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Integrative taxonomy identifies a new species of *Trimeresurus* Lacépède, 1804 (Reptilia: Serpentes: Viperidae) from Yunnan Province, China

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ABSTRACT

The genus *Trimeresurus* currently contains at least 56 recognized species of venomous terrestrial to arboreal species distributed across South and Southeast Asia. We collected several specimens of the subgenus *Viridovipera* in Yunnan Province, China in recent years. Based on morphological characters and phylogenetic analysis, we confirm that *Trimeresurus yunnanensis* is distributed in the west of the Honghe River in Yunnan Province and the *Trimeresurus* species living along the lower reaches of the Honghe River Basin and adjacent areas is an undescribed taxon. The new species *Trimeresurus honghee*nsi*s* **sp. nov.** can be distinguished from all known congeners by the pairwise genetic divergence in the mitochondrial cytochrome-*b* (p-distance≥5.0%) and 16S rRNA gene fragment (p-distance≥0.5%), and morphologically by the combination of the following characters: (1) hemipenes short and strongly spinose, with deep bifurcation; (2) a white postocular stripe bordered above and below by red or only a white postocular stripe present in males; postocular stripe white or absent in females; (3) the ventrolateral stripe is red (below) and white (above) in males and white in females; (4) iris brick red or sepia in males; iris yellow or rusty-red in females; (5) VEN 150–165 in males and 157–165 in females; SC 61–76 in males and 56–61 in females; (6) dorsal tail mostly rusty red; (7) 9–12 cephalic scales; (8) 19 or 21 dorsal scale rows at mid-body; (9) first supralabial completely separated from the nasal scale.

Keywords: Mitochondrial DNA; Morphology; Honghe River; Phylogenetics; *Trimeresurus hongheensis* sp. nov.; *Viridovipera*

INTRODUCTION

The subgenus *Viridovipera* is characterized by a short and strong hemipenis, with large stout spines sparsely distributed at its base (Malhotra & Thorpe, 2004a; Malhotra et al., 2004). Most species of the subgenus *Viridovipera* share a common color pattern consisting of a uniform green coloration with a white ventrolateral stripe on the first dorsal scale row, often also with red ventrolateral stripe and postocular stripes (e.g., Gumprecht et al., 2004; Guo et al., 2009; Malhotra & Thorpe, 2004a). Most species have marked morphological similarities,

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with considerable geographic variation and sexual dimorphism within species, which results in inter-specific differences that are often difficult to distinguish, making classification difficult and confusing (e.g., David et al., 2001b; Guo & Wang, 2011; Guo et al., 2015; Malhotra & Thorpe, 2004b; Regenass & Kramer, 1981; Vogel et al., 2004; Zhu et al., 2016). Currently, seven species have been described in the subgenus *Viridovipera*, namely *Trimeresurus stejnegeri* Schmidt, 1925, *Trimeresurus yunnanensis* Schmidt, 1925, *Trimeresurus medoensis* Wang & Zhao, 1998, *Trimeresurus vogeli* David, Vidal & Pauwels, 2001, *Trimeresurus truongsonensis* Orlov, Ryabov, Thanh & Hô, 2004, *Trimeresurus mayaae* Rathee, Purkayastha, Lalremsanga, Dalal, Biakzuala, Muansanga & Mirza, 2022, *Trimeresurus nujiang* Liang, Ding, Vogel, Chen & Wu, 2025.

Trimeresurus yunnanensis was described from Tengyueh (now Tengchong City), Yunnan Province, China (Schmidt, 1925). Due to its morphological similarity to *T. stejnegeri*, *T. yunnanensis* was recognized as a subspecies of *T. stejnegeri* for a long time (Pope, 1935). It was not until 1995 that Zhao (1995) raised it to specific rank based on its scalation and geographical distribution compared to *T. stejnegeri*. However, the original description of *T. yunnanensis* is relatively sparse, with only a few brief lines, such as it is closely allied to *T. stejnegeri* and can be distinguished by having 19 rows of dorsal scales at mid-body and 21 rows of dorsal scales at neck (vs. 21 at mid-body and 23–25 at neck in *T. stejnegeri*) (Schmidt, 1925). Therefore, 19 dorsal scale rows at mid-body are an important diagnostic criterion for *T. yunnanensis*. Guo et al., (2009) conducted molecular phylogenetic analysis on two *Trimeresurus* specimens from Huili City, Liangshan Prefecture, Sichuan Province, China for the first time, combined with the decreasing pattern of dorsal scale rows at mid-body and morphometric analysis, identified the two specimens as *T. yunnanensis*, leading to a redescription of the holotype of *T. yunnanensis*. However, since the type specimen of *T. yunnanensis* was an old museum specimen without any available molecular data, the reliability of the classification conclusion based solely on morphological analysis to identify specimens collected in Huili, Sichuan Province as *T. yunnanensis* remains to be further verified. Additionally, the samples from Huili, Sichuan Province, exhibit significant morphological differences in the hemipenis compared to the type specimen of *T. yunnanensis*, suggesting that they may belong to different species. Therefore, whether the *Trimeresurus* specimens from Huili, Sichuan Province, are truly *T. yunnanensis* remains uncertain.

Trimeresurus gumprechti David, Vogel, Pauwels & Vidal, 2002, a green pitviper of the subgenus *Viridovipera*, was described from Phu Luang Wildlife Sanctuary, Loei Province, northern Thailand (David et al., 2002). Subsequently, the distribution of this species was also reported from Laos, Vietnam, Myanmar, and Yunnan Province, China, among which Malhotra & Thorpe (2004b) first mentioned *T. gumprechti* from Yunnan Province, China. Malhotra & Thorpe (2004b) argued that *T. gumprechti* and *T. yunnanensis* might be conspecific based on the following evidence: *T. gumprechti* (as determined by DNA analysis) was present at the type locality of *T. yunnanensis*, and the female paratype of *T. yunnanensis* (the holotype had not been examined at that time) was morphologically similar to *T. gumprechti*. Liang et al., (2025) really synonymized that *T. gumprechti* is a subjective junior synonym of *T. yunnanensis* based on molecular and morphological analyses. The departing point of our discussion follows this taxonomic revision.

Due to the wide distribution of the species, morphological variability and the lack of molecular data for *Trimeresurus* from northeast India, this could lead to misidentification of some taxa (e.g., Mirza et al., 2020; Nguyen et al., 2025; Rathee et al., 2022). For example, David & Mathew (2005) previously identified the *Trimeresurus* specimens from the state of Mizoram and Meghalaya as *T. gumprechti*. However, recently, Rathee et al. (2022) redescribed this population as *T. mayaae*. Previous studies have shown that there are more than one taxa present in Southwestern China (e.g., Gumprecht et al., 2004; Guo et al., 2015; Zhao et al., 1998). At the same time, Guo et al., (2015) explored the species diversity of Asian green pitvipers occurring in Yunnan Province, China and the non-monophyly of *T. gumprechti*, which the study indicates that the specimens from Southern Yunnan province may be an undescribed taxon. As previously noted, the subgenus *Viridovipera* is known to include several undescribed species that require further analysis and classification. Whether the green pitviper found in Southern Yunnan Province represents a cryptic species remains to be determined.

In this study, we extensively investigated and sampled *Trimeresurus* (*Viridovipera*) specimens from Yunnan Province, China. Based on the available morphological and molecular data from the literature, as well as our newly collected data, we describe a green pitviper found in the area surrounding the Honghe River Basin as a new species.

MATERIALS AND METHODS

Sampling

Seventeen *Trimeresurus* (*Viridovipera*) specimens (10 males and 7 females) were collected from Yunnan Province, China from 2017 to 2019. The muscle or liver used for molecular analysis were preserved in 99.9% ethanol and stored at −80°C. Vouchered specimens used in this study were deposited at the Guangxi Normal University (GXNU), Guangxi, China.

Molecular analysis

Total genomic DNA was extracted from ethanol-preserved liver or muscle tissue samples of 17 specimens using TsingKE Animals DNA Kit. Using the polymerase chain reaction (PCR), we amplified and sequenced fragments of mitochondrial cytochrome *b* (cyt *b*), NADH dehydrogenase subunit 4 (*ND4*), 12S ribosomal RNA (12S rRNA) and 16S ribosomal RNA (16S rRNA) genes using the primer pairs Gludg/H16064 (Burbrink et al., 2000; Palumbi, 1996), NADH4/H12763V (Arevalo et al., 1994), S12S471L1/S16S2489H1 (Li et al., 2020), and S12S471L2/S16S2489H2 (Li et al., 2020), respectively. The PCR amplification was performed in a 30 μl reaction volume with the following conditions: initial denaturation for 3min at 98°C, followed by 37 cycles: denaturation at 98°C for 10sec, annealing temperature 55°C for cyt *b*, 60°C for ND4, 56°C for 12S rRNA and 58°C for 16S rRNA for 15sec, elongation at 72°C for 15sec, and a final extending step of 5min at 72°C. The PCR products were sent to Beijing TsingKE Biotech Co., Ltd. (Chengdu, China) for purification and bidirectional sequencing.

The phylogenetic tree was reconstructed from a concatenated alignment of four mitochondrial DNA sequences (cyt *b*, ND4, 12S rRNA and 16S rRNA) from 93 samples.

Sequences of *Protobothrops elegans* (Gray) and *Azemiops feae* Boulenger were added to the dataset as outgroups (Chen et al., 2020; Malhotra & Thorpe, 2004b). Detailed information on these samples is shown in Supplementary Table S1. DNA sequences were aligned in MEGA 11.0 (Kumar et al., 2018). Phylogenetic relationships were analyzed using Maximum likelihood (ML) and Bayesian inference (BI). A maximum-likelihood phylogeny was constructed in RAxML v.8.2.4 (Stamatakis, 2014) with 1000 ultrafast bootstraps to assess support for inferred clades. Bayesian inference was performed in MrBayes 3.2 (Ronquist et al., 2012), and the best-fit partitioning strategy and models were obtained for the concatenated sequences by the Bayesian inference criteria (BIC) (Kalyaanamoorthy et al., 2017; Zhang et al., 2020) in PartitionFinder 2.1.1 software (Lanfear et al., 2017). The BI analyses were run for 20 million generations, with parameters and topology sampling every 1000 generations. Nodes in the phylogenetic trees were considered strongly supported when Bayesian posterior probabilities (BPP) were≥0.95 and the ML ultrafast bootstrap value (UFB) was≥95% (Huelsenbeck et al., 2001; Wilcox et al., 2002). Uncorrected pairwise *p*-distances (% of sequence divergence) were calculated using MEGA 11.0 (Kumar et al., 2018).

Morphological analysis

After preservation, measurements were taken with digital calipers to the nearest 0.1 mm and those for tail length and snout to vent length were taken with a string, which was then measured with a tape ruler to the nearest 1 mm. Ventral scales were counted in accordance with Dowling (1951). The enlarged plate(s) anterior to the first ventral were regarded as preventral(s). The first subcaudal scales were defined as the first pair of post-cloacal scales that were in contact with each other, and the unpaired terminal scute was not included in the subcaudal scale count. Cephalic scales were counted on a straight line between the middle of the supraoculars. The numbers of dorsal scale rows were given at one head length behind the head, at mid-body, and at one head length before the vent, respectively. The sex was determined by dissection of the ventral tail base in preserved specimens.

Abbreviations used in the text: **TL:** total length (from the tip of snout to the tip of tail); **SVL:** snout-vent length (from tip of snout to anterior margin of cloaca); **TaL:** tail length (from posterior margin of cloaca to the tip of tail); **TaL/TL:** ratio of tail length to total length; **HL:** head length (from the snout tip to the posterior margin of the mandible); **HW:** head width (measured at the widest part of the head); **HH:** head height (measured at the maximum highest part of the head); **VED:** vertical eye diameter; **DEL:** distance lower eye margin–edge of the lip; **DSR:** dorsal scale rows; **MSR:** dorsal scale rows at mid-body; **VEN:** ventral scales; **SC:** subcaudal scales; **Cep:** cephalic scales; **IL:** infralabial scales; **SL:** supralabial scales. Bilateral scale counts were given as left/right.

Comparative morphological data from other species of subgenus *Viridovipera* found in Southeast Asia and China were obtained from examined specimens (Appendix 1) and literatures (David et al., 2001a, 2001b, 2002; Guo et al., 2009; Liang et al., 2025; Nguyen et al., 2025; Orlov et al., 2004; Rathee et al., 2022; Schmidt, 1925; Wang & Zhao, 1998; Yang & Rao, 2008; Zhao et al., 1998).

Institutional acronyms

CAS: California Academy of Sciences, San Francisco, USA; **CIB:** Chengdu Institute of Biology, Sichuan, China; **FMNH:** Field Museum of Natural History, Chicago, USA; **GXNU:** Guangxi Normal University, Guangxi, China; **IEBR:** Institute of Ecology and Biological Resources, Hanoi, Vietnam; **KIZ:** Kunming Institute of Zoology, Yunnan, China; **MH:** Mian Hou's private collection, Sichuan, China; **MHNG:** Muséum d'Histoire Naturelle de la Ville de Genève, Genève, Switzerland; **NHMUK** (formerly BMNH)**:** Natural History Museum, London, UK; **NHMW:** Naturhistorisches Museum Wien, Austria; **RMNH:** Naturalis-Nationaal Natuurhistorisch Museum [formerly Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands; **VNMN:** Vietnam National Museum of Nature, Hanoi, Vietnam; **SMF:** Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany; **ZFMK:** Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; **ZMH:** Zoologisches Museum Hamburg [formerly Zoologisches Institut und Museum], Universität Hamburg, Hamburg, Germany.

RESULTS

Phylogenetic analysis

The ML and BI phylogenetic trees were constructed based on concatenated DNA sequences of the mitochondrial cyt *b* (1074 bp), ND4 (690 bp), 12S rRNA (903 bp) and 16S rRNA (525 bp) genes with a total length of 3192 bp, which selected GTR+I+G for 12S rRNA, 16S rRNA, the first codon position of cyt *b* and ND4; HKY+I+G for the second codon position of cyt *b* and ND4; GTR+G for the third codon position of cyt *b* and ND4 as the best-fit evolutionary model. ML and BI analysis obtained similar phylogenetic topologies, so we only show the BI tree, but included ML ultrafast bootstrap support and Bayesian posterior probabilities (Figure 1). The phylogenetic tree showed that twenty-three specimens (Serial No. 54–76) collected from near the Honghe River Basin, Yunnan Province, including Honghe County, Jinping County, Pingbian County, Yuanjiang County, and Mengzi City, form a monophyletic evolutionary branch with high bootstrap support (BPP 1.00/UFB 99), belonging to a member of the subgenus *Viridovipera*. These twenty-three specimens (Serial No. 54–76) form a sister taxon to *T. stejnegeri*, although this relationship received low node support. Subsequently, together these taxa clustered with *T. yunnanensis* (BPP 1.00/UFB 97).

Uncorrected pairwise genetic distances indicated that mitochondrial divergence ranged from 5.0% (*T. stejnegeri*) to 15.5% (*Trimeresurus hageni* (Lidth De Jeude)) in cyt *b* and ranged from 0.5% (*T. yunnanensis*) to 4.1% (*Trimeresurus popeiorum* Smith) in 16S rRNA between new species and other congeneric species (see Supplementary Tables S2–S3). The divergence is clearly at the inter-specific level since the uncorrected *p*-distances are larger than those of some known species pairs (e.g. 4.2% in cyt *b* and 2.6% in 16S rRNA between *Trimeresurus phuketensis* Sumontha, Kunya, Pauwels, Nitikul & Punnadee and *T. popeiorum*). Twenty-three specimens (Serial No. 54–76) collected from near the Honghe River Basin, are grouped together with little genetic variation between each other ($P≤0.1\%$) (see Supplementary Tables S2–S3). In summary, the phylogenetic analyses demonstrated that the *Trimeresurus* (*Viridovipera*) taxon from Honghe, Jinping, Pingbian, and Yuanjiang counties, and Mengzi City (Yunnan Province, China), represents a divergent lineage of pitvipers. Taken together, both morphological distinctions (e.g., scalation, coloration, and hemipenis structure) and

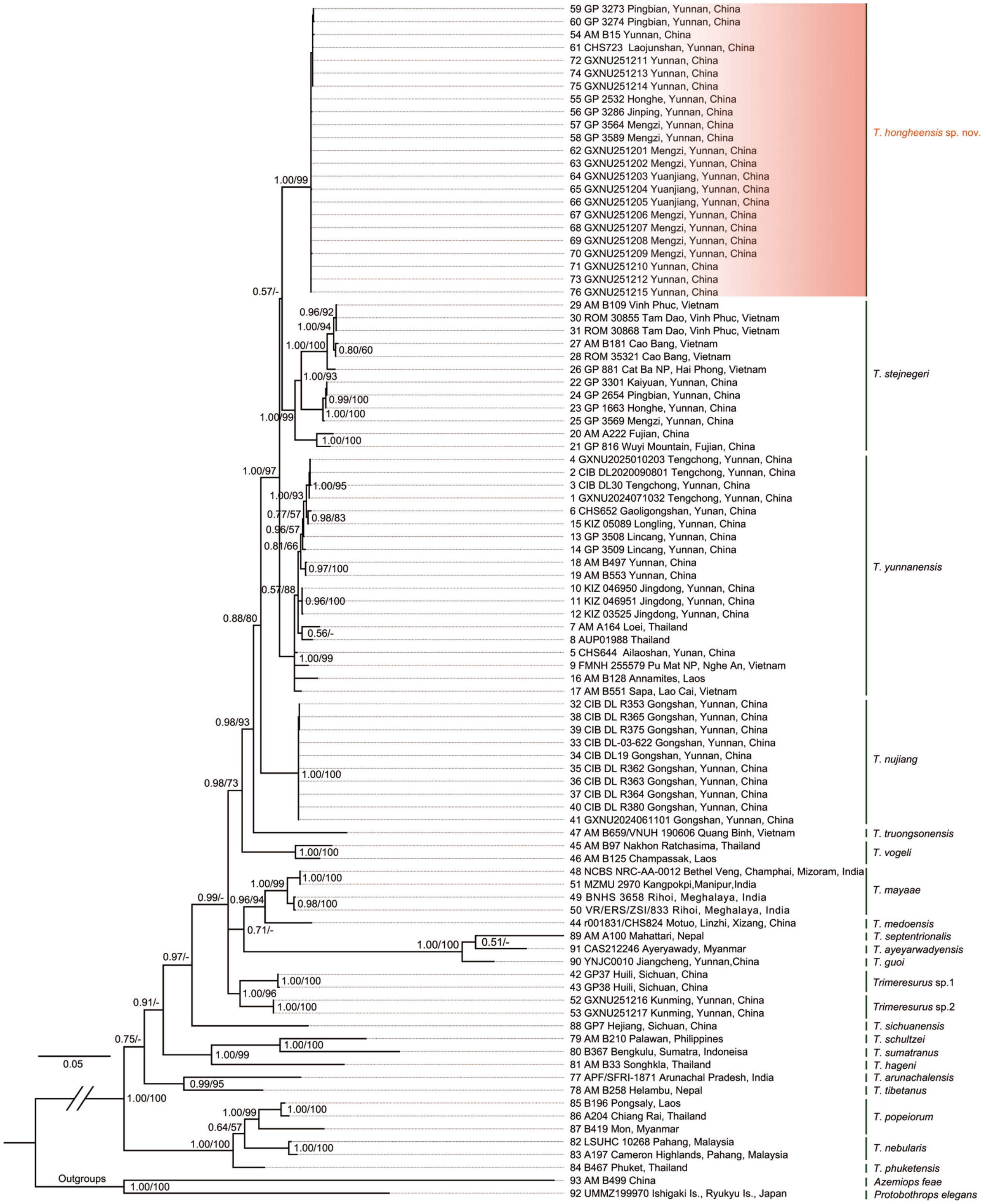

Figure 1 Phylogenetic tree of the genus *Trimeresurus* constructed based on cyt *b*, *ND4*, 12S rRNA, and 16S rRNA gene fragments

Bayesian posterior probability and ML ultrafast bootstrap support (BPP/UFB) are denoted beside each node, and "–" indicates<50%.

molecular evidence clearly support the separation of this population from all known congeners. Accordingly, we describe it as a new species in the following section.

The phylogenetic tree shows that two *Trimeresurus* specimens from Huili, Sichuan Province, China (GP37, GP38) and two specimens from Kunming, Yunnan Province, China (GXNU251216, GXNU251217) form two strongly supported, independent evolutionary branches (BPP 1.00/UFB 100), which together constitute a pair of strongly supported sister clades (BPP 1.00/UFB 96). Genetic distance analysis revealed significant genetic divergence between this lineage and other *Trimeresurus* (*Viridovipera*) species (see Supplementary Tables S2–S3). The uncorrected pairwise distances between the two specimens (GP37 and GP38 from

Huili, Sichuan Province, China) and other species of the genus *Trimeresurus* vary from 5.0% (GXNU251216 and GXNU251217 from Kunming, Yunnan Province, China) to 14.3% (*Trimeresurus septentrionalis* Kramer) in cyt *b* gene and vary from 0.5% (GXNU251216 and GXNU251217 from Kunming, Yunnan Province, China) to 4.6% (*Trimeresurus sumatranus*) in 16S rRNA gene. The uncorrected pairwise distances between the two specimens (GP37 and GP38 from Huili, Sichuan Province, China) and *T. yunnanensis* were 9.2% for cyt *b* and 1.4% for 16S rRNA, while the uncorrected pairwise distances between the two specimens (GP37 and GP38 from Huili, Sichuan Province, China) and *Trimeresurus* sp. near Honghe River population were 7.4% for cyt *b* and 1.0% for 16S rRNA. Based on phylogenetic analysis and genetic distance analysis, this study concludes that the two specimens collected from Huili, Sichuan Province, China, should not represent the true *T. yunnanensis*, but instead belong to an undescribed species. The unnamed *Trimeresurus* samples from Kunming, Yunnan Province, China (GXNU251216 and GXNU251217) and other *Trimeresurus* species are genetically differentiated from each other with the uncorrected *p*-distance≥3.6% (*T. mayaae*) for cyt *b* and 0.5% (*Trimeresurus* sp., GP37 and GP38) for 16S rRNA (Supplementary Tables S2–S3). The two specimens (GXNU251216 and GXNU251217) and other *T. yunnanensis* complex species are genetically differentiated from each other (Supplementary Tables S2–S3). In this study, we refer to these two specimens from Kunming, Yunnan Province, China as *Trimeresurus* sp. and their taxonomic status remains unresolved.

Taxonomy

Trimeresurus hongheensis **sp. nov.** (Figures 2–5)

Chresonymy

Viridovipera gumprechti — Malhotra & Thorpe, 2004a (part.)
Viridovipera gumprechti — Dawson et al., 2008 (part.)
Viridovipera gumprechti — Wallach et al., 2014 (part.)
Viridovipera gumprechti — Guo et al., 2015 (part.)
Viridovipera gumprechti — Wang et al., 2022 (part.)
Trimeresurus gumprechti— Rathee et al., 2022 (part.)
Trimeresurus (*Viridovipera*) *gumprechti* — Mirza et al., 2023 (part.)
Trimeresurus (*Viridovipera*) *hongheensis* Liang et al., 2025

Holotype: GXNU251201, an adult male, collected from Mingjiu Town, Mengzi City, Honghe Hani and Yi Autonomous Prefecture, Yunnan Province, China (N103.646°, E23.431°; elevation 1 735 m above sea level) by Li Ding on 31 August 2018.

Paratypes: (*n*=9, all from Yunnan Province, China; for detailed information, see Table 1) Mengzi City: GXNU251202 (adult male), GXNU251206 (adult male), GXNU251207 (adult male), GXNU251208 (subadult male), GXNU251209 (subadult male); Yuanjiang Hani, Yi and Dai Autonomous County: GXNU251203 (adult female), GXNU251204 (adult male), GXNU251205 (adult female); Mountain Dawei, Pingbian County: GXNU251219 (adult male). These specimens were collected by Li Ding except the sample GXNU251219 by Sheng-Chao Shi.

Other specimens: (*n*=7, all from Yunnan Province, China; for detailed information, see Table 1) Mengzi City: GXNU251218 (subadult female); Yunnan Province: GXNU251210 (adult female), GXNU251211 (adult female), GXNU251212 (adult female), GXNU251213 (junior male), GXNU251214 (junior male), GXNU251215 (adult female), collected by Li Ding.

Etymology: The new species name "*hongheensis*" refers to its type locality, the area around the Honghe River Basin, which is a boundary of the new species and *T. yunnanensis*. For common name we suggested as "Honghe green pit-viper" in English and "Hóng hé Zhú Yè Qīng (红河竹叶青)" in Chinese.

Diagnosis: (1) Head and body dorsum dark green, venter yellow green or light green. (2) 80% of the tail is rusty red, gradually fusing backwards, with dark red at the end of the tail. (3) Interstitial skin black. (4) Head dark green above, light yellow or light green below, clearly defined. (5) Iris brick red or sepia in males; iris yellow or rusty-red in females. (6) A white postocular stripe bordered above and below by red or only a white postocular stripe present in males, occupying only about 1–2 rows of scales across; postocular stripe white or absent in females. (7) Vivid, broad, bicolored ventrolateral stripe, red below and white above in males, covering 1–2 scales thick; thin white ventrolateral stripe present on the first row of DSR in females. (8) First supralabials separated from nasals. (9) Internasals separated by 0–2 scale. (10) Supraoculars separated by 9–12 smooth cephalic scales. (11) Head scales feebly keeled; 19 or 21 dorsal scale rows at mid-body, feebly keeled except for the outermost rows; VEN 150–165 in males (*n*=10), 157–165 in females (*n*=7); SC 61–76 in males (*n*=7), 56–61 in females (*n*=7). (12) Tail length to total length ratio (TaL/TL) 0.172–0.204 in males (*n*=7), 0.145–0.160 in females (*n*=7). (13) Hemipenes short and strongly spinose, with deep bifurcation.

Description of holotype: (Figure 3)**.** Body cylindrical, long and thin; head triangular in dorsal view, elongate, clearly distinct from the neck (HL 28.3 mm, HW 16.2 mm, HH 10.0 mm, ratio HL/HW 1.75%, HL/HH 2.83%), HL accounts for 4.3% of TL; snout moderate (snout length 8.74 mm), counting for 30.9% of HL; eye moderately sized (VED 3.27 mm), counting for 11.6% of HL, pupil vertically elliptic. The eye diameter is less than the distance from eye to lip (DEL 3.96 mm). Nostril elliptical about one-fourth of the eye diameter.

SVL: 542 mm; TaL: 116 mm; TL: 658 mm; TaL/TL: 17.6%.

VEN: 159 (plus 2 preventrals); SC: 61, all paired; anal shield entire.

DSR: 23–19–15, rhomboid, feebly keeled, first row smooth.

Rostral overall trapezoidal in front view, lower margin of rostral nearly 2.5 times wider than upper margin, height about 2 times as wide as top, front edge obtusely visible from lateral view, subtriangular slightly visible when viewed from above; nasal large, sub-rectangular and intact, completely free from first supralabial; temporal and occipital scales flat and feebly keeled; 9 small and irregular cephalic scales arranged in a line between midpoint of supraoculars; 10/11 supralabials; 2nd supralabials completely contact with the anterior margin of pit; one small scale between nasal and 2nd supralabials at left and two small scales at right; 3th supralabials largest and in contact with the subocular; 4th and 5th supralabials separated from subocular by one row of scales; 3 preoculars, elongated, the lower two scales border the pit with 2nd supralabials; 2/2 postoculars, 1/1 supraocular; 1/1 subocular; 12/13 infralabials; the first pair of infralabials meet each other behind the mental; the first three pairs in contact with chin-shields; single pair of chin-shields; six pairs of gulars aligned between the chin-shields and the 1st preventral; internasals not touching and separated by one scale.

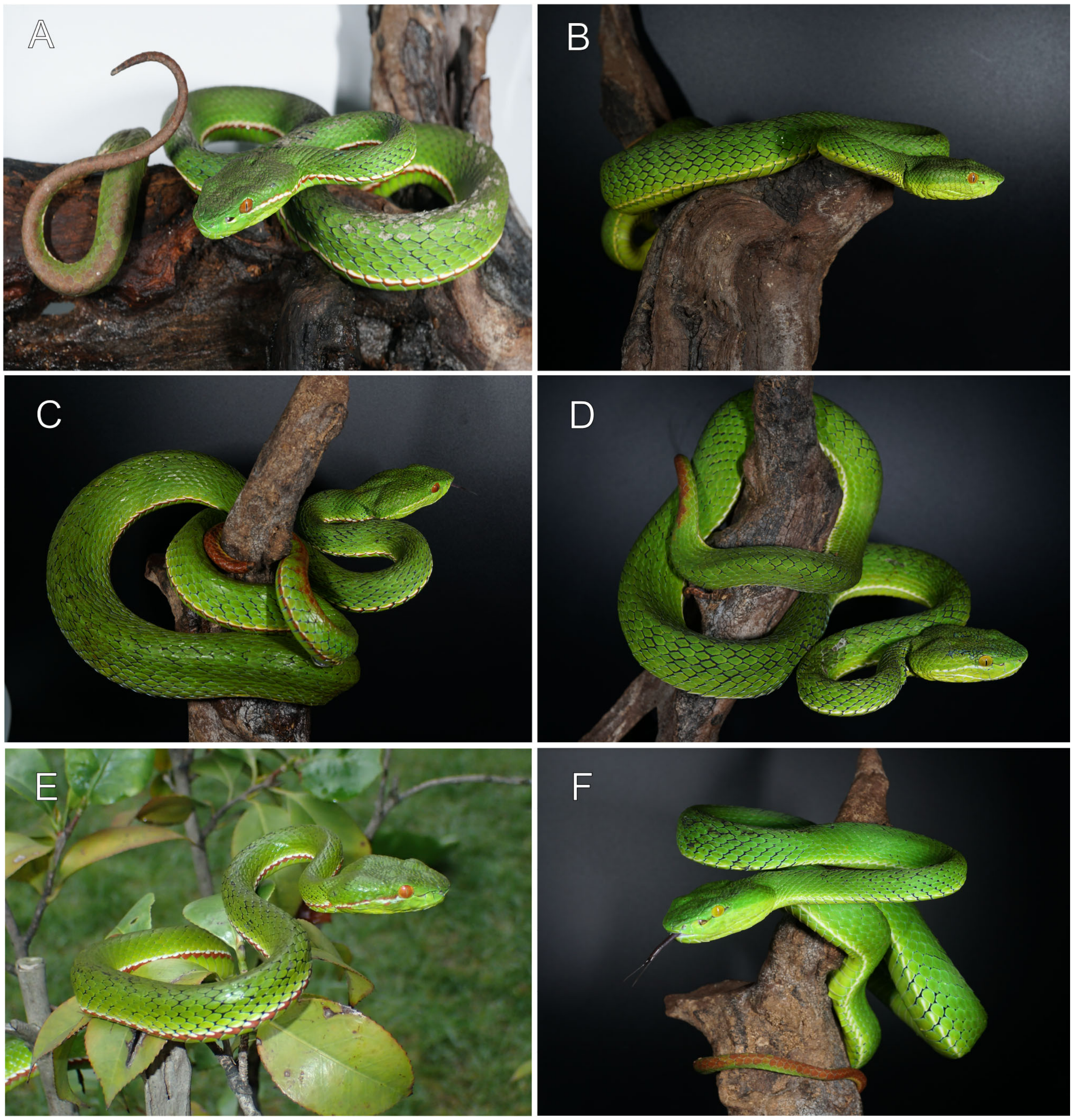

Figure 2 *Trimeresurus hongheensis* sp. nov. in Yunnan, China, males (Left) and females (Right) in life

A: Mingjiu, Mengzi (Holotype GXNU251201). B: Mingjiu, Mengzi (GXNU251218). C: Yuanjiang (Paratype GXNU251204). D: Yuanjiang (Paratype GXNU251205). E: Mt. Dawei, Pingbian County, Yunnan (Paratype GXNU251219). F: Yuanjiang (Paratype GXNU251203). Photos by Li Ding.

Coloration in preservation: Overall dorsum in a shade of dark green, ventral body yellow green or light green. Interstitial skin grey-black. The dorsal head is dark green, and the green coloration fades to a lighter shade towards the lateral portion of the head. Lateral head dark green above lower margin of eye, gradually turning into grass green, then yellow green or light green. Eye bright red, blood red, greenish-gold and blue in males; eye yellow, rusty red and greyish-blue in females. In males, the red postocular stripe has faded and is replaced by a faint white stripe extending from behind the eyes to the angle of the jaw; in females, a white postocular stripe is present or absent. The ventrolateral stripe is bicolored (white above and red or greyish-brown below) and 1–2 scales wide in males; ventrolateral stripe faint and thin white, present on the first row of DSR in females. More than half of the posterior part of the tail is rusty red in both sexes.

Hemipenes: (Figure 4). The description is based on the holotype GXNU251201. Hemipenes short, bilobed, more deeply forked, extending to the ninth subcaudal scale. The hemipenes are birfurcated at around three-fifths of the length measured from the base. Some enlarged and strong spines are present at one-quarter of the length from the base. There are about 9–11 stout spines on the outside (asulcal) side of each hemipenes, with the remainder of the hemipenes being covered with calyces or microspines, apart from the bifurcated regions of the hemipenes, which are without spines. *Sulcus spermaticus* divides at around one-quarter of the length of the hemipenes from the base and extends to the tip of the

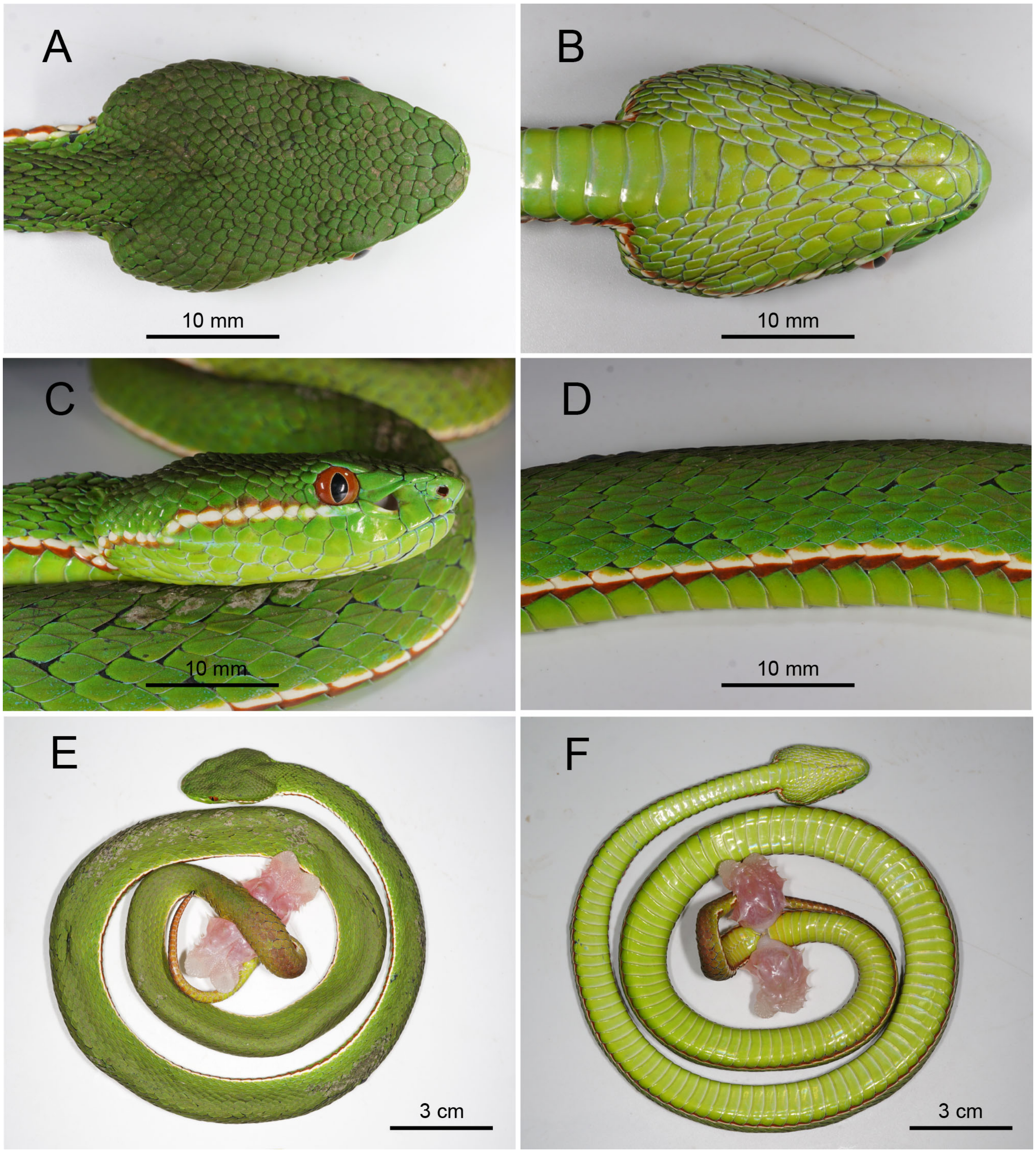

Figure 3 Holotype (adult male GXNU251201) of *Trimeresurus hongheensis* sp. nov.

A: Dorsal view of head; B: Ventral view of head; C: Lateral view of head; D: Lateral view of middle body; E: Dorsal view of the specimen; F: Ventral view of the specimen. Photos by Sheng-Chao Shi. Scale bars: 10 mm (A, B, C, D); 3 cm (E, F).

bifurcated region of the hemipenes.

Intraspecific morphological variation: (Table 1, Figure 5). Measurements and body proportions of type series of *T. hongheensis* **sp. nov.** are given in Table 1. All seventeen specimens have similar body patterns, but there are still some intraspecific morphological differences. A postocular streak is usually present and conspicuous in males, while postocular stripe is absent or white in females. The ventrolateral stripe is bicolored in males and only white in females. Both sexes show two types of skull shape, a longer skull or a shorter skull. Iris color differs between the sexes: males typically display brick red or sepia hues, while females show yellow or rusty-red irises. VEN 150–165 in males (*n*=10), while 157–165 in females (*n*=7). SC 61–76 in males (*n*=7), while 56–61 in females (*n*=7). The number of dorsal scale rows at MSR varies between 19 (9 specimens, 52.94%) and 21 (8 specimens, 47.06%) (*n*=17). SL vary from 9 to 11 (*n*=17); IL vary from 11 to 13 (*n*=17); Cep vary from 9 to 12 (*n*=17).

Comparison: According to the molecular data and hemipenes structure, *T. hongheensis* **sp. nov.** is a member of the subgenus *Viridovipera*. The species differs from all the known members of subgenus *Viridovipera* by the following characters

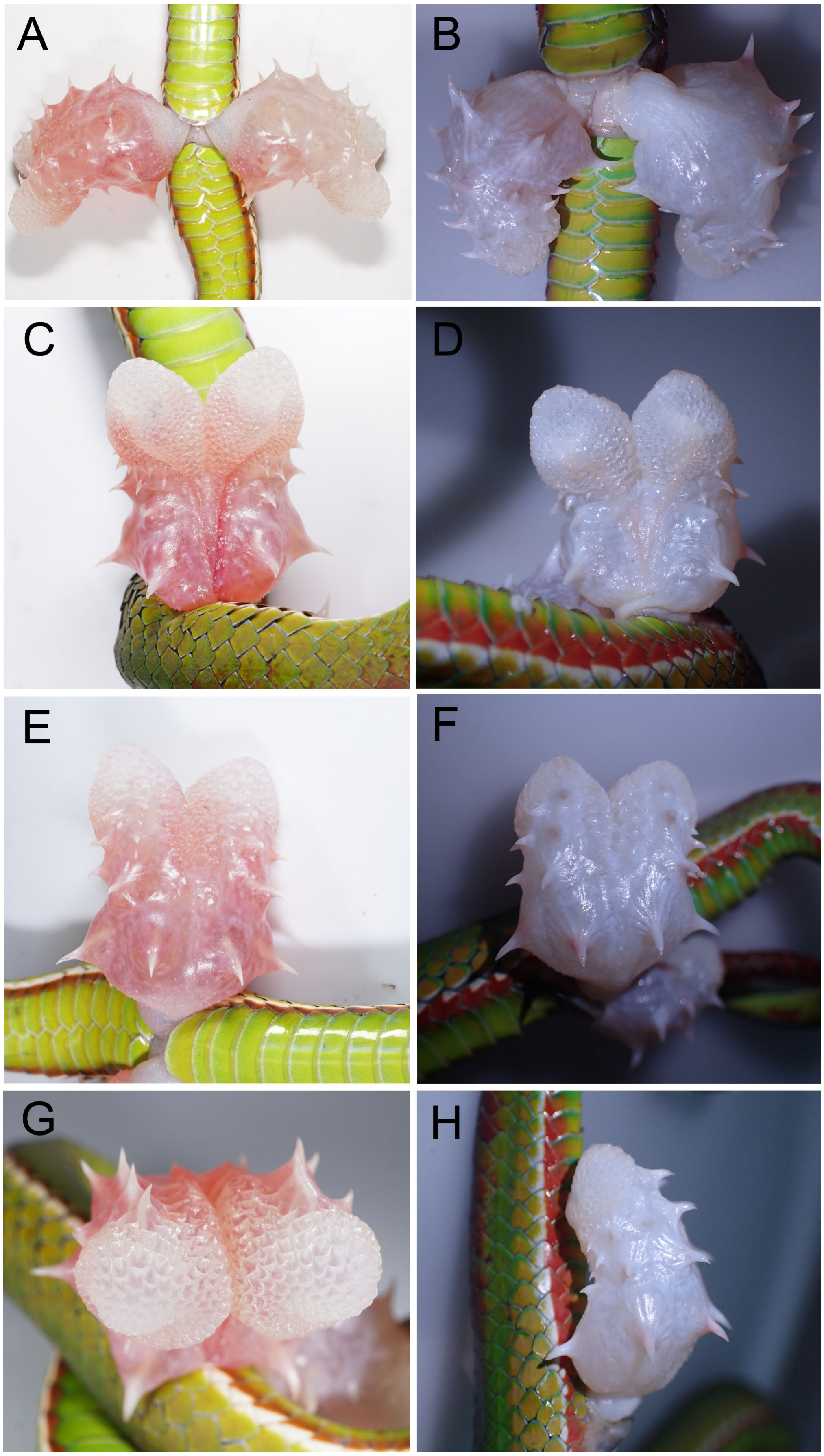

Figure 4 Hemipenes of *Trimeresurus hongheensis* sp. nov.

A, C, E & G: Holotype GXNU251201; B, D, F & H: Paratype GXNU251219. A & B: Ventral view of the tail with the everted hemipenes; C & D: Sulcate view; E & F: Asulcate view; G: Top view of hemipenes; H: Lateral view of hemipenes. Photos by Sheng-Chao Shi.

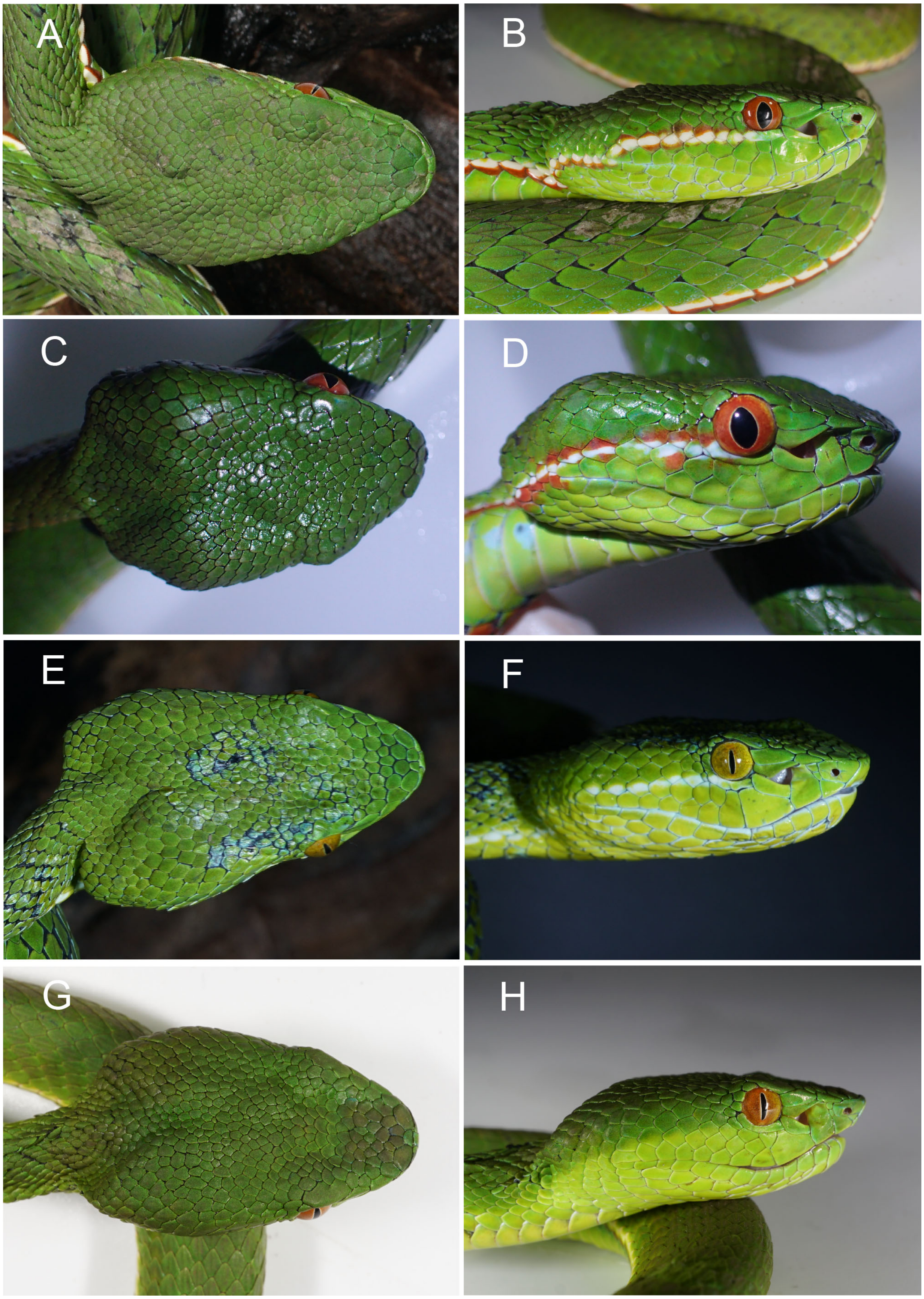

Figure 5 Comparison of head shape and coloration between males and females in *Trimeresurus hongheensis* sp. nov.

Left, dorsal view of head; right, lateral view of head. A & B: Specimen GXNU251201 (holotype, male); C & D: Specimen GXNU251219 (paratype, male); E & F: Specimen GXNU251205 (paratype, female); G & H: GXNU251218 (female). A & C: Different head shape in males (more elongated skull vs short skull); B & D: Different iris color in males (brick red vs sepia); E & G: Different head shape in females (more elongated skull vs short skull); F & H: Different postocular stripe (present vs absent) and different iris color (yellow vs rusty-red) in females. Photos by Sheng-Chao Shi.

Table 1 Measurements (to 0.1 mm) of *Trimeresurus hongheensis* sp. nov. Missing data are denoted with "–". "" represents holotype, "*" represents paratype.**

No.	Voucher	Sex	DSR	Pre-Ven	VEN	SC	Cep	SL	IL	SVL (mm)	TaL (mm)	TL (mm)	TaL/TL	HL (mm)	HW (mm)	HH (mm)
1	GXNU251201**	M	23–19–15	2	159	61	9	10/11	12/13	542	116	658	0.176	28.3	16.2	10.0
2	GXNU251202*	M	21–19–15	2	157	16+	10	10/10	11/12	563	32+	595+	–	26.1	16.5	11.9
3	GXNU251204*	M	22–21–15	2	151	41+	10	11/10	11/13	658	105+	763	–	32.2	16.6	15.1
4	GXNU251206*	M	22–21–15	0	164	65	11	10/10	11/12	566	136	702	0.193	27.1	17.2	9.5
5	GXNU251207*	M	21–21–15	3	163	64+	10	10/11	12/13	656	94+	750+	–	23.9	17.8	7.5
6	GXNU251208*	M	21–19–15	2	150	66	11	10/10	11/12	274	57	331	0.172	16.1	10.3	6.4
7	GXNU251209*	M	21–19–15	0	164	71	10	9/10	11/11	388	84	472	0.178	18.4	11	7.4
8	GXNU251213	M	21–19–15	1	159	68	10	11/11	12/12	207	44	251	0.175	13.3	8.9	4.1
9	GXNU251214	M	21–21–15	2	165	69	10	11/10	12/13	209	47	256	0.184	13.4	8.6	5.1
10	GXNU251219*	M	21–19–13	4	155	76	12	10/10	12/13	605	155	760	0.204	29.1	21.5	11.9
11	GXNU251203*	F	21–19–15	1	164	59	9	9/9	12/12	650	120	770	0.156	31.9	18.4	13.5
12	GXNU251205*	F	21–19–15	2	165	56	10	11/11	12/13	603	102	705	0.145	29.9	17.1	13.7
13	GXNU251218	F	21–21–15	2	159	59	10	11/11	13/13	330	60	390	0.154	18.9	13.3	7.2
14	GXNU251210	F	23–21–15	0	161	61	10	10/10	13/13	685	129	814	0.158	25.5	20.4	13.7
15	GXNU251211	F	21–21–19	2	157	56	11	10/10	13/13	662	124	786	0.158	32.7	18.6	13.5
16	GXNU251212	F	21–21–15	0	162	60	12	11/10	12/12	–	–	–	–	36.9	23.6	17.1
17	GXNU251215	F	22–19–15	0	160	58	11	10/10	12/13	722	138	860	0.16	38	21.5	17.1

(Supplementary Table S4):

Trimeresurus hongheensis **sp. nov.** is distinct from *T. yunnanensis* by: (1) No sexual dimorphism in body size vs. present in *T. yunnanensis* (658 mm vs. 700 mm in males, 722 mm vs. 1 047 mm in females). (2) A white postocular stripe bordered above and below by red or only white in males vs. white (below) and red (above) or white in *T. yunnanensis*. (3) Different color of ventrolateral stripe, ventrolateral stripe red (below) and white (above) in males vs. bright or deep red (below) and white (above) in *T. yunnanensis*; a white ventrolateral stripe is always present in females vs. sometimes present or absent in *T. yunnanensis*. (4) Different color of iris in females, yellow or rusty-red vs. yellow in *T. yunnanensis*. (5) Hemipenes are forked more deeply vs. shallow bifurcation in *T. yunnanensis*.

Trimeresurus hongheensis **sp. nov.** is distinct from *T. nujiang* by: (1) Higher max SVL in both sexes (658 mm vs. 649 mm in males, 722 mm vs. 682 mm in females). (2) Lower number of VEN in both sexes (150–165 [$\bar{x}$=158.7] vs. 164–173 [$\bar{x}$=168.7] in males; 157–165 [$\bar{x}$=161.1] vs. 165–168 [$\bar{x}$=166.6] in females). (3) Higher number of SC in males (61–76 [$\bar{x}$=68.0] vs. 59–68 [$\bar{x}$=62.8]). (4) Internasals usually in contact or separated by 1–2 scales vs. internasals not in contact in *T. nujiang*. (5) 19/21 DSR at mid-body vs. 19 in *T. nujiang*. (6) Postocular stripe always present in males vs. absent in *T. nujiang*; postocular stripe present or absent in females vs. always absent in *T. nujiang*. (7) Ventrolateral stripe red (below) and white (above) in males vs. dark red (below) and white (above) in *T. nujiang*. (8) Iris color brick red or sepia vs. golden-yellow in males; yellow or rusty-red vs. golden-yellow in females.

Trimeresurus hongheensis **sp. nov.** is distinct from *T. stejnegeri* by having: (1) Higher max SVL in both sexes (658 mm vs. 610 mm in males, 722 mm vs. 627 mm in females). (2) Internasals are in contact or separated by 1–2 scales vs. internasals are always not in contact in *T. stejnegeri*. (3) MSR 19/21 vs. MSR 21 in *T. stejnegeri*. (4) Postocular streak white bordered above and below by red or only white in males vs. white below and red above or white in *T. stejnegeri*. (5) Ventrolateral line red (below) and white (above) occupying 1–2 scales in males vs. red (below) and white (above) or white occupying the whole of the outermost scale row and a portion of the second row in *T. stejnegeri*. (6) Different color of eyes, brick red or sepia vs. bright red or amber or yellow in males in *T. stejnegeri*; yellow or rusty-red vs. yellow or amber in females in *T. stejnegeri*.

Trimeresurus hongheensis **sp. nov.** is distinct from *T. medoensis* by: (1) Higher max SVL in both sexes (658 mm vs. 573 mm in males, 722 mm vs. 555 mm in females). (2) Higher number of VEN in both sexes (150–165 [$\bar{x}$=158.7] vs. 138–149 [$\bar{x}$=144.7] in males, 157–165 [$\bar{x}$=161.1] vs. 138–149 [$\bar{x}$=143.6] in females). (3) Higher number of SC in both sexes (61–76 [$\bar{x}$=68.0] vs. 53–63 [$\bar{x}$=58.3] in males, 56–61 [$\bar{x}$=58.4] vs. 52–60 [$\bar{x}$=55.7] in females). (4) Higher total number of VEN+SC in both sexes (216–235 [$\bar{x}$=227.4] vs. 192–208 [$\bar{x}$=202.8] in males, 213–223 [$\bar{x}$=219.6] vs. 195–206 [$\bar{x}$=199.2] in females). (5) More cephalic scales, 9–12 vs. 6–9 (rarely 10) in *T. medoensis*. (6) MSR 19/21 vs. MSR 17 in *T. medoensis*. (7) Postocular stripe always present in males vs. absent in *T. medoensis*; postocular stripe present or absent in females vs. absent in *T. medoensis*. (8) Ventrolateral stripe white in females vs. red (below) and white (above) or only white which occupies the whole of the outermost scale row and a portion of the second row in *T. medoensis*.

Trimeresurus hongheensis **sp. nov.** is different from *T. vogeli* by: (1) Lower max SVL in both sexes (658 mm vs. 692 mm in males, 722 mm vs. 947 mm in females). (2) Fewer number of VEN in both sexes (150–165 [$\bar{x}$=158.7] vs. 154–169 [$\bar{x}$=162.2] in males, 157–165 [$\bar{x}$=161.1] vs. 157–173 [$\bar{x}$=166.3] in females). (3) Lower total number of VEN+SC in females (213–223 [$\bar{x}$=219.6] vs. 218–233 [$\bar{x}$=227.2]). (4) Fewer cephalic scales, 9–12 vs. 11–14 in *T. vogeli*. (5) DSR 19/21 at mid-body vs. 21 (rarely 20) in *T. vogeli*. (6) Postocular streak always present, white bordered above and below by red or only white in males vs. whitish yellow and rather faint or absent in *T. vogeli*; postocular streak white or absent in females vs. often absent in *T. vogeli*. (7) 80% of the tail rusty red vs. no more than about 25% of its tail rusty red in *T. vogeli*.

Trimeresurus hongheensis **sp. nov.** is different from *T. truongsonensis* by: (1) Higher max SVL in both genders (658 mm vs. 521 mm in males, 722 mm vs. 462 mm in females). (2)

Fewer number of ventral scales in both genders (150–165 [$\bar{x}$=158.7] vs. 166–176 [$\bar{x}$=171.8] in males, 157–165 [$\bar{x}$=161.1] vs. 165 in females). (3) Lower subcaudal scales in females (56–61 [$\bar{x}$=58.4] vs. 70). (4) Fewer total number of VEN+SC in both genders (216–235 [$\bar{x}$=227.4] vs. 235–243 [$\bar{x}$=238.5] in males, 213–223 [$\bar{x}$=219.6] vs. 235 in females). (5) Dorsal scale rows at mid-body 19/21 vs. 21 in *T. truongsonensis*. (6) Different dorsal color, dark green without bands or markings vs. greenish blue with brown broad bands in males and light-brown in females in *T. truongsonensis*. (7) Different ventral color, yellow green or light green vs. gray-bluish in *T. truongsonensis*. (8) Postocular stripe present in males vs. absent in *T. truongsonensis*; white or absent in females vs. absent in *T. truongsonensis*. (9) Different ventrolateral stripe, red (below) and white (above) in males vs. red-brown (below) and light greenish-blue (above) or white in *T. truongsonensis*. (10) Different eye color in males, brick red or sepia vs. greenish-yellow in *T. truongsonensis*. (11) Different coloration in dorsal tail, tip of tail dark red vs. yellow-orange in *T. truongsonensis*. (12) No bands present on tail vs. red-brown bands present on tail.

Trimeresurus hongheensis **sp. nov.** is different from *T. mayaae* by: (1) Higher max SVL in both genders (658 mm vs. 610 mm in males, 722 mm vs. 590 mm in females). (2) More ventral scales in females (157–165 [$\bar{x}$=161.1] vs. 153 [$\bar{x}$=153.0]). (3) More subcaudal scales in both genders (61–76 [$\bar{x}$=68.0] vs. 54–69 [$\bar{x}$=62.0]) in males, 56–61 [$\bar{x}$=58.4] vs. 54–55 [$\bar{x}$=54.5] in females). (4) Higher total number of VEN+SC in both genders (216–235 [$\bar{x}$=227.4] vs. 211–231 [$\bar{x}$=220.0] in males, 213–223 [$\bar{x}$=219.6] vs. 207–208 [$\bar{x}$=207.5] in females). (5) More cephalic scales, 9–12 vs. 9–10 in *T. mayaae*. (6) Dorsal scale rows at mid-body 19 (52.94%) or 21 (47.06%) vs. 19 (15.80%) or 20 (7.69%) or 21 (69.23%) in *T. mayaae*. (7) Postocular stripe present in males, white bordered above and below by red or only white vs. thin and white below, wide and bright red above or white in *T. mayaae*. (8) Different iris color, brick red or sepia vs. rust in males; yellow or rusty-red vs. green in females.

Trimeresurus hongheensis **sp. nov.** is different from *Trimeresurus pretiosus* by: (1) Higher max SVL in both genders (658 mm vs. 516 mm in males, 722 mm vs. 512 mm in females). (2) Higher number of VEN in both genders (150–165 [$\bar{x}$=158.7] vs. 140–143 [$\bar{x}$=141.5] in males, 157–165 [$\bar{x}$=161.1] vs. 142 in females). (3) Higher number of SC in both sexes (61–76 [$\bar{x}$=68.0] vs. 56–58 [$\bar{x}$=57.0]) in males, 56–61 [$\bar{x}$=58.4] vs. 54 in females). (4) Higher total number of VEN+SC in both sexes (216–235 [$\bar{x}$=227.4] vs. 198–199 [$\bar{x}$=198.5] in males, 213–223 [$\bar{x}$=219.6] vs. 196 in females). (5) Internasals are frequently either in contact or separate, whereas they are typically not in contact in *T. pretiosus*. (6) MSR 19 or 21 vs. 19 in *T. pretiosus*. (7) Postocular stripe always present in males, white bordered above and below by red or only white vs. a faint white postocular stripe present or absent in *T. pretiosus*; postocular stripe white or absent in females vs. absent in *T. pretiosus*. (8) Eyes brick red or sepia in males vs. reddish-brown in *T. pretiosus*; yellow or rusty-red in females vs. orange-yellow in *T. pretiosus*. (9) Subcaudal scales all paired vs. partially arranged in a single row in *T. pretiosus*.

Trimeresurus hongheensis **sp. nov.** differs from other species of the genus *Trimeresurus* occurring in Yunnan Province, China by the following characteristics:

Trimeresurus hongheensis **sp. nov.** can easily be distinguished from *Trimeresurus albolabris*, *Trimeresurus caudornatus* Chen, Ding, Vogel & Shi, *Trimeresurus guoi* Chen, Shi, Vogel & Ding, by having 1st supralabial completely distinct from nasal scale (vs. partially or completely fused to the nasal scale) and the structure of the hemipenes (see Chen et al., 2020, 2021; Nguyen et al., 2024; Vogel et al., 2023).

Trimeresurus hongheensis **sp. nov.** can be distinguished from *T. popeiorum* (see Idiiatullina et al., 2024) by: (1) Fewer ventral scales, 150–165 vs. 159–173 in *T. popeiorum*. (2) MSR 19 (52.94%) or 21 (47.06%) vs. 21 in *T. popeiorum*. (3) Different colors of dorsal surfaces, dark green vs. various shades of green, bluish-green or even turquoise blue. (4) Postocular streak always present in males vs. absent in *T. popeiorum*. (5) Different ventrolateral stripe in females, white or absent vs. thin and white or yellow in *T. popeiorum*. (6) Different color of eyes, brick red or sepia in males and yellow or rusty-red in females vs. red to deep red in both sexes in *T. popeiorum*. (7) Hemipenes short and strongly spinose vs. long and forked, without spines.

Trimeresurus hongheensis **sp. nov.** is distinguishable from *Trimeresurus lanna* Idiiatullina, Nguyen, Pawangkhanant, Suwannapoom, Chanhome, Mirza, David, Vogel & Poyarkov (see Idiiatullina et al., 2024) as follows: (1) Ventral body yellow green or light green vs. dark green in *T. lanna*. (2) Postocular streak bicolored in males, white bordered above and below by red or only a white postocular streak, occupying only about 1–2 rows of scales across vs. white and thin ventrally, broad and bright red dorsally, covering two or three temporal scales. (3) Ventrolateral line bicolored, red (below) and white (above) in males vs. bright and deep red (below) and white (above) in *T. lanna*; ventrolateral stripe white in females vs. thin, pale yellow anteriorly and whitish posteriorly in *T. lanna*. (4) Different eye color, brick red or sepia in males and yellow or rusty-red in females vs. red to deep red in both males and females in *T. lanna*. (5) MSR 19 (52.94%) or 21 (47.06%) vs. 21 (93.3%) or rarely 20 (6.7%) in *T. lanna*. (6) Hemipenes short and stout with relatively few, large, basal spines vs. hemipenes long and forked without spines in *T. lanna*.

Distribution: (Figure 6). *Trimeresurus hongheensis* **sp. nov.** is known to occur near the Honghe River Basin in Yunnan Province, China, including Honghe, Jinping, Pingbian, Yuanjiang counties, and Mengzi City. According to the source of the samples, it is known that *T. yunnanensis* and *T. hongheensis* **sp. nov.** are divided by the Ailao Mountain and Honghe River Basin, with *T. yunnanensis* distributed in the west of the Honghe River and *T. hongheensis* **sp. nov.** occurring along the lower reaches of the Honghe River Basin and adjacent areas in Yunnan Province, China.

DISCUSSION

Previous research suggested that *Trimeresurus* specimens (GP37 and GP38) collected in Huili, Sichuan Province, China were attributable to *T. yunnanensis* (Guo et al., 2009) and have subsequently been used as such in the construction of phylogenetic trees (e.g., Dawson et al., 2008). However, there are significant differences in the hemipenial morphology between *Trimeresurus* specimens collected in Huili, Sichuan Province, China and the type series of *T. yunnanensis*, which shows that the hemipenes structure of *T. yunnanensis* is short and strong, with shallow bifurcation, and the demarcation between spinous area and calyculate area is distinct (Pope, 1935), while the specimens collected in Huili, Sichuan Province, China have deep bifurcation, and the distinction

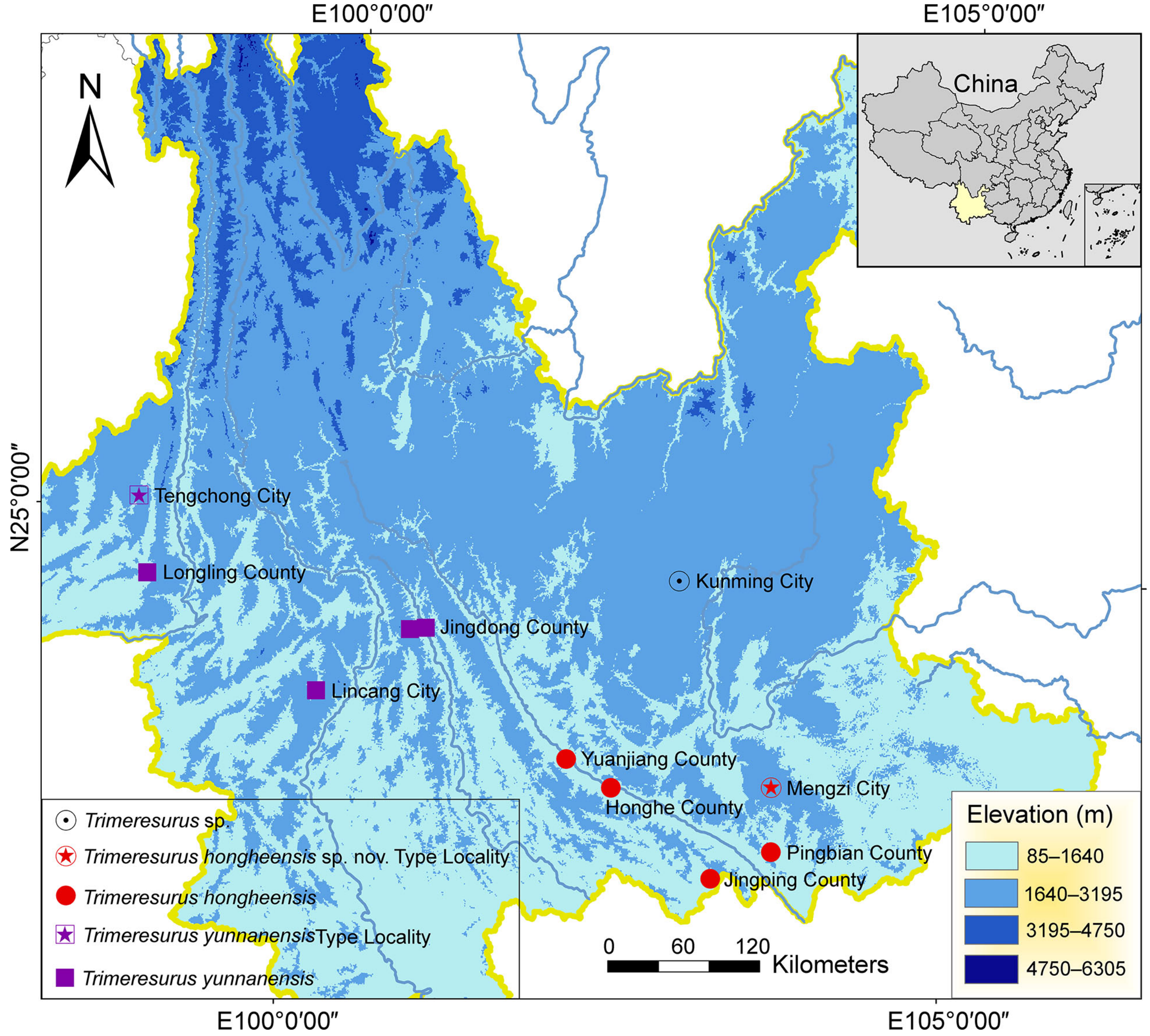

Figure 6 Distribution map of *T. hongheensis* sp. nov., *T. yunnanensis* and *Trimeresurus* sp. recorded in Yunnan Province, China

between spinous area and calyculate area is not significant (Guo et al., 2006). The highly stable morphological characteristics of the hemipenis in male snakes make it a valuable taxonomic marker in systematic studies. Molecular phylogenetic analyses indicate that the *Trimeresurus* specimens collected from Huili, Sichuan Province, China are not conspecific with *T. yunnanensis*, but instead represent a previously undescribed new species. This study named the two specimens (GP37 and GP38) as *Trimeresurus* sp., whose formal taxonomic status is subject to further confirmation by subsequent morphological studies and the designation of type specimens.

Trimeresurus "*gumprechti*" was initially recognized as a new species based on five individuals collected from northern Thailand (David et al., 2002; Gumprecht, 1997). However, Guo et al., (2015) found that the samples previously assigned to *T.* "*gumprechti*" did not form a monophyletic clade. Instead, they clustered into two distinct clades with strong phylogenetic support. Consequently, it was hypothesized that the specimens from Southern Yunnan Province might represent an undescribed taxon. After more extensive investigation, sampling and using more molecular markers, the problem has been solved by Liang et al., (2025), which synonymized *T. gumprechti* David, Vogel, Pauwels & Vidal, 2002 with *T. yunnanensis* Schmidt, 1925. Based on the currently known geographic distribution, we can roughly delineate the distribution areas of *T. yunnanensis* and *T. hongheensis* **sp. nov.,** i.e., they are bounded by the Ailao Mountain and Honghe River Basin, with *T. yunnanensis* distributed in the west of the Honghe River and *T. hongheensis* **sp. nov.** along the lower reaches of the Honghe River Basin and adjacent areas. Although *T. hongheensis* **sp. nov.** represents a valid taxon, which in parts of its range is sympatric with *T. albolabris*, the exact geographical limits of this species remain unclear. Moreover, this study identified a cryptic species within the genus *Trimeresurus* in the Kunming region of Yunnan Province, that requires further comprehensive analysis, including detailed morphological comparison, to be formally described. The precise distribution of the *T. yunnanensis* complex in Yunnan Province, requires further comprehensive investigation. Therefore, extensive sampling across its distribution range, including type localities, is essential to resolve taxonomic ambiguities in complex groups such as *Trimeresurus*.

Yunnan Province, China is located in the Hengduan Mountains region and Yunnan-Guizhou Plateau in the

Southwest of China, bordering Vietnam and Laos in the South and Myanmar in the west and the Southwest. Due to its complex geographical topology, unique location and changeable climate, the region is rich in biodiversity, and some species are endemic to the region. As new species continue to be discovered and reported, there are currently at least 9 species of the genus *Trimeresurus* occurring in Yunnan Province: *T. albolabris*, *T. stejnegeri*, *T. yunnanensis*, *T. popeiorum*, *T. caudornatus*, *T. guoi*, *T. lanna*, *T. nujiang* and *T. hongheensis* **sp. nov.** (Chen et al., 2019, 2020, 2021; Gray, 1842; Idiiatullina et al., 2024; Liang et al., 2025; Nguyen et al., 2024; Schmidt, 1925; This study). The description of increasing numbers of new taxa in this region recently lends support to the view that the biodiversity of the region is greatly underestimated. The Honghe River is one of the major international rivers that originates in the central part of Yunnan Province of China, flows Southeast to Hekou and enters Vietnam, branching off in Hanoi to flow into the Gulf of Tonkin in the Pacific Ocean. To date, the newly discovered species is confined to Yunnan Province. There is a strong likelihood that it may also inhabit regions proximate to the Honghe River Basin or even extend its range into adjacent countries. These indicate that more integrated studies are needed on the populations of the genus *Trimeresurus* in Southern China and neighbouring countries, in order to fully determine the *Trimeresurus* geographic distribution and to enhance our understanding of its ecological role and conservation status.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Sample collections in the field were conducted following the Wildlife Protection Law of the People's Republic of China. All laboratory experiments followed the Animal Experiment Guidelines of Guangxi Normal University.

DATA AVAILABILITY

The Supplementary Table S1–S4 are accessible on Science Data Bank (https://www.scidb.cn/) under DOI: https://doi.org/10.57760/sciencedb.zrdc.00042. The cyt *b*, ND4, 12S rRNA, and 16S rRNA gene sequencing data are available in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under accession NO. PQ789720–PQ789749, PQ801146–PQ801153, PX069568–PX069578, PX516277–PX516280, PX605308–PX605310.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Y.T.L. performed data analyses and wrote the initial manuscript. L.D., Z.N.C., and S.C.S. conducted field sampling. L.D., X.W., V.G., and X.G. provided key technical support and species taxonomy. Z.N.C., and Z.J.W. provided key technical support and funding support. All authors read and approved the final version of the manuscript.

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