

On the validity of *Hebius sauteri maximus* (Malnate, 1962) (Squamata, Natricidae), with the redescription of *H. maximus* comb. nov. and *H. sauteri* (Boulenger, 1909)

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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 of the *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 that *H. s. maximus* is morphologically distinguishable from the nominative subspecies. Therefore, our results support the validity of *H. s. maximus* and we elevate it to full species status, namely *Hebius maximus* comb. nov. The distribution range of *H. sauteri* is revised 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 humid or riparian habitats (Narayanan et al. 2020; Peng et al. 2022). The genus *Hebius* Thompson, 1913 is the most speciose group within Natricidae; members of the genus *Hebius* are widely distributed across South and East Asia, as well as Southeast Asia (Guo et al. 2014). The genus *Hebius* was previously combined with the genus *Amphiesma* Duméril, Bibron, &

Duméril, 1854 *sensu lato* and was recently resurrected by Guo et al. (2014). Currently, the genus *Hebius* includes 48 species, of which 23 species are known from China (Wang et al. 2020; David et al. 2021; Hou et al. 2021; Hauser et al. 2022; Ren et al. 2022; Uetz et al. 2022).

Hebius sauteri (Boulenger, 1909) is a small to medium-sized snake inhabiting moist mountains and often found near water. Described based on two specimens from Taiwan Island, southeastern 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 ventral and subcaudal scale counts and coloration, 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) has been 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* a monotypic species (Wallach et al. 2014). No recent study has yet examined the controversial taxonomy of the subspecies of *H. sauteri*.

Based on the examination of voucher specimens in natural history collection and individuals newly collected from the field, we re-evaluated the taxonomic status of *H. s. sauteri* and *H. s. maximus* by using morphological and molecular phylogenetic data, and discussed the taxonomic status of *H. s. bourreti*.

Materials and methods

Sampling

During field surveys conducted in the last five years, nine specimens of *H. sauteri* were collected in Sichuan, Guizhou, Guangdong, and Fujian, including one specimen near the type locality of *H. s. maximus* (CIB 118635). Specimens collected in the field were euthanatized and preserved in 10% formalin and then transferred to 75% ethanol, and all newly collected specimens were deposited in the Herpetological Museum, Chengdu Institute of Biology (CIB), Chinese Academy of Sciences, Chengdu, China, and the Museum of Biology, School of Life Sciences, Sun Yat-Sen University (SYS), Guangzhou, China. Other specimens or tissue samples used in this study were obtained from institution collections (see collection abbreviations).

Morphological analysis

A total of 44 specimens of *H. sauteri* were examined in this study. The description and measurements of morphological characters were obtained according to Zhao (2006), Ren et al. (2018) and Ren (2019). A tape measure with 1 mm accuracy was used to measure the total length (ToL) and tail length (TL). The head length (HL), head width (HW), eye width (EW), and distance between the lower margins of eye and lip (SoL) were taken with a slide-caliper with a minimum accuracy of 0.01 mm. Other pholidosis counts were also examined for comparison, including the number of internasal (IN), prefrontal (PrF), loreal (L), frontal (F), parietal (P), preocular (PrO), postocular (PtO), supraocular (SpO), supralabial (SpL), infralabial (IfL), temporal (TEM), chin-shield (CS), dor-

sal scale rows (DSR), ventral (V) and subcaudal (SC). Additionally, the number and shape of maxillary teeth (MT), and keeling status of the dorsal scale rows (KDSR) were also described.

The hemipenes of one adult specimen of *H. s. maximus* near the type locality (CIB 118635) and one adult 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). The 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 is preserved in 95% ethanol. 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 using polymerase chain reaction (PCR), primers used in amplification 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), 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) analy-

Table 1. DNA sequences used in this study.

Taxon	Voucher number	Locality	GenBank accession number				Reference
			<i>Cyt b</i>	<i>C-mos</i>	<i>NT3</i>	<i>Rag1</i>	
<i>Hebius atemporalis</i>	HS 11001 (CHS 153)	Mengzi, Yunnan, China	MK201299	–	–	MK194367	Li et al. (2020)
<i>Hebius atemporalis</i>	GP 1626	Guangdong, China	KJ685680	KJ685630	KJ685732	KJ685572	Guo et al. (2014)
<i>Hebius boulengeri</i>	SYS r001506 (CHS 757)	Dawuling, Guangdong, China	MK201509	–	–	–	Li et al. (2020)
<i>Hebius boulengeri</i>	RE55 (CHS 291)	Chebaling, Guangdong, China	MK201380	–	–	MK194448	Li et al. (2020)
<i>Hebius boulengeri</i>	GP 1789	Guangdong, China	KJ685684	KJ685634	KJ685736	KJ685576	Guo et al. (2014)
<i>Hebius clerki</i>	CAS 215036	Yunnan, China	KJ685666	KJ685615	KJ685716	KJ685559	Guo et al. (2014)
<i>Hebius conelarus</i>	KUZ: R20253 (AB 989268)	Miyakojimashi, Japan	AB989268	AB989271	LC047778	LC047774	Kaito and Toda (2016)
<i>Hebius conelarus</i>	KUZ: R20255 (AB 989272)	Miyakojimashi, Japan	AB989272	–	–	–	Kaito and Toda (2016)
<i>Hebius craspedogaster</i>	GP 139	Sichuan, China	JQ687437	JQ687429	KJ685730	KJ685569	Guo et al. (2014)
<i>Hebius craspedogaster</i>	HS 13020 (CHS 155)	Huangshan, Anhui, China	MK201301	–	–	MK194369	Li et al. (2020)
<i>Hebius craspedogaster</i>	SYS r000910 (CHS 602)	Huangshan, Anhui, China	MK201428	–	–	MK194505	Li et al. (2020)
<i>Hebius igneus</i>	AMNH 148575	Ha Giang, Vietnam	KJ685665	KJ685614	KJ685715	KJ685558	Guo et al. (2014)
<i>Hebius ishigakiensis</i>	KUZ: R33044	Iriomotejima, Japan	AB989294	–	–	–	Kaito and Toda (2016)
<i>Hebius ishigakiensis</i>	KUZ: R33045	Iriomotejima, Japan	AB989296	–	–	–	Kaito and Toda (2016)
<i>Hebius johannis</i>	GP 1569	Yunnan, China	KJ685678	KJ685628	KJ685731	KJ685571	Guo et al. (2014)
<i>Hebius johannis</i>	GP 897	Yunnan, China	KJ685708	KJ685658	KJ685767	KJ685605	Guo et al. (2014)
<i>Hebius khasiensis</i>	CAS 221504	Kachin, Myanmar	KJ685668	KJ685617	KJ685718	KJ685561	Guo et al. (2014)
<i>Hebius khasiensis</i>	CAS 221525	Kachin, Myanmar	KJ685669	KJ685618	KJ685719	KJ685562	Guo et al. (2014)
<i>Hebius metusia</i>	HS 11158 (CHS 152)	Pingshan, Yibin, Sichuan, China	MK201298	–	–	MK194366	Li et al. (2020)
<i>Hebius metusia</i>	GP 871	Sichuan, China	KJ685707	KJ685657	KJ685766	–	Guo et al. (2014)
<i>Hebius metusia</i>	GP 1712	Sichuan, China	KJ685682	KJ685632	KJ685734	KJ685574	Guo et al. (2014)
<i>Hebius modestus</i>	CAS 234262	Yunnan, China	KJ685671	KJ685620	KJ685721	KJ685564	Guo et al. (2014)
<i>Hebius optatus</i>	HS 11143 (CHS 151)	Mangshan, Hunan, China	MK201297	–	–	MK194365	Li et al. (2020)
<i>Hebius optatus</i>	GP 1885	Guizhou, China	KJ685687	KJ685637	KJ685739	KJ685579	Guo et al. (2014)
<i>Hebius optatus</i>	AMNH 147155	Vinh Phu, Vietnam	KJ685662	KJ685611	KJ685712	KJ685555	Guo et al. (2014)
<i>Hebius popei</i>	GP 2169	Hainan, China	KJ685692	KJ685642	KJ685744	KJ685584	Guo et al. (2014)
<i>Hebius popei</i>	GP 2386	Guizhou, China	KJ685697	KJ685647	KJ685749	KJ685588	Guo et al. (2014)
<i>Hebius pryori</i>	KUZ: R67983	Amamioshima, Japan	AB989102	AB989105	LC047779	LC047776	Kaito and Toda (2016)
<i>Hebius sangzhiensis</i>	SYNU 08070350	Sangzhi, Hunan, China	MK340763	–	–	–	Zhou et al. (2019)
<i>Hebius sauteri</i>	CIB 118516	Guangdong, China	OP937178	OP965807	OP965801	OP965796	This study
<i>Hebius sauteri</i>	SYS r001766	Hunan, China	OP937182	OP965802	OP965797	OP965792	This study
<i>Hebius sauteri</i>	SYS r001258	Jiangxi, China	OP937180	OP965805	OP965799	OP965794	This study
<i>Hebius sauteri</i>	SYS r001266	Jiangxi, China	OP937181	OP965804	OP965798	OP965793	This study
<i>Hebius sauteri</i>	GP 1790	Guangdong, China	KJ685685	KJ685635	KJ685737	KJ685577	Guo et al. (2014)
<i>Hebius sauteri</i>	GP 2549	Taiwan, China	KJ685701	KJ685651	KJ685754	KJ685592	Guo et al. (2014)
<i>Hebius sauteri</i>	CIB 118517	Fujian, China	OP937179	OP965806	OP965800	OP965795	This study
<i>Hebius sauteri</i>	SYS r002087	Hunan, China	OP937183	OP965803	–	–	This study
<i>Hebius maximus</i>	HS 11157 (CHS 156)	Mianyang, Sichuan, China	MK201302	–	–	MK194370	Li et al. (2020)
<i>Hebius maximus</i>	GP 864	Sichuan, China	KJ685706	KJ685656	KJ685765	KJ685603	Guo et al. (2014)
<i>Hebius maximus</i>	GP 2382	Sichuan, China	KJ685696	KJ685646	KJ685748	–	Guo et al. (2014)
<i>Hebius maximus</i>	CIB 118518	Dayi, Sichuan, China	OP937186	OP937189	OP937192	OP965791	This study
<i>Hebius maximus</i>	SYS r002041	Bijie, Guizhou, China	OP937184	OP937190	OP937191	OP965790	This study
<i>Hebius maximus</i>	CIB 118072	Bijie, Guizhou, China	OP937188	–	–	–	This study
<i>Hebius maximus</i>	CIB 118074	Bijie, Guizhou, China	OP937187	–	–	–	This study
<i>Hebius maximus</i>	CIB 118635	Yibin, Sichuan, China	OP937185	–	–	–	This study
<i>Hebius vibakari</i>	KUZ: R21587	Kyoto, Japan	AB989302	AB989305	–	–	Kaito and Toda (2016)
<i>Hebius vibakari</i>	HS 14026 (CHS 149)	Harbin, China	MK201296	–	–	MK194363	Li et al. (2020)
<i>Hebius vibakari</i>	GP 1352	Heilongjiang, China	KJ685677	KJ685627	KJ685729	KJ685568	Guo et al. (2014)
<i>Hebius yanbianensis</i>	GP 4006	Yanbian, Sichuan, China	MH532291	–	–	–	Liu et al. (2018)
<i>Herpetoreas tpser</i>	JK 201710 (CHS 849)	Mêdog, Tibet, China	MK201567	–	–	–	Li et al. (2020)

sis 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 sam-

Table 2. Primers used for DNA amplification.

Gene	Primers	Primer sequences (from 5' to 3')	Reference
Cyt <i>b</i>	L14919	AACCACCGTTGTTATTCAACT	Burbrink et al. (2000)
	H16064	CTTTGGTTTACAAGAACAATGCTTTA	(2000)
<i>C-mos</i>	S77	CATGGACTGGGATCAGTTATG	Lawson et al. (2005)
	S78	CCTTGGGTGTGATTTCTCACCT	(2005)
<i>Rag1</i>	R13	TCTGAATGGAAATCAAGCTGTT	Groth and Barrowclough (1999)
	R18	GATGCTGCCTCGGTCGGCCACCTTT	(1999)
<i>NT3</i>	NT3F	ATATTCTGGCTTTTCTCTGTGGC	Noonan and Chippindale (2006)
	NT3R	CGGTTTCATAAAATATTGTTTGACCGG	(2006)

pled every 100 generations. The first 25% of all searched trees were discarded as burn-in. Bayesian posterior probability (BPP) $\geq 95\%$ 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* was chosen as the outgroup.

Collection abbreviations

NHMUK: 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 Sciences, San Francisco, USA; **FMNH:** Field Museum of Natural History, Chicago, Illinois, USA; **SYS:** The Museum of Biology, School of Life Sciences, Sun Yat-Sen University, Guangzhou, China; **USNM:** Nation-

al 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* = 1,070 bp; *C-mos* = 587 bp; *NT3* = 476 bp; *Rag1* = 954 bp). The topological structure of the phylogenetic tree (Fig. 1) was largely consistent with previous studies (Guo et al. 2014; Kizirian et al. 2018; Liu et al. 2018; Zhou et al. 2019). Although higher relationships of *Hebius* congeners remain 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. conelarus*; Fig. 1).

The uncorrected pairwise distance of Cyt *b* sequences between *H. s. maximus* and *H. s. sauteri* varies 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).

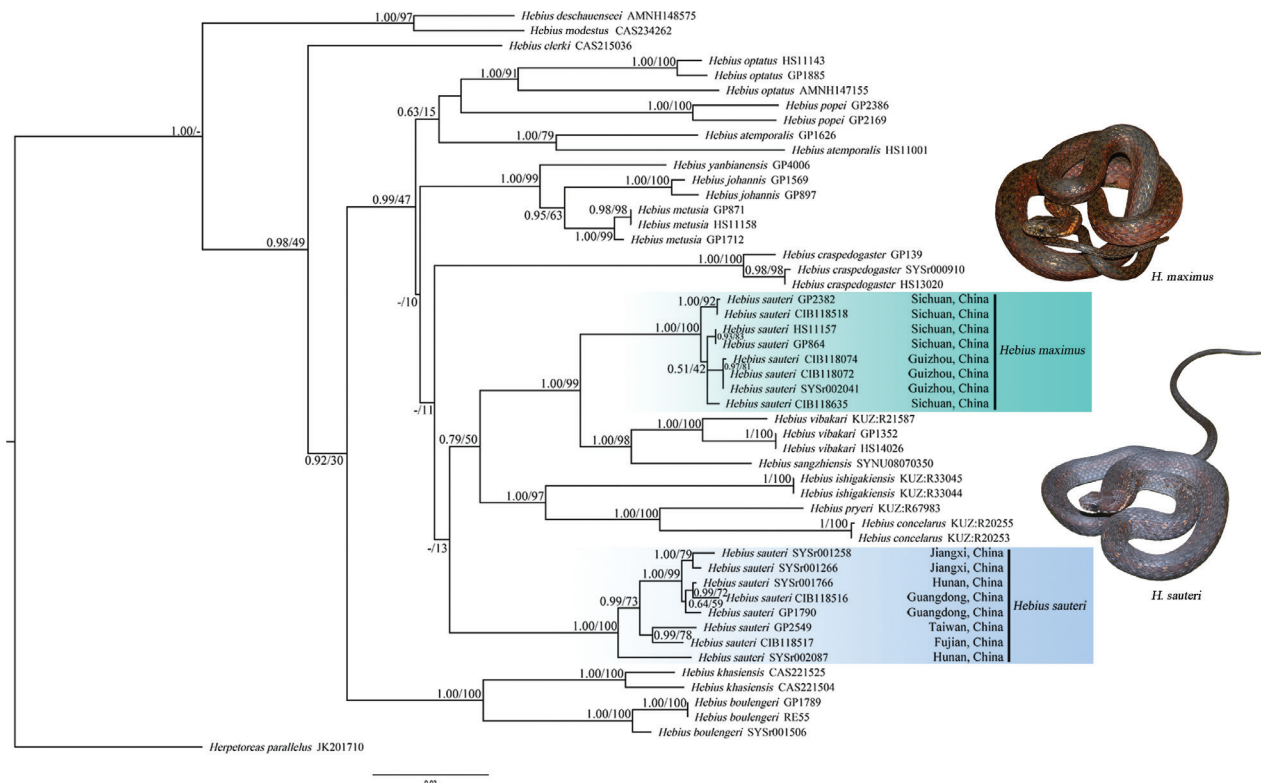


Figure 1. Maximum likelihood (ML) tree of the genus *Hebius* based on Cyt *b*, *NT3*, *C-mos* and *Rag1*, showing phylogenetic position of *Hebius sauteri* (blue) and *Hebius maximus* comb. nov. (green).

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	<i>Hebius atemporalis</i>	GP 1626															
2	<i>Hebius conelarus</i>	KUZ: R20255	0.174														
3	<i>Hebius craspedogaster</i>	GP 139	0.152	0.164													
4	<i>Hebius igneus</i>	AMNH 148575	0.155	0.174	0.168												
5	<i>Hebius ishigakiensis</i>	KUZ: R33044	0.136	0.133	0.159	0.159											
6	<i>Hebius metusia</i>	GP 871	0.131	0.150	0.131	0.143	0.136										
7	<i>Hebius optatus</i>	AMNH 147155	0.145	0.144	0.157	0.163	0.131	0.136									
8	<i>Hebius pryeri</i>	KUZ: R67983	0.153	0.093	0.171	0.176	0.117	0.139	0.151								
9	<i>Hebius sangzhiensis</i>	SYNU 08070350	0.151	0.132	0.152	0.162	0.123	0.139	0.139	0.120							
10	<i>Hebius sauteri</i>	CIB 118516	0.138	0.151	0.143	0.162	0.123	0.119	0.120	0.141	0.132						
11	<i>Hebius sauteri</i>	SYS r001258	0.136	0.151	0.139	0.162	0.125	0.117	0.120	0.137	0.133	0.009					
12	<i>Hebius sauteri</i>	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	<i>Hebius maximus</i>	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	<i>Hebius maximus</i>	CIB 118072	0.133	0.154	0.136	0.150	0.122	0.134	0.122	0.139	0.084	0.123	0.124	0.116	0.007		
15	<i>Hebius maximus</i>	CIB 118635	0.139	0.151	0.137	0.150	0.128	0.136	0.125	0.136	0.085	0.124	0.125	0.117	0.007	0.007	
16	<i>Hebius yanbianensis</i>	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

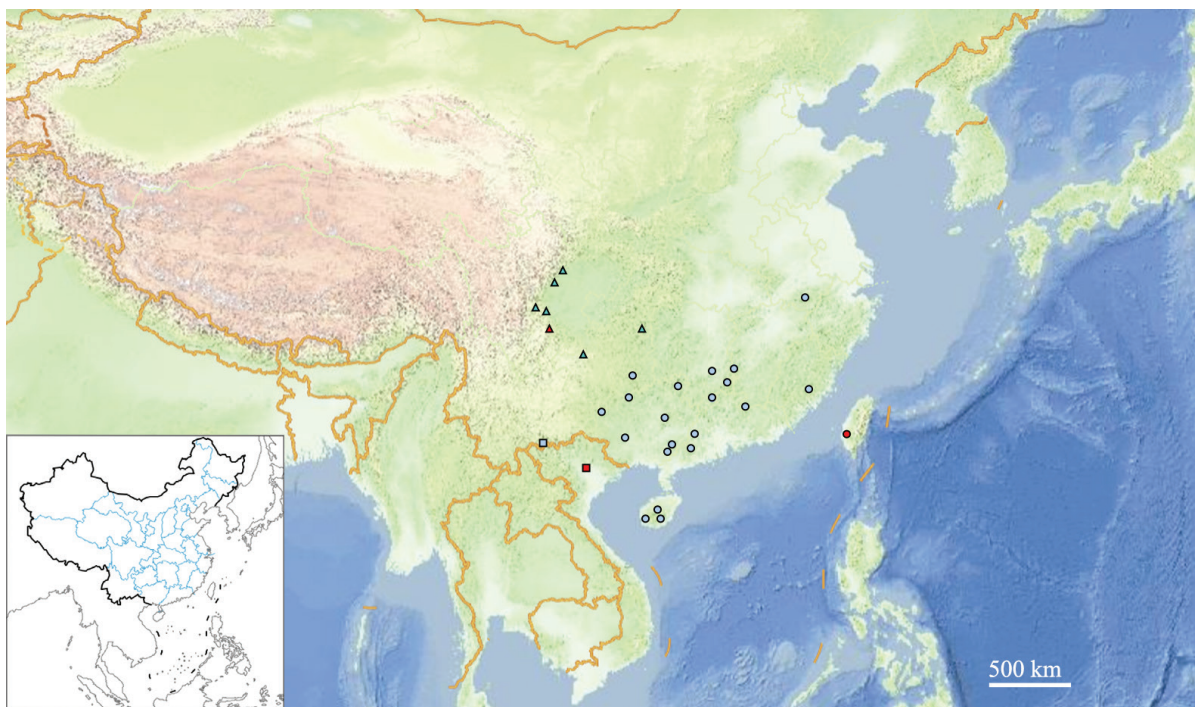


Figure 2. Distribution of *Hebius maximus* comb. nov. and re-defined distribution of *H. sauteri* in China based on museum collections, previous studies, and this study (Triangle: *Hebius maximus* comb. nov., round: *H. sauteri sauteri*, square: *H. sauteri bourreti*. Type localities are colored red).

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 the 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); 2 preoculars 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 subspecies *H. s. maximus* in this study.

Although superficially similar to *H. s. sauteri*, *H. s. maximus* can be distinguished from *H. s. sauteri* by

having a higher number of ventrals (132–138 in males, 135–143 in females in *H. s. maximus* vs. 125–130 in males, 116–133 in females 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 (usually white with black edge on the posterior part of 1st–3rd IfL only in *H. s. maximus* vs. white with black edge between each IfL in *H. s. sauteri*) (Table 4, 5; Fig. 3).

Consequently, all available data support the recognition 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 an expanded morphological description of both *H. s. sauteri* and *H. maximus* comb. nov.

Taxonomic accounts

Hebius sauteri (Boulenger, 1909)

Figs 2–6

Tropidonotus sauteri 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).

Amphiesma sauteri sauteri — Malnate 1962: 272.

Amphiesma 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)

Types. Syntypes. NHMUK (formerly BMNH) 1946.1.13.38–39, a male and a female.

Referred specimens. 19 specimens of *H. s. sauteri* were examined in this study: CHINA ($n = 19$) – **Taiwan Prov.** 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, Xingcun Township. – **Anhui Prov.** CIB 8483, Huangshan City. – **Jiangxi Prov.** 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 Prov.** 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 on outmost one or two rows; (3) ventral scales 116–133, subcaudals 60–86, 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 border the loreal; (7) infralabials 6–9, mostly edged with black on their posterior border; (8) single white to orange stripe extends 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 males, 145–455 mm in females), TL/ToL 0.24–0.33 (0.27–0.31 in males, 0.24–0.33 in females). Eye large, pupil round.

Dentition. Maxillary teeth 23–27 without diastema, gradually enlarged posteriorly, last two or three 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 males, 116–133 in females); subcaudals 60–86 (60–86 in females, 65–84 in males), paired.

Head scalation. Rostral broad, visible from above; internasals paired, nearly triangular, curved outwards, not in contact with loreal; prefrontals paired, nearly in a diamond shape, wider than long, border on loreal laterally, preocular and supraocular posteriorly; frontal hexagonal, longer than wide, embedded into parietal posteriorly; parietal paired, much longer than wide; nasals 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 in contact behind the mental, iFl 1–3, 1–4 or 1–5 border the anterior chin shields; temporals variable, in two or three rows, 1–2 + 1–3 + 0/2–3; chin shields paired, posterior pair longer (Figs 3, 5, Table 4).

Hemipenis. The description of the hemipenis is based on an adult 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 is 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 (Fig. 6).

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

Coloration in life. Based on two adult female specimens from Guangdong (CIB 118516) and Fujian (CIB 118517), China. Dorsal surface of the head reddish-brown with irregular grayish-green spots, a pair of elliptic orangish spots symmetrically present on inner sides of parietals, just separated by parietal sutures; ventral side of head whitish; 1st–5th supralabials white with black edges posteriorly, 6th or 6–7th brown on their upper part; infralabials white with black edge between each scale; an orange stripe extends from *angulus oris* to dorsal side of neck, 1–2 scales wide; dorsal surface of body and tail dark brown to reddish-brown, top with or without an ill-defined dark olive stripe scattered with black spots extends from neck to the end, a reddish-brown lateral streak on 4th–6th body scale rows extends from neck to tail

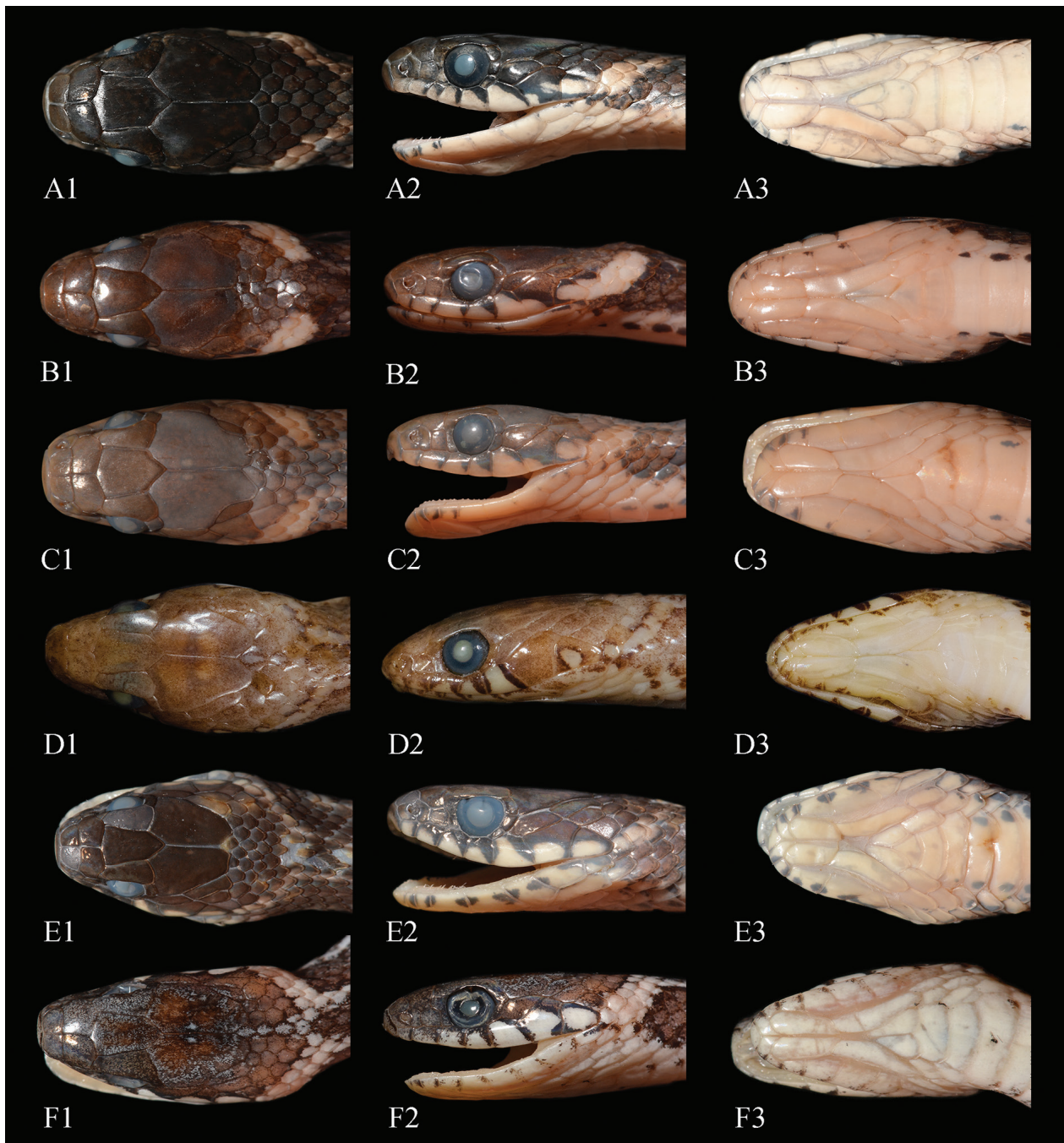


Figure 3. Dorsal (left), lateral (middle) and ventral (right) of the head comparisons between *Hebius sauteri* and *Hebius maximus* comb. nov. Row D photographed by Kai Wang, others were photographed by Jun-Jie Huang. **A–C.** *Hebius maximus* comb. nov. (A. CIB 118635, Mt. Laojun, Pingshan County, Sichuan, China; B. CIB 8482, Bijie City, Guizhou, China; C. CIB 8458, Yingjing County, Sichuan, China) **D–F.** *H. sauteri* (CAS 18984, Pingtung County, Taiwan, China; CIB 118516, Yinpingshan, Dongguan City, Guangdong, China; CIB 118517, Daiyun, Dehua County, Fujian, China).

with series of orange spots separated by 2–3 scales above; ventral and subcaudal sides cream white, with black spots on both ends of the ventral scale forming a chain-like pattern on the ventral view; sclera brown (Fig. 4).

Coloration in preservative. Largely the same as in life except dorsal side of head brown to dark brown, scattered with small black spots; ventral side of head cream white; a pale yellow stripe extends from *angulus oris* to dorsal side of neck, 1–2 scales wide; dorsal of body and tail brown to

dark brown, a lighter lateral streak on 4th–6th body scale rows presents or not, covered with series of cream white spots separated by 2–3 scales; ventral and subcaudal sides cream to pale white; sclera black (Figs 3, 5).

Etymology. *Hebius sauteri* was named after the collector of the type specimens, Hans Sauter (1871–1943), a German naturalist (Boulenger 1909). We suggest that the Chinese common name of this species remains unchanged, as “Zōng Hēi Fù Liàn Shé (棕黑腹链蛇)”.



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

Table 4. Morphological characters of *H. maximus* and *H. sauteri*. For specimens with asymmetrical cephalic scales, the scale count was given as “left/right”, “-” indicates missing data.

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

Natural history. This species inhabits flatlands and mountain regions up to 1,500 m and prefers terrestrial microhabitat such as grassland, woodland, and bushes near water bodies; diurnal, occasionally found at night, preys include earthworms, slugs, snails and tadpoles; oviparous (this study; Pope 1935; Zhao 2006; Xiang et al. 2009).

Distribution. *Hebius sauteri* is currently known to be reported in Vietnam (Ngan Son, Lang Son, Tam Dao and Ba Vi), and China, including Taiwan (Kaohsiung County [type locality]), Fujian (Dehua County), Anhui (Huangshan County), Jiangxi (Jinggangshan City, 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 (Qiongzong County,

Wuzhishan County, Baisha County, Lingshui County) (Deuve 1970; Wu 1985; Zhao 2006; Yang et al. 2008; Nguyen et al. 2009; Zhang 2009; Li 2011; Shen 2014; this study) (Fig. 2).

Remarks. *Natrix copei* (Van Denburgh, 1909) was described by Van Denburgh (1909) based on specimen form “Kanshirei” (now Guanziling), Tainan County, Taiwan Province, China, the description of this species was published just 20 days after that of *Tropidonotus sauteri* by Boulenger (1909) (now *Hebius sauteri*) (Stejneger 1910), Stejneger (1910) considered *Natrix copei* a synonym of *Natrix sauteri*. We examined the paratype of *Natrix copei*, and its morphological characters are in the range of variation of *H. sauteri*, which also supports the treatment of *Natrix copei* as an objective synonym by Stejneger (1910). The taxonomic status of the subspecies *H. s. bourreti* is discussed below.



Figure 5. Preserved specimen of *H. sauteri* (CAS 18988), from the type locality of the species, Guanziling, Tainan City, Taiwan, China. Not to scale. Photographs by Kai Wang.

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

Figs 2, 3, 7–11

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

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

Amphiesma sauteri maximus — Malnate 1962: 272.

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

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

Types. Holotype. FMNH 18796 (formerly CHNM 18796), a 457 mm adult female specimen (Fig. 7).

Paratypes. FMNH 18797, USNM 71570, USNM 84362.

Referred specimens. 25 specimens of *H. maximus* were examined in this study: CHINA ($n = 25$) – **Sichuan Prov.** CIB 118635, Pingshan County, Mt. Laojun near the type locality; CIB 8451–8452, CIB 8455, CIB 8464, CIB 8467, CIB 8470–8471, Emeishan City, Mt. Emei; CIB 8458, Yingjing County; CIB 8457, Hongya County; CIB 118518, CIB 107645–646, CIB 107649, Dayi County; YBU 18170, Dujiangyan City; CIB 94215–94216, Mianyang City. – **Chongqing.** CIB 8448, Youyang Tujia & Miao Autonomous County; YBU 11258, Xiushan Tujia & Miao Autonomous County. – **Guizhou Prov.** CIB 8482, SYS r002041, CIB 8484, CIB 118072–118074, Bijie City, Qixingguan District.

Diagnosis. *Hebius maximus* comb. nov. can be distinguished from its congeners by the following morphological characters: (1) body size small to medium, maximum ToL 597 mm; (2) dorsal scales rows 17-17-17, all weekly keeled or smooth at outmost one or two rows; (3) ventral scales 132–143, cloacal plates divided, subcaudals 64–92, paired; (4) maxillary teeth 24, last two distinct-

ly enlarged, without diastema; (5) supralabials 7–8; (6) infralabials 7–9, generally edged with black at posterior border on 1st–3rd scales only; (7) a light orange stripe extends from *angulus oris* to the neck; (8) dorsal body reddish brown or grayish brown, with an ill-defined dark olive streak scattered with black spots extending from neck to end at medium of the dorsal.

Description. Body elongated, small to medium-sized, ToL 175–597 mm (260–470 mm in males, 175–597 mm in females); tail relatively long, TL/ToL 0.25–0.33 (0.25–0.33 in males, 0.25–0.31 in females). Eye large, pupil round.

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

Body scalation. Dorsal scales in 17-17-17 rows, weekly keeled except outer 1–4 rows at anterior body, outer 0–2 rows smooth at midbody and outer 0–1 row smooth posteriorly; ventrals 132–143 (132–138 in males, 135–143 in females); cloacal plates divided; subcaudals 64–92 (72–92 in males, 64–82 in females), paired.

Head scalation. Rostral broad, visible from above; internasals paired, nearly triangular, curved outwards, not bordering loreal; prefrontals paired, nearly in a diamond

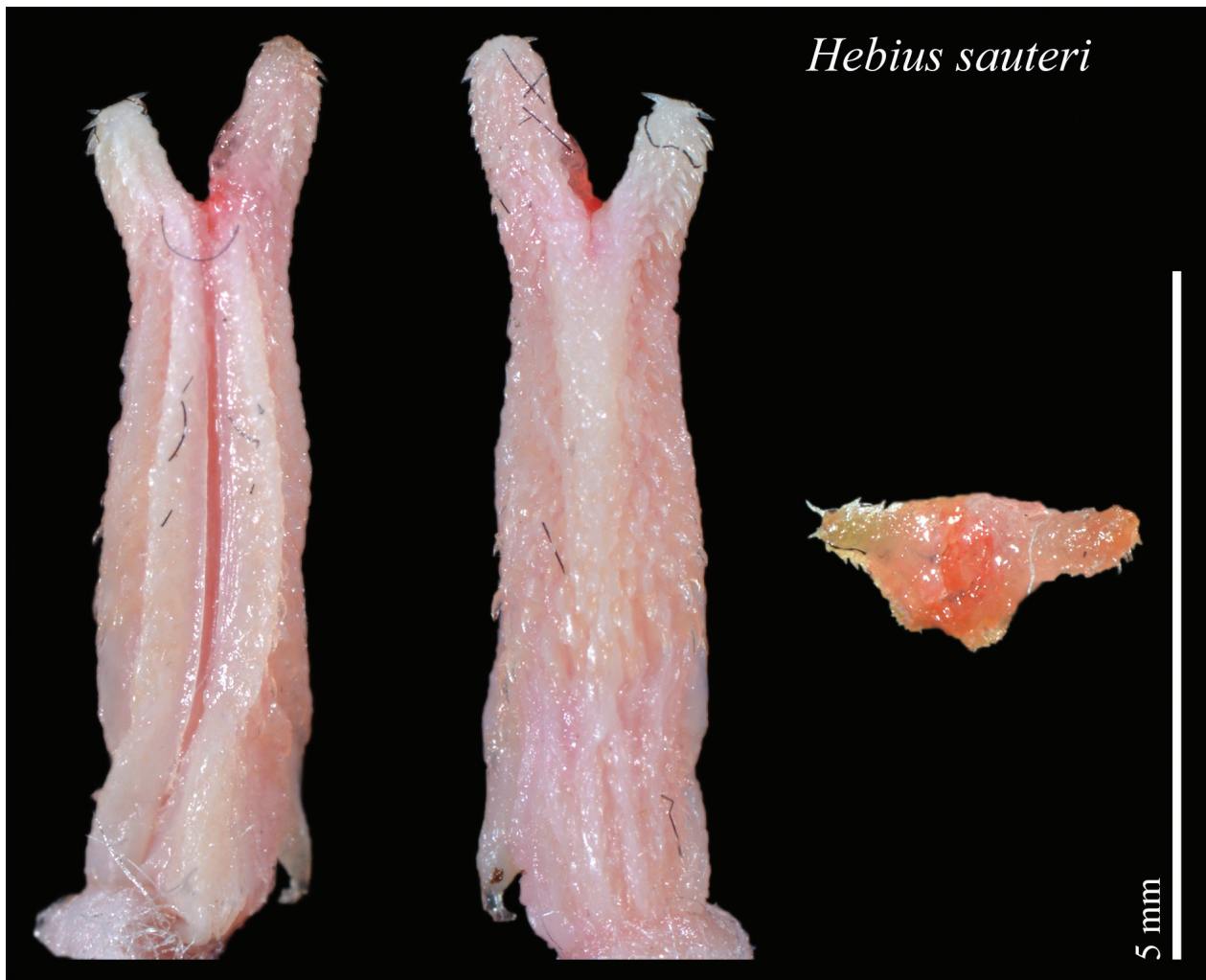


Figure 6. Photographs of the hemipenis of *H. sauteri* (SYS r000323, Mt. Jinggang, Jiangxi Province, China), photos from left to right showing sulcate, asulcate, and apical sides of the hemipenis. Photographs by Jun-Jie Huang.

shape, wider than long, borders the loreal, preocular, and supraocular; frontal hexagonal, longer than wide, embedded into parietals posteriorly; parietals paired, not bordering preocular; nasals wider than high, divided at lower half, borders 1st–2nd supralabials; loreal single, borders 2nd or 2nd–3rd supralabials, not entering orbit; preocular single, higher than wide, rarely divided (CIB 8484, CIB 8467, SYS r002041); supraocular single, narrowed anteriorly, much wider than high; postoculars 2–3; supralabials 7–8, 6th or 7th highest, 3rd–4th or 4th–5th entering orbit; temporals 1–2 + 1–3 + 0/2–4; infralabials 7–9, first pair in contact behind the mental, IfL 1–3, 1–4 or 1–5 border the anterior chin shields; chin shields paired, posterior pair longer (Figs 3, 8, Table 4).

Hemipenis. The description of hemipenis based on an adult specimen (CIB 118635) near the type locality, Yibin, Sichuan, southwestern China. The left side of hemipenis fully everted, whereas the right side remained *in situ* for description of retracted condition.

Hemipenis thin and short, hemipenial total length (HTL) 7.14 mm, hemipenial total width (HTW) 1.57 mm. HTL/HTW 4.55; Y-shaped, shallowly bilobed, hemipenial truncus length (HCL): 5.75 mm, HCL/HTL 0.81. Both sulcate and asulcate surfaces densely ornamented with spinules, a large basal hook present at the 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 (Fig. 10).

In situ hemipenis extends up to 5th SC with its crotch extending to 4th SC; crotch of *m. retractor penis magnus* extending to 6th SC, origin of *m. retractor penis magnus* invariably at level of 20th SC.

Coloration in life. Based on one male adult specimen near the type locality (CIB 118635). Dorsal side of head reddish brown with irregular dark and olive spots above; ventral side of head cream white; 1st–6th supralabials whitish with dark edges on posterior part; 7th supralabial reddish-brown at upper part and white with dark edge at lower part, 8th supralabial cream white, gradually turning to orange posteriorly; infralabials white, edged with black on posterior border on 1st–3rd scales only; an orange stripe extends from *angulus oris* to dorsal side of neck, two scales wide; dorsal body and tail reddish-brown with an ill-defined dark olive dorsal streak scattered with black spots extending from 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 (Fig. 8).

Coloration in preservative. Largely the same as in life except dorsal head brown to seal brown, with or



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



Figure 8. *Hebius maximus* comb. nov. **A.** SYS r002041, adult male, Wujing, Bijie, Guizhou, China; **B.** CIB 118635, adult male, Mt. Laojun, Pingshan, Sichuan, China; **C.** adult female, Mt. Emei, Sichuan, China. Photographs by Zhi-Tong Lyu (**A**) and Mao-Liang Li (**B, C**).

without irregular dark spots; supralabials cream white to pale gray, 1st–6th supralabials with black edge or spots posteriorly, upper half of the highest supralabial brown to black; a pale orange to yellow short stripe extends from *angulus oris* to neck; dorsal of 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 pale grey; sclera black (Fig. 9).

Sexual dimorphism. Males *H. maximus* comb. nov. exhibit a lower number of ventral scales [132–138

(136 ± 2) in male vs. 135–143 (138 ± 3) in female] and a higher number of subcaudal scale counts [72–92 (81 ± 6) in male vs. 64–82 (72 ± 5) in female] than female ($n = 13$ male and 12 female) (Tables 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. conelarus*, *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 vs. 19-19-17 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* (Peters 1871; Malkmus et al. 2002; David et al. 2005; David et al. 2015; Purkayastha and David 2019; David et al. 2021).

Hebius maximus comb. nov. differs from *H. atemporalis* by (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 usually on 1st–3rd scales only vs. white with black edge between each scale (Fig. 3, Tables 4, 5).

Etymology. *Hebius maximus* comb. nov. is named for 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.

Table 5. Comparison of main morphological characters of *H. maximus*, *H. s. sauteri*, “–” indicates missing data.

Species	TL/ToL		V		SC		V + SC		MT	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<i>H. maximus</i>	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	–
<i>H. s. sauteri</i>	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



Figure 9. Preserved specimen of *Hebius maximus* comb. nov., CIB 118635, adult male near the type locality of the species, Mt. Laojun, Pingshan Country, Sichuan, China. Photographs by Jun-Jie Huang.

Natural history. *Hebius maximus* comb. nov. inhabits subtropical mountain regions around 812–1,200 m above sea level, including coniferous forest and large forest clearings (Inger et al. 1990; This study). One specimen near the type locality (CIB 118635) was found on a road near a stream at dusk, emerging from a

cornfield. 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



Figure 10. Photographs of the hemipenis of *Hebius maximus* comb. nov., CIB 118635, Mt. Laojun, Pingshan, Sichuan, China, photos from left to right showing sulcate, asulcate, and apical sides of the hemipenis. Photographs by Jun-Jie Huang.

City), Sichuan, China, while 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 Yibin, Sichuan, China (Fig. 11).

Distribution. *Hebius maximus* comb. nov. is currently known to be 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 City, Mianyang City, Leshan City) and Guizhou (Qixingguan District, Bijie City) (this study; Wu 1985) (Fig. 2).

Discussion

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

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



Figure 11. Natural habitat of *Hebius maximus* comb. nov. on Mt. Laojun, Pingshan, Yibin, Sichuan, China. **A.** Macrohabitat; **B.** Microhabitat. Photographs by Mao-Liang Li.

H. maximus in having 35 maxillary teeth in No. 83017 vs. 24 in specimens from Sichuan. Thus, this record should be further studied in the future, and we doubt the distribution record of *H. maximus* from Yunnan, China. Consequently, we revised the distribution of *H. sauteri* and *H. maximus*, where *H. sauteri* is currently distributed in north Vietnam and southern China, including Taiwan Island and Hainan Island; while *H. maximus* is restricted in the mountain region of southwestern China (Fig. 2).

Despite the high resemblance between *H. maximus* and *H. sauteri*, which leads to great difficulty in species identification, *H. sauteri* and *H. maximus* are shown to be two distantly related clades (Fig. 1). Both species inhabit mountain regions and prey on earthworms, slugs, and tadpoles (Pope 1935; Wu 1985; Zhao et al. 1998; Zhao 2006). Combining with the phylogenetic relationships, it is supposed that this morphological resemblance may arise from convergent evolution, which should be discussed in further research (Wang et al. 2022).

Taxonomic status of *Hebius sauteri bourreti*

Three subspecies of *Hebius sauteri* were previously recognized based on the counts of ventral and subcaudal scales, i.e., *H. s. sauteri*, *H. s. bourreti*, and *H. s. maximus*. In the current study, *H. s. maximus* is recognized as a distinct

species, i.e. *Hebius maximus* (see above). However, the taxonomic identity of the subspecies *H. s. bourreti* still remained elusive. The taxa *H. s. bourreti* was originally described by Malnate (1962) based on six specimens from Tam Dao, Vinh Phuc Province, northern Vietnam, which differs from the other two subspecies by having a fewer number of ventrals (123–130) than in *H. s. sauteri* (116–133) and in *H. s. maximus* (132–143), a fewer number of subcaudals (60–73) than in *H. s. sauteri* (69–86) and in *H. s. maximus* (64–92) and by the color pattern (supralabials posterior to the eye often in the form of a light, dark-edged stripe, continuous with the nuchal crescent; dorsal color dark brown; ventral pattern strongly developed, especially subcaudally).

Yang et al. (2008: 266) reported one specimen of *H. s. bourreti* from Adebo Town, Jinping County, Yunnan China (Fig. 2). No other specimen of *H. s. bourreti* has been recorded in China. Our extended examination of *H. s. sauteri* reveals that the body and head scale counts of *H. s. bourreti* are largely overlapping 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 body; another specimen of *H. sauteri* (CIB 118516) from Guangdong, China also shows strong ventral pattern, which is similar to *H. s. bourreti*.

Table 6. Morphological comparison of *H. s. sauteri* and *H. s. bourreti*.

Subspecies	PrO	PtO	SpL	Ifl	TEM	V	SC	TL/ToL
<i>H. s. sauteri</i>	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
<i>H. s. bourreti</i>	1	2–3	2–2–3	7–8	1(2) + 1(2)	123–130	60–73	0.27–0.30

Based on the comparisons discussed above, none of these morphology characters provided by Malnate (1962) could accurately distinguish *H. s. bourreti* from *H. s. sauteri*. Therefore, we suggest that *H. s. bourreti* is likely to be a synonym of *H. s. sauteri* which would make *H. sauteri* a monotypic species. More molecular evidence is needed to further confirm this suggestion.

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