

A new species of krait of the genus *Bungarus* (Squamata, Elapidae) from Ratchaburi Province, western Thailand

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Abstract

We described a new species of elapid snake genus *Bungarus* from the Tenasserim Mountain Range in Ratchaburi Province, western Thailand. *Bungarus sagittatus* sp. nov. can be distinguished from all congeners by having the combination of 15 dorsal scale rows; 215–217 ventral scales; 48–56 undivided subcaudal; prefrontal suture 2.4–2.6 times length of internasal suture; anterior chin shields larger than posterior chin shields; head of adult uniform black while juvenile black with small dim white patches on temporal and parietal areas; dorsal body black, with 25–31 white narrow bands, white and black bands at midbody covering 1.5–3.0 and 4.5–6.0 vertebral scales, respectively; dorsal body black bands not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales; ventral surface of body immaculate white; ventral side of tail white with a row of dark brown triangular patches on middle pointing posteriorly; tail relatively long, tail length/total length 0.140–0.143. Genetically, the new species has uncorrected pairwise divergences of $\geq 8.29\%$ of the mitochondrial cytochrome *b* from other *Bungarus* species. Currently, the new species is only known from the type locality.

Key Words

biodiversity, snake, Southeast Asia, systematics, Tenasserim

Introduction

The kraits, genus *Bungarus* Daudin, 1803, are a group of highly venomous snakes in the family Elapidae, with 17 recognized species that are distributed across Asia, from Southeast Asia and China, westwards through the South Asia to Iran (Smith 1943; Slowinski 1994; Abtin et al. 2014; Ahsan and Rahman 2017; Chen et al. 2021; Uetz et al. 2023). In Thailand, five species are currently reported, including *B. candidus* (Linnaeus, 1758), *B. fasciatus* (Schneider, 1801), *B. flaviceps* Reinhardt, 1843, *B. slowinskii* Kuch, Kizirian, Nguyen, Lawson, Donnelly & Mebs, 2005 and *B. wanghaotingi* Pope, 1928 (Smith 1943; Taylor 1965; Cox 1991; Leviton et al. 2003, 2008; Das 2010; Cox et al. 2012, 2018; Smits and Hauser 2019; Chen et al.

2021). Among the members of the genus *Bungarus*, the species with black-and-white crossbands are some of the most taxonomically confusing groups due to their highly similar color patterns and morphological characteristics (Pope 1928; Leviton et al. 2003, 2008; Xie et al. 2018; Chen et al. 2021; Yuan et al. 2022). Recently, Chen et al. (2021) investigated the taxonomic status of the *B. candidus/multicinctus/wanghaotingi* complex (black-and-white banded kraits) from China and some parts of Southeast Asia using the multiple lines of evidence (mitochondrial DNA, external morphology and cranial osteology). The combination of molecular phylogeny and morphological data supported the validity of three species in the complex (*B. candidus*, *B. multicinctus* and *B. wanghaotingi*) and uncovered a new species, *B. suzhenae* Chen, Shi, Vogel,

Ding & Shi, 2021 from Yunnan Province, China (Chen et al. 2021). Yuan et al. (2022) also investigated the molecular phylogeny of *B. multicinctus* Blyth, 1861 in Hong Kong and verified the occurrence of *B. multicinctus* and *B. wanghaotingi*.

Khao (mountain) Krachom is part of Tenasserim Mountain Range that is located at Suan Phueng District, Ratchaburi Province, western Thailand. The area lies on the Thai–Myanmar border and contains a variety of forest habitats ranging from 200 meters to more than 1,100 meters in elevation (The Office of Her Royal Highness Princess Maha Chakri Sirindhorn's Projects 2005; Pawangkhanant et al. 2018; Grismer et al. 2020b; Phuthai et al. 2021). Recently, several new species of herpetofauna were described from the area (e.g., Pawangkhanant et al. 2018; Grismer et al. 2020a, 2020b, 2021; Poyarkov et al. 2020, 2022; Suwannapoom et al. 2021), indicating a high diversity of herpetofauna.

During our field surveys in 2022, specimens of black-and-white banded *Bungarus* were collected from Suan Phueng District, Ratchaburi Province in western Thailand. These specimens closely resemble *B. candidus/multicinctus/wanghaotingi* complex in color pattern. The combination of morphological and molecular analyses revealed that the Ratchaburi specimens differed from all recognized *Bungarus* species. Thus, we herein describe it as a new species.

Methods

Sampling

Three *Bungarus* samples were collected during field surveys by hand and pitfall trap from Khao Krachom, Suan Phueng District, Ratchaburi Province from, May to June 2022 (Fig. 1). Geographical coordinates with elevation of

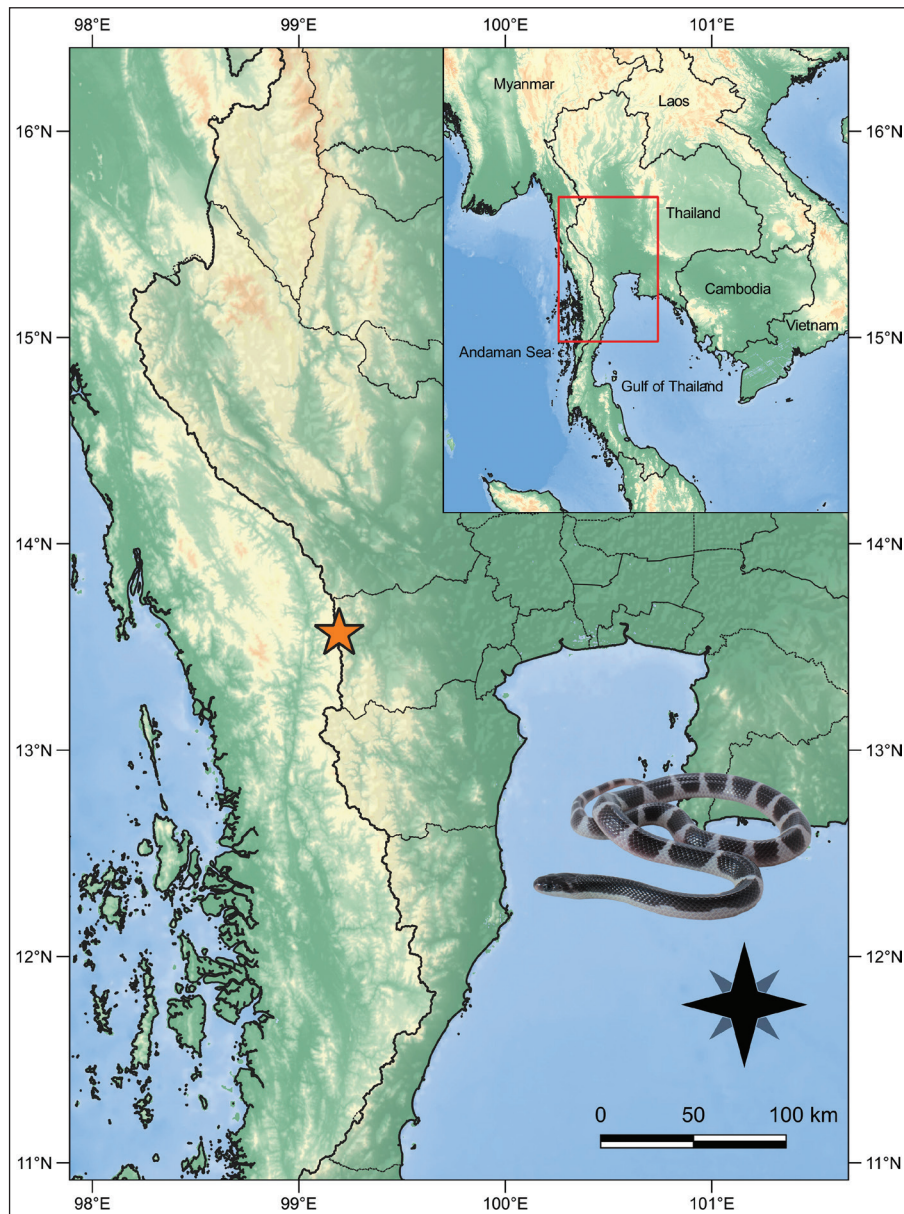


Figure 1. Map showing the type locality of *Bungarus sagittatus* sp. nov. (orange star) in Khao Krachom, Suan Phueng District, Ratchaburi Province.

each specimen were collected using a Garmin GPSMAP 64st. Ambient air temperature and relative humidity were collected with Kestrel 4000 Weather Meter. The specimens were humanely euthanized using tricaine methanesulfonate (MS-222) solution (Simmons 2015). Liver tissue was immediately cut from a euthanized individual, preserved in 95% ethyl alcohol, and stored at -20 °C for genetic analysis. Voucher specimens were then initially fixed in 10% formaldehyde solution and later transferred to 70% ethyl alcohol for long-term preservation. All type series and tissue samples were deposited in herpetological collection of Zoological Museum, Kasetsart University, Bangkok, Thailand (ZMKU). An additional specimen was examined at herpetological collection of the Rabbit in the Moon Foundation (RIM), Suan Phueng District, Ratchaburi Province.

DNA extraction and PCR amplification

We extracted genomic DNA from liver tissue of three individuals of *Bungarus* from Ratchaburi Province (Suppl. material 1) using the DNeasy (Qiagen, German) Blood and Tissue Kit according to manufacturer's protocol. A 1,041 base pairs of mitochondrial cytochrome *b* (*cyt b*) was amplified by the polymerase chain reaction (PCR), using the light strand primer L14910 (5'-AACCACCGTTG-TACATCAACT-3') and heavy strand primer H16064 (5'-CTTTGGCTTACAAGAACAATGCTTTA-3') (Burbrink et al. 2000). PCR conditions were as follows: initial denaturation at 95 °C for 2 min, followed by a second denaturation at 95 °C for 40 s, annealing at 57 °C for 25 s, followed by a cycle extension at 72 °C for 15 s, for 35 cycles with a final extension at 72 °C for 2 min. PCR amplifications were carried out in a Mastercycler[®] nexus gradient thermocycler (Eppendorf SE, Germany). Amplified PCR products were run on a 1.5% agarose gel and viewed with a Molecular Imager[®] Gel Doc[™] XR system (Bio-Rad Laboratories, USA) to confirm the PCR amplification. PCR products were purified using a QIAquick PCR Purification Kit (Qiagen, Germany). PCR products were sequenced in both forward and reverse directions using the same amplifying primers at Biobasic Asia Inc. (Singapore) on an ABI 3730XL automatic sequencer (Applied Biosystems, CA, USA). Bidirectional sequences were visually checked and edited in Geneious Prime 2022.2.1 (Biomatters, Ltd, Auckland, New Zealand). The protein-coding region of *cyt b* was translated to amino acids and checked to confirm the lack of premature termination codons. All new sequences were deposited in GenBank under accession numbers PP131180 to PP131182 (Suppl. material 1).

Phylogenetic analyses

Additional homologous *cyt b* sequences from 43 individuals of *Bungarus* species and the outgroups were downloaded from GenBank, based on previous *Bungarus* studies (Kuch et al. 2005; Xie et al. 2018; Biakzuala et al. 2021b, 2023; Chen et al. 2021) (Suppl. material 1).

Naja naja (Linnaeus, 1758) and *Elapsoidea sundevallii* Smith, 1848 were selected as outgroups to root the tree following Xie et al. (2018) and Chen et al. (2021). The three newly generated *Bungarus* sequences and GenBank dataset were aligned using the MUSCLE alignment function (Edgar 2004) with default setting in Geneious Prime 2022.2.1 (Biomatters, Ltd, Auckland, New Zealand). The aligned dataset was partitioned into three partitions (1st–3th *cyt b* codon positions). We used ModelFinder (Kalyaanamoorthy et al. 2017) to identify the best-fit model of sequence evolution for each partition as determined by the Bayesian Information Criterion (BIC). The best-fit evolutionary models were TIM2+F+G4, TN+F+G4 and TN+F+I+G4 for *cyt b* codon position 1, 2, and 3, respectively.

Maximum Likelihood (ML) and Bayesian Inference (BI) were used to estimate phylogenetic relationships. The ML analysis was conducted using the IQ-TREE 1.6.12 web server available at "<http://iqtree.cibiv.univie.ac.at>" (Trifinopoulos et al. 2016) with 1,000 bootstrap replicates using the ultrafast bootstrap analysis (Minh et al. 2013; Hoang et al. 2018). The BI analysis was carried out using MrBayes v3.2 (Ronquist et al. 2012) on CIPRES Science Gateway V. 3.3 (Miller et al. 2010) with default prior setting. Two independent runs, each with three heated and one cold chain, were performed using Metropolis-coupled Markov Chain Monte Carlo (MCMC). The MCMC chains were run for 10,000,000 generations, with trees sampled every 1,000 generations, and the first 25% of each run was discarded as burn-in. Stationarity was evaluated by ensuring that effective sample sizes (ESS) exceeded 200 for all parameters in Tracer v. 1.7 (Rambaut et al. 2018). Nodal support for ML and BI was quantified using Ultrafast bootstrap support values (UFB) and Bayesian posterior probabilities (BPP), respectively. UFB values ≥ 95 and BPP ≥ 0.95 are considered highly supported (Huelsenbeck and Ronquist 2001; Wilcox et al. 2002; Minh et al. 2013). The phylogenetic trees from the ML and BI analyses were visualized and edited using Fig-Tree v. 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>). Uncorrected pairwise sequence divergences (*p*-distances) were calculated in MEGA 11 (Tamura et al. 2021) using the pairwise deletion option to remove gaps and missing data from the alignment prior to analysis.

Morphological analyses

Morphological measurements were taken with digital calipers to the nearest 0.1 mm (except SVL and TaL, which were measured to the nearest 1 mm). The morphological characters and abbreviations used were modified from the previous studies of the genus *Bungarus* (Slowinski 1994; Kuch et al. 2005; Chen et al. 2021). The following morphometric and meristic characters were recorded: snout-vent length (SVL); tail length (TaL); head length (HL), from the tip of snout to the posterior edge of mouth; head width (HW), the widest part of head; head height (HH), the highest part of head in vertical; eye diameter (ED), the

horizontal length of eye ball; distance between eyes (DE), was measured from the margin of upper eye contacting supraocular to opposite side; the length of internasal suture (IS), the length of suture between left and right internasal scales; the length of prefrontal suture (PS), the length of suture between left and right prefrontal scales; supralabials (SL); infralabials (IL); dorsal scale rows (DSR), were counted at one head length behind the angle of jaw, at midbody, and at one head length before the cloaca; ventral scales (VS), were counted following Dowling (1951); and subcaudals (SC). The number of white bands on dorsal body (BB) and white bands on tail (TB) were counted, while incomplete white bands were counted as one.

Comparative morphological data from other species of *Bungarus* were obtained from the original descriptions and literature (Boulenger 1890, 1897; Wall 1907, 1908; Pope 1928; Smith 1943; Biswas and Sanyal 1978; Slowinski 1994; Leviton et al. 2003; Kuch et al. 2005; Faiz et al. 2010; Cox et al. 2012, 2018; Chanhom 2013; Abtin

et al. 2014; Knierim et al. 2017; Luu and Ha 2018; Xie et al. 2018; Smits and Hauser 2019; Biakzuala et al. 2021b; Chen et al. 2021) (Suppl. material 3).

Results

The final alignment of *cyt b* contained 1,137 characters of 46 taxa (44 individuals of *Bungarus* and two individuals of the outgroup species). The standard deviation of split frequencies among the four Bayesian runs was 0.003186 and the ESS values of all parameters were greater than or equal to 6,531. The best tree in ML analysis had a maximum likelihood value of -6,833.101. The ML and BI analyses recovered trees with similar topologies (Fig. 2). The three Ratchaburi samples formed a strongly supported monophyletic lineage (100 UFB, 1.00 BPP) and nested within the genus *Bungarus*. The Ratchaburi population was a strongly supported sister lineage (97 UFB,

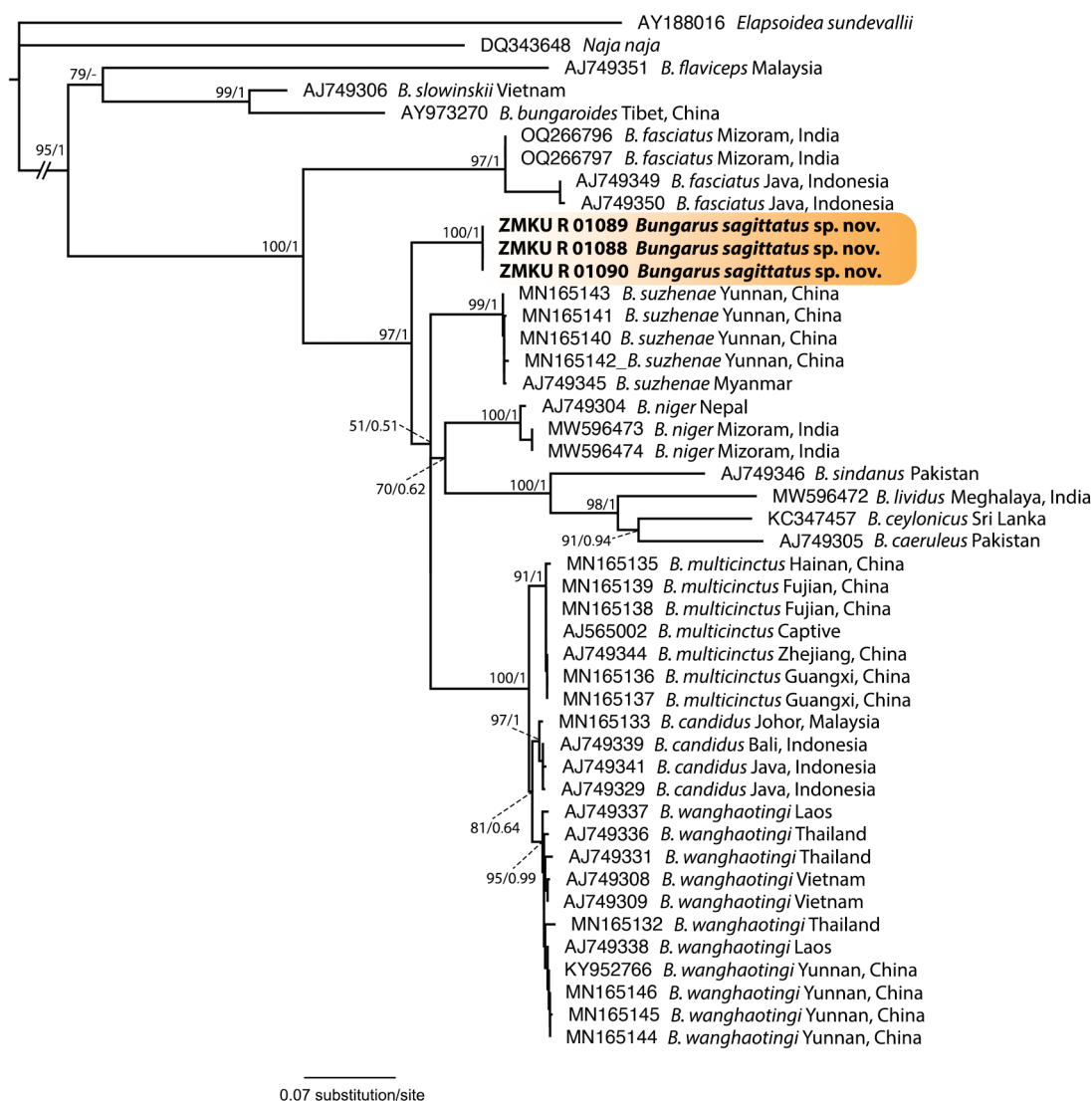


Figure 2. The best tree resulting from Maximum Likelihood analysis of 1,137 aligned characters of the mitochondrial cytochrome *b* gene of *Bungarus* species. Nodal support is indicated by Ultrafast bootstrap (UFB) values and Bayesian posterior probabilities (BPP), respectively. GenBank accession numbers and locality data for sequenced samples are provided in Suppl. material 1.

1.00 BPP) to a clade containing *B. caeruleus* (Schneider, 1801), *B. candidus/multicinctus/wanghaotingi* complex, *B. ceylonicus* Günther, 1864, *B. lividus* Cantor, 1839, *B. niger* Wall, 1908, *B. sindanus* Boulenger, 1897 and *B. suzhenae*. However, the relationships among the Indian subcontinent clade (*B. caeruleus*, *B. ceylonicus*, *B. lividus*, *B. niger* and *B. sindanus*), *B. candidus/multicinctus/wanghaotingi* complex clade and *B. suzhenae* were not resolved representing as a polytomy. Uncorrected pairwise genetic divergences (*p*-distances) among *Bungarus* species ranged from 1.77–20.46% (Suppl. material 2). The uncorrected *p*-distances between Ratchaburi population and all other *Bungarus* species ranged from 8.29–19.42%, being most similar to *B. suzhenae* and most distant to *B. bungaroides* (Cantor, 1839). The uncorrected *p*-distances within the Ratchaburi population were 0.00%.

Taxonomic hypotheses

The samples of *Bungarus* from Suan Phueng District, Ratchaburi Province, western Thailand differed from congeners in mtDNA and morphological comparisons (see below). Based on these corroborated lines of support, we hypothesize that this population represents a distinct species, which is described as a new species below.

Taxonomy

Bungarus sagittatus sp. nov.

<https://zoobank.org/F19C3493-FA00-4F4A-A9B1-4A39B5C5FF0A>

Figs 3–5

Type material. *Holotype* (Fig. 3). ZMKU R 01089, adult female collected from Thailand, Ratchaburi Province, Suan Phueng District, Suan Phueng Subdistrict, Khao Krachom (13°33'57"N, 99°11'43"E, 834 m elevation), on 15 May 2022 by Akrachai Aksornneam, Mali Naiduangchan, Kritsada Rungrot, Purinut Numuan, Suphap Sisuk and Goe Wongdee.

Paratypes (Figs 4, 5A–D). ZMKU R 01088 (subadult female) bear the same locality data as the holotype. ZMKU R 01090 (juvenile) collected from Thailand, Ratchaburi Province, Suan Phueng District, Suan Phueng Subdistrict, Khao Krachom (13°33'41"N, 99°12'18"E, 619 m elevation), on 15 June 2022, by Akrachai Aksornneam and Naka Taou.

Referred specimen (Fig. 5E, F). RIM00012 (subadult male) collected from Thailand, Ratchaburi Province, Suan Phueng District, Suan Phueng Subdistrict, Khao Krachom (13°34'53"N, 99°10'43"E, 987 m elevation), on 16 April 2021, by Parinya Pawangkhanant and Boontorn Wongdee.

Diagnosis. *Bungarus sagittatus* sp. nov. is assigned to the genus *Bungarus* by its recovered phylogenetic position and having enlarged, hexagonal-shaped, midbody vertebrae scales (Smith 1943; Slowinski 1994). This species can be distinguished from other species of *Bungarus*

by the following combination of characters: 15–15–15 dorsal scale rows; 215–217 ventral scales; 48–56 undivided subcaudal; prefrontal suture 2.4–2.6 times length of internasal suture; anterior chin shields larger than posterior chin shields; head of adult uniform black while juvenile black with small dim white patches on temporal and parietal areas; dorsal surface of body black, with 25–31 white narrow bands, white and black bands at midbody covering 1.5–3.0 and 4.5–6.0 vertebral scales, respectively; dorsal black bands of body not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales; ventral surface immaculate white; ventral side of tail white with a row of dark brown triangular patches on middle pointing posteriorly; tail relatively long, tail length/total length = 0.140–0.143.

Description of holotype. Adult female. Head length 19.9 mm, head width 16.8 mm; head height 10.7 mm, head 1.2 times longer than wide, distance between eyes 9.2 mm. Body length (SVL) 791 mm; tail incomplete, 132 mm; total length 923 mm.

Body scalation. Dorsal scales smooth, in 15–15–15 rows; vertebral scales enlarged, hexagonal, largest at midbody, wider than long. Ventrals 216, preentrals 3, anterior edge of first ventral starting at level of oral rictus. Cloacal plate undivided. Subcaudals 48 undivided, tail incomplete.

Head. Head scales smooth. Δ -shaped rostral visible from above 1.6 times wider than tall. Nasal large, divided into one irregular quadrilateral-shaped prenasal and one crescent-shaped postnasal on both side; prenasal and postnasal bordered by internasal and first supralabial; prenasal contacted with rostral; postnasal surrounded by prefrontal, preocular and second supralabial. External nares large, vertically oval-shaped, about half size of eye diameter. Preoculars 1/1 (left/right) hexagonal-shaped, bordered by orbit, supraocular, prefrontal, postnasal, second and third supralabials. Two internasals, 1.03 times wider than long, surrounded by rostral, prenasal, postnasal and prefrontal. Prefrontals large, 1.06 times wider than long, prefrontals suture length 2.6 times of internasals suture. Frontal shield-shaped, pointing backward to parietals, 1.3 times longer than wide, bordered by prefrontals, supraoculars and parietals; anterior suture of frontal pointed toward prefrontal suture. Supraocular 1/1 small, 1.6 times longer than wide, in contact with preocular, orbit, upper postocular, parietal, frontal and prefrontal. Parietals large and long, 2 times longer than wide, 1.6 times longer than frontal length; left parietal anteriorly and laterally bordered by frontal, supraocular, upper postocular, anterior temporal and upper posterior temporal; right parietal anteriorly and laterally bordered by frontal, supraocular, upper postocular, lower postocular, anterior temporal and upper posterior temporal; posterolateral margins of parietals bordered by 1/1 enlarged elongate scales that anteriorly contact upper posterior temporals; posteriormost extensions of parietals pointed, divided by one of three small dorsal scales bordering posterior end of parietals. Eyes small, oval-shaped, horizontal diameter 2.6 mm, vertical diameter 2.3 mm. Postoculars 2/2, relatively small with one-third size of

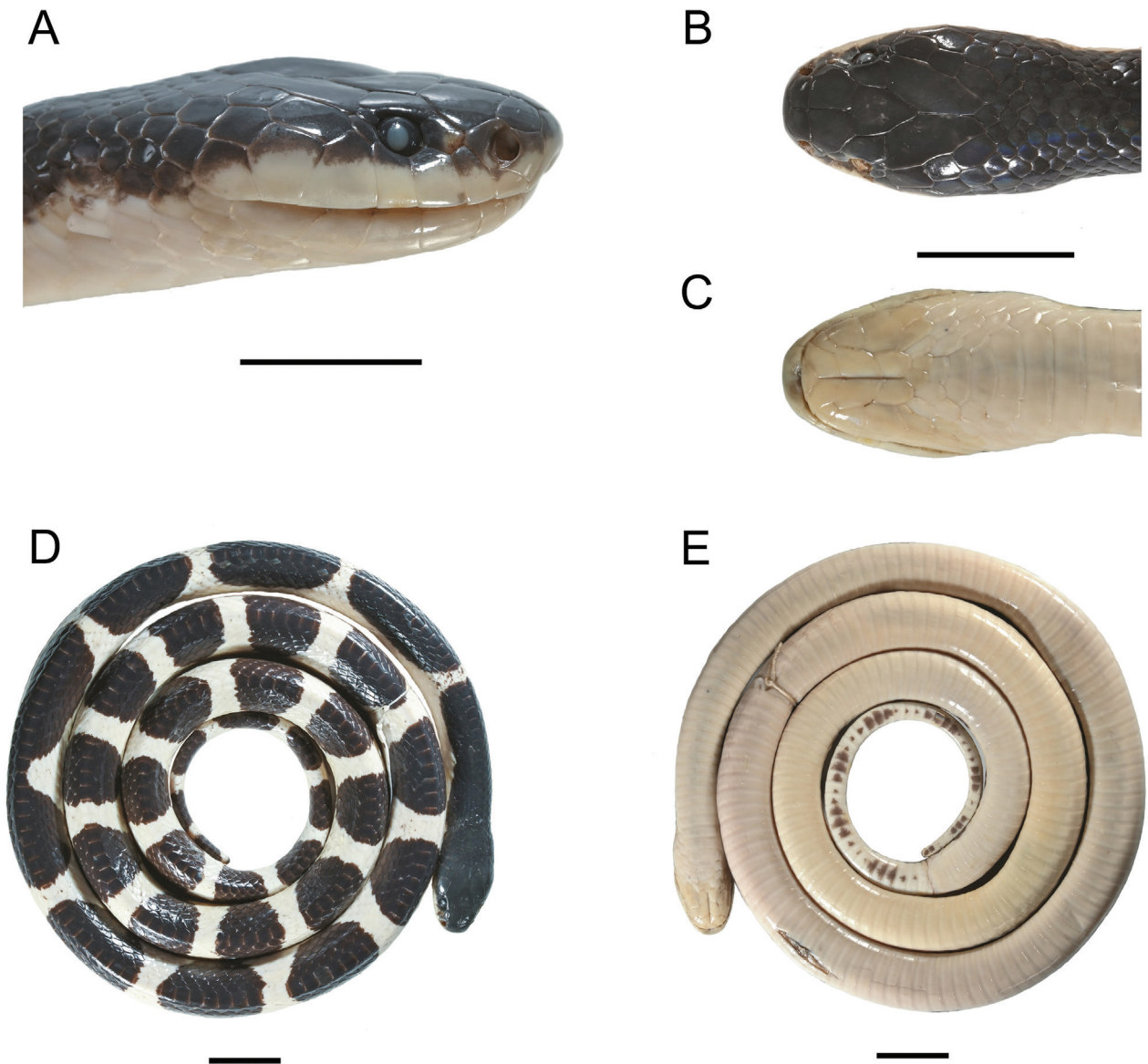


Figure 3. Holotype of *Bungarus sagittatus* sp. nov. (ZMKU R 01089) in preservation. **A.** Lateral view; **B.** Dorsal view and **C.** Ventral view; **D.** Dorsal view; **E.** Ventral view. Scale bars: 20 mm.

preoculars; on right side, lower postocular bordered by orbit, fourth and fifth supralabials, anterior temporal, parietal and upper postocular; on left side, lower postocular bordered by orbit, fourth and fifth supralabials, anterior temporal and upper postocular; on right side, upper postocular bordered by orbit, lower postocular, parietal and supraocular; on left side, upper postocular bordered by orbit, lower postocular, anterior temporal, parietal and supraocular. Anterior temporals 1/1, long and subhexagonal-shaped, 1.6 times longer than wide; right anterior temporal bordered by lower postocular, fifth and sixth supralabials, lower posterior temporal, upper posterior temporal and parietal; left anterior temporal bordered by upper postocular, lower postocular, fifth and sixth supralabials, lower posterior temporal, upper posterior temporal and parietal. Posterior temporals 2/2 surrounded by parietals, anterior temporals, sixth and seventh supralabials and dorsal scales. Supralabials 7/7, the third and fourth su-

pralabials touching lower margin of orbit; first supralabials small, subtriangular, 1.2 times wider than height; other supralabials in different pentagonal shapes; second supralabials height pentagonal-shaped, larger than the first, 1.8 times higher than wide; the third supralabial larger than first, second and fourth supralabials, 1.3 times higher than wide; fourth supralabials with 1.5 times higher than wide; fifth and sixth supralabials are two largest, both height equal to width, but fifth supralabials wider at lower part while the sixth supralabials is wider at the upper part; seventh supralabials is the third largest, 1.2 times higher than wide. Mental triangular-shaped, 1.4 times shorter than width of rostral, in contact with first infralabials, mental groove distinct. Infralabials 7/7, first infralabials pentagonal-shaped, long and narrow, 1.6 times longer than wide, in contact behind the mental and anterior chin shields; second infralabials square-shaped, one-third size of the first, 2.1 times longer than wide, in contact with anterior chin



Figure 4. Paratypes in life showing the variation in different age class. **A.** Subadult female (ZMKU R 01088); **B.** Juvenile (ZMKU R 01090).

shields; the third infralabials enlarged, in contact with anterior chin shields, 1.1 times longer than wide; the fourth is largest infralabial, pentagonal shaped, in contact with anterior and posterior chin shields, 1.2 times longer than wide; fifth infralabials in form of a square, half size of the fourth, 1.2 times longer than wide; the sixth is widest infralabial, 1.9 times wider than long; seventh infralabials is smallest, 1.4 times wider than long. Anterior chin shields larger than posterior chin shields; anterior chin shield suture 2 times the length of the posterior chin shield suture; posterior chin shields bordered by anterior chin shields, fourth infralabials, 2/2 sublabials and three gulars. Three gulars between first ventral and posteriormost extension of posterior chin shield; one gular and three preventrals between first ventral and suture of posterior chin shields.

Coloration in preservative. Dorsal surface and lateral sides of head, including upper part of supralabial, upper part of rostral uniform black; lower part of head, including portions of lower supralabials and rostral to ventral head uniform creamy white. Dorsal body black with 26 white

crossbands (the fifth band incomplete). Some white bands on the body scattered with few dark spots, most bands nearly immaculate creamy white. The white bands cover 0.5 to 2.0 times vertebral scales (average 1.5 ± 0.4 , $n = 26$; 1.5 vertebral scales at midbody), bands widening on flanks before merging with the immaculate creamy white ventral scales. The first white band starts at 16th ventral, 11 vertebral scales between first and second bands and five vertebral scales between 25th and 26th bands. A dark spot is present at the junction between white bands and ventral scales at midbody positions. Black bands on body wide, covering 6.0 vertebral scales at midbody positions, generally not intruding white ventral scales; some bands slightly intruding ventral scales less than 0.5 times width of outer lateral dorsal scales.

Dorsal surface of tail black with eight creamy white bands on dorsal part, covering 1.0–1.5 times of vertebral scales. Ventral surface of tail creamy white with a row of dark brown triangular patches pointing posteriorly at the middle of subcaudals, starting from second subcaudal to the tip of tail.

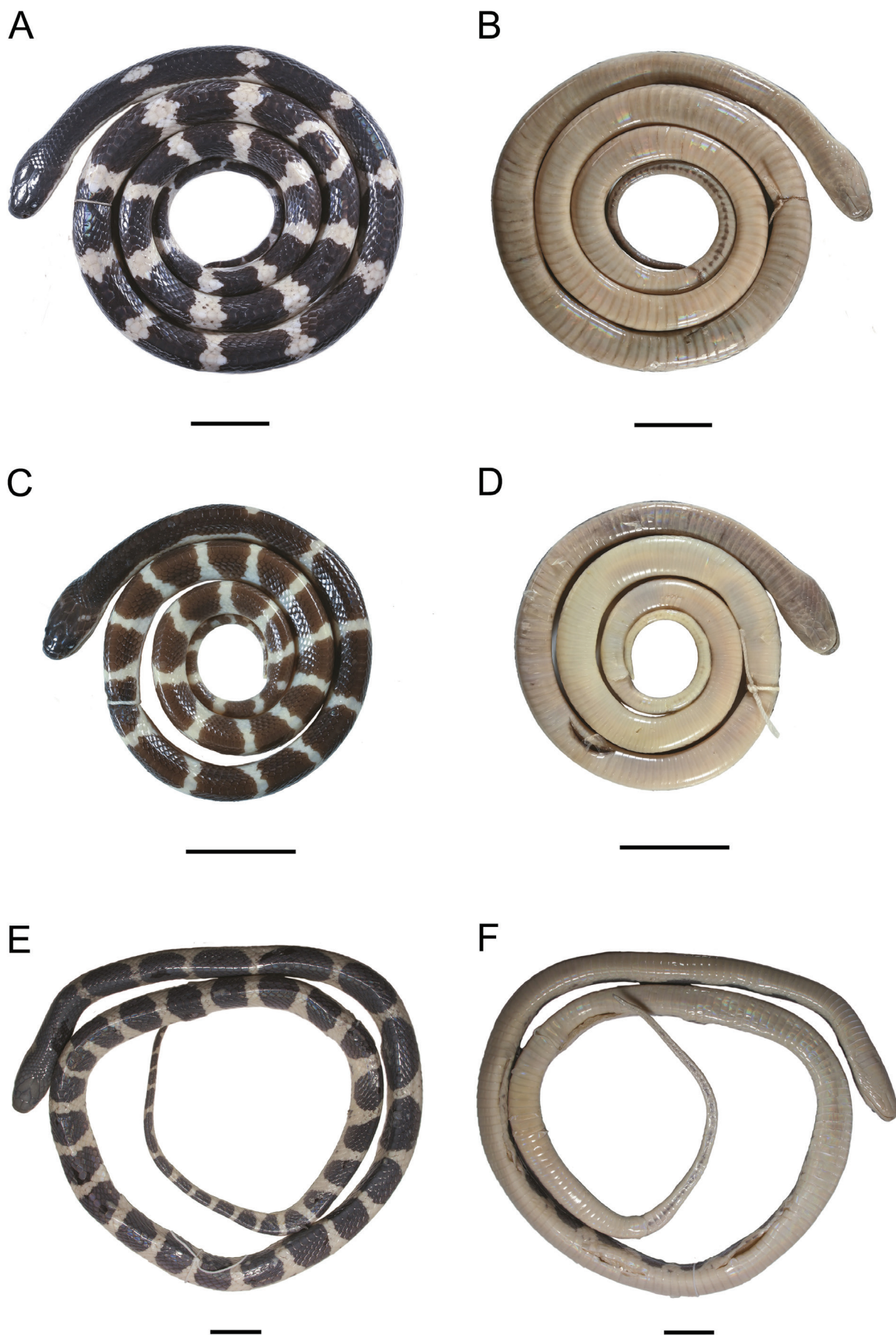


Figure 5. Paratypes and referred specimen in preservation. **A.** Dorsal and **B.** Ventral view of subadult female (ZMKU R 01088); **C.** Dorsal and **D.** Ventral view of juvenile (ZMKU R 01090); **E.** Dorsal and **F.** Ventral view of subadult male (RIM00012). Scale bars: 20 mm.

Variation. Paratypes and referred specimens closely resemble the holotype in general aspects of morphology and color pattern. First and second white bands on dorsum of ZMKU R 01090 (juvenile) are disconnected. In ZMKU R 01088 (subadult female), the first white band on dorsum is disconnected; the second and third are incompletely connected on lateral side of body. Twentieth white band on dorsum of RIM00012 (subadult male) is incomplete (present only on left side). Juvenile (ZMKU R 01090) head black with small dim white patches on temporal and parietal areas. A row of dark brown triangular patches on ventral surface of tail in juvenile is indistinct. Other variations in measurements, meristics and color pattern among the type series and referred specimen are shown in Table 1.

Etymology. The specific epithet *sagittatus* is derived from *sagittata* (L.) meaning arrow and in reference to the dark triangular shape on subcaudals which resembles a barbed arrow.

Distribution. *Bungarus sagittatus* sp. nov. is currently known from type locality: Khao Krachom, Suan Phueng District, Ratchaburi Province. The area is part of Tenasserim Mountain Range, which lies on Thai-Myanmar borderline.

Ecology. Most observations of *Bungarus sagittatus* sp. nov. occurred at night, three specimens (ZMKU R 01088, ZMKU R 01089 and RIM00012) were collected in hill evergreen forest (834 m to 987 m elevation; Fig. 6) between

2050 and 2210 h with air temperature 24.1 °C and relative humidity 91.7%. One juvenile (ZMKU R 01090) was collected in a pitfall trap at daytime in mixed deciduous forest (619 m elevation). One subadult (not collected) was found swallowing an adult scincid lizard, *Scincella reevesii* (Gray, 1839), on forest floor in hill evergreen forest (1,049 m elevation) on 6 November 2022 at 2154 h (Fig. 7).

The new species was found sympatrically with other snake species such as *Ahaetulla prasina* (Boie, 1827), *Boiga cyanea* (Duméril, Bibron & Duméril, 1854), *Coelognathus flavolineatus* (Schlegel, 1837), *Gonyosoma oxycephalum* (Boie, 1827), *Lycodon ophiophagus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009, *Ptyas carinata* (Günther, 1858), *Rhabdophis chryseus* (Schlegel, 1837), *Psammodynastes pulverulentus* (Boie, 1827), *Pareas carinatus* Wagler, 1830, *Argyrophis diardii* (Schlegel, 1839), *Naja kaouthia* Lesson, 1831, *Bungarus flaviceps*, *Ophiophagus hannah* (Cantor, 1836) and *Trimeresurus* cf. *popeiorum* Smith, 1937.

Comparison. *Bungarus sagittatus* sp. nov. is distinguished from all other *Bungarus* by a combination of morphological and color pattern characteristics (see Suppl. material 3). *Bungarus sagittatus* sp. nov. differed from *B. andamanensis* Biswas & Sanyal, 1978 by having 215–217 ventral scales (vs. 192–197); 48–56 subcaudals (vs. 45–47); TaL/TL 0.140–0.143 (vs. 0.156–0.161); 25–31

Table 1. Descriptive measurement (millimeters), meristics (left/right) and color pattern of *Bungarus sagittatus* sp. nov. Morphological abbreviations are defined in Methods.

Character	ZMKU R 01089	ZMKU R 01088	ZMKU R 01090	RIM00012
Sex	Female	Subadult female	Juvenile	Subadult male
Type	Holotype	Paratype	Paratype	Referred specimen
Measurement				
SVL	791	550	300	710
TaL	132	92	49	118
HL	19.9	15.0	10.2	17.8
HW	16.8	11.2	8.1	12.6
HH	10.7	7.0	5.5	9.0
ED	2.6	2.1	1.8	2.1
DE	9.2	6.7	4.6	7.4
IS	1.6	1.2	0.8	1.3
PS	4.1	2.9	1.9	3.2
TaL/TL	0.143	0.143	0.140	0.143
PS/IS	2.56	2.42	2.38	2.46
Meristics				
SL	7/7	7/7	7/7	7/7
IL	7/7	7/7	7/7	7/7
DSR	15/15/15	15/15/15	15/15/15	15/15/15
VS	216	215	216	217
SC	48	53	56	55
BB	26	25	25	31
TB	8	7	11	12
Color pattern				
Black bands intruding ventrals	Yes	No	No	No
Head color	Uniform black	Black with small dim white patches	Black with small dim white patches	Uniform black
Vertebral scales covered by white bands at midbody	1.5 scales	3.0 scales	1.5 scales	1.5 scales
Vertebral scales covered by black bands at midbody	6.0 scales	5.5 scales	6.0 scales	4.5 scales

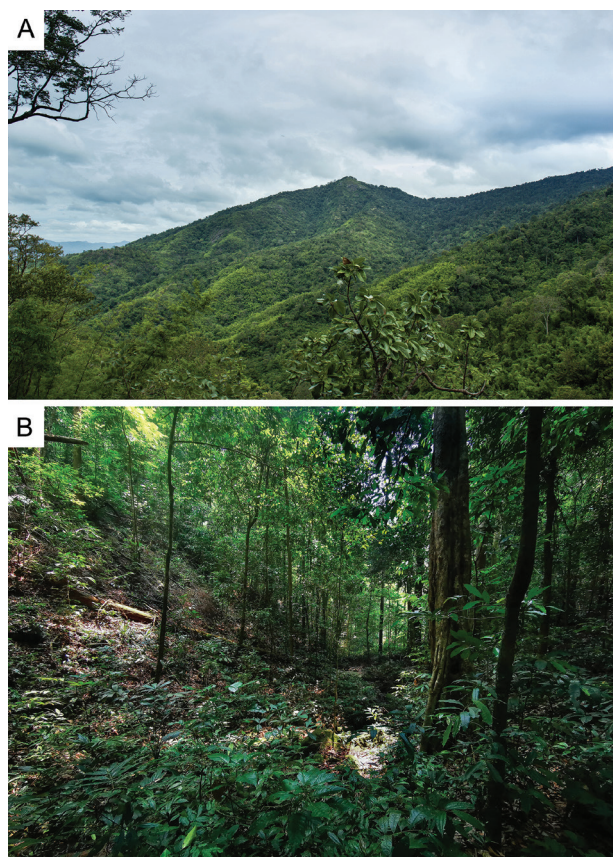


Figure 6. Habitat of *Bungarus sagittatus* sp. nov. **A.** Macrohabitat at Khao Laem Summit (1,130 m elevation), Khao Krachom, Suan Phueng District, Ratchaburi Province; **B.** Hill evergreen forest at 1,000 m elevation.



Figure 7. Feeding behavior of *Bungarus sagittatus* sp. nov. (not collected) on smooth skink (*Scincella reevesii*) from the type locality, in hill evergreen forest at 1,049 m elevation. Red arrows indicate the tail part of skink.

narrow white body bands (vs. 39–47 yellow or white bands mottled with brown); head uniform black (vs. head brown chocolate); and ventral surface of body immaculate white (vs. anterior and margin of ventral scales tinged with brown).

Bungarus sagittatus sp. nov. differed from *B. bungaroides* by having 215–217 ventral scales (vs. 220–237);

TaL/TL 0.140–0.143 (vs. 0.114–0.130); subcaudals undivided (vs. divided); dorsal body with 25–31 narrow white bands (vs. 46–60 narrow white bands consisting of small white spots); dorsal body with larger black bands covering 4.5–6.0 vertebral scales at midbody (vs. 3.0–4.5 vertebral scales); and ventral surface of body immaculate white (vs. blackish with irregular yellowish white pattern).

Bungarus sagittatus sp. nov. differed from *B. caeruleus* (Schneider, 1801) by having TaL/TL 0.140–0.143 (vs. 0.111); 25–31 narrow white body bands (vs. 29–65 white bands); and white bands not in pairs (vs. white bands in pairs).

Bungarus sagittatus sp. nov. differed from *B. candidus* by having prefrontal suture length 2.4–2.6 times of internasal suture (vs. 1.4–2.4 times); TaL/TL 0.140–0.143 (vs. 0.112–0.130); white bands on dorsal body covering 1.5–3.0 vertebral scales at midbody (vs. 3.0–5.0 vertebral scales); black bands on dorsal body covering 4.5–6.0 vertebral scales at midbody (vs. 3.0–5.0 vertebral scales); dorsal body black bands not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales (vs. 1.0–2.0 times); adult head uniform black (vs. temporal area and lateral neck stained white); juvenile head black with small dim white patches on temporal and parietal areas (vs. creamy white head); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. broad dark crossbars).

Bungarus sagittatus sp. nov. differed from *B. ceylonicus* by having 215–217 ventral scales (vs. 219–235); 48–56 subcaudals (vs. 33–40); 25–31 narrow white body bands (vs. 15–21 narrow white bands); TaL/TL 0.140–0.143 (vs. 0.087); and ventral surface of body immaculate white (vs. broad dark crossbands).

Bungarus sagittatus sp. nov. differed from *B. fasciatus* by having 48–56 subcaudals (vs. 23–39); TaL/TL 0.140–0.143 (vs. 0.074–0.096); dorsal body and tail black with narrow white bands (vs. broad yellow and black bands); ventral surface of body immaculate white (vs. yellow and black bands); dorsal body black bands not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales (vs. black bands encircling ventrals); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. yellow and black bands).

Bungarus sagittatus sp. nov. differed from *B. flaviceps* by having 15 dorsal scale rows (vs. 13 rows); dorsal body and tail black with narrow white bands (vs. body black with or without light vertebral and paraventral stripes, tail bright red); and head uniform black (vs. head red).

Bungarus sagittatus sp. nov. differed from *B. lividus* by having vertebral scales distinctly enlarged (vs. slightly enlarged on the anterior body); 48–56 subcaudals (vs. 35–43); TaL/TL 0.140–0.143 (vs. 0.118); and dorsal body black with narrow white bands (vs. black without bands).

Bungarus sagittatus sp. nov. differed from *B. magnimaculatus* Wall & Evans, 1901 by having 48–56 subcaudals (vs. 40–48); TaL/TL 0.140–0.143 (vs. 0.115);

and 25–31 narrow white body bands (vs. 11–14 broad white bands).

Bungarus sagittatus sp. nov. differed from *B. multicinctus* by having 25–31 white bands on dorsal body (vs. 31–50); black bands on dorsal body covering 4.5–6.0 vertebral scales at midbody (vs. 3.0–4.0 vertebral scales); dorsal body black bands not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales (vs. 1.2–2.0 times); ventral surface of body immaculate white (vs. white with dense brown pigments); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. dense black bands and patches).

Bungarus sagittatus sp. nov. differed from *B. niger* by having dorsal body black with mostly complete narrow white bands (vs. body bands absent); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. immaculate white).

Bungarus sagittatus sp. nov. differed from *B. percicus* Abtin, Nilson, Mobaraki, Hosseini & Dehgannejhad, 2014 by having 15 dorsal scale rows (vs. 17); 215–217 ventral scales (vs. 236–238); TaL/TL 0.140–0.143 (vs. 0.127–0.134); loreal scale absent (vs. present); and dorsal body black with mostly complete narrow white bands (vs. black with light triangular-shaped crossbars, ending in pairs of rectangular whitish dots or crossbars along the vertebral area).

Bungarus sagittatus sp. nov. differed from *B. sindanus* by having 15 dorsal scale rows (vs. 17); 215–217 ventral scales (vs. 220–237); and dorsal body black with mostly complete narrow white bands (vs. black with white bands formed by series of white spots).

Bungarus sagittatus sp. nov. differed from *B. slowinskii* by having 215–217 ventral scales (vs. 225–230); 48–56 subcaudals (vs. 33–41); TaL/TL 0.140–0.143 (vs. 0.120); subcaudals undivided (vs. divided); ventral surface of body immaculate white (vs. black bands encircling with irregular yellowish white pattern); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. black bands encircling with irregular yellowish white pattern).

Bungarus sagittatus sp. nov. differed from *B. suzhenae* by having prefrontal suture 2.4–2.6 times of internasal suture (vs. 2.7–3.4 times); 215–217 ventral scales (vs. 220–229); 25–31 narrow white body bands (vs. 26–38); head of juvenile black with small dim white patches on temporal and parietal areas (vs. uniform black head); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. immaculate white or with small brown dots).

Bungarus sagittatus sp. nov. differed from *B. walli* Wall, 1907 by having 15 dorsal scale rows (vs. 17); 215–217 ventral scales (vs. 198–207); and dorsal body black with mostly complete narrow white bands (vs. black with white bands formed by series of white spots).

Bungarus sagittatus sp. nov. differed from *B. wanghaotingi* by having TaL/TL 0.140–0.143 (vs. 0.114–0.132); dorsal body black bands not intruding ventrals or intruding ventrals less than 0.5 times of width of outer dorsal scales (vs. 0.5–1.5 times); head of juvenile black with

small dim white patches on temporal and parietal areas (vs. light brown); and ventral surface of tail creamy white with a row of dark brown triangular patches on middle (vs. a row of small light brown dots on middle).

Discussion

The combination of phylogenetic and morphological analyses revealed that the populations of *Bungarus* from Ratchaburi Province should be recognized as a distinct species, which is described here as *Bungarus sagittatus* sp. nov. Based on general morphology and color pattern, *Bungarus sagittatus* sp. nov. superficially resembles the members of the *B. candidus/multicinctus/wanghaotingi* complex, but phylogenetic analyses revealed that the new species is not closely related to those species. Moreover, the new species has high uncorrected pairwise divergences based on *cyt b* gene ($\geq 8.29\%$) from other *Bungarus* species whereas members of the *B. candidus/multicinctus/wanghaotingi* complex have uncorrected pairwise divergences of 1.6–3.3% (in Chen et al. 2021) and 1.8–3.1% (this study; Suppl. material 2).

In this study, the new species was observed preying on scincid lizard, *Scincella reevesii*, which revealed that the new species could prey on other reptiles or non-snake prey animals e.g., amphibians, rodents or birds (not strictly on snakes) as reported in other *Bungarus* species (see Knierim et al. 2017; Luu and Ha 2018; Biakzuala et al. 2019a, 2019b, 2021a; Mohalik et al. 2019; Pandey et al. 2020; Hong et al. 2021; Hruaia et al. 2023; Subba et al. 2023). The ecology and natural history of this species should be further investigated. Furthermore, the report on their venom composition is still lacking. Since kraits are recognized as highly venomous snakes, this data is needed for snake bite management and development of effective antivenom (Fry et al. 2003; Sunagar et al. 2021; Talukdar et al. 2023).

Bungarus sagittatus sp. nov. is currently known only from the lowland hill forest at 600 meters to over 1,000 meters elevation in Khao Krachom, Suan Phueng District, Ratchaburi Province, western Thailand. Additional field surveys in the Tenasserim Range including Thai-Myanmar border and examination of museum specimens are needed to investigate the geographic range of the new species. Description of *Bungarus sagittatus* sp. nov. brings the total number of *Bungarus* to 18 species (Chen et al. 2021; Uetz et al. 2023). The discovery of this new *Bungarus* species and recent studies from Tenasserim Range highlight that this area is a potential stronghold for amphibians and reptiles, and also act as an important herpetofaunal exchange (dispersal) between Indochina and Sundaland in the past (see Grismer et al. 2017, 2020a; Suwannapoom et al. 2018).

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Supplementary material 1

Samples used in the molecular analyses

Authors: Akrachai Aksornneam, Attapol Rujirawan, Yik-Hei Sung, Siriporn Yodthong, Anchalee Aowphol
 Data type: pdf
 Explanation note: Samples used in the molecular analyses, including their locality, voucher number and GenBank accession number.
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 Link: <https://doi.org/10.3897/zse.100.116601.suppl1>

Supplementary material 2

Mean (minimum-maximum) percentages of uncorrected pairwise sequence divergences (*p*-distances) of *Bungarus* species compared to *Bungarus sagittatus* sp. nov.

Authors: Akrachai Aksornneam, Attapol Rujirawan, Yik-Hei Sung, Siriporn Yodthong, Anchalee Aowphol
 Data type: pdf
 Explanation note: Mean (minimum-maximum) percentages of uncorrected pairwise sequence divergences (*p*-distances) of *Bungarus* species compared to *Bungarus sagittatus* sp. nov., based on 1,137 aligned characters of the mitochondrial cytochrome *b* gene. Intra-specific *p*-distances are in bold font. Key: NA = data unavailable or not applicable.
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 Link: <https://doi.org/10.3897/zse.100.116601.suppl2>

Supplementary material 3

Diagnostic morphological and color pattern characteristics distinguishing *Bungarus sagittatus* sp. nov. from other *Bungarus* species

Authors: Akrachai Aksornneam, Attapol Rujirawan, Yik-Hei Sung, Siriporn Yodthong, Anchalee Aowphol
 Data type: pdf
 Explanation note: Diagnostic morphological and color pattern characteristics distinguishing *Bungarus sagittatus* sp. nov. from other *Bungarus* species. Key: / = data unavailable or not applicable. Morphological abbreviations are defined in Methods.
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