




## Article

# Taxonomic Review of the Genus *Herpetoreas* (Serpentes: Natricidae), with the Description of a New Species from Tibet, China

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**Abstract:** The taxonomic history of the *Amphiesma sensu lato* has long been confused, and this complex was recently divided into three genera, i.e., *Amphiesma* Duméril, Bibron, and Duméril, 1854 *sensu stricto*, *Hebius* Thompson, 1913, and *Herpetoreas* Günther, 1860. Being the least known genus, *Herpetoreas* is reviewed herein through an integrative taxonomic approach. Our results indicate that specimens previously referred to *Hebius parallelus* (Boulenger, 1890) from Mêdog, Tibet, China, represent a new species. We describe here this new species and refer it to the genus *Herpetoreas*; therefore, we remove *Hebius parallelus* from the Chinese herpetofauna. A diagnostic key to all the species of *Herpetoreas* is also provided. Furthermore, we re-evaluate the diagnostic characters of the three genera formerly confused with *Amphiesma*, namely, *Amphiesma*, *Hebius*, and *Herpetoreas*. We provide a key to these three morphologically similar genera. We also emphasize the importance of the maxillary teeth and hemipenial morphology in the generic diagnosis in the family Natricidae.

**Keywords:** diagnostic key; hemipenis; Himalayas; misidentification; taxonomic revision



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## 1. Introduction

The taxonomic history of the genus *Amphiesma* Duméril, Bibron, and Duméril, 1854 has long been confused and controversial mainly due to their morphological similarities, wide distribution, and cryptic diversity [1–3]. Species of this genus have successively been placed in the genera *Tropidonotus* Boie, 1826 and *Natrix* Laurenti, 1768 [1,4–6]. A first wide-scale revision of the genus *Natrix sensu lato* was provided by Malnate [1]. Guo et al. [3] subsequently divided *Amphiesma* into three genera, i.e., *Amphiesma*, *Hebius* Thompson, 1913, and *Herpetoreas* Günther, 1860 based on phylogenetic analysis. After this generic division, the genus *Amphiesma* became monotypic, including only the well-known species *Amphiesma stolatum* (Duméril, Bibron, and Duméril, 1854) while the genus *Hebius* represents the most speciose genus of Natricidae [3]. The third genus, in contrast, *Herpetoreas* mainly distributed in the southern foothills of the Himalayas, represents a lesser-known group among the three former genera of *Amphiesma sensu lato* [3,7].

After its revalidation, the genus *Herpetoreas* (type species: *Herpetoreas sieboldii* Günther, 1860, by monotypy) included only three species, namely, *Her. sieboldii*, *Her. platyceps* (Blyth, 1854), and a newly described species, *Her. burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang & Pyron, 2014. Guo et al. [3] suggested that *Herpetoreas* might include additional species temporarily referred to *Hebius*. Two more *Hebius* species, i.e., *Heb. xenura* (Wall, 1907) and *Heb. pealii* (Sclater, 1891), were successively found to be nested within the genus

*Herpetoreas* instead of *Hebius* and thus moved to the former genus [7,8]. However, little remains known about *Herpetoreas* species, mainly because some are known only from a handful of specimens [8]. Previous old records have not been re-evaluated [3,9]. Although Guo et al. [3] recommended that further taxonomic revision may be necessary in the future, previous studies only focused on generic assignments of the *Herpetoreas* members. No taxonomic review of the genus *Herpetoreas* had been previously published [7,8].

More importantly, the generic assignments of many species of *Amphiesma sensu lato* remain elusive. For example, many species were found to be assigned to the wrong genus [7,8]. Most recently, Deepak et al. [10] also indicated the non-monophyly of the genus *Hebius*, and transferred *Heb. monticola* (Jerdon, 1854) to the genus *Amphiesma* (to be *Amphiesma monticulum*) based on their multilocus phylogeny of natricid snakes. Such a widespread wrong generic affiliations within the genus *Amphiesma sensu lato* were mainly due to their morphological similarities [3]. Thus, the re-evaluation of the definition of generic boundaries is sorely needed.

In the genus *Hebius*, David et al. [11] revised the complex of species of *Hebius parallelus* (Boulenger, 1890). These authors revalidated *Hebius clerki* (Wall, 1925), long considered a synonym of *Heb. parallelus*, and confined the distribution area of *Heb. parallelus* to the Khasi Hills and Naga Hills, in Northeast India. On the contrary, *Heb. clerki* has a much wider distribution, from Sikkim (Northeast India) to Yunnan Province (southwestern China) across northern Myanmar. As a consequence, records of *Heb. parallelus* from Yunnan were referred to *Heb. clerki* [11].

Zhao et al. [12] recorded *Heb. parallelus* (as *Amphiesma parallela*) based on two specimens from Mêdog County, Xizang Autonomous Region (Tibet), China. Their identifications have not been re-evaluated and still remain unknown; no comment on the generic assignment of these specimens was provided by David et al. [11]. Che et al. [13] recently found specimens from Tibet, identified as *Hebius cf. parallelus*, to be clustered within *Herpetoreas* lineages and sister to *Her. burbrinki*, and thus transferred *Hebius cf. parallelus* to *Herpetoreas*, as *Herpetoreas cf. parallelus*. However, the taxonomic identity of *Herpetoreas cf. parallelus* recorded from Mêdog, Tibet, remained unsettled since major morphological differences exist between the Tibetan population and the original description of *Heb. parallelus* [13,14].

In the present study, we re-evaluate the taxonomic status of the *Herpetoreas* specimens from China through an integrative taxonomy approach. Results indicate that specimens of *Herpetoreas cf. parallelus* from Mêdog (Tibet) are clearly different from *Hebius parallelus* and other members of *Herpetoreas*. Specimens from Mêdog represent an undescribed species that we describe here. Furthermore, we provide detailed taxonomic accounts of the genus *Herpetoreas* and a diagnostic key to all members of this genus. To avoid further taxonomic confusions of *Amphiesma sensu lato*, a preliminary diagnostic key to the genera *Amphiesma*, *Hebius*, and *Herpetoreas* is also provided based on pholidosis, maxillary teeth, and hemipenial morphology.

## 2. Materials and Methods

**Sampling.** Two female specimens were newly collected from Mêdog, Tibet, PR China. After collection, snakes were euthanized, and fresh liver tissues were taken and preserved in 95% ethanol prior to the fixation of specimens in 10% buffered formalin. Specimens were transferred to 75% ethanol after three days for permanent storage, and deposited in the Herpetological Museum, Chengdu Institute of Biology, Chinese Academy of Sciences (CIB), PR China. Other *Herpetoreas* specimens were also examined based on museum collections (Appendix A), additional museum abbreviations see below.

**Museum abbreviations.** ANU—Anhui Normal University Museum, Wuhu, China. CAS—California Academy of Sciences, San Francisco, USA. BNHS—Bombay Natural History Society, Museum, Mumbai, India. CIB—Herpetological Museum, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China. FMNH—The Field Museum, Chicago, USA. IMC—Indian Museum, Calcutta, India (no longer extant, now = ZSI). KIZ—Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China. KSC—

Kohima Science College, Kohima, India. **MCZ**—Department of Herpetology, Museum of Comparative Zoology, Harvard University, Cambridge, USA. **MHNG**—Museum d’Histoire Naturelle, Geneva, Switzerland. **MNHN**—Muséum National d’Histoire Naturelle, Paris, France. **NHMUK** (formerly BMNH)—The Natural History Museum, London, United Kingdom. **NMW**—Naturhistorisches Museum Wien, Vienna, Austria. **ROM**—Royal Ontario Museum, Toronto, Canada. **SICAU**—Sichuan Agricultural University, Ya’an, China. **SYS**—The Museum of Biology, Sun Yat-sen University, Guangzhou, China. **UMMZ**—Museum of Zoology, University of Michigan, Ann Arbor, USA. **USNM**—National Museum of Natural History [formerly United States National Museum], Smithsonian Institution, Washington, D.C., USA. **VNMN**—Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi, Vietnam. **YBU**—Yibin University, Yibin, China. **ZISP**—Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia. **ZMB**—Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany. **ZSI/ERS**—Zoological Survey of India (Eastern Regional Station), Shillong, India.

**Morphological data.** Definitions of pholidosis characters and their counting methods mainly followed Zhao [15], as follows: internasals (IN), prefrontals (PrF), frontals (F), parietals (P), loreals (L), preoculars (PrO), postoculars (PtO), supraoculars (SpO), suboculars (SbO), supralabials (SpL), infralabials (IfL), anterior temporals (aTEM), posterior temporals (pTEM), chin shields (CS), dorsal scale rows (DSR), ventrals (VEN), and subcaudals (SC). Dorsal scale rows were taken at one head length behind head, at midbody, and at one head length before cloaca, respectively. The number of ventral plates is counted according to Dowling [16], the counting method of supracaudal scales reduction followed Malnate et al. [17]. Symmetric characters were given as left/right and averages were used in the analyses. In addition, maxillary teeth (MT) of the left sides were also counted under microscope.

External measurements and methods followed Ren et al. [2], all measurements were made with digital calipers to the nearest 0.1 mm. Morphometric characters and measurements were taken as follows: total length (TL): distance from the tip of the snout to the tip of tail; snout-vent length (SVL): distance from the tip of the snout to the posterior margin of cloaca; tail length (TaL): distance from the posterior margin of cloaca to the tail tip; head length (HL): distance from the tip of the snout to the posterior margins of the parietals; head width (HW): maximum head width. The following ratios were also obtained from raw measurements, including TaL/TL: ratio tail length/total length; HL/HW: ratio head length/head width.

**Hemipenial morphology.** The hemipenial materials were prepared from left side of preserved, adult male specimens, everting methods were adapted from Myers et al. [18], Pesantes [19], Zaher et al. [20], Jiang [21]. The descriptive terminology of hemipenial morphology follows Cope [22], Dowling et al. [23], Zhang et al. [24]. Everted hemipenes were 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 (Helicon Soft Ltd., Kharkiv, Ukraine).

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

**Molecular analyses.** Genomic DNA was extracted from macerated liver or muscle tissue samples using an Ezup Column Animal Genomic DNA Purification Kit (Sangon Biotech, China), according to the protocols of the manufacturer. Primer pairs used for amplification and sequencing included L14910/H16064 [25] for cytochrome b (Cyt *b*), 16Sar-L/16Sar-H [26] for 16S rRNA (16S), and S77/S78 [27] for oocyte maturation factor MOS

(CMOS). PCR products were purified and then sequenced in both directions using an ABI 3730xL sequencer by Sangon Biotech Co., Ltd. (Chengdu, China).

Initial nucleotide sequences were verified using Geneious Pro 4.8.4 [28] and translated into amino-acid sequences for quality check, and then deposited in GenBank (Table 1). In addition to our newly generated sequences, we included homologous sequences of all available *Herpetoreas* members from GenBank. *Sibynophis subpunctatus* was chosen to root the tree based on previous phylogenetic studies [29]. Sequences were aligned using MEGA 10.1.6 [30] with default settings and checked visually for minor manual justifications.

**Table 1.** Sequences of *Herpetoreas* and related taxa used in this study.

Species	Voucher No.	Locality	GenBank Accession No.		
			Cyt <i>b</i>	16S	CMOS
<i>Afronatrix anoscopus</i>	ROM 19842	Liberia	AF420073	-	AF471123
<i>Amphiesma stolatum</i>	GP 901	China: Guizhou	JQ687432	-	JQ687450
<i>Amphiesma stolatum</i>	GP 2213	China: Guangdong	KJ685693	-	KJ685643
<i>Amphiesma stolatum</i>	GP 2250	China: Taiwan	KJ685702	-	KJ685652
<i>Blythia hmuifang</i>	PUCZM/X/SL2	India: Mizoram	MN993854	MT003011	MN993862
<i>Blythia hmuifang</i>	MZMU 715	India: Mizoram	MN993853	MT003010	MN993861
<i>Blythia reticulata</i>	AD5618	India	-	MT003015	MN993890
<i>Blythia reticulata</i>	PUCZM/X/SL223	India: Mizoram	MN993855	MT003012	MN993863
<i>Fowlea yunnanensis</i>	CIB 106884	China: Yunnan	MT199264	-	-
<i>Hebius atemporalis</i>	GP 2318	China: Yunnan	KJ685695	-	KJ685645
<i>Hebius bitaeniatus</i>	GP 2402	China: Guizhou	KJ685698	-	KJ685648
<i>Hebius bouleengeri</i>	GP 2134	China: Hainan	KJ685691	-	KJ685641
<i>Hebius chapaensis</i>	VNMN 06102	Vietnam: Lao Cai	MH778702	-	-
<i>Hebius clerki</i>	CAS 215036	China: Yunnan	KJ685666	-	KJ685615
<i>Hebius craspedogaster</i>	GP 139	China: Sichuan	JQ687429	-	JQ687437
<i>Hebius johannis</i>	GP 897	China: Yunnan	KJ685708	-	KJ685658
<i>Hebius khasiensis</i>	CAS 221525	Myanmar: KaChin state	KJ685669	-	KJ685618
<i>Hebius modestus</i>	CAS 234262	China: Yunnan	KJ685671	-	KJ685620
<i>Hebius popei</i>	GP 2169	China: Hainan	KJ685692	-	KJ685642
<i>Hebius sauteri</i>	GP 2549	China: Taiwan	KJ685701	-	KJ685651
<i>Hebius venningi</i>	CAS 233206	Myanmar: KaChin state	KJ685670	-	KJ685619
<i>Hebius vibakari</i>	GP 1352	China: Heilongjiang	KJ685677	-	KJ685627
<i>Herpetoreas burbrinki</i>	YBU 071128	China: Tibet	GQ281781	-	JQ687443
<i>Herpetoreas pealii</i>	WII-ADR547	India	MT571586	MT578065	MT571590
<i>Herpetoreas platyceps</i>	GP 2096	China: Tibet	KJ685690	-	KJ685640
<i>Herpetoreas platyceps</i>	KIZ YPX26317	China: Tibet, Gyirong	MW111464	-	MW111514
<i>Herpetoreas cf. platyceps</i>	WII-ADR183	India	MT571587	MT578066	-
<i>Herpetoreas tpser</i> <b>sp.nov.</b>	CIB 107855	China: Tibet, Mêdog	OM313292	OM339162	OM313294
<i>Herpetoreas tpser</i> <b>sp.nov.</b>	CIB 118524	China: Tibet, Mêdog	OM313293	OM339163	OM313295
<i>Herpetoreas tpser</i> <b>sp.nov.</b>	KIZ 06681	China: Tibet, Mêdog	MW111476	-	MW111503
<i>Herpetoreas xenura</i>	PUCZM/X/SL1	India: Mizoram	MN993850	MT003007	MN993858
<i>Herpetoreas xenura</i>	PUCZM/X/SL16	India: Mizoram	MN993851	MT003008	MN993859
<i>Herpetoreas xenura</i>	PUCZM/X/SL17	India: Mizoram	MN993852	MT003009	MN993860
<i>Lycognathophis seychellensis</i>	SM165	Seychelles: Mahé	MW711494	MW699983	MW711550
<i>Macropisthodon rudis</i>	GP 1266	China: Guizhou	JQ687434	-	JQ687452
<i>Natriciteres olivacea</i>	CAS 220640	DR Congo	AF471058	-	AF471146
<i>Natrix natrix</i>	LSUMZ 41506	England: Kent	AY866544	-	AF471121
<i>Opisthotropis latouchii</i>	GP 647	China: Fujian	GQ281783	-	JQ687446
<i>Rhabdophis nuchalis</i>	GP 251	China: Sichuan	GQ281786	-	JQ687438
<i>Rhabdophis tigrinus</i>	GP 613	China: Liaoning	GQ281785	-	JQ687444
<i>Sibynophis subpunctatus</i>	RAP 0491	-	KC347471	KC347373	KC347411
<i>Thamnophis sirtalis</i>	-	-	AF402929	-	DQ902094
<i>Trachischium fuscum</i>	AD5608	India	-	MT003016	MN993886
<i>Trachischium guentheri</i>	ADR502	India	MN993892	MT003017	MN993887
<i>Trachischium laeve</i>	AD5763	India	-	MT003018	MN993888
<i>Trachischium monticola</i>	GP 1487	China: Tibet	JQ687435	-	JQ687453
<i>Trachischium tenuiceps</i>	KIZ 011134	China: Tibet	MN306289	-	MW111500
<i>Trimerodytes annularis</i>	GP 889	China: Jiangxi	JQ687431	-	JQ687449

"-" indicates missing data.

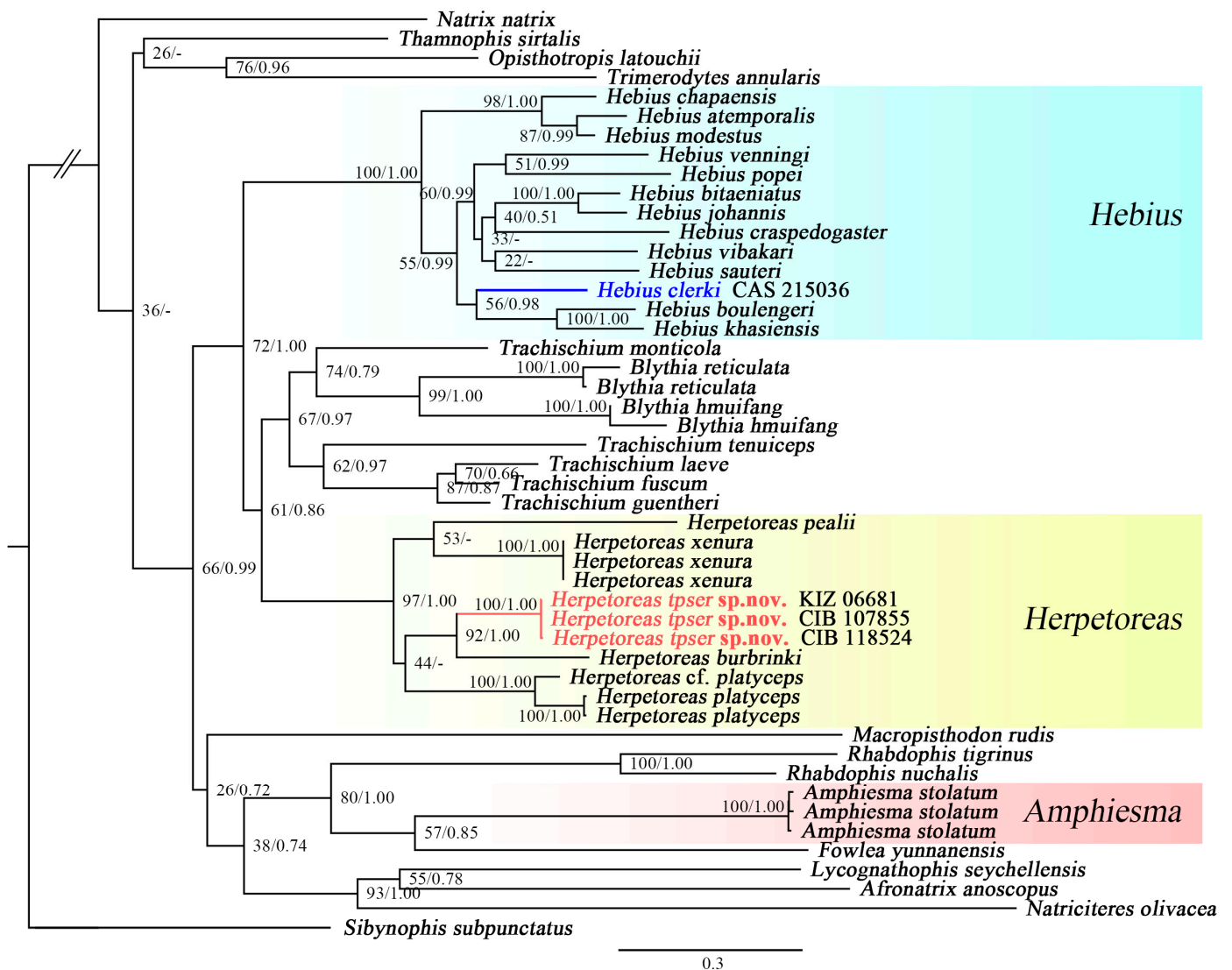
Maximum likelihood (ML) analysis was conducted in RAxML v8.2.10 [31] under the best-fit substitution model (GTRGAMMA) based on the AIC criterion, as implemented in PartitionFinder 2 [32]. Bootstrap proportions (BSP) were investigated with 1000 bootstrap

replicates using the fast-bootstrapping algorithm, otherwise under default parameters. Bayesian inference (BI) analyses were performed in MrBayes 3.2.6 [33], two Markov chain Monte Carlo (MCMC) initiated from random trees and run for  $1 \times 10^7$  generations and sampled every 100 generations, the first 25% of trees were discarded as “burn-in”. Convergence of MCMC chains and effective sampling size (ESS) were checked in Tracer 1.6 [34], ensuring a sample size > 200 for all parameters.

### 3. Results

#### 3.1. Phylogenetic Analyses

The final alignment of the three gene dataset consisted of 2149 bp, and includes 1074 bp from Cyt *b*, 503 bp from 16S, and 572 bp from CMOS. GTR+G was selected as the best-fit model for both ML and BI analysis. For phylogenetic analyses, a majority rule consensus tree inferred from BI was consistent with the ML tree, and the topologies of our results are largely agreeing with previous analysis (Figure 1) [3,8,10,13].



**Figure 1.** Maximum likelihood (ML) phylogenetic tree inferred from mtDNA Cyt *b*, 16S, and nuDNA gene CMOS, depicting phylogenetic relationships of *Herpetoreas* and related genera in Natricidae. Numbers above branches are bootstrap proportions and Bayesian posterior probability (BSP/BPP), respectively. “-” indicates different topologies between Bayesian inference phylogenetic tree and ML tree.

Among our sample, three genera of *Amphiesma sensu lato* were recovered as strongly supported clades within the family Natricidae, that were highly diverged with long basal branch lengths. The genus *Herpetoreas* was recovered as monophyletic with current samplings (BSP = 97/BPP = 1.00). Although interspecific relationships among congeners within *Herpetoreas* were not fully resolved, the final consensus tree yielded high supportive values (BSP > 70; BPP > 0.95) for key nodes concerning the relationship between the Tibetan population with recognized congeners. The Tibetan population was recovered as a highly diverged monophyletic clade (BSP = 100/BPP = 1.00) within *Herpetoreas*, which was sister to *Herpetoreas burbrinki* (BSP = 92/BPP = 1.00). The sequences considered to be *Herpetoreas* cf. *parallelus* (KIZ 06681) by Che et al. [13] showed no genetic divergence to our newly sequenced Tibetan population (marked in red), and we consider them to be conspecific. The sample of *Hebius clerki* (CAS 215036, marked in blue) from Nujiang County, Yunnan Province, China, previously misidentified as *Hebius parallelus*, was nested within the genus *Hebius* (Figure 1; Table 1).

Although the Tibetan population was previously identified as *Hebius parallelus*, morphological comparisons indicate that the Tibetan population is easily distinguished by a suit of characters against *Hebius parallelus* (see Comparison below). Furthermore, the Tibetan population is recovered to be a distinct evolutionary lineage of the genus *Herpetoreas* (Figure 1), and morphologically differs from all known species of this genus (Table 2). Therefore, we describe the Mêdog population of *Herpetoreas* as a new species herein. On the generic level, we review the taxonomic history of *Herpetoreas*. Moreover, in despite of the fact that phylogenetic definitions of *Amphiesma sensu lato* have been clarified [3], the morphological difference of *Amphiesma sensu lato* still remains unknown. Based on morphological comparisons of specimens from *Amphiesma sensu lato*, we provide diagnostic characters and a diagnostic key to the genera *Amphiesma*, *Hebius*, and *Herpetoreas*.

**Table 2.** Morphological comparisons among congeners of the genus *Herpetoreas*. “-” indicates missing data.

Species	<i>Herpetoreas platyceps</i>	<i>Herpetoreas sieboldii</i>	<i>Herpetoreas pealii</i>	<i>Herpetoreas xenura</i>	<i>Herpetoreas burbrinki</i>	<i>Herpetoreas tpser</i> sp. nov.
	<i>n</i> = 29	<i>n</i> = 54	<i>n</i> = 2	<i>n</i> = 3	<i>n</i> = 2	<i>n</i> = 6
TL	755–927	729–943	451–660	590–660	646–757	387–679
TaL	-	-	117–150	160–190	184–230	108–207
TaL/TL	0.232–0.286	0.242–0.300	0.227–0.259	0.271–0.302	0.285–0.304	0.262–0.317
DSR	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17
cloacal	divided	divided	single	single	divided	divided
SC condition	divided	divided	divided	single	divided	divided
VEN	180–234	168–216	136–142	158–165	169–172	153–167
SC	78–99	81–111	69–77	82–105	94–96	79–97
1st SC6	9th	25th–28th	-	-	22th–23th	13th–30th
SC6	23	27–38	-	-	40–41	25–31
SC4	33	20	-	-	-	33–41
SC4/SC6	1.43	0.53	-	-	-	1.06–1.64
SpL	2-3-3	2-3-3	3-2-4	3-2-4	2-3-3	2-3-3 or 3-3-3
IfL	8–10	9–10 (11)	10	9–10	10	9–10 (8)
PrO	1	1	1	1	1–2	1 (2)
PtO	3	3	3	3	3	3 (2)
aTEM	1–2	1–2	2	2	2–3	1–2 or (1 + 1/1)
pTEM	1–2 (3)	1–2	2	2	2	2, 1–2 + 2 or 1/(1 + 2)
Maxillary teeth	18–22	19–23	13–21	22–23	21	20–21
Posterior	last two	last two	last two	gradually	? 1	last two
maxillary teeth	enlarged	enlarged	enlarged	enlarged	? 1	enlarged
Diastema	present, small gap	present, small gap	present, small gap <sup>2</sup>	present, small gap <sup>2</sup>	? 1	present, small gap

Table 2. Cont.

Species	<i>Herpetoreas platyceps</i>	<i>Herpetoreas sieboldii</i>	<i>Herpetoreas pealii</i>	<i>Herpetoreas xenura</i>	<i>Herpetoreas burbrinki</i>	<i>Herpetoreas tpser</i> sp. nov.
<i>sulcus spermaticus</i>	single, extends to tip	single, extends to tip	single	-	-	single, extends to crotch
VEN color	usually immaculate	darkened posteriorly	pale with brown patches	whitish or yellowish	creamish-beige	reddish orange
VEN lateral blotch	present or absent	usually absent	present, continuous	present, discontinuous	present, discontinuous	present, discontinuous
Source	Das et al. [8], Malnate [35], this work	Das et al. [8], Malnate [35]	Das et al. [8]	Smith [6], Das et al. [8], Wall [36]	Guo et al. [3], Peng et al. [37], this work	This work

<sup>1</sup> Data missing in holotype because of damage; given in Peng et al. [37] as “Maxillary teeth are 21 in continuous series, last 15 enlarged”, which is a highly isolated condition in the genus *Herpetoreas*, further confirmation is needed. <sup>2</sup> Given in Das et al. [8] as “a small gap but without diastema”, whereas we consider that the “small gap” is homologous with diastema, thus referred both of them as “diastema” in this work.

### 3.2. Taxonomic Account

#### *Herpetoreas* Günther, 1860

Figures 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11A.

*Herpetoreas* Günther, 1860, *Proc. Zool. Soc. London*, 1860 (1): 156–157 [38]. Type species: *Herpetoreas sieboldii* Günther, 1860.

**Type species.** *Herpetoreas sieboldii* Günther, 1860 by monotypy.

**Contents.** The genus *Herpetoreas* currently includes six species:

*Herpetoreas platyceps* (Blyth, 1854)

*Herpetoreas sieboldii* Günther, 1860

*Herpetoreas pealii* (Sclater, 1891)

*Herpetoreas xenura* (Wall, 1907)

*Herpetoreas burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang, and Pyron, 2014

*Herpetoreas tpser* sp. nov., herein described.

**Diagnosis.** (1) Head moderately distinct from neck; (2) body cylindrical, maximum TL 660–943 mm; (3) tail relatively long, TaL/TL 0.227–0.317; (4) nostrils and eye directed laterally; (5) supralabials 8–9, usually 3rd–5th or 4th and 5th entering orbit; (6) dorsal scale rows 19–19–17; weakly to distinctly keeled, notched at their apical part; (7) ventrals 136–234; (8) cloacal plate and subcaudals divided or not; (9) maxillary teeth 13–23, slightly enlarged posteriorly, last two to three distinctly enlarged, separated from anterior teeth by a small diastema; (10) hemipenis short and thin, shallowly bilobed, spinous throughout with single basal hook; (11) *sulcus spermaticus* single, centripetal, extends to the inner right lobe or to the crotch only; (12) apical naked area on the crotch weakly developed, not protruding, not visible from asulcate surface; (13) venter yellowish-beige, each ventral scale decorated with dark spots at lateral edge or not (Figures 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11A).

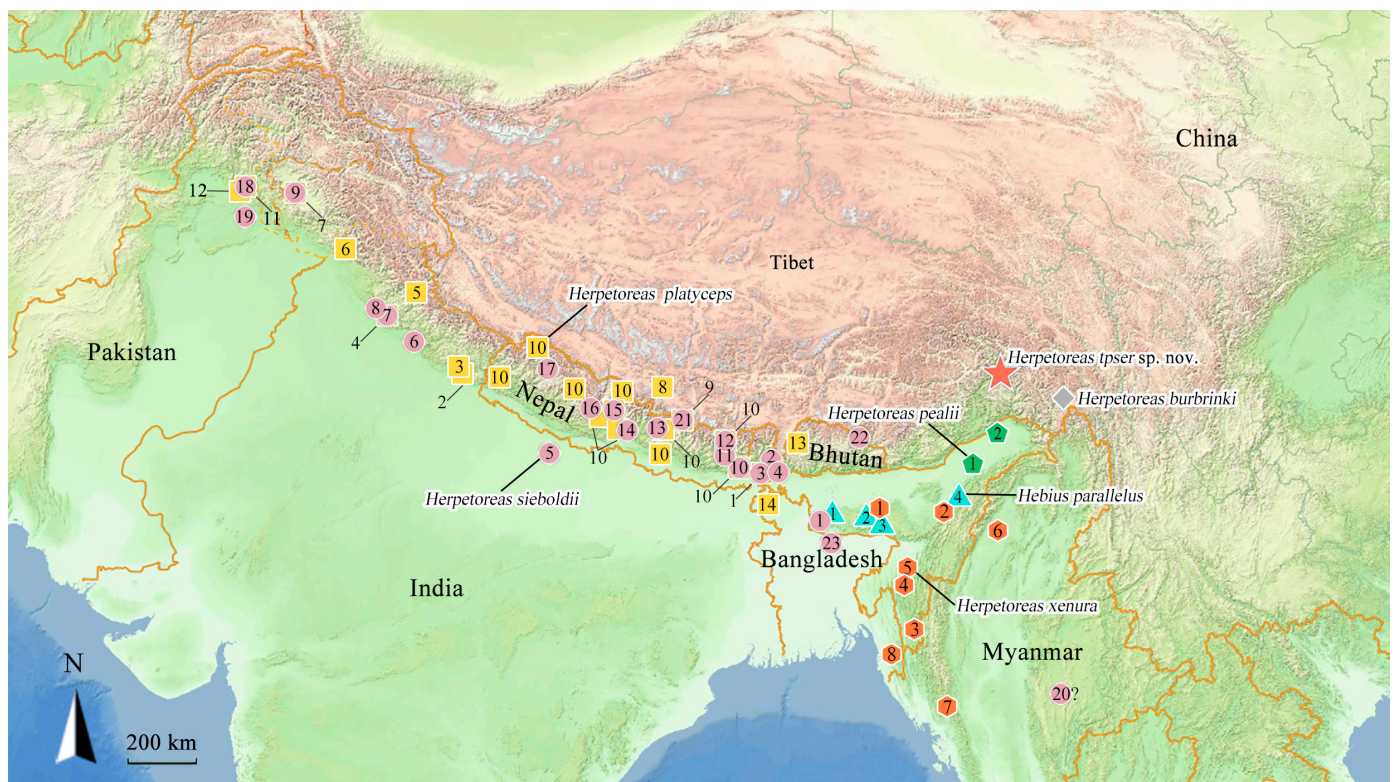
#### Key to species of *Herpetoreas*

- 1A Subcaudals single.....*H. xenura*
- 1B Subcaudals divided.....2
- 2A Cloacal plate single.....*H. pealii*
- 2B Cloacal plate divided.....3
- 3A Ventrals fewer than 168..... *H. tpser* sp. nov.
- 3B Ventrals no less than 168.....4
- 4A Tail relatively long, TaL/TL > 0.300.....*H. burbrinki*
- 4B Tail relatively short, TaL/TL ≤ 0.300.....5
- 5A A high proportion of the length of the tail with 4 supracaudal scale rows to that with 6 supracaudal scale rows high, SC4/SC6 = 1.43.....*H. platyceps*
- 5B A low proportion of the length of the tail with 4 supracaudal scale rows to that with 6 supracaudal scale rows high, SC4/SC6 = 0.53.....*H. sieboldii*

**Etymology.** The etymology of the genus nomen of *Herpetoreas* was not specified by Günther [38]. It consists of the Greek noun “*herpeton*”, meaning “reptiles”, and of the Greek substantive *ορειος*, oreios, seemingly latinized in *oreas*, meaning “living or inhabiting mountains”. Based on this substantive, the grammatical gender of *Herpetoreas* is masculine.

We suggest “Himalaya Mountain Keelback” as its English common name, and Xǐ Shān Fù Liàn Shé Shǔ (喜山腹链蛇属) as its Chinese common name.

**Distribution.** The distribution pattern of *Herpetoreas* species is typical of distinct biogeographic boundaries, members of this genus are mainly known from southern foothills of the Himalaya Mountains as well as Eastern Himalayas, including northeastern Pakistan, northern and northeastern India, southwestern China (Tibet), Nepal, Bangladesh, Bhutan, and Myanmar (Figure 2).



**Figure 2.** General distribution map of members of *Herpetoreas* and *Hebius parallelus*, star represents the type locality of *Herpetoreas tpser* sp. nov. from Mêdog County, Xizang Autonomous Region (Tibet), China; rhombus represents the locality of *Her. burbrinki*; pentagon: *Her. pealii*; hexagon: *Her. xenura*; square: *Her. platyceps*; circle: *Her. sieboldii*; triangle: *Heb. parallelus*. Detailed information of numbers of the localities were listed in Appendix B.

### 3.2.1. *Herpetoreas platyceps* (Blyth, 1854)

Figures 3 and 4

*Tropidonotus platyceps* Blyth, 1854, *J. Asiat. Soc. Bengal*, 23 (3): 297 [39]. Type locality: “Darjeeling, Bengal” [= Darjeeling, West Bengal, North India, 27°02′ N, 88°16′ E, elevation ca. 2100 m] via lectotype selection.

*Tropidonotus platyceps*—Blyth, 1854: 297 (in part) [39]; Günther, 1860: 162 [38]; Günther, 1861: 217 [40]; Günther, 1862: 53 [41]; Günther, 1864: 264, plate 22: Figure D [5]; Theobald, 1868: 55 [42]; Stoliczka, 1870: 191 [43]; Anderson, 1871: 176 [44]; Stoliczka, 1872: 130 [45]; Blanford, 1875: 196 [46]; Theobald, 1876: 174 [47]; Blanford, 1878: 23 [48]; Atkinson, 1882: 76 [49]; Hubrecht, 1882: 142 [50]; Boulenger, 1888: 598 [51]; Phipson, 1888: 51 [52]; Boulenger, 1890: 343 [14]; Boulenger, 1893: 248 [53]; Cardew, 1897: 592 [54]; Wall, 1909:



340 [55]; Annandale, 1912: 49 [56]; Cataly, 1914: 30 [57]; Werner, 1929: 28 [58]; Prater, 1933: 393 [59].

*Rhabdophis platyceps*—Wall, 1923: 604 [60].

*Natrix platyceps*—Shaw et al. 1939: 118 [61]; Smith, 1943: 305 [6]; Smith, 1951: 728 [62]; Smith and Battersby, 1953: 703 [63]; Swan and Leviton, 1962: 114 [64]; Deoras, 1965: 87 [65]; Waltner, 1975: 18 [66]; Zhao et al. 1977: 64 (in part) [67]; Khan, 1980: 136 [68]; Hu et al. 1980: 76 [69]; Khan, 1982: 4 [70].

*Natrix (Rhabdophis) platyceps*—Smith, 1951: 728 [62].

*Amphiesma platyceps*—Malnate, 1960: 50 [1]; Malnate, 1966: 11 [35]; Fleming and Fleming, 1974: 430 [71]; Kramer, 1977: 729 [72]; Nanhoe and Ouboter, 1987: 33 [73]; Zhao and Adler, 1993: 228 [74]; Das, 1994: 31 [75]; Das, 1996: 53 [76]; Das et al. 1998: 152 [77]; Zhao et al. 1998: 76 [78]; Rao, 2000: 112 [79]; Das, 2002: 18 [80]; Khan, 2002: 82 [81]; Schleich et al., 2002: 435 (plate 84, Figure 250), 813 [82]; Das, 2003: 473 [83]; Tillack, 2003: 21 [84]; Khan, 2004: 196 [85]; Whitaker and Captain, 2004: 26, 206 [86]; Zhao, 2006: 170 [15]; Zhao, 2006: 93, Figure 55, 1–2 [87]; Sharma, 2007: 212 [88]; Ahsan et al., 2009: 116 [89]; Li et al., 2010: 167 [9]; Reza, 2010: 64 [90]; Wangyal, 2011: 118 [91]; Wangyal, 2013: 4777 [92]; Wallach et al. 2014: 32 [93]; David et al. 2015: 391–393 [11]; Sahi and Koul, 2020: 893 [94].

*Natrix (Amphiesma) platyceps*—Mertens, 1969: 64 [95].

*Amphiesma cf. platyceps*—Ahmed et al. 2009: 155 [96].

*Herpetoreas platyceps*—Guo et al. 2014: 437 [3]; Aengals et al. 2018: 21 [97]; Che et al. 2020: 677 [13]; Wang et al. 2020: Appendix 16 [98]; Boundy, 2021: 95 [99]; Huang, 2021: 424 [100].

*Tropidonotus dipsas* Blyth, 1854, *J. Asiat. Soc. Bengal*, 23 (3): 297 [39]. Type locality: “Vicinity of Darjiling”.

*Zamenis himalayanus* Steindachner, 1867, *Verh. Der Kais.-Königlichen Zool.-Bot. Ges. Wien.*, 17: 513 [101]. Types: NMW, Nos. 18569, 18570: 1–2. Type locality: “Simla und Kulu (Himalaya)” [=Shimla and Kullu, Himachal Pradesh, India].

*Tropidonotus firthi* Wall, 1914, *J. Bombay Nat. Hist. Soc.*, 23 (1), 166–167 [102]. Type locality: “Takdah in the Eastern Himalayas”.

*Tropidonotus himalayanus*—Anderson, 1871: 178 [44].

*Zamenis himalayanus*—Steindachner, 1867: 513 [101]; Günther, 1872: 14 [103]; Hubrecht, 1882: 141 [50].

*Rhabdophis firthi*—Wall, 1923: 606 [60].

*Tropidonotus firthi*—Werner, 1929: 29 [58].

**Type.** Lectotype, ZSI 7482 (formerly IMC 7482), a 692+ mm specimen (W.S. Sherwill, 1843–1854), designated by Malnate [35]: 11.

**Referred specimens** ( $n = 29$ ).—**India** ( $n = 25$ ). West Bengal: NMW 22383: 2, NMW 22383: 5, Darjeeling; BNHS 80-11, Turjun tea estate, Darjeeling. Sikkim: FMNH 15827, “Mangpu, Sikkim”; BMNH 60.3.19.1354, no specific locality. Uttarakhand: BNHS 80-3, Almora; BMNH 1911.9.8.2, Binsar. Himachal Pradesh: NMW 18569, NMW 18570: 1–2, “Simla and Kulu (Himalaya)”, now Shimla and Kullu; BNHS 80-2, Dalhousie, about 1828 m; BNHS 80-5 (b), 80-7, Shimla; BMNH 1911.5.9.1, Upper Sutlej Valley, about 2133 m. Jammu and Kashmir: MNHN 1988.6484, above Doda, between Makabagi and Ularbagi, Udamphur District, about 2,800 m; ZMB 7293, “Kashmir”; BMNH 96.11.20.5–6, Kashmir, Gulmarg. No specific locality: BMNH 70.1 1.30.36A–D, about 3048 m; BMNH 1903.6.22.23; USNM 48469–70).—**Pakistan** ( $n = 1$ ). Khyber Pakhtunkhwa. BNHS 580, Thandiani.—**China** ( $n = 1$ ). Xizang A.R.: CIB 8420, Zhangmu, Nyalam, about 2400 m.—**Nepal** ( $n = 2$ ). Jumla: BMNH 1953. 1. 1. 63, 7600 feet. No specific locality: BMNH 45. 1. 12. 570. Of these, nine specimens were physically examined (see Appendix A), and data of 20 other specimens were obtained from the literature [35].



**Figure 3.** *Herpetoreas platyceps* showing color in life, Gyirong County, Xizang Autonomous Region, China. (A) general view; (B) close-up of dorsal scale rows at anterior body, showing moderate keeling on outer rows; (C) lateral head view. Photographs by Shuo Qi.

**Diagnosis.** (1) body cylindrical, TL 755–927 mm; (2) tail moderate, TaL/TL 0.232–0.286; (3) dorsal scale rows 19-19-17; weekly keeled only on five to seven mid-dorsal scale rows, namely, on the 3rd–9th to 5th–9th dorsal scale rows plus the vertebral row; (4) ventrals 180–234; (5) cloacal plate and subcaudals divided; (6) subcaudals 78–99; (7) supralabials 8, 3rd, 4th and 5th entering orbit; (8) maxillary teeth 18–22, slightly enlarged posteriorly, last two distinctly enlarged, separated from anterior teeth by small diastema; (9) hemipenis short and thin, shallowly bilobed, spinous throughout with single basal hook; (10) *sulcus spermaticus* single, centripetal, extends to the tip of inner right lobe; (11) the upper edge of the supralabials bordered by dark postocular streak; (12) dorsal color highly variable,

dorsum frequently speckled with small dark spots; (13) venter yellowish-beige, each ventral decorated with a pair of dark spots at lateral edges or not.

**Distribution.** This species is widely distributed across Southern Asia, including northern Pakistan, northern India, southwestern China (Tibet), Nepal, Bangladesh, and western Bhutan (Paro), 1250–3700 m a.s.l. [93] (Figure 2).

**Comments.** Although *Herpetoreas platyceps* has been widely recorded across southern Asia, few studies have focused on the cryptic diversity of this highly variable species. For example, previously considered a junior synonym of *Her. platyceps*, the type species of *Herpetoreas*, *Her. sieboldii* is morphologically similar to *Her. platyceps* [6,35]. Malnate [35] revised and re-described both *Her. sieboldii* and *Her. platyceps*, indicating that the dorsal scale rows of *Her. platyceps* are feebly keeled only on five to seven mid-dorsal scale rows without exception. However, *Her. platyceps* specimens from Gyirong County, Tibet, China are distinctly differ from descriptions provided by Malnate [35] in having stronger keeled dorsal scales along the anterior body (Figure 3B). Further phylogenetic work is recommended to incorporate the topotype of *Her. platyceps* to clarify whether this variation is caused by cryptic diversity or intraspecific variation. In addition, see comments under *Her. sieboldii*.



**Figure 4.** Preserved specimen of *Herpetoreas* cf. *platyceps*, CIB 8420, adult female, Nyalam County, Xizang Autonomous Region, China. Photographs by Jun-Jie Huang.

### 3.2.2. *Herpetoreas sieboldii* Günther, 1860

#### Figure 5

*Herpetoreas sieboldii* Günther, 1860, *Proc. Zool Soc. London*, 28 (1): 156–157 [38]. Type locality: “Sikkim, Himalaya (7500 feet above the level of the sea)” [=Sikkim State, Northeast India, elevation 2286 m a.s.l.].

*Herpetoreas sieboldii*—Günther, 1860: 156 [38]; Günther, 1864: 257 [5]; Theobald, 1868: 54 [42]; Theobald, 1876: 172 [47]; Guo et al. 2014: 437 [3]; Aengals et al. 2018: 21 [97]; Boundy, 2021: 95 [99].

*Amphiesma sieboldii*—Malnate, 1966: 14 [35]; Dierl and Gruber, 1979: 45 [104]; Welch, 1988: 34 [105]; Das, 1994: 31 [75]; Das, 1996: 53 [76]; Das, 1997: 40 [106]; David et al. 1998: 92 [107]; Kahn, 2002: 83 [81]; Das, 2003: 473 [83]; Khan, 2004: 196 [85]; Whitaker and Captain, 2004: 26 [86]; David et al. 2005: 174 [108]; Ahsan et al. 2009: 116 [89]; Das, 2010: 334, plate 68 [109]; Reza, 2010: 64 [90]; Wangyal, 2011: 120 [91]; Das, 2012: 117 [110]; Wallach et al. 2014: 33 [93]; David et al. 2015: 375 [11].

*Natrix platyceps*—Smith, 1943: 305 (in part) [6]; Schleich et al. 2002: 813 (in part) [82]; Tillack, 2003: 21 (in part) [84].

*Natrix sieboldii*—Khan, 1980: 136 [68]; Khan, 1982: 4 [70].

**Type.** Holotype, NHMUK (formerly BMNH) 1946.1.13.16, a 917 mm male (H.R.A. von Schlagintweit, A. von Schlagintweit, and R. von Schlagintweit, 1854–1858).

**Referred specimens** ( $n = 54$ ).—**India** ( $n = 22$ ). **Assam**: BNHS 80-8, Garo Hills, Tura. **Sikkim**: BNHS 80-10, Gangtok. **West Bengal**: CAS-SU 15973, NMW 22383: 1, NMW 22383: 3–4, BMNH 70.11.30.37M–N, Darjeeling; BNHS 1835, Lebong; MCZ 58238–40, Takdah; BNHS 80-15, BMNH 53.8.12.30K–L, BMNH 60.3.19.1352, no specific locality. **Uttar Pradesh**: BNHS 80-9, Gonda. **Uttarakhand**: BMNH 1905.10.27.1, UMMZ 77237, Mussoorie, 1828–2133 m. **Himachal Pradesh**: BNHS 582, 80-5a, Shimla; BNHS 80-6, Taradevi hill, near Shimla.—**Pakistan** ( $n = 2$ ). **Khyber Pakhtunkhwa**: BNHS 581, Thandiani. **Punjab**: BNHS 80-14, Rawalpindi, Ghora Galli.—**China** ( $n = 3$ ). **Xizang A. R.**: CAS 177474, between Chinese check point at Zhangmu (Khasa) (28°07' N–85°59' E) and the Nepal border on the Lhasa-Kathmandu Rd., Nyalam county, Xigaze Prefecture, 2000–2100 m; CAS 177672–177673, locality same to CAS 177474, 2300–2500 m.—**Nepal** ( $n = 26$ ). BMNH 1913.5.22.1, “Maikola Valley, E. Nepal”, now Mai Kola, 2133–3048 m; CAS 90690, “above Deppur”, about 1676 m; FMNH 109762, Amp Pipal, about 1219 m; FMNH 131966, Chapa-gaon, Kathmandu Valley; FMNH 131967, Kathmandu Valley; FMNH 190856, Arun Valley, at Num Bridge across Arun River; FMNH 204499, above Num, 6400' in forest area; MHNG 1355.72–73, Astam, near Hyangcha, 1600 m; MNHN 2003.3614, east of Mounasko Pass, between Surkie Pass and Chheskam, Eastern Region, 2400 m; ZMB 4551, “Himalaya”; ZMB 10231, Sikkim; FMNH 204500–504, no specific locality. BMNH 1953.1.1.64, Balangra Pass, about 3657 m; BMNH 1962.1047, Hatia, Arun River, about 1981 m; BMNH 1955.1.13.71, Lumsum, NW. Beni, 1981 m; BMNH 1962.1048, Maewa khola, Sangwe, 1981 m; BMNH 1955.1.13.69–70, Taglung, S. Tukucha, 2895 m; BMNH 1950.1.5.59–60, Thangjet, 1524 m; BMNH 45.1.12.572, no specific locality.—**Myanmar** (? See below) ( $n = 1$ ). **Shan State**, BNHS 80.4, Taung-gyi. Of these, 24 specimens were physically examined (see Appendix A), and data of 30 other specimens were obtained from the literature [35].

**Diagnosis.** (1) body cylindrical, TL 729–943 mm; (2) tail relatively long, TaL/TL 0.242–0.300; (3) dorsal scale rows 19-19-17; all keeled but some may not be keeled in outermost rows; (4) ventrals 168–216; (5) cloacal plate and subcaudals divided; (6) subcaudals 81–111; (7) supralabials 8, 3rd, 4th and 5th entering orbit; (8) maxillary teeth 19–23, slightly enlarged posteriorly, last two distinctly enlarged, separated from anterior teeth by small diastema; (9) hemipenis short and thin, shallowly bilobed, spinous throughout with single basal hook; (10) *sulcus spermaticus* single, centripetal, extends to the tip of lobe; (11) a light, dark-bordered crescent extends from the last supralabial up and back over the nape; (12) dorsum frequently speckled with small light spots; (13) venter often darkened posteriorly or usually with a lateral series of dark streaks.

**Comparison.** *Herpetoreas sieboldii* differs from *Her. platyceps* by having (1) all dorsal scale rows keeled vs. keeled on five to seven mid-dorsal scale rows; (2) 168–216 ventrals vs. 180–234 ventrals; (3) A low proportion of the length of the tail with 4 supracaudal scale rows to that with 6 supracaudal scale rows,  $SC4/SC6 = 0.53$  vs.  $SC4/SC6 = 1.43$ ; (4) ventral surface of body mostly darkened posteriorly vs. usually immaculate.

**Distribution.** India, Nepal, China (Tibet), Bhutan, Bangladesh, Myanmar (? See below), and Pakistan, 1219–3657 m a.s.l. (Figure 2).

**Comments.** The genus *Herpetoreas* has long been regarded as a junior synonym of *Amphiesma* [1], of which the species *Her. sieboldii* has long been synonymized with *Her. platyceps* [6,84]. Although Malnate [35] revalidated *sieboldii* as a separate species and provided distinctive characters between *Her. sieboldii* and *Her. platyceps*, the number of ventrals in *Her. sieboldii* listed by Malnate [35] is distinctly lower than its original description (168–207 vs. 216) [38], thus further pholidosis confirmation is needed especially for the holotype. Guo et al. [3] revalidated the genus *Herpetoreas* to accommodate the following three species: *Her. sieboldii*, *Her. platyceps*, and *Her. burbrinki*. However, no genetic data are available for *Her. sieboldii* to our knowledge [7,8,13]. Further study is also recommended to clarify the relationships between *Her. sieboldii* and *Her. platyceps*. In addition, see comments under *Her. platyceps*.

David et al. [11] reported three specimens (CAS 177474, 177672–177673,) of *Her. sieboldii* from Zhangmu, Xizang Autonomous Region (Tibet), China. However, no morphological data was provided and the species is previously not listed from Chinese herpetofauna [98]. The distribution record from Myanmar provided by Malnate [35] was based on a single specimen (BNHS 80.4) from Shan State (Figure 2), which was considered to be highly isolated. We question the Burmese record of *Her. sieboldii* pending further confirmation.



**Figure 5.** Preserved specimen of *Herpetoreas sieboldii*, NMW 22383: 1, adult male, Darjeeling, West Bengal, India. Not to scale. Photographs by Gernot Vogel.

### 3.2.3. *Herpetoreas pealii* (Sclater, 1891)

*Tropidonotus pealii* Sclater, 1891, *J. Asiat. Soc. Bengal*, 60 (3): 241, pl. 6, figs. 4a–c [111]. Type locality: “Sibsagar district of Assam” [= Sibsagar District, North Assam State, Northeast India, ca. 26°59' N, 94°38' E, elevation ca. 100 m].

*Tropidonotus pealii*—Boulenger, 1893: 214 [53].

*Natrix peali* [sic]—Wall, 1923: 600 [60]; Smith, 1943: 291 [6].

*Amphiesma peali* [sic]—Malnate, 1960: 50 [1]; Sharma, 2007: 206 [88].

*Paranatrix pealii*—Mahendra, 1984.

*Amphiesma pealii*—Das, 1994: 31 [75]; Das, 1996: 53 [76]; Das et al. 1998: 151 [77]; Das, 2003: 473 [83]; Whitaker and Captain, 2004: 25 [86]; Ahmed et al. 2009: 19 [96]; Wallach et al. 2014: 32 [93].

*Hebius pealii*—Guo et al. 2014: 438 [3]; Das and Das, 2017: 168 [112]; Aengals et al. 2018: 21 [97]; Purkayastha and David, 2019: 86 [113]; Boundy, 2021: 92 [99].

*Herpetoreas pealii*—Das et al. 2020: 309 [8].

**Type.** Syntypes (2), BMNH 1946.1.13.43 and ZSI 4034 (formerly IMC), two males, longer syntype 508 mm (S.E. Peal, 1872–1891).

**Referred specimens** ( $n = 2$ ). —**India.** BMNH 1946.1.13.43, Sibsagar district, Assam; WII-ADR547, Siang district, northeast India. Data were obtained from the literature [8,113].

**Diagnosis.** (1) Body cylindrical, TL 451–660 mm; (2) tail moderate long, TaL/TL 0.227–0.259; (3) dorsal scale rows 19-19-17; moderately keeled except for outermost row at anterior and midbody; (4) ventrals 136–142; (5) cloacal plate single, subcaudals divided; (6) subcaudals 69–77; (7) supralabials 9, 4th and 5th entering orbit; (8) maxillary teeth 13–21, slightly enlarged posteriorly, last two distinctly enlarged, separated from anterior teeth by small diastema; (9) hemipenis short and thin, shallowly bilobed, spinous throughout with single basal hook; (10) *sulcus spermaticus* single; (11) dorsum dark brown above with paler and darker spots; (12) venter yellowish-beige, each ventral decorated with a pair of dark spots at lateral edges that are connected to form a continuous ventrolateral line.

**Comparison.** *Herpetoreas pealii* differs from both *Her. platyceps* and *Her. sieboldii* by having (1) single cloacal plate vs. divided cloacal plate; (2) fewer ventral scales 136–142 vs. 180–234 in *Her. platyceps* and 168–216 in *Her. sieboldii*; (3) fewer subcaudals 69–77 vs. 78–99 in *Her. platyceps* and 81–111 *Her. sieboldii*; (4) only two supralabials entering orbit, supralabial formula 3-2-4 vs. three supralabial entering orbit, supralabial formula 2-3-3.

**Distribution.** Northeastern India, 100–120 m a.s.l. (Figure 2).

**Comments.** This is a poorly known species with only three specimens known up to now [8]. Das et al. [8] redescribed the species based on newly obtained specimen and transferred the species to the current genus *Herpetoreas* according to their phylogenetic results.

### 3.2.4. *Herpetoreas xenura* (Wall, 1907)

*Tropidonotus xenura* Wall, 1907, *J. Bombay Nat. Hist. Soc.* (1906–1907), 17 (3): 616–617, pl. 1, Figure 2 [36].

*Natrix xenurus*—Wall, 1923: 601 [60].

*Natrix xenura*—Smith, 1943: 292 [6]; Romer, 1945: 431 [114].

*Paranatrix xenura*—Mahendra, 1984.

*Amphiesma xenura*—Das, 1994: 31 [75]; Das, 1996: 54 [76]; Pawar and Birand, 2001: 102 [115]; Das, 2003: 474 [83]; Whitaker and Captain, 2004: 152, 190 [86]; David et al. 2007: 54 [116]; Sharma, 2007: 210 [88]; Wogan et al. 2008: 87 [117]; Ahsan et al. 2009: 118 [89]; Das, 2010: 335 plate 68 [109]; Reza, 2010: 64 [90]; Das, 2012: 118 [110]; Wallach et al. 2014: 35 [93].

*Hebius xenura*—Guo et al. 2014: 438 [3]; Aengals et al. 2018: 21 [97]; Purkayastha and David, 2019: 85 [113].

*Herpetoreas xenura*—Lalronunga et al. 2020: 196 [7]; Muansanga et al. 2021: 82 [118].

**Type.** Holotype, IMC, lost *fide* Smith [6]: 292.

**Type locality.** Unknown.

**Referred specimens** ( $n = 3$ ). Detailed voucher unknown. Data were obtained from the literature [6,8,36].

**Diagnosis.** (1) Body cylindrical, TL 590–660 mm; (2) tail relatively long, TaL/TL 0.271–0.302; (3) dorsal scale rows 19-19-17; all strongly keeled; (4) ventrals 158–165; (5) cloacal plate usually single, subcaudals single; (6) subcaudals 82–105; (7) supralabials 9 (10), 4th–5th entering orbit; (8) maxillary teeth 22–23, gradually enlarged posteriorly, last two distinctly enlarged, separated from anterior teeth by a small diastema; (9) hemipenis short and thin, shallowly bilobed, extends to 8th subcaudals; (10) *sulcus spermaticus* single; (11) dorsum dark olive-brown with indistinct narrow blackish cross-bars or series of spots; (12) venter off-whitish, each ventral decorated with a pair of dark brown square spots on their lateral edges.

**Comparison.** *Herpetoreas xenura* differs from *Her. platyceps*, *Her. sieboldii* and *Her. pealii* by having single subcaudals vs. divided subcaudals. Particularly, *Her. xenura* differs from *Her. platyceps* and *Her. sieboldii* in having fewer ventrals 158–165 vs. 180–234 in *Her. platyceps* and 168–216 in *Her. sieboldii*; only two supralabials entering orbit, supralabial formula 3-2-4 vs. three supralabial entering orbit, supralabial formula 2-3-3; from *Her. pealii* by having more ventrals 158–165 vs. 136–142, a longer tail, TaL/TL 0.271–0.302 vs. TaL/TL 0.227–0.259, and more subcaudals 82–105 vs. 69–77.

**Distribution.** Northeast India, Bangladesh and Myanmar, 124–1444 m a.s.l. (Figure 2).

**Comments.** A morphologically distinct but poorly known species, Wall [36] indicated that both the cloacal and subcaudal scales are in a single row when describing the species. Particularly, the supracaudal scales are arranged in even rows though the subcaudals are entire, which is distinct among many groups of snakes such as *Bungarus* (Elapidae), *Aspidura* (Natricidae), *Achalinus* (Xenodermidae), etc. [36]. Lalronunga et al. [7] transferred the species into *Herpetoreas* based on their phylogenetic trees, whereas no redescription was provided especially for the maxillary teeth.

### 3.2.5. *Herpetoreas burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang, and Pyron, 2014

#### Figure 6

*Herpetoreas burbrinki* Guo Zhu, Liu, Zhang, Li, Huang, and Pyron, 2014, *Zootaxa*, 3873 (4): 438, Figure 3 [3]. Type locality: “Zayu County, Xizang A. R., China, at an elevation of 1889 m above sea level”.

*Amphiesma* cf. *craspedogaster* Guo et al. 2008: 658, Figure 2 [119].

*Herpetoreas burbrinki* Guo et al. 2014: 438 [3]; Che et al. 2020: 671 [13]; Das et al. 2020: 313 [8]; Wang et al. 2020: Appendix 16 [98]; Boundy, 2021: 94 [99]; Huang, 2021: 426 [100]; Peng et al. 2021: 434 [37].

**Type.** Holotype. YBU 071128, a 757 mm adult male specimen.

**Referred specimens** ( $n = 2$ ).—**China.** Xizang A. R.: YBU 071128, Zayü County, ANU 20210006 Xiachayu Town, Zayu County. Of these, the holotype was physically examined (see Appendix A), and data of another specimen was obtained from the literature [37].

**Diagnosis.** (1) Tail relatively long, TaL/TL 0.285–0.304; (2) dorsal scale rows 19-19-17; moderately keeled, notched at apex; (3) supralabials 8 (9), 3rd–5th entering orbit; (4) one (two) preoculars; (5) three postoculars; (6) ventrals 169–172; (7) cloacal plate and subcaudals divided, subcaudals 94–96; (8) reduction of dorsal scales rows from 19 to 17 scale occurring above ventral scale position 105–108; (9) reduction of the supracaudal scales rows from 8 to 6 (SC8TO6) occurring above subcaudal 62–63; (10) venter yellowish-beige in preservative, each ventral decorated with a pair of dark spots at lateral edges (Figure 6).

**Comparison.** *Herpetoreas burbrinki* differs from *Her. platyceps* by having a longer tail, TaL/TL 0.285–0.304 vs. TaL/TL 0.232–0.286, fewer ventrals 169–172 vs. 180–234; from *Her. sieboldii* by having 1st SC6 22th–23th vs. 25th–28th, SC6 40–41 vs. 27–38, a clear ventral color pattern with a pair of dark spots on each side of ventral scale vs. ventral surface darkened posteriorly with a greyish suffusion of variable intensity; from *Her. pealii* by having divided cloacal plate and subcaudals vs. cloacal plate single, subcaudals paired in *Her. pealii* and both cloacal plate and subcaudals paired in *Her. xenura*.

**Distribution.** Zayü County, Xizang Autonomous Region, China, this species is still known only from its type locality; 1889–1938 m a.s.l. (Figure 2).

**Comments.** *Herpetoreas burbrinki* is still known only from two specimens to our best knowledge [37]. The holotype of *Her. burbrinki* (YBU 071128) was firstly reported as *Amphiesma* cf. *craspedogaster* from Tibet, China by Guo et al. [119], and its measurement provided by Guo et al. [3] is consistent with Guo et al. [119], i.e., SVL 495 mm, TaL 130 mm. However, we re-examined the holotype of *Her. burbrinki* (YBU 071128) and found our observations are mostly in agreement with previous studies for most of characters except for a longer SVL (527 mm vs. 495 mm) and a distinctly longer tail (TaL 230 mm vs. 130 mm; TaL/TL 0.304 vs 0.208) [3,119]. The measurements of the holotype of *Her. burbrinki* provided by the current study were based on our data, which were also similar to the newly reported female specimen TaL/TL 0.304 vs. 0.285 (ANU 20210006) [37].



**Figure 6.** Preserved holotype of *Herpetoreas burbrinki*, YBU 071128, adult male, Zayü County, Xizang Autonomous Region, China. Photographs by Jin-Long Ren.

### 3.2.6. *Herpetoreas tpser* sp. nov.

<http://zoobank.org/CAB44C8A-1C8C-4962-ADAC-5AFF2FE4F6C0> (accessed on 26 November 2021)

Figures 7, 8, 9, 10 and 11A

#### **Chresonymy.**

*Amphiesma khasiensis*—Zhao and Li, 1985: 106 [120]; Zhao et al. 1986: 201 [121].

*Amphiesma parallela*—Zhao and Li, 1987: 49 [12].



*Amphiesma parallelum*—Zhao and Adler, 1993: 227 (in part) [74]; Li et al. 1995: 264 [122]; Zhao et al. 1998: 74 (in part) [78]; Zhao, 2006: 169 (in part) [15]; Zhao, 2006: 92, Figure 54 [87]; Li et al. 2010: 166 [9].

*Hebius parallelum*—Guo et al. 2014: 438 (in part) [3].

*Herpetoreas cf. parallelum*—Che et al. 2020: 673 [13].

**Holotype.** CIB 8418 (field no. 73II5194), adult male, from Beibeng Town to De'ergong Village, Mêdog County, Nyingchi City, Xizang Autonomous Region, China (ca. 1300 m a.s.l.), collected by Er-Mi Zhao and Xue-En Wu, on 28 July 1973.

**Paratypes** CIB 8419 (field no. T8370131), adult female, from Ani Bridge, Beibeng Town, Mêdog County, Nyingchi City, Xizang Autonomous Region, China (ca. 1200 m a.s.l.), collected by Sheng-Quan Li, on 18 July 1983. CIB 118523 (field no. JK202005293), adult female, from Ani Bridge (29°3289' N, 95°1780' E, ca. 1087 m a.s.l.), Beibeng Town, Mêdog County, Nyingchi City, Xizang Autonomous Region, China, collected by Xiao-Yong Ding in May, 2016. CIB 118524 (field no. LAB2019437), adult female, from the forest near Hanmi (29°3809' N, 95°112' E, ca. 2280 m a.s.l.), Mêdog County, Nyingchi City, Xizang Autonomous Region, China, collected by Xiao-Yong Ding in September, 2019.

**Diagnosis.** (1) Body cylindrical, TL 387–679 mm; (2) tail relatively long, TaL/TL 0.262–0.317; (3) dorsal scale rows 19-19-17; all keeled or may not be so on outermost rows; (4) ventrals 153–167; (5) cloacal plate and subcaudals divided; (6) subcaudals 79–97; (7) supralabials 8–9, 3rd–5th or 4th–6th entering orbit; (8) maxillary teeth 20–21, slightly enlarged posteriorly, last two distinctly enlarged, separated from anterior teeth by small diastema; (9) hemipenis short and thin, shallowly bilobed, spinous throughout with a single basal hook; (10) *sulcus spermaticus* single, centripetal, extends to crotch; (11) a light, dark-bordered crescent extending from the last supralabial up and back over the nape; (12) dorsum reddish-brown in life, speckled with short dark stripes; (13) venter reddish-orange in life, each ventral decorated with dark spots at lateral edge (Figure 7).

**Description of the holotype.** Body slender, TL 519 mm, cylindrical and elongate; head moderately large, HL/SVL 0.03, HL/HW 1.49, moderately distinct from neck; snout broad, obtuse as seen from above; eye large, EW 2.65 mm, EW/SOL 2.64; pupils round; nostrils crescentic, piercing in the middle of the nasal, directed laterally.

Dorsal scale rows 19-19-17, moderately keeled throughout, scales of the first dorsal scales keeled just after neck; notched at apex.

Dorsal scale row reductions (Formula (1)):

$$19 \frac{3 + 4 \rightarrow 3 \text{ (VEN 101)}}{3 + 4 \rightarrow 3 \text{ (VEN 100)}} 17 \quad (1)$$

Two preventrals, ventrals 158; tail complete, particularly long, TaL 165 mm, TaL/TL 0.317, tapering posteriorly; subcaudals 96, all paired, with single terminal rod; cloacal plate divided.

Position of the reduction to 6 suprascale rows around the tail at 20th SC. Range, in number of subcaudals spanned, of the portion of the tail with 6 supracaudal scale rows from 20th–44th SC, 25 subcaudals in total; range of the length of tail with 4 supracaudal scale rows: 47th–87th SC, 41 subcaudals in total; ratio: length with 4 supracaudal scale rows/length of the portion of tail with 6 supracaudal scale rows: 1.64.



**Figure 7.** *Herpetoreas tpser* sp. nov. showing color in life, KIZ 06681, adult female, from 80K, Mèdog County, Xizang Autonomous Region, China. (A) dorsolateral view; (B) ventral view. Photographs by Mian Hou.

Dorsal side of head scales complete including 2 internasals, 2 prefrontals, 2 supraoculars, 1 frontal, and 2 parietals. Rostral wider than high, width approximately twice as long as high, visible from above; nasals subpentagonal, slightly elongate, about 1.2 times longer than high, completely divided, anterior part slightly larger than the posterior one; nostrils located on the anterior part of nasals; internasals subtriangular, in broad contact with each other, not in contact with loreal, about equal length to width, distinctly narrowing anteriorly, the width of the posterior margin approximately twice as long as the anterior margin; 2 prefrontals, subhexagonal, slightly broader than long, about 1.3 times longer than internasals; prefrontal sutures about equal length to internasal sutures; frontal pentagonal, elongate, length 1.45 times longer than width, about twice as long as prefrontal; supraocular 1/1, rectangular, elongate, narrowed anteriorly, about 2.1 times longer than width; parietals large, length 1.95 times longer than width, 1.5 times longer than frontal; parietals in broad

contact with each other, parietal suture subequal to length of frontal. Loreal 1/1, subquadrate, small, about equal in length to depth, in contact with 2nd–3rd supralabials, not entering orbit; preoculars 1/1, depth about 1.7 times longer than width, about two times higher than loreal; postoculars 3/3, size decreasing from top to bottom; supralabials 9/8, 2nd–3rd in contact with the loreal, 4th–6th entering orbit on the left side, 3rd–5th entering orbit on the right side, penultimate one largest; temporals in 3 rows, elongate, variable and asymmetric, anterior temporals 2 (left) and (1 + 1/1) (right), broadly in contact with supralabials 7–8 on the left side, supralabials 6–7 on the right side, followed by 2 + 2 (left) and 1 + 2 (right) posterior temporals; mental subtriangular, width 2.5 times longer than high; 10/9 infralabials, first pair in contact with each other after mental, 1st–5th/1st–4th in contact with anterior chin shields; chin shields pairs two; posterior chin shields 1.3 times longer than anterior ones, separated from each other by small scales; mental groove apparent (Figure 8).



**Figure 8.** *Herpetoreas tpser* sp. nov. showing color in life, KIZ 06681, adult female, from 80K, Mèdog County, Xizang Autonomous Region, China. (A) dorsal head view; (B) ventral head view; (C) right side of head view; (D) left side of head view. Photographs by Mian Hou.

Maxillary teeth 19 + 2, slightly enlarged posteriorly, last two distinctly enlarged, separate from anterior maxillary teeth by a small diastema, not grooved.

The left side of hemipenis is missing, the description of hemipenis in retracted condition is based on the right side. The organ is shallowly bilobed, retracted hemipenis extending to SC 7 with its crotch extending to SC 6; the fork point of *m. retractor penis magnus* extending to SC 8, origin of *m. retractor penis magnus* at level of SC 21.

**Coloration in preservative.** Dorsal surface of head overall creamish-beige, yellowish-brown or blackish-brown, usually more distinctly paler on anterior half of head (Figure 9). Upper surfaces of internasals, anterior sides of prefrontals, and central part of frontal yellowish-beige, sparsely decorated with irregular blackish-brown spots. Upper cephalic scales irregularly and incompletely edged with blackish brown; these dark outlines of

dorsal head scales usually become more distinct on their posterior margins. Lateral sides of parietals distinctly darker, almost forming two thick lateral stripes along the outer margins. Parietals speckled with dark brown, a pair of elliptic beige spots symmetrically present on inner sides of corresponding scales, just separated by parietal sutures. A six-scales-long, two-scales-wide beige sagittal line extends just behind parietal suture. Coloration of sides of the head distinctly separated by a narrow, oblique, dark streak, which originates from posterior margins of nasals, goes through upper edges of loreal and preocular, extends from middle postocular downwards to last supralabials until corner of mouth. Coloration above this dark streak as upper surface of head, whereas that below uniformly creamish-beige. Posterior edges of supralabials 1–3, upper margins of 4th–6th (left) or 3rd–5th (right) supralabials bordered by darker stripes. Posterior bottom corners of penultimate supralabials with a dark spot. Chin and throat uniformly creamish-yellow; anterior margin of mental and posterior corners of last two infralabials with faint, darker edges.

Dorsal surface of body umber or dark brown. Some dorsal scales are slightly darker, each dorsal scale more or less scattered with paler spots. A conspicuous, pale (cream or pale yellow), V or Y-shaped chevron extends onto neck, starting on each side from behind last supralabial and reaching upper surface of neck, pointing backwards, not in contact with beige sagittal line just behind parietal suture. Venter uniformly creamish-yellow, with outer edges of ventral scales dark brown or blackish-brown, in contact with the short streaks of lower edges of 1st DSR. Ventral surface of subcaudals uniformly colored as venter (Figure 9).

**Description of paratypes and variation.** Paratypes and other specimens known generally resemble the holotype in morphological characters, except for having a wider range of total length (TL 387–679 mm vs. 519 mm) and a slightly shorter tail (TaL/TL 0.262–0.313 vs. 0.317). They have 153–167 ventrals (vs. 158 in the holotype), 79–97 subcaudals (vs. 96), and the following dorsal scale row reductions (Formula (2)):

$$19 \frac{3 + 4 \rightarrow 3 \text{ (VEN 82-106)}}{3(4) + 4(5) \rightarrow 3(4) \text{ (VEN 82-106)}} 17 \quad (2)$$

Notably, CIB 8419 has a different dorsal scale row formula 18-19-17 (vs. 19-19-17); CIB 107855 has two preoculars and two postoculars on both sides, 8 infralabials on the left side; CIB 107855 and CIB 118524 have divided subcaudals but the 8th and 7th–9th are single, respectively. Both the anterior and posterior temporals are asymmetric and highly variable, aTEM 1–2 or (1 + 1/1) and pTEM in 2, 1–2 + 2 or 1/(1 + 2) (Figure 10; Table 3).

**Coloration in life.** In life, dorsal surface of head and neck are bright yellowish brown; the background color of supralabials, loreals, and lower part of preoculars is yellowish off-white; posterior corner of eye streak is bordered with reddish orange (Figures 7 and 8). The sagittal line just behind the parietal suture and the chevrons along each side of neck are bright reddish orange, slightly paler than the background color of neck, barely visible in general view. The dorsal surface of body is yellowish-brown, brownish-red, or reddish-ochre, gradually tending to become darker towards the posterior part of the body, sparsely speckled with small dark blotches and spots, especially on the outer margins of dorsal scales. The background color of the lateral surface is darker than dorsal body surface, giving a dark maroon hue; caudal scales are narrowly edged with dark grey, forming several continuous or not, dark zigzag streaks on the posterior part of the tail.

The ventral surface of head is creamish-white, speckled with dark, grey, and beige, especially on the posterior margin of the infralabials. The first preventral is as throat, whereas the second preventral is decorated with bright reddish-orange. The ventral surface of body is glossy bright jacinth, reddish-orange or even scarlet posteriorly, distinctly separated from ventral head surface from the first ventral scale and throat. Ventral scales are ornated with a pair of more or less conspicuous blackish-brown spots on both sides, these spots progressively become larger and more distinct posteriorly and do not connect with each other. The ventral part of the tail is the same as the venter, whereas the subcaudals are more or less decorated with lateral blackish spots and nearly immaculate towards tail tip.



**Figure 9.** Preserved holotype of *Herpetoreas tpser* sp. nov., CIB 8418, adult male, Beibeng, Mêdog County, Xizang Autonomous Region, China. Photographs by Jun-Jie Huang.

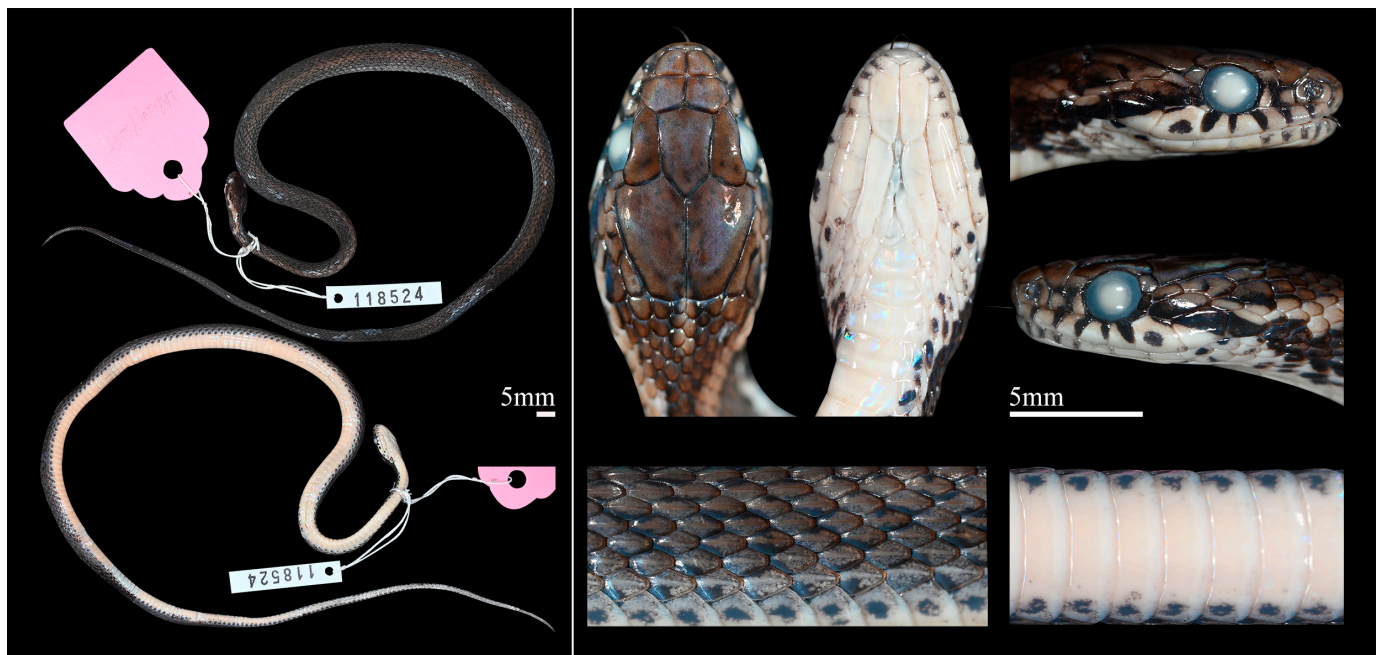
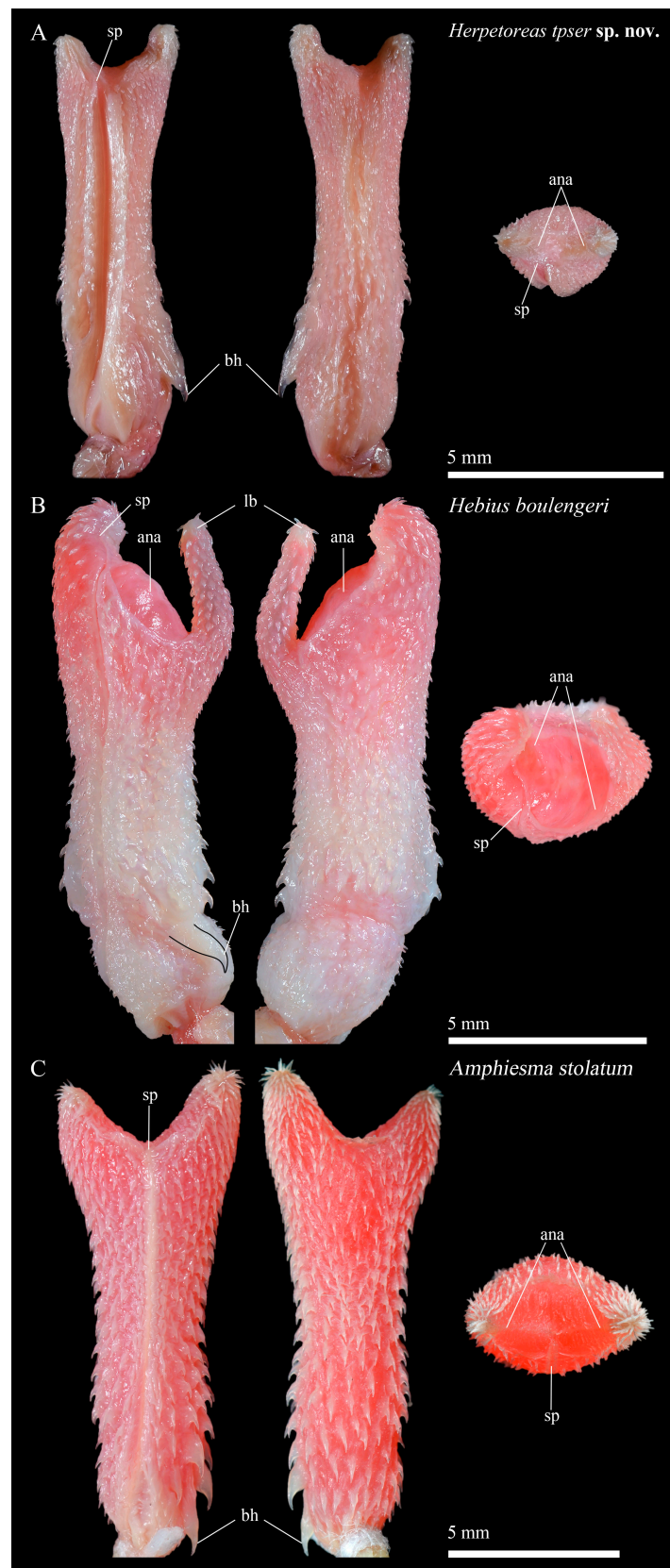


Figure 10. Preserved paratype of *Herpetoreas tpser* sp. nov., CIB 118524, subadult, Médog County, Xizang Autonomous Region, China. Photographs by Jun-Jie Huang.

Table 3. Morphological characters of *Herpetoreas tpser* sp. nov. specimens.

Voucher	CIB 8418	CIB 107855	CIB 8419	CIB 118523	CIB 118524	KIZ 06681	Range		Total (n = 6)
Sex	M	M	F	F	F	F	M (n = 2)	F (n = 4)	Total (n = 6)
Locality	Beibeng, Médog, Tibet	Hanmi, Médog, Tibet	Aniqiao, Médog, Tibet	Médog, Tibet	Médog, Tibet	80K, Médog, Tibet	Médog, Tibet	Médog, Tibet	Médog, Tibet
TL	519	649	662	594	387	679	519–649	387–679	387–679
TaL	165	170+	207	176	108	188	165–170+	108–207	108–207
SVL	355	479	455	418	279	491	355–479	279–491	279–491
TaL/TL	0.317	0.262+	0.313	0.296	0.279	0.277	0.262–0.317	0.277–0.313	0.262–0.317
HL	10.95	13.56	12.83	10.96	9.60	-	10.95–13.56	9.60–12.83	9.60–13.56
HW	7.34	9.54	8.97	7.26	6.91	-	7.34–9.54	6.91–8.97	6.91–9.54
HL/HW	1.49	1.42	1.43	1.51	1.39	-	1.42–1.49	1.39–1.51	1.39–1.51
PrO	1/1	2/2	1/1	1/1	1/1	1/1	1–2	1	1 (2)
PtO	3/3	2/2	3/3	3/3	3/3	3/3	2–3	3	3 (2)
SL	3-3-3/2-3-3	3-3-3/3-3-3	2-3-3/2-3-3	2-3-3/2-3-3	2-3-3/2-3-3	2-3-3/2-3-3	2-3-3 or 3-3-3	2-3-3	2-3-3 or 3-3-3
SL-N	1-2/1-2	1-2/1-2	1-2/1-2	1-2/1-2	1-2/1-2	1-2/1-2	1-2	1-2	1-2
SL-L	2-3/2-3	2-4/2-3	2-3/2-3	2-3/2-3	2-3/2-3	2-3/2-3	2-3 (2-4)	2-3	2-3 (2-4)
IL	10/9	8/9	10/10	-/9	10/10	9/9	9–10 (8)	9–10	9–10 (8)
aTEM	2/(1+1/1)	(1+1/1)/(1+1/1)	2/2	2/2	2/2	1/1	(1+1/1) or 2	1–2	1–2 or (1+1/1)
pTEM	2+2/1+2	2/2	1+2/1+2	[1+2/(1+1)]/1+2+2/[1/(1+2)]		2/2	2+2, 1+2, or 2	1+2, 2+2, or 1/(1+2)	2, 1-2+2 or 1/(1+2)
CS	2	2	2	2	2	2	2	2	2
IL-CS	1-5/1-4	1-4//1-5	1-5/1-4	1-4/1-4	1-5/1-5	1-4/1-4	1-4 or 1-5	1-4 or 1-5	1-4 or 1-5
DSR	19-19-17	19-19-17	18-19-17	19-19-17	19-19-17	19-19-17	19-19-17	19 (18)-19-17	19-19-17
Keel DSR	++	++	++	++	++	++	++	++	++
VEN	158	165	156	153	162	167	158–165	153–167	153–167
SC	96	79+	97	86	89	81	79–96	81–97	79–97
SC s/p	all paired	SC8 single	all paired	all paired	SC7–9 single	-	all paired or SC8 single	all paired or SC7–9 single	all paired or SC7–9 single
1st SC6	20	30	14	13	20	-	20–30	13–20	13–30
SC6	25	26	27	31	28	-	25–26	27–31	25–31
SC4	41	22+	37	33	34	-	41	33–37	33–41
SC4/SC6	1.64	-	1.37	1.06	1.21	-	1.64	1.06–1.37	1.06–1.64
MT	19+d+2	19+d+2	18+d+2	-	19+d+2	-	19+d+2	18–19+d+2	18–19+d+2



**Figure 11.** Sulcate, asulcate, and apical sides of the hemipenis distinguishing different genera of *Amphiesma sensu lato*. (A) *Amphiesma stolatum*, SYS r001727; (B) *Hebius boulengeri*, SYS r001680; (C) *Herpetoreas tpser* sp. nov., CIB 107855. Photographs by Jun-Jie Huang (A,C) and Jin-Long Ren (B). Legend—sp: sulcus spermaticus; bh: basal hook; ana: apical naked area; lb: left lobe of hemipenis.

**Hemipenis.** The description of hemipenis in everted condition is based on the left side of CIB 107855 (Figure 11A). The organ is thin and short, hemipenial total length (HTL) 10.7 mm, hemipenial total width (HTW) 3.0 mm. HTL/HTW 3.6; Y-shaped, shallowly bilobed, hemipenial truncus length (HCL): 9.8 mm, HCL/HTL 0.92. Both the sulcate and asulcate surfaces are densely ornamented with spines and spinules; a large basal hook is present at the proximal part of truncus, which at least two times higher than the adjacent spines. The *sulcus spermaticus* is single, extending to the base of inner right lobe where it takes a centripetal position. Sulcus lip highly developed and raised, walls covered with spinules.

In situ, the hemipenis extends up to SC 6–7 with its crotch extending to SC 4–6; the fork point of *m. retractor penis magnus* extends to SC 7–8, the origin of *m. retractor penis magnus* invariably at level of SC 21.

**Comparisons.** *Herpetoreas tpser* **sp. nov.** was previously misidentified as *Hebius parallelus* [13]. The new species differs from *Heb. parallelus* by having (1) a longer tail (TaL/TL 0.262–0.317 vs. 0.221–0.252), (2) more subcaudals (79–97 vs. 63–77), (3) fewer preoculars (usually a single preocular vs. 2 preoculars); (4) more strongly keeled dorsal scales (1st dorsal scale row moderately keeled throughout vs. smooth or at best feebly keeled); (5) the presence of a chevron on the upper part of the neck (vs. absent); (6) a different ventral color in life (ventral surface of body and tail bright jacinth, reddish-orange to scarlet vs. pale yellow).

*Herpetoreas tpser* **sp. nov.** is the sister taxon of *Her. burbrinki* with current samplings in our molecular phylogeny (Figure 1). It can be separated from the latter species by having (1) a shorter body length (maximum TL 679 mm vs. 757 mm in *Her. burbrinki*), (2) fewer ventrals (153–167 vs. 169–172), (3) a more restricted range of subcaudals with 6 supracaudal scale rows (25–31 scales vs. 40–41 scales), and (4) a different dorsal color pattern (dorsal scales irregularly speckled with small dark blotches or spots with no definite pattern vs. each side of body with a faint yellowish dorsolateral stripe).

For the other four congeners, *Herpetoreas tpser* **sp. nov.** differs from *Her. platyceps* by having 153–167 ventrals (vs. 180–234 ventrals), the location of the 1st subcaudal at which the tail has 6 supracaudal scale rows (1st SC6) between SC 13th–30th (vs. SC 9th), *sulcus spermaticus* extending to the crotch (vs. extending to the tip); from *Her. sieboldii* by having 153–167 ventrals (vs. 168–207 ventrals), the proportion of the length of the tail with 4 supracaudal scale rows to that with 6 supracaudal scale rows (SC4/SC6) 1.06–1.64 (vs. 0.53), *sulcus spermaticus* extending to the crotch only vs. extending to the tip of the lobes; from *Her. pealii* and *Her. xenura* by having divided cloacal plate and subcaudals (vs. cloacal single in *Her. pealii* and *Her. xenura*, and subcaudals all single in *Her. xenura*).

In addition, *Herpetoreas tpser* **sp. nov.** may be confused with *Hebius clerki*; it can be distinguished from the latter species by the presence of a diastema before the enlarged maxillary teeth (vs. absent in *Heb. clerki*), a different ventral color in life (ventral surface of body and tail bright jacinth, reddish-orange to scarlet vs. bright yellow to white). For the morphological differences with reference to other members of the genera *Amphiesma* and *Hebius*, see the discussion below.

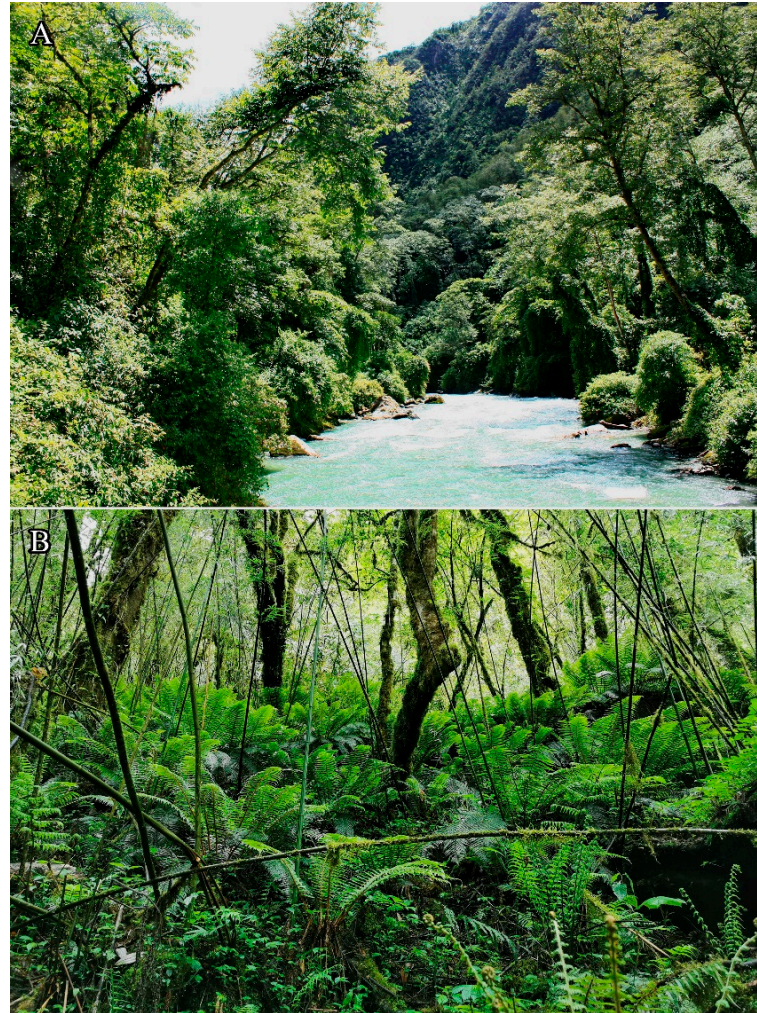
**Etymology.** The specific epithet *tpser* (pronounced as “/tʰpsər/”) is the acronym of “Tibetan Plateau Scientific Expedition and Research” of China, which greatly promoted the scientific research of the Qinghai-Tibet Plateau. All specimens of *Herpetoreas tpser* **sp. nov.** were collected during The First/The Second Tibetan Plateau Scientific Expedition and Research.

We suggest “Mêdog Himalayas Keelback” as its English common name, and Mò Tuō Fù Liàn Shé (墨脱腹链蛇) as its Chinese common name.

**Distribution and Natural history.** *Herpetoreas tpser* **sp. nov.** is presently only known from Beibeng and adjacent Ani Bridge, Hanmi, and 80K, Mêdog County, southeastern Xizang Autonomous Region (Tibet), southwestern China, at an altitude of 1087–2280 m a.s.l. This species inhabits evergreen broad-leaf forest or the moist fields of forest margins covered with dense vegetation close to the water (Figure 12). All known specimens were



collected in daytime, on a cloudy or mildly rainy day; this species is possibly diurnal. The species has a fierce disposition and bites when handled, often holding the mouth open while on the defensive.



**Figure 12.** Habitat of *Herpetoreas tpser* **sp. nov.** in Mêdog County, southwestern Xizang Autonomous Region, southwestern China. (A) Ani Bridge; (B) Hanmi. Photographs by Ke Jiang.

*Herpetoreas tpser* **sp. nov.** was observed sympatrically with *Amolops aniqiaoensis*, *Trimeresurus medoensis*, *Protobothrops kaulbacki*, and *Elaphe taeniura* in Ani Bridge (~1100 m a.s.l.), with *Polypedates braueri*, *Zhangixalus burmanus*, *Nanorana medogensis*, *Japalura austeni-ana*, *Asymblepharus nyingchiensis*, and *Ovophis zayuensis* in 80 K (~2100 m a.s.l.), with *Amolops medogensis*, *Nanorana medogensis*, *Ovophis zayuensis*, *Protobothrops jerdonii*, and *Pseudoxenodon macrops* in Hanmi (~2200 m a.s.l.).

**Comments.** *Herpetoreas tpser* **sp. nov.** was previously misidentified as *Hebius parallelus*. Although the Tibetan record of *Heb. parallelus* has been clarified in this work, other records outside China still need to be studied. For example, another specimen (KSC 414) reported from Nagaland, northeastern India largely agrees with *Herpetoreas tpser* **sp. nov.** but differs from the latter in its strongly colored and patterned dorsal coloration (see Ao et al. [123]: Figures 1 and 2), which should be identified as *Heb. clerki* [11]. Furthermore, Kramer [72] doubted the occurrence of *Heb. parallelus* west of 88° E and supposed that the Nepalese records might be questionable. The description of *Heb. cf. parallelus* from Nepal provided by Schleich et al. [82] is similar to *Herpetoreas tpser* **sp. nov.** except for having a slightly higher number of ventrals (163–172 vs. 153–167) and a pair of parietal spots (vs. absent). Thus,

the systematics of the genus *Herpetoreas* still remain poorly known, and its biodiversity probably has been underestimated.

#### 4. Discussion

##### 4.1. Morphological Characters of the Genera Previously Confused with *Amphiesma*

The genus *Herpetoreas* has long been considered as a synonym of the genus *Amphiesma*, mainly due to its morphological similarities [1,3,14]. Guo et al. [3] divided the genus *Amphiesma auctorum* into three genera—*Amphiesma*, *Hebius*, and *Herpetoreas* based on their phylogenetic results. The morphological diagnoses of these three genera have long remained to be elusive [3], which broadly caused taxonomic confusions [7,8]. Although the diagnostic key provided by Ren et al. [2] includes three genera of the former genus *Amphiesma sensu lato*, it could be only applied to species known from China and Vietnam. More importantly, it has been a challenging task to elucidate a morphological diagnosis of these three morphologically similar and speciose genera, especially for their conservativeness of pholidosis characters and general appearance. For example, these three genera previously confused with *Amphiesma* are similar to each other in having the following key generic diagnosis in the family Natricidae [124,125]: (1) head moderately distinct from neck; (2) nostrils situated and directed laterally or dorsolaterally; (3) eyes relatively moderate to large; (4) prefrontals mostly paired; (5) common dorsal scale rows, as 19-19-17; (6) largely overlapped ventral scale counts, as 118–158 in *Amphiesma*, both min. and max. in *A. stolatum* [6]; as 101–187 in *Hebius*, min. in *Heb. viperinus* [126], max. in *Heb. arquus* [127]; as 136–234 in *Herpetoreas*, min. in *Her. pealii*, max. in *Her. platyceps* (Table 2). Thus, the general morphological features cannot distinguish *Amphiesma sensu lato*.

Hemipenial morphology has been widely applied for diagnosis in the family Natricidae, especially at a genus level [1,24,128]. Malnate [1]: 47 also highlighted the effectiveness of hemipenial morphology and maxillary teeth in generic identifications of natricid taxa. We compared pholidosis, hemipenial morphology, and maxillary teeth of *Amphiesma sensu lato*, and found that different genera could be readily distinguished by a suit of characters including (1) the number of supralabials in contact with the nasals; (2) the diastema before the distinctly enlarged posterior maxillary teeth; (3) the direction of progression of the *sulcus spermaticus*; (4) the position of the distal end of *sulcus spermaticus*; (5) the relative size of the basal hook of the hemipenis; (6) the degree of heterogeneity between the left and right lobe of the hemipenis; (7) the conditions of apical naked areas of the hemipenis (protruding or not); and (8) the visibility of apical naked area from asulcate surface (Figure 11; Table 4).

**Table 4.** Morphological comparisons among different genera of *Amphiesma sensu lato*.

	<i>Amphiesma</i>	<i>Hebius</i>	<i>Herpetoreas</i>
SpL-N maxillary diastema	1st present	1st–2nd absent	1st–2nd present
<i>sulcus spermaticus</i>	extends to the middle of crotch	extends to the base or tip of inner right side of lobe	extends to the base or tip of inner right side of lobe
basal hook length of left lobe <sup>1</sup>	single, weakly developed left lobe slightly longer	single, developed left lobe distinctly longer or not developed, protruding to a greater (morph I) or lesser (morph II) extent	single, developed left lobe slightly longer
apical naked area on crotch	developed, not protruding		weakly developed, not protruding
apical naked area visible or not from asulcate surface	invisible	visible	invisible
distribution	South Asia and Indochina	South Asia, East Asia, and Southeast Asia	Southern foothills of Himalayas and Eastern Himalayas

<sup>1</sup> The left lobe is defined to be the left lobe when face to the sulcus side of hemipenis in some studies [128,129], the orientation of hemipenis is followed Zhang et al. [24] in this study.

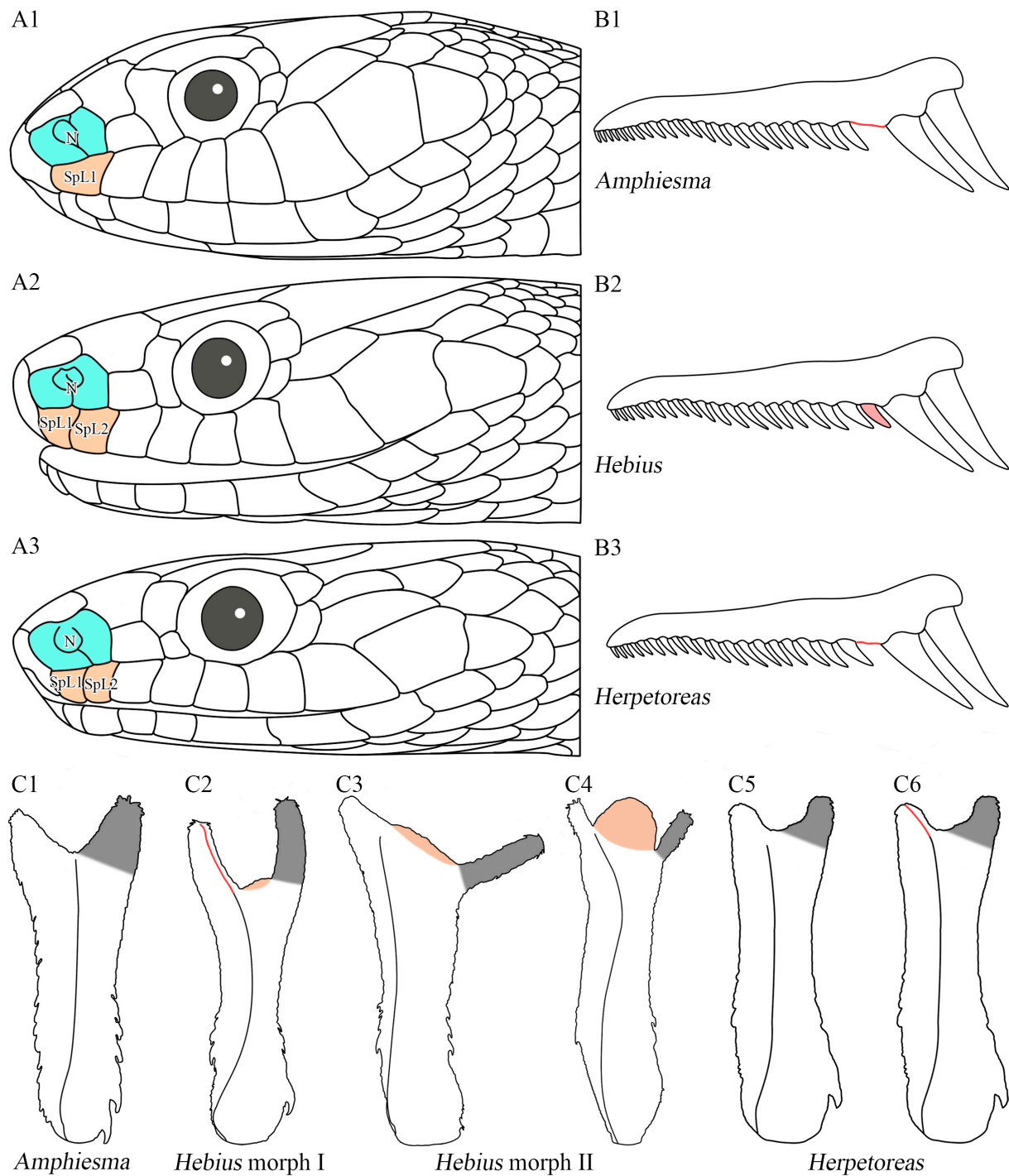
Specifically, the genus *Amphiesma* is the most morphologically distinct genus among the three different genera of *Amphiesma sensu lato*, which could be also reflected by its distant related phylogenetic relationship with reference to both *Hebius* and *Herpetoreas* (Figure 1, also see Deepak et al. [10]). The genus *Amphiesma* differs from both *Hebius* and *Herpetoreas*

in having (1) only the 1st supralabial in contact with nasal vs. 1st–2nd supralabials in contact with nasal; (2) *sulcus spermaticus* extends to the middle of crotch vs. extends to the base or the tip of inner side of right lobe; (3) basal hook slightly higher than the adjacent spines vs. basal hook at least two times higher than the adjacent spines; (4) hemipenis sparsely ornamented with spines vs. densely ornamented with spines (Figure 11; Table 4). Furthermore, the genus *Amphiesma* differs from *Hebius* in having a diastema before the distinctly enlarged diastema vs. absent. Although the hemipenial morphology is currently unknown for *A. monticolum*, a second member of *Amphiesma* [10], the character that 1st supralabial in contact with nasal is still capable of identification.

Secondly, *Herpetoreas* is different from *Hebius* in the morphology of maxillary teeth and hemipenis. *Herpetoreas* differs from *Hebius* in having the presence of diastema before the distinctly enlarged posterior maxillary teeth vs. absent in *Hebius*. The morphology of dentition has been considered as key diagnosis in the taxonomic history of natricid snake since Malnate [1], and this character is proved to be conservative within a given genus, such as *Fowlea* [130,131], *Rhabdophis* (only except for some ecological specialists) [132], and *Opisthotropis* [125]. Thus, the dentition is considered to be of significant value in distinguishing *Herpetoreas* from *Hebius*.

Additionally, although it has been broadly demonstrated that hemipenial morphology is a key morphological diagnosis in the taxonomy of Reptilia [23,133,134], very few are known in the genus *Hebius* and *Herpetoreas* [8,24,128,129]. Das et al. [8] briefly compared the hemipenial morphology within the genus *Herpetoreas*, while their differences among *Amphiesma sensu lato* remained unknown. Nevertheless, based on our current samplings, *Hebius* and *Herpetoreas* could also be distinguished from each other by hemipenial morphology. The morphology of hemipenis in *Hebius* has been depicted as shallowly bilobed, densely spinose, with nude crotch and a single *sulcus spermaticus* mostly extending to the base (sometimes the tip) of short lobes [24,128,129]. The apical naked area in the genus *Hebius* is highly developed, which extends proximally onto the asulcate surface (e.g., in *Heb. venningi*, see Cadle [128]: 9) or protrudes from crotch to different degree (e.g., in *Heb. optatus*, see Zhang et al. [24]: 41, Figure 52B and Appendix C, Figure A1H). Although this apical naked area has been previously recorded, few attentions have been given to the distinct hemipenial character, which is rare in other Asian natricid taxa and regarded to be significant [128,133,134]. In the current study, two distinct morphs of hemipenis are defined in the genus *Hebius*, based on the degree of crotch protrusion and the shape of lobes, which includes (1) morph I: apical naked area slightly protruded with relatively long and slender lobes (Figure 13C2); (2) morph II: apical naked area distinctly protruded with relatively short and vestigial lobes (Figures 11B and 13(C3,C4), Appendix C). The genus *Herpetoreas*, in contrast to *Hebius*, differs from all the two *Hebius* morphs in having less developed apical nude area, which is invisible from asulcate surface vs. well-developed apical nude area, which is visible from the asulcate surface in *Hebius* (Figure 13).

Consequently, we emphasize the importance of hemipenial morphology and maxillary teeth in generic identifications of the Family Natricidae, due to the conservative evolution of pholidosis characters in natricid snakes [1]. Nevertheless, *Hebius* is the most speciose genus in Natricidae (~47 species) [99,135], and morphological data of more species are also needed to improve the diagnosis.



**Figure 13.** Comparisons of morphological features of *Amphiesma sensu lato*, showing diagnostic characters among the genera *Amphiesma*, *Hebius*, and *Herpetoreas*. (A) lateral head view, showing different numbers of supralabials (SpL, in orange) in contact with nasals (N, in blue) in different genera: (A1). *Amphiesma stolatium*, YBU 12081A; (A2). *Hebius boulengeri*, SYS r001680; (A3). *Herpetoreas tpser* sp. nov., CIB 107855. (B) schematic diagrams of maxillary teeth and diastema (in red) in different genera: (B1). *Amphiesma*, diastema present; (B2). *Hebius*, diastema absent; (B3). *Herpetoreas*, small diastema present. (C) schematic diagrams of hemipenial morphology in different genera, showing differences in direction and the position of the distal end of *sulcus spermaticus* (in red); the area of apical naked areas (in orange); and the condition of the left lobe of hemipenis (in grey). Not to scale. Line drawings by Jin-Long Ren.

**Key to the three genera of previously confused with *Amphiesma***

- 1A Nasal in contact with 1st supralabial only; *sulcus spermaticus* extends straight to the center of the crotch.....*Amphiesma*
- 1B Nasal in contact with 1st–2nd supralabials; *sulcus spermaticus* laterally extends to the side of crotch or inner right side of lobe.....2
- 2A Diastema before enlarged posterior maxillary teeth present; (hemipenis) apical naked area on the crotch weakly developed, not protruding, not visible from asulcate surface.....*Herpetoreas*
- 2B Diastema before enlarged posterior maxillary teeth absent; (hemipenis) apical naked area highly developed, protruding to different degree, visible from asulcate surface.....*Hebius*

**4.2. Generic Assignment of Some *Hebius* Snakes**

After the taxonomic revision of *Amphiesma sensu lato*, *Hebius parallelus* was considered as a member of *Hebius* based on molecular phylogenetic results [3]. David et al. [11] subsequently confined *Heb. parallelus* to northeastern India only, and revalidated *Amphiesma clerki* to the genus *Hebius* to accommodate populations from the Eastern Himalayas, northern Myanmar, and western Yunnan, China. Therefore, the sample of *Heb. parallelus* (CAS 215036) from Yunnan, China used in Guo et al. [3] would actually represent *Hebius clerki* (Figure 1; Table 1). Recently, Che et al. [13] reconstructed the phylogenetic tree of the genus *Herpetoreas* with inclusion of sample of *Hebius* cf. *parallelus* from Mêdog, Tibet, China and transferred the species to *Herpetoreas*. However, our results indicated that the taxon identified as *Hebius* cf. *parallelus* from Mêdog, Tibet, China is a misidentification of the new species *Herpetoreas tpser* described above.

We cannot here ascertain the generic position of *Hebius parallelus* (*Tropidonotus parallelus* Boulenger, 1890: 345. Type locality, by virtue of lectotype designation: “Sikhim”, i.e., now Sikkim, India). The lectotype was designated by Kramer [72]: NHMUK 1946.1.13.53, adult male; collected and deposited by Sir Joseph Dalton Hooker. No genetic sequence of this rare species is available. However, we noticed that *Heb. parallelus* is similar to species currently referred to *Herpetoreas* in having (1) a similar number of maxillary teeth, 21–22 vs. 13–23 min. in *Her. pealii*, max. in *Her. xenura*, (2) posterior teeth distinctly enlarged, (3) the presence of diastema before the enlarged maxillary teeth. Nevertheless, we here refrain from referring *Hebius parallelus* to the genus *Herpetoreas* pending the availability of phylogenetic analyses.

Since the diagnostic characters of species previously referred to *Amphiesma sensu lato* have long been unclear, the generic assignments of several *Hebius* taxa to the genus *Hebius* were recently found to be inappropriate [7,8]. Moreover, Guo et al. [3] also rightly suggested that the genus *Herpetoreas* may contain additional species then referred to *Hebius*. Particularly, the generic allocation of a newly described species, namely, *Hebius lacrima* Purkayastha and David, 2019, needs to be further ascertained. *Hebius lacrima* agrees with the diagnosis of *Herpetoreas* in having “24 gradually enlarged maxillary teeth, followed, with a diastema, by 3 distinctly enlarged posterior teeth”, a major difference from the genus *Hebius* [113] (Table 4; Figure 13B). The morphological differences provided by Purkayastha et al. [113] also cannot distinguish it from *Herpetoreas* when one takes all present members of the latter genus into account, including (1) ventrals scales counts 147 in *Heb. lacrima* vs. 136–234 (min. in *Her. pealii*; max. in *Her. platyceps*), and tail length ratio TaL/TL, 0.301 in *Heb. lacrima* vs. 0.227–0.317 (min. in *Her. pealii*; max. in *Her. tpser*). The distribution range of *Hebius lacrima* also falls within the known distribution range of *Herpetoreas*. Therefore, we question the generic assignment of *Hebius lacrima*, and recommend further molecular phylogenetic analyses to clarify the taxonomic confusions still present among species of the former genus *Amphiesma sensu lato*.

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and P.D.; visualization, J.-J.H.; supervision, J.-T.L.; project administration, J.-T.L. and K.J.; funding acquisition, J.-T.L. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the Animal Ethics Committee of Chengdu Institute of Biology, Chinese Academy of Sciences (CIBDWLL2021023, 21 December 2021). Research procedures were carried out in accordance with national and institutional regulations.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Names of the new species were formally registered in the database ZooBank (<http://zoobank.org> (accessed on 26 November 2021)). Specimens were deposited in the Herpetological Museum, Chengdu Institute of Biology, Chinese Academy of Sciences (CIB). The newly generated sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank> (accessed on 26 November 2021)).

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**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A. Specimens Examined ( $n = 225$ ). \* Indicates Hemipenes Examined

### Genus *Amphiesma* Duméril, Bibron, and Duméril, 1854 ( $n = 5$ )

*Amphiesma stolatum* ( $n = 5$ ) **China**. Guangdong Province. SYS r000052, Renhua County, Mt. Danxia; SYS r002147, Xinyi City, Dawuling. Guangxi Zhuang Autonomous Region. SYS r001727\*, Chongzuo City, Longzhou County; KIZ 7I0015, Chongzuo City, Nalong, 230 m. Yunnan Province. KIZ 79012, Pingbian County, Qianjin, 960 m.

### Genus *Hebius* Thompson, 1913 ( $n = 180$ )

*Hebius annamensis* ( $n = 1$ ). **Vietnam**. Quang Tri Province. ROM 33290, “Bau Cap”.

*Hebius atemporalis* ( $n = 5$ ). **China**. Yunnan Province. KIZ 090312, KIZ 09124, YBU 14259, Mengzi County; KIZ 79013, Pingbian County, Qianjin; KIZ 91II0001, Kunming City, Huahongdong, 2100 m.

*Hebius cf. bitaeniatus* ( $n = 9$ ) **China**. Yunnan Province. KIZ 90I165, KIZ 90I174, Dayao County, Santai, 2100 m. Guangxi Zhuang Autonomous Region. YBU 11204–05, Tianlin County, Cenwanglaoshan. Guizhou Province. SYS r002171\*, Shuicheng County, Yezhong; YBU 11136–37, YBU 14137, Leishan County, Mt. Leigong; YBU 12150, Rongjiang County, Pingyang.

*Hebius boulengeri* ( $n = 17$ ). **China**. Guangdong Province. SYS r001506, SYS r001680\*, SYS r001685, SYS r001900, CIB 118637\*, Xinyi City, Dawuling; SYS r001749, SYS r001801, SYS r002016, Gaozhou City, Xianrendong; SYS r000223, Fengkai County, Heishiding; SYS r001179, Chaozhou City, Jiaoshuikeng Village; SYS r002210, Shixing County, Chebaling. Fujian Province. YBU 12163, Dehua County, Mt. Daiyun. Jiangxi Province. SYS r001003, Xunwu County, Jilong Village; SYS r001371, Xinfeng County, Mt. Jinpen. Guangxi Zhuang Autonomous Region. SYS r001552, Huanjiang, Mt. Jiuwan. Yunnan Province. KIZ 79I034, Cangyuan County, 1200 m. **Vietnam**. Vinh Phuc Province. VNMN 06218, Tamdao, 687 m.

*Hebius chapaensis* ( $n = 10$ ). **Vietnam**. Lao Cai Province. VNMN 05791, VNMN 06102–106, Sa Pa; VNMN 3277, Bat Xat, Y Ty, 2030 m. **China**. Yunnan Province. YBU 14026,

Pingbian County, Mt. Dawei, 1993 m; CIB 110718\*, Mengla County; SYS r001240, Mengla County, Zhushihe Village, 930 m.

***Hebius craspedogaster* (n = 11) China.** Zhejiang Province. SYS r002253, SYS r002469, Suichang County, Wangcunkou Town, 780–810 m; YBU 17186, Dongyang City, Xujiashuang. Fujian Province. CIB 8250–52, Nanping City, Mt. Wuyi, 730–1100 m. Jiangxi Province. SYS r000735, SYS r000901, Shangrao City, Mt. Tongbo. Hunan Province. SYS r000878\*, SYS r002093, Shuangpai County, Mt. Yangming. Guizhou Province. KIZ 7620755, Leishan County.

***Hebius johannis* (n = 3) China.** Yunnan Province. CIB 103939, Yulong County, Shuhe Ancient Town, 2457 m; KIZ 79001, Ninglang County; SYS r002402, Chengjiang County.

***Hebius khasiensis* (n = 4) China.** Yunnan Province. SYS r002568, Yingjiang County; CIB 118636\*, CIB 118641\*, Mengla County; KIZ 75I399, Menglian County, Lafu Village, 1620 m.

***Hebius metusia* (n = 23) China.** Sichuan Province. CIB 78163–64, SYS r001604\*, Hongya County, Mt. Wawu; CIB 8168, Hongya, Liujiang; CIB 101971–72, Tianquan County, Xingou Town, 1400 m; YBU 16129, Yingjing County, Xinmiao Town; CIB 101973, CIB 106522, YBU 16142, YBU 19076, Shimian County, Liziping, 2030 m; YBU 16143, Shimian County, Dahongshan; YBU 17254, Shimian, Tianwan Town; YBU 17255, Shimian County, Huilong Town; CIB 102742, Lushan County, Dachuanhe, 2017 m; CIB 8176, SYS r000725, Leshan City, Mt. Emei, 1100 m; YBU 18231–233, Ebian County, Heizhugou; YBU 15178–79, Muchuan County; CIB 118638\*, Mianning County, Yele Town.

***Hebius modestus* (n = 10) China.** Yunnan Province. CIB 72352–53, Tengchong City, Dakun Village, 1720 m; CIB 8275, Baoshan City, Bawan Village, 1800 m; KIZ 79I098, KIZ 79I300, Yongde County, 1560–1900 m; KIZ 75I324, Menglian County, Lafu Village, 1620 m; SYS r002185\*, Xiping County. Guizhou Province. CIB 8276–67, Luodian County, Bamao Town, 920 m. Guangxi Zhuang Autonomous Region. SYS r001557, Tianlin County, Cenwanglaoshan, 1500 m.

***Hebius octolineatus* (n = 7). China.** Yunnan Province. YBU 14425–26, Xundian County, Qixing Town; KIZ II0492, KIZ II0495, Ludian County, 2500 m; KIZ 94602, Kunming City, Xima Village. Guizhou Province. KIZ 781105, KIZ 781308, Weining County.

***Hebius optatus* (n = 6) China.** Guangxi Zhuang Autonomous Region. KIZ 750001, Daxin County; KIZ 780378, Quanzhou County, Dongshan; SYS r001629, Longshen County, Huaping, 800 m. Guizhou Province. SYSr002081–SYSr002082, Jishou City, Aizhai Town. Sichuan Province. Unlabeled\*, Yibin City.

***Hebius parallelus* (n = 18). India.** Sikkim (?). BMNH 1946.1.13.53 (lectotype of *Tropidonotus parallelus* Boulenger, 1890), “Sikkim”. Meghalaya. BMNH 1946.1.12.83–84, BMNH 1946.1.13.48 (3 former syntypes of *Tropidonotus parallelus* Boulenger, 1890), “Khasi Hills”; ZSI 3852, “Shillong”; ZSI/ERS 112, ZSI/ERS 205, ZSI/ERS 2785, ZSI/ERS 3076–3077, Shillong, Risa Colony; ZSI/ERS 272, ZSI/ERS 9059, Shillong, Tripura Castle Road; ZSI/ERS 450, ZSI/ERS 970, Shillong, Fruit Garden; ZSI/ERS 3253, East Khasi Hills District, Mawlai; ZSI/ERS 8262, East Khasi Hills, Mawphlang; ZSI/ERS 9060, Garo Hills, Selbelgiri. Nagaland. Unpreserved specimen, near the Tragopan Sanctuary (25.63549N-094.01261E), Khonoma. No locality. ZSI 4397, “Madras Hills”, in error.

***Hebius popei* (n = 16) China.** Hainan Province. CIB 118640\*, Lingshui County, Mt. Diaoluo; YBU 17001, Ledong County, Jianfengling. Guangdong Province. SYS r002252\*, Yingde City, Shimentai; SYS r000091, SYS r000558, SYS r001065, Renhua County. Guangxi Zhuang Autonomous Region. SYS r001532, Guanyang County, Qianjiadong, 1000 m; SYS r001634, Longsheng County, Huaping, 600 m; SYS r002517, SYS r002519, Guiping City, 73–293 m; YBU 19016, Cangwu County, Mushuang Town. Jiangxi Province. SYS r000073, SYS r000081, Guixi City, Yangjifeng. Hunan Province. SYS r002091, Shuangpai County, Mt. Yangming. Guizhou Province. KIZ 791143, Libo County, Chengguan; SYS r000237, Libo County, Maolan.

*Hebius sangzhiensis* ( $n = 3$ ) **China**. Hunan Province. SYS r001397 (paratype of *Hebius sangzhiensis*), CIB 118639\*, Sangzhi County, Mt. Tianping; YBU 16145, Sangzhi County, Mt. Badagong.

*Hebius sauteri sauteri* ( $n = 10$ ) **China**. Taiwan Province. CAS 18984, Pingtung County; CAS 18988 (paratype of *Natrix copei* Van Denburgh, 1909), Tainan City, Guanziling. Hainan Province. YBU 17001, Ledong County, Jianfengling. Jiangxi Province. SYS r000323\*, Ji'an City, Mt. Jinggang; SYS r000162, SYS r001258, SYS r001266\*, Longnan County, Mt. Jiulian, 400 m. Hunan Province. SYS r001766\*, Guidong County, Mt. Bamian. Guangdong Province. SYS r001150, Xinyi City, Sihe Town. Guizhou Province. SYS r000275, Libo County, Maolan.

*Hebius sauteri maximus* ( $n = 3$ ) **China**. Sichuan Province. CIB 118635\*, Yibin City, Mt. Laojun; YBU 18170, Dujiangyan City, Jiezi Town. Guizhou Province. SYS r002041\*, Bijie City, Xiachang Village.

*Hebius septemlineatus* ( $n = 10$ ) **China**. Yunnan Province. KIZ 74II0177, KIZ 74II0183, Tengchong County, Dakuang, 1800 m; SYS r001223, SYS r001225\*, Tengchong County, Mt. Gaoligong, 2040 m; YBU 15161–62, Tengchong County, Mazhan Town; KIZ 75II0235, KIZ 75II0236, Yingjiang County, Tongbiguan, 1350 m; KIZ II0511, KIZ II0520, Longchuan County, 800–1300 m.

*Hebius venningi* ( $n = 5$ ) **Myanmar**. Kachin State. CAS 238901, Myitkyina District, Moenyin Township, 358 m. Chin State. CAS 233206, Phalum District, Haka Township, 1634 m; CAS 235175, Mindat District, Mindat Township, 992 m; CAS 234777, Mindat District, Kanpatlat Township, 1238 m. No locality. YBU 18229.

*Hebius vibakari* ( $n = 3$ ) **China**. Jilin Province. SYS r002217, Huinan County, Longwan. **Russia**. ZISP 15546, ZISP 16073, “Far East”.

*Hebius weixiensis* ( $n = 5$ ) **China**. Yunnan Province. CIB 8257–59, KIZ II0501, Yulong County, Ludian Town, 2500 m; SICAU 2020082701\*, Weixi County, Gongnong Village, 2127 m.

*Hebius yanbianensis* ( $n = 1$ ) **China**. YBU 15018 (holotype of *Hebius yanbianensis*), Yanbian County, Zemulong Town.

**Genus *Herpetoreas* Günther, 1860** ( $n = 40$ )

*Herpetoreas burbrinki* ( $n = 1$ ) **China**. Xizang Autonomous Region. YBU 071128 (holotype of *Herpetoreas burbrinki*), Zayü County.

*Herpetoreas platyceps* ( $n = 9$ ). **India**. Sikkim. FMNH 15827, “Mangpu, Sikkim”. West Bengal. NMW 22383:2, NMW 22383:5, Darjeeling. Himachal Pradesh. NMW 18569, NMW 18570:1–2, Shimla and Kullu (Syntypes of *Zamenis himalayanus* Steindachner, 1867). Jammu and Kashmir. MNHN 1988.6484, Udamphur District, between Makabagi and Ularbagi, above Doda, about 2800 m; ZMB 7293, “Kashmir”. **China**. Xizang Autonomous Region. CIB 8420, Nyalam County, Zhangmu, 2400 m.

*Herpetoreas sieboldii* ( $n = 24$ ). **India**. Sikkim. ZMB 10231, no precise locality. West Bengal. CAS-SU 15973, Darjeeling; NMW 22383:1, NMW 22383:3–4, Darjeeling. **China**. Xizang Autonomous Region. CAS 177474, CAS 177672–177673, Nyalam County, Zhangmu, 2000–2500 m. **Nepal**. BMNH 1913.5.22.1, Mai Kola; CAS 90690, above Deppur, 1676 m; FMNH 109762, Amp Pipal, 1219 m; FMNH 131966, Chapagaon, Kathmandu Valley; FMNH 131967, Kathmandu Valley; FMNH 190856, Num Bridge across Arun River, Arun Valley; FMNH 204499, above Num, in forest area, 1950 m; MHNG 1355.72–73, near Hyangcha, Astam, 1600 m; MNHN 2003.3614, Eastern Region, between Surkie Pass and Chheskam, east of Mounasko Pass, 2400 m; ZMB 4551, “Himalaya”; FMNH 204500–504, no precise locality.

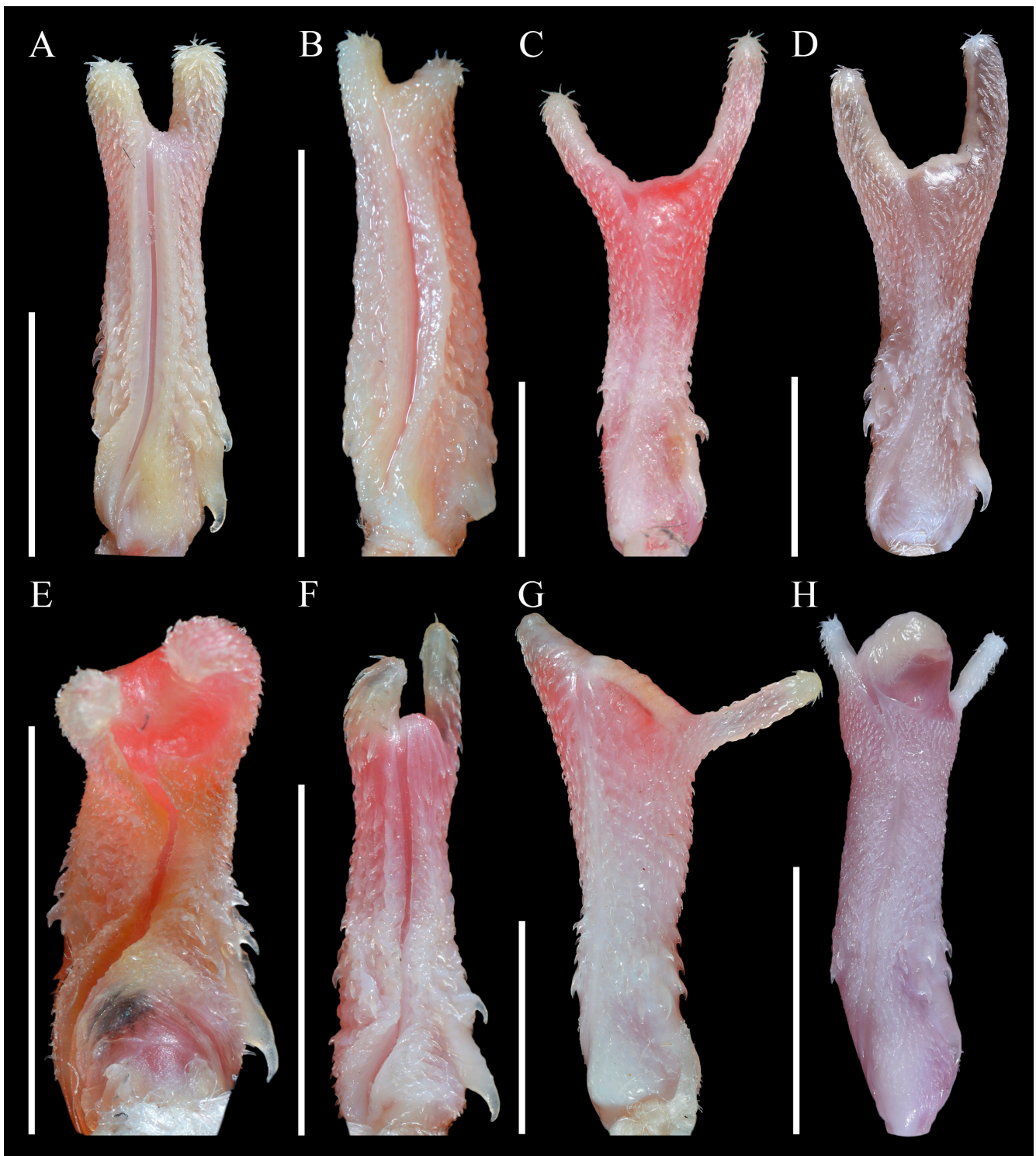
*Herpetoreas tpser* ( $n = 6$ ) **China**. Xizang Autonomous Region. CIB 8418 (holotype of *Herpetoreas tpser*), Médog County, Beibeng, 1300 m; CIB 8419, CIB 118523 (paratypes of *Herpetoreas tpser*), Médog County, Ani Bridge, 1087–1200 m; CIB 118524 (paratype of *Herpetoreas tpser*), Médog County, Hanmi, 2280 m; CIB 107855\*, Médog County, Hanmi, 2127 m; KIZ 06681, Médog County, 80K.



## Appendix B

Table A1. Detailed information of the distribution sites showed in Figure 2.

Taxon Name	Authority	Symbol	No.	Locality	Source
<i>Herpetoreas platyceps</i>	(Blyth, 1854)	square	1	India: West Bengal, Darjeeling	Malnate [35]
			2	India: Uttarakhand, Almora	Malnate [35]
			3	India: Uttarakhand, Binsar	Malnate [35]
			4	India: Himachal Pradesh, Shimla	Malnate [35]
			5	India: Himachal, Upper Sutlej	Malnate [35]
			6	India: Himachal Pradesh, Dalhousie	Malnate [35]
			7	India: Jammu and Kashmir, Gulmarg	Malnate [35]
			8	China: Xizang (Tibet), Gyirong	Che et al. [13]
			9	China: Xizang (Tibet), Nyalam	Che et al. [13]
			10	Nepal: widely distributed	Nanhoe et al. [73], Schleich et al. [82]
			11	Pakistan: Punjab, Rawalpindi	Malnate [35]
			12	Pakistan: Khyber Pakhtunkhwa, Changla Gali	Khan [81]
			13	Bhutan: Paro District, Pachu Bank	Wangyal [92]
			14	Bangladesh: "northwest and northern part"	Ahsan et al. [89]
<i>Herpetoreas sieboldii</i>	Günther, 1860	circle	1	India: Assam, Garo Hills, Tura	Malnate [35]
			2	India: Sikkim, Gvangtok	Malnate [35]
			3	India: West Bengal, Darjeeling	Malnate [35]
			4	India: West Bengal, Takdah	Malnate [35]
			5	India: Uttar Pradesh, Gonda	Malnate [35]
			6	India: Uttarakhand, Mussoorie	Malnate [35]
			7	India: Himachal Pradesh, Shimla	Malnate [35]
			8	India: Himachal Pradesh, Tara devi hill	Malnate [35]
			9	India: Jammu and Kashmir, Gulmarg	Malnate [35]
			10	Nepal: Province No. 1, Mai Kola	Malnate [35]
			11	Nepal: Province No. 1, Maiwa Khola	Malnate [35]
			12	Nepal: Province No. 1, Hatia	Malnate [35]
			13	Nepal: Bagmati Province, Thangjet	Malnate [35]
			14	Nepal: Gandaki Province, Ampipal	Malnate [35]
15	Nepal: Gandaki Province, Taglung	Malnate [35]			
16	Nepal: Gandaki Province, Lumsum	Malnate [35]			
17	Nepal: Karnali Province, Balangra Pass	Malnate [35]			
18	Pakistan: Khyber Pakhtunkhwa, Thandiani	Malnate [35]			
19	Pakistan: Punjab, Rawalpindi	Malnate [35]			
20	Myanmar (?): Shan State, Taunggyi	Malnate [35]			
21	China: Xizang (Tibet), Nyalam	David et al. [11]			
22	Bhutan: Trashiyangtse, Bumdeling	Wangyal [91]			
23	Bangladesh: no specific locality	Ahsan et al. [89]			
<i>Herpetoreas pealii</i>	(Sclater, 1891)	pentagon	1	India: Assam, Sibsagar district	Sclater [111]
			2	India: Northeast India, Siang district	Das et al. [8]
<i>Herpetoreas xenura</i>	(Wall, 1907)	hexagon	1	India: Meghalaya, Khasi Hills	Smith [6]
			2	India: Nagaland, Kohima	Romer [114]
			3	India: Mizoram, Pala Lake Area	Pawar et al. [115]
			4	India: Mizoram, Aizawl	Pawar et al. [115]
			5	India: Mizoram, North Hlimen	Muansanga et al. [118]
			6	Myanmar: northwest Sagaing	Wogan et al. [117]
			7	Myanmar: Rakhine, Rakhine Hills	Wogan et al. [117]
			8	Bangladesh: Bandarban District, Keokradong	Ahsan et al. [89]
<i>Herpetoreas burbrinki</i>	Guo, Zhu, Liu, Zhang, Li, Huang, and Pyron, 2014	rhombus	-	China: Xizang (Tibet), Zayü	Guo et al. [3]
<i>Herpetoreas tpser</i>	This study	star	-	China: Xizang (Tibet), Médog	This study
<i>Hebius parallelus</i>	(Boulenger, 1890)	triangle	1	India: Meghalaya, Selbalgiri	David et al. [11]
			2	India: Meghalaya, Shillong and its vicinity	David et al. [11]
			3	India: Meghalaya, Mawphlang	David et al. [11]
			4	India: Nagaland, Khonoma	David et al. [11]

Appendix C. Sulcate Surfaces of Hemipenis in the Genus *Hebius*

**Figure A1.** (A). *Hebius bitaeniatus*, SYS r002171; (B). *Hebius septemlineatus*, SYS r001225, basal hook broken; (C). *Hebius weixiensis*, SICAU 2020082701; (D). *Hebius metusia*, CIB 118638; (E). *Hebius sauteri*, SYS r002041; (F). *Hebius popei*, SYS r002252; (G). *Hebius boulengeri*, CIB 118637; (H). *Hebius optatus*, unlabeled. Information see Appendix A. Scale bar = 5 mm. Photographs by Jun-Jie Huang and Jin-Long Ren.

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