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Morphological and molecular evidence for the first occurrence of *Takydromus kuehnei vietnamensis* Ziegler & Bischoff, 1999 (Squamata, Lacertidae) in Guangxi, China

Xue-Fang Jiang[1,2,3*], Jia-Song He[4*], Zheng-Jun Wu[1,2,3], You-Bang Li[1,2,3], Ze-Ning Chen[1,2,3]

1 *Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection (Guangxi Normal University), Ministry of Education, Guilin 541006, Guangxi, China*

2 *Guangxi Key Laboratory of Rare and Endangered Animal Ecology, Guangxi Normal University, Guilin 541006, Guangxi, China*

3 *School of Life Sciences, Guangxi Normal University, Guilin 541006, Guangxi, China*

4 *Guangxi Daguishan Crocodile Lizard National Nature Reserve, Hezhou 542800, China*

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Corresponding authors: You-Bang Li (lyb_2001@126.com); Ze-Ning Chen (chenzn@gxnu.edu.cn)

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Abstract

The first occurrence of the grass lizard subspecies *Takydromus kuehnei vietnamensis* Ziegler & Bischoff, 1999 in China is documented based on two specimens collected from Fangchenggang, Guangxi. Morphological features and molecular phylogenetic evidence from mitochondrial COI and Cyt *b* sequences concordantly identify these samples as *T. k. vietnamensis*, which forms a well-supported clade sister to the nominate subspecies *T. k. kuehnei*. The observed genetic divergence (6.4–7.9% for Cyt *b*; 8.2–11.5% for COI) is consistent with deep lineage differentiation. This new record further complements the distributional data for *T. k. vietnamensis* and provides the first molecular resources for this poorly documented subspecies. The findings underscore the close biogeographic connection between southern China and northern Vietnam and emphasize the need for intensified surveys in cross-border regions.

Key Words

COI, Cyt *b*, genetic divergence, *Takydromus*, Vietnam

Introduction

The genus *Takydromus* Daudin, 1802, commonly known as Asian grass lizards, comprises small-bodied, oviparous, diurnal lizards. This genus is widely distributed across East and Southeast Asia, including continental regions and numerous offshore islands (Arnold 1997; Arnold et al. 2007). To date, 26 valid species have been formally recognized in *Takydromus* (Guo et al. 2024; Uetz et al. 2026), 16 of which occur in China: *T. albomaculosus*, *T. amurensis*, *T. formosanus*, *T. guilinensis*, *T. hsuehshanensis*, *T. intermedius*, *T. luyeanus*, *T. sauteri*, *T. septentrionalis*, *T. sexlineatus*, *T. stejnegeri*, *T. sylvaticus*, *T. viridipunctatus*, *T. wolteri*, *T. yunkaiensis*, and *T. kuehnei*.

Ziegler and Bischoff (1999) formally described the subspecies *Takydromus kuehnei vietnamensis* based on specimens collected from northern Vietnam, distinguishing it from the nominate subspecies *T. k. kuehnei* using a suite of stable scalation and color-pattern morphological characters. In their original taxonomic account, the authors provided detailed meristic data and dorsal and lateral photographs of the holotype (ZFMK 70342, Fig. 1) and paratypes, all of which are deposited at the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Germany.

* These authors contributed equally to this work.

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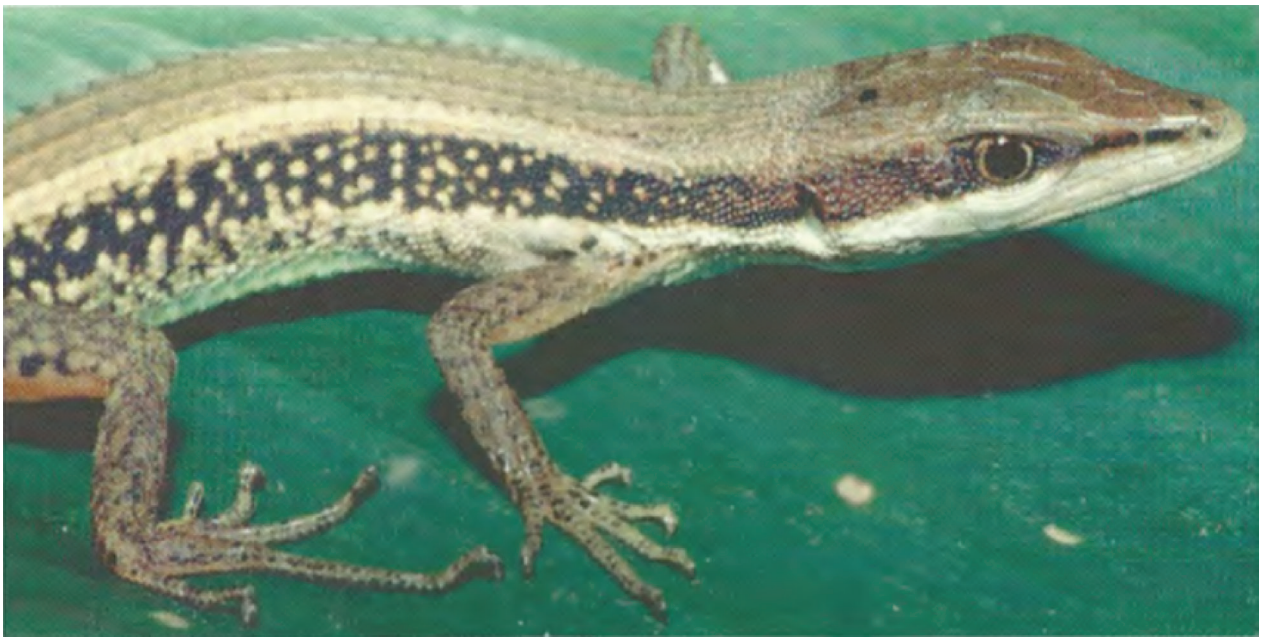

Figure 1. Live portrait of the holotype specimen (ZFMK 70342, male) of *T. k. vietnamensis*. Photo credit: T. Ziegler (Ziegler and Bischoff 1999).

They also conducted detailed morphological comparisons between Vietnamese populations and conspecifics from mainland China and Taiwan, China. The diagnostic traits of *T. k. vietnamensis* summarized in the original description include separated interparietal and occipital scales, higher numbers of supratemporals and supraciliary granules, distinctly enlarged lower flank scales in females, and faint lateral striping in males. Nevertheless, subsequent faunal surveys in northern Vietnam have routinely recorded these grass lizards only at the species level (*T. kuehnei*), without assigning them to any subspecies (Nguyen et al. 2009; Hecht et al. 2013; Pham et al. 2017, 2018). This limited taxonomic recognition of the subspecies stems from two major research gaps: the absence of independent molecular evidence supporting its morphologically defined differentiation and the lack of consistent diagnostic traits for reliable subspecies identification in the field.

Field surveys conducted from May to October 2025 in Nasuo Town, Fangcheng District, Fangchenggang City, Guangxi Zhuang Autonomous Region, yielded two lacertid specimens referable to the genus *Takydromus*. Morphological examinations confirmed that these specimens conform to the diagnostic characters given in the original taxonomic description of *T. k. vietnamensis*. Molecular phylogenetic analyses further recovered the two Guangxi samples as a well-supported lineage sister to the nominate subspecies *T. k. kuehnei*, with pairwise genetic distances exceeding typical interspecific divergence thresholds within *Takydromus*. Geographically, Fangchenggang shares contiguous terrain with northern Vietnam; the two areas exhibit comparable elevational ranges and lack prominent topographic barriers that would hinder faunal exchange. Based on integrated morphological and molecular evidence, the examined specimens are unequivocally assigned to *T. k. vietnamensis*. This study documents the first record of this subspecies for China and provides the first mitochondrial sequence data for this taxon, establishing a crucial baseline for future diagnostic, taxonomic, and phylogenetic investigations.

Materials and methods

Sampling

Field sampling was carried out from May to October 2025, yielding three *Takydromus* specimens from the Guangxi Zhuang Autonomous Region and Guangdong Province, China. The first specimen, an adult male (voucher GXNU2025051263), was collected on 8 May 2025 by Shufa Yan at Nasuo Town, Fangchenggang (21.74876287°N, 108.04627105°E; 85 m a.s.l.). The second specimen, an adult female (voucher GXNU2025101523), was obtained on 11 October 2025 by Zhenhong Kong at Nasuo Town, Fangchenggang (21.74836499°N, 108.06745464°E; 249 m a.s.l.). The third *Takydromus* specimen (voucher GXNU2025072603) was collected by Zhenhong Kong on 15 July 2025 from Ruyuan Yao Autonomous County, Shaoguan City, Guangdong Province (24.88780473°N, 113.05154473°E; 833 m a.s.l.). All individuals were initially fixed in 95% ethanol and later stored long term in 80% ethanol. The entire series is deposited in the zoological collection of the School of Life Sciences, Guangxi Normal University.

Molecular phylogenetic analysis

Genomic DNA was isolated from muscle tissue with the TIANamp Marine Animals DNA Kit (TIANGEN Biotech). Fragments of the COI gene were amplified using

the primer pair COI-L/COI-H (Tseng et al. 2015), while Cyt *b* sequences were amplified using primers L14910/H16064 (Burbrink et al. 2000). All PCR amplifications were performed in a total reaction volume of 25 μL, comprising 12.5 μL 2× SanTaq PCR Master Mix (containing Blue Dye), 10 μL ddH_2O, 1 μL forward primer, 1 μL reverse primer, and 0.5 μL template DNA. The thermal cycling profile comprised an initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 48.5 °C for 45 s, and extension at 72 °C for 35 s, with a terminal extension step at 72 °C for 10 min. Purified PCR amplicons were submitted to Sangon Biotechnologies Co., Ltd. (Shanghai, China) for bidirectional Sanger sequencing using the same forward and reverse primer sets.

Sequencing chromatograms were manually inspected and edited. A total of 38 COI and 38 Cyt *b* sequences of *Takydromus* were retrieved from GenBank (Table 1). *Eremias vermiculata* was chosen as the outgroup. All sequences were aligned using MEGA X (Kumar et al. 2018). PartitionFinder 2 was employed to identify the best-fit nucleotide-substitution model for the concatenated COI and Cyt *b* dataset according to the Akaike information criterion (AIC) (Lanfear et al. 2017). Phylogenetic reconstructions were carried out using PhyloSuite 1.2.3 (Zhang et al. 2020). Maximum likelihood (ML) analysis

Table 1. Samples used for molecular phylogenetic analysis of the COI and Cyt *b* genes in this study.

No.	Taxa	Voucher	Locality	COI	Cyt *b*	Reference
1	*T. k. vietnamensis*	GXNU2025051263	Nasuo, Guangxi, China	PZ869530	PZ879522	This study
2	*T. k. vietnamensis*	GXNU2025101523	Nasuo, Guangxi, China	PZ869531	—	This study
3	*T. k. kuehnei*	GXNU2025072603	Ruyuan, Guangdong, China	PZ869532	PZ879523	This study
4	*T. tachydromoides*	TAC201	Kyoto, Japan	AY248555	AY248479	Tseng et al. 2015
5		TAC103	Yakushima, Japan	AY248554	AY248478	Tseng et al. 2015
6	*T. septentrionalis*	SEP0202	Fujian, China	AY248545	AY248469	Tseng et al. 2015
7		HS17112	Huangshan, Anhui, China	MK630237	MK630237	Hu et al. 2019
8	*T. formosanus*	FOR2807	Taiwan, China	AY248604	AY248533	Tseng et al. 2015
9		FOR2802, FOR2805	Taiwan, China	AY248603	AY248532	Tseng et al. 2015
10	*T. hsuehshanensis*	HSU0501	Taiwan, China	AY248562	AY248486	Tseng et al. 2015
11		HSU0304–HSU0301	Taiwan, China	AY248560	AY248484	Tseng et al. 2015
12	*T. wolteri*	WOL101	China	AY248557	AY248481	Tseng et al. 2015
13		NIBRRP0000100350	Inje-gun, Gangwon-do, South Korea	JQ844542	JQ798812	Jeong et al. 2013
14	*T. toyamai*	TOY101	Miyako Island, the Ryukyus, Japan	AY248556	AY248480	Tseng et al. 2015
15	*T. stejnegeri*	STE1001	Ping- dong, Taiwan, China	AY248553	AY248477	Tseng et al. 2015
16		STE0601	Taipei, Taiwan, China	AY248552	AY248476	Tseng et al. 2015
17	*T. smaragdinus*	SMA103	Okinawa Island, Ryukyu, Japan	AY248551	AY248475	Tseng et al. 2015
18		SMA102	Okinawa Island, Ryukyu, Japan	AY248550	AY248474	Tseng et al. 2015
19		SMA101	Okinawa Island, Ryukyu, Japan	AY248549	AY248473	Tseng et al. 2015
20	*T. sexlineatus*	—	Guangxi, China	KF425529	KF425529	Qin et al. 2015
21		SEX101	Hong Kong, China	AY248546	AY248470	Tseng et al. 2015
22	*T. sauteri*	SAU0401	Lanyu, Taiwan, China	AY248543	AY248467	Tseng et al. 2015
23		SAU0301	Pingdong, Taiwan, China	AY248542	AY248466	Tseng et al. 2015
24		SAU0101	Pingdong, Taiwan, China	AY248541	AY248465	Tseng et al. 2015
25	*T. k. kuehnei*	KUE0201	Taipei, Taiwan, China	AY248540	AY248464	Tseng et al. 2015
26		KUE0102	Taipei, Taiwan, China	AY248539	AY248463	Tseng et al. 2015
27		LSU20210413QLG001	qvzhou, Zhejiang, China	MZ435950	MZ435950	Chen et al. 2022
28		SYS r001268	Longnan, Jiangxi, China	MF631863	MN239964	Wang et al. 2017, 2019
29		SYS r001338	Fengkai, Guangdong, China	MF631864	MN239965	Wang et al. 2017, 2019
30	*T. intermedius*	SYS r001602	Mt. Emei, Sichuan, China	MF631859	MN239958	Wang et al. 2017, 2019
31		SYS r000856	Libo, Guizhou, China	MF631860	MN239959	Wang et al. 2017, 2019
32	*T. dorsalis*	DOR102	Ishigaki Island, Ryukyu, Japan	AY248537	AY248461	Tseng et al. 2015
33		DOR101	Ishigaki Island, Ryukyu, Japan	AY248536	AY248460	Tseng et al. 2015
34	*T. amurensis*	AMU103	Seoul, South Korea	AY248535	AY248459	Tseng et al. 2015
35		AMU102	Seoul, South Korea	AY248534	AY248458	Tseng et al. 2015
36	*T. sylvaticus*	—	Xiuning, Anhui, China	JX290083	JX290083	Tang et al. 2014
37		SYS r001276	Shaowu, Fujian, China	MF631871	—	Wang et al. 2017
38	*T. albomaculosus*	SYS r001292	Ruyuan, Guangdong, China	MF631870	—	Wang et al. 2017
39	*T. yunkaiensis*	SYS r001514	Gaozhou, Guangdong, China	—	MN239955	Wang et al. 2019
40		SYS r001513	Gaozhou, Guangdong, China	—	MN239954	Wang et al. 2019
41	*T. guilinensis*	sim1	Guilin, Guangxi, China	OR667005	OR820954	Guo et al. 2024
42		sim2	Guilin, Guangxi, China	OR667006	OR820955	Guo et al. 2024
43		sim3	Guilin, Guangxi, China	OR667007	OR820956	Guo et al. 2024
44	*Eremias vermiculata*	Guo26028	Dunhuang Basin, Gansu, China	MK261078	MK261078	Chen et al. 2019

was implemented in IQ-TREE (Nguyen et al. 2015) under the best-fit TVM+I+G model with 5,000 ultrafast bootstrap replicates. Bayesian inference (BI) analyses were performed using MrBayes 3.2.7 (Ronquist et al. 2012) under the same optimal model for 2,000,000 generations, with the initial 25% of sampled data discarded as burn-in.

Morphological analysis

All morphological measurements were taken with a digital caliper to an accuracy of 0.1 mm. Morphometric abbreviations follow Lue and Lin (2008): arm-leg length (ALL), from forelimb insertion to hindlimb insertion; head height (HH), maximum vertical depth of the head; head length (HL), snout tip to anterior margin of the ear opening; hindlimb length (HLL), groin to tip of the fourth toe; head width (HW), maximum head width; fourth-toe length excluding the claw (LTL); radius-ulna length (RUL); snout-to-forelimb length (SAL), snout tip to anterior forelimb insertion; snout-eye length (SEL), snout tip to anterior orbital margin; skull length (SKL), snout tip to posterior edge of the occiput; snout-vent length (SVL), snout tip to anterior margin of the cloaca; tail length (TaL), cloaca to tail tip; tibia-fibula length (TFL).

Nineteen external morphological characters were examined for the three specimens (Table 2). Abbreviations for these characters follow Arnold (1997) and Wang et al. (2017), with modifications as follows: anterior dorsal scale rows (ADSR), distinctly enlarged and keeled scales on the anterior dorsum, counted transversely at the level of the forelimbs; chin-shields (CS); caudal scale rows (CSR), counted around the tail in the position of the 11th to 13th subcaudal scales; enlarged and keeled lateral scales in longitudinal rows above ventrals on the lower flanks (ESRF); femoral pores (FP); infralabials (IFL); longitudinal dorsal scale number (LDSN), counted longitudinally from the posterior margin of the occiput to the posterior margin of the hind limbs; mid-body scale rows (MBSR), transverse scale rows at mid-body, including ventrals; transverse dorsal scale rows at mid-body (MDSR); posterior dorsal scale rows (PDSR), counted transversely at the position of the hind limbs; subdigital lamellae under the fourth finger (SDLF-IV); subdigital lamellae under the fourth toe (SDLT-IV); supraciliaries (SPC); supralabials (SPL); supraoculars (SPO); supratemporals (SPT); small,

Table 2. Measurements (in mm) of two specimens of *T. k. vietnamensis* (GXNU2025051263 and GXNU2025101523) and one specimen of *T. k. kuehnei* (GXNU2025072603). Abbreviations are defined in the Materials and methods section.

Voucher/sex	GXNU2025051263 adult male	GXNU2025101523 adult female	GXNU2025072603 adult female
CS	4/4	5/4	4/4
SPL	6/6	6/7	6/6
IFL	6/6	6/7	6/6
SPO	4/4	4/4	4/4
SPC	4/4	4/4	4/3
SPT	6/6	5/5	3/4
FP	3/3	4/4	3/3
ADSR	7	7	7
MDSR	8	6	7
PDSR	6	6	6
LDSN	42	44	44
MBSR	44	48	45
SSRF	16	18	16
VR	6	6	6
VN	26	26	28
CSR	12	12	12
ESRF	1	1	1
SDLF-IV	20	19	15
SDLT-IV	25	25	22
SVL	56.44	51.63	52.1
TaL	—	165.66	—
HL	13.56	12.70	11.78
HW	7.64	7.24	6.18
HH	5.55	5.28	5.04
SKL	15.37	12.96	12.07
SEL	5.60	4.64	4.10
SAL	20.85	19.27	17.94
ALL	26.70	24.29	27.08
RUL	6.99	6.27	5.68
HLL	32.27	28.84	23.73
TFL	6.92	6.68	5.96
LTL	10.64	10.28	9.62

flat, granular scales in a transverse row on the flank at mid-body (SSRF); ventral scale number (VN), counted longitudinally from the posterior margin of the collar to the anterior margin of the precloacal scales; ventral scale rows (VR), counted transversely at mid-body.

Result

Morphological results

Morphologically, the two *Takydromus* specimens collected from Nasuo Town, Fangchenggang, fully agree with the original taxonomic description of *T. k. vietnamensis* Ziegler & Bischoff, 1999. The individuals show a suite of diagnostic traits characteristic of this subspecies: interparietal and occipital scales separated and not in contact; a higher number of supratemporal scales than in *T. k. kuehnei*, with the anterior supratemporal conspicuously enlarged (Fig. 3A–C); and a cyan-green ventral coloration. Geographically, Nasuo Town and the type locality (Ky Anh–Ke Go Nature Reserve, Ha Tinh Province, Vietnam) both lie within the coastal zone of the Gulf of Tonkin, with a straight-line distance of approximately 400 km between the two localities (Fig. 2).

Molecular results

The concatenated molecular dataset comprised 44 samples and 1,819 base pairs. The topologies recovered from both ML and BI phylogenetic analyses were highly consistent. The two *Takydromus* specimens from Fangchenggang (GXNU2025051263, GXNU2025101523) formed a strongly supported monophyletic lineage (Fig. 3D; BPP = 1.00/UFS = 100) and were retrieved as the sister group of *T. k. kuehnei*.

After exclusion of the outgroup, uncorrected pairwise *p*-distances among *Takydromus* species were calculated in MEGA X (Appendix 1). Genetic distances between the Fangchenggang specimens and 18 congeners ranged from 6.4 to 22.4% for Cyt *b* and from 8.2 to 24.7% for COI. The smallest genetic divergences occurred between the Fangchenggang specimens and *T. k. kuehnei*, with values of 6.4–7.9% for Cyt *b* and 8.2–11.5% for COI.

Systematics

Description of GXNU2025051263. Adult male. Rostral large, pentagonal; posteriorly in contact with the first supralabials on both sides and dorsolaterally with the supranasals. Nostril bordered on each side by one supranasal, one postnasal, and the first supralabial. A single, large supranasal is present on each side; the paired supranasals meet along the dorsomedial midline, separating the rostral from the frontonasal and contacting the anterior loreal posteriorly. One postnasal occurs on each side, touching the supranasal dorsally, the anterior loreal posteriorly, and the first supralabial ventrally. Six supralabials on each side; the fifth supralabial is the largest and is situated ventral to the orbit. Two loreals per side; the anterior loreal is smaller than the posterior one, with the posterior loreal contacting the anteriormost supraocular and anteriormost supraciliary scale posteriorly. Four

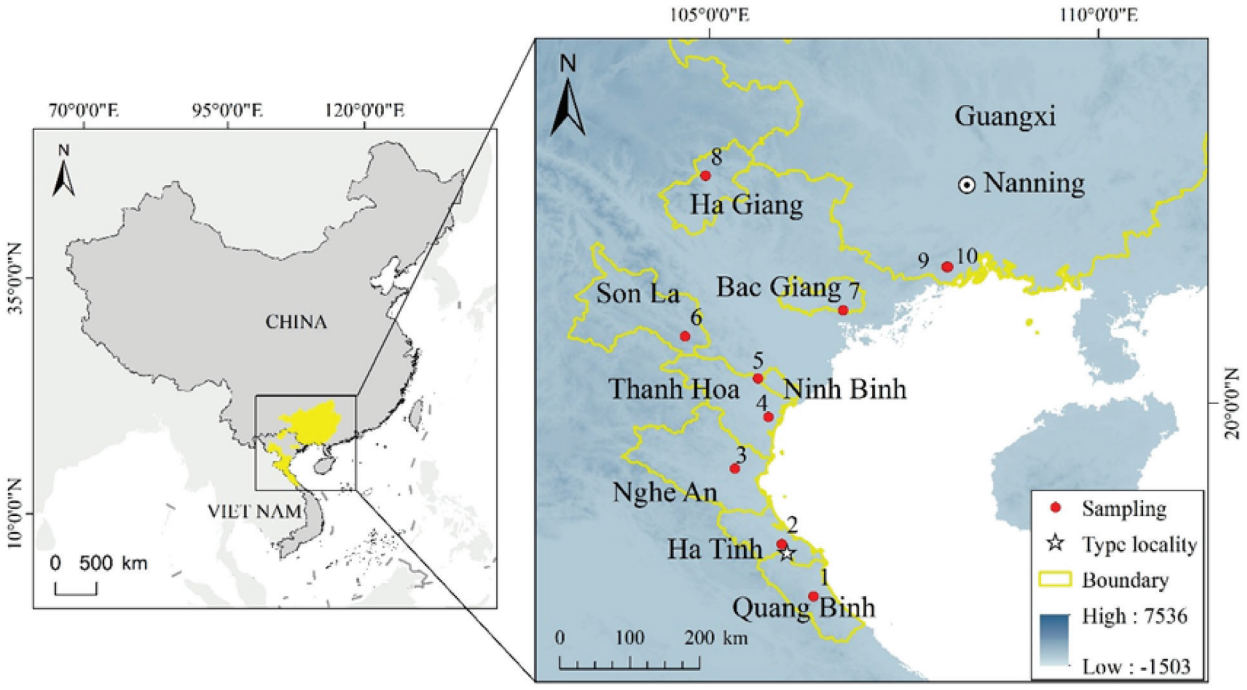

Figure 2. Distribution of *T. k. vietnamensis*. Sampling localities: 1. Quang Binh Province; 2. Ke Go Nature Reserve, Ha Tinh Province; 3. Tan Ky, Nghe An Province; 4. Ben En, Thanh Hoa Province; 5. Cuc Phuong National Park, Ninh Binh Province; 6. Son La Province; 7. Tay Yen Tu Nature Reserve, Bac Giang Province; 8. Phong Quang Nature Reserve, Ha Giang Province; 9, 10. Nasuo Town, Fangchenggang, Guangxi, China. The white star denotes the type locality: Ky Anh–Ke Go Nature Reserve, Ha Tinh Province.

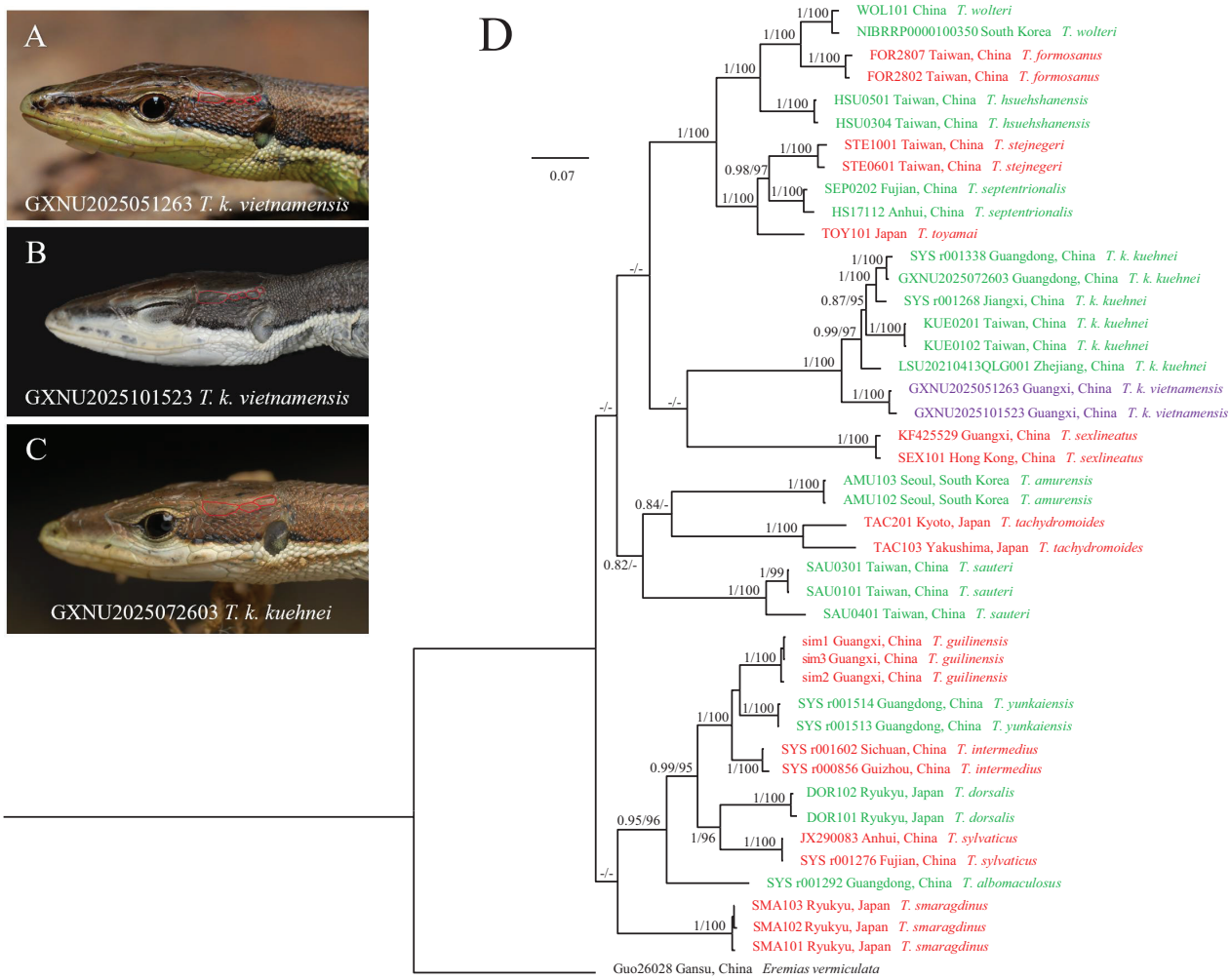

Figure 3. A–C. Comparison of supratemporals between *T. k. vietnamensis* and *T. k. kuehnei*; **D.** Combined phylogeny obtained by ML and BI analyses, with high bootstrap support values (≥70) and Bayesian posterior probabilities (≥0.7).

supraoculars on each side; the first and fourth supraoculars are distinctly smaller than the middle ones. Four supraciliaries on each side; the second supraciliary is the longest. The posterior three supraciliaries are separated from the supraocular series by eight supraciliary granules. Frontonasal large and smooth, separated from the frontal by a pair of prefrontals. Two weakly keeled prefrontals are present, contacting one another medially, articulating with the frontal and the first two supraoculars posteriorly, and touching the loreals laterally. A single pentagonal frontal scale is weakly keeled; it contacts the two largest supraoculars laterally and the paired frontoparietals posteriorly. Two subpentagonal frontoparietals meet along the midline, each associated with a parietal and the interparietal scale posteriorly. The quadrilateral interparietal scale is longer than wide, surrounded by two frontoparietals and two parietals, and separated from the occipital scale by small granular scales. The paired parietals represent the largest cephalic scales and do not contact medially; a single occipital scale lies between the paired parietals. Temporal scales are granular and weakly keeled. Six supratemporals occur on each side, with the anterior supratemporal distinctly enlarged. The mental scale is large and semicircular, and six infralabials are present on each side. Four pairs of chin-shields are observed; the anterior two pairs contact medially, whereas the posterior two pairs are separated by longitudinal gular scales. The flanks bear black markings interspersed with brown spots; the dorsal surfaces of the limbs are densely dotted with brownish-black spots; caudal scales exhibit distinct dark maculations.

Description of GXNU2025101523. Adult female. This specimen exhibits a cephalic scalation pattern nearly identical to that of the male GXNU2025051263. The only notable cranial difference is the contact between the parietal and occipital scales in this female. Furthermore, this individual lacks flank markings and bears only a few dark spots on the caudal scales.

Color in Life. Dorsal surfaces of the head, body, limbs, and tail are brown; the venter of the head is yellowish-green; the belly is cyan-green; and the ventral bases of the limbs and tail are green, whereas their remaining portions are brown. The male bears prominent black blotches on the flanks; females lack distinct flank markings. A well-defined black stripe runs from the nostril through the lower orbit to the forelimb insertion (Fig. 4A–D).

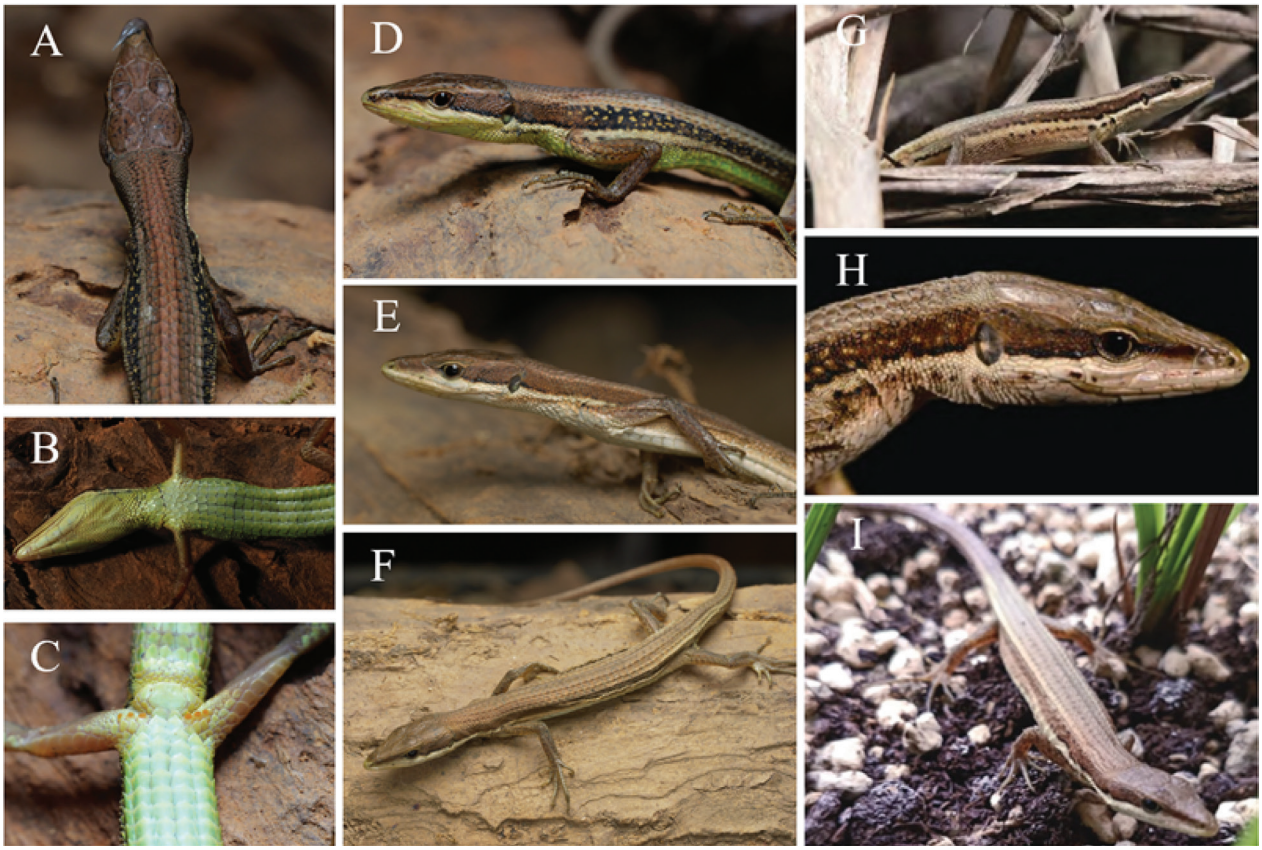

Figure 4. Comparison of *T. k. vietnamensis* and *T. k. kuehnei*: **A–D.** *T. k. vietnamensis* (GXNU2025051263) from Nasuo Town, Fangchenggang, Guangxi, China; **E, F.** *T. k. kuehnei* (GXNU2025072603) from Ruyuan Yao Autonomous County, Shaoguan, Guangdong, China; **G.** *T. k. kuehnei* from Qinshan Town, Fenyi County, Xinyu, Jiangxi, China (Zhang et al. 2024); **H.** *T. k. kuehnei* from Quzhou, Zhejiang, China (Chen et al. 2022); **I.** *T. k. kuehnei* from Huangshan Scenic Area, Huangshan, Anhui, China (Hong et al. 2023).

Color in preservative. In 80% ethanol, the dorsal surfaces of the head, body, and tail base are grayish brown, with the remaining tail portion light brown; the labial series and ventral head surface are pale bluish white; the ventral body and tail base are grayish blue; and the remaining ventral tail is light gray in males and light brown in females. Flank markings are dark blue in males and bluish gray in females (Fig. 5).

Variation. Consistent with Ziegler and Bischoff (1999), this subspecies exhibits clear sexual dimorphism. Females possess distinctly enlarged lower-flank scales, with indistinct flank markings and sparse caudal spots. In contrast, males show prominent flank patterns and relatively distinct caudal maculations. Meristic variation is as follows: supraciliary granules 6–15; supratemporals 4–7; scales between the tympanum and supratemporals 2–4; subdigital lamellae under the fourth toe 21–25.

Comparison with *T. k. kuehnei*. *T. k. vietnamensis* differs from the nominate subspecies by possessing a cyan-green venter (vs. pale brownish-yellow); an interparietal usually not contacting the occipital (vs. usually in contact); and higher counts of supratemporals, supraciliary granules, and scales between the tympanum and supratemporals (Fig. 4).

Diagnosis. *T. k. vietnamensis* is diagnosed by the following combination of characters: (1) interparietal usually not adjacent to the occipital; (2) venter creamy-white to cyan-green in life; (3) a well-defined black stripe running from the nostril through the inferior orbital margin to the forelimb insertion; (4) males with more than five supratemporal scales, the anterior one distinctly enlarged; and (5) males bearing distinct alternating black and yellowish-brown flank markings, with females lacking such markings.

Distribution and ecology. Ziegler and Bischoff (1999) documented *T. k. vietnamensis* from Ha Tinh, Nghe An, Ninh Binh, and Thanh Hoa provinces, Vietnam, based on verified voucher specimens ZFMK 70339–70345 (Ha Tinh), ZFMK 70346 (Nghe An), and ZIN 19809 (Ninh Binh); no voucher catalog numbers were provided for the Thanh Hoa population in their work. Hecht et al. (2013) reported *T. k. vietnamensis* from Bac Giang Province using voucher VNMN 1330. Pham et al. (2017) confirmed its occurrence in Ha Giang Province on the basis of two examined specimens, TNUEPQ 849 and TNUEPQ 850. Although Nguyen et al. (2009) and Pham et al. (2018) recorded *T. k. vietnamensis* for Son La Province, no corresponding voucher numbers were published for this locality. Bobrov and Semenov (2008) noted *T. k. vietnamensis* in Quang Binh Province without citing supporting

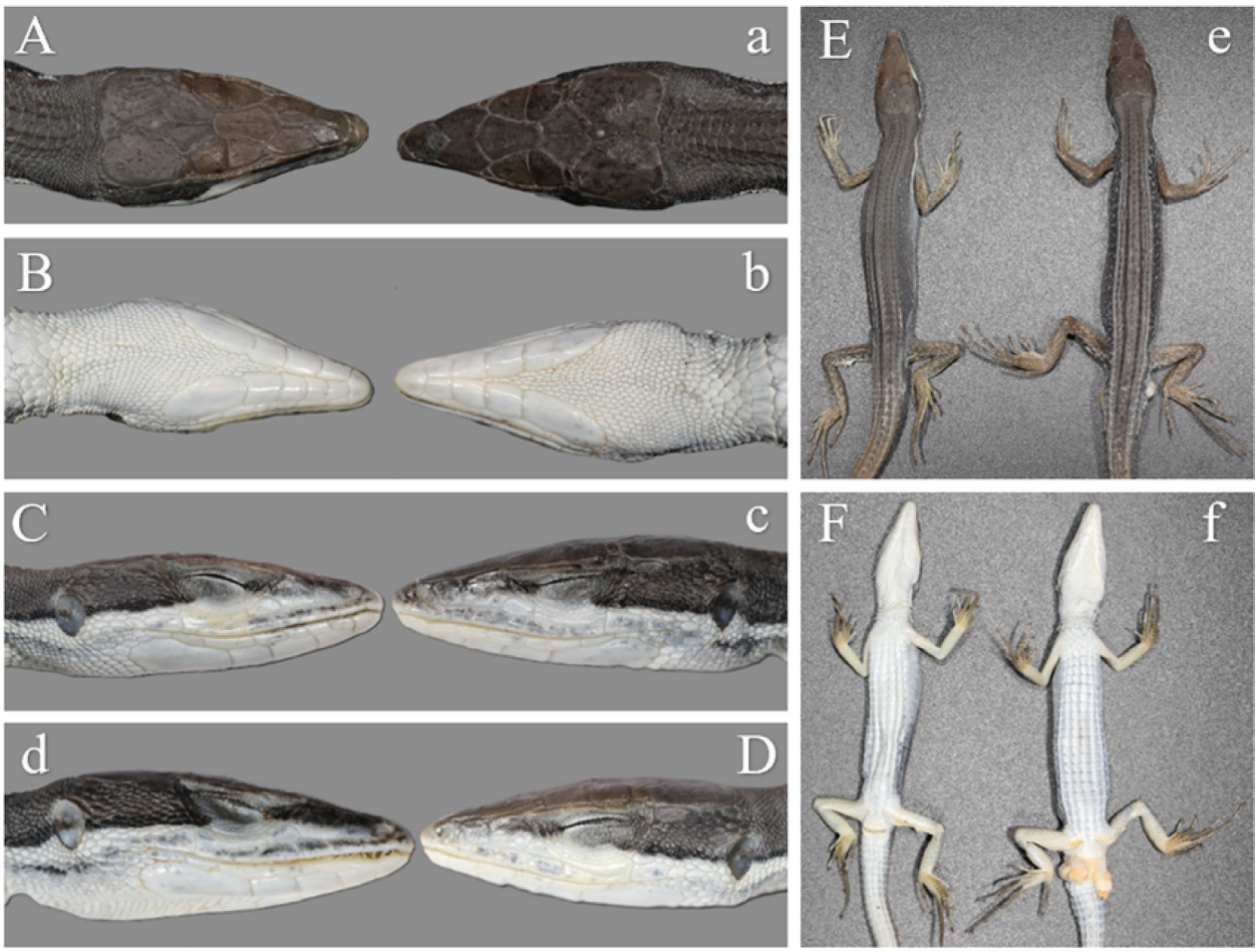

Figure 5. *T. k. vietnamensis* (**A–F:** GXNU2025101523; **a–f:** GXNU2025051263) preserved in 80% ethanol: **A.** Dorsal view of head; **B.** Ventral view of head; **C, D.** Left and right lateral views of head; **E.** Dorsal view of body; **F.** Ventral view of body.

vouchers, and this provincial record is further validated in The Reptile Database (Uetz et al. 2026). The finding from Fangchenggang, Guangxi, represents the first record of this subspecies for China and extends its known distribution northeastward into southern China (Fig. 2). The immediate habitat of the two *Takydromus* specimens from Nasuo comprises secondary evergreen broad-leaved forest with dense shrubs, ferns, and vines (Fig. 6). Within this area, the subspecies occurs sympatrically with *Ptyas multicincta* (Roux, 1907), *Ahaetulla prasina* (Boie, 1827), *Sphenomorphus cryptotis* Darevsky, Orlov & Cuc, 2004, *Odorrana graminea* (Boulenger, 1899), and *Hylarana maosonensis* Bourret, 1937.

Discussion

It should be noted that all previous records of *T. kuehnei* from northern and central Vietnam are attributable to *T. k. vietnamensis*. In the present study, two specimens collected from Fangchenggang were assigned to *T. k. vietnamensis* based on morphological evidence and mitochondrial sequence data for COI and Cyt *b*, representing the first national record of this subspecies for China. Prior to this study, no molecular data were available for *T. k. vietnamensis*. The phylogenetic analyses recovered this subspecies as a strongly supported sister lineage to the nominate subspecies *T. k. kuehnei*. Uncorrected pairwise genetic distances reached 6.4–7.9% (Cyt *b*) and 8.2–11.5% (COI), approaching typical interspecific divergence values reported for *Takydromus* lizards. Its subspecific rank is retained herein based on the following comprehensive evidence.

First, morphological differences between the two populations are restricted to continuous quantitative traits (e.g., ventral coloration and head-scale proportions), without fixed discrete diagnostic characters sufficient for species-level delimitation. No distinct morphological gap exists between the two taxa.

Second, although the two lineages are geographically allopatric, continuous forest habitats extend across northern Vietnam, connecting the type locality of *T. k. vietnamensis* to the China–Vietnam border; no impassable geographic barrier has historically restricted potential gene flow.

Third, despite substantial mitochondrial divergence, *T. kuehnei* forms a single well-defined monophyletic group encompassing both clades. Elevating these two subspecies to full species status would render *T. kuehnei* paraphyletic. Currently, nuclear genetic data and direct evidence of reproductive isolation remain lacking, precluding formal elevation to full species rank.

Figure 6. Habitat of *T. k. vietnamensis* (GXNU2025051263 and GXNU2025101523), Nasuo Town, Fangchenggang, Guangxi Zhuang Autonomous Region, China.

In China, all previously known native populations of *T. kuehnei* belong to the nominate subspecies. The present new record extends the distribution range of *T. k. vietnamensis* to southern Guangxi, demonstrating close biogeographic affinities between southern China and northern Vietnam. Further field surveys along the Sino-Vietnamese border and analyses of multilocus nuclear datasets are required to clarify their precise distributional boundaries and refine their taxonomic status in future studies.

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Appendix 1

Table A1. Uncorrected *p*-distances (in %) among *Takydromus* species. Lower diagonal: COI (789 bp); upper diagonal: Cyt *b* (930 bp).

Taxa	No.	1–2	3	4–5	6–7	8–9	10–11	12–13	14	15–16	17–19
T. k. vietnamensis	1–2		6.7	18.2–20.2	17.6–17.7	20.1–20.3	18.1–18.8	19.5–20.7	18.7	19.1–19.6	20.6
T. k. kuehnei	3	10.6		18.9–19.8	16.0–16.7	18.5–18.7	17.4–17.6	18.3–19.2	18.4	17.9–18.4	18.4–18.7
T. tachydromoides	4–5	19.9–20.5	19.1–19.4		18.6–20.0	20.8–21.4	20.9–22.0	20.4–22.4	18.9–20.8	20.4–20.9	14.8–16.4
T. septentrionalis	6–7	18.7–20.1	19.5–19.6	23.0–24.0		14.1–15.4	13.9–14.5	14.5–15.4	8.4–9.3	9.5–10.4	19.0–19.2
T. formosanus	8–9	18.3–19.3	18.4	23.1–24.1	12.0–13.3		12.2–13.1	7.1–7.6	14.8–15.6	14.1–14.7	19.0–19.9
T. hsuehshanensis	10–11	18.2	15.9–16.8	22.4–23.4	10.7–11.1	10.7–11.5		9.4–11.0	13.4–13.6	12.8–13.6	18.0–18.5
T. wolteri	12–13	19.7–20.2	18.3–18.8	21.7–22.8	12.5–13.7	6.7–7.4	11.1–11.9		15.2–15.6	15.2–15.8	17.8–18.7
T. toyamai	14	21.1	23.5	24–24.5	8.2–8.7	13.3–14.2	11.2	14.7		9.5–10.4	17.9–18.4
T. stejnegeri	15–16	20.1–21	20.1	22.1–23.0	6.2–7.4	12.8–13.7	11.9	13.7–16.3	8.2–9.4		17.0–17.3
T. smaragdinus	17–19	19.0–19.9	18.5	17.6–23.8	18.9–19.3	20.6–21.6	17.2–18.1	18.7–20.1	20	20.3–21.6	
T. sexlineatus	20–21	22.4–22.9	23.9	18.5–21.0	19.4–20.9	20.9–22.0	16.6–18.5	19.0–20.6	20.0–20.5	18.4–20.2	20.5–22.1
T. sauteri	22–24	18.0–19.4	18.5–18.9	19.7–20.4	17.0–19.0	17.8–18.1	16.3–17.5	19.6–21.0	19.7–19.8	18.8–19.8	18.3–20.2
T. k. kuehnei	25–29	8.2–11.5	1.4–7.4	19.0–22.4	18.8–23.9	18.6–21.2	16.7–20.9	18.5–21.7	23.1–26.0	19.6–23.5	18.1–22.3
T. intermedius	30–31	17.8–18.3	17.8–18.3	17.5–19.5	17.8–19.2	16.9–17.5	15.4–16.4	18.4–19.4	20.2–20.8	18.7–20.1	18.1–19.5
T. dorsalis	32–33	17.9–18.4	20.3–20.7	18.0–19.7	19.7–21.3	18.5–20.0	18.8–20.2	17.7–18.6	20.4–20.9	22.7–23.6	17.2–18.6
T. amurensis	34–35	16.9–17.3	17.8–18.2	22.7–24.7	16.4–17.4	17.4–18.8	18.1–18.5	16.5–17.4	17.4–17.8	16.0–18.1	19.7–20.6
T. sylvaticus	36–37	17.9	17.3	15.7–17.0	22.0–22.1	20.9–21.0	18.5–19.4	21.0–21.5	25.7	22.0–23.4	20.7–21.7
T. albomaculosus	38	19.9	22.4	23.5–24.0	18.2–18.7	18.6	19.1	18.6–19.1	22.6	21.0–22.5	15.8
T. yunkaiensis	39–40	—	—	—	—	—	—	—	—	—	—
T. guilinensis	41–43	17.0–17.5	19.3–20.3	16.6–18.5	18.8–20.1	18.9–20.8	18.7–20.6	18.0–19.4	19.8–20.4	20.7–22.6	18.5–19.4

Table A1. Continued.

Taxa	20–21	22–24	25–29	30–31	32–33	34–35	36–37	38	39–40	41–43
T. k. vietnamensis	17.7–17.9	20.6–22.0	6.4–7.9	20.3–20.5	19.3–20.1	18.3–18.5	19.1	—	18.7–19.0	20.7
T. k. kuehnei	18.0–18.3	19.1–20.2	0.6–4.0	19.5–19.7	18.8–19.3	19.5–19.7	19.4	—	19.0–19.3	21.3
T. tachydromoides	20.1–21.4	19.1–21.3	18.9–20.9	17.2–18.5	15.8–18.8	16.4–17.2	16.6–17.7	—	16.6–17.4	19.8–20.6
T. septentrionalis	17.9–18.5	18.0–19.6	15.8–17.3	17.4–18.8	19.8–20.5	17.6–17.7	18.2–18.7	—	19.0–20.2	20.6–21.2
T. formosanus	19.5–20.0	18.4–19.8	19.1–20.2	19.3–19.5	19.5–20.1	17.9–18.4	20.2–20.5	—	20.5–20.8	20.7–21.3
T. hsuehshanensis	20.1–21.0	18.3–18.6	15.7–17.6	17.0–17.7	18.2–19.0	19.7–20.0	15.6–16.0	—	17.4–18.0	18.2
T. wolteri	20.2–20.6	17.1–18.7	18.3–20.8	19.4–19.9	18.2–19.8	16.8–17.3	18.7–19.1	—	19.1–19.6	20.2–20.6
T. toyamai	16.7–16.9	18.7–19.2	18.2–18.6	17.5–17.7	18.0–18.5	16.9	17.2	—	17.8–18.1	18.6
T. stejnegeri	19.6–20.6	17.8–20.0	17.3–19.1	18.4–19.6	19.4–19.8	16.8–17.2	17.2–17.6	—	19.0–20.1	19.9–20.0
T. smaragdinus	20.5–21.0	15.8–16.5	18.7–19.1	14.7–14.9	16.1	16.2–16.4	13.5–14.1	—	14.7–15.1	17.6
T. sexlineatus		20.0–22.0	18.5–20.1	18.3–18.7	19	21.3–21.8	18.4	—	16.5–16.9	20.0–20.3
T. sauteri	15.6–18.9		19.3–22.3	18.7–19.8	18.3–20.6	17.5–19.5	19.3	—	19.7–21.5	19.2–19.9
T. k. kuehnei	22.5–24.5	16.1–21.8		19.0–20.0	18.2–20.4	19.2–20.2	17.5–19.8	—	19.3–20.0	20.9–22.7
T. intermedius	18.6–19.5	14.8–15.7	19.6		10.9–11.7	15.4–15.8	10.5–10.6	—	6.3–6.7	6.7–6.8
T. dorsalis	20.1–21.1	19.8–21.4	17.9–20.8	11.6–13.4		17.9–18.5	11.3–11.6	—	10.6–11.5	13.0–13.4
T. amurensis	21.6–22.5	15.1–17.3	18.3–19.6	17.0–18.5	18.8–19.7		17.6–17.8	—	16.2–16.6	16.6–16.8
T. sylvaticus	18.3–18.8	17.2–18.2	17.8–21.9	12.5	11.9–12.7	21.0–21.4		—	11.5–11.8	13.1
T. albomaculosus	19.2–20.2	18.0–19.1	20.2–22.5	13.0–13.9	14.2–14.7	19.8–20.2	17.3		—	—
T. yunkaiensis	—	—	—	—	—	—	—	—		7.3–7.5
T. guilinensis	18.2–19.7	17.1–20.0	18.4–21.6	7.1–8.3	11.1–11.6	16.1–17.1	13.3–14.2	10.0–11.3	—	

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Author contributions

Xue-Fang Jiang: Methodology, Formal analysis, Investigation, Data curation, Writing – Original Draft, Visualization. Jia-Song He: Methodology, Investigation, Data curation, Writing – Review & Editing. Zheng-Jun Wu: Investigation, Resources, Data curation. You-Bang Li: Supervision, Writing – Review & Editing, Project administration, Funding acquisition. Ze-Ning Chen: Supervision, Writing – Review & Editing, Project administration, Funding acquisition.

Author ORCIDs

Z.-N. Chen https://orcid.org/0000-0002-2266-7776

Data availability

All of the data that support the findings of this study are available in the main text.