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On the validity of *Hebius sauteri maximus* (Squamata, Natricidae), with redescription of *H. maximus* comb. nov. and *H. sauteri* from China

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Abstract

Hebius sauteri (Boulenger, 1909) has been long recognized as a widely distributed species with three subspecies, namely *Hebius sauteri sauteri* from Taiwan Island and southeastern China, *Hebius sauteri bourreti* (Malnate, 1962) from northern Vietnam, and *Hebius sauteri maximus* (Malnate, 1962) from Sichuan, southwestern China. However, the validity of these subspecies partition of *H. sauteri* complex has not been evaluated. In the current study, we re-evaluate the taxonomic status of *H. s. maximus* based on morphological and molecular evidence. Molecular phylogenetic results indicate that *H. s. maximus* is a distantly diverged clade with respect to *H. s. sauteri*, and *H. s. maximus* is morphologically distinguishable from the latter nominate subspecies. Therefore, we support the validity of *H. s. maximus* and elevate it to full species status, namely *Hebius maximus* **comb. nov.**, and we revise the distribution range of *H. sauteri* according to our proposed taxonomic change. Furthermore, detailed redescription, natural history, and coloration of both *H. sauteri* and *H.*

maximus and comments on the validity of *H. s. bourreti* are also provided.

Key Words

distribution, hemipenis, revision, subspecies, taxonomic confusion

Introduction

Keelback snakes of the family Natricidae Bonaparte, 1840 represent a remarkable radiation of snakes in the world, which show unique adaptation to water habitats (Narayanan et al. 2020; Peng et al. 2022). The genus *Hebius* Thompson, 1913 is the most specious group within Natricidae, of which members are widely distributed across South and East Asia, as well as Southeast Asia (Guo et al. 2014). The genus *Hebius* was previously confused with the genus *Amphiesma sensu lato* Duméril, Bibron, and Duméril, 1854 and was recently resurrected by Guo et al. (2014). Currently, the genus *Hebius* includes 47 species, of which 23 species are known from China (David et al. 2021; Hou et al. 2021; Ren et al. 2022; Uetz et al. 2022).

Hebius sauteri (Boulenger, 1909) is a small to medium size snake inhabiting moist mountains and often found near water. First described based on two specimens from Taiwan Island, southeast China, the species was subsequently reported across southern China and northern Vietnam (Boulenger 1909; Zhao 2006). Malnate (1962) divided *H. sauteri* into three subspecies according to the ventral and subcaudal scale counts, namely *H. sauteri sauteri* from Taiwan Island and southeastern mainland China, *H. sauteri bourreti* from northern Vietnam, and *H. sauteri maximus* from Sichuan, southwestern China. However, the systematic status of three subspecies in *H. sauteri* has long remained inconclusive (Zhao et al. 1998; Zhao 2006; Guo et al. 2014). Although the taxonomic treatment of Malnate (1962) have accepted by most authors (e.g., Zhao et al. 1998; Zhao 2006; Yang and Rao 2008; Nguyen et al. 2009; Xiang et al. 2009; Zhang 2009;), some studies consider *H. sauteri* is a monotpyic species (Wallach et al. 2014). To date, no study has yet examined the controversial taxonomy of the subspecies of *H. sauteri* to our best knowledge.

Based on the examination of voucher specimens in natural history collection and

77 individuals newly collected from the field, we re-evaluate the taxonomic statuses of
78 *H. s. sauteri* and *H. s. maximus* by using morphological and molecular phylogenetic
79 data, and discuss the taxonomic status of *H. s. bourreti*.
80
81 **Materials and methods**
82
83 **Sampling**
84 During field surveys conducted in the last five years, nine specimens of *H.*
85 *sauteri* were collected in Sichuan, Guizhou, Guangdong, and Fujian Provinces,
86 including one topotype of *H. s. maximus* (CIB 118635). Specimens collected in the
87 field were euthanatized and preserved in 10% formalin and then transferred to 75%
88 ethyl alcohol, all newly collected specimens were deposited in the Herpetological
89 Museum, Chengdu Institute of Biology (CIB), Chinese Academy of Sciences,
90 Chengdu, China, and the Museum of Biology, School of Life Sciences, Sun Yat-Sen
91 University (SYS), Guangzhou, China. Other specimens or tissue samples used in this
92 study were obtained from institution collections (see collection abbreviations).
93
94 **Morphological analysis**
95 A total of 44 specimens of *H. sauteri* were examined in this study. The
96 description and measurement of morphological characters were according to Zhao
97 (2006) and Ren (2019). A tape measure with 1 mm accuracy was used to measure the
98 total length (ToL) and tail length (TL) of the specimen. The head length (HL) and
99 head wide (HW) were taken with a slide-caliper with a minimum accuracy of 0.01
100 mm. Other pholidosis counts were also examined for comparison, including the
101 number of internasal (IN), prefrontal (PrF), loreal (L), frontal (F), parietal (P),
102 preocular (PrO), postocular (PtO), supraocular (SpO), supralabial (SpL), infralabial
103 (IfL), temporal (TEM), chin-shield (CS), dorsal scale rows (DSR), ventral (V),
104 subcaudal (SC). Additionally, number and shape of maxillary teeth (MT) and keel
105 status at dorsal scale rows (KDSR) were also described.
106 The hemipenes of one adult male specimen of *H. s. maximus* (CIB 118635,

topotype) and one adult male specimen of *H. s. sauteri* (SYS r000323) were everted from the left side and used for hemipenial description, the preparation method of hemipenis eversion followed Jiang (2010). The description of hemipenial characters followed Zhang *et al*. (1984). Everted hemipenis was re-inflated with colored petroleum jelly. We photographed the hemipenis using a digital camera attached to a tripod head and performed the combination and montage of multifocal photographs using the Helicon Focus (7.0.2 Pro) software.

The following measurements were also used for hemipenial description: hemipenial total length (HTL): distance from the bottom of the truncus to the tip of the most distant point in the vertical direction; hemipenial truncus length (HCL): distance from the bottom of the truncus to the tip of crotch in the vertical direction; hemipenial total width (HTW): the widest distance of the hemipenis in the horizontal direction. The following ratios were also obtained from raw measurements, including HTL/HTW, HCL/HTL.

Additional morphological data were also obtained from published literature (Malnate 1962; Zhao et al. 1998; Zhao 2006; Yang et al. 2008).

Molecular analysis

Sequences of 39 specimens of 20 species were obtained from GenBank (Table 1). Liver or muscle tissue of new specimens collected from fieldwork was preserved in 95% ethyl alcohol. Genomic DNA was extracted using a commercially-available DNA extraction kit (Sangon Biotech Co., Ltd.).

A single mitochondrial gene (mitochondrial cytochrome b, Cyt *b*) and three nuclear genes (oocyte maturation factor mos, *C-mos*; recombination-activating gene 1, *Rag1*; neurotrophin 3, *NT3*) were amplified by polymerase chain reaction (PCR), primers used in amplification followed are listed in Table 2. PCR cycling and running program of Cyt *b* is performed as a denaturing step at 94°C for 7 min; followed by 40 cycles of 94°C for 40 s, 46°C for 30 s, and 72°C for 1 min; and a final extension step at 72°C for 8 min. The cycling and running program for *C-mos*, *Rag1*, and *NT3* amplification followed Kelly (2011) and Kaito and Toda (2016). PCR products were

purified and then sequenced in both directions by Sangon Biotech Co., Ltd. (Shanghai, China). Sequences alignment and calculation of the uncorrected pairwise distance (*p*-distance) were conducted by using MEGA X (Kumar et al., 2018). Four gene sequences were concatenated in PhyloSuite v1.2.2 (Zhang et al. 2020).

The best model of sequence evolution for Maximum Likelihood (ML) and Bayesian inference (BI) analysis were selected using PartitionFinder v2.1.1 (Lanfear et al. 2016). The best evolution model for concatenated sequences is TIM+I+G for *Rag 1*, *C-mos*, *NT3,* and GTR+I+G for Cyt *b*. MrBayes ver. 3.2.6 (Stamatakis 2014) was used for the BI analyses, searches were conducted with three independent runs, each run started with a random tree, set as four Markov chain Monte Carlo (MCMC) iterated for 10 million generations and sampled every 100 generations. The first 25% of all searched trees were discarded as burn-in. Bayesian posterior probability (BPP) ≥ 95% is regarded as strongly supported. RAxML ver. 8.2.1 (Ronquist and Huelsenbeck 2003) was used to search for the best maximum likelihood tree with 1000 bootstraps. *Herpetoreas tpser* is chosen as the outgroup.

Collection abbreviations

BMNH: The Natural History Museum [formerly British Museum (Natural History)], London, England, UK; **CIB:** Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China; **CAS:** California Academy of Science, San Francisco, USA; **FMNH:** Division of Amphibians and Reptiles, Field Museum of Natural History, Chicago, Illinois, USA; **SYS:** The Museum of Biology, School of Life Sciences, Sun Yat-Sen University, Guangzhou, China; **USNM:** National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, District of Columbia, USA; **YBU:** Yibin University, Yibin, China.

Results

Phylogeny

Aligned sequences concatenation is 3,087 bp in length (Cyt *b* = 1070 bp; *C-mos* = 587 bp; *NT3* = 476 bp; *Rag1* = 954 bp). The topological structure of the phylogenetic tree (Figure 1) was largely consistent with previous studies (Guo et al. 2014; Liu et al. 2018; Zhou et al. 2019). Although higher relationships of *Hebius* congeners were remained to be not fully resolved, the phylogenetic relationships of our targeted species were strongly supported. In both BI and ML phylogenetic trees, *H. s. maximus* and *H. s. sauteri* formed two well-supported (BS = 100, BPP = 1.00) clades, and the two subspecies were paraphyletic with respect to recognized species (including *H. vibakari*, *H. sangzhiensis*, *H. ishigakiensis*, and *H. pryeri*, and *H. concelarus*; Figure 1).

The uncorrected pairwise distance of Cyt *b* sequences between *H. s. maximus* and *H. s. sauteri* varied from 12.05 to 12.65% (Table 3), which is higher than the overall mean distance of selected taxa apart from *Hebius* clade (12.1%) (Ren et al. 2018).

Morphology

Specimens of *H. s. maximus* from Sichuan and Guizhou Provinces in southwestern China largely agree with the original description of *H. s. maximus* as follows (data from original description in parenthesis): ventrals 132–143 (vs. 137–141); SpL 7–8 (vs. 7); IfL 7–9 on both sides of the head, IfL 1–3, 1–4, or 1–5 border the anterior chin-shields (vs. IfL 8/9, IfL 1–4 in contact with the anterior chin-shields); preocular 2 in two specimens (on both sides in CIB 8484, on the right side only in CIB 8467) (vs. 1); postocular 2–3 (vs. 2); anterior temporals 1–2 (vs. 2) (Malnate 1962). Thus, we confirm the identity of the sampled population as the true subspecies *H. s. maximus* in this study.

Although superficially similar to *H. s. sauteri*, *H. s. maximus* could be distinguished with *H. s. sauteri* by having a higher number of ventrals (132–138 in male, 135–143 in female in *H. s. maximus* vs. 125–130 in male, 116–133 in female in

H. s. sauteri), a higher number of ventrals + subcaudals (207–225 in *H. s. maximus* vs. 187–212 in *H. s. sauteri*), and a different coloration of infralabials (white with black edge on the posterior part of 1st–3rd IfL in *H. s. maximus* vs. white with black edge between each IfL in *H. s. sauteri*) (Table 4; Table 5; Figure 3).

Consequently, all available data support the recognization of *H. s. maximus* as a distinct species rather than a subspecies of *H. sauteri*. Herein, we elevate the subspecies *H. s. maximus* to a full species status, i.e., *Hebius maximus* (Malnate 1962) **comb. nov**. Furthermore, based on historical collections and newly collected specimens, we provide the expanded morphological description of both *H. s. sauteri* and *H. maximus*.

Taxonomic accounts

Hebius sauteri (Boulenger, 1909)

Figures 2–6

Tropidonotus sauteri G. A. Boulenger 1909, Ann. Mag. Nat. Hist., London. ser.8, 4, 495. Type locality: Kosempo (= Chiahsien, Kaohsiung County), Taiwan, China.

Natrix sauteri — Mell 1931 [1929]: 204; Moichiro 1931: 30; Bourret 1934a: 4; Bourret 1935: 2; Pope 1935: 125 (in part); Smith 1943: 287.

Amphiesma sauteri — Malnate 1960: 51; Zhao and Adler 1993: 228 (in part); Xie et al. 1998: 82; Zhao et al. 1998: 80 (in part); Orlov et al. 2000: 72; David et al. 2007: 60 (in part); Nguyen et al. 2009: 357; Xiang et al. 2012: 230; Wallach et al. 2014: 33 (in part).

Amphiema sauteri sauteri — Malnate 1962: 272.

Amphiema sauteri bourreti — Malnate 1962: 273.

Natrix copei Van Denburgh 1909, Proc. California Acad. Sci. 3(3): 52–53. Type locality: “Kanshirei, Formosa” (= Guanziling, Tainan County, Taiwan, China)

Natrix copei — Van Denburgh 1909: 52.

Types. Syntypes. BMNH 1946.1.13.38–39, a male and female.

Referred specimens. 19 specimens of *H. s. sauteri* were referred in this study: CHINA (*n* = 19) – **Taiwan.** CAS 18984, Pingtung County; CAS 18988 (paratype of *Natrix copei* Van Denburgh, 1909), Tainan City, Guanziling. – **Fujian Prov.** CIB 8476–8479, CIB 78046, Dehua County, Daiyun; CIB 118517, Dehua County, Xinyong Village; CIB 8480, Wuyishan City, Xing Village. – **Anhui Prov.** CIB 8483, Huangshan City. Jiangxi. SYS r000323, Jinggangshan City, Mt. Jinggang; SYS r001258, SYS r001266, Longnan County, Jiulianshan. – **Hainan Prov.** YBU 17001, Ledong Li Autonomous County, Jianfengling; CIB 8481. Guangdong. SYS r001150, Xinyi City, Sihe Township; CIB 118516, Dongguan City, Yinpingshan. – **Guizhou Prov.** SYS r000275, Libo County, Maolan National Natural Reserve. – **Hunan Prov.** SYS r001766, Guidong County, Bamianshan.

Diagnosis. *Hebius sauteri* can be distinguished from its congeners by the following features: (1) body size small to medium, maximum ToL 455 mm; (2) dorsal scales rows 17-17-17, all weekly keeled or smooth at outmost one or two rows; (3) ventral scales 116–133, subcaudals 69–86, paired; (4) maxillary teeth 23–27, last two or three distinctly enlarged teeth, without diastema; (5) preocular single, occasionally two; (6) supralabials 6–8, 2nd or 2nd–3rd touches the loreal; (7) infralabials 6–9, mostly edged with black at their posterior border; (8) single white to orange stripe extended from *angulus oris* to neck; (9) dorsal body brown to reddish brown, with or without single series of white spots or short band on lateral.

Description. Head moderately distinct from neck; body size small to medium, ToL 145–455 mm (282–370 mm in male, 145–455 mm in female), TL/ToL 0.24–0.33 (0.27–0.31 in male, 0.24–0.33 in female). Eye relatively large, pupil round.

Dentition. Maxillary teeth 23–27 without diastema, gradually enlarged posteriorly, last 2 or 3 distinctly enlarged.

Body scalation. Body scale in 17-17-17 rows, weekly keeled except outer 1–4 rows smooth anteriorly, outer 0–2 rows smooth at midbody and outer 0–1 row smooth posteriorly; ventrals 116–133 (125–130 in male, 116–133 in female); subcaudals 69–86 (69–86 in female, 74–84 in male), paired.

Head scalation. Rostral broad, visible from above; internasal paired, nearly triangular, curved outwards, not in contact with loreal; prefrontals paired, nearly rhombus, broader than long, border on loreal laterally, preocular and supraocular posteriorly; frontal hexagon, longer than wide, embedded into parietal posteriorly; parietal paired, much longer than width; nasal wider than high, divided below nostril, borders 1st–2nd supralabials; loreal single, rarely divided (right side of CIB 8481), borders 2nd or 2nd–3rd supralabials, not entering orbit; preocular 1–2; supraocular single, narrowed anteriorly, much wider than high, not in contact with parietal; postoculars 2–3, rarely 4 (left side of CIB 8483); supralabials 6–8, 5th, 6th or 7th highest, 3rd –4th entering orbit, rarely 2nd–3rd (right side of CIB 8480), 3rd only (both sides of CIB 8479) or 4th–5th (left side of CIB 8477); infralabials 6–9, first pair contact behind the mental, IfL 1–3, 1–4 or 1–5 border the anterior chin shields; temporals variable, two to three rows, 1–2 + 1–3 + 0/2–3; chin shields paired, posterior pair longer (Figure 3, 5; Table 4).

Hemipenis. The description of hemipenis based on an adult male specimen (SYS r000323) from Mt. Jinggang, Jiangxi, southeastern China. Left side of hemipenis fully everted, right side remained *in situ* for description of retracted condition.

The everted hemipenis thin and short, Y-shaped, shallowly bilobed. Both sulcate and asulcate surfaces densely ornamented with spinules, a large basal hook present at proximal part. *Sulcus spermaticus* single, extending to base of inner right lobe where it takes a centripetal position. Sulcus lip highly developed and raised, walls covered with spinules (Figure 6).

In situ the hemipenis extends to 7th SC with its crotch extending to 6th SC; the fork point of *m. retractor penis magnus* extending to 8th SC, origin of *m. retractor penis magnus* at the level of 20th SC.

Coloration in life. Based on two adult female specimens from Guangdong (CIB 118516) and Fujian (CIB 118517), China. Dorsal of the head reddish brown with irregular greyish green spots, a pair of elliptic orangish spots symmetrically present on inner sides of corresponding scales, just separated by parietal sutures; ventral of the head whitish; 1st–5th supralabials white with black edges posteriorly, 6th or 6–7th

brown at upper part; infralabials white with black edge between each scale; an orange stripe extended from *angulus oris* to dorsal side of the neck, 1–2 scales wide; dorsal body and tail dark brown to reddish brown, with or without an ill-defined dark olive streak scattered with black spots extended from neck to the end at medium, an reddish brown lateral streak on 4th–6th body scale rows extended from neck to tail with series of orange spots separated by 2–3 scales above; ventral and subcaudal cream white, with black spots on both ends of the ventral scale forms a chain-like pattern on the ventral view; sclera brown (Figure 4).

Coloration in preservation. Largely the same as in life except dorsal side of the head brown to dark brown, scattered with small black spots; ventral of the head cream white; a yellowish white stripe extended from *angulus oris* to dorsal side of the neck, 1–2 scales wide; dorsal of the body and tail brown to dark brown, a lighter lateral streak on 4^{th}–6^{th} body scale rows presents or not, covered with series of cream white spots separated by 2–3 scales; ventral and subcaudal cream to pale white, with black spots on both ends of the ventral scale forms a chain-like pattern on the ventral view; sclera black with round pupil (Figure 3, 5).

Sex dimorphism. TL/ToL 0.27–0.31 (0.30 ± 0.02) in male, 0.24–0.33 (0.28 ± 0.02) in female; ventral scales 125–130 (128 ± 2) in male, 116–133 (129 ± 4) in female; subcaudal scales 74–84 (78 ± 4) in male, 69–86 (74 ± 5) in female (n = 5 male and 15 female) (Table 4, 5).

Extended comparison. *Hebius sauteri* can be distinguished from *H. maximus* **comb. nov.** by (1) ventrals 125–130 in male, 116–133 in female vs. 132–138 in male, 135–143 in female; (2) ventrals + subcaudals 187–215 vs. 207–225; (3) maxillary teeth 23–27 vs. 24; (4) infralabials white with black edge between each scale vs. edged with black at the posterior border on 1^{st}–3^{rd} scales only (Figure 3; Table 4, 5).

Etymology. *Hebius sauteri* was named after the collector of the type specimen, Hans Sauter (Boulenger 1909). We suggest the Chinese common name of this species remain to be unchanged, as “Zōng Hēi Fù Liàn Shé (棕黑腹链蛇)”.

Natural history. This species inhabits flatlands and mountain region up to 1500 m and prefer terrestrial microhabitat such as grassland, woodland, and bushes near

water body; diurnal, occasionally found at night, preys include earthworms, slugs, snails, and tadpoles; oviparous (this study; Xiang et al. 2009; Zhao 2006; Pope 1935).

Distribution. *Hebius sauteri* is currently known distributed in Vietnam (Ngan Son, Lang Son, Tam Dao and Ba Vi), northern Laos, and China, including Taiwan (type locality), Fujian (Dehua County), Anhui (Huangshan County), Jiangxi (Jinggangshan County, Longnan County), Hunan (Yizhang County), Guangdong (Lianping County, Xinyi County, Deqing County, Ruyuan County, Dongguan City), Guangxi (Jinxiu County, Quanzhou County, Rongxian County, Beiliu County, Long'an County), Guizhou (Libo County, Leishan County), Yunnan (Jinping County), Hainan (Qiongzhong County, Wuzhishan County, Baisha County, Lingshui County) (Deuve 1970; Wu 1984; Shen 2002; Zhao 2006; Yang et al. 2008; Nguyen et al. 2009; Zhang 2009; Li 2011; this study) (Figure 2).

Remarks. *Natrix copei* (Van Denburgh, 1909) is described by Van Denburgh (1909) based on specimens form "Kanshirei" (now Guanziling), Tainan County, Taiwan Province, China, this name was published just 20 days later than the description of *Tropidonotus sauteri* by Boulenger (1909) (now *Hebius sauteri*) (Stejneger 1910), Stejneger (1910) considered *Natrix copei* as a synonym of *Natrix sauteri* (now *Hebius sauteri*), our research examined the paratype of *Natrix copei* and its morphological features is in the range of *H.sauteri* which also supports the treatment of *Natrix copei* by Stejneger (1910). The taxonomic status of its subspecies *H. s. bourreti* see discussion.

Hebius maximus **(Malnate, 1962) comb. nov.**

Figures 2, 7–11

Amphiesma sauteri maximus Malnate 1962, Proc. Acad. Nat. Sci. Philadelphia, 114, 251–299. Type locality: "Hsaioyangchi, Szechwan, China." (= Xiaoyangxi, Mabian County, Leshan City, Sichuan Province, China)

Natrix sauteri — Pope 1935: 125 (in part); Wu 1985: 209 (in part).

343 *Amphiesma sauteri maximus* — Malnate 1962: 272.

344 *Amphiesma sauteri* — Inger et al. 1990: 20; Zhao and Adler 1993: 228 (in part);
345 Zhao et al. 1998: 80 (in part); Zhao 2003: 140; David et al. 2007: 60 (in part); Wallach
346 et al. 2014: 33 (in part).

347 *Hebius sauteri* — Guo et al. 2014: 428 (in part); David et al. 2021 (in part).

348 **Types.** Holotype. FMNH 18796 (formerly CHNM 18796), a 457 mm adult
349 female specimen (Figure 7). Paratypes. FMNH 18797, USNM 71570, USNM 84362.

350 **Referred specimens.** 25 specimens of *H. maximus* were referred in this study:
351 CHINA (*n* = 25) – **Sichuan Prov.** CIB 118635, Pingshan county, Mt. Laojun
352 (topotype); CIB 8451–8452, CIB 8455, CIB 8464, CIB 8467, CIB 8470–8471,
353 Emeishan City, Mt. Emei; CIB 8458, Yingjing County; CIB 8457, Hongya County;
354 CIB 118518, CIB 107645–646, CIB 107649, Dayi County; YBU 18170, Dujiangyan
355 County; CIB 94215–94216, Anzhou District. – **Chongqing.** CIB 8448, Youyang Tujia
356 & Miao Autonomous County; YBU 11258, Xiushan Tujia & Miao Autonomous
357 County. – **Guizhou Prov.** CIB 8482, SYS r002041, CIB 8484, CIB 118072–118074,
358 Qixingguan District.

359 **Diagnosis.** *Hebius maximus* **comb. nov.** can be distinguished from its congeners
360 by the following morphological characters: (1) body size small to medium, maximum
361 ToL 597 mm; (2) dorsal scales rows 17-17-17, all weekly keeled or smooth at outmost
362 one or two rows; (3) ventral scales 132–143, cloacal plate divided, subcaudal 64–92,
363 paired; (4) maxillary teeth 24, last two distinctly enlarged, without diastema; (5)
364 supralabials 7–8; (6) infralabials 7–9, generally edged with black at posterior border
365 on 1st–3rd scales only; (7) a light orange stripe extended from *angulus oris* to the neck;
366 (8) dorsal body reddish brown or greyish brown, with an ill-defined dark olive streak
367 scattered with black spots extended from neck to end at medium of the dorsal.

368 **Description.** Body elongated, small to medium, ToL 175–597 mm (260–470 mm
369 in male, 175–597 mm in female); tail relatively long, TL/ToL 0.25–0.33 (0.25–0.33 in
370 male, 0.25–0.31 in female). Eye relatively large, pupil round.

371 *Dentition.* Maxillary teeth 24, without diastema, gradually enlarged posteriorly,
372 last two distinctly enlarged.

373 *Body scalation.* Dorsal scales in 17-17-17 rows, weekly keeled except outer 1–4
374 rows at the anterior body, outer 0–2 rows smooth at midbody and outer 0–1 row
375 smooth posteriorly; ventrals 132–143 (132–138 in male, 135–143 in female); cloacal
376 divided; subcaudal 64–92 (64–82 in female, 72–92 in male), paired.
377 *Head scalation.* Rostral broad, visible from above; internasal paired, nearly
378 triangular, curved outwards, not border on loreal; prefrontals paired, nearly rhombus,
379 broader than long, border on loreal, preocular, and supraocular; frontal hexagon,
380 longer than wide, embedded into parietal posteriorly; parietal paired, not borders
381 preocular; nasal wider than high, divided at lower half, borders 1st–2nd supralabials;
382 loreal single, borders 2nd or 2nd–3rd supralabials, not entering orbit; preocular single,
383 higher than wide, rarely divided (CIB 8484, CIB 8467, SYS r002041); supraocular
384 single, narrowed anteriorly, much wider than high; postoculars 2–3; supralabials 7–8,
385 6th or 7th highest, 3rd–4th or 4th–5th entering orbit; infralabials 7–9, first pair contact
386 behind the mental, IfL 1–3, 1–4 or 1–5 border the anterior chin shields; temporals 1–2
387 + 1–3 + 0/2–4; chin shields paired, posterior pair longer (Figure 3, 8; Table 4).
388 *Hemipenis.* The description of hemipenis based on an adult male specimen (CIB
389 118635, topotype) from Yibin, Sichuan, southwestern China. The left side of
390 hemipenis fully everted, whereas the right side remained *in situ* for description of
391 retracted condition.
392 Hemipenis thin and short, hemipenial total length (HTL) 7.14 mm, hemipenial
393 total width (HTW) 1.57 mm. HTL/HTW 4.55; Y-shaped, shallowly bilobed,
394 hemipenial truncus length (HCL): 5.75 mm, HCL/HTL 0.81. Both sulcate and
395 asulcate surfaces densely ornamented with spinules, a large basal hook present at the
396 proximal part. *Sulcus spermaticus* single, extending to base of the inner right lobe
397 where it takes a centripetal position. Sulcus lip highly developed and raised, walls
398 covered with spinules (Figure 9).
399 *In situ* hemipenis extends up to 5th SC with its crotch extending to 4th SC; fork
400 point of *m. retractor penis magnus* extending to 6th SC, origin of *m. retractor penis*
401 *magnus* invariably at level of 20th SC.
402 **Coloration in life.** Based on one male adult specimen (CIB 118635, topotype).

Dorsal side of the head reddish brown with irregular dark and olive spots above; ventral of head cream white; 1st–6th supralabials whitish with dark edge on posterior part; 7th supralabial reddish brown at the upper part and white with dark edge at the lower part, 8th supralabial cream white, gradually turning to orange posteriorly; infralabials white, edged with black at the posterior border on 1st–3rd scales only; an orange stripe extended from *angulus oris* to dorsal of the neck, two scales wide; dorsal body and tail reddish brown with an ill-defined dark olive dorsal streak scattered with black spots extended from the neck to tail, lateral with a series of orange spots separated by 2–3 scales on 4th–5th body scale rows, gradually faded posteriorly; ventral and subcaudal cream white with black spots on outer edge of each scale; sclera yellow with black round pupil (Figure 8B).

Coloration in preservation. Largely the same as in life except dorsal head brown to seal brown, with or without irregular dark spots; supralabials cream white to greyish white, 1st–6th supralabials have black edge or spots posteriorly, the upper half of the highest supralabial brown to black; a pale orange to yellow short stripe extended from *angulus oris* to neck; infralabials white with black edges posteriorly, usually on 1st–3rd scales; dorsal of the body and tail brown to seal brown, slightly darker posteriorly, with or without a series of white spots or short band separated by 2–3 scales on 4–6 body scale rows; ventral and subcaudal cream white to greyish white; sclera black (Figure 9).

Sex dimorphism. Male *H. maximus* **comb. nov.** exhibits longer tail length [TL/ToL 0.25–0.33 (0.29 ± 0.02) in male vs. 0.24–0.31 (0.27 ± 0.02) in female], lower count of ventral scales [132–138 (136 ± 2) in male vs. 135–143 (138 ± 3) in female] and higher count of subcaudal scale counts [72–92 (81 ± 6) in male vs. 64–73 (72 ± 5) in female] than female (n = 13 male and 12 female) (Table 4, 5).

Comparison. *Hebius maximus* **comb. nov.** differs from *H. andreae*, *H. annamensis*, *H. arquus*, *H. beddomei*, *H. bitaeniatus*, *H. boulengeri*, *H. celebicus*, *H. clerki*, *H. concelarus*, *H. craspedogaster*, *H. deschauenseei*, *H. flavifrons*, *H. groundwateri*, *H. igneus*, *H. inas*, *H. ishigakiensis*, *H. johannis*, *H. kerinciensis*, *H.*

khasiensis, *H. lacrima*, *H. leucomystax*, *H. metusia*, *H. miyajimae*, *H. modestus*, *H. monticola*, *H. nicobariensis*, *H. octolineatus*, *H. optatus*, *H. parallelus*, *H. petersii*, *H. popei*, *H. pryeri*, *H. sangzhiensis*, *H. sanguineus*, *H. sarasinorum*, *H. septemlineatus*, *H. vibakari*, H. *viperinus*, *H. weixiensis*, *H. xenura* and *H. yanbianensis* by having 17-17-17 dorsal scale rows.

Hebius maximus **comb. nov.** differs from *H. chapaensis*, *H. frenatus*, *H. nigriventer*, *H. sarawacensis* and *H. taronensis* by (1) maxillary teeth 24 vs. 29–34 in *H. chapaensis*, 28–33 in *H. nigriventer*, 28–32 in *H. taronensis*; (2) ventrals 132–143 vs. 159–177 in *H. chapaensis*, 164–166 in *H. frenatus*, 155–168 in *H. nigriventer*, 145–150 in *H. sarawacensis*, 158–176 in *H. taronensis* (David et al. 2021; Malkmus et al. 2002; Peters 1871).

Hebius maximus **comb. nov.** differs from *H. atemporalis* in having (1) temporals present, supralabial not in contact with parietal vs. usually absent or a small triangular temporal between postocular and supralabial, supralabial in contact with parietal; (2) maxillary teeth 24 vs. 27–32 (Bourret 1934b; Zhao et al. 1998; Table 4).

Lastly, *H. maximus* **comb. nov.** was previously confused with *H. sauteri*, *H. maximus* differs from the latter species in having (1) more ventrals 132–138 in male, 135–143 in female vs. 125–130 in male, 116–133 in female; (2) more ventrals + subcaudals counts, 207–225 vs. 187–215 (3) fewer maxillary teeth 24 vs. 23–27 (Zhao et al. 1998; this study); (4) infralabials white edged with black at the posterior border on 1st–3rd scales only vs. white with black edge between each scale (Figure 3; Table 4, 5).

Etymology. *Hebius maximus* **comb. nov.** is named after its highest count of ventral scales among three previous subspecies of *H. sauteri* (Malnate 1962). Since *Hebius maximus* **comb. nov.** is mainly distributed in southwestern China (Sichuan, Chongqing, and Guizhou), we suggest its common name as “Western China Keelback” in English and “Huá Xī Fù Liàn Shé (华西腹链蛇)” in Chinese.

Natural history. *Hebius maximus* **comb. nov.** inhabits subtropical mountain regions around 812–1200 m above sea level, including coniferous forest and large forest clearings, one topotype (CIB 118635) was found on a road near a stream at

dusk, emerging from a cornfield (Inger et al. 1990; This study); the species is diurnal and is active at dusk, it has been reported to prey on earthworms, slugs, and tadpoles (Wu et al. 1985; Zhao 2006); oviparous, Pope (1935) reported five well-developed eggs inside with very small embryos in one specimen (USNM 84362) from Chouchiakou (= Zhoujiakou), Suchow (= Yibin City), Sichuan, China, Inger *et al*. (1990) reported two females collected from Washan, Sichuan had one enlarged egg in each ovary; the specimens of *H. maximus* **comb. nov.** we collected exhibit no tendency to bite when handled; *Hebius maximus* **comb. nov.** is found sympatric with *Cyclophiops major*, *Achalinus spinalis*, *Protobothrops mucrosquamatus*, *Lycodon ruhstrati*, *Rhabdophis tigrinus*, *Sphenomorphus indicus*, *Rana omeimontis*, *Odorrana graminea* and *Bufo gargarizans* in field observations during fieldwork conducted in August 2021 (Figure 11).

Distribution. *Hebius maximus* **comb. nov.** is currently known distributed in southwestern China, including Chongqing (Youyang Tujia & Miao Autonomous County, Xiushan Tujia & Miao Autonomous County), Sichuan (Mabian County, Pingshan County, Yingjing County, Hongya County, Dujiangyan County, Anzhou District, Mt. Emei) and Guizhou (Qixingguan District) (this study; Wu 1984) (Figure 2).

Discussion

Taxonomic revision of *Hebius maximus* and *Hebius sauteri*

The Asian keelback snakes, genus *Hebius*, had long been considered difficult to identify due to the morphological resemblance among species, and *H. maximus* and *H. sauteri* were previously confused in the past six decades (Malnate 1962). Combined with diagnostic morphological characters and molecular phylogeny, we elevated the previous subspecies *H. s. maximus* to full species status, which is currently known distributed in Sichuan, Chongqing, and Guizhou, China (Figure 2). However, some previous records are also seemed to be doubtful. For example, Yang et al. (2008) reported "*H. s. maximus*" from Kunming, Yunnan, southwest China, based on a single specimen (Field number: No. 83017), whereas the number of maxillary teeth

492 distinctly differs from the known range of *H. maximus* in having 35 maxillary teeth in
493 No. 83017 vs. 24 in specimens from Sichuan). Thus, this record is still to be further
494 studied in the future, and we doubt the distribution record of *H. maximus* from
495 Yunnan, China. Consequently, we revised the distribution of *H. sauteri* and *H.*
496 *maximus*, where *H. sauteri* is currently distributed in north Vietnam, Laos, and
497 southern China, including Taiwan Island and Hainan Island; while *H. maximus* is
498 restricted in the mountain region of southwestern China (Figure 2).

499 Despite the high resemblance between *H. maximus* and *H. sauteri*, which leads to
500 great difficulty in species identification, *H. satueri* and *H. maximus* are recovered to
501 be two distantly related clades (Figure 1). Both species inhabit mountain region and
502 prey on earthworms, slugs, and tadpoles (Pope 1935; Wu 1984; Zhao et al. 1998;
503 Zhao 2006), combining with the phylogenetic relationships, it is supposed that this
504 morphological resemblance may arise from convergent evolution, this situation
505 should be discussed in further research (Wang et al. 2022).

506 **Taxonomic status of *Hebius sauteri bourreti***

507 Three subspecies of *Hebius sauteri* were previously recognized based on the
508 counts of ventral and subcaudal scales, i.e., *H. s. sauteri*, *H. s. bourreti*, and *H. s.*
509 *maximus*. In the current study, *H. s. maximus* was recognized as a distinct species, i.e.
510 *Hebius maximus* (see above). However, the taxonomic identity of the subspecies *H. s.*
511 *bourreti* still remained elusive, *H.s. bourreti* was originally described by Malnate
512 (1962) based on six specimens from Tam Dao, northern Vietnam, which differs from
513 the other two subspecies by having fewer number of ventrals (123–130) vs. in *H. s.*
514 *sauteri* (116–133) in *H. s. maximus* (132–143), fewer number of subcaudals (60–73)
515 vs. in *H. s. sauteri* (69–86) in *H. s. maximus* (64–92) and color pattern (supralabials
516 posterior to the eye often in the form of a light, dark-edged stripe, continuous with the
517 nuchal crescent; dorsal color dark brown; strong ventral pattern strongly developed,
518 especially subcaudally).

519 Yang et al. (2008: 266) reported one specimen of *H. s. bourreti* from Adebo
520 Town, Jinping County, Yunnan China. No other specimen of *H. s. bourreti* has been
521 recorded in China. Our extended examination of *H. s. sauteri* reveals that the body

and head scale counts of *H. s. bourreti* are largely overlapped with the range of *H. s. sauteri* (Table 6), and the high variability of the color pattern of *H. sauteri* suggests coloration may be unreliable in identifying this subspecies, one specimen of *H. s. sauteri* (CIB 8480) from Fujian, China presents highly similar color pattern of *H. s. bourreti* in supralabials, dorsal, and ventral, another specimen of *H. s. sauteri* (CIB 118516) from Guangdong, China also shows strong ventral pattern, which is similar to *H. s. bourreti*. Based on the comparisons discussed above, none of these morphology diagnosis provided by Malnate (1962) could accurately distinguish *H. s. bourreti* from *H. s. sauteri*. Therefore, we suggest *H. s. bourreti* is likely to be a synonym of *H. s. sauteri* which makes *H. sauteri* to be a monotypic species, more molecular evidence is needed to further confirm this suggestion.

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738 # Tables

739 ## Table 1. DNA sequences used in this study

Taxon	Voucher number	Locality	GenBank accession number				Reference
			Cyt *b*	*C-mos*	*NT3*	*Rag1*	
Hebius atemporalis	HS 11001 (CHS 153)	Mengzi, Yunnan, China	MK201299	-	-	MK194367	Li et al., (2020)
Hebius atemporalis	GP 1626	Guangdong, China	KJ685680	KJ685630	KJ685732	KJ685572	Guo et al., (2014)
Hebius boulengeri	SYS r001506 (CHS 757)	Dawuling, Guangdong, China	MK201509	-	-	-	Li et al., (2020)
Hebius boulengeri	RE55 (CHS 291)	Chebaling, Guangdong, China	MK201380	-	-	MK194448	Li et al., (2020)
Hebius boulengeri	GP 1789	Guangdong, China	KJ685684	KJ685634	KJ685736	KJ685576	Guo et al., (2014)
Hebius clerki	CAS 215036	Yunnan, China	KJ685666	KJ685615	KJ685716	KJ685559	Guo et al., (2014)
Hebius concelarus	KUZ: R20253 (AB 989268)	Miyakojimashi, Japan	AB989268	AB989271	LC047778	LC047774	Kaito & Toda, (2016)
Hebius concelarus	KUZ: R20255 (AB 989272)	Miyakojimashi, Japan	AB989272	-	-	-	Kaito & Toda, (2016)
Hebius craspedogaster	GP 139	Sichuan, China	JQ687437	JQ687429	KJ685730	KJ685569	Guo et al., (2014)
Hebius craspedogaster	HS 13020 (CHS 155)	HuangShan, Anhui, China	MK201301	-	-	MK194369	Li et al., (2020)
Hebius craspedogaster	SYS r000910 (CHS 602)	Huangshan, Anhui, China	MK201428	-	-	MK194505	Li et al., (2020)
Hebius deschauenseei	AMNH 148575	Ha Giang, Vietnam	KJ685665	KJ685614	KJ685715	KJ685558	Guo et al., (2014)
Hebius ishigakiense	KUZ: R33044	Iriomotejima, Japan	AB989294	-	-	-	Kaito & Toda, (2016)
Hebius ishigakiense	KUZ: R33045	Iriomotejima, Japan	AB989296	-	-	-	Kaito & Toda, (2016)
Hebius johannis	GP 1569	Yunnan, China	KJ685678	KJ685628	KJ685731	KJ685571	Guo et al., (2014)
Hebius johannis	GP 897	Yunnan, China	KJ685708	KJ685658	KJ685767	KJ685605	Guo et al., (2014)
Hebius khasiensis	CAS 221504	KaChin state, Myanmar	KJ685668	KJ685617	KJ685718	KJ685561	Guo et al., (2014)
Hebius khasiensis	CAS 221525	KaChin state, Myanmar	KJ685669	KJ685618	KJ685719	KJ685562	Guo et al., (2014)
Hebius metusia	HS 11158 (CHS 152)	Pingshan, Yibin, Sichuan, China	MK201298	-	-	MK194366	Li et al., (2020)
Hebius metusia	GP 871	Sichuan, China	KJ685707	KJ685657	KJ685766	-	Guo et al., (2014)
Hebius metusia	GP 1712	Sichuan, China	KJ685682	KJ685632	KJ685734	KJ685574	Guo et al., (2014)
Hebius modestus	CAS 234262	Yunnan, China	KJ685671	KJ685620	KJ685721	KJ685564	Guo et al., (2014)
Hebius optatus	HS 11143 (CHS 151)	Mangshan, Hunan, China	MK201297	-	-	MK194365	Li et al., (2020)
Hebius optatus	GP 1885	Guizhou, China	KJ685687	KJ685637	KJ685739	KJ685579	Guo et al., (2014)

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742 **Table 1.** (Continued)

Taxon	Voucher number	Locality	GenBank accession number				Reference
			Cyt *b*	*C-mos*	*NT3*	*Rag1*	
Hebius optatus	AMNH 147155	Vinh Phu, Vietnam	KJ685662	KJ685611	KJ685712	KJ685555	Guo et al., (2014)
Hebius popei	GP 2169	Hainan, China	KJ685692	KJ685642	KJ685744	KJ685584	Guo et al., (2014)
Hebius popei	GP 2386	Guizhou, China	KJ685697	KJ685647	KJ685749	KJ685588	Guo et al., (2014)
Hebius pryeri	KUZ: R67983	Amamioshima, Japan	AB989102	AB989105	LC047779	LC047776	Kaito & Toda, (2016)
Hebius sangzhiensis	SYNU 08070350	Sangzhi, Hunan, China	MK340763	-	-	-	Zhou et al., (2019)
Hebius satueri	CIB 118516	Guangdong, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius satueri	SYS r001766	Hunan, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius satueri	SYS r001258	Jiangxi, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius satueri	SYS r001266	Jiangxi, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius satueri	GP 1790	Guangdong, China	KJ685685	KJ685635	KJ685737	KJ685577	Guo et al., (2014)
Hebius satueri	GP 2549	Taiwan, China	KJ685701	KJ685651	KJ685754	KJ685592	Guo et al., (2014)
Hebius satueri	CIB 118517	Fujian, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius satueri	SYS r002087	Hunan, China	upon acceptance	upon acceptance	upon acceptance	-	This study
Hebius maximus	HS 11157 (CHS 156)	Mianyang, Sichuan, China	MK201302	-	-	MK194370	Li et al., (2020)
Hebius maximus	GP 864	Sichuan, China	KJ685706	KJ685656	KJ685765	KJ685603	Guo et al., (2014)
Hebius maximus	GP 2382	Sichuan, China	KJ685696	KJ685646	KJ685748	-	Guo et al., (2014)
Hebius maximus	CIB 118518	Dayi, Sichuan, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius maximus	SYS r002041	Bijie, Guizhou, China	upon acceptance	upon acceptance	upon acceptance	upon acceptance	This study
Hebius maximus	CIB 118072	Bijie, Guizhou, China	upon acceptance	-	-	-	This study
Hebius maximus	CIB 118074	Bijie, Guizhou, China	upon acceptance	-	-	-	This study
Hebius maximus	CIB 118635	Yibin, Sichuan, China	upon acceptance	-	-	-	This study
Hebius vibakari	KUZ: R21587	Kyoto, Japan	AB989302	AB989305	-	-	Kaito & Toda, (2016)
Hebius vibakari	HS 14026 (CHS 149)	Harbin, China	MK201296	-	-	MK194363	Li et al., (2020)
Hebius vibakari	GP 1352	Heilongjiang, China	KJ685677	KJ685627	KJ685729	KJ685568	Guo et al., (2014)
Hebius yanbianensis	GP 4006	Yanbian, Sichuan, China	MH532291	-	-	-	Liu et al., (2018)
Herpetoreas tpser	JK 201710 (CHS 849)	Mêdog, Linzhi, Tibet, China	MK201567	-	-	-	Li et al., (2020)

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744 **Table 2.** Primers used for DNA amplification

Gene	Primers	Primer sequences (from 5' to 3')	Reference
Cyt *b*	L14919	AACCACCGTTGTTATTCA ACT	Burbrink et al., (2000)
	H16064	CTTTGGTTTACAAGA ACAATGCTTTA	
C-mos	S77	CATGGACTGGGATCAGTTATG	Lawson et al., (2005)
	S78	CCTTGGGTGTGATTTTCTCACCT	
Rag1	R13	TCTGAATGGAAATTCAAGCTGTT	Groth & Barrowclough (1999)
	R18	GATGCTGCCTCGGTCGGCCACCT TT	
NT3	NT3F	ATATTTCTGGCTTTTCTCTGTGGC	Noonan & Chippindale (2006)
	NT3R	GCGTTTCATAAAAATATTGTTTGACCGG	

745 **Table 3.** Uncorrected *p*-distance between *Hebius* species based on 1070 base pairs from the mitochondrial genes Cyt *b*

Number	Species	Voucher	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*Hebius atemporalis*	GP 1626															
2	*Hebius concelarus*	KUZ: R20255	0.174														
3	*Hebius craspedogaster*	GP 139	0.152	0.164													
4	*Hebius deschauenseei*	AMNH 148575	0.155	0.174	0.168												
5	*Hebius ishigakiensis*	KUZ: R33044	0.136	0.133	0.159	0.159											
6	*Hebius metusia*	GP 871	0.131	0.150	0.131	0.143	0.136										
7	*Hebius optatus*	AMNH 147155	0.145	0.144	0.157	0.163	0.131	0.136									
8	*Hebius pryeri*	KUZ: R67983	0.153	0.093	0.171	0.176	0.117	0.139	0.151								
9	*Hebius sangzhiensis*	SYNU 08070350	0.151	0.132	0.152	0.162	0.123	0.139	0.139	0.120							
10	*Hebius satueri*	CIB 118516	0.138	0.151	0.143	0.162	0.123	0.119	0.120	0.141	0.132						
11	*Hebius satueri*	SYS r001258	0.136	0.151	0.139	0.162	0.125	0.117	0.120	0.137	0.133	0.009					
12	*Hebius sauteri*	CIB 118517	0.124	0.139	0.138	0.158	0.115	0.110	0.112	0.132	0.126	0.030	0.029				
13	*Hebius maximus*	CIB 118518	0.133	0.157	0.133	0.144	0.125	0.124	0.124	0.139	0.082	0.125	0.126	0.116			
14	*Hebius maximus*	CIB118 072	0.133	0.154	0.136	0.150	0.122	0.134	0.122	0.139	0.084	0.123	0.124	0.007	0.116		
15	*Hebius maximus*	CIB 118635	0.139	0.151	0.137	0.150	0.128	0.136	0.125	0.136	0.085	0.124	0.125	0.007	0.117	0.007	
16	*Hebius yanbianensis*	GP 4006	0.130	0.152	0.139	0.150	0.134	0.057	0.141	0.135	0.126	0.126	0.124	0.120	0.119	0.125	0.129

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747 **Table 4.** Measured morphological characters of *H. maximus* and *H. sauteri*. For specimens with asymmetrical facial scales, the scale
748 count was given as "left/right"

749

Species	Voucher number	Locality	Sex	ToL (mm)	TL (mm)	SpL	IfL	PtO	DSR	V	SC	V+SC	MT
H. maximus	CIB 118635 (topotype)	Sichuan, China	M	470	141	3-2-3	8	3	17-17-17	138	87+1	225	22+2
H. maximus	CIB 118518	Sichuan, China	M	433	137+?	-	-	2	17-17-17	137	74+?	-	-
H. maximus	CIB 8482	Guizhou, China	M	352	117	3/2-2-2	7/8	2	17-17-17	136	83+1	219	-
H. maximus	YBU 18170	Sichuan, China	M	260	66	2-2-3	9	3/2	17-17-17	137	72+1	209	22+2
H. maximus	YBU 11258	Chongqing, China	M	365	111	2-2-3	7	2/3	17-17-17	133	92+1	225	22+2
H. maximus	CIB 118072	Guizhou, China	F	384	106	3/2-2-3	7/8	3	17-17-17	141	73+1	214	-
H. maximus	CIB 107649	Sichuan, China	F	496	131	2-2-3	8	2/3	17-17-17	135	73+1	208	-
H. maximus	CIB 8484	Guizhou, China	F	300	70	2-2-3	8	3/2	17-17-17	143	64+1	207	-
H. maximus	CIB 8470	Sichuan, China	F	333	93	2/3-3/2-3	7	2	17-17-17	135	72+1	207	-
H. maximus	CIB 94216	Sichuan, China	F	523	162	3-2-3	8	2/3	17-17-17	135	82+1	217	-
H. sauteri	SYS r001766	Hunan, China	M	320	96	2-2-3	7/8	3/2	17-17-17	128	76+1	204	24+2
H. sauteri	SYS r001266	Jiangxi, China	M	282	88	2-2-3	8	2/3	17-17-17	129	84+1	213	23+2
H. sauteri	CIB 8481	Hainan, China	M	347	95	3/2-2-? /2	-/8	3	17-17-17	125	74+1	199	-
H. sauteri	CAS 18984 (topotype)	Taiwan, China	F	303	99	2-2-3	7	3	17-17-17	116	71+1	187	-
H. sauteri	CAS 18988 (topotype)	Taiwan, China	-	299	83	2-2-3	7	3	17-17-17	128	77+1	205	-
H. sauteri	YBU 17001	Hainan, China	F	225	58	2-2-3	7	3	17-17-17	126	76+1	202	25+2
H. sauteri	CIB 118517	Fujian, China	F	412	120	2-2-3	8	2/3	17-17-17	133	79+1	212	24+3
H. sauteri	CIB 118516	Guangdong, China	F	324	88	2-2-3	7	3	17-17-17	129	69+1	198	-
H. sauteri	SYS r001150	Guangdong, China	F	145	38	2-2-3	7	3	17-17-17	129	70+1	199	21+2
H. sauteri	SYS r000275	Guizhou, China	F	306	77	2-2-3	7	3/2	17-17-17	132	66+?	-	-

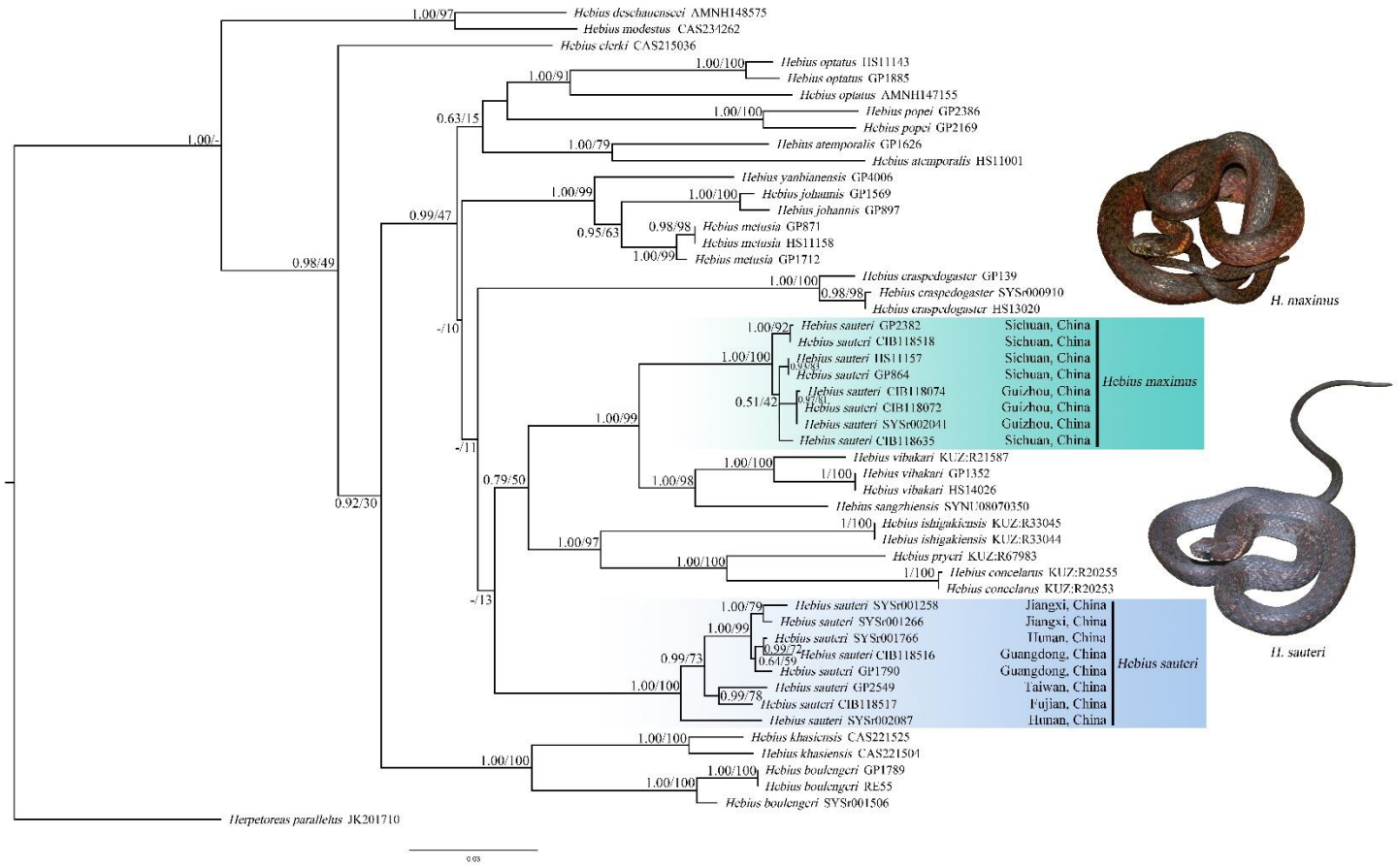
Table 5. Comparison between main morphological characters of *H. maximus*, *H. sauteri*, "-" indicates missing data

Species	TL/ToL		V		SC		V + SC		MT	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
H. maximus	0.25–0.33 (0.29 ± 0.02)	0.25–0.31 (0.27 ± 0.02)	132–138 (136 ± 2)	135–143 (138 ± 3)	72–92 (81 ± 6)	64–82 (72 ± 5)	209–225 (216 ± 6)	207–217 (210 ± 3)	24	-
H. sauteri	0.27–0.31 (0.30 ± 0.02)	0.24–0.33 (0.28 ± 0.02)	125–130 (128 ± 2)	116–133 (129 ± 4)	74–84 (78 ± 4)	69–86 (74 ± 5)	199–213 (205 ± 6)	187–215 (203 ± 7)	25–27	23–27

Table 6. Morphological comaparison between *H. s. sauteri* and *H. s. bourreti*

Species	PrO	PtO	SpL	IfL	TEM	V	SC	TL/ToL
H. s. sauteri	1–2	2–3	2(3)-2(1)-3(2)	6–9	1(2) + 1(2, 3) + 0(2, 3)	116–133	69–86	0.24–0.33
H. s. bourreti	1	2–3	2-2-3	7–8	1(2) + 1(2)	123–130	60–73	0.27–0.30

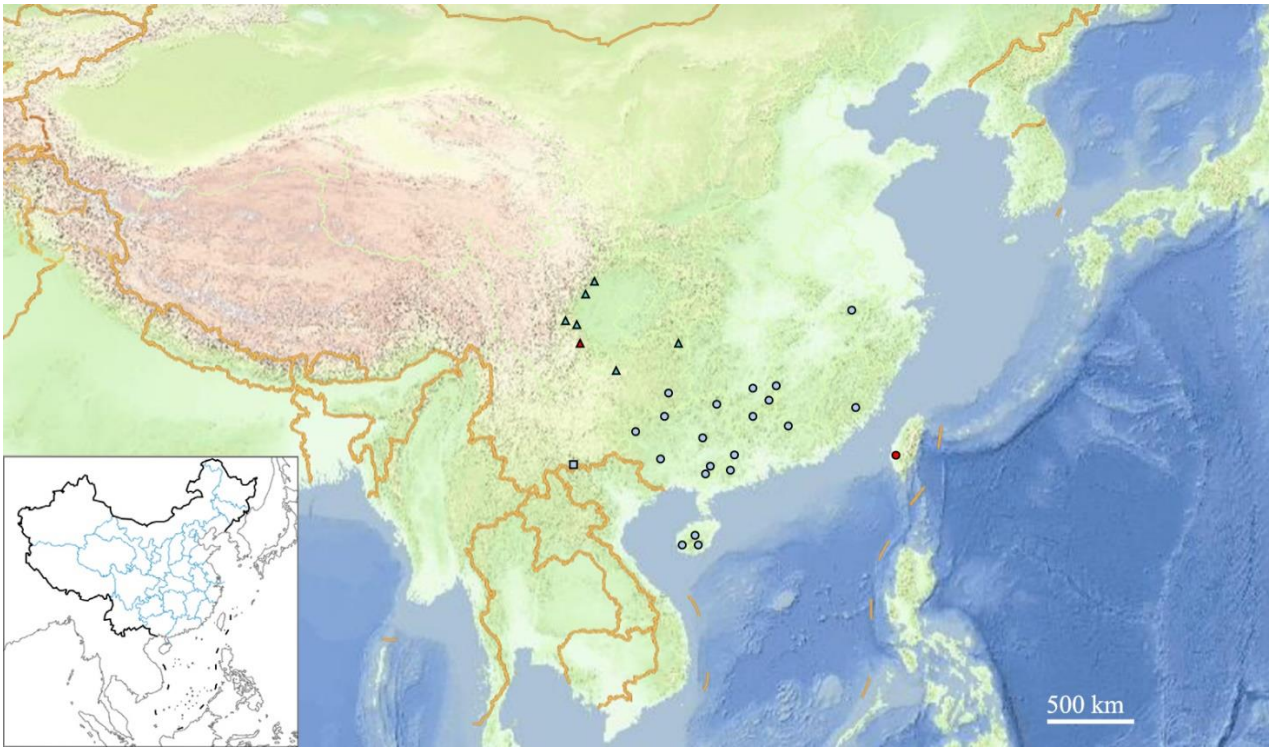
760 **FIGURES**



761

762 **Figure 1.** Maximum likelihood (ML) tree of the genus *Hebius* based on Cyt *b*, *NT3*, *C-mos* and

763 *Rag1*, showing phylogenetic position of *Hebius sauteri* (blue) and *Hebius maximus* **comb. nov.** (green).



764

765 **Figure 2.** Distribution of *Hebius maximus* **comb. nov.** and re-defined distribution of *H. sauteri* in China

766 based on museum collections, previous studies and this study (Triangle: *Hebius maximus* **comb. nov.**, round:

767 *H. sauteri sauteri*, square: *H. sauteri bourreti*. Type localities are colored red).

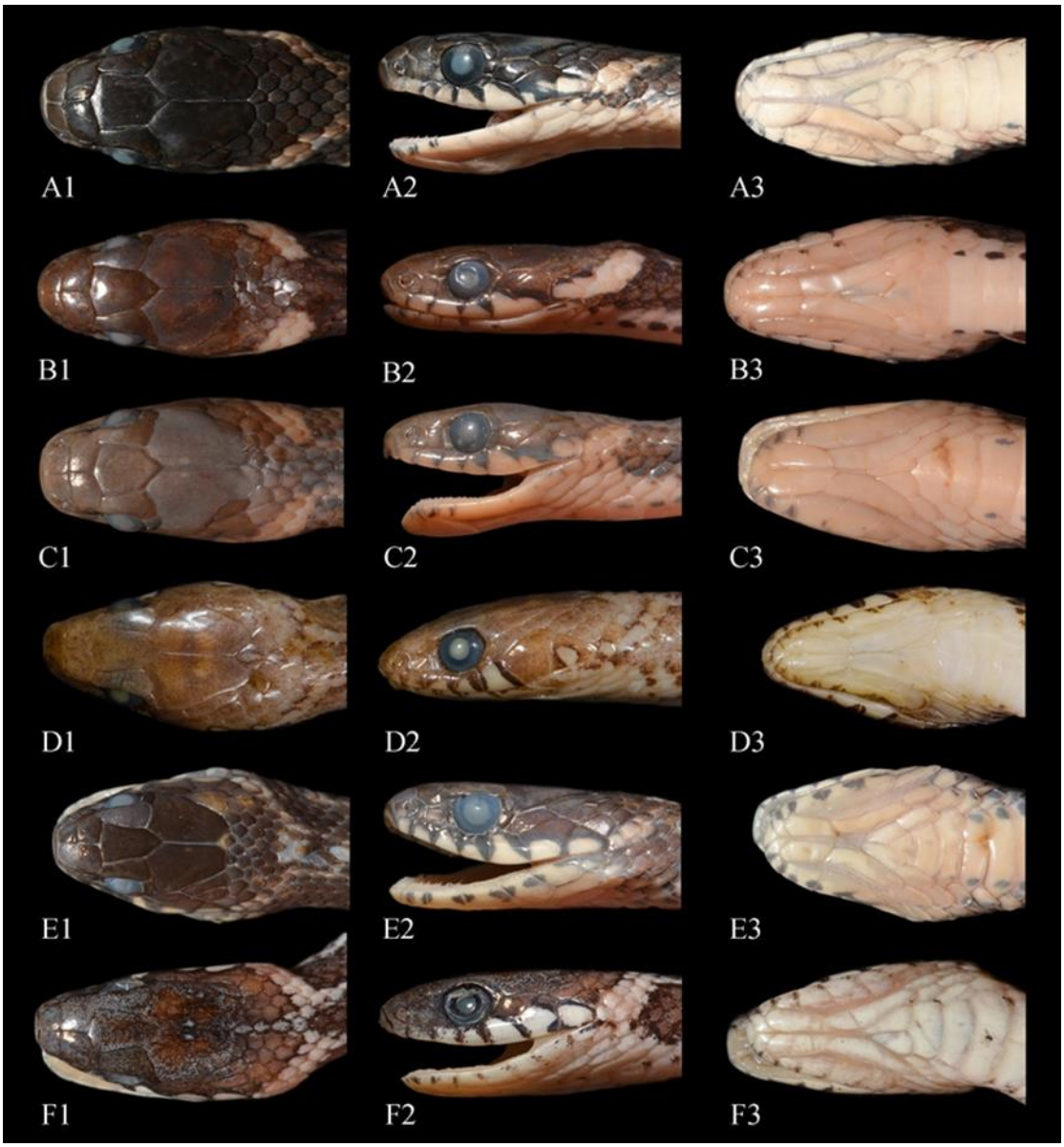


Figure 3. Dorsal (left), lateral (middle) and ventral (right) of the head comparisons between *Hebius sauteri* and *Hebius maximus* **comb. nov.** Row D photographed by Kai Wang, others were photographed by Jun-Jie Huang.

A–C: *Hebius maximus* **comb. nov.** (A: Topotype CIB 118635, Mt. Laojun, Pingshan County, Sichuan, China; B: CIB 8482, Qixingguan District, Guizhou, China; C: CIB 8458, Yingjing County, Sichuan, China) D–F: *H. sauteri* (Topotype CAS 18984, Pingtung County, Taiwan; CIB 118516, Yinpingshan, Dongguan City, Guangdong, China; CIB 118517, Daiyun, Dehua County, Fujian, China)

Figure 4. *Hebius sauteri* in life, A: CIB 118516, Yinpingshan, Dongguan City, Guangdong, China; B: CIB 118517, Xinyong Village, Dehua County, Fujian, China. Photographs by Jin-Long Ren.

Figure 5. Topotype of *H. sauteri* (CAS 18988), Guanziling, Tainan City, Taiwan, China. Not to scale. Photographs by Kai Wang.

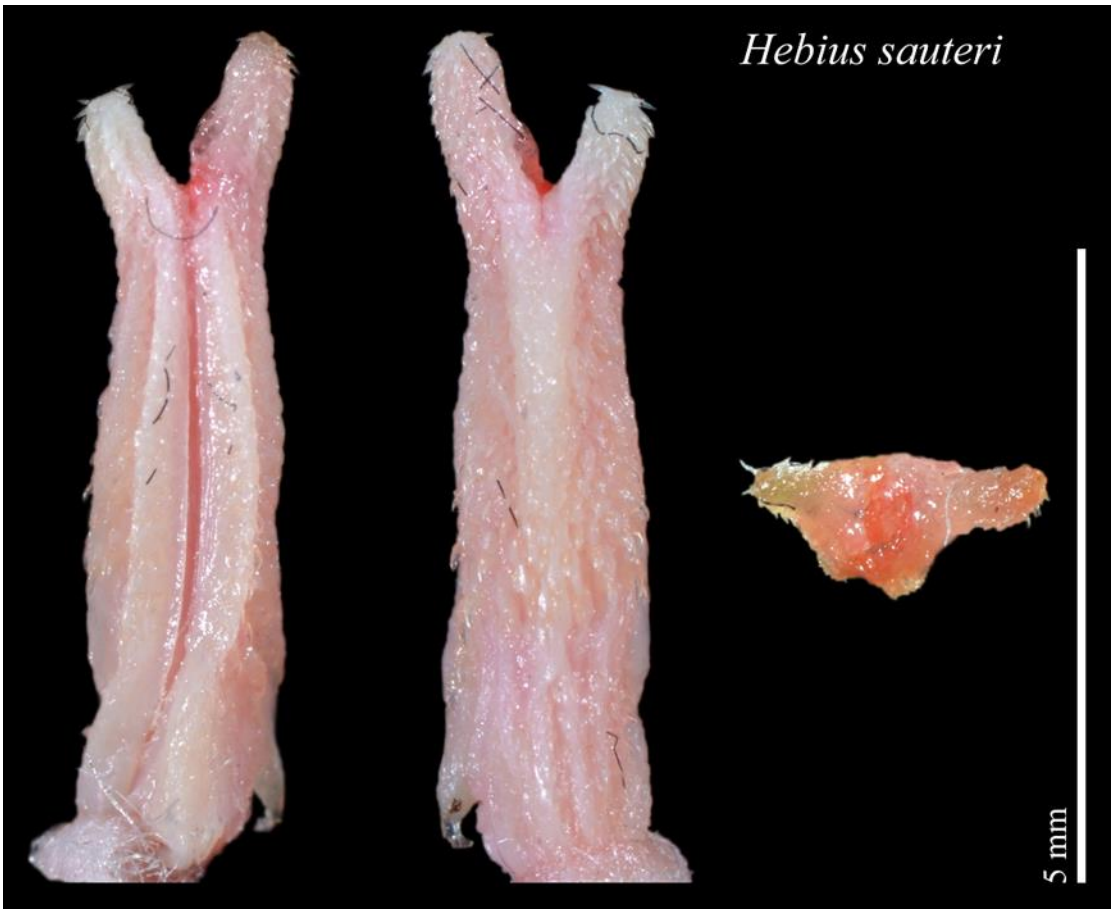


Figure 6. Photographs of the hemipenis of *H. sauteri* (SYS r000323, Mt. Jinggang, Jiangxi Province, China). Photographs by Jun-Jie Huang.

Figure 7. Holotype of *Hebius maximus* **comb. nov.** (FMNH 18796), photographs from Field Museum of Natural History (https://collections-zoology.fieldmuseum.org/catalogue/1846011).

788

789 **Figure 8.** *Hebius maximus* **comb. nov.** in life, A: SYS r002041, adult male, Wuqing, Bijie, Guizhou, China;

790 B: CIB 118635, adult male, Mt. Laojun, Pingshan County, Sichuan, China; C: adult female, Emeishan,

791 Sichuan, China. Photographs by Zhi-Tong Lyu (A) and Mao-Liang Li (B and C).

Figure 9. Topotype of *Hebius maximus* **comb. nov.**, CIB 118635, adult male, Mt. Laojun, Pingshan County, Sichuan, China, in preservation. Photographs by Jun-Jie Huang.

Figure 10. Photographs of the hemipenis of *Hebius maximus* **comb. nov.**, CIB 118635, Mt. Laojun, Pingshan County, Sichuan, China. Photographs by Jun-Jie Huang.

Figure 11. Natural habitat of *Hebius maximus* **comb. nov.** in Mt. Laojun, Pingshan county, Yibin City, Sichuan, China, A: macrohabitat; B: microhabitat. Photographs by Mao-Liang Li.