3) OTU3 (mtDNA Clade F) includes populations from the northern Tenasserim Mountains, in the peninsular part of southwestern Thailand and southeastern Myanmar. The identification of this clade strongly supports the hypothesis of Mulcahy et al. (2017) that an undescribed species exists in this region. We describe OTU3 as a new species below. We also report on a significant divergence between the populations of OTU3 on the opposite sides of the Tenasserim Range in peninsular Myanmar and Thailand (subclades F1 and F2).

The three mainland Asian OTUs of the subgenus *Popeia* are superficially similar in external morphology and coloration relative to other members of the subgenus, and are characterized by a green dorsal background color with varying degrees of patterning, SL1 separated from the nasal by a distinct suture, comparatively small cephalic scales (i.e., not enlarged into plates), and long and slender, deeply forked and calyculate hemipenes. Based on our results, we therefore recognize three distinct species-level taxa in the Indo-Burma Region, namely *T. popeiorum* s. str. and two undescribed species, which we formally describe below.

Trimeresurus popeiorum Smith, 1937

Figs 4–6, 7A–E; Tables S3, S4

Synonymy.

Trimeresurus [sic] *elegans* Gray, 1853: 391. – Holotype: NHMUK 1946.1.19.20, a subadult female from “Sikkim”, India, donated by Joseph D. Hooker. A nomen dubium based on its original description, but here considered both a senior subjective synonym of *T. popeiorum* Smith, 1937 and a nomen oblitum after examination of the holotype (see below.)

Trimeresurus popeiorum Smith, 1937: 730. – Lectotype: NHMUK 1872.4.17.137A, an adult male from “Khasi Hills” [Meghalaya State, India; ca. 25.60°N, 91.65°E], donated by Thomas C. Jerdon; designated by Taylor and Elbel (1958: 1174).

Trimeresurus yingjiangensis Chen et al., 2019: 9. – Holotype: CIB DL2017070101, an adult male from Heihe Village, Kachang Town, Yingjiang County, Yunnan Province, China (24.782°N, 97.878°E; elevation 1112 m). According to Mirza et al. (2023), a subjective junior synonym of *T. popeiorum* Smith, 1937.

Etymology. The species name is a patronym, in genitive plural, created in honour of Clifford H. Pope (1899–1974) and his wife Sarah H. Pope (1901–1995); see below for a discussion of the correct spelling. We recommend the following common names for this species: “Pō pǔ zhú yè qīng” (坡普竹叶青) (in Chinese), “Pope’s green pitviper” (in English), “Ngu Khiew Hang Mai Thong Khiew Assam” (งูเขียวหางไหม้ทองเขียวอัสสัม) (in Thai), “Trimérésure vert des Pope” (in French), “Popes Bambusotter” (in German), and “Bambukovaya kufiya Poupov” (in Russian).

Systematics and nomenclature. Before Smith (1937), the species *Trimeresurus popeiorum* s. str. was widely mentioned in the literature under the combinations *T.*

gramineus or *Lachesis gramineus* (non *Coluber gramineus* Shaw, 1802, a distinct, valid species from Peninsular India; see, for example, Pope and Pope 1933: 9). As explained above, Regenass and Kramer (1981) divided this species into three subspecies, retaining the nominative one, *T. p. popeiorum*, for populations of the Asian mainland. Currently, following Vogel et al. (2004), Westl et al. (2016), and the present work, *Trimeresurus popeiorum* s. str. is monotypic.

We take this opportunity to mention the taxon *Coluber viridicaeruleus* La Cépède, 1789, which Wallach et al. (2014: 575) placed in the synonymy of *T. popeiorum*. La Cépède (1789: 122 and 306) erected this taxon as a replacement name for *Coluber cyaneus* Linnaeus, 1758. Based on its scalation characters, such as a head covered with large plates and 110 subcaudals, this taxon is obviously not a pitviper, but may represent a nearctic or neotropical colubrid species, as it was stated to have originated from “Les Amériques”. Therefore, we formally remove *Coluber viridicaeruleus* from the synonymy of *Trimeresurus popeiorum*, while the taxonomic identity of *Coluber viridicaeruleus* La Cépède, 1789 remains unclear.

The species nomen *popeiorum*. A nomenclatural problem arose when Smith (1943: 518) stated in a footnote that the spelling *popeiorum* in his earlier paper was a clerical error and, on the same page, corrected it into *popeorum*. As a result, the spelling *popeorum* has been widely used in the literature, for example by Haas (1950), Taylor and Elbel (1958), Klemmer (1963), Werler and Keegan (1963), Taylor (1965), Leviton (1968), Harding and Welch (1980), and Regenass and Kramer (1981). David and Vogel (1996: 163) were the first authors to discuss the spelling problem and pointed out that, based on Art. 32 (c) (ii) of the Code (ICZN 1985), the original spelling had to be retained even though Smith (1943) tried to correct the original spelling. According to Art. 32.5.1 of the Code (ICZN 1999), the initial spelling was an incorrect transliteration or Latinization and does not allow for “correction of an incorrect original spelling”. According to the Art. 33.4, the use of a termination *-orum* in a subsequent spelling of a species-group name that is a genitive based upon a personal name in which the correct original spelling terminates with *-iorum*, is an incorrect subsequent spelling, even if the change is deliberate. The original spelling, *popeiorum*, must therefore be conserved. McDiarmid et al. (1999) and Orlov et al. (2002a, 2002b) challenged this interpretation and argued that the spelling *popeorum* was the correct one. However, these authors have not been followed.

The status of *Trimeresurus elegans* Gray, 1853. This taxon has long been forgotten or considered a synonym of *Trimeresurus gramineus*. For example, Uetz et al. (2024) currently list this taxon in the synonymy of *Craspedocephalus gramineus* (Shaw, 1802) based on Stejneger (1907, 1927). These authors apparently overlooked the fact that Stejneger confused several green pitvipers under the combination *Trimeresurus gramineus*. The type locality of *Trimeresurus elegans* makes clear that it can-

not be a synonym of *T. gramineus*, as currently defined, a species endemic to southeastern Peninsular India (see Mallik et al. 2021).

The brief original description of *Trimeresurus elegans* does not allow a formal identification of the species. However, its holotype (NHMUK 1946.1.19.20), which we examined, is indeed a subadult female referable to *Trimeresurus popeiorum* s. str. as defined here. On this basis, *Trimeresurus elegans* Gray, 1853 should be considered a senior subjective synonym of *T. popeiorum*. Such a conclusion would be problematic in terms of nomenclatural stability, as the species name *elegans* has seemingly never been used as valid after its establishment by Gray (1853), while the *popeiorum* has been used as valid in dozens of publications since 1937 in the genera *Trimeresurus* or *Popeia*.

For this reason, in order to protect the binomen *Trimeresurus popeiorum* Smith, 1937, we here make use of Art. 23.9 of the Code to reverse precedence (ICZN 1999). In order to apply this Article, two conditions must be fulfilled: Art. 23.9.1.1 states that the senior synonym must not have been used as a valid nomen after 1899; and Article 23.9.1.2 states that the junior synonym must have been used for a particular taxon, as its presumed valid nomen, “in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years” (ICZN 1999).

In the present case, the first condition is met because to the best of our knowledge, the specific epithet *elegans*, as proposed by Gray (1853), has never been used as valid for any pitviper after 1853. It should be noted that *Craspedocephalus elegans* Gray, 1849, now *Protobothrops elegans*, a valid species inhabiting Japan, was placed in the genus *Trimeresurus* by Stejneger (1907). In this case, *Trimeresurus elegans* Gray, 1853 also becomes a secondary homonym of *Craspedocephalus elegans* Gray, 1849 in the genus *Trimeresurus*.

In order to fulfil the second condition, the epithet *popeiorum* should have been used as valid in the genus *Trimeresurus*, even if under the erroneous spelling *popeorum*, by at least 25 authors since 1972. We provide below a list of 25 works published from 1972 onwards in which the epithet *popeiorum* (or *popeorum*) has been used as valid: Harding and Welch (1980: 74); Regenass and Kramer (1981: 186; as *T. p. popeorum*); Tweedie (1983: 139, 158); Toriba in Golay et al. (1993: 103; as *T. popeorum*); David and Ineich (1999: 288); Leviton et al. (2003: 446); Gumprecht et al. (2004: 37, 256; as *Trimeresurus popeiorum popeiorum*); Malhotra and Thorpe (2004: 97); Sanders et al. (2004: 183); Vogel et al. (2004: 19); Castoe and Parkinson (2006: 105); Sanders et al. (2006: 361); Vogel (2006: 107); Leviton et al. (2008: 80); Das (2010: 307); Malhotra et al. (2010: 175); Teynié and David (2010: 268); Wallach et al. (2014: 575); Visser (2015: 387); Guo et al. (2015: 267); Chan-ard et al. (2015: 345); Das et al. (2016: 275-276); Wostl et al. (2016: 637); Chen et al. (2019: 20); Nguyen et al. (2020: 239); Liu et al. (2022: 86); and Rathee et al. (2022: 3)

The foregoing sources allow to conclude that Art. 23.9 can be applied to *Trimeresurus elegans* and precedence can

be reversed. We therefore declare *Trimeresurus elegans* Gray, 1853 to be a subjective senior synonym of *Trimeresurus popeiorum* Smith, 1937 and a nomen oblitum. In so doing, *Trimeresurus popeiorum* Smith, 1937, and also becomes a nomen protectum and the binomen can be used for green pitvipers from Southeast Asia.

Referred specimens (n = 15). **Nepal.** NHMUK 1874.4.29.881 (adult female), “Himalayas”. — **India.** Meghalaya State: NHMUK 1872.4.17.137A (lectotype of *Trimeresurus popeiorum*, adult male), from Khasi Hillis; Sikkim State: NHMUK 1946.1.19.20 (holotype of *Trimeresurus elegans* Gray, 1853, subadult female); West Bengal State: NHMUK 1872.4.17.377 (paralectotype of *Trimeresurus popeiorum*, adult male), NHMUK 1872.4.17.378 and NHMUK 1891.9.11.28–29 (three adult females) from Darjeeling District; Mizoram State: MZMU ZOO-GV 001 (adult male); Arunachal Pradesh: NCBS NRC-AA-4548 (adult male) from Kamlang WS., NCBS NRC-AA-4549 (adult male) and NCBS NRC-AA-4534 (adult female) from Eaglenest WS. **China.** Yunnan Province: CIB DL201070102 and CIB DL201070103 (paratypes of *T. yingjiangensis*, two adult males) from Heihe Village, Kachang Town, Yingjiang Country. — **Myanmar.** Kachin State: ZMMU NAP-09445 (adult male) from Inn Gyin Taung Mt., Indawgyi NR., Mohnyin Township; Sagaing Region: ZMMU NAP-09522 (subadult male) from Zalon Taung Mt., Ban Mau District.

Diagnosis. *Trimeresurus popeiorum* differs from all other members of the subgenus *Popeia* by the combination of the following morphological characters: (1) dorsal surfaces in various shades of green, bluish-green or even turquoise blue; (2) in males, a vivid, wide bicolored ventrolateral stripe, bright and deep red below, white above; in females, stripe thin, white or yellow; (3) males with a conspicuous, bicolored postocular streak, thin and white ventrally, wide and bright red dorsally; streak absent in females; (4) eyes red to deep red in both males and females; (5) 21 dorsal scale rows at midbody, more or less strongly keeled in males, weakly keeled in females, scales of the first dorsal scale row always smooth; (6) first supralabial entirely separated from nasal scale by a distinct suture; (7) supraoculars much narrower than internasals; (8) internasals never in contact, separated by one or two scales; (9) 159–173 ventrals; 55–76 subcaudals, all paired; (10) hemipenes long and forked, reaching at least to the 25th subcaudal, without spines; (11) 11–13 cephalic scales between the supraoculars in males, 10–12 in females; (12) relative tail length 0.18–0.21 in males, 0.14–0.19 in females.

Description of the holotype (NHMUK 1946.1.19.20) of *Trimeresurus elegans* Gray, 1853 (Fig. 4). A subadult female in a relatively good state of preservation after more than 150 years in preservative.

Morphology. Body cylindrical, long, and laterally compressed (SVL 322 mm, TaL 62 mm, TL 384 mm, TaL/TL 0.161). Head triangular in dorsal view, elongate, clear-

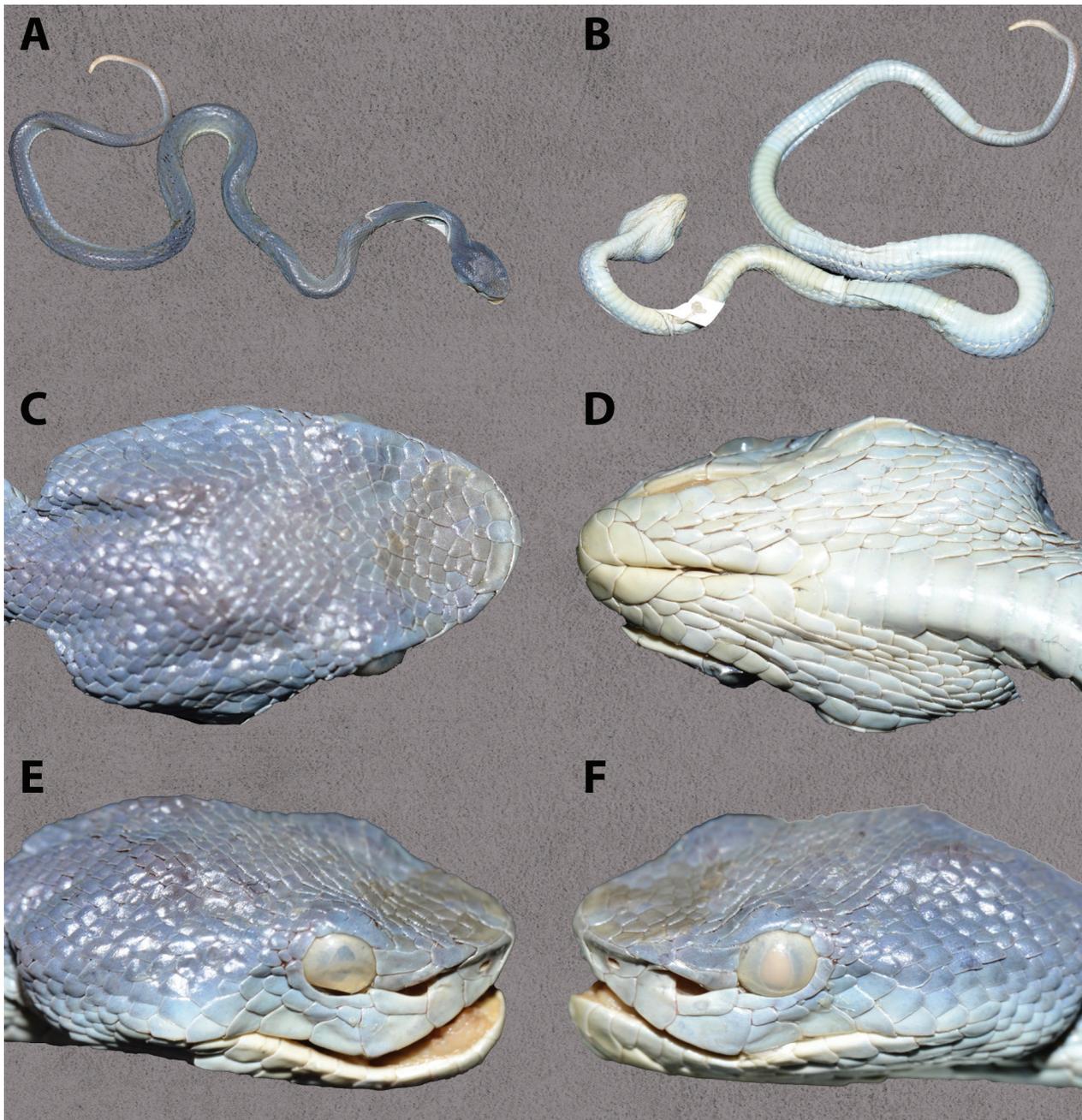


Figure 4. *Trimeresurus popeiorum* in preservative – specimen NHMUK 1946.1.19.20 (holotype of *Trimeresurus elegans*, subadult female) **A** General dorsal view; **B** General ventral view; **C** Dorsal view of the head; **D** Ventral view of the head; **E** Lateral view of the head, right side; **F** Lateral view of the head, left side. Photos by P. D. Campbell.

ly distinct from the neck (HL 18.4 mm, HL/SVL 0.06), snout elongate, flattened, and rounded when seen from above, rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; loreal pit present, triangular in shape. Eye average (ED 3.1 mm, SnL 5.2 mm, ED/SnL 0.58); pupil vertical, elliptic.

Body scalation. Dorsal scales in 25-21-15 rows; dorsal scales all moderately keeled, except the first row, the scales of which are smooth; 167 ventrals (plus single pre-ventral); cloacal plate single; 61 subcaudals, all divided.

Head scalation. Rostral slightly visible from above, triangular; one large pair of enlarged internasals, separated

by a one small scale; nostril completely included in nasal scale; nasal scale completely separated from the first supralabial; 1/2 small scales between nasal and second supralabial; scales on the upper snout surface and in the interorbital region smooth, irregular, barely imbricate; temporal and occipital scales strongly keeled; two elongate upper preoculars above the loreal pit; lower preocular forming the lower margin of the loreal pit; one supraocular on each side, large, broader than the internasals; 13 irregular cephalic scales between the supraoculars; one long, thin, crescent-like subocular scale (Fig. 4C); 9/9 supralabials, third largest and separated from the subocular by one scale on each side, fourth and fifth supralabials separated from subocular by one scale on each side; 2/2

postoculars (Fig. 4E, F); 13/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields and the first preventral (Fig. 4D).

Coloration and pattern. Body green, beneath paler, whitish; scales of the back moderate, smooth, not keeled, the lateral series rather broader, the first lateral series green, with a small white spot on the hind part of the upper edge forming an interrupted lateral line.

Description of the lectotype (NHMUK 1872.4.17.137A) of *Trimeresurus popeiorum* Smith, 1937 (Fig. 5). An adult male in a relatively good state of preservation after more than 150 years in preservative.

Morphology. Body cylindrical, long, and laterally compressed (SVL 758 mm, TaL 167 mm, TL 925 mm, TaL/TL 0.181). Head triangular in dorsal view, elongate, clearly distinct from the neck, snout elongate, flattened, and rounded when seen from above (Fig. 5C), rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; loreal pit present, triangular in shape (Fig. 5E). Eye average; pupil vertically elliptic (Fig. 5E).

Body scalation. Dorsal scales in 23-21-15 rows; dorsal scales all moderately keeled, except the first row, the scales of which are smooth; 165 ventrals (plus single pre-ventral); cloacal plate single; 70 subcaudals, all divided.

Head scalation. Rostral slightly visible from above, triangular; one large pair of enlarged internasals, separated by one small scale (Fig. 5C); nostril completely included in an entire nasal scale; nasal scale completely separated from the first supralabial; 1/2 small scales between nasal and the second supralabial; scales on the upper snout surface and in the interorbital region smooth, irregular, barely imbricate; temporal and occipital scales strongly keeled; two elongate upper preoculars above the loreal pit; lower preocular forming the lower margin of the loreal pit (Fig. 5E); one supraocular on each side, large, broader than the internasals; ten irregular cephalic scales on a line between the supraoculars (Fig. 5C); one long, thin, crescent-like subocular scale; 9/10 supralabials, third largest and separated from the subocular by one scale on each side; fourth and fifth supralabials separated from subocular by one or two scales on each side; 2/2 postoculars (Fig. 5E); 12/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields and the first preventral (Fig. 5D).

Coloration and pattern. Color uniform green above; paler green below. First row of scales on each side brown with yellow tip, second row yellow below the median keel. The narrow bicolor lateral stripe thus formed ending just behind head anteriorly and at vent posteriorly,

incompletely developed on tail. Tip of tail pale reddish. Head without pattern or postocular stripe (Fig. 5A, B, F).

Redescription of the paratype (CIB DL201070102) of *Trimeresurus yingjiangensis* Chen et al. (Fig. 6). Below we provide a brief redescription of the paratype of *T. yingjiangensis* (CIB DL201070102), examined by one of us (GV), in order to provide a detailed morphological data justifying the synonymy of this taxon with *T. popeiorum*, as proposed based on molecular data by Mirza et al. (2023).

An adult male in a very good state of preservation.

Morphology. Body cylindrical, long, and laterally compressed; SVL 594 mm, TaL 148 mm, TL 742 mm, TaL/TL 0.199. Head triangular in dorsal view, elongate, clearly distinct from the neck (HL 29.8 mm, HW 18.1 mm, HL/SVL 0.05); snout elongate, flattened, and rounded when seen from above, rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; loreal pit present, triangular in shape. Eye average (ED 12.9 mm); pupil vertically elliptic.

Body scalation. Dorsal scales in 21-21-15 rows; dorsal scales all moderately keeled, except the first row the scales of which are smooth; 164 ventrals (plus single pre-ventral); cloacal plate single; 76 subcaudals, all divided. Hemipenes long, reaching to 23–24 SC, forked opposite fifth to sixth subcaudal scale, no spines (Fig. 6H).

Head scalation. Rostral slightly visible from above, triangular, broader than high; one enlarged internasal on each side, internasals separated by one small scale behind the top of rostral (Fig. 6E); nostril completely included in the entire nasal scale, pentagonal, not divided, elongate, as long as high; nasal scale completely separated from the first supralabial (Fig. 6C, D); one internasal on each side, pentagonal, curved, wide, transversely elongate, separated by one small scale; two small scales between the nasal and the second supralabial; scales on the upper snout surface and in the interorbital region smooth, irregular, barely imbricate; 3/3 canthal scales, slightly larger than adjacent snout scales, bordering the canthus rostralis between the internasals and corresponding supraocular; temporal and occipital scales obtusely keeled; one relatively large triangular loreal between the upper preocular and the nasal; two elongate upper preoculars above loreal pit, lower one bordering the upper margin of loreal pit, upper one visible from above, both elongate and in contact with loreal; lower preocular forming lower margin of loreal pit; one supraocular on each side, long, much longer than wide, cephalic scales relatively small, irregular or slightly rounded, juxtaposed, flat and smooth; 11 irregular cephalic scales between the supraoculars; one long, thin, crescent-like subocular scale; occipital scales rhombohedral, distinctly but obtusely keeled; 2/2 small postoculars; 10/11 supralabials, first supralabial short, entirely separated from the nasal by a distinct suture; second supralabial tall, forming the anterior border of loreal pit; third supralabial largest and in contact with the subocu-

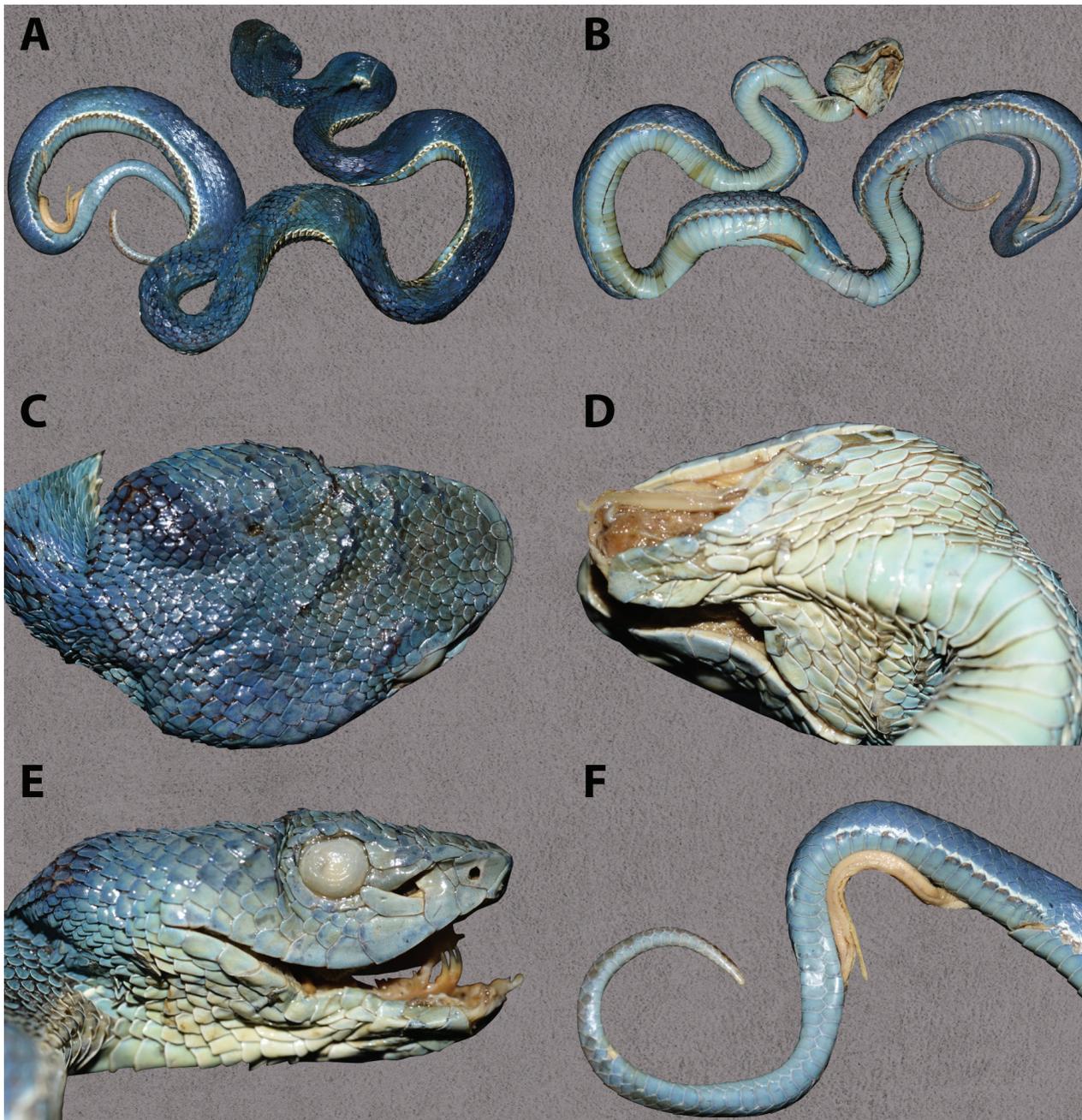


Figure 5. *Trimeresurus popeiorum* in preservative – specimen NHMUK 1872.4.17.137 (Lectotype, adult male) **A** General dorsal view; **B** General ventral view; **C** Dorsal view of the head; **D** Ventral view of the head; **E** Lateral view of the head, right side; **F** Latero-ventral view of the tail. Photos by P. D. Campbell.

lar on each side; fourth and fifth supralabials much lower than the third one, separated from the subocular by one scale on each side (Fig. 6C, D); 12/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields and the first preventral (Fig. 6F).

Coloration in preservative (Fig. 6 and Fig. 1D in Chen et al. 2019). The body is uniform deep bluish-green (bright grass-green in life), without darker areas or cross-bands; a conspicuous, bicolored ventrolateral stripe extends from the beginning of the neck to the vent, pinkish-brown (bright deep red in life) ventrally, this color

covering nearly the whole surface of scales of the first dorsal scale row except their upper posterior corner that is cream (white in life), same as the lower half of scales of the second row. The tail is bluish-green like the dorsum; the ventrolateral stripe extends up to the first third of the tail; near its end, the dorsal surface of the tail is irregularly mottled with pinkish-orange (rusty-red in life).

The dorsal surface of the head and temporal region are bluish-green like the body; the side of the head below the eye, i.e., the sides of the snout, nasal scale, anterior supralabials and lower temporals, is distinctly paler than the dorsal surface of the head, namely pale bluish-green (pale green in life); thin and short bicolored postocular strip (red and white), runs from the posterior part of the suboc-

ular to the angle of the jaw. The chin and throat are pale sea-green (yellow green in life), uniform but with few faint darker areas on infralabials sometimes. The eye is grey but it was deep fire-red in life. The venter is uniform pale sea-green (yellow green in life); dorsal tail heavily mottled with dark red blotches, the dark red blotches contiguous posteriorly; the ventral surface of the tail is as the venter anteriorly, tip of tail red on dorsal while dark salmon on ventral.

Variation. This description is based on the ten specimens examined by us, supplemented by data from 15 specimens published by Das et al. (2016), Chen et al. (2019), Liu et al. (2022), and Mirza et al. (2023) (see Table S3).

Morphology. The maximum known total length is 925 mm in males (NHMUK 1872.4.17.137), 848 mm in females (NHMUK 1891.9.11.28). The body is robust but relatively slender in males, thicker in large females, laterally compressed; head triangular, elongate, wide posteriorly, flattened in males, moderately thick in females, clearly distinct from the neck; snout elongate, distinctly flattened, rounded seen from above, angular and obliquely truncated in profile view, with a distinct canthus rostralis; nostril piercing in the middle of nasal scale; eye average, amounting for 0.9–1.2 times in males and 0.7–1.1 times in females the distance between the lower margin of eye and upper lip border; tail average to long, progressively tapering and distinctly prehensile; ratio TaL/TL 0.140–0.219, with a weak sexual dimorphism (males: 0.179–0.219; females: 0.140–0.191).

Body scalation. Dorsal scales rhombohedral, more or less strongly keeled in males, weakly keeled in females, in 21–21–15 (73%) or 23–21–15 (23%) rows (exceptionally in 25–21–15 rows; 4%); scales of the first dorsal scale row smooth and not enlarged; 159–173 ventrals (plus one or two preentrals), rounded; 57–76 paired subcaudal scales with overlapping sexual dimorphism (64–76 in males, 57–70 in females); cloacal plate entire.

Head scalation. Rostral much broader than high, triangular, well visible from above; nasal subrectangular, entire, elongate, longer than high; one internasal on each side, pentagonal, curved, wide, transversely elongate, separated by one (90%) or rarely two (10%) small scales; four or five canthal scales, slightly larger than adjacent snout scales, bordering the canthus rostralis between the internasal and corresponding supraocular; one relatively large triangular loreal between the upper preocular and nasal; two upper preoculars above loreal pit, lower one bordering the upper margin of loreal pit, upper one visible from above, both elongate and in contact with loreal; lower preocular forming lower margin of loreal pit; one supraocular on each side, entire, elongate and rather narrow, about 2.7–3.3 times longer than wide, about 0.5–0.9 times as wide as the internasals, indented on their inner margins by the upper head scales; cephalic scales relatively small, irregular or slightly rounded, juxtaposed, flat and smooth; 10–13 cephalic scales on a line between supraoc-

ulars; occipital scales rhombohedral, moderately or more frequently distinctly keeled in males, smooth or weakly keeled in females; temporals rhombohedral, distinctly keeled or less frequently smooth in males, always smooth in females; on each side, one thin, elongate, subocular scale, crescent-shaped; 2–3 small postoculars; 9–13 (usually 10–12) supralabials; first supralabial short, entirely separated from the nasal by a distinct suture; second supralabial tall, always forming the anterior border of loreal pit, separated from the nasal by one or two small scales; third supralabial the longest and highest, rather tall, usually separated from the subocular by one scale on each side (77.8%), rarely in contact (22.2%); fourth supralabial as long as high, lower than third supralabial, separated from subocular by one scale; fifth supralabial smaller than the fourth one, separated from the subocular by one or two scales of similar size; 10–15 (generally 12 or 13) infralabials, those of the first pair in contact with each other, the first three pairs in contact with the chin shields.

Coloration and pattern. In life, the body is uniform bright green, grass-green, deep green, bluish-green or even turquoise blue (Wall 1909). In preservative, the general background color remains green or turns to bluish-green, reddish-brown, brown or even black. Generally, numerous faint, dark transversal bands due to the dark brown or dark grey skin between the dorsal scales; in males, a broad and conspicuous, bicolored ventrolateral stripe, bright red, deep red or rusty brown on its lower part covering the lower half of the scales of the first dorsal scale row, white or whitish-yellow above on the upper posterior half of scales of the first row and on the lower part of scales of the second row, extends from the angle of the mouth to the base of the tail; in females, the ventrolateral stripe is thinner, white or creamish-yellow anteriorly, white or cream posteriorly, conspicuous and extends from the neck to the base of the tail on the first dorsal scale row. The tail is of the same green color than the dorsum, irregularly mottled with reddish-brown or rusty brown, without a clear demarcation between the red and green colors, entirely reddish-brown posteriorly; the ventrolateral stripe extends up to the first third to half-length of the tail.

The dorsal surface of the head and temporal region are uniform green or bluish-green like the body; the side of the head below the eye, i.e., the lower sides of the snout, nasal scale, and anterior supralabials and lower temporals, is distinctly paler than the dorsal surface of the head, generally pale green, yellowish-green or pale bluish-green; in males, a vivid, broad, bicolored postocular streak, the lower part narrow and white, the upper part broad and bright red, rusty-red or brownish-red, present at any age, extends from the postoculars obliquely towards the angle of the mouth then to the lower side of the neck where it connects to the ventrolateral stripe; in females, the postocular streak is usually absent, or present as a white and thin line. The chin and throat are generally pale yellowish-green, with infralabials sometimes bright yellow or marked with green. The eye is bright red, fire-red or deep red in life in adult specimens of both sexes (Fig. 7A–E).

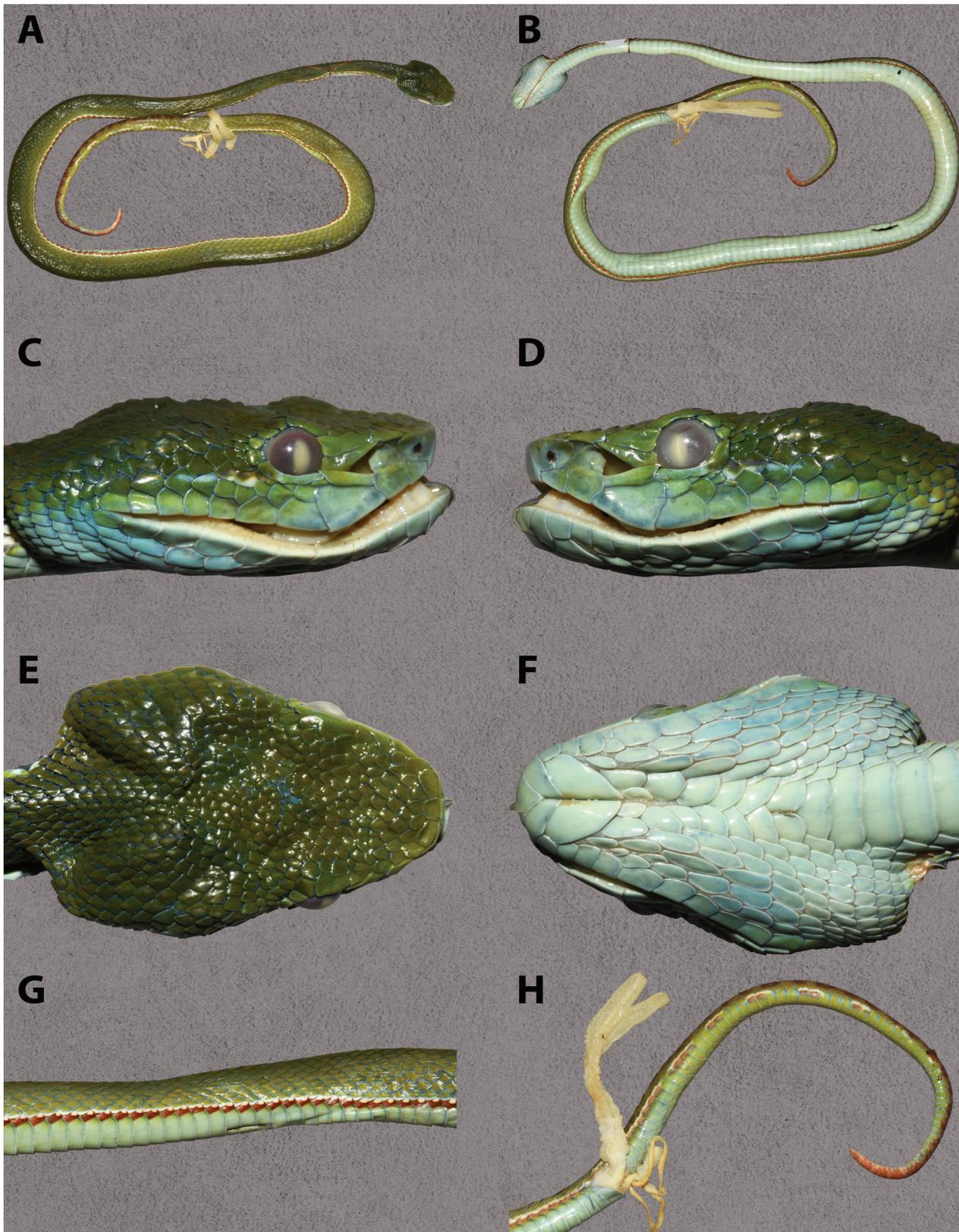


Figure 6. *Trimeresurus popeiorum* in preservative – specimen CIB DL201070102 (Paratype of *T. yingjiangensis*, adult male) **A** General dorsal view; **B** General ventral view; **C** Lateral view of the head, right side; **D** Lateral view of the head, left side; **E** Dorsal view of the head; **F** Ventral view of the head; **G** Latero-ventral aspect of the body; **H** Latero-ventral aspect of the tail. Photos by G. Vogel.

The venter is uniform yellowish-green or pale green; tips of ventrals red as the lower part of the ventrolateral stripe. The ventral surface of the tail is as the venter anteriorly, becoming rusty-red on its posterior half to third.

Hemipenis. The organ is long and thin, deeply forked, extending to the 25th or 26th subcaudal scale in situ, forked opposite at the level of the sixth to eighth subcaudal scales; the base of the organ, up to the point of bifurca-

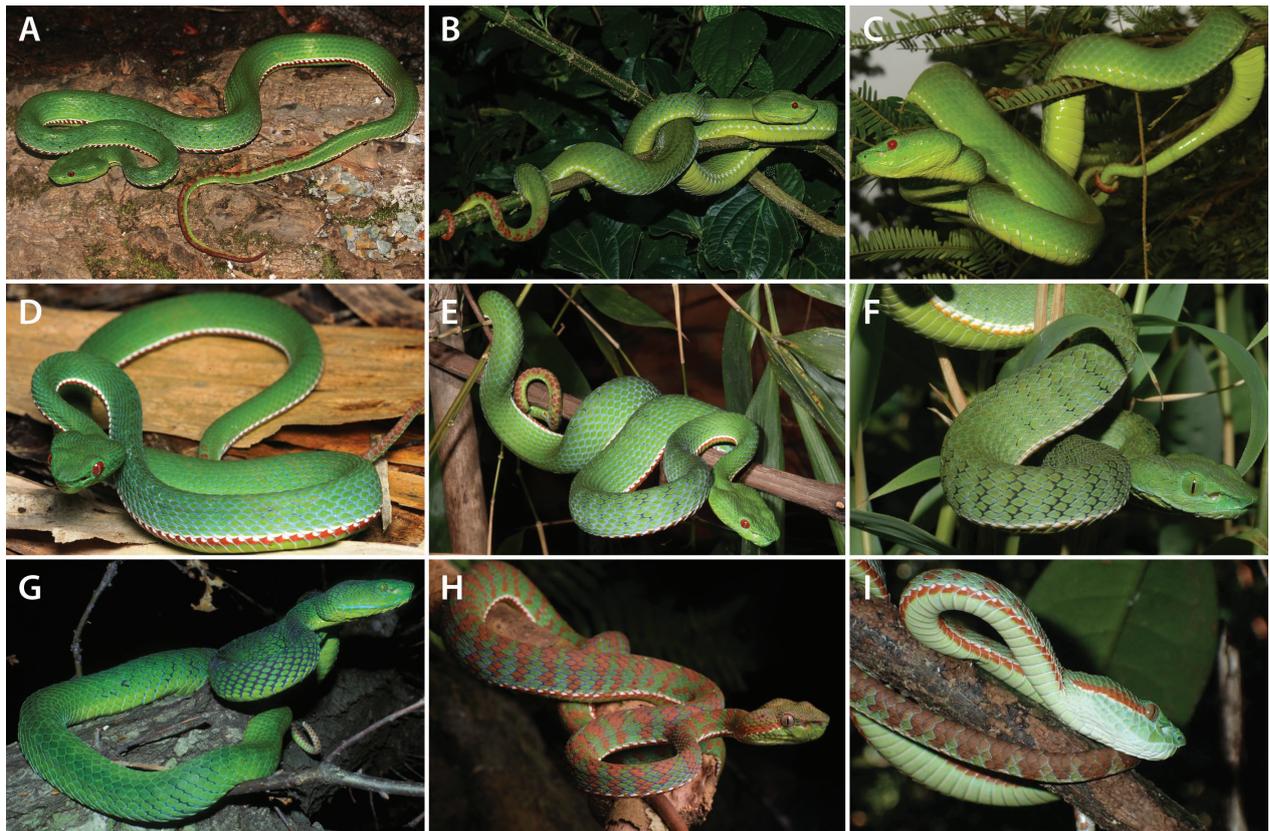


Figure 7. *Trimeresurus popeiorum*, *T. nebularis*, and *T. phuketensis* in life. – *Trimeresurus popeiorum*: **A** Buxa Tiger Reserve, West Bengal, India (adult male); **B** Karimganj, Assam, India (adult female); **C** Aizawl, Mizoram, India (adult female); **D** Inn Gyin Taung Mt., Kachin, Myanmar (male); **E** Yingjiang, Yunnan, China (adult male); *T. nebularis*: **F**, **G** Cameron Highlands, Pahang, Malaysia (adult male and adult female, respectively); *T. phuketensis*: **H** Phuket Is., Phuket, Thailand (adult male); **I** Sri Phang Nga NP, Phang Nga, Thailand (adult male). Photos by: P. Ray (A), R. Gassah (B), G. Vogel (C, E-G), N. A. Poyarkov (D), R. Grassby-Lewis (H), and S. Plongnui (I)

tion, is entirely smooth with longitudinal folds, except for the sulcus spermaticus; from the point of bifurcation up to the tip of the organ, each fork is finely calyculate. The sulcus is prominent; it divides near the base of the organ and ends near the tip of the fork (based on Smith 1937; Chen et al. 2019; Mirza et al. 2023; our data).

Dentition. Maxilla with one functional and 5–6 replacement fangs; palatine with four teeth, pterygoid with eight teeth, 10–12 dentary teeth (based on Mirza et al. 2023; and our data).

Distribution (Fig. 1). Based on our definition of *T. popeiorum*, we establish its range as follows: **India** (northeastern part of the country, in the states of Sikkim, West Bengal, Meghalaya, Assam, Arunachal Pradesh, and Mizoram); **Bhutan** (south); **Nepal** (east); **Bangladesh** (southeast: Chittagong Province), **China** (western Yunnan Province: Dehong Dai and Jingpo Autonomous Prefecture), and **Myanmar** (northern and southwestern parts of the country, in Kachin and Chin States, and Sagaing Region). The southernmost record for this species is from Ngape Township, Rakhine Yoma, Rakhine State, Myanmar (our data). The occurrence of this species in the states of Nagaland and Manipur, India, is expected.

Natural history notes. *Trimeresurus popeiorum* inhabits hilly and montane regions covered with humid tropical and subtropical submontane and montane evergreen forests and semi-evergreen forests. Chen et al. (2019) stated that at the type locality of *T. yingjiangensis* in Yunnan Province this species prefers to inhabit sites near streams at an elevation of about 1000 m, and can be found perched on branches waiting for prey in ambush. In contrast, in Myanmar, Liu et al. (2022) found individuals perched on small or big trees at elevations of only 155–176 m, and no rivers or streams were nearby. In the Dampa Tiger Reserve, Mizoram State, India, Malsawmdawnliana et al. (2022) noted that this species was quite common in their study area. These authors encountered more than ten individuals among roadside vegetation and along forest trails, and a female perched in ambush position on a small guava tree near the guest house. In Mizoram State, one of the authors of the present paper (GV) found a large female, on a tree trunk at about 1.7 m above the ground, in a secondary forest at an elevation of about 800 m. Moreover, *T. popeiorum* appears to be common across lower-elevation forests of Arunachal Pradesh State. Most individuals were observed perched on vegetation along roads, but we observed a higher number of individuals along streams. The species is found in sympatry with *T. salazar* Mirza, Bhosale, Phansalkar, Sawant, Gowande & Patel in

Arunachal Pradesh and Assam states and *T. erythrurus* (Cantor) in Meghalaya and Mizoram states.

Trimeresurus lanna sp. nov.

<https://zoobank.org/D1682045-34E5-458B-936D-B91434FEE-ADE>

Figs 8, 9; Tables S3, S4

Chresonymy.

Trimeresurus gramineus (non *Coluber gramineus* Shaw, 1802) – Pope and Pope (1933: 9, in part).

Trimeresurus popeiorum (non *Trimeresurus popeiorum* Smith, 1937) – Smith (1943: 518–519, in part); Taylor and Elbel (1958: 1171, in part), Taylor (1965: 1073–1075, in part); Malhotra and Thorpe (2000: 201, in part); Nabhitabhata (2000: 142, in part); David et al. (2001: 221, in part), Gumprecht (2001: 20–30, in part), Leviton et al. (2003: 446–447, in part); Malhotra and Thorpe (2004: 97, in part); Vogel et al. (2004: 19, in part); Sanders et al. (2004: 183–184, in part); Gumprecht et al. (2004: 36 in part, 257–258); Sanders et al. (2006: 361, in part); Castoe and Parkinson (2006: 105, in part); Leviton et al. (2008: 80–81, in part); Das (2010: 307, in part); Malhotra et al. (2010: 175, in part); Teynié and David (2010: 268–270); Chanhome et al. (2011: 325–326, in part); Chuaynkern and Chuaynkern (2012: 148, in part); Wallach et al. (2014: 575–576, in part); Guo et al. (2015: 267–268, 274, in part); Chan-ard et al. (2015: 345–346, in part); Wostl et al. (2016: 637, in part); Chen et al. (2019: 20, in part); Nguyen et al. (2020: 239, 241, in part); Wang et al. (2020: 205); Janzen (2021: 14, 20–21, in part); Liu et al. (2022: 86–87); Maury et al. (2022: 90); Ngo et al. (2023: 592, 594–595; in part), Vogel et al. (2022: 348, 363), Wang et al. (2022: 6); David et al. (2023: 59, 68–69, 92, 98, 105 [all *T. lanna*] and 813–820, in part); Poyarkov et al. (2023: 142, in part); Uetz et al. (2024, page “*Trimeresurus popeiorum*”, in part).

Popeia popeiorum [sic] – Guo et al. (2009: 153, in part), Liu et al. (2015: 266), Li et al. (2020); Wu et al. (2023: Table S1).

Trimeresurus popeiorum popeiorum (non *Trimeresurus popeiorum* Smith, 1937) – Regenass and Kramer (1981: 186–187, in part).

Popeia sp. 1 – Mirza et al. (2023: 94).

Trimeresurus cf. *popeiorum* 1 – Idiatiullina et al. (2023: 701), Idiatiullina et al. (2024: 17).

Holotype. AUP-00180, an adult male from Siriphum Waterfall, Doi Inthanon National Park (18.5467°N, 98.5124°E; elevation 1450 m), Chiang Mai Province, Thailand; collected by P. Pawangkhanant, C. Suwannapoom, and N. A. Poyarkov on 30 August 2017.

Paratypes (n = 8). **Thailand.** Chiang Mai Province: AUP-00178 (adult male), AUP-01574 (adult female) data same with holotype; FMNH 178656 (adult male), collected by O.G. Young, and NHMUK 1937.2.1.25 (adult male), collected by M.A. Smith in 1937, no specific locality. Lampang Province: IRSNB 2736 (formerly IRSNB 16545; adult male) and IRSNB 2737 (formerly IRSNB 16546; subadult female) from Chae Son NP. **Laos.** Phongsaly Province: FMNH 14430 (adult male) from Ban Muangyo, collected by R.E. Wheeler on 9

May 1929; MNHN-RA-2004.0262 (adult male), between Nathen and Long Nai, collected on 26 July 2004.

Referred specimens (n = 21). **Thailand.** Chiang Mai Province: MNHN-RA-1987.3836 (adult male), PSGV S0062 (subadult male), and AUP-00181, PSGV S0063 (two subadult females) from Doi Inthanon NP.; USNM 84757 (subadult female) from Khun Chae NP.; NHMW 27947 (adult male), FMNH 178655, FMNH 178658 (two subadult males), and NHMUK 1937.2.1.24, NHMUK 1937.2.1.26 (two subadult females), no specific localities. — **Laos.** Luangphrabang or Xaignabouli provinces: NHMUK 1862.7.28.4 (adult male) and NHMUK 1862.7.28.1 (adult female), “Lao Mountains, Cochinchina”, now Luangphrabang Range, western Laos, probably between Paklay (Xaignabouli Province) and Luangphrabang (Luangphrabang Province). — **Myanmar.** Mon Sate: CAS 222195, CAS 240640 (two adult males), and CAS 216609 (subadult male) all from Kyaik Hti Yo WS. Bago Reigon: CAS 205847 (adult female) from Bago Yoma City. Kayah State: NHMB 2596-97, NHMW 23923:1-2, and ZMB 11637 (five adult males) from Monts Karen Mt.

Etymology. The new species name “*lanna*” represents a noun in apposition and is given in reference to the Lan Na Kingdom, or “Kingdom of a Million Rice Fields”. The Kingdom of Lan Na, also known as Lannathai, was centered in present-day northern Thailand from the 13th–18th centuries. The territories and cultural influence of the Lan Na Kingdom spread from easternmost Myanmar to northern Laos and southernmost present-day Yunnan of China, a geographic area that matches well the range of the new species. Though eventually the Lan Na Kingdom was united with the Siamese State in the early 19th century, its culture had a profound influence on different parts of northern Indochina. We suggest the following common names for the new species: “Ngu Khiew Hang Mai Thong Khiew Nua” (เผ็ดหางไหม้ทองเขียวหนือ) (in Thai), “Lán nà zhú yè qīng” (蘭納竹叶青) (in Chinese), “Lanna green pitviper” (in English), “Trimérésure vert du Lanna” (in French), “Lanna Bambusotter” (in German), and “Chiangmaiskaya bambukovaya kufiya” (in Russian).

Diagnosis. *Trimeresurus lanna* differs from other members of the subgenus *Popeia* by the combination of the following morphological characters: (1) dorsal surfaces deep green, without crossbands; (2) in males, a vivid, wide, bicolored ventrolateral stripe, bright and deep red below, white above; in females, ventrolateral stripe thin, pale yellow anteriorly, whitish posteriorly; (3) in males, a conspicuous, bicolored postocular streak, white and thin ventrally, broad and bright red dorsally, covering two or three temporal scales; in females, streak absent or only white; (4) eyes red to deep red in both males and females; (5) 21 (93.3%) or rarely 20 (6.7%) dorsal scales rows at midbody, strongly keeled except those of the first dorsal scale row, always smooth; (6) 145–167 ventral plates (145–167 in males; 157–166 in females); 56–75 paired subcaudal scales with weak sexual dimorphism (59–75

in males, 56–64 in females); (7) first supralabial entirely separated from the nasal scale by a distinct suture; (8) supraoculars relatively narrow, narrower than internasals, separated by 10–13 cephalic scales; (9) internasals never in contact, separated by one or two scales; (10) hemipenes long and forked, reaching at least 25th SC, without spines; (11) 9–14 cephalic scales between the supraoculars in males, 11–13 in females; (12) relative tail length 0.18–0.21 in males, 0.16–0.17 in females.

Description of the holotype (Fig. 8A–D). An adult male, specimen in a very good state of preservation.

Morphology. Body cylindrical, long, and laterally compressed; SVL 640 mm, TaL 175 mm, TL 815 mm, TaL/TL 0.215. Head triangular in dorsal view, elongate, clearly distinct from the neck (HL 36.8 mm, HL/SVL 0.06); snout elongate, flattened, and rounded when seen from above, rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; loreal pit present, triangular in shape. Eye average (ED 4.5 mm, SnL 11.3 mm, ED/SnL 0.40); pupil vertically elliptic.

Body scalation. Dorsal scales in 23-21-15 rows; dorsal scales all moderately keeled, except the first row the scales of which are smooth; 157 ventrals (plus single pre-ventral); cloacal plate single; 71 subcaudals, all divided.

Head scalation. Rostral slightly visible from above, triangular, broader than high; one enlarged internasal on each side, internasals separated by one small scale behind the top of rostral (Fig. 8A); nostril completely included in the entire nasal scale, pentagonal, undivided, elongate, as long as high; nasal scale completely separated from the first supralabial (Fig. 8C); one internasal on each side, pentagonal, curved, wide, transversely elongate, separated by one small scale; two small scales between the nasal and the second supralabial; scales on the upper snout surface and in the interorbital region smooth, irregular, barely imbricate; 3/3 canthal scales, slightly larger than adjacent snout scales, bordering the canthus rostralis between the internasal and corresponding supraocular; temporal and occipital scales obtusely keeled; one relatively large triangular loreal between the upper preocular and the nasal; two elongate upper preoculars above loreal pit, lower one bordering the upper margin of loreal pit, upper one visible from above, both elongate and in contact with loreal; lower preocular forming lower margin of loreal pit; one supraocular on each side, long, much longer than wide, 0.7/0.8 times as wide as the internasals; cephalic scales relatively small, irregular or slightly rounded, juxtaposed, flat and smooth; 11 irregular cephalic scales between the supraoculars; one long, thin, crescent-like subocular scale; occipital scales rhombohedral, distinctly but obtusely keeled; 2/2 small postoculars; 10/10 supralabials, first supralabial short, entirely separated from the nasal by a distinct suture; second supralabial tall, forming the anterior border of loreal pit; third supralabial the largest and in contact with the subocular on each side; fourth and fifth supralabials much lower than the third

one, separated from the subocular by one scale on each side (Fig. 8C); 12/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields and the first pre-ventral (Fig. 8B).

Coloration in preservative (Fig. 8A–D). The body is uniform deep bluish-green (bright grass-green in life), without darker areas or crossbands; a conspicuous, bicolored ventrolateral stripe extends from the beginning of the neck to the vent, pinkish-brown (bright deep red in life) ventrally, this color covering nearly the whole scales of the first dorsal scale row except their upper posterior corner that is cream, and dorsally cream (white in life) on the lower half of scales of the second row. The tail is bluish-green like the dorsum; the ventrolateral stripe extends up to the first third of the tail; near its end, the dorsal surface of the tail is irregularly mottled with pinkish-orange (rusty-red in life).

The dorsal surface of the head and the temporal region are bluish-green like the body; the side of the head below the eye (i.e., the sides of the snout, nasal scale, anterior supralabials and lower temporals) is distinctly paler than the dorsal surface of the head, namely pale bluish-green (pale green in life); a broad, bicolored postocular streak, its ventral part narrow and cream (white in life) covering the lower row of temporals, its upper part, broader (two rows of temporals), pinkish-brown (bright deep red in life), extends from the postoculars obliquely towards the angle of the mouth but the postocular streak does not connect with the ventrolateral stripe. The chin and throat are pale sea-green (pale green in life), uniform but with few faint darker areas on infralabials sometimes. The eye is grey but it was deep fire-red in life. The venter is uniform pale sea-green (pale green in life); tips of ventrals of the same green color, not red. The ventral surface of the tail is as the venter anteriorly, becoming pinkish-orange in its posterior quarter (reddish-brown in life).

Description of hemipenes (based on adult male CAS 240640, Fig. 8H). The organ is long and thin, deeply forked, extending to the 18th subcaudal scale in situ, forked at the level of fifth to sixth subcaudal scales; the base of the organ, up to the point of bifurcation, is entirely smooth with longitudinal folds, except for the sulcus spermaticus; from the point of bifurcation up to the tip of the organ, each fork is finely calyculate. The sulcus is prominent; it divides near the base of the organ and ends near the tip of the fork.

Variation. See also Table S3.

Morphology. The longest known specimen is 845 mm long (SVL 709 mm, TaL 136 mm; female, NHMUK 1862.7.28.1). The longest known male is 815 mm long (SVL 640 mm, TaL 175 mm; holotype). The body is robust, relatively slender in males, thicker in large females, laterally compressed; head triangular, elongate, wide posteriorly, flattened in males, moderately thick in females,

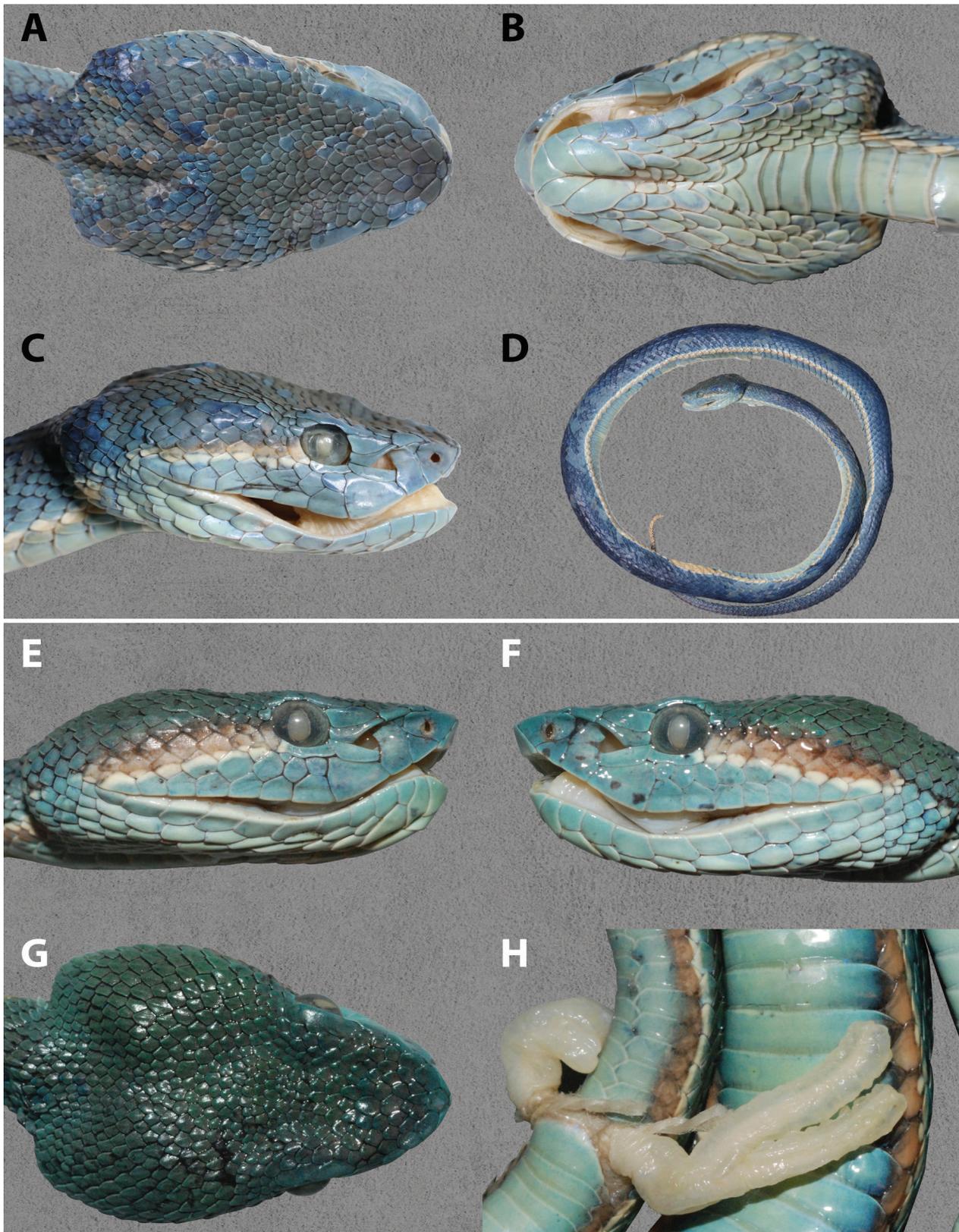


Figure 8. *Trimeresurus lanna* sp. nov. in preservative. Specimen AUP-00180 (holotype, adult male): **A** Dorsal view of the head; **B** Ventral view of the head; **C** Lateral view of the head, right side; **D** General dorsal view. Specimen CAS 240640 (adult male): **E** Lateral view of the head, right side; **F** Lateral view of the head, left side; **G** Dorsal view of the head; **H** Hemipenis in asulcal aspect. Photos by: P. Pawangkhanant (A–D), and G. Vogel (E–H).

clearly distinct from the neck; snout elongate, distinctly flattened, rounded seen from above, angular and obliquely truncated in profile view, with a distinct canthus rostralis;

nostril piercing in the middle of nasal scale; eye average, amounting for 0.9–1.2 times in males and 0.7–1.0 times in females the distance between the lower margin of eye

and upper lip border; tail average to long, progressively tapering and distinctly prehensile; ratio TaL/TL 0.149–0.211, with a sexual dimorphism (males: 0.182–0.211; females: 0.149–0.173).

Body scalation. Dorsal scales in 23–21–15 (50%), 21–21–15 (36.7%), or rarely 25–21–15 (10%) and 22–21–15 (3.3%) rows, moderately or strongly keeled; scales of the first dorsal scale row smooth and not enlarged; 145–167 ventral plates (plus one or two preventrals), rounded; 56–75 subcaudal scales with a weak sexual dimorphism (59–75 in males, 56–64 in females), all paired; total number of VEN+SC: 213–241, without sexual dimorphism; cloacal plate entire.

Head scalation. The head scalation is as described for the holotype, with the following variation: internasals separated by one (84%) or rarely two (16%) small scales; three or four canthal scales bordering the canthus rostralis between the internasal and corresponding supraocular; one supraocular on each side, entire and rather narrow, about 0.7–0.9 times as wide as the internasals, indented on their inner margins by the upper head scales; cephalic scales juxtaposed, flat and smooth; 10–13 cephalic scales on a line between supraoculars; occipital scales rhombohedral, distinctly obtusely keeled in males, weakly keeled or even smooth in females; temporals generally moderately but distinctly keeled (80%), rarely smooth (20%) in males, always smooth in females; on each side, one thin, elongate subocular scale, crescent-shaped; two or three small postoculars; 9–11 supralabials; third supralabial the longest and highest, rather tall, in contact with the subocular or separated from this latter scale by one scale; fourth supralabial separated from the subocular by one scale in all examined specimens; fifth supralabial smaller than the fourth one, separated from the subocular by one or two scales of similar size; 10–14 (generally 12–13) infralabials, those of the first pair in contact with each other.

Coloration and pattern (Figs 8, 9). In life or in freshly preserved animals, the body is uniform bright green, grass-green, emerald-green or deep green (in preservative, the general background color remains green or turns to bluish-green); no dark transversal crossbands or white vertebral dots; in males, the broad, bicolored ventrolateral stripe is as described above, namely bright red, deep red or rusty brown on its lower part, white or whitish-yellow above, always present and conspicuous; in females, the ventrolateral stripe is absent or thin and faint, white or cream. The tail is of the same green color than the dorsum, irregularly mottled with reddish-brown or rusty brown posteriorly.

The dorsal surface of the head and the temporal region are uniform green or bluish-green like the body; the sides of the head below the eye, i.e., the lower sides of the snout, nasal scale, and anterior supralabials and lower temporals are distinctly paler than the dorsal surface of the head, pale green or pale bluish-green; in males, the vivid, broad, bicolored postocular streak, white ventrally, bright red, rusty-red or brownish-red dorsally, is always

present; in females, the postocular streak is usually absent (85.7%) or present as a white and thin line (14.3%). The chin and throat are pale green or pale sea-green, uniform or with infralabials marbled with green. The eye is bright red, fire-red or deep red in specimens of both sexes. The venter is uniform pale green or pale sea-green; tips of ventrals green. The ventral surface of the tail is as the venter anteriorly, becoming rusty-red on its posterior half to third.

Comparisons. We here compare *T. lanna* with the four other species of the subgenus *Popeia* (*T. nebularis*, *T. phuketensis*, *T. popeiorum*, and the *T. sabahi* complex). The main diagnostic characters separating the new species from these four species are summarized in Table S4.

Trimeresurus lanna is morphologically very similar to *T. popeiorum* but it is distinguished from this latter species by having: (1) lower max TL in males (815 mm vs. 925 mm), but higher max TL in females (884 mm vs. 854 mm); (2) slightly lower number of ventral plates in males (145–167, $\bar{x} = 159.9$ vs. 162–171, $\bar{x} = 165.7$; $p = 0.0004$); (3) slightly lower total number of VEN+SC in males (213–241, $\bar{x} = 227.81$ vs. 229–240, $\bar{x} = 234.71$; $p = 0.0004$); (4) bicolor postocular streak in males broad, covering 2–3 temporal scales vs. narrow, covering 1–2 temporal scales; (5) temporals strongly keeled in males (vs. feebly keeled).

Trimeresurus lanna is distinguished from *T. nebularis* by having: (1) eye color deep red in both sexes vs. usually green; (2) bicolor postocular streak present in males vs. absent; presence of a white ventrolateral stripe in females vs. absent; (3) lower max TL in both sexes (815 mm in males, 854 mm in females vs. 1002 mm in males, 948 mm in females); (4) higher total number of VEN+SC in both sexes (213–241, $\bar{x} = 228.1$ vs. 210–218, $\bar{x} = 214.0$ in males; $p = 0.007$; 213–229, $\bar{x} = 221.2$ vs. 197–210, $\bar{x} = 205.6$ in females; $p = 0.021$).

Trimeresurus lanna differs from *T. phuketensis* by having: (1) higher max TL in both sexes (815 mm in males, 854 mm in females vs. 640 in males, 748 mm in females); (2) lower total number of VEN+SC in both sexes (213–241, $\bar{x} = 227.8$ vs. 242–249, $\bar{x} = 246.4$ in males; $p = 0.0032$; 213–229, $\bar{x} = 221.2$ vs. 226–237, $\bar{x} = 230.6$ in females; $p = 0.015$); (3) eye color deep red in both sexes vs. copper; (4) body without dorsal crossbands vs. present and conspicuous.

Trimeresurus lanna can be further differentiated from the five subspecies of *T. sabahi* as follows:

- from *T. s. barati* by having: (1) 21 dorsal scales rows at midbody (vs. 17–19); (2) eye color deep red in both sexes vs. deep orange; (3) bicolor postocular streak present in males vs. absent; (4) slightly higher max TL in both sexes (815 mm in males, 854 mm in females vs. 740 mm in males, 720 mm in females);
- from *T. s. buniana* by having: (1) dorsum uniform bright green vs. dark bluish-green or verdigris with

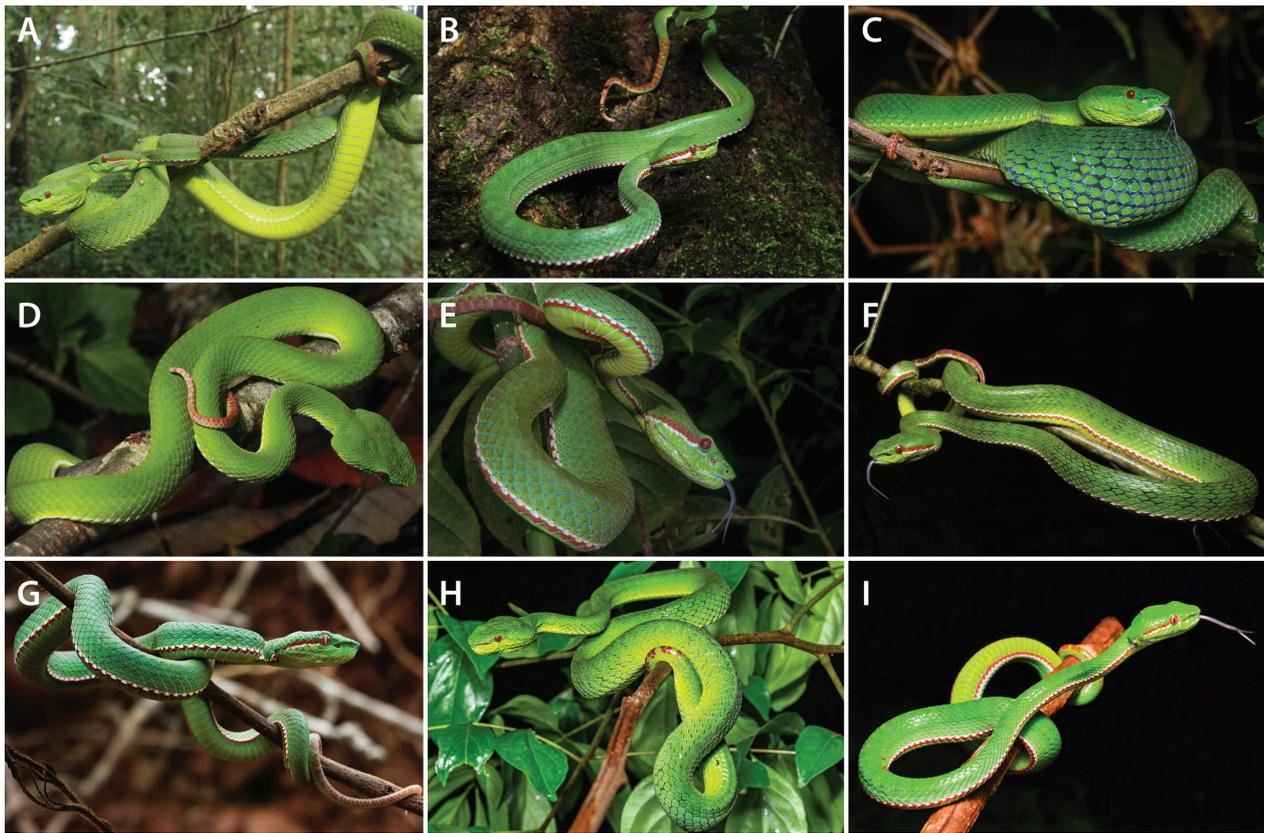


Figure 9. *Trimeresurus lanna* sp. nov. in life. **Thailand:** A Doi Inthanon NP, Chiangmai (mating adult couple); B, C Doi Phu Kha NP, Nan, Thailand; D Doi Suthep-Pui NP., Chiangmai (subadult female); E Doi Luang Mt., Chiang Rai (adult male); F Umphang, Tak (adult male). **Laos:** G, H Phongsaly (adult male and female, respectively). **China:** I Mengla, Xishuangbanna, Yunnan, China (adult male). Photos by: P. Pawangkhanant (A, D), T. Smith (B, E, F), R. Jaihan (C), T. Calame (G), P. Brakels (H), and J. Ming (I).

- conspicuous reddish-brown or violet, irregular crossbands; (2) eye color deep red in both sexes vs. copper; (3) bicolor postocular streak (red plus white) present in males vs. postocular streak reddish-brown; (4) slightly lower ratio TaL/SVL in both sexes (0.18–0.21, \bar{x} = 0.20 vs. 0.22–0.23, \bar{x} = 0.22 in males; p = 0.007; 0.14–0.17, \bar{x} = 0.16 vs. 0.21 in females); (5) lower total number of VEN+SC in both sexes (213–241, \bar{x} = 228.5 vs. 246–250, \bar{x} = 248.0 in males; p = 0.0004; 213–229, \bar{x} = 221.4 vs. 231 in females);
- from *T. s. fucatus* by having: (1) slightly lower ratio TaL/TL in both sexes (0.18–0.21, \bar{x} = 0.20, vs. 0.19–0.24, \bar{x} = 0.22 in males; p = 0.000002; 0.14–0.17, \bar{x} = 0.16 vs. 0.16–0.19, \bar{x} = 0.17 in females; p = 0.05; (2) eye color deep red in both sexes vs. copper; (3) dorsal crossbands absent in males vs. present; (4) white vertebral spots absent vs. present; (5) bicolor postocular streak wide (red plus white) present in male vs. sometimes absent, or white, or white with its upper part dark red and thin;
 - from *T. s. toba* by having: (1) eye color deep red in both sexes vs. deep orange; (2) ventrolateral stripe bicolor, wide in males vs. white and thin; (3) slightly higher max TL in both sexes (815 mm in males, 854 mm in females vs. 730 mm in males, 798 mm in females);
 - from *T. s. sabahi* by having: (1) bicolor postocular streak present in males vs. absent; (2) slightly lower TaL/TL ratio in both sexes (0.18–0.21, \bar{x} = 0.20 vs. 0.19–0.24, \bar{x} = 0.21 in males; p = 0.05; 0.14–0.17, \bar{x} = 0.16 vs.

0.17–0.18, \bar{x} = 0.18 in females; p = 0.04); (3) slightly higher total number of VEN+SC in females (213–229, \bar{x} = 221.2 vs. 212–217, \bar{x} = 214.7; p = 0.034).

Furthermore, in western Laos and northern Thailand *T. lanna* may be recorded in sympatry with the superficially similar *T. (Viridovipera) gumprehti* David et al., 2002. The two species can be easily distinguished from each other by hemipenial morphology: in the new species hemipenes are long, slender and deeply forked, reaching in situ at least the 25th subcaudal, lacking spines (vs. hemipenes short, thick, barely forked and strongly spinous, extending at most up to the 13th–15th subcaudals in *T. gumprehti*). Furthermore the eye of *T. lanna* is always deep red or fire-red in life in both sexes (vs. eye in life red in males, copper or yellow in females in *T. gumprehti*); and the head is flat with a distinctly obliquely truncated snout (vs. snout barely obliquely truncated, rather rectangular or rounded in *T. gumprehti*).

Distribution. *Trimeresurus lanna* is currently known from a large expanse in northern Indochina around the infamous “Golden Triangle”, including southeastern Myanmar. Based on our data, we establish the distribution of this species as follows: **Myanmar** (southeastern part of the country: Mon and Kayah States, and the Bago Region). **China** (Yunnan Province: Puer, Jinghong, and Mengla Counties). **Laos** (Houaphan, Luangnamtha, Lu-

angphrabang, Oudomxay, Phongsali, Xaignabouli, and Vientiane Provinces). **Thailand** (northern and western parts of the country: Chiang Mai, Chiang Rai, Kamphaeng Phet, Kanchanaburi, Lampang, Mae Hong Son, Nan, Tak, and Uthai Thani Provinces; the southern limit of the range is in Sri Sa Wat District, Kanchanaburi). The occurrence of the new species in Shan and Kayin States of Myanmar, in the province of Bokeo in Laos, and in Phayao and Phrae Provinces in Thailand, is strongly anticipated.

Natural history notes. *Trimeresurus lanna* typically inhabits humid tropical submontane primary evergreen and secondary forests, subtropical montane evergreen, semi-evergreen and mixed forests, as well as mixed secondary submontane forest, generally at elevations between 600 and 2000 m but it can be found at much lower elevations in suitable cool and humid habitats. It feels also at home in moist monsoon and other deciduous forests, bamboo thickets, and plantations. In Chiang Mai Province, Thailand, it is normally found in evergreen submontane and montane forest at elevations between 500 and 1700 m. It occurs in regions where winter temperatures can be as low as 3–7°C. The preferred microhabitats of this pitviper are markedly cool, humid, and shaded places. It is generally associated with dense shrubs, thickets, bushes, scrubs, the foliage of low trees, and tall grasses. This species is generally found in the low, humid vegetation of riparian areas, especially in the vicinity of freshwater habitats. Wogan and Chan-ard (2012, 2022; reported as *T. popeiorum*) stated that individuals can often be found hanging over streams and in bushes. It is also often seen along the edges of forest clearings and sides of forest tracks.

Trimeresurus lanna is arboreal, crepuscular, and nocturnal. It is usually found coiled up above small streams or sometimes as high as 4 or 5 m above the ground. In Tak Province, Thailand, GV observed an individual on the ground in a submontane forest. In Oudomxay Province, Laos, Nguyen et al. (2020; reported as *T. popeiorum*) found individuals perched at night (1900–2300 h) from 0.5–4 m above the ground along a road in a forested valley. Still in Laos, Maury et al. (2022) recorded many specimens during the day and at night between elevations of 450–1300 m, the species being more abundant near streams and other freshwater habitats. Snakes were perched high in trees, between about 2 m and 10 m during dry days, where they were probably resting. At night, especially during rainy weather, specimens were found much closer to the ground, at heights between 10 cm and 2 m. This pitviper feeds mainly on frogs and lizards, especially geckos, also small mammals, and birds. It is ovoviviparous. On Doi Suthep Mt., Chiang Mai Province, Thailand, one of the authors (P. Pawangkhanant) observed a mating pair in October; mating started after a big rainfall around 1750 h, the adult male stayed near the female for almost two weeks. Newborns have been observed along a small stream on Doi Inthanon NP, Chiang Mai Province, Thailand (elevation ca. 1230 m) in late April to May.

Conservation status. Further research is required to clarify the extent of the distribution, population size and trends before the conservation status of this new species can be assessed. *Trimeresurus lanna* is distributed over a large area including many protected areas. Across its range the new species generally seems to be quite common. The density of some populations may be high as Maury et al. (2022) found up to 25 individuals in a single evening. These authors stated that it was common to find over 15 individuals at the same place in secondary forest. Thus, we tentatively suggest *T. lanna* be considered a species of Least Concern (LC) following the IUCN's Red List categories (IUCN Standards and Petitions Committee 2019).

Trimeresurus tenasserimensis sp. nov.

<https://zoobank.org/BE72A92E-E498-4C84-9BC1-8EF0EDB44905>

Figs 10, 11; Tables 3, 4

Chresonymy.

Trimeresurus gramineus (non *Coluber gramineus* Shaw, 1802) – Pope and Pope (1933: 9, in part).

Trimeresurus popeiorum (non *Trimeresurus popeiorum* Smith, 1937) – Smith (1943: 518–519, in part); Nabhitabhata (2000: 142, in part); Gumprecht (2001: 20–30, in part); Leviton et al. (2003: 446–447, in part); Malhotra and Thorpe (2004: 97, in part); Vogel et al. (2004: 19, in part); Sanders et al. (2004: 183–184, in part); Castoe and Parkinson (2006: 105, in part); Sanders et al. (2006: 361, in part); Leviton et al. (2008: 80–81, in part); Das (2010: 307, in part); Malhotra et al. (2010: 175, in part); Chanhome et al. (2011: 325–326, in part); Chuaynkern and Chuaynkern (2012: 148, in part); Wallach et al. (2014: 575–576, in part); Chan-ard et al. (2015: 345–346 in part); Zug and Mulcahy (2020: 164); Poyarkov et al. (2023: 392, in part); Uetz et al. (2024, page “*Trimeresurus popeiorum*”, in part).

Trimeresurus popeiorum popeiorum – Regenass and Kramer (1981: 186–187, in part).

Trimeresurus sp. nov. – Mulcahy et al. (2017: 310–311).

Trimeresurus cf. *popeiorum* – Platt et al. (2018: 93).

Popeia sp. 2 – Mirza et al. (2023: 94).

Trimeresurus stejnegeri (non *Trimeresurus stejnegeri* Schmidt, 1925) – Leviton et al. (2003: 448, in part).

Viridovipera stejnegeri – Leviton et al. (2008: 91–92, in part).

Popeia fucata (non *Trimeresurus fucatus* Vogel, David & Pauwels, 2004, now *Trimeresurus sabahi fucatus*) – Leviton et al. (2008: 78–79, in part); Pauwels and Chan-ard (2006: 100, 103), Pauwels et al. (2009: 14).

Trimeresurus cf. *popeiorum* 2 – Idiatullina et al. (2023: 701); Idiatullina et al. (2024: 17).

Holotype. ZMMU Re-17668 (adult male) from Suan Phueng District, Ratchaburi Province, Thailand (13.55358°N, 99.20528°E; elevation 640 m) collected by P. Pawangkhanant on 7 June 2019.

Paratypes (n = 4). **Thailand.** ZMMU Re-17671 (adult female) collected on 3 June 2019, same information

than the holotype. — **Myanmar.** Tanintharyi Region: NHMUK 1924.5.20.38 (adult male) from Paya Taung Mt., Dawei City; CAS 247870 (adult male) and CAS 247754 (adult female) from Kawthaung District.

Referred specimens (n = 5). **Thailand.** ZMMU Re-17672 (subadult male) and ZMMU Re-17670 (subadult female) collected on 3 June 2019, ZMMU Re-17673 (subadult male) collected on 17 July 2019, all same information with holotype. — **Myanmar.** Tanintharyi Region: NHMUK 1856.5.6.105 from Myeik Is., Myeik District; NHMUK 1940.3.9.43 (adult male) from Kisseraing Is, Myeik District.

Referred materials from the literature (n = 4). **Myanmar.** Tanintharyi Region: USNM 587920 (subadult female), USNM 587921 (adult male) from Kawthaung District; USNM 587588 (adult female) Lenya Area; and USNM 587919 (adult female) from Ywahilu Village (see detail from Mulcahy et al. 2017).

Etymology. The species name “*tenasserimensis*” is a modern Latin toponymical adjective in nominative singular, adopting the masculine gender of the genus name *Trimeresurus*, combining the name of the Tenasserim Mountain Range in western Thailand and southeastern Myanmar, where the new species occurs, and the Latin suffix *-ensis* (*-is*, *-e*), meaning “from”. The species nomen therefore means “from Tenasserim”. We suggest the following common names for the new species: “Ngu Khiew Hang Mai Thong Khiew Tanao Sri” (งูเขียวหางไหมทอง เตี้ยตะนาอศรี) (in Thai), “Dān nà shā lín zhú yè qīng” (丹那沙林竹叶青) (in Chinese), “Tenasserim green pitviper” (in English), “Tenasserim Bambusotter” (in German), “Trimérésure vert du Tenasserim” (In French) and “Tenasserimskaya bambukovaya kufiya” (in Russian).

Diagnosis. *Trimeresurus tenasserimensis* differs from other members of the subgenus *Popeia* by the combination of the following morphological characters: (1) dorsal surfaces deep green, with faint dark, interstitial crossbands; (2) in males, a wide, bicolored ventrolateral stripe, bright red ventrally, white dorsally; in females, ventrolateral stripe thin, pale yellow anteriorly, whitish posteriorly; (3) in males, a conspicuous, bicolored postocular streak, white and thin ventrally, broad and bright red dorsally, covering two or three temporal scales; in females, streak absent or only white; (4) eyes red to deep red in both males and females; (5) 21 dorsal scales rows at midbody, strongly keeled except those of the first dorsal scale row, always smooth; (6) 159–176 ventrals (159–170 in males, 154–176 in females); 57–74 subcaudals with slightly overlapping sexual dimorphism (66–74 in males, 57–66 in females), all paired; (7) first supralabial entirely separated from the nasal scale by a distinct suture; (8) supraoculars relatively narrow, narrower than internasals, separated by 9–11 cephalic scales; (9) internasals not in contact, separated by one scale; (10) 10–11 cephalic scales between the supraoculars in both sexes; (11) relative tail length 0.20–0.23 in males, 0.14–0.16 in females.

Description of the holotype (Fig. 10A–F). Adult male, specimen in a good state of preservation. Especially, it had still retained its color in life at the time of writing this paper.

Morphology. Body cylindrical, long, and laterally compressed (SVL 502 mm, TaL 127 mm, TL 629 mm, TaL/TL 0.202). Head triangular in dorsal view, elongate, clearly distinct from the neck (HL 30.2 mm, HL/SVL 0.06), snout elongate, flattened and rounded when seen from above, rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; loreal pit present, triangular in shape. Eye average (ED 3.3 mm, SnL 8.4 mm, ED/SnL 0.39); pupil vertically elliptic.

Body scalation. Dorsal scales in 21-21-15 rows; dorsal scales all moderately keeled, except the first row of which scales are smooth; 160 ventrals (plus two prefrontals); cloacal plate single; 66 subcaudals, all divided.

Head scalation. Rostral slightly visible from above, triangular; one internasal on each side, pentagonal, distinctly transversely elongate, internasals separated by one small scale behind the top of rostral (Fig. 10E); nostril completely included in nasal scale, pentagonal, entire, elongate, as long as high; nasal scale completely separated from the first supralabial; one small scale between nasal and the second supralabial; scales on the upper snout surface and in the interorbital region smooth, irregular, barely imbricate; 4/4 canthal scales, slightly larger than adjacent snout scales, bordering the canthus rostralis between the internasal and corresponding supraocular; temporal and occipital scales distinctly but obtusely keeled; one relatively large triangular loreal between the upper preocular and the nasal; two elongate upper preoculars above loreal pit, lower one bordering the upper margin of loreal pit, upper one visible from above, both elongate and in contact with loreal; lower preocular forming lower margin of loreal pit (Fig 10C, D); one supraocular on each side, long, much longer than wide, 0.7/0.8 times as wide as the internasals; cephalic scales relatively small, irregular or slightly rounded, juxtaposed, flat and smooth; ten irregular cephalic scales between the supraoculars; one long, thin, crescent-like subocular scale; occipital scales rhombohedral, distinctly but obtusely keeled (Fig. 10E); 2/2 small postoculars; 10/11 supralabials, first supralabial short, entirely separated from the nasal by a distinct suture; second supralabial tall, forming the anterior border of loreal pit; third supralabial largest and in contact with the subocular on each side; fourth and fifth supralabials, much lower than the third one, separated from the subocular by one scale on each side (Fig. 10C, D); 13/12 infralabials, those of the first pair in contact with each other behind the mental, the first three pairs in contact with the single pair of chin shields. Five pairs of gulars aligned between the chin shields and the first prefrontal (Fig. 10F).

Coloration in life (Fig. 10A–F). The body is uniform bright grass-green, with faint darker areas forming cross-

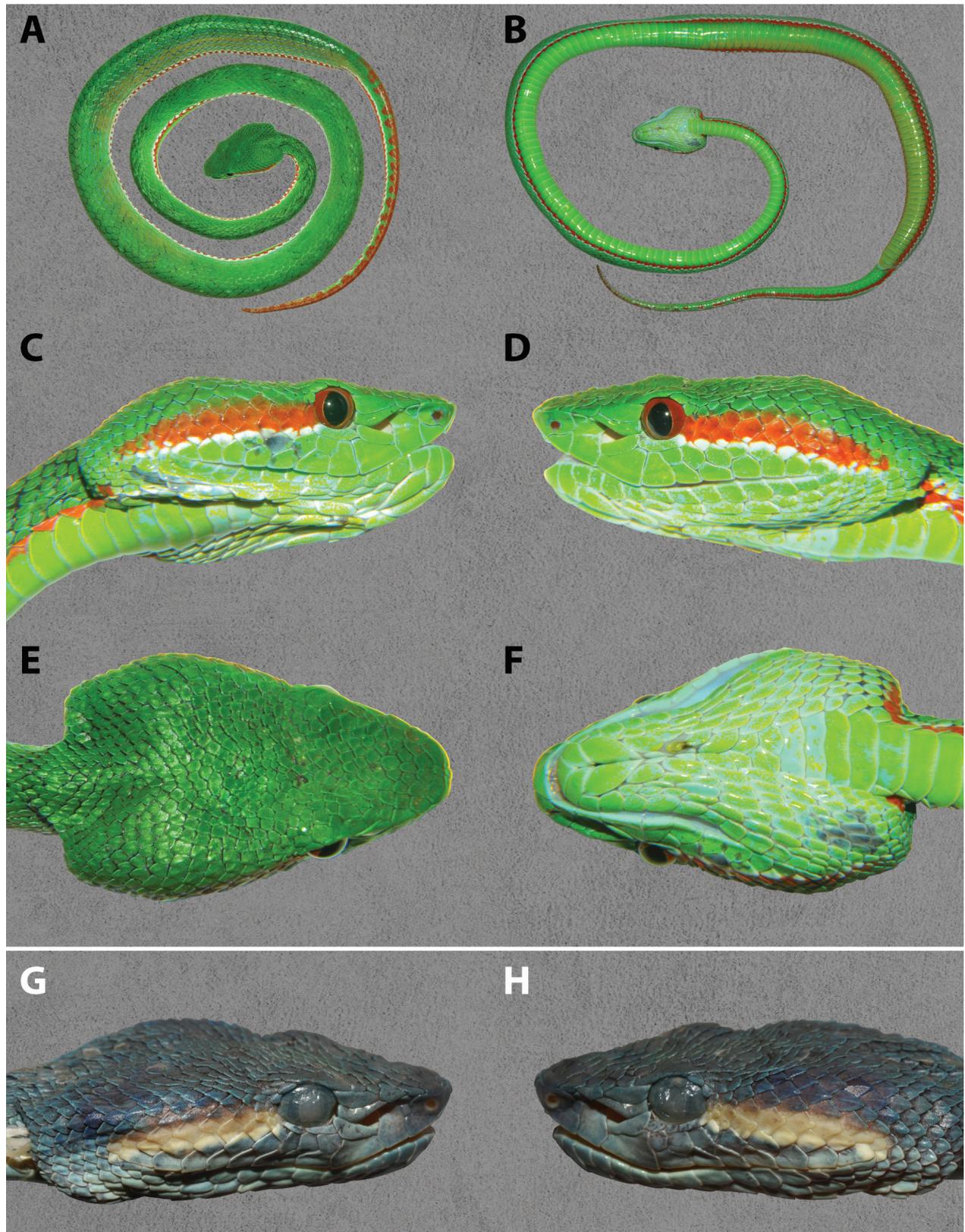


Figure 10. *Trimeresurus tenasserimensis* sp. nov. Specimen ZMMU Re-17668 (holotype, adult male; before preservation): **A** General dorsal view; **B** General ventral view; **C** Lateral view of the head, right side; **D** Lateral view of the head, left side; **E** Dorsal view of the head; **F** Ventral view of the head. Specimen CAS 247870 (paratype, adult male; in preservative): **G** Dorsal view of the head; **H** Ventral view of the head. Photos by: N. A. Poyarkov (A–F), and G. Vogel (G–H).

bands due to the darker interstitial skin; a conspicuous, bicolored ventrolateral stripe extends from the beginning of the neck to the vent, bright deep red ventrally, this col-

or covering a large part of the scales of the first dorsal scale row except their upper posterior corner or half that is white, and dorsally white on the lower half of scales

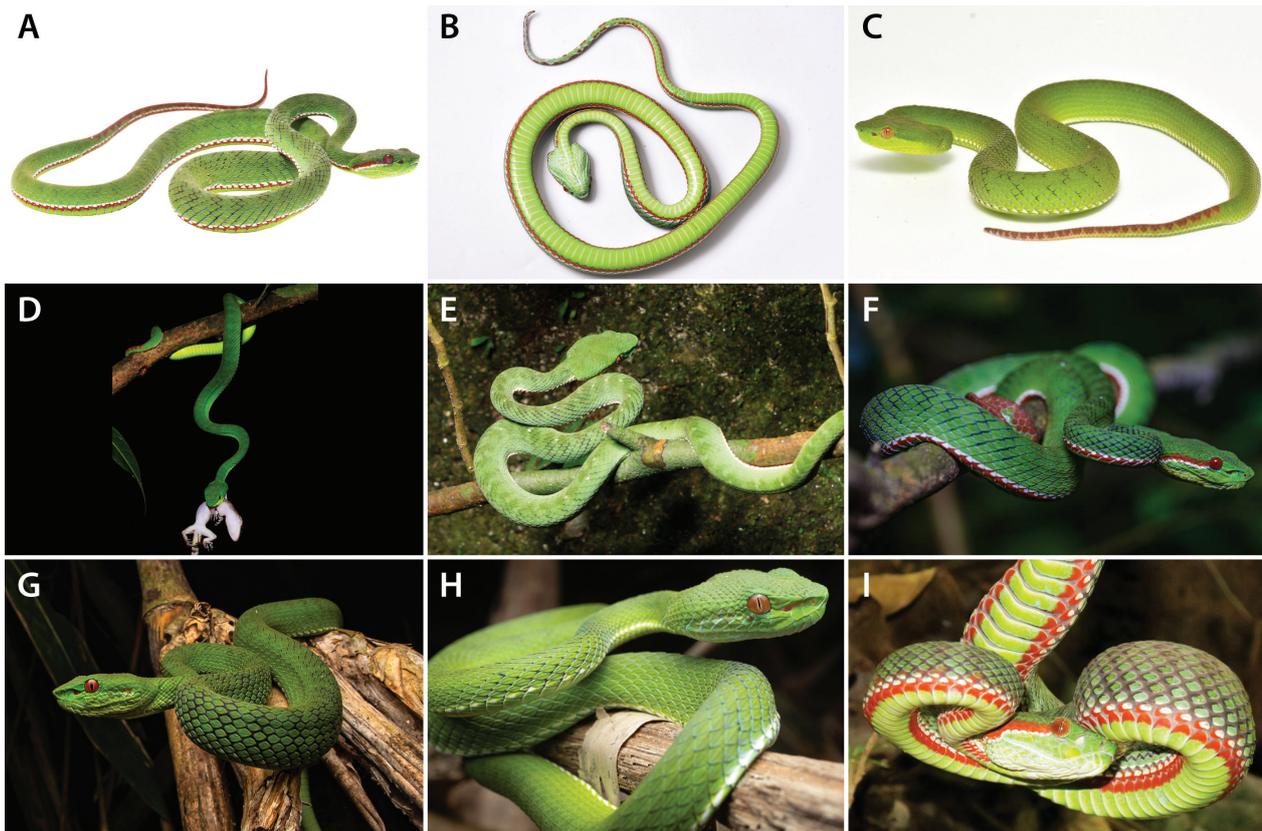


Figure 11. *Trimeresurus tenasserimensis* sp. nov. in life. **Thailand:** A–D Khao Kra Jom Mt, Suan Phueng, Ratchaburi, adult male (A, B), adult female (C), and subadult female (D), respectively; E Khao Laem Mt., Suan Phueng, Ratchaburi (subadult male); F–G Kaeng Krachan NP, Phetchaburi (adult male and adult female, respectively); H Namtok Huai Yang NP, Prachuap Khiri Khan (adult female). **Myanmar:** I Lampi Marine NP, Mergui, Tanintharyi (adult male). Photos by: P. Pawangkhanant (A–E), R. Jaihan (F), A. Tomaszek (G), T. Smith (H), and P. Brakels (I).

of the second row; the large white areas on the red first dorsal scale row makes this ventrolateral stripe seeming red alternately with white; elongate white dots, faint, one scale long, widely spaced on scales of the vertebral row, more visible anteriorly. The tail is bright green like the dorsum, ornate above and on its sides by about 15, distinct large blotches crossing the vertebral line of the tail, hexagonal or subrectangular, bright rusty-red, extending downwards to the mid-height of the sides, in contact each with the other on the vertebral row, progressively fused posteriorly as an irregular stripe; the ventrolateral stripe of the body extends at least up to half of the tail length before vanishing as red blotches; near its end, the dorsal surface of the tail is irregularly mottled with rusty-red.

The dorsal surface of the head and the temporal region are bright grass-green like the body; the side of the head below the eye, i.e., the sides of the snout, nasal scale, anterior supralabials and lower temporals, is paler green than the dorsal surface of the head; a broad, bicolored postocular streak, its ventral part narrow and white, covering the lower part of the second row and, posteriorly, the first lower row of temporals, its upper part, broader, covering the second and third rows of temporals, bright rusty-red, extends from the postoculars obliquely towards the angle of the mouth; the postocular streak does not connect with the ventrolateral stripe. The chin and throat are uniform pale green. The eye is deep brownish-red.

The venter is uniform pale green; tips of ventrals of the same green color, not red. The ventral surface of the tail is as the venter anteriorly, with the bright red ventrolateral stripe on each side, becoming greenish-grey near its tip with reddish-brown dots but not completely reddish-brown.

Variation (see also Table S3). The longest-known specimen is 736 mm long (SVL 587 mm, TaL 149 mm; male, CAS 247870). The longest-known female is 532 mm long (SVL 452 mm, TaL 80 mm; USNM 587919). The body is quite slender in males, more robust in large females, laterally compressed; head triangular, elongate, wide posteriorly, flattened in males, moderately thick in females, clearly distinct from the neck; snout elongate, distinctly flattened, rounded seen from above, angular and obliquely truncated in profile view, with a distinct canthus rostralis; nostril centered in the nasal scale; size of the eye average, 0.7–0.9 times the distance between the lower margin of the eye and the border of the upper lip; tail average to long, progressively tapering and distinctly prehensile; TaL/TL 0.177–0.230 in males, 0.136–0.161 in females.

Body scalation. Generally 23-21-15 dorsal scale rows (50%), less frequently 21-21-15 (30%) or 22-21-15 (20%) dorsal scale rows; 154–176 distinctly keeled ventrals (159–170 in males, 154–176 in females); scales of

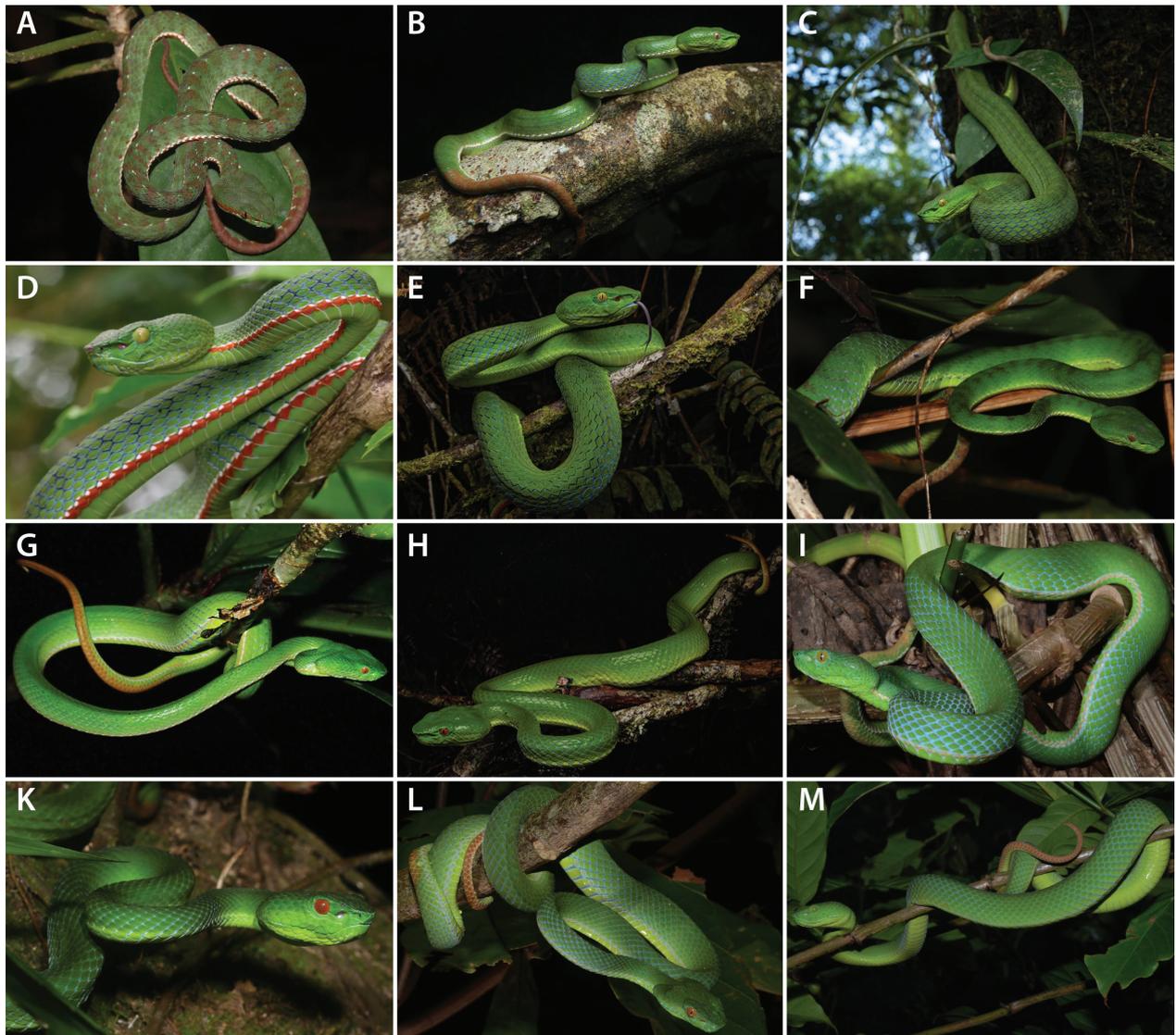


Figure 12. *Trimeresurus sabahi* complex in life. **Thailand** (*T. sabahi fucatus*): **A** Krung Ching Waterfall, Nakhon Si Thammarat (adult male), **B, C** Ron Phibun, Nakhon Si Thammarat (adult male and adult female, respectively). **West Malaysia:** **D–E** Raub, Pahang (adult male and adult female of *T. sabahi fucatus*, respectively); **F** Tioman Is., Pahang (adult female of *T. sabahi buniana*). **East Malaysia** (*T. sabahi sabahi*): **G** Kota Belud, Sabah (adult male), **H** Ranau, Sabah, (adult female). **Indonesia:** **I** North Sumatra, (adult male of *T. sabahi toba*), **J** Karo, North Sumatra, (adult female of *T. sabahi toba*); **K, L** West Sumatra (adult male and adult female of *T. sabahi barati*, respectively). Photos by: R. Grassby-Lewis (A), T. Smith (B, C), R. Harris (D), A. Tomaszek (E, H), O.B. Claesson (F, J), A. Kang (G), and G. Vogel (I, K, L).

the first dorsal scale row smooth and not enlarged; subcaudals sexually dimorphic with slight overlap, 66–74 in males, 57–66 in females; total number of VEN+SC: 222–242; cloacal plate entire.

Head scalation. The head scalation is as described for the holotype, with the following variation: internasals separated by one small scale in all examined specimens; four or five canthal scales bordering the canthus rostralis between the internasal and corresponding supraocular; one supraocular on each side, entire and rather narrow, about 0.7–0.9 times as wide as the internasals, indented on its inner margin by the upper head scales; cephalic scales juxtaposed, flat and smooth; 9–14 (10–11 in most examined specimens) cephalic scales on a line between supraoculars; occipital scales rhombohedral, distinctly obtusely keeled

in males, weakly keeled or even smooth in females; temporals generally moderately but distinctly keeled in most males (71.5%), sometimes smooth (28.6%); smooth in all examined females; 9–11 supralabials; third supralabial the longest and highest, rather tall, in contact with the subocular or separated from this latter scale by one scale; fourth supralabial separated from the subocular by one scale in all examined specimens; fifth supralabial smaller than the fourth one, separated from the subocular by one or two scales of similar size; 11–14 (generally 12 or 13) infralabials, those of the first pair in contact with each other.

Coloration and pattern (Figs 10–11). In life or in freshly preserved animals, the body is uniform bright green, grass-green or emerald-green (in preservative, the general background color remains green or turns to bluish-green

or brown); dark, transversal interstitial crossbands faint in males, absent in females; white, elongate vertebral dots present in males; in males, the broad, bicolored ventrolateral stripe is as described above, bright red or fire-red on its lower part, on most scales of the first dorsal scale rows, white above, on scales of the second dorsal scale row and on the upper posterior part of scales of the first row, always present and conspicuous; in females, the ventrolateral stripe is absent (83.3%) or sometimes present as thin white line (16.7%). The tail is of the same green color than the dorsum, with above and on the sides a series of 15–25 large, bright rusty-red blotches, subrectangular or hexagonal, crossing the vertebral line of the tail, either distinct throughout the tail or progressively fused together posteriorly as an irregular stripe.

The dorsal surface of the head and the temporal region are uniform bright green or deep green like the body; the sides of the head below the eye, are more or less distinctly paler than the dorsal surface of the head, namely usually pale yellowish-green or pale green; in males, the vivid, broad, bicolored postocular streak associating a thin and white ventral part with a broad and bright red, rusty-red dorsal part, is always present (Fig. 10C, D, G, H); in females, the postocular streak is usually absent or present as a thin, faint white line. The chin and throat are pale yellowish-green or pale sea-green, uniform or with some darker green areas. The eye is bright red, fire-red, or deep red in specimens of both sexes.

The venter is uniformly pale green or pale yellowish-green; tips of ventrals usually green like the venter but we saw a male, especially colorful, in which the bright red part of the ventrolateral stripe also extended onto the outer parts of ventral plates. The ventral surface of the tail is like the venter with the tips of the red dorsal blotches extending onto the outer parts of some subcaudal scales; posterior part of the tail mixed rusty-red and green.

Comparisons. *Trimeresurus tenasserimensis* is distinguished from *T. lanna* (described above) by having: (1) lower max TL in both sexes (736 mm in males, 532 mm in females vs. 815 mm in males, 854 mm in females); (2) slightly higher total number of VEN+SC in males (226–242, \bar{x} = 235.3 vs. 213–241, \bar{x} = 227.8 in males; p = 0.018); (3) a slightly lower ratio ED/SnL in males (0.39–0.62, \bar{x} = 0.50 vs. 0.46–0.66, \bar{x} = 0.58 in males; p = 0.05); (4) elongate, white vertebral spots generally present in juvenile and subadult specimens in both sexes (vs. absent).

Trimeresurus tenasserimensis is distinguished from *T. popeiorum* by having: (1) lower max TL in both sexes (736 mm in males, 532 mm in females vs. 925 mm in males, 884 mm in females); (2) slightly lower ratio TaL/TL in females (0.136–0.161, \bar{x} = 0.152 vs. 0.14–0.19, \bar{x} = 0.166; p = 0.017); (3) bicolor postocular streak in males very broad, covering 2–3 temporal scales (vs. thin, covering 1–2 temporal scales); (4) temporals strong keeled in males (vs. feebly keeled). Furthermore, *T. tenasserimensis* is widely separated from *T. popeiorum* on a geographical basis as this latter species inhabits only northeastern

India, Nepal, Bhutan, Bangladesh, southwestern China, and northern Myanmar. Moreover, the ranges of both species are separated by that of *T. lanna*.

Trimeresurus tenasserimensis is distinguished from *T. nebularis* by having: (1) lower max TL in both sexes (736 mm in males, 532 mm in females vs. 1002 mm in males, 948 mm in females); (2) higher total number of VEN+SC in both sexes (226–242, \bar{x} = 235.3 vs. 210–218, \bar{x} = 214.0 in males; p = 0.02; 222–242, \bar{x} = 231.0 vs. 197–210, \bar{x} = 205.6 in females; p = 0.01); (3) eye bright or deep red in both sexes vs. usually green; (4) bicolored postocular streak present in males vs. absent; (5) ventrolateral streak present in females vs. absent; (6) ventral color green vs. usually yellowish in both sexes.

Trimeresurus tenasserimensis differs from *T. phuketensis* by having: (1) higher max TL in males (736 mm vs. 640 mm), but lower max TL in females (532 mm vs. 748 mm); (2) lower ratio TaL/TL in both females (0.14–0.16, \bar{x} = 0.15 vs. 0.17–0.18, \bar{x} = 0.17; p = 0.003); (3) higher total number of VEN+SC in males (226–242, \bar{x} = 235.3 vs. 242–249, \bar{x} = 246.4; p = 0.004); (4) eye color deep red in both sexes vs. copper; (5) no dorsal crossbands vs. irregular, conspicuous reddish-brown crossbands usually present.

Lastly, *T. tenasserimensis* can be further differentiated from the five subspecies of *T. sabahi* as follows:

- from *T. s. barati* by having: (1) higher total number of VEN+SC in both sexes (226–242, \bar{x} = 235.3 vs. 208–225, \bar{x} = 217.7 in males; p = 0.0006; 222–242, \bar{x} = 231.0 vs. 201–219, \bar{x} = 207.0 in females; p = 0.001); (2) 21 dorsal scales rows at midbody vs. 17–19; (3) eye color deep red in both sexes vs. deep orange; (4) bicolored postocular streak present in males vs. absent;
- from *T. s. buniana* by having: (1) lower total number of VEN+SC in males (226–242, \bar{x} = 235.3 vs. 246–250, \bar{x} = 248.0; p = 0.02); (2) lower number of cephalic scales in both sexes (9–11, \bar{x} = 10.0 vs. 11–12, \bar{x} = 11.7 in males; p = 0.03; 11–13 vs. 14 in female); (3) eye color deep red in both sexes vs. copper; (4) dorsum uniform bright green vs. dark bluish-green or verdigris with conspicuous reddish-brown or violet, irregular crossbands; (5) bicolored postocular streak, red and white, in males vs. postocular streak reddish-brown;
- from *T. s. fucatus* by having: (1) lower max TL in both sexes (736 mm in males, 532 mm in females vs. 834 mm in males, 826 mm in females); (2) lower ratio TaL/TL in females (0.14–0.16, \bar{x} = 0.15 vs. 0.16–0.19, \bar{x} = 0.17; p = 0.002); (3) eye color deep red in both sexes vs. copper; (4) solid dorsal crossbands in males absent vs. present; (5) wide bicolor postocular streak, red and white, present in males vs. sometimes absent, or white, or thin, white with a dark red upper part;
- from *T. s. toba* by having: (1) lower max TL in females (532 mm vs. 798 mm); (2) slightly higher total number of VEN+SC in females (222–242, \bar{x} = 231.0 vs.

- 204–218, \bar{x} = 212.5; p = 0.02); (3) eye color deep red in both sexes vs. deep orange; (4) in males, ventrolateral stripe bicolored, wide, vs. white and thin.
- from *T. s. sabahi* by having: (1) slightly lower ratio TaL/TL in females (0.14–0.16, \bar{x} = 0.15 vs. 0.17–0.18, \bar{x} = 0.18; p = 0.02); (2) higher total number of VEN+SC in both sexes (226–242, \bar{x} = 235.3 vs. 216–226, \bar{x} = 222.0 in males; p = 0.01; 222–242, \bar{x} = 231.0 vs. 212–217, \bar{x} = 214.7 in females; p = 0.02); (3) bicolored postocular streak present in males vs. absent.

Distribution (Fig. 1). Currently, *T. tenasserimensis* is likely to be restricted to the northern part of the Isthmus Kra, in the Tenneserim Range of peninsular Myanmar and Thailand. Based on our data, we establish the distribution of this species as follows: **Peninsular Thailand** (Ratchaburi, Kanchanaburi, Phetchaburi, and Prachuap Khiri Khan provinces), and **southeastern Myanmar** (Tanintharyi Region).

Natural history notes. *Trimeresurus tenasserimensis* inhabits a wide variety of habitats, from lowland bamboo forest and dry evergreen forest to submontane forest, at elevations from 200–1500 m. This pitviper usually occurs near small streams or in wet habitats. In Lampi Marine NP., Tanintharyi Region, Myanmar, this species was found coiled in trailside vegetation (ca. 50 cm above the ground) in undisturbed tropical evergreen forest on ridgeline (Platt et al. 2018). Arboreal and nocturnal, it is mostly found hanging above streams, sometimes at 6–8 m above water. Breeding starts around August, and newborn snakes appear around mid-December (personal observations). Diet in the wild is mostly based on frogs and geckos such as *Cyrtodactylus* cf. *oldhami* (Theobald). Large females sometimes feed on small rodents (personal observations).

Conservation status. Further research is required to clarify the extent of the distribution, population trends and conservation status of the new species. *Trimeresurus tenasserimensis* is distributed over a relatively small region, but inhabits several protected areas. Across its range, the new species is quite common. Thus, we tentatively suggest that *T. tenasserimensis* be assessed as Least Concern (LC) following the IUCN's Red List categories (IUCN Standards and Petitions Committee 2019).

Discussion and Conclusions

Updated taxonomy of the subgenus *Popeia* and unresolved questions

The genus *Trimeresurus* has been one of the most taxonomically challenging groups of Asian snakes. Due to a high degree of morphological similarity between species, many *Trimeresurus* species have been misidentified in the past, and the interspecific and intrageneric classification

of most of its members, including the subgenus *Popeia*, have remained contentious (Vogel et al. 2004; Sanders et al. 2006; Mirza et al. 2023). According to previously published molecular phylogenies, the subgenus *Popeia* diverged from its most recent common ancestors ca. 15 MYA ago (Alencar et al. 2016). Several recent studies of *Popeia* have demonstrated that this subgenus has a high level of hidden and undescribed diversity (Mulcahy et al. 2017; Mirza et al. 2023). Our new samples from the type localities of focal taxa as well as a re-examination of type specimens allowed us to provide detailed insights into the taxonomy of the *T. popeiorum* group. In particular, a redefinition of *T. popeiorum* allowed us to resolve the status of previously unattended populations from the Indo-Burma Biodiversity Hotspot. With this contribution, we were able to substantially improve the taxonomy of the subgenus *Popeia* at the species level. Furthermore, the combination of molecular and morphological data allowed us to clarify the validity and distributional limits of the taxa included in the *T. popeiorum* group. Our study revealed six major OTUs that represent distinct species, each with significant genetic and morphological differences from each other (see Results). Our study also confirms the earlier conclusions of Mirza et al. (2023) that *T. yingjiangensis* represents a subjective junior synonym of *T. popeiorum* Smith, 1937, and we were also able to resolve the previously unnoticed nomenclatural problem of *T. elegans* Gray, 1853.

We also provide additional information on the morphological variation and distribution of *T. popeiorum* and restrict the distribution of this species to northeastern India, eastern Nepal, southern Bhutan, southeastern Bangladesh, western Yunnan (China), and northern and southwestern Myanmar. As a consequence, we propose to remove *T. popeiorum* from the snake faunas of Thailand, Laos, southern Yunnan Province (China), and southeastern Myanmar. We further describe the mainland Asian populations previously assigned to *T. popeiorum* as two new species: *T. lanna* for the populations from southern Yunnan, western Laos, northern Thailand and eastern mainland Myanmar, and *T. tenasserimensis* for the populations from Tenneserim Mountains in southeastern Myanmar and western Thailand.

Furthermore, we demonstrate that *T. lanna* consists of two divergent subclades, one in Thailand, Laos, and China, and the other in southeastern Myanmar. These two subclades differ by a significant genetic divergence, with a mean *cyt b* pairwise distance of 3.4%. The low sample size of the specimens from Myanmar examined in our study and the superficial morphological similarity between the specimens of the two clades of *T. lanna* hinders further assessment of their taxonomic status. Therefore, further studies are required to elucidate the taxonomic status of *T. lanna* populations from southeastern Myanmar.

As the present study is focused on the taxonomic relationships of the continental populations of the *T. popeiorum* species group, we do not provide significant insights on taxonomy of the populations inhabiting the islands of Southeast Asia and the Malay Peninsula, which was partially addressed in previous works (e.g., Wostl et al. 2016). Nevertheless, our study further confirms the distinctive-

ness and full species status of *T. nebularis*, restricted to the highlands of peninsular Malaysia. Moreover, our data suggest that the taxonomy of the *T. sabahi* complex still remains unresolved. Despite the significant degree of morphological differentiation among the populations of *Popeia* inhabiting Sumatra, Borneo, the Malay Peninsula, and some offshore islands (Regenass and Kramer 1981; Vogel et al. 2004; Grismer et al. 2006; David et al. 2009), they show shallow divergences in mtDNA sequences, which suggests that each taxon emerged relatively rapidly. In our mtDNA-based genealogy, the *T. sabahi* complex contains seven geographically circumscribed lineages. This result agrees well with the data presented in earlier works on this group (Wostl et al. 2016; Mulcahy et al. 2017). Wostl et al. (2016) suggested that the taxa of the subgenus *Popeia* described from the Southeast Asian islands, along with *T. s. fucatus* from the mainland, should all be regarded as junior synonyms of *T. sabahi*, whereas Mulcahy et al. (2017) suggested that these taxa were better regarded as subspecies of *T. sabahi*. In this study, we follow the suggestion of Mulcahy et al. (2017) and treat the intraspecific lineages of the *T. sabahi* complex as subspecies based on five geographical regions, which correspond morphological characters for each species. Our study confirms the distinctiveness and monophyly of *T. s. sabahi* from eastern Borneo, of *T. s. toba* from northern Sumatra, and *T. s. buniana* from Pulau Tioman. At the same time, two subspecies, namely *T. s. barati* from western and southern Sumatra and *T. s. fucatus* from peninsular Thailand and Malaysia, were non-monophyletic in our mtDNA-based genealogy, and are comprised of a number of mitochondrial lineages. Furthermore, we also noticed a high degree of morphological variation among the examined specimens of these subspecies (Figs 3, 12). Given the significant morphological differentiation of the *T. sabahi* complex (Fig. 3), lumping all included lineages into a single species without recognizing different subspecies would likely affect the morphological diagnosability of *T. sabahi* and the subgenus *Popeia* as a whole. Future integrative studies based on morphological and molecular data along with additional sampling efforts are needed to elucidate the taxonomy and distribution of the *T. sabahi* complex.

In summary, our phylogenetic analyses of the subgenus *Popeia* suggest that several lineages are still poorly resolved and that most recognized species and subspecies constitute a rapid radiation, which likely speciated during a comparatively short time period. A phylogenetic resolution of the subgenus *Popeia* would likely require genomic-scale data, which would help establish the degree of isolation and gene flow among the OTUs reported in this work. Overall, the description of *T. lanna* and *T. tenasserimensis* brings the total number of species in the subgenus *Popeia* to six.

Distribution of species of the subgenus *Popeia*

The distribution of the subgenus *Popeia* in mainland Asia seems to be shaped by the physical geography of

the region. *Trimeresurus popeiorum*, according to our data, is distributed across the hilly and mountainous areas of Northeast India, the eastern Himalayas, northern Myanmar, and the westernmost part of Yunnan Province, China. Some other members of the herpetofauna show similar distribution patterns covering the northern part of the Indo-Burma Biodiversity Hotspot (e.g., Than Zaw et al. 2019; Vogel et al. 2020; Decemson et al. 2023).

The distribution of *T. lanna* is restricted to the mountainous areas of the Northwest Thai Uplands and the Northeast Thai–Lao Uplands (see Poyarkov et al. 2023). It is distributed from the montane forests of the Dawna Mts. in the south (eastern Myanmar and northwestern Thailand), to the Thanon Thing Chai Mts. (northern Thailand), Daen Lao Mts. (eastern Myanmar and northern Thailand), Khun Tan Mts. (northern Thailand), Phi Pan Nam Mts. (northern Thailand and extreme western Laos), and Luang Prabang Mts. in the north (northwestern Laos). In the north, the distribution of this species reaches the southernmost part of Yunnan Province of China (Mengla County), a region that shows significant faunal similarity with the rest of northern Indochina (e.g., Poyarkov et al. 2021, 2023). In the south, the distribution of *T. lanna* is likely limited by the Three Pagodas Fault (see Fig. 1), which was reported as a zone of herpetofaunal turnover between the herpetofauna of Northern Tenasserim and the mainland Indochina (Poyarkov et al. 2021, 2023). In the west, *T. lanna* penetrates in the eastern part of Myanmar. According to the genetic results of our study, the populations of this species from the Bago and Mon regions of Myanmar form a clade that is highly divergent from other *T. lanna* from northern Indochina (clade 2, Fig. 2). Due to the limited sampling available from Myanmar, the actual distribution of this lineage remains unclear, though it is highly likely that the ranges of the two clades of *T. lanna* are separated by the Salween River (see Fig. 1). This river is one of the largest in the Golden Triangle Region, comprising parts of southern China, southeastern Myanmar, northern Thailand, and northern Laos. Thus, the Salween River may serve as a physical barrier, or, rather, as a ‘biogeographic filter’, following the concept proposed by McKenna (1973) and Das (1996), which would restrict gene flow between the two lineages of *T. lanna*. Similar biogeographic patterns were recently revealed in a number of other reptile groups, such as *Draco* flying lizards (Klabacka et al. 2020). Further studies including additional sampling efforts in eastern Myanmar and western Thailand are needed to clarify the extent of distribution and the taxonomic status of the lineages within *T. lanna*.

The distribution of *T. tenasserimensis* is restricted to the Tenasserim Range, a chain of hills and mountains that exhibit high levels of herpetofaunal diversity and endemism (e.g., Poyarkov et al. 2021, 2023). In the north, the range of *T. tenasserimensis* is probably limited by the Three Pagodas Fault zone, however further studies on *Popeia* populations in Kanchanaburi Province of Thailand are required to clarify the actual extent of its distribution. In the south, *T. tenasserimensis* reaches the southernmost foothills of the Tenasserim Mountains and is likely limited by the Isthmus of Kra. The importance

of the Isthmus of Kra as an area of herpetofaunal turnover was demonstrated in numerous recent publications; this narrow area likely shaped radiation in many groups of reptiles and amphibians inhabiting Southeast Asia (e.g., Pauwels et al. 2003; Matsui et al. 2005; Chen et al. 2018; Pawangkhanant et al. 2018; Suwannapoom et al. 2018, 2020, 2021, 2022; Poyarkov et al. 2019, 2020, 2021, 2022, 2023; Gorin et al. 2020; Grismer et al. 2020a, 2020b, 2022; Chomdej et al. 2021).

However, the taxonomic status of the *Popeia* populations distributed between the Isthmus of Kra and the Khlong – Marui Fault (Ta Pi Line of Poyarkov et al. 2021, 2023) requires additional research. At present the populations in this area (populations 13–16, see Fig. 1) are assigned to *T. s. fucatus*, though further research on their phylogenetic position is needed. Two clades were revealed within *T. tenasserimensis*, which seem to be restricted to the eastern and the western slopes of Tenasserim Mountain Range (clade 1 and clade 2, respectively; see Fig. 1).

Despite receiving much taxonomic interest from the 1930s to the present day, the existing reports on distribution of species of the subgenus *Popeia* both at the national and regional levels remained highly controversial. Below we will address some long-standing questions of *Popeia* species distribution in Bhutan, China, Myanmar, Thailand, and Laos.

In Bhutan. Wangyal (2012: 29) reported *T. albolabris* from Lodari, Sarpang District and Gelephu, Sarpang District. However, these records appear to be based on misidentifications of *T. popeiorum* (J. T. Wangyal, pers. comm. on 1 September 2023). Furthermore, Das et al. (2016: 275–276) also recorded *T. popeiorum* from Royal Manas NP, Zemgang District, approximately 40 km from the two localities reported by Wangyal et al. (2012). The white-lipped pitviper, *T. albolabris*, is currently considered to be distributed in southern China, northern Vietnam, and northern Laos (see Vogel et al. 2023), and records of this species in Bhutan are probably based on misidentified specimens of *T. salazar* Mirza et al., 2020 (see Vogel et al. 2022) or *T. popeiorum*. As a consequence, we propose to remove *T. albolabris* from the snake fauna of Bhutan.

In China. Guo et al. (2015) first reported *T. popeiorum* from China based on 13 specimens collected in Mengla County, Yunnan Province. Furthermore, based on molecular data, Liu et al. (2015) and Wu et al. (2023) reported this species in Xishuangbanna and Jinghong Counties, complementing to the previous records from Mengla County, Yunnan. In this study, we demonstrate that specimens from Mengla are nested in the same clade as *T. lanna* and also coincide morphologically with that species. Therefore, we propose that the populations from Mengla, Xishuangbanna and Jinghong counties should be assigned to *T. lanna*, and recommend removing *T. popeiorum* from the snake fauna of southern Yunnan Province (Puer City, Jinghong City, and Mengla County, both located in Xishuangbanna Dai Autonomous Prefecture). As

indicated above, *T. popeiorum* is indeed present in China, but is present only in westernmost Yunnan Province in Dehong Dai and Jingpo Autonomous Prefecture.

In Myanmar. Vogel et al. (2004: 27) reported two male specimens, namely, NHMUK 1856.5.6.105 and NHMUK 1940.3.9.43, both from Myeik District, Taninthayi Region, under the name *T. fucatus*, which we in the present paper regard as a subspecies of *T. sabahi*. This record was repeated by Leviton et al. (2008: 78–79). At the same time, Leviton et al. (2008: 91–92) recorded *T. (Viridovipera) stejneri* from Kawthaung District, Taninthayi Region, based on examination of specimen CAS 247870 (G. Zug, pers. comm.). At present, *T. stejneri* is considered to be distributed in southern and southeastern China, Taiwan, northern Vietnam, and northeastern Laos (see David et al. 2023; Poyarkov et al. 2023). However, after re-examination of the three Burmese specimens mentioned above (CAS 247870, NHMUK 1856.5.6.105, NHMUK 1940.3.9.43) we conclude that they should be assigned to *T. tenasserimensis* (see Table S3). As a consequence, we propose to remove *T. s. fucatus* and *T. stejneri* from the snake fauna of Myanmar. Furthermore, as noted above, the Isthmus of Kra represents an important geographical boundary separating the herpetofauna of Indochina from Sundaland (Poyarkov et al. 2021, 2023). The non-overlapping ranges of *T. tenasserimensis* and *T. sabahi* imply that the Isthmus Kra may serve as a barrier or, at least, a filter, for gene flow among these species. Therefore, based on data examined by us, the occurrence of *T. s. fucatus* in Myanmar appears unlikely, though further studies in the extreme south of Myanmar including the offshore islands of the Taninthayi Region are required to clarify the distribution extent of *Popeia* pitvipers in Myanmar.

In Thailand. Chuaynkern and Chuaynkern (2012: 147–148), followed by Chan-ard et al. (2015) and Lee and Zug (2019), mentioned the occurrence of *T. nebularis* in Narathiwat Province, but did not provide information on voucher specimens or any other details. According to our data, this species seems to be restricted to the central and southern parts of the Titiwangsa Range in Peninsular Malaysia (Fig. 1). Moreover, two of us (PP and NAP) have conducted numerous field trips in Narathiwat Province and did not record any specimens of *T. nebularis*. Therefore, the existing records of this species from Thailand likely represent misidentifications with *T. s. fucatus*, which is a very common snake species in this area. Therefore, we propose removing *T. nebularis* from the snake fauna of Thailand until voucher specimens are available for confirmation.

Similarly, Wüster (1992, Fig. 6) reported *T. popeiorum* from Ban Pala-U, Prachuap Khiri Khan Province (subsequently followed by Pauwels et al. 2003). This record appears to be a misidentified specimen belonging to the *T. albolabris* species group. Pauwels and Chan-ard (2006, Fig. 4 in 101, 102) reported the occurrence of *T. s. fucatus* (under the name *Popeia fucata*) from Kaeng Krachan NP, Phetchaburi Province (based on specimen FMNH

263429). However, the morphological and scalation characters of this specimen, and its coloration pattern match the characteristics of *T. tenasserimensis*.

Previous studies (Sumontha et al. 2011) suggested that *T. phuketensis* was distributed exclusively on Phuket Island and was not recorded in the adjacent areas of Phang Nga Province, which is separated from Phuket by a narrow strait. However, in the present study, we present molecular evidence supporting the occurrence of *T. phuketensis* on mainland Thailand in Phang Nga Province (specimen B467, locality 2; see Fig. 1). Previously, Mulcahy et al. (2017) listed this sample as *T. cf. phuketensis*. In a similar way, Sumontha et al. (2021), in the description of *T. kuiburi*, included a novel genetic sample of *T. phuketensis* that was recovered sister to sample B467. These authors, and our data, definitively confirm the suspicions of Mulcahy et al. (2017). Further studies are required to clarify the taxonomic status of *T. phuketensis* and *T. s. fucatus* populations from Phang Nga Province.

In Laos. Under the combination *T. popeiorum*, Teynié and David (2010) and David et al. (2023) mentioned the occurrence of *T. lanna* in the provinces of Luangnamtha, Luangphrabang, Oudomxay, Phongsaly, Vientiane, and Xayabury, namely in the north and northwest of the country. However, a picture published on iNaturalist (<https://www.inaturalist.org/observations/141981742>; last accessed on 10 September 2023) depicted a specimen of “*T. popeiorum*” originating from Nam Et-Phou Louey National Protected Area, a large national park located in Houaphan Province, northeastern Laos. Although this locality is located somewhat apart from the main portion of *T. lanna*’s species range in Laos, our phylogenetic analysis confirmed the occurrence of this species in Houaphan Province (VNMN 6339, collected from Houaphan, locality 27; Figs 1, 2). Additional studies are needed to clarify the full distribution of *T. lanna* in Laos.

Indo-Burma hosts a high diversity of *Trimeresurus* pitvipers

The Indo-Burma Biodiversity Hotspot is known for its rich biodiversity, including herpetofauna (Myers et al. 2000; Bain and Hurley 2011; Poyarkov et al. 2021, 2023). The present work further underscores that the herpetofaunal diversity across this region still remains largely unexplored. Further sampling efforts along with integrative taxonomic assessments combining molecular and morphological data will likely result in the discovery of many more undescribed species. Several relationships within the subgenus *Popeia* remain unresolved in our analysis. However a high amount of genetic diversity is present within this group in western Indochina, particularly in the mountains of western Thailand and the Thai-Malay Peninsula. We deem it plausible that this region may represent an area of origin of the subgenus *Popeia*, since this region is known to act as a “stepping stone” that connects mainland Asia with Sundaland, and is also as an important center of origin for many other groups of amphibians

and reptiles (e.g., Chen et al. 2018; Suwannapoom et al. 2018; Gorin et al. 2020; Chomdej et al. 2021; Poyarkov et al. 2021, 2022, 2023; Grismer et al. 2022).

Furthermore, the Indo-Burma Region, as currently known, hosts the highest number of species of *Trimeresurus* pitvipers in the world. With the description of two new species of the subgenus *Popeia*, the present study brings the total number of *Trimeresurus* species recorded in this region to 32, including: 17 species of the subgenus *Trimeresurus*: *T. albolabris*; *T. ayeyarwadyensis* Chan et al., 2023; *T. cardamomensis* (Malhotra et al., 2011); *T. caudornatus* Chen et al., 2020; *T. ciliaris* Idiatullina et al., 2023; *T. erythrurus*; *T. guoi* Chen et al., 2021; *T. honsonensis* (Grismer et al., 2008); *T. kanburiensis* Smith, 1943; *T. kraensis* Idiatullina et al., 2024; *T. kuiburi* Sumontha et al., 2021; *T. macrops* Kramer, 1977; *T. purpureomaculatus* (Gray, 1832); *T. rubeus* (Malhotra et al., 2011); *T. salazar* Mirza et al., 2020; *T. uetzi* Vogel et al., 2023; and *T. venustus* Vogel, 1991; two species of the subgenus *Parias*: *T. hageni* (Lidth de Jeude, 1886); and *T. sumatranus* (Raffles, 1822); six species of the subgenus *Popeia* (listed above); seven species of the subgenus *Viridovipera*: *T. gumprechtii* David et al., 2002; *T. mayaae* Rathee et al., 2022; *T. medoensis* Djao in Djao & Jiang, 1977; *T. stejnegeri* Schmidt, 1925; *T. truongsongensis* Orlov et al., 2004; *T. vogeli* David et al., 2001; and *T. yunnanensis* Schmidt, 1925 (Chan et al. 2023; Idiatullina et al. 2023, 2024; Poyarkov et al. 2023; Vogel et al. 2023).

Despite recent progress on the taxonomy of Asian pitvipers, our knowledge of the diversity and distribution of several species still remains incomplete. Furthermore, along with the venomous elapid snakes (such as *Naja* spp. and *Bungarus* spp.), members of the genus *Trimeresurus* are responsible for a large percentage of the documented cases of snakebites in Southeast Asia and their medical importance cannot be underestimated (e.g., Patikorn et al. 2022). Therefore, we emphasize the need for further research efforts on the taxonomy, distribution, ecology, and toxicology of *Trimeresurus* pitvipers in Southeast Asia. There is also a particularly large gap in our knowledge on the evolution, ecology (including behavior and reproduction), population sizes and trends, venom variation, and conservation status of the two new species described here, as well as other species in the *Popeia* subgenus. We recommend for additional research in these directions. Finally, we would like to stress that most people across Southeast Asia are unaware of their local venomous snakes, especially *Trimeresurus* pitvipers, and more outreach is needed to increase public awareness on ways to correctly identify these species and prevent snakebites. Only coordinated actions by scientists, educators, the general public, nature conservation organizations, and local governments can give hope for the future for these fascinating snakes.

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Supplementary Material 1

Tables S1–S4

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Data type: .pdf

Explanation notes: **Table S1.** Species-level scientific names erected for the members of the subgenus *Popeia*. — **Table S2.** Resulting p-values from univariate morphological analyses comparing the geographic populations of the *Trimeresurus popeiorum* group from the Indo-Burma Region: Northeast India, northern Myanmar, and western Indochina. — **Table S3.** Main measurements and meristic characters of the type series and other specimens of *Trimeresurus popeiorum* s. str. (OTU1), *T. lanna* **sp. nov.** (OTU2), and *T. tenasserimensis* **sp. nov.** (OTU3). — **Table S4 (Part 1–4).** Comparison of morphological characteristics of *Trimeresurus lanna* **sp. nov.** (OTU2) and *T. tenasserimensis* **sp. nov.** (OTU3) with those of the subgenus *Popeia*.

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Supplementary Material 2

Appendices I–VIII

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Data type: .docx

Explanation notes: **Appendix I.** Primers used in this study. — **Appendix II.** Sequences and voucher specimens of the genus *Trimeresurus* and outgroup taxa used in This study. Locality number corresponds to those shown on the map in Figure 1. — **Appendix III.** Comparative material examined for the subgenus *Popeia*. — **Appendix IV.** List of morphological variables recorded from each specimen examined. — **Appendix V.** Characteristics of analyzed mtDNA sequences and the proposed optimal evolutionary models for gene and codon partitions as estimated in PartitionFinder v1.0.1. — **Appendix VI.** Uncorrected p distances (percentage, presented below the diagonal; calculation error presented above the diagonal) between the sequences of the *cyt b* gene for species of the subgenus *Popeia* included in the phylogenetic analyses. — **Appendix VII.** Summary of PC scores and statistics for the Principal Components Analysis (PCA) consisting of members of the subgenus *Popeia*. Abbreviations are listed in the materials and methods. — **Appendix VIII.** Literature used for the revised distribution of species of the subgenus *Popeia*. Locality numbers correspond to those shown on the map in Figure 1.

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