

## Research article

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**Taxonomic reassessment of the *Herpetoreas xenura* (Wall, 1907)  
(Squamata: Serpentes: Natricidae) from Myanmar  
with description of a new species**Tan Van NGUYEN<sup>1,\*</sup>, Hmar Tlawmte LALREMSANGA<sup>2</sup>,  
Lal BIAKZUALA<sup>3</sup> & Gernot VOGEL<sup>4,\*</sup><sup>1</sup>Institute for Research and Training in Medicine, Biology and Pharmacy, Duy Tan University,  
Da Nang, 550000, Vietnam.<sup>1</sup>College of Medicine and Pharmacy, Duy Tan University, 120 Hoang Minh Thao,  
Lien Chieu, Da Nang, 550000, Vietnam.<sup>2,3</sup>Developmental Biology and Herpetology Laboratory, Department of Zoology, Mizoram University,  
796004 Tanhril, Mizoram, India.<sup>4</sup>Society for South East Asian Herpetology, Im Sand-3, Heidelberg, Germany.

\*Corresponding authors: tan.sifasv@gmail.com; Gernot.Vogel@t-online.de

<sup>2</sup>Email: htlrta@yahoo.co.in<sup>3</sup>Email: bzachawngthu123@gmail.com<sup>1</sup>urn:lsid:zoobank.org:author:94EABB6E-180C-424E-8E9C-60DB36125550<sup>2</sup>urn:lsid:zoobank.org:author:F7D2FBD8-87EB-4962-BC8E-87AD754F7E8C<sup>3</sup>urn:lsid:zoobank.org:author:D4198FBC-CB58-453B-B0E1-568F47ECE876<sup>4</sup>urn:lsid:zoobank.org:author:26C84E11-E43F-4076-B268-28C32E9FD2D0

**Abstract.** The review of the taxonomic status of *Herpetoreas xenura* species complex, based on morphological and molecular data, revealed a new species from Myanmar, which we describe as *Herpetoreas davidi* sp. nov. from the Rakhine Yoma Elephant Wildlife Sanctuary in Rakhine State. It is suggested to be a sister species to *Herpetoreas pealii* and *Herpetoreas xenura* sensu stricto, and can be separated from the latter species by a combination of morphological and scalation characters, and by its pattern. Another population from the Htamanthi Wildlife Sanctuary, Sagaing Region, was previously confused with *H. xenura*. However, as a closer examination of its morphology, shows it to be closer to *Hebius khasiensis*, we herein tentatively refer to this population as *Hebius khasiensis*, pending further molecular data confirming its taxonomic status. Consequently, we propose to temporarily remove *Herpetoreas xenura* from the fauna of Myanmar. Further studies, especially in the northwestern region of Myanmar, such as near border with India in Chin Hills and Naga Hills, are required. An updated key for the species of *Herpetoreas* is also provided.

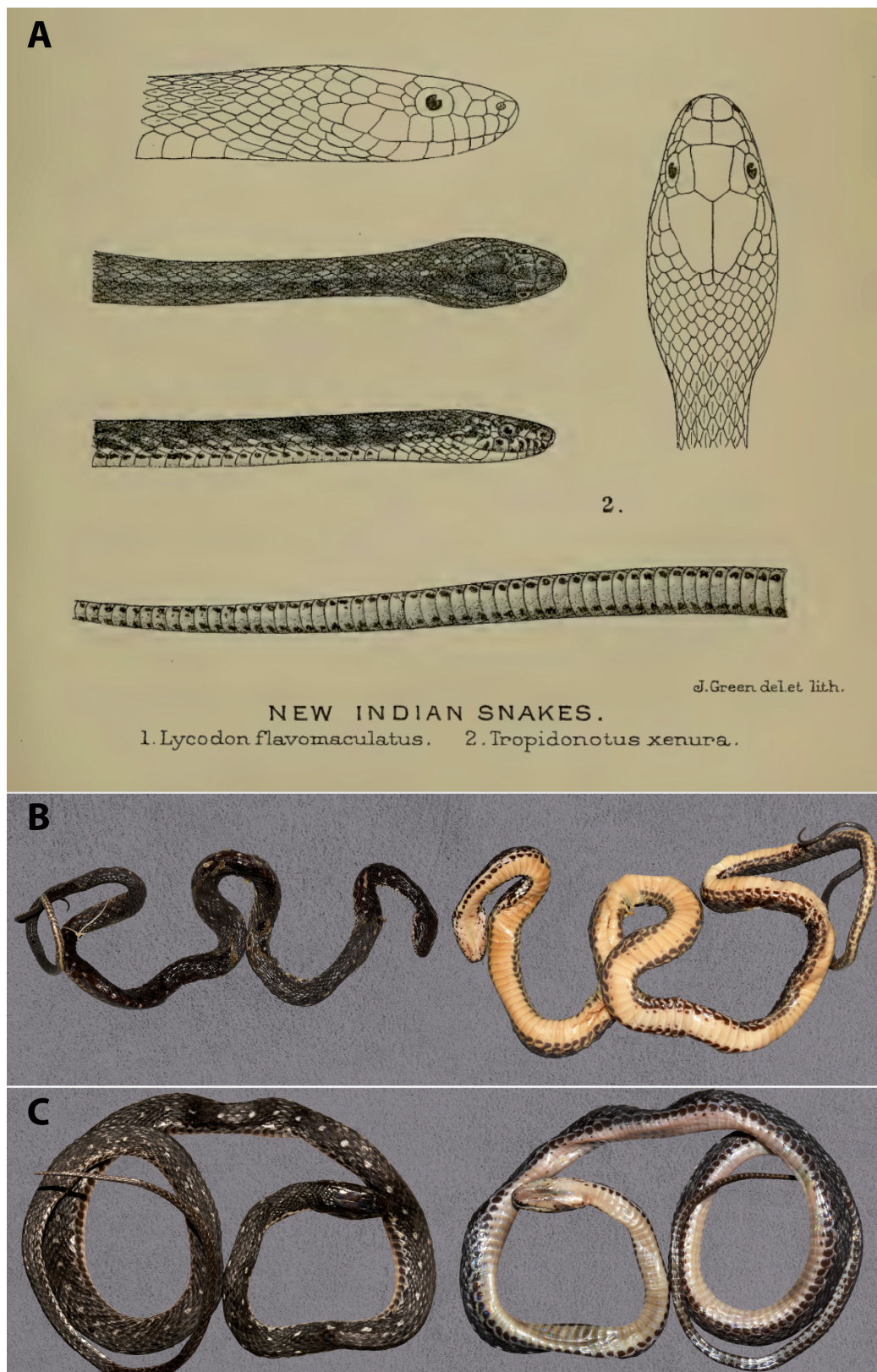
**Keywords.** Distribution, *Herpetoreas davidi* sp. nov., Indo-Burmese region, Naga Hills, Rakhine Hills, taxonomy.

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## Introduction

The Himalaya mountain keelbacks of the genus *Herpetoreas* Günther, 1860 are widely distributed across the southern foothills of the Himalaya Mountains as well as Eastern Himalayas, including northeastern Pakistan, northern and northeastern India, southwestern China (Region of Tibet), Nepal, Bhutan, Bangladesh, and Myanmar (Lalremsanga *et al.* 2022; Ren *et al.* 2022). Several recent studies have demonstrated that the diversity of *Herpetoreas* is still underestimated and the species received much controversy and confusion with species of the genera *Amphiesma* Duméril, Bibron & Duméril, 1854 and, especially, *Hebius* Thompson, 1913 (Smith 1943; Malnate 1966; Guo *et al.* 2014; Peng *et al.* 2021; Deepak *et al.* 2022; Lalremsanga *et al.* 2022; Ren *et al.* 2022). The genus *Herpetoreas* is morphologically characterised by: head moderately distinct from neck; body cylindrical, maximum TL 943 mm; tail relatively long, TaL/TL 0.227–0.317; nostrils and eye directed laterally; supralabials 8–9, usually 3<sup>rd</sup>–5<sup>th</sup> or 4<sup>th</sup> and 5<sup>th</sup> entering orbit; dorsal scale rows 19–19–17; scales weakly to distinctly keeled, notched at their apical part; ventrals 136–234; cloacal plate and subcaudals divided or not; maxillary teeth 13–23, slightly increasing in size, last two to three teeth distinctly enlarged, separated from anterior teeth by a small diastema; hemipenis short and thin, shallowly bilobed, spinous throughout with single basal hook; sulcus spermaticus single, centripetal, extends to the inner right lobe or to the crotch only; apical naked area on the crotch weakly developed, not protruding, not visible from asulcate surface; venter yellowish-beige, each ventral scale decorated with dark spots at lateral edge or not (Günther 1860; Guo *et al.* 2014; Ren *et al.* 2022). Currently, the genus *Herpetoreas* comprises seven species, namely: *Herpetoreas burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang & Pyron, 2014; *H. murlen* Lalremsanga, Bal, Vogel & Biakzuala, 2022; *H. pealii* (Slater, 1891); *H. platyceps* (Blyth, 1854); *H. sieboldii* Günther, 1860; *H. xenura* (Wall, 1907); and *H. tpser* Ren, Jiang, Huang, David & Li, 2022 (Lalremsanga *et al.* 2022; Ren *et al.* 2022).

The Strange-tailed keelback or Wall's Keelback, *Herpetoreas xenura*, was described by Wall (1907) based on a specimen in bad condition from an unknown type locality (see Fig. 1A), and, furthermore, the holotype of this species has been lost (Smith 1943). Subsequently, Wall (1909) reported about four additional specimens of this species from Cherrapunji in the Khasi Hills, Assam (now Meghalaya State) which were discovered in the Indian Museum (now the Zoological Survey of India [ZSI], Kolkata [Calcutta], West Bengal, India). These specimens were labelled *Hebius modestus* (Günther, 1875), to which the species bears resemblance in general coloration but is differentiated by its undivided subcaudals, number of preoculars, number of temporals, and number of keeled scales on body (Wall 1907). Therefore, “Khasi Hill, Meghalaya State, India” is assumed to be the type locality. The semi-aquatic species *Herpetoreas xenura* has been reported to be distributed from Northeast India to Bangladesh and Myanmar (Wall 1907; Wogan *et al.* 2008; Ren *et al.* 2022; Uetz *et al.* 2023). But the records of this species from Rakhine State and Sagaing Region of Myanmar, however, were not accompanied by information on morphology or molecular data. During examination of the herpetological collections of the California Academy of Sciences (CAS, USA), one of us (G. Vogel) encountered six specimens of *Herpetoreas* from Myanmar (five from Rakhine State and one from Sagaing Region), which were originally identified as *Herpetoreas xenura* by Wogan *et al.* (2008). However, a more detailed morphological re-examination of these six specimens revealed morphological differences between these two populations. In the present study, we provide a detailed morphological description and comparison of the populations of *Herpetoreas* in Myanmar and demonstrate that they belong to two taxa that are morphologically distinct from true *H. xenura* and other congeners. Molecular analyses based on mitochondrial cytochrome b (Cytb) confirm the distinctiveness of the Rakhine population,



**Fig. 1.** *Herpetoreas xenura* (Wall, 1907), in preservative. **A.** Holotype (lost), sex unknown. **B.** ♂, general dorsal, ventral, and head view (MZMU 1211). **C.** ♀, general dorsal and ventral view (MZMU 3271). Drawing (A) by J. Green Delet Lith in Wall (1907). Photos by G. Vogel (A–C).



which is formally described below as a new species. Meanwhile the population at Sagaing should be assigned to *Hebius khasiensis* (Boulenger, 1890).

## Material and methods

### Material examined

For this study, a total of 19 preserved specimens of the *Herpetoreas xenura* group were examined for their external morphological characters (five specimens from Rakhine State and one specimen from Sagaing Region, Myanmar; and 13 specimens of *Herpetoreas xenura* from India, see Table 1). The other 58 examined specimens of Natricidae Bonaparte, 1838, including *Hebius khasiensis* (28 specimens), *Herpetoreas sieboldii* (19 specimens), and *Herpetoreas platyceps* (six specimens), are listed in Appendix 1. Measurements were taken with a slide calliper to the nearest 0.1 mm, except for body and tail lengths, which were measured to the nearest mm with a measuring tape.

The following morphometric and meristic characters were recorded:

ATEM	=	anterior temporals
CS	=	condition of the cloacal plate
DSR	=	dorsal scale rows
E-Ns	=	eye to nostril distance
E-Sn	=	eye to snout distance
ED	=	eye diameter
FL	=	length of frontal
HD	=	head depth
HL	=	head length
HW	=	head width
IL	=	infralabials
INL	=	length of internasal scales
Lor	=	loreal
PFL	=	length of prefrontals
PL	=	length of parietals
PoO	=	postoculars
PrO	=	preoculars
PTEM	=	posterior temporals
PVEN	=	pre-ventrals
SC	=	subcaudals
SL	=	supralabials
SL-E	=	supralabials contacting the eye
SVL	=	snout-vent length
SW	=	snout width
TaL	=	tail length
TL	=	total length
VEN	=	ventrals

The number of ventral scales was counted according to Dowling (1951). Dorsal scales were counted at one head length posterior to the neck, at the midpoint of snout-vent length, and at one head length anterior to the cloacal plate. Subcaudals were counted from immediately posterior to the anal scute to the tail tip, but excluding the terminal scute. Values for paired head characters were recorded on both sides of the head and were reported in a left/right order. The sex was determined by dissection of the ventral tail base.



**Table 1** (continued on next page). Main measurements and meristic characters of the *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890). Abbreviations: F = adult female; *Heb.* = *Hebius*; *Her.* = *Herpetoreas*; M = adult male; N/a = not available; SF = subadult female; SM = subadult male.

No.	Previously taxa	Propose taxa	Locality	Number	Sex	Status	SVL (mm)	TaL (mm)
1	<i>Hep. xenura</i>	<i>Hep. davidi</i> sp. nov.	Gawa, Rakhine, Myanmar	CAS 222969	M	Holotype	384	168
2	<i>Hep. xenura</i>	<i>Hep. davidi</i> sp. nov.	Gawa, Rakhine, Myanmar	CAS 220378	SM	Paratype	292	126
3	<i>Hep. xenura</i>	<i>Hep. davidi</i> sp. nov.	Gawa, Rakhine, Myanmar	CAS 220550	F	Paratype	397	178
4	<i>Hep. xenura</i>	<i>Hep. davidi</i> sp. nov.	Gawa, Rakhine, Myanmar	CAS 220256	F	Paratype	482	N/a
5	<i>Hep. xenura</i>	<i>Hep. davidi</i> sp. nov.	Gawa, Rakhine, Myanmar	CAS 220332	SF	Paratype	259	115
6	<i>Hep. xenura</i>	<i>Heb. khasiensis</i>	Khandi, Sagaing, Myanmar	CAS 232203	F		153	72
7	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 810	M		650	N/a
8	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 811	M		635	195
9	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 812	M		675	195
10	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 813	M		620	175
11	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 814	M		670	200
12	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 816	M		635	185
13	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 817	M		560	170
14	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 818	M		480	143
15	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 1211	M		501	198
16	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 819	F		565	180
17	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 820	F		424	124
18	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 3271	F		417	161
19	<i>Hep. xenura</i>	<i>Hep. xenura</i>	Mizoram, India	MZMU 815	SF		110	N/a

**Table 1** (continued). Main measurements and meristic characters of the *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890). Abbreviations: F = adult female; *Heb.* = *Hebius*; *Her.* = *Herpetoreas*; M = adult male; N/a = not available; SF = subadult female; SM = subadult male.

No.	Propose taxa	Number	Sex	VEN	SC	SC	CP	DSR	SL	SL-E	IL
1	<i>Hep. davidi</i> sp. nov.	CAS 222969	M	154	99	single	single	19–19–17	9/9	4–6	9/10
2	<i>Hep. davidi</i> sp. nov.	CAS 220378	SM	156	97	single	single	19–19–17	9/9	4–6	10/10
3	<i>Hep. davidi</i> sp. nov.	CAS 220550	F	151	97	single	single	19–19–17	9/9	4–6	10/10
4	<i>Hep. davidi</i> sp. nov.	CAS 220256	F	155	N/a	single	single	19–19–17	9/9	4–6	10/10
5	<i>Hep. davidi</i> sp. nov.	CAS 220332	SF	152	100	single	single	19–19–17	9/9	4–6	10/9
6	<i>Heb. khasiensis</i>	CAS 232203	F	134	92	divided	divided	19–19–17	9/9	4–6	9/10
7	<i>Hep. xenura</i>	MZMU 810	M	160	N/a	single	single	19–19–17	9/9	4–6	9/9
8	<i>Hep. xenura</i>	MZMU 811	M	159	102	single	single	19–19–17	9/9	4–6	9/9
9	<i>Hep. xenura</i>	MZMU 812	M	158	86	single	single	19–19–17	7/8	4–6	8/8
10	<i>Hep. xenura</i>	MZMU 813	M	158	95	single	single	19–19–17	7/8	4–6	8/8
11	<i>Hep. xenura</i>	MZMU 814	M	164	103	single	single	19–19–17	7/7	4–5/4–6	7/7
12	<i>Hep. xenura</i>	MZMU 816	M	161	86	single	single	19–19–17	9/9	4–6	9/9
13	<i>Hep. xenura</i>	MZMU 817	M	160	92	single	single	19–19–17	8/8	4–6	8/8
14	<i>Hep. xenura</i>	MZMU 818	M	160	101	single	single	19–19–17	8/8	4–6	8/8
15	<i>Hep. xenura</i>	MZMU 1211	M	165	105	single	single	19–19–17	9/9	4–6	9/10
16	<i>Hep. xenura</i>	MZMU 819	F	165	110	single	single	19–19–17	9/9	4–6	9/9
17	<i>Hep. xenura</i>	MZMU 820	F	158	97	single	single	19–19–17	8/8	4–6	8/8
18	<i>Hep. xenura</i>	MZMU 3271	F	155	87	single	single	19–19–17	9/9	4–6	10/10
19	<i>Hep. xenura</i>	MZMU 815	SF	164	87	single	single	19–19–17	8/8	4–6	7/7

For comparison with other taxa, we relied on previously published data (e.g., Wall 1907, 1909; Smith 1943; Malnate 1966; Mathew & Meetei 2004; Reza 2010; Guo *et al.* 2014; Das *et al.* 2020; Malsawmdawngliana *et al.* 2021; Peng *et al.* 2021; Lalremsanga *et al.* 2022; Ren *et al.* 2022); and our examined specimens. The distribution map was prepared in QGIS ver. 3.16.2.

### Museum abbreviations

AUP	=	School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand
BNHS	=	Bombay Natural History Society, Mumbai, India
CAS	=	California Academy of Science, San Francisco, USA
CHS	=	Private catalogue of Huang Song (China)
CIB	=	Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, Sichuan, China
FMNH	=	The Field Museum, Chicago, USA
GP	=	Private catalogue of Guo Peng (China)
JU	=	Jahangirnagar University, Dhaka, Bangladesh
KIZ	=	Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China
KUZ	=	Kyoto University, Department of Zoology Museum, Japan
MNHN	=	Muséum national d'histoire naturelle, Paris, France
MZMU	=	Departmental Museum of Zoology, Mizoram University, India
NHMUK	=	The Natural History Museum (formerly BMNH), London, United Kingdom
NHMW	=	Naturhistorisches Museum (formerly NMW), Wien, Austria
PUCZM	=	Pachhunga University College, Mizoram University, Mizoram, India
QSMI	=	Queen Saovabha Memorial Institute, Bangkok, Thailand
RMNH	=	Naturalis-Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands
SYNU	=	Shenyang Normal University, Shenyang, China
USNM	=	National Museum of Natural History, Smithsonian Institution, Washington, USA
VNMN	=	Vietnam National Museum of Nature, Hanoi, Vietnam
VNUF	=	Vietnam National University of Forestry, Hanoi, Vietnam
WII	=	Wildlife Institute of India, Uttarakhand, India
YBU	=	Yibin University, Sichuan, China
ZMMU	=	Zoological Museum of Moscow, Moscow, Russia
ZSI	=	Zoological Survey of India (formerly ZSIC), Kolkata, West Bengal, India

### Molecular analyses

We extracted the Genomic DNA from the liver tissues using QIAamp DNA Mini Kit following the manufacturer's procedure. The fragment of *Cytb* was amplified using the forward (L14910) and reverse (H16064) primers (Burbrink *et al.* 2000) at the thermal conditions of 94°C for 3 min, followed by 35 cycles of 94°C for 30 sec, 49°C for 40 sec, 72°C for 30 sec, and with a final extension at 72°C for 5 min. The amplified products were purified and sequenced using Sanger's dideoxy method at Barcode BioSciences, Bangalore, India.

The datasets of natricid snakes comprise the sequence of *Cytb* gene of *Herpetoreas* sp. (CAS 220256) from Rakhine State, Myanmar, and *Hebius venningi* (Wall, 1910) (MZMU 1313 [isolate A, B] with sequence accession numbers: OR389974-75, respectively) from Mizoram State, India along with 52 congeneric sequences and outgroups obtained from the NCBI database (see Appendix 2). The dataset was aligned with the MUSCLE algorithm (Edgar 2004) using default parameters in MEGA 11 (Tamura *et al.* 2021). The dataset was partitioned by codon positions. PartitionFinder ver. 2 (Lanfear *et al.* 2016) was employed for selecting the best partitioning schemes and for evolutionary model searching under the Bayesian Information Criterion (Appendix 2). Bayesian Inference (BI) and Maximum Likelihood (ML) phylogenies were performed in Mr.Bayes ver. 2.3.5 (Ronquist *et al.* 2012) and in IQTREE (Nguyen *et al.* 2015), respectively. In the BI analyses, four independent runs with one cold and three hot



chains were conducted for 20 million generations and sampled every 5000 generations. The trace plots generated by the MCMC runs were viewed in Tracer ver. 1.7 (Rambaut *et al.* 2018) and the first 25% of samples were discarded as burnin. The ML analysis was performed using the partitioning schemes selected by PartitionFinder ver. 2 (Lanfear *et al.* 2016), and the models selected under BIC scores by ModelFinder (Kalyaanamoorthy *et al.* 2017) implemented in the IQTREE (Nguyen *et al.* 2015) at 10000 Ultrafast Bootstrap (UFB) (Minh *et al.* 2013). The uncorrected p-distances were estimated in MEGA 11 (Tamura *et al.* 2021). The standardized p-distances were further utilized for multivariate Principal Coordinate Analysis (PCoA) (Gower 1966) to visualize the genetic differentiation among the study taxa in PAST ver. 4.13 (Hammer *et al.* 2001). We applied Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al.* 2021), a single locus-based species delimitation method. This method produced species partitions based on the probabilities and barcode gap width; these two metrics are combined into a single ASAP-score for ranking the partitions, the lower the ASAP-score, the better the partition (Puillandre *et al.* 2021).

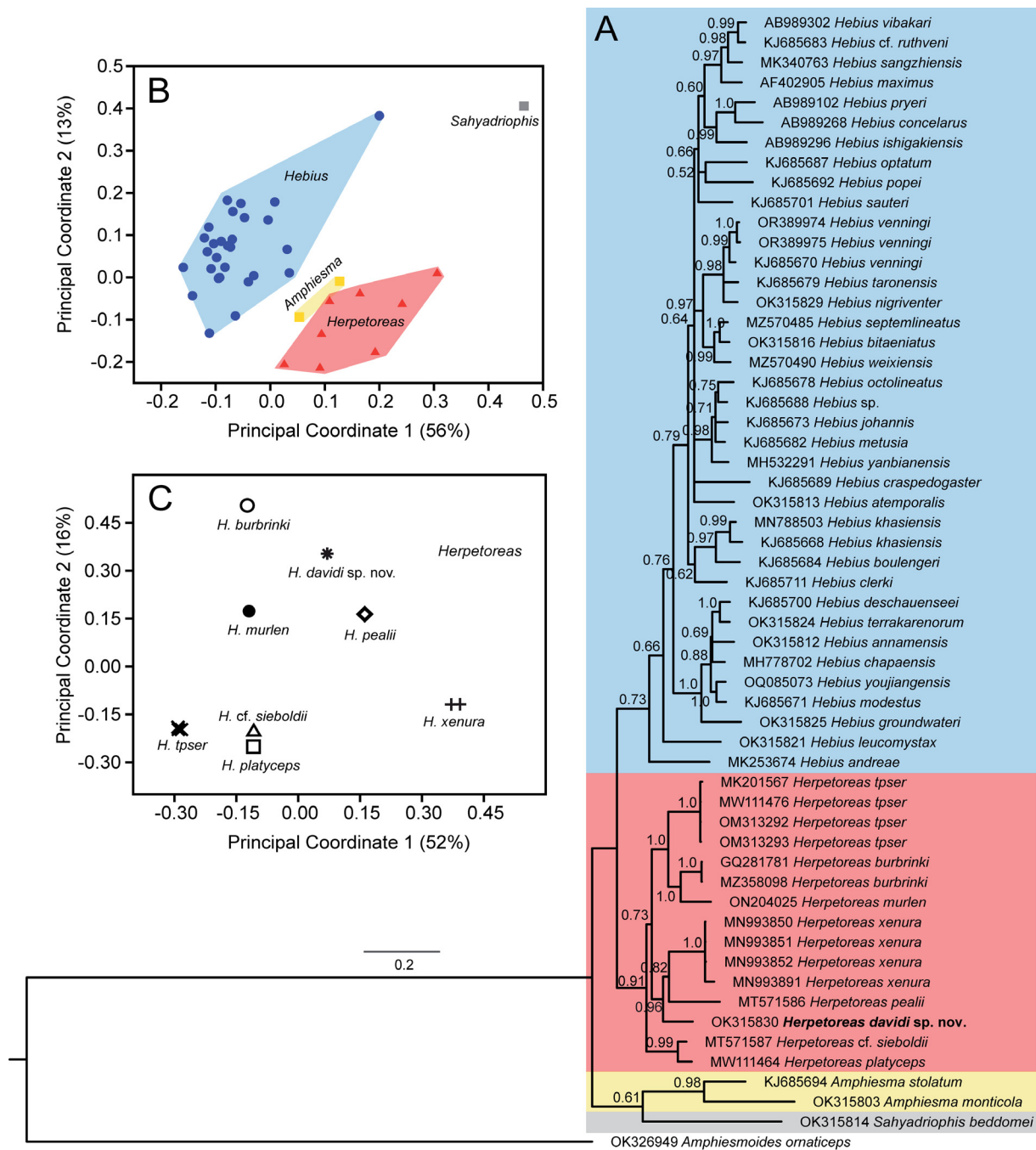
## Results

### *Phylogenetic relationships*

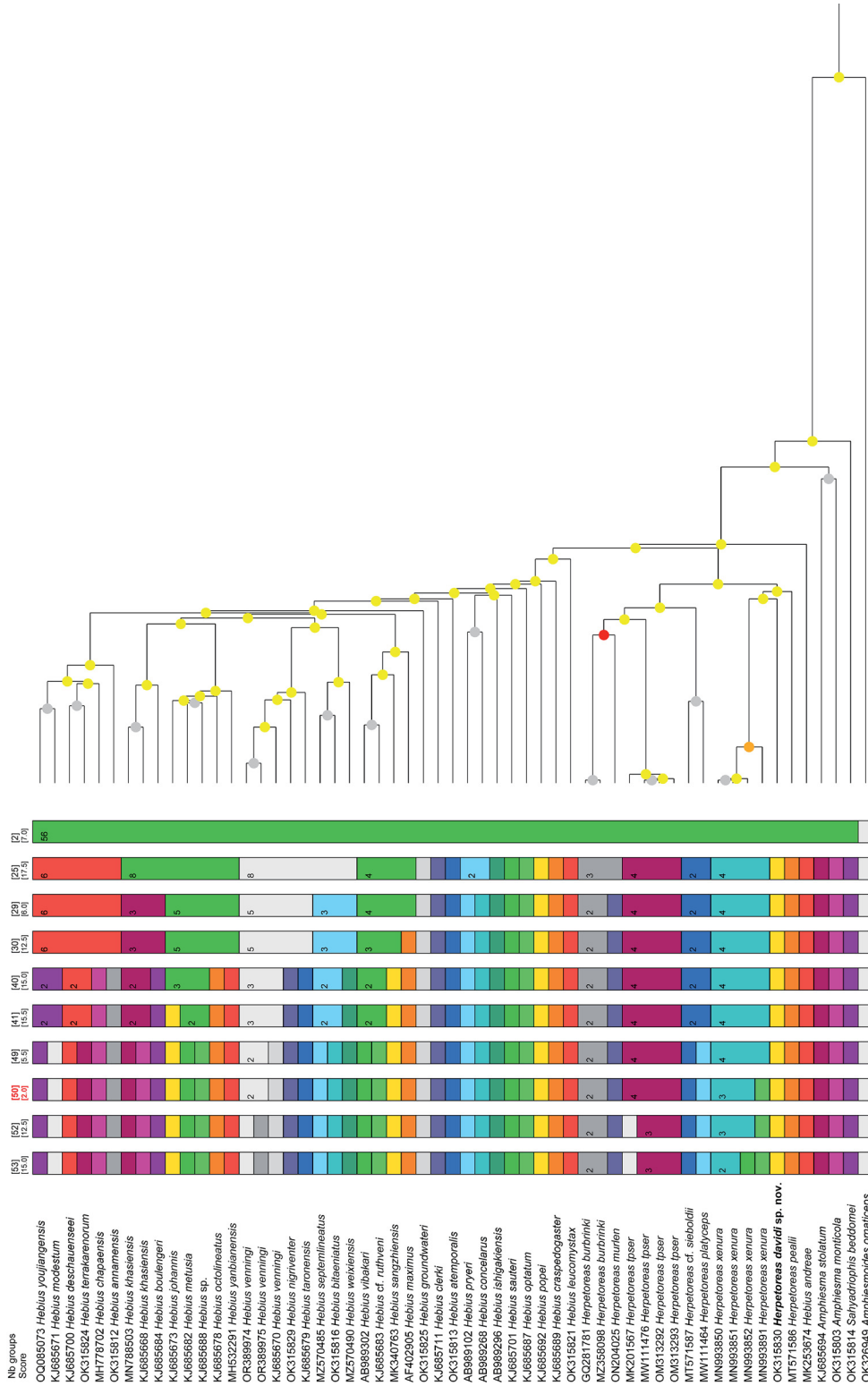
The Cytb dataset of the natricid species contained 1124 bp aligned characters. Two types of partitioned phylogenetic analyses (BI and ML) were performed, which largely inferred consistent tree topologies (Fig. 2A; Supp. file 1). In our phylogenetic analyses of the natricid group, the specimen of *Herpetoreas* cf. *xenura* from Rakhine, Myanmar, is nested with the putative *Herpetoreas* clade and forms a sister lineage to the sub-clade consisting of *H. pealii* and *H. xenura* sensu stricto with well-supported Bayesian posterior probabilities (PP) and UFB values (PP=0.96; UFB=98). It is also distinct from the other species of *Herpetoreas* by considerable genetic divergences of 19.2% (to *H. murlen*) to 30.8% (to *H. tpser*), and 26.9–30.8% with *H. xenura* sensu stricto; while 26.9% genetic distances are recovered with the two species of *Amphiesma*, and 38.5% genetic divergence from *Sahyadriophis beddomei* (Günther, 1864); the genetic divergence with species of *Hebius* ranged from 15.4–38.5% (to *Hebius andreae* (Ziegler & Le, 2006) and *H. pryeri* (Boulenger, 1887), respectively) and 46.2% to the outgroup (*Amphiesmoides ornaticeps* (Werner, 1924)) (Appendix 3). The ordination of the genetic divergence along the first two Principal Coordinate (PCo) axes also reveal the discrete clustering of the genera: *Amphiesma*, *Hebius*, *Herpetoreas* and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023 (Fig. 2B). The Rakhine specimen of *H. cf. xenura* is also clearly discriminated from *H. xenura* sensu stricto as well as from the other species of *Herpetoreas* (Fig. 2C). The molecular species delimitation produced 10 partitions, out of which 90% of the partitions including the optimal partition selected (ASAP-score = 2.0) inferred *H. cf. xenura* (Rakhine) as distinct species (Fig. 3).

### *Taxonomy*

The morphological features in five specimens of *Herpetoreas* cf. *xenura* from Rakhine Yoma Elephant Sanctuary, Rakhine State, agree with the generic characters of *Herpetoreas* provided by Guo *et al.* (2014) and Ren *et al.* (2022), but exhibit a distinct lineage with strong genetic divergence from the seven nominal species of *Herpetoreas*. Overall, both molecular and morphological differentiation leave no doubt that the species of *Herpetoreas* from Rakhine State represents a distinct undescribed species. Another juvenile specimen (CAS 232203) originally classified as *Herpetoreas* cf. *xenura* from Htamanthi Wildlife Sanctuary, Sagaing Region, Myanmar (Wogan *et al.* 2008), was examined. The morphological characteristics (pholidosis and colour pattern) of CAS 232203 are not consistent with the generic characters of *Herpetoreas*. The important morphological characters and photos of the specimen CAS 232203 are presented in Table 1 and Fig. 4A–F. However, the specimen CAS 232203 is very similar to the diagnostic characters of *Hebius khasiensis* see Table 2 and Figs 4G–H, 6G–H. Due to the lack of genetic information for the Sagaing specimen, we herein tentatively refer to this specimen as *Hebius*

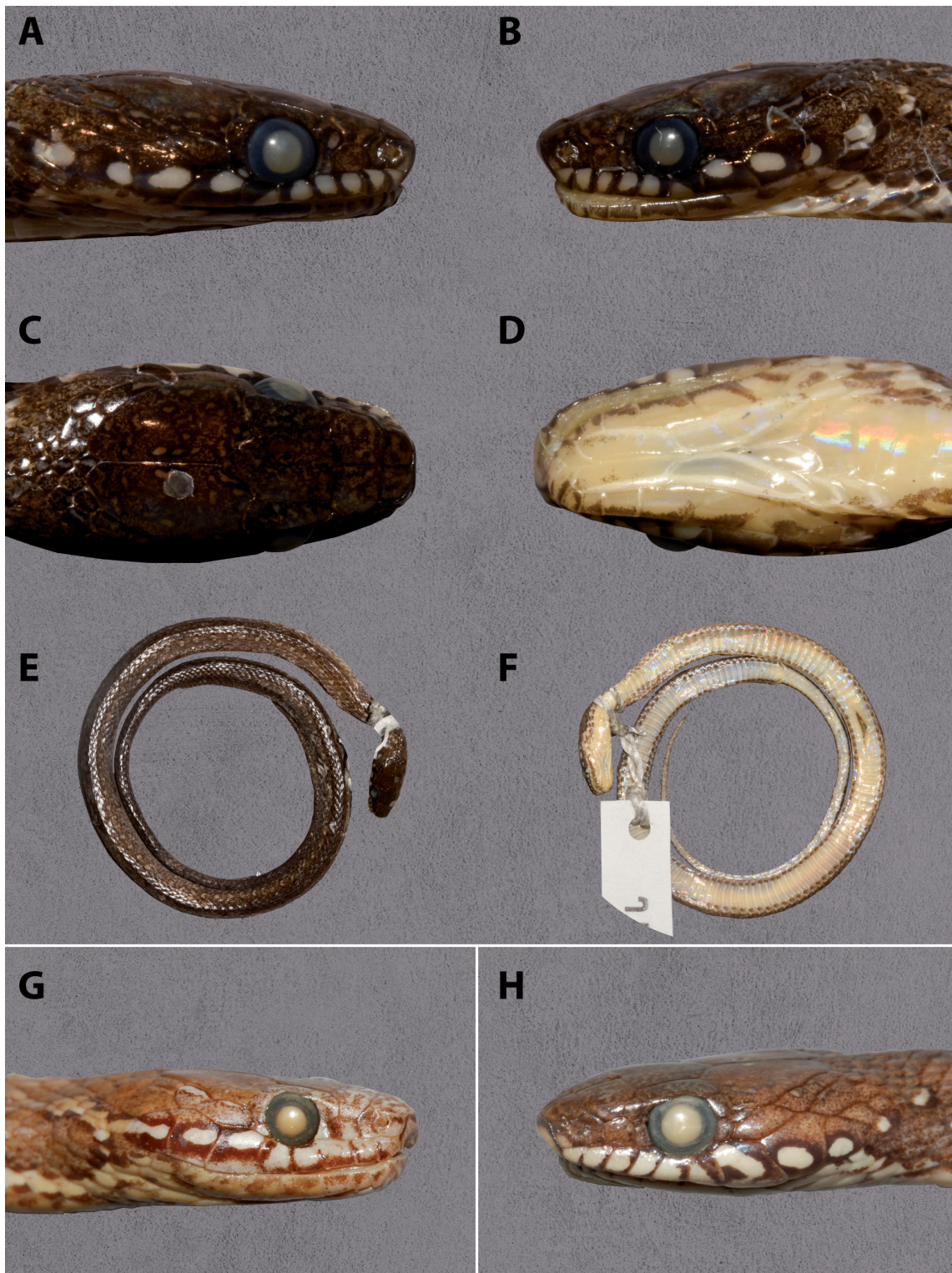


**Fig. 2.** A. Bayesian Inference (BI) phylogenetic tree based on the fragment of mitochondrial cytochrome b gene among the genera: *Amphiesma* Duméril, Bibron & Duméril, 1854, *Amphiesmoides* Malnate, 1961, *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023. The posterior probability (PP) support values are given at each branch. B. Ordination of standardized p-distance of the genera: *Amphiesma*, *Amphiesmoides*, *Hebius*, *Herpetoreas*, and *Sahyadriophis* (excluding outgroup) along the first and second principal coordinate (PCo) axes where a total of 56% and 13% of variance are captured by PCo1 and PCo2, respectively. C. Ordination of standardized p-distance of *Herpetoreas* along the first and second PCo axes where a total of 52% and 16% of variance are captured by PCo1 and PCo2, respectively.



**Fig. 3.** Species delimitation by ASAP using Cytb gene sequence of the genera *Amphiesma* Duméril, Bibron & Duméril, 1854, *Amphiesmoides* Malnate, 1961, *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023. The columns represent the different species group partitions, and the colours depict species hypothesis in each partition. The values above the column represent the number of inferred species in the partition (upper value) and the ASAP-score (lower value). The ASAP-score of the best partition selected is indicated in red. The Neighbour-joining cladogram (right) supports the species delimitation on the bar charts (left). The colour dots correspond to the probability of the nodes, darker colour depicts lower probability, and uncalculated probability is shown in grey dot.





**Fig. 4.** *Hebius khasiensis* (Boulenger, 1890). **A–F.** Specimen juvenile, sex unknown, in preservative (CAS 232203). **A.** Lateral view of the head, right side. **B.** Lateral view of the head, left side. **C.** Dorsal view of the head. **D.** Ventral view of the head. **E.** General dorsal view. **F.** General ventral view. **G.** *Tropidonotus khasiensis*, syntype, ♂ (NHMUK 1946.1.13.62), lateral view of the head, right side. **H.** *Natrix gilhodesi* Wall, 1925, holotype, ♂ (NHMUK 1946.1.12.81), lateral view of the head, right side. Photos by G. Vogel.

**Table 2** (continued on next two pages). Comparison of morphological characteristics of *Herpetoreas davidi* sp. nov. with those of the genus *Herpetoreas* Günther, 1860. Abbreviations: *Heb.* = *Hebius*; *Her.* = *Herpetoreas*; N/a = not available.

No.	Species	SVL (mm)		TaL (mm)		TaL/TL (mm)		VEN	
		Males	Females	Males	Females	Males	Females	Males	Females
1	<i>Hep. davidi</i> sp. nov.	292–384 [ $\bar{x}$ = 338.0, n = 2]	259–482 [ $\bar{x}$ = 379.3, n = 3]	126–168 [ $\bar{x}$ = 147.0, n = 2]	115–178 [ $\bar{x}$ = 146.5, n = 2]	0.301–0.304 [ $\bar{x}$ = 0.303, n = 2]	0.207–0.310 [ $\bar{x}$ = 0.309, n = 2]	154–156 [ $\bar{x}$ = 155, n = 2]	151–155 [ $\bar{x}$ = 152.7, n = 3]
2	<i>Hep. xenura</i>	480–675 [ $\bar{x}$ = 590.6, n = 10]	417–565 [ $\bar{x}$ = 468.7, n = 3]	143–200 [ $\bar{x}$ = 182.9, n = 10]	124–180 [ $\bar{x}$ = 155.0, n = 3]	0.220–0.283 [ $\bar{x}$ = 0.240, n = 9]	0.226–0.279 [ $\bar{x}$ = 0.249, n = 3]	158–165 [ $\bar{x}$ = 160.7, n = 9]	155–165 [ $\bar{x}$ = 160.5, n = 4]
3	<i>Hep. burbrinki</i>	527 [n = 1]	462 [n = 1]	230 [n = 1]	184 [n = 1]	0.304 [n = 1]	0.304 [n = 1]	172 [n = 1]	169 [n = 1]
4	<i>Hep. murlen</i>	355 [n = 1]	N/a [n = 1]	106 [n = 1]	N/a [n = 1]	0.230 [n = 1]	N/a [n = 1]	179 [n = 1]	N/a [n = 1]
5	<i>Hep. pealii</i>	334 [n = 1]	511 [n = 1]	117 [n = 1]	150 [n = 1]	0.259 [n = 1]	0.227 [n = 1]	142–144 [n = 2]	136 [n = 1]
6	<i>Hep. platyceps</i>	N/a [n = 1]	402–546 [ $\bar{x}$ = 480.7, n = 6]	N/a [n = 1]	106–216 [ $\bar{x}$ = 160.2, n = 5]	0.243–0.267 [ $\bar{x}$ = 0.252, n = 5]	0.232–0.273 [ $\bar{x}$ = 0.248, n = 10]	205–234 [ $\bar{x}$ = 220.8, n = 8]	191–216 [ $\bar{x}$ = 202.1, n = 13]
7	<i>Hep. sieboldii</i>	328–584 [ $\bar{x}$ = 476, n = 13]	318–552 [ $\bar{x}$ = 485.7, n = 6]	115–203 [ $\bar{x}$ = 170.6, n = 9]	102–224 [ $\bar{x}$ = 174.0, n = 3]	0.246–0.294 [ $\bar{x}$ = 0.273, n = 9]	0.243–0.296 [ $\bar{x}$ = 0.270, n = 3]	193–207 [ $\bar{x}$ = 200.3, n = 13]	174–185 [ $\bar{x}$ = 181.2, n = 6]
8	<i>Hep. tpser</i>	355–479 [ $\bar{x}$ = 417.0, n = 2]	279–491 [ $\bar{x}$ = 410.8, n = 4]	165 [n = 1]	108–207 [ $\bar{x}$ = 169.8, n = 4]	0.318 [n = 1]	0.277–0.313 [ $\bar{x}$ = 0.293, n = 4]	158–165 [ $\bar{x}$ = 161.5, n = 2]	153–167 [ $\bar{x}$ = 159.5, n = 4]
9	<i>Heb. khasiensis</i>	271–412 [ $\bar{x}$ = 333.4, n = 13]	113–435 [ $\bar{x}$ = 281.4, n = 20]	138–183 [ $\bar{x}$ = 164.7, n = 10]	53–192 [ $\bar{x}$ = 122.5, n = 15]	0.320–0.346 [ $\bar{x}$ = 0.338, n = 10]	0.296–0.329 [ $\bar{x}$ = 0.312, n = 15]	142–154 [ $\bar{x}$ = 148.2, n = 13]	141–152 [ $\bar{x}$ = 147.7, n = 20]
10	<i>Heb. khasiensis</i>	N/a [n = 1]	153 [n = 1]	N/a [n = 1]	72 [n = 1]	N/a [n = 1]	0.320 [n = 1]	N/a [n = 1]	134 [n = 1]
11	<i>Hep. cf. sieboldii</i>	N/a [n = 1]	407 [n = 1]	N/a [n = 1]	153 [n = 1]	N/a [n = 1]	0.273 [n = 1]	N/a [n = 1]	200 [n = 1]

**Table 2** (continued). Comparison of morphological characteristics of *Herpetoreas davidi* sp. nov. with those of the genus *Herpetoreas* Günther, 1860. Abbreviations: *Heb.* = *Hebius*; *Her.* = *Herpetoreas*; N/a = not available.

No.	Species	SC		VEN+CS		DSR	Lor	AS	SC
		Males	Females	Males	Females				
1	<i>Hep. davidi</i> sp. nov.	97–99 [ $\bar{x}$ = 98.0, n = 2]	97–100 [ $\bar{x}$ = 98.5, n = 2]	253 [n = 2]	248–252 [ $\bar{x}$ = 250.0, n = 2]	19–19–17	1	Single	Single
2	<i>Hep. xenura</i>	86–105 [ $\bar{x}$ = 96.6, n = 9]	87–110 [ $\bar{x}$ = 95.3, n = 4]	244–270 [ $\bar{x}$ = 257.3, n = 9]	242–275 [ $\bar{x}$ = 255.8, n = 4]	19–19(17)–17	1	Single	Single
3	<i>Hep. burbrinki</i>	96 [n = 1]	94 [n = 1]	268 [n = 1]	263 [n = 1]	19–19–17	1 or 2	Divided	Divided
4	<i>Hep. murlen</i>	78 [n = 1]	N/a	257 [n = 1]	N/a	19–19–17	1	Divided	Divided
5	<i>Hep. pealii</i>	75–77 [n = 1]	69 [n = 1]	219 [n = 2]	205 [n = 1]	19–19–17	1	Single	Divided
6	<i>Hep. platyceps</i>	88–98 [ $\bar{x}$ = 92.2, n = 6]	78–96 [ $\bar{x}$ = 86.1, n = 11]	308–326 [ $\bar{x}$ = 316.7, n = 6]	271–302 [ $\bar{x}$ = 287.3, n = 11]	19–19–17	1	Divided	Divided
7	<i>Hep. sieboldii</i>	91–109 [ $\bar{x}$ = 102.3, n = 9]	97–106 [ $\bar{x}$ = 100.7, n = 3]	296–314 [ $\bar{x}$ = 303.0, n = 9]	279–287 [ $\bar{x}$ = 283.3, n = 3]	19–19–17	1	Divided	Divided
8	<i>Hep. tpser</i>	96 [n = 1]	81–97 [ $\bar{x}$ = 88.3, n = 4]	255 [n = 1]	239–253 [ $\bar{x}$ = 247.8, n = 4]	19–19–17	1	Divided	Divided
9	<i>Heb. khashensis</i>	96–111 [ $\bar{x}$ = 103.3, n = 10]	87–99 [ $\bar{x}$ = 93.8, n = 15]	238–264 [ $\bar{x}$ = 250.7, n = 10]	230–251 [ $\bar{x}$ = 241.9, n = 15]	19–19–17	1	Divided	Divided
10	<i>Heb. khashensis</i>	N/a	92 [n = 1]	N/a	226 [n = 1]	19–19–17	1	Divided	Divided
11	<i>Hep. cf. sieboldii</i>	N/a	107 [n = 1]	N/a	310 [n = 1]	19–19–17	1	Divided	Divided



**Table 2** (continued). Comparison of morphological characteristics of *Herpetoreas davidi* sp. nov. with those of the genus *Herpetoreas* Günther, 1860. Abbreviations: *Heb.* = *Hebius*; *Her.* = *Herpetoreas*; N/a = not available.

No.	Species	SL	SL-E	IL	Pr-O	Po-O	A TEM	P TEM	MT	VEN colours	VEN lateral blotch	Distributions	Sources
1	<i>Hep. davidi</i> sp. nov.	9	4–6	9 or 10	1	3	1–2	2	N/a	whitish or yellowish	barely present, discontinuous	Myanmar	our data
2	<i>Hep. xenura</i>	9 (8 or 7)	4–6 (4–5)	9–9	1	3	1–2	1–2	22–23	whitish or yellowish	present, discontinuous	India, Bangladesh	Wall (1907, 1909); Mathew & Meetei (2004); Reza (2010); Malsawmdawngliana <i>et al.</i> (2021); our data
3	<i>Hep. burbrinki</i>	8 (9)	3–5	10	1–2	3	2–3	2	21	creamish-beige	present, discontinuous	China	Guo <i>et al.</i> (2014); Peng <i>et al.</i> (2021)
4	<i>Hep. murlen</i>	8	3–5	9–9	1	3	1	1	13	light sandbrown	present, discontinuous	India	Lahremisanga <i>et al.</i> (2022)
5	<i>Hep. pealii</i>	9	4–5	10	1	3 (2)	2	2	13–21	pale with brown patches	continuous present	India	Smith (1943); Das <i>et al.</i> (2020)
6	<i>Hep. platyceps</i>	8	3–5	8 or 9	1	3	1–2	1–2 (3)	18–22	usually immaculate	present or absent	India, Nepal, Pakistan, Bhutan, China, Bangladesh	Malnate (1966); our data
7	<i>Hep. sieboldii</i>	8	3–5	10	1	3	1–2	1–2	19–23	darkened posteriorly	usually absent	Pakistan, India, Nepal, Bhutan, Bangladesh	Malnate (1966); our data
8	<i>Hep. tpser</i>	8 or 9	3–5 or 4–6	9–10 (8)	1	3 (2)	1–2	2 (1)	20–21	reddish orange	present, discontinuous	China	Ren <i>et al.</i> (2022)
9	<i>Heb. khasiensis</i>	9	4–6	10 (9)	1	2	1 (2)	2 (1)	21–26	whitish or yellowish	usually absent	India, Myanmar, China, Thailand	our data
10	<i>Heb. khasiensis</i>	9	4–6	9 or 10	1	3	1	1	N/a	whitish	barely present, discontinuous	Myanmar	our data
11	<i>Hep. cf. sieboldii</i>	9	3–5 or 4–5	9–9	1	2	1	2	N/a	whitish	absent	Myanmar	our data

*khasiensis* with pending further molecular data for confirming its taxonomic status. The taxonomic status of the *Hebius khasiensis-boulengeri* complex of species is being re-evaluated in another project (T.V. Nguyen *et al.* unpubl. data).

In contrast, based on the morphological and genetic distinctiveness of specimens of the Rakhine population from other congeners, we have no hesitation in considering them representing a new species of the genus *Herpetoreas* described below:

Class Reptilia Laurenti, 1768  
Order Squamata Oppel, 1811  
Suborder Serpentes Linnaeus, 1758  
Family Natricidae Bonaparte, 1838  
Genus *Herpetoreas* Günther, 1860

***Herpetoreas davidi* sp. nov.**

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Fig. 5; Tables 1–2

*Amphiesma xenura* (non *Herpetoreas xenura* Wall, 1907) – Wogan *et al.* 2008: 87, in part. — Das 2010: 335, in part. — Reza 2010: 64, in part. — Wallach *et al.* 2014: 35, in part.

*Herpetoreas xenura* – Ren *et al.* 2022: 79, in part. — Uetz *et al.* 2023: page “*Herpetoreas xenura*”, in part.

*Herpetoreas* sp. – Deepak *et al.* 2022: 285, in part. — Patel *et al.* 2023: 431 in supplementary materials.

**Diagnosis**

*Herpetoreas davidi* sp. nov. differs from all other members of the genus *Herpetoreas* by the combination of the following morphological characters: (1) body cylindrical, small size, max. TL 552 mm; (2) tail relatively long in both sexes, TaL/TL 0.301–0.310; (3) dorsal scale rows 19–19–17; all strongly keeled; (4) ventrals 151–156; cloacal plate single, subcaudals single; subcaudals 97–100; (5) supralabials 9, 4<sup>th</sup>–6<sup>th</sup> entering orbit; (6) head with a faint off-white sagittal line just behind the parietal; (7) dorsum dark olive-brown or dark brown with indistinct series of pale spots; (8) venter off-whitish, each ventral decorated with a pair of indistinct and faint dark-brown spots on their lateral edges.

**Etymology**

The species epithet is an eponym in honour of Patrick David (MNHN, Paris, France), a French reptile taxonomist, for his contribution to the systematics of snakes of the family Natricidae and to the Asian snake fauna in general. We suggest “Rakhine Keelback” as its English common name.

**Type material**

**Holotype**

MYANMAR • ♂ adult; Daung Stream, within Rakhine Yoma Elephant Sanctuary, Gwa Township, Rakhine State; 17.5844166667° N, 94.6812777778° E, WGS 84; ca 120 m a.s.l.; 23 Jan. 2002; G.O.U. Wogan and S.W. Kyi leg.; CAS 222969.

**Paratypes**

MYANMAR • 1 ♀ adult, 1 ♀ subadult, 1 ♂ subadult; Kyat Stream, Rakhine Yoma Elephant Sanctuary, Gwa Township, Rakhine State; 17.7038888889° N, 94.6484166667° E, WGS 84; ca 175 m a.s.l.; 26–27 and 29 Apr. 2021, respectively; J.B. Slowinski, G.O.U. Wogan, H. Win, T. Thin, and K.S. Lwin leg.; CAS 220256, CAS 220332, CAS 220378, respectively • 1 ♂ adult; Daung Stream, Rakhine Yoma

Elephant Sanctuary, Gwa Township, Rakhine State; 17.5841833333° N, 94.67815° E, WGS 84; ca 125 m a.s.l.; 1 May 2021; J.B. Slowinski, G.O.U. Wogan, H. Win, T. Thin, and K.S. Lwin leg.; CAS 220550.

### **Description of the holotype** (Fig. 5)

**MORPHOLOGY.** Body slender, cylindrical, and elongate (SVL 384 mm, TaL 168 mm, TL 552 mm, ratio TaL/TL 0.304). Head moderately large, moderately distinct from neck (ratio HL/SVL 0.048, ratio HW/HL 0.512), moderately distinct from neck (Fig. 5E–F); snout broad, obtuse as seen from above; eye large (ED 2.86 mm, ratio ED/E–Sn 1.036, ratio ED/E–Ns 2.000); pupils round; nostrils crescentic, piercing in the middle of the nasal, oriented laterally (Fig. 5A–B).

**BODY SCALATION.** Dorsal scales in 19–19–17 rows; all scales strongly keeled, notched at apex; 154 ventrals (plus 2 preentrals); cloacal plate single; 99 subcaudals, all single.

**HEAD SCALATION.** Rostral wider than high, width approximately twice as long as high, visible from above (Fig. 5D); nasals pentagonal, slightly elongate, completely divided, anterior part slightly smaller than the posterior one; nostrils located on the middle of nasals (Fig. 5A–B); internasals subtriangular, in broad contact with each other, not in contact with loreal, about equal length to width, slightly, but distinctly narrowing anteriorly, the width of the posterior margin approximately twice as long as the anterior margin; 2 prefrontals, hexagonal, slightly broader than long, about 1.3 times as long as internasals; prefrontal sutures slightly longer than length internasal sutures; frontal pentagonal, elongate, length 1.4 times as long as width, about twice as long as prefrontal; supraocular 1/1, rectangular, elongate, narrowed anteriorly, broadly in contact with prefrontal, with supraocular two-thirds as broad as the frontal; parietals in broad contact with each other, parietal suture subequal to length of frontal (Fig. 5D). Loreal 1/1, subrectangular, small, about equal in length to depth, in contact with 2<sup>nd</sup>–3<sup>rd</sup> supralabials, not entering orbit; preoculars 1/1; postoculars 3/3, size decreasing from top to bottom; supralabials 9/9, 2<sup>nd</sup>–3<sup>rd</sup> in contact with the loreal, 4<sup>th</sup>–6<sup>th</sup> entering orbit, 8<sup>th</sup> largest; temporals 2+3 on both sides; mental subtriangular, wide, 2.5 times as long as high (Fig. 5A–B); 9/10 infralabials, first pair in contact with each other behind mental, 1<sup>st</sup>–5<sup>th</sup> in contact with anterior chin shields; two pairs of chin shields; posterior chin shields 1.3 times as long as anterior ones, separated from each other by small scales; mental groove apparent (Fig. 5C).

### **Coloration in preservative**

Dorsal surface of head dark brown, with two small and white stripes run from the posterior edge of the 8<sup>th</sup> supralabials to the nape. Ventral surface of head uniform whitish. Dorsal surface of body and tail pale dark brown with irregular brown speckling on either side. Ventral surface of body and tail whitish with scales bordered on either side by a blackish-brown stripe. According to CAS staff, no photographs of living specimens of the type series of *Herpetoreas davidi* sp. nov. were taken.

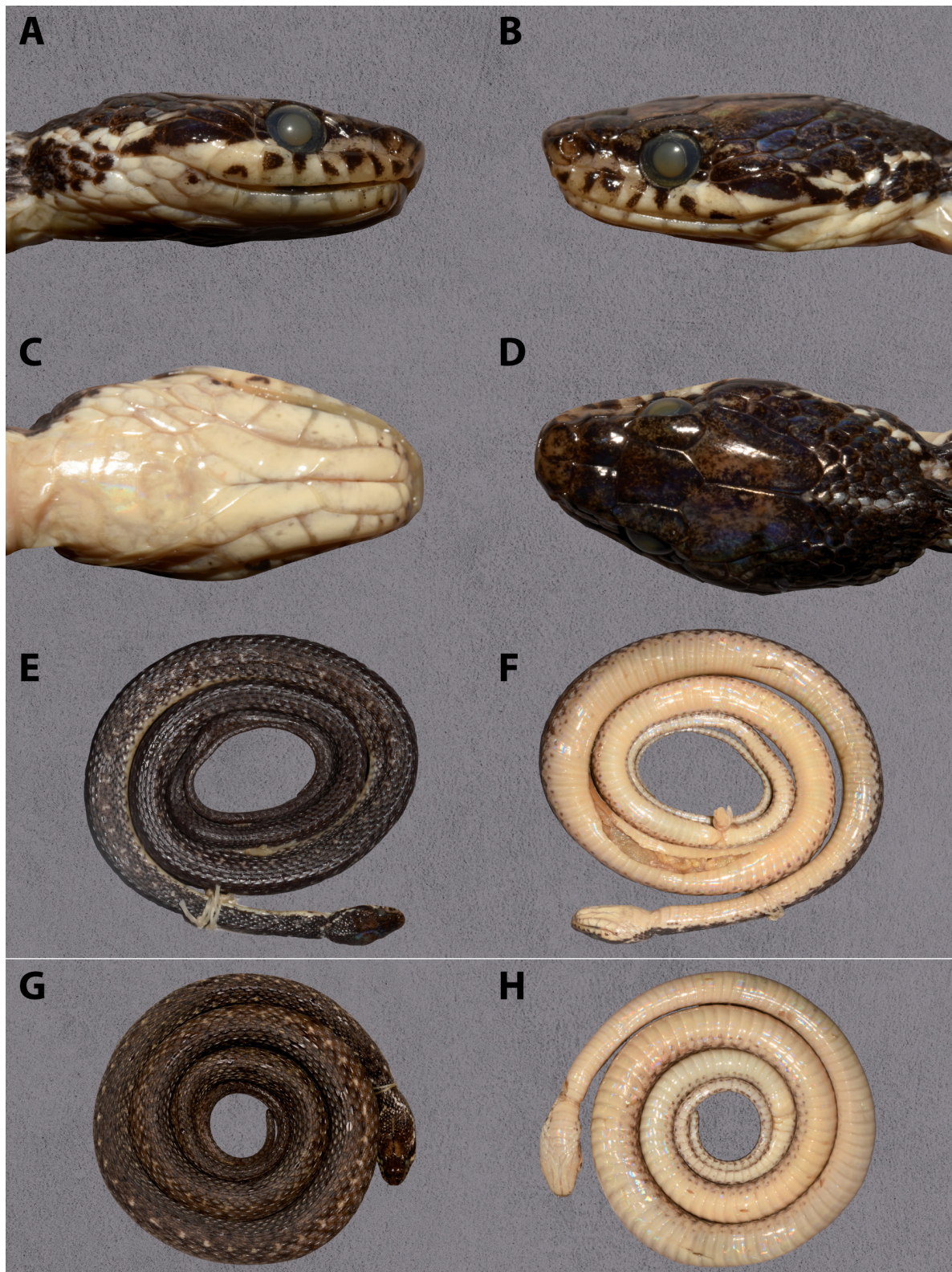
### **Variation** (for details of information's see Table 1 and Fig. 5)

The longest known specimen is 575 mm long (SVL 397 mm, TaL 178 mm, female; CAS 220550).

**BODY SCALATION.** 19–19–17 DSR; 151–156 VEN, 97–100 SC, single in all examined specimens, total number of VEN+SC 248–253, without sexual dimorphism. SL: 9 in all occurrences, IL: 9–10.

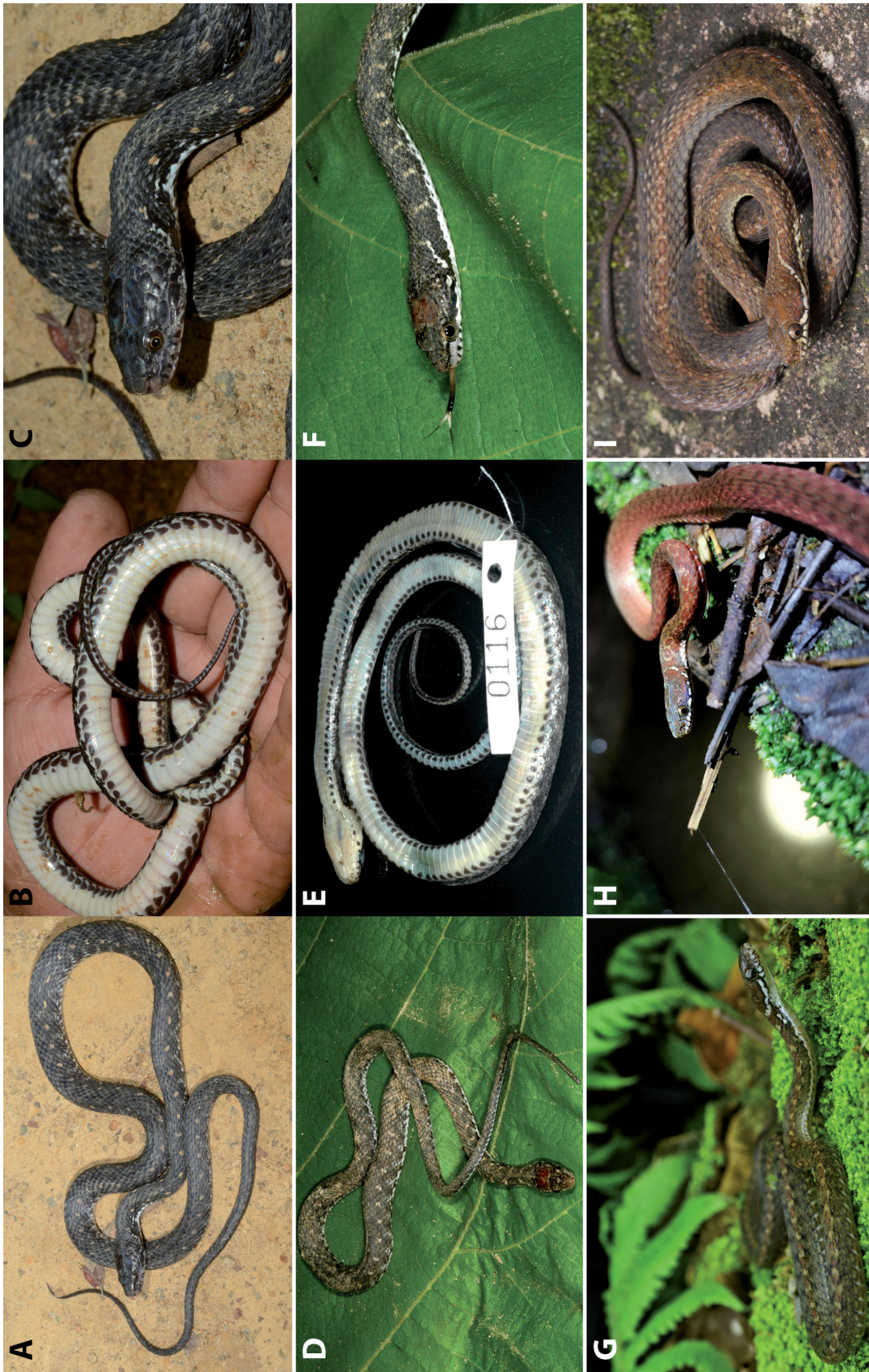
**MAIN CHARACTERS OF PATTERN.** Head olive-brown with two small, faint off-white spots on the parietals and a faint off-white sagittal line just behind the parietal. Dorsum dark olive-brown or dark brown with indistinct narrow blackish cross-bars or series of spots; venter off-whitish or cream, each ventral decorated with a pair of dark brown square spots on their lateral edges.





**Fig. 5.** *Herpetoreas davidi* sp. nov. **A–F.** Holotype, ♂ (CAS 222969) in preservation. **A.** Lateral view of the head, right side. **B.** Lateral view of the head, left side. **C.** Ventral view of the head. **D.** Dorsal view of the head. **E.** General dorsal view. **F.** General ventral view. **G–H.** Paratype, ♀ (CAS 220256). **G.** General dorsal view. **H.** General ventral view. Photos by G. Vogel.





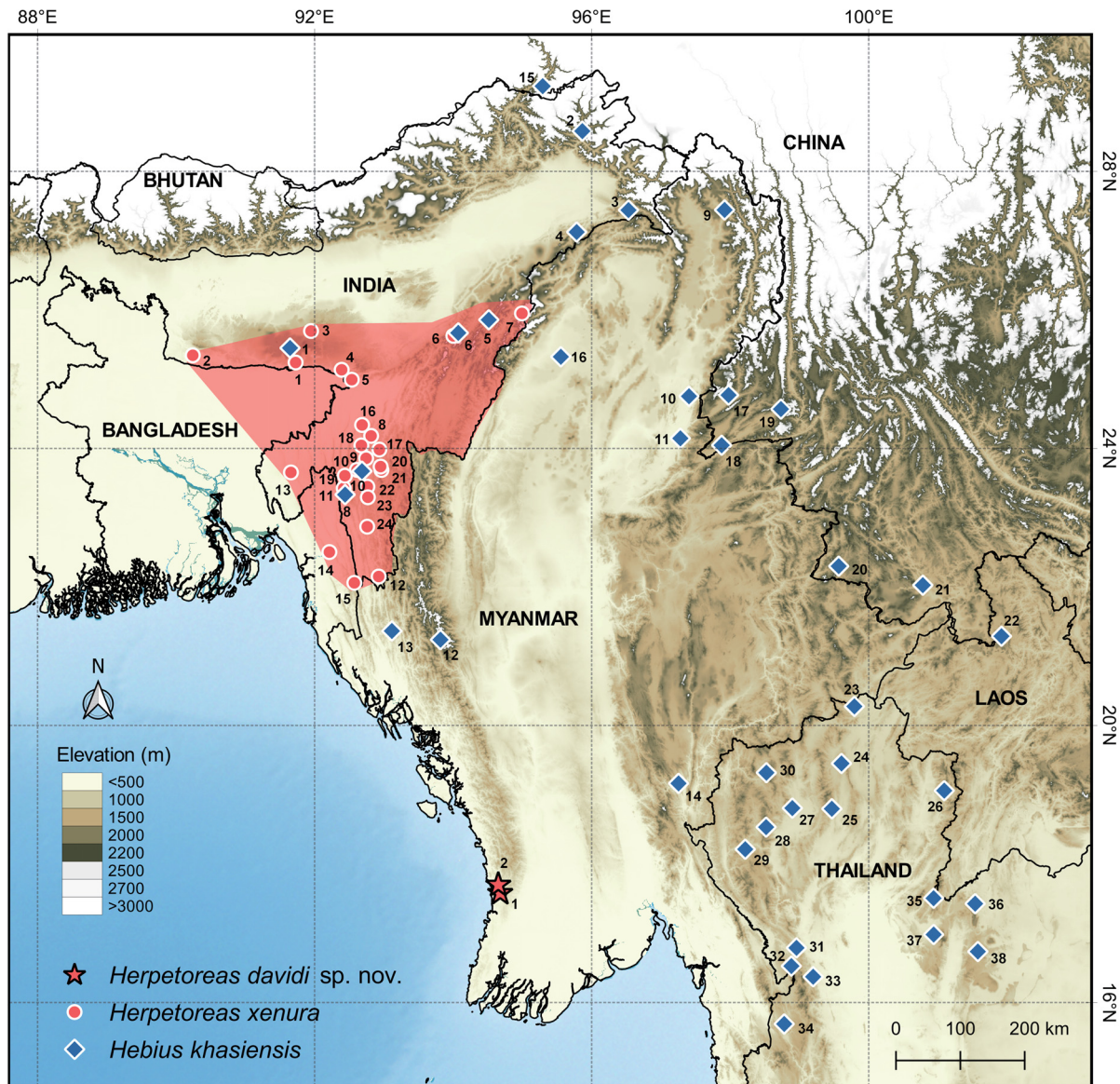
**Fig. 6.** A–F. *Herpetoreas xenura* (Wall, 1907) in life. A–C. Mizoram, India. D–F. Kaptai National Park, Chittagong, Bangladesh. G–I. *Hebius khasiensis* (Boulenger, 1890) in life. G. Tamdil, Mizoram, India. H. Bhamo, Kachin, Myanmar. I. Nakhon Thai, Phitsanulok, Thailand. Photos by G. Vogel (A–C), Reza (2010) (D–E), P. Shinde (G), K.C. Ouyang (H), and P. Pawangkhanant (I).



## Comparison

We summarize the main characters separating *Herpetoreas davidi* sp. nov. from the other seven species of the genus *Herpetoreas* in Table 2. More specifically, the comparisons with these species are as follows:

*Herpetoreas davidi* sp. nov. is easily distinguished from *H. burbrinki*, *H. murlen*, *H. pealii*, *H. platyceps*, *H. sieboldii*, and *H. tpser* by having single subcaudals vs divided subcaudals. Particularly, *Herpetoreas davidi* differs from *H. burbrinki*, *H. murlen*, *H. platyceps*, *H. sieboldii*, and *H. tpser* by having a single cloacal plate (vs divided) and fewer ventrals VEN 151–156 (vs 169–172 in *H. burbrinki*, 179 in *H.*



**Fig. 7.** Map showing the distribution of *Herpetoreas davidi* sp. nov. in Rakhine Yoma Elephant Sanctuary, Rakhine, Myanmar (red stars). 1. Daung Stream (type locality). 2. Kyat Stream. *Herpetoreas xenura* (Wall, 1907) sensu stricto in red circles, *Hebius khasiensis* (Boulenger, 1890) in blue diamonds, and *Hebius* cf. *khasiensis* in blue triangle. Our estimated distribution range for *Herpetoreas xenura* sensu stricto is shaded in red. See Appendix IV for the corresponding locality numbers of the other taxa presented in the map.

*murlen*, 191–234 in *H. platyceps*, and 174–207 in *H. sieboldii*); differs from *H. pealii* by having more ventrals VEN 151–156 (vs 136–144); and differs from *H. tpser* by having a smaller size in both sexes (max TL 552 mm in males, 575 mm in females vs 584 mm in males, 679 mm in females).

Finally, *Herpetoreas davidi* sp. nov. can be distinguished from the superficially similar species *H. xenura* by having a smaller size in both sexes (max TL 552 mm in males, 575 mm in females vs 870 mm in males, 754 mm in females), higher ratio TaL/TL in both sexes (0.301–0.304 in males, 0.307–0.310 in females vs 0.220–0.283 in males, 0.226–0.279 in females), and slightly lower number of VEN in both sexes (154–156 in males, 151–155 in females vs 158–165 in males, 155–165 in females).

### **Distribution and natural history notes**

*Herpetoreas davidi* sp. nov. is so far known only from mountain forests in two locations within Rakhine Yoma Elephant Sanctuary, Gwa Township, Rakhine State, Myanmar (Fig. 7; Appendix 4). Further studies in neighbouring areas, especially in the northern Rakhine Hills, Myanmar, are required to determine the actual distribution and population size and trend of this new species. According to data recorded for specimens deposited in the collections of CAS (<http://portal.vortnet.org/search?q=Amphiesma+xenura+CAS+Myanmar>), specimens of *Herpetoreas davidi* were collected both during the day and at night on the ground near streams. The air temperature varied from 28°C to 31°C, and relative humidity was 94%. This species seems to be distributed at low elevations. The stomach of the holotype CAS 222969 contained a frog of the family Ranidae Batsch, 1796.

### **Conservation status**

*Herpetoreas davidi* sp. nov. is currently known only from Rakhine Yoma Elephant Sanctuary, Gwa Township, Rakhine State, Myanmar, a protected area. In absence of other biological data to assess its population status and potential threat, we suggest that the species should be considered a Data Deficient (DD) species, following the IUCN's Red List categories (IUCN Standards and Petitions Committee 2019).

### **Discussion**

In this study, we re-evaluate the taxonomy of the species *Herpetoreas xenura* previously reported in Myanmar by Wogan *et al.* (2008). The evidence from the molecular inferences and morphology clearly signified that the *Herpetoreas xenura* population in Rakhine State sensu Wogan *et al.* (2008) is distinct from the other nominal species of *Herpetoreas* that we describe here as *Herpetoreas davidi* sp. nov. Furthermore, the new species *Herpetoreas davidi* is completely geographically isolated from the species of *Herpetoreas* (mainly distributed in the Himalayan foothills), thus also supporting the validity of the new species. It is the most southern representative of the genus *Herpetoreas*, the closest distance to the north to the genus *Herpetoreas* (represented by *Herpetoreas xenura* in Pala Lake Area, Mizoram State, India, location 12 in Fig. 7) is more than 500 km. Meanwhile, the other population previously identified as *Herpetoreas* cf. *xenura* in Sagaing Region should be referred to as *Hebius khasiensis*.

Despite some recent progress in the taxonomy of the genus *Herpetoreas*, the diversity within this genus is still underestimated (Lalremsanga *et al.* 2022; Ren *et al.* 2022). For instance, similar to the case of *Herpetoreas* cf. *xenura* in Myanmar (Wogan *et al.* 2008), we strongly presume that the record of *Herpetoreas* cf. *sieboldii* from Taunggyi City, Shan State, Myanmar cited by Malnate (1966) based on female specimen BNHS 1567 (formerly BNHS 80.4) is also ambiguous. Re-examination of this specimen BNHS 1567 (by O. Adhikari, BNHS) revealed a higher total number of VEN+SC (310 vs 279–287 in *H. sieboldii*, see Table 2). Furthermore, this locality in Shan State is also reasonably isolated from the range of the true *Herpetoreas sieboldii* that inhabits the foothills of the Himalayas. This locality



is at about 880 km southeast from the type locality of *H. sieboldii*. Therefore, we stress the need for additional specimens to clarify its taxonomic status (see also Ren *et al.* 2022).

The present ASAP analysis produced 10 unidentical species partitions, and a total of 50 species are inferred by the best partition selected. Notably, this method detected *H. venningi* (MZMU 1313) from Mizoram State, India as distinct to *Hebius venningi* (CAS 233206) from Kachin State, Myanmar, with a genetic divergence of 3.8% between them; *Hebius khasiensis* (MZMU 1304) from Mizoram State, India, as distinct to *Hebius khasiensis* (CAS 221504) from Kachin State, with a genetic divergence of 3.8% between them; and *Herpetoreas xenura* (AD 633) from Assam State, India, as distinct to the other three conspecific specimens (PUCZM/X/SL1, 16–17) from Mizoram State, with a genetic divergence of 3.8% each from them. Comparably, inter-specific genetic divergence ranged between 3.8% and 46.2% across the present dataset excluding the outgroup taxon (see Appendix 4). The substantially high inter-specific genetic divergence (46.2%) estimated from *Sahyadriophis beddomei* with respect to three species of *Hebius*, viz. *H. craspedogaster* (Boulenger, 1899), *H. conelarus* (Malnate, 1963), and *H. leucomystax* (David, Bain, Nguyen, Orlov, Vogel, Vu & Ziegler, 2007), further corroborates the generic status of the recently erected *Sahyadriophis* (Patel *et al.* 2023). Henceforth, our genetic divergence estimation reveals the absence of a barcode gap in the dataset and further evinces cryptic diversity within *Hebius venningi*, *H. khasiensis*, and *Herpetoreas xenura* by taking into account their respective intra-specific genetic divergence (3.8%) and the species inferences in ASAP. The aforesaid evidence necessitates a systematic review particularly for these three taxa and will be addressed in a future study with more holistic data (T.V. Nguyen *et al.* unpubl. data). Concerning *Herpetoreas sieboldii* and *H. platyceps*, two widely distributed species that received controversies in the past and little interest from taxonomists, the best ASAP partition inferred the two specimens of *Herpetoreas platyceps* (KIZ YPX26317, WII AD.R183) as two distinct species despite the fact that the genetic divergence-based PCoA ordination and phylogenetic inferences suggested their close relationship with a shallow genetic differentiation between them. Nonetheless, seeing the minimum inter-specific genetic divergence estimated across the dataset (3.8%), the genetic divergence between them (7.7%) propounded to refer the specimen of *Herpetoreas platyceps* (WII AD.R183) to as *H. cf. sieboldii*. Conforming to our molecular inferences, we further propose to amend the status of the following specimens: *Amphiesma stolatum* (Linnaeus, 1758) (USNM 524073) into *Hebius clerki* (Wall, 1925), *Amphiesma sauteri* (Boulenger, 1909) (FMNH 232808) into *Hebius maximus* (Malnate, 1962), *Amphiesma craspedogaster* (YBU 071128) into *Herpetoreas burbrinki*, *Hebius venningi* (GP 2468, from Chiang Mai, Thailand) into *Hebius deschauenseei* (Taylor, 1934) [a re-identification in full agreement with David *et al.* 2021; Hauser *et al.* 2022], *Hebius venningi* (ZMMU NAP-08395) into *Hebius nigriventer* (Wall, 1925) [a re-identification in full agreement with David *et al.* 2021], *Hebius octolineatus* (Boulenger, 1904) (GP 1242) into *Hebius johannis* (Boulenger, 1908), *Hebius craspedogaster* (GP 1712) into *Hebius metusia* (Inger, Zhao, Shaffer & Wu, 1990), *Hebius johannis* (GP 1569) into *Hebius octolineatus* (Boulenger, 1904), *Hebius* sp. (GP 1766) into *Hebius cf. ruthveni* (Van Denburgh, 1923), *Hebius* sp. (GP 1790) into *Hebius sauteri* (Boulenger, 1909), *Hebius* sp. (GP 1618) into *Hebius taronensis* (Smith, 1940), *Hebius* sp. (ZMMU NAP-06638) into *Hebius terrakarenorum* Hauser, Smits & David, 2022, *Hebius* sp. in to (AUP NAP-06639) *Hebius cf. groundwateri* (Smith, 1922), *Hebius bitaeniatum* (Wall, 1925) (GP 1940) into *Hebius* sp., and *Hebius parallelum* (Boulenger, 1890) (CHS 849; KIZ 06681) into *Herpetoreas tpser* (see Appendix 2).

As the holotype of the *Herpetoreas xenura* was lost, a neotype designation from the four samples (stored at ZSI, India) reported by Wall (1909) was required to ensure taxonomy stability of this species. In the present study, we update the diagnosis of *Herpetoreas xenura* as follows (Wall 1907, 1909; Mathew & Meetei 2004; Reza 2010; Malsawmdawngliana *et al.* 2022; Ren *et al.* 2022; and our specimens): body cylindrical, maximum TL 870 mm; tail relatively long, TaL/TL 0.220–0.283; dorsal scale rows 19–19–17; all strongly keeled; ventrals 155–165; cloacal plate single, subcaudals single; subcaudals 81–110; supralabials 9(10), 4<sup>th</sup>–6<sup>th</sup> entering orbit; maxillary teeth 22–23, gradually enlarged posteriorly,

last two distinctly enlarged, separated from anterior teeth by a small diastema; hemipenis short and thin, shallowly bilobed, extends to 8<sup>th</sup> subcaudals; sulcus spermaticus single; dorsum dark olive-brown with indistinct narrow blackish cross-bars or series of spots; venter off-white each ventral decorated with a pair of dark brown square spots on their lateral edges (see Fig. 6A–F). The known distribution of *Herpetoreas xenura* is restricted to northeastern India (from West Garo Hills and Khasi Hills in Meghalaya through Atharamura Range in Tripura, Menam Mikir Punjee in Assam, and extending towards south in Lushai Hills and up to Naga Hills towards northeast), southeastern Bangladesh (Keokradong Mountain), and possibly to the northeastern parts of Bangladesh as well as the Chin Hills of Myanmar (Fig. 7; Appendix 4). According to our observations and secondary information, we argue that there are well thriving populations of this species within its distribution range in Northeast India. Consequently, we speculate the current IUCN’s categorization of this species as “Near Threatened” due to the small distribution area and reduced quality of forest freshwater habitat may be overstated (see Wogan *et al.* 2021), therefore we suggest an amendment on its conservation status into “Least Concern” species concurring to the IUCN’s Red List categories (IUCN Standards and Petitions Committee 2019).

Based on literature (Lalremsanga *et al.* 2022; Ren *et al.* 2022); and our material, we propose an updated key to the genus *Herpetoreas*.

1. Subcaudals single ..... 2
  - Subcaudals divided ..... 3
2. Max TL up to 575 mm, ventrals < 155 ..... *H. davidi* sp. nov.
  - Max TL up to 870 mm, ventrals > 155 ..... *H. xenura* (Wall, 1907)
3. Cloacal plate single ..... *H. pealii* (Sclater, 1891)
  - Cloacal plate divided ..... 4
4. Ventrals fewer than 168 ..... *H. tpser* Ren, Jiang, Huang, David & Li, 2022
  - Ventrals no less than 168 ..... 5
5. Tail relatively long,  $TaL/TL > 0.300$  .....
  - ..... *H. burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang & Pyron, 2014
  - Tail relatively short,  $TaL/TL \leq 0.300$  ..... 6
6. Ventrals < 190 ..... *H. murlen* Lalremsanga, Bal, Vogel & Biakzuala, 2022
  - Ventrals  $\geq 190$  ..... 7
7. A higher proportion of the length of the tail with 4 supracaudal scale rows than that with 6 supracaudal scale rows high,  $SC4/SC6 = 1.43$ ; weekly keeled only on five to seven mid-dorsal scale rows; VEN 205–234 [ $\bar{x} = 220.8$ ] in males, 191–216 [ $\bar{x} = 202.1$ ] in females ..... *H. platyceps* (Blyth, 1854)
  - A lower proportion of the length of the tail with 4 supracaudal scale rows than that with 6 supracaudal scale rows high,  $SC4/SC6 = 0.53$ ; all keeled but some may not be keeled in outermost mid-dorsal scale rows; VEN 193–207 [ $\bar{x} = 200.3$ ] in males, 174–185 [ $\bar{x} = 181.2$ ] in females .....
    - ..... *H. sieboldii* Günther, 1860

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## Supplementary files

**Supp. file 1.** Maximum Likelihood (ML) phylogenetic tree based on the fragment of mitochondrial Cytochrome b (cytb) gene among the genera *Amphiesma* Duméril, Bibron & Duméril, 1854, *Amphiesmoides* Malnate, 1961, *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023. The ultrafast bootstrap (UFB) support values are given at each branch. <https://doi.org/10.5852/ejt.2024.932.2519.11303>

**Supp. file 2.** *Herpetoreas* cf. *sieboldii* (Günther, 1860), specimen ♀ (BNHS 1567). **A.** Lateral view of the head, right side. **B.** Lateral view of the head, left side. **C.** Dorsal view of the head. **D.** Ventral view of the head. **E.** General dorsal view. **F.** General ventral view. Photos by O. Adhikari. <https://doi.org/10.5852/ejt.2024.932.2519.11305>

**Appendix 1** (continued on next page). List of examined specimens of *Hebius khasiensis* (Boulenger, 1890), *Herpetoreas sieboldi* (Günther, 1860), and *Her. platyceps* (Blyth, 1854).

No.	Species	Number	Location	Sex
1	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.11	Putao, Kachin, Myanmar	M
2	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.13	Putao, Kachin, Myanmar	M
3	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.14	Putao, Kachin, Myanmar	M
4	<i>Hebius khasiensis</i>	NHMUK 1946.1.12.81 (syntypes of <i>Tropidonotus khasiensis</i> )	Khasi Hills, Meghalaya, India	M
5	<i>Hebius khasiensis</i>	NHMUK 1946.1.12.82 (syntypes of <i>Tropidonotus khasiensis</i> )	Khasi Hills, Meghalaya, India	M
6	<i>Hebius khasiensis</i>	NHMUK 1946.1.13.62 (holotype of <i>Natrix gilhodesi</i> )	Putao, Kachin, Myanmar	M
7	<i>Hebius khasiensis</i>	NHMUK 1946.1.13.63	Putao, Kachin, Myanmar	M
8	<i>Hebius khasiensis</i>	CAS 220023	Nat Ma Taung NP., Chin, Myanmar	M
9	<i>Hebius khasiensis</i>	CIB 2000 I 0009	Ruili, Dehong, Yunnan, China	M
10	<i>Hebius khasiensis</i>	FMNH 251781	Chiang Mai, Thailand	M
11	<i>Hebius khasiensis</i>	KSC 140	Kohima, Nagaland, India	M
12	<i>Hebius khasiensis</i>	NRCT 980504	Doi Inthanon NP., Chiang Mai, Thailand	M
13	<i>Hebius khasiensis</i>	378 P	Dibang, Arunachal Pradesh, India	M
14	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.10	Putao, Kachin, Myanmar	F
15	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.12	Putao, Kachin, Myanmar	F
16	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.15	Putao, Kachin, Myanmar	F
17	<i>Hebius khasiensis</i>	NHMUK 1925.4.2.15A	Putao, Kachin, Myanmar	F
18	<i>Hebius khasiensis</i>	NHMUK 1946.1.12.80	Khasi Hills, Meghalaya, India	F
19	<i>Hebius khasiensis</i>	NHMUK 1946.1.13.45	Khasi Hills, Meghalaya, India	F
20	<i>Hebius khasiensis</i>	NHMUK 1974.884	Putao, Kachin, Myanmar	F
21	<i>Hebius khasiensis</i>	CAS 221504	Putao, Kachin, Myanmar	F
22	<i>Hebius khasiensis</i>	CAS 221525	Putao, Kachin, Myanmar	F
23	<i>Hebius khasiensis</i>	CAS 221543	Putao, Kachin, Myanmar	F
24	<i>Hebius khasiensis</i>	CAS 224654	Putao, Kachin, Myanmar	F
25	<i>Hebius khasiensis</i>	CAS 224694	Putao, Kachin, Myanmar	F
26	<i>Hebius khasiensis</i>	CIB Xi0089	Xichuangbanna, Yunnan, China	F
27	<i>Hebius khasiensis</i>	FMNH 251780	Chiang Mai, Thailand	F
28	<i>Hebius khasiensis</i>	MNHN 1893.0399	Karen Hills, Shan, Myanmar	F
29	<i>Hebius khasiensis</i>	MNHN 2004.0248	Boun Tay, Phongsaly, Laos	F
30	<i>Hebius khasiensis</i>	QSMI 0273	Phu Luang, Loei, Thailand	F
31	<i>Hebius khasiensis</i>	ZSI 23926	Changlang, Arunachal Pradesh, India	F
32	<i>Hebius khasiensis</i>	377 P	Dibang, Arunachal Pradesh, India	F
33	<i>Hebius khasiensis</i>	379 P	Dibang, Arunachal Pradesh, India	F
34	<i>Herpetoreas sieboldii</i>	NHMUK 1913.5.22.1	Maikola Valley, Nepal	M
35	<i>Herpetoreas sieboldii</i>	CAS 177672	Tibet, China	M
36	<i>Herpetoreas sieboldii</i>	CAS 177673	Tibet, China	M



**Appendix 1** (continued). List of examined specimens of *Hebius khasiensis* (Boulenger, 1890), *Herpetoreas sieboldi* (Günther, 1860), and *Her. platyceps* (Blyth, 1854).

No.	Species	Number	Location	Sex
37	<i>Herpetoreas sieboldii</i>	CAS 90690	Nepal	M
38	<i>Herpetoreas sieboldii</i>	FMNH 204502	Nepal	M
39	<i>Herpetoreas sieboldii</i>	FMNH 204504	Nepal	M
40	<i>Herpetoreas sieboldii</i>	FMNH 190856	Nepal	M
41	<i>Herpetoreas sieboldii</i>	FMNH 131966	Nepal	M
42	<i>Herpetoreas sieboldii</i>	FMNH 204499	Nepal	M
43	<i>Herpetoreas sieboldii</i>	FMNH 204501	Nepal	M
44	<i>Herpetoreas sieboldii</i>	NHMW 22383:1	Darjeeling, West Bengal, India	M
45	<i>Herpetoreas sieboldii</i>	NHMW 22383:3	Darjeeling, West Bengal, India	M
46	<i>Herpetoreas sieboldii</i>	NHMW 22383:4	Darjeeling, West Bengal, India	M
47	<i>Herpetoreas sieboldii</i>	CAS 15973	Darjeeling, West Bengal, India	F
48	<i>Herpetoreas sieboldii</i>	CAS 177674	Tibet, China	F
49	<i>Herpetoreas sieboldii</i>	MNHG 1355.73	Nepal	F
50	<i>Herpetoreas sieboldii</i>	FMNH 109762	Gorkha, Nepal	F
51	<i>Herpetoreas sieboldii</i>	FMNH 204500	Nepal	F
52	<i>Herpetoreas sieboldii</i>	FMNH 204503	Nepal	F
53	<i>Herpetoreas platyceps</i>	NHMW 22383:5	Darjeeling, West Bengal, India	F
54	<i>Herpetoreas platyceps</i>	NHMW 18570:1 (syntypes of <i>Zamenis himalayanus</i> )	Shimla and Kullu, Himachal Pradesh, India	F
55	<i>Herpetoreas platyceps</i>	NHMW 18570:2 (syntypes of <i>Zamenis himalayanus</i> )	Shimla and Kullu, Himachal Pradesh, India	F
56	<i>Herpetoreas platyceps</i>	NHMW 18569	Himachal Pradesh, India	F
57	<i>Herpetoreas platyceps</i>	MNHN 4197	Himachal Pradesh, India	F
58	<i>Herpetoreas platyceps</i>	RMNH 20502	Landrang, Nepal	F

**Appendix 2** (continued on next two pages). Sequences of the *Herpetoreas* Günther, 1860 and related taxa used in this study. Remark: “?” = request verification.

No	Previous identification	New identification	Revised distributions	Voucher number	Cytb	Locality	References
1	<i>Amphiesma monticolium</i>	<i>Amphiesma monticola</i>	India	SN 009	OK315803	Wayanad, India	Deepak <i>et al.</i> 2022
2	<i>Amphiesma stolatum</i>	<i>Amphiesma stolatum</i>	India, Nepal, Pakistan, Sri Lanka, Myanmar, China <sup>?</sup> , Taiwan <sup>?</sup> , Thailand <sup>?</sup> , Vietnam <sup>?</sup> , Laos <sup>?</sup> , Cambodia <sup>?</sup>	GP 2239	KJ685694	Guangdong, China	Guo <i>et al.</i> 2014; Poyarkov <i>et al.</i> 2023; our data
3	<i>Amphiesmoides ornaticeps</i>	<i>Amphiesmoides ornaticeps</i>	China, Vietnam	ZMMU R16289	OK326949	Pu Hoat, Nghe An, Vietnam	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023;
4	<i>Hebius andreae</i>	<i>Hebius andreae</i>	Vietnam, Laos	VNUF R.2017.25	MK253674	Khammouane, Laos	Ziegler <i>et al.</i> 2019; Poyarkov <i>et al.</i> 2023
5	<i>Hebius annamensis</i>	<i>Hebius annamensis</i>	Vietnam, Laos	FMNH 258637	OK315812	Kaleum, Xekong, Laos	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
6	<i>Hebius atemporalis</i>	<i>Hebius atemporalis</i>	Vietnam, China	ZMMU NAP07877	OK315813	Pu Hoat, Nghe An, Vietnam	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
7	<i>Hebius bitaeniatus</i>	<i>Hebius bitaeniatus</i>	Myanmar, Thailand, Vietnam, China <sup>?</sup>	AUP 00062	OK315816	Chiang Mai, Thailand	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
8	<i>Hebius boulengeri</i>	<i>Hebius boulengeri</i>	China, Vietnam, Thailand <sup>?</sup> , Laos <sup>?</sup> , Cambodia <sup>?</sup>	GP 1789	KJ685684	Guangdong, China	Guo <i>et al.</i> 2014; Poyarkov <i>et al.</i> 2023
9	<i>Hebius chapaensis</i>	<i>Hebius chapaensis</i>	Vietnam, Laos, China	VNMN 06102	MH778702	Sapa, Lao Cai, Vietnam	Ren <i>et al.</i> 2018; Poyarkov <i>et al.</i> 2023
10	<i>Amphiesma stolatum</i>	<i>Hebius clerki</i>	Myanmar, China	USNM 524073	KJ685711	Chatthin, Sagaing, Myanmar	Guo <i>et al.</i> 2014
11	<i>Hebius concelarus</i>	<i>Hebius concelarus</i>	Japan	KUZ R20253	AB989268	Okimawa, Ryukyu, Japan	Kaito & Toda 2016
12	<i>Hebius craspedogaster</i>	<i>Hebius craspedogaster</i>	China	GP 1963	KJ685689	Sichuan, China	Guo <i>et al.</i> 2014
13	<i>Hebius venningi</i>	<i>Hebius deschauenseei</i>	Thailand	GP 2468	KJ685700	Chiang Mai, Thailand	Guo <i>et al.</i> 2014; Poyarkov <i>et al.</i> 2023
14	<i>Hebius sp.</i>	<i>Hebius cf. groundwateri</i>	Thailand	AUP NAP-06639	OK315825	Ratchaburi, Thailand	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
15	<i>Hebius ishigakiensis</i>	<i>Hebius ishigakiensis</i>	Japan	KUZ R33045	AB989296	Okimawa, Ryukyu, Japan	Kaito & Toda 2016
16	<i>Hebius octolineatus</i>	<i>Hebius johannis</i>	China	GP 1242	KJ685673	Guizhou, China	Guo <i>et al.</i> 2014
17	<i>Hebius khaensis</i>	<i>Hebius khaensis</i>	Myanmar, China, Thailand	CAS 221504	KJ685668	Putao, Kachin, China	Guo <i>et al.</i> 2014; Poyarkov <i>et al.</i> 2023
18	<i>Hebius leucomystax</i>	<i>Hebius leucomystax</i>	Vietnam, Laos, Cambodia, Thailand	ZMMU R. 14807	OK315821	Quang Binh, Vietnam	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
19	<i>Amphiesma sauteri</i>	<i>Hebius maximus</i>	China	FMNH 232808	AF402905	Hongya, Sichuan, China	Alfaro & Arnold 2001; Li <i>et al.</i> 2022
20	<i>Hebius craspedogaster</i>	<i>Hebius metusia</i>	China	GP 1712	KJ685682	Baoxing, Sichuan, China	Guo <i>et al.</i> 2014

**Appendix 2** (continued). Sequences of the *Herpetoreas* Günther, 1860 and related taxa used in this study. Remark: “?” = request verification.

No	Previous identification	New identification	Revised distributions	Voucher number	Cytb	Locality	References
21	<i>Hebius modestum</i>	<i>Hebius modestum</i>	India, Myanmar, China	CAS 234262	KJ685671	Dehong, Yunnan, China	Guo <i>et al.</i> 2014; David <i>et al.</i> 2021
22	<i>Hebius venningi</i>	<i>Hebius nigriventer</i>	Myanmar, China	ZMMU NAP-08395	OK315829	Kachin, Myanmar	David <i>et al.</i> 2021; Deepak <i>et al.</i> 2022
23	<i>Hebius johannis</i>	<i>Hebius octolineatus</i>	China	GP 1569	KJ685678	Yunnan, China	Guo <i>et al.</i> 2014
24	<i>Hebius optatus</i>	<i>Hebius optatus</i>	China, Vietnam?	GP 1885	KJ685687	Libo, Guangxi, China	Guo <i>et al.</i> 2014; Poyarkov <i>et al.</i> 2023
25	<i>Hebius popei</i>	<i>Hebius popei</i>	China	GP 2169	KJ685692	Qiongzhang, Hainan, China	Guo <i>et al.</i> 2014
26	<i>Hebius pryeri</i>	<i>Hebius pryeri</i>	Japan	KUZ R67983	AB989102	Ryukyu, Japan	Kaito & Toda 2016
27	<i>Hebius</i> sp.	<i>Hebius</i> cf. <i>ruthveni</i>	China	GP 1766	KJ685683	Jiangxi, China	Guo <i>et al.</i> 2014; Kaito & Toda 2016
28	<i>Hebius sangzhiensis</i>	<i>Hebius sangzhiensis</i>	China	SYNU 08070350	MK340763	Sangzhi, Hunan, China	Zhou <i>et al.</i> 2019
29	<i>Hebius</i> sp.	<i>Hebius sauteri</i>	China, Taiwan	GP 1790	KJ685685	Guangdong, China	Guo <i>et al.</i> 2014; Li <i>et al.</i> 2022
30	<i>Hebius septemlineatus</i>	<i>Hebius septemlineatus</i>	China	KIZ 037706	MZ570485	Tengchong, Yunnan, China	Hou <i>et al.</i> 2021
31	<i>Hebius</i> sp.	<i>Hebius taronensis</i>	Myanmar, India	GP1618	KJ685679	Myanmar	Guo <i>et al.</i> 2014; David <i>et al.</i> 2021
32	<i>Hebius</i> sp.	<i>Hebius terrakarenorum</i>	Thailand	ZMMU NAP-06638	OK315824	Tak, Thailand	Deepak <i>et al.</i> 2022; Poyarkov <i>et al.</i> 2023
33	<i>Hebius venningi</i>	<i>Hebius venningi</i>	India, Myanmar	CAS 233206	KJ685670	Phalum, Chin, Myanmar	Guo <i>et al.</i> 2014; David <i>et al.</i> 2021
34	<i>Hebius venningi</i>	<i>Hebius venningi</i>		MZMU1313 (isolate A)	OR389974	Mizoram, India	<b>This study</b>
35	<i>Hebius venningi</i>	<i>Hebius venningi</i>		MZMU1313 (isolate B)	OR389975	Mizoram, India	<b>This study</b>
36	<i>Hebius vibakari</i>	<i>Hebius vibakari</i>	Japan	KUZ R21587	AB989302	Kansai, Japan	Kaito & Toda 2016
37	<i>Hebius weixiensis</i>	<i>Hebius weixiensis</i>	China	KIZ 035776	MZ570490	Weixi, Yunnan, China	Hou <i>et al.</i> 2021
38	<i>Hebius yanbianensis</i>	<i>Hebius yanbianensis</i>	China	GP 4006	MH532291	Yanbian, Sichuan, China	Liu <i>et al.</i> 2018
39	<i>Hebius bitaeniatum</i>	<i>Hebius</i> sp.	China	GP 1940	KJ685688	Guangxi, China	Guo <i>et al.</i> 2014
40	<i>Hebius youjiangensis</i>	<i>Hebius youjiangensis</i>	China	HSR 22184	OQ085073	Baise, Guangxi, China	Xu <i>et al.</i> 2023
41	<i>Amphitesma craspedogaster</i>	<i>Herpetoreas burbrinki</i>	China	YBU 071128	GQ281781	Tibet, China	Guo <i>et al.</i> 2012
42	<i>Herpetoreas burbrinki</i>	<i>Herpetoreas burbrinki</i>	China	HSR 19252	MZ358098	Tibet, China	Peng & Huang unpubl. data; Ren <i>et al.</i> 2022
43	<i>Herpetoreas xenura</i>	<i>Herpetoreas davidi</i> sp. nov.	Myanmar	CAS 220256	OK315830	Gwa, Rakhine, Myanmar	Deepak <i>et al.</i> 2022

**Appendix 2** (continued). Sequences of the *Herpetoreas* Günther, 1860 and related taxa used in this study. Remark: “?” = request verification.

No	Previous identification	New identification	Revised distributions	Voucher number	Cytb	Locality	References
44	<i>Herpetoreas murlen</i>	<i>Herpetoreas murlen</i>	India	MZMU 2473	ON204025	Mizoram, India	Lalremsanga <i>et al.</i> 2022
45	<i>Herpetoreas pedtii</i>	<i>Herpetoreas pealii</i>	India	WII ADR547	MT571586	Arunachal Pradesh, India	Das <i>et al.</i> 2020
46	<i>Herpetoreas platyceps</i>	<i>Herpetoreas platyceps</i>	India, Nepal, Pakistan, Bhutan, China, Bangladesh	KIZ YPX26317	MW111464	Gyirong, Tibet, China	Xu <i>et al.</i> 2021
47	<i>Herpetoreas platyceps</i>	<i>Herpetoreas cf. sieboldii</i>	Pakistan, India, Nepal, Bhutan, Bangladesh	WII AD.R183	MT571587	Chamoli, Uttarakhand, India	Das <i>et al.</i> 2020
48	<i>Hebius parallelum</i>	<i>Herpetoreas tpser</i>		CHS 849	MK201567	Tibet, China	Li <i>et al.</i> 2020
49	<i>Hebius parallelum</i>	<i>Herpetoreas tpser</i>	China	KIZ 06681	MW111476	Tibet, China	Xu <i>et al.</i> 2021
50	<i>Herpetoreas tpser</i>	<i>Herpetoreas tpser</i>		CIB 107855	OM313292	Medog, Tibet, China	Ren <i>et al.</i> 2022
51	<i>Herpetoreas tpser</i>	<i>Herpetoreas tpser</i>		CIB 118524	OM313293	Medog Tibet, China	Ren <i>et al.</i> 2022
52	<i>Herpetoreas xenura</i>	<i>Herpetoreas xenura</i>	India, Bangladesh	PUCZMX SL1	MN993850	Mizoram, India	Lalronunga <i>et al.</i> 2020
53	<i>Herpetoreas xenura</i>	<i>Herpetoreas xenura</i>		PUCZM X SL17	MN993852	Mizoram, India	Lalronunga <i>et al.</i> 2020
54	<i>Herpetoreas xenura</i>	<i>Herpetoreas xenura</i>		PUCZM X SL16	MN993851	Mizoram, India	Lalronunga <i>et al.</i> 2020
55	<i>Herpetoreas xenura</i>	<i>Herpetoreas xenura</i>		AD 633	MN993891	Assam, India	Lalronunga <i>et al.</i> 2020
56	<i>Sahyadriophis beddomei</i>	<i>Sahyadriophis beddomei</i>	India	SN 013	OK315814	Valparai, India	Deepak <i>et al.</i> 2022



**Appendix 3.** The best partitioning schemes and nucleotide substitution models selected for the partitioned Bayesian Inference and Maximum Likelihood phylogenies in the present study.

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<b>Partitions</b>	<b>Sites</b>	<b>For Bayesian Inference (Partition Finder)</b>	<b>For Maximum Likelihood (ModelFinder)</b>
I	Cytbpos1	TIM+I+G	TN+F+R7
II	Cytbpos2, Cytbpos3	HKY+I+G	TPM2+F+I+G4

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**Appendix 4** (continued on next seven pages). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	OK315830 <i>Herpetoreas davidi</i> sp. nov																		
2	ON204025 <i>Herpetoreas murlen</i>	0.192																	
3	MZ358098 <i>Herpetoreas burbrinki</i>	0.231	0.154																
4	GQ281781 <i>Herpetoreas burbrinki</i>	0.231	0.154	0.000															
5	MW111464 <i>Herpetoreas platyceps</i>	0.231	0.231	0.231	0.231														
6	MT571587 <i>Herpetoreas</i> cf. <i>sieboldii</i>	0.231	0.231	0.231	0.231	0.077													
7	MT571586 <i>Herpetoreas pealii</i>	0.269	0.308	0.385	0.385	0.269	0.269												
8	MN993850 <i>Herpetoreas xenura</i>	0.269	0.308	0.308	0.308	0.231	0.154	0.308											
9	MN993852 <i>Herpetoreas xenura</i>	0.269	0.308	0.308	0.308	0.231	0.154	0.308	0.000										
10	MN993851 <i>Herpetoreas xenura</i>	0.269	0.308	0.308	0.308	0.231	0.154	0.308	0.000	0.000									
11	MN993891 <i>Herpetoreas xenura</i>	0.308	0.346	0.346	0.346	0.269	0.192	0.346	0.038	0.038	0.038								
12	MW111476 <i>Herpetoreas ipser</i>	0.308	0.231	0.269	0.269	0.154	0.231	0.231	0.346	0.346	0.346	0.385							
13	OM313293 <i>Herpetoreas ipser</i>	0.308	0.231	0.269	0.269	0.154	0.231	0.231	0.346	0.346	0.346	0.385	0.000						
14	OM313292 <i>Herpetoreas ipser</i>	0.308	0.231	0.269	0.269	0.154	0.231	0.231	0.346	0.346	0.346	0.385	0.000	0.000					
15	MK201567 <i>Herpetoreas ipser</i>	0.308	0.231	0.269	0.269	0.154	0.231	0.231	0.346	0.346	0.346	0.385	0.000	0.000	0.000				
16	MK253674 <i>Hebius andreae</i>	0.154	0.231	0.231	0.231	0.231	0.154	0.346	0.269	0.269	0.269	0.308	0.308	0.308	0.308	0.308			
17	OK315812 <i>Hebius annamensis</i>	0.192	0.192	0.269	0.269	0.192	0.192	0.269	0.308	0.308	0.308	0.346	0.192	0.192	0.192	0.192	0.115		
18	KJ685671 <i>Hebius modestum</i>	0.192	0.192	0.269	0.269	0.192	0.192	0.269	0.308	0.308	0.308	0.346	0.192	0.192	0.192	0.192	0.115	0.000	
19	KJ685684 <i>Hebius boulengeri</i>	0.192	0.231	0.308	0.308	0.231	0.231	0.308	0.269	0.269	0.269	0.308	0.231	0.231	0.231	0.231	0.231	0.115	0.115
20	KJ685700 <i>Hebius deschaenseei</i>	0.192	0.192	0.269	0.269	0.192	0.192	0.269	0.308	0.308	0.308	0.346	0.192	0.192	0.192	0.192	0.115	0.000	0.000
21	MH778702 <i>Hebius chapaensis</i>	0.192	0.192	0.269	0.269	0.192	0.192	0.269	0.308	0.308	0.308	0.346	0.192	0.192	0.192	0.192	0.115	0.000	0.000
22	MN788503 <i>Hebius khaasiensis</i>	0.231	0.231	0.308	0.308	0.231	0.231	0.308	0.346	0.346	0.346	0.385	0.231	0.231	0.231	0.231	0.154	0.038	0.038
23	KJ685668 <i>Hebius khaasiensis</i>	0.231	0.269	0.346	0.346	0.269	0.269	0.346	0.308	0.308	0.308	0.346	0.269	0.269	0.269	0.269	0.192	0.077	0.077
24	KJ685683 <i>Hebius</i> cf. <i>ruthveni</i>	0.231	0.231	0.308	0.308	0.231	0.231	0.269	0.346	0.346	0.346	0.385	0.192	0.192	0.192	0.192	0.154	0.038	0.038
25	OQ085073 <i>Hebius youjiangensis</i>	0.231	0.231	0.308	0.308	0.231	0.231	0.231	0.346	0.346	0.346	0.385	0.154	0.154	0.154	0.154	0.154	0.038	0.038
26	KJ685711 <i>Hebius clerki</i>	0.231	0.231	0.269	0.269	0.154	0.154	0.231	0.269	0.269	0.269	0.308	0.154	0.154	0.154	0.154	0.154	0.038	0.038
27	AF402905 <i>Hebius maximus</i>	0.231	0.231	0.308	0.308	0.231	0.231	0.269	0.346	0.346	0.346	0.385	0.192	0.192	0.192	0.192	0.154	0.038	0.038

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
28	KJ685687 <i>Hebius optatum</i>	0.231	0.269	0.346	0.346	0.269	0.269	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.192	0.077	0.077
29	MZ570490 <i>Hebius weixiensis</i>	0.231	0.269	0.346	0.346	0.269	0.269	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.231	0.115	0.115
30	OK315813 <i>Hebius atemporalis</i>	0.231	0.269	0.346	0.346	0.269	0.269	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.192	0.077	0.077
31	KJ685673 <i>Hebius johannis</i>	0.231	0.231	0.308	0.308	0.231	0.231	0.269	0.346	0.346	0.346	0.385	0.192	0.192	0.192	0.192	0.154	0.038	0.038
32	OK315824 <i>Hebius terrakarenorum</i>	0.231	0.192	0.269	0.269	0.231	0.231	0.308	0.346	0.346	0.346	0.385	0.231	0.231	0.231	0.231	0.154	0.038	0.038
33	MZ570485 <i>Hebius septemlineatus</i>	0.231	0.269	0.346	0.346	0.269	0.269	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.231	0.115	0.115
34	AB989302 <i>Hebius vibakari</i>	0.269	0.231	0.308	0.308	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.192	0.192	0.192	0.192	0.192	0.077	0.077
35	KJ685678 <i>Hebius octolineatus</i>	0.269	0.269	0.346	0.346	0.269	0.192	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.115	0.077	0.077
36	KJ685682 <i>Hebius metusia</i>	0.269	0.231	0.308	0.308	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.192	0.192	0.192	0.192	0.192	0.077	0.077
37	KJ685688 <i>Hebius</i> sp.	0.269	0.231	0.308	0.308	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.192	0.192	0.192	0.192	0.192	0.077	0.077
38	MH532291 <i>Hebius yambianensis</i>	0.269	0.269	0.346	0.346	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.231	0.231	0.231	0.231	0.192	0.077	0.077
39	OK315816 <i>Hebius bitaeniatus</i>	0.269	0.308	0.385	0.385	0.308	0.308	0.308	0.269	0.269	0.269	0.308	0.269	0.269	0.269	0.269	0.269	0.154	0.154
40	KJ685689 <i>Hebius craspedogaster</i>	0.269	0.192	0.346	0.346	0.346	0.346	0.346	0.346	0.346	0.346	0.385	0.308	0.308	0.308	0.308	0.308	0.192	0.192
41	MK340763 <i>Hebius sangzhiensis</i>	0.269	0.231	0.308	0.308	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.192	0.192	0.192	0.192	0.231	0.115	0.115
42	OK315825 <i>Hebius groundwateri</i>	0.269	0.231	0.308	0.308	0.269	0.269	0.269	0.385	0.385	0.385	0.423	0.192	0.192	0.192	0.192	0.192	0.077	0.077
43	KJ685670 <i>Hebius venningi</i>	0.269	0.269	0.269	0.269	0.231	0.231	0.308	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.231	0.115	0.115
44	OR389974 <i>Hebius venningi</i>	0.308	0.308	0.269	0.269	0.192	0.192	0.269	0.269	0.269	0.269	0.308	0.192	0.192	0.192	0.192	0.269	0.154	0.154
45	OR389975 <i>Hebius venningi</i>	0.308	0.308	0.269	0.269	0.192	0.192	0.269	0.269	0.269	0.269	0.308	0.192	0.192	0.192	0.192	0.269	0.154	0.154
46	KJ685701 <i>Hebius sauteri</i>	0.308	0.269	0.423	0.423	0.346	0.269	0.308	0.269	0.269	0.269	0.308	0.308	0.308	0.308	0.308	0.192	0.154	0.154
47	AB989296 <i>Hebius ishigakiensis</i>	0.308	0.308	0.308	0.308	0.269	0.269	0.346	0.346	0.346	0.346	0.385	0.269	0.269	0.269	0.269	0.231	0.115	0.115
48	KJ685692 <i>Hebius popei</i>	0.308	0.308	0.346	0.346	0.231	0.231	0.269	0.346	0.346	0.346	0.385	0.192	0.192	0.192	0.192	0.231	0.115	0.115
49	KJ685679 <i>Hebius taronensis</i>	0.308	0.308	0.269	0.269	0.192	0.192	0.269	0.269	0.269	0.269	0.308	0.192	0.192	0.192	0.192	0.269	0.154	0.154

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
50	OK315829 <i>Hebius nigriventer</i>	0.308	0.308	0.269	0.269	0.192	0.192	0.269	0.269	0.269	0.269	0.308	0.192	0.192	0.192	0.192	0.269	0.154	0.154
51	AB989268 <i>Hebius conelarus</i>	0.346	0.269	0.308	0.308	0.269	0.269	0.308	0.385	0.385	0.385	0.423	0.231	0.231	0.231	0.231	0.308	0.192	0.192
52	OK315821 <i>Hebius leucomystax</i>	0.346	0.385	0.462	0.462	0.385	0.308	0.423	0.269	0.269	0.269	0.308	0.385	0.385	0.385	0.385	0.269	0.231	0.231
53	AB989102 <i>Hebius pryori</i>	0.385	0.385	0.385	0.385	0.269	0.269	0.308	0.308	0.308	0.346	0.346	0.269	0.269	0.269	0.269	0.346	0.231	0.231
54	KJ685694 <i>Amphiesma stolatum</i>	0.269	0.192	0.308	0.308	0.231	0.231	0.269	0.308	0.308	0.308	0.346	0.231	0.231	0.231	0.231	0.308	0.192	0.192
55	OK315803 <i>Amphiesma monticola</i>	0.269	0.231	0.231	0.231	0.269	0.308	0.423	0.346	0.346	0.346	0.385	0.269	0.269	0.269	0.269	0.346	0.231	0.231
56	OK315814 <i>Sahyadriophis beddomei</i>	0.385	0.346	0.346	0.346	0.346	0.269	0.346	0.346	0.346	0.346	0.308	0.385	0.385	0.385	0.385	0.308	0.308	0.308
57	OK326949 <i>Amphiesmoides ornateiceps</i>	0.462	0.538	0.500	0.500	0.385	0.462	0.500	0.577	0.577	0.577	0.538	0.423	0.423	0.423	0.423	0.385	0.385	0.385

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
1	OK315830 <i>Herpetoreas davidi</i> sp. nov																			
2	ON204025 <i>Herpetoreas murlen</i>																			
3	MZ358098 <i>Herpetoreas burbrinki</i>																			
4	GQ281781 <i>Herpetoreas burbrinki</i>																			
5	MW111464 <i>Herpetoreas platyceps</i>																			
6	MT571587 <i>Herpetoreas</i> cf. <i>sieboldii</i>																			
7	MT571586 <i>Herpetoreas pealii</i>																			
8	MN993850 <i>Herpetoreas xenura</i>																			
9	MN993852 <i>Herpetoreas xenura</i>																			
10	MN993851 <i>Herpetoreas xenura</i>																			
11	MN993891 <i>Herpetoreas xenura</i>																			
12	MW111476 <i>Herpetoreas tpser</i>																			
13	OM313293 <i>Herpetoreas tpser</i>																			
14	OM313292 <i>Herpetoreas tpser</i>																			
15	MK201567 <i>Herpetoreas tpser</i>																			
16	MK253674 <i>Hebius andreae</i>																			
17	OK315812 <i>Hebius annamensis</i>																			
18	KJ685671 <i>Hebius modestum</i>																			
19	KJ685684 <i>Hebius Boulengeri</i>																			
20	KJ685700 <i>Hebius deschauenseei</i>	0.115																		
21	MH778702 <i>Hebius chapaensis</i>	0.115	0.000																	
22	MN788503 <i>Hebius khasiensis</i>	0.077	0.038	0.038																
23	KJ685668 <i>Hebius khasiensis</i>	0.038	0.077	0.077	0.038															
24	KJ685683 <i>Hebius</i> cf. <i>ruthveni</i>	0.154	0.038	0.038	0.077	0.115														
25	OQ085073 <i>Hebius youjiangensis</i>	0.154	0.038	0.038	0.077	0.115	0.038													



**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
26	KJ685711 <i>Hebius clerki</i>	0.154	0.038	0.038	0.077	0.115	0.077	0.077												
27	AF402905 <i>Hebius maximus</i>	0.154	0.038	0.038	0.077	0.115	0.000	0.038	0.077											
28	KJ685687 <i>Hebius optatum</i>	0.115	0.077	0.077	0.115	0.077	0.038	0.077	0.115	0.038										
29	MZ570490 <i>Hebius weixiensis</i>	0.115	0.115	0.115	0.154	0.115	0.115	0.115	0.154	0.115	0.077									
30	OK315813 <i>Hebius atemporalis</i>	0.115	0.077	0.077	0.115	0.077	0.077	0.077	0.115	0.077	0.038	0.038								
31	KJ685673 <i>Hebius johannis</i>	0.154	0.038	0.038	0.077	0.115	0.000	0.038	0.077	0.000	0.038	0.115	0.077							
32	OK315824 <i>Hebius terrakarenorum</i>	0.154	0.038	0.038	0.077	0.115	0.077	0.077	0.077	0.077	0.115	0.154	0.115	0.077						
33	MZ570485 <i>Hebius septemlineatus</i>	0.115	0.115	0.115	0.154	0.115	0.077	0.115	0.154	0.077	0.038	0.038	0.077	0.077	0.154					
34	AB989302 <i>Hebius vibakari</i>	0.192	0.077	0.077	0.115	0.154	0.038	0.077	0.115	0.038	0.077	0.154	0.115	0.038	0.115	0.115				
35	KJ685678 <i>Hebius octolineatus</i>	0.192	0.077	0.077	0.115	0.154	0.038	0.077	0.115	0.038	0.077	0.154	0.115	0.038	0.115	0.115	0.077			
36	KJ685682 <i>Hebius metusia</i>	0.192	0.077	0.077	0.115	0.154	0.038	0.077	0.115	0.038	0.077	0.154	0.115	0.038	0.115	0.115	0.000	0.077		
37	KJ685688 <i>Hebius sp.</i>	0.192	0.077	0.077	0.115	0.154	0.038	0.077	0.115	0.038	0.077	0.154	0.115	0.038	0.115	0.115	0.000	0.077	0.000	
38	MH522291 <i>Hebius yanzianensis</i>	0.115	0.077	0.077	0.038	0.077	0.038	0.077	0.115	0.038	0.077	0.154	0.115	0.038	0.115	0.115	0.077	0.077		
39	OK315816 <i>Hebius bitaeniatius</i>	0.154	0.154	0.154	0.192	0.154	0.115	0.154	0.192	0.115	0.077	0.077	0.115	0.115	0.192	0.038	0.154	0.154	0.154	
40	KJ685689 <i>Hebius craspedogaster</i>	0.192	0.192	0.192	0.231	0.192	0.154	0.192	0.231	0.154	0.115	0.115	0.115	0.154	0.192	0.077	0.192	0.192	0.192	
41	MK340763 <i>Hebius sang-hiensiensis</i>	0.192	0.115	0.115	0.154	0.192	0.077	0.115	0.154	0.077	0.115	0.154	0.115	0.154	0.077	0.154	0.077	0.038	0.115	0.038
42	OK315825 <i>Hebius groundwateri</i>	0.192	0.077	0.077	0.115	0.154	0.077	0.038	0.115	0.077	0.115	0.154	0.115	0.154	0.077	0.154	0.115	0.115	0.115	
43	KJ685670 <i>Hebius vanningi</i>	0.192	0.115	0.115	0.154	0.192	0.077	0.115	0.154	0.077	0.115	0.115	0.154	0.077	0.154	0.077	0.115	0.115	0.115	
44	OR389974 <i>Hebius vanningi</i>	0.231	0.154	0.154	0.192	0.231	0.115	0.154	0.115	0.115	0.154	0.154	0.192	0.115	0.192	0.115	0.154	0.154	0.154	
45	OR389975 <i>Hebius vanningi</i>	0.231	0.154	0.154	0.192	0.231	0.115	0.154	0.115	0.115	0.154	0.154	0.192	0.115	0.192	0.115	0.154	0.154	0.154	
46	KJ685701 <i>Hebius sauteri</i>	0.269	0.154	0.154	0.192	0.231	0.115	0.154	0.192	0.115	0.154	0.231	0.192	0.115	0.192	0.192	0.154	0.077	0.154	
47	AB989296 <i>Hebius ishigakiensis</i>	0.154	0.115	0.115	0.077	0.115	0.077	0.115	0.154	0.077	0.115	0.192	0.154	0.077	0.154	0.115	0.115	0.115	0.115	
48	KJ685692 <i>Hebius popei</i>	0.154	0.115	0.115	0.077	0.115	0.077	0.115	0.077	0.077	0.115	0.192	0.154	0.077	0.154	0.115	0.115	0.115	0.115	
49	KJ685679 <i>Hebius taronensis</i>	0.231	0.154	0.154	0.192	0.231	0.115	0.154	0.115	0.115	0.154	0.154	0.192	0.115	0.192	0.115	0.154	0.154	0.154	
50	OK315829 <i>Hebius nigriventer</i>	0.231	0.154	0.154	0.192	0.231	0.115	0.154	0.115	0.115	0.154	0.154	0.192	0.115	0.192	0.115	0.154	0.154	0.154	
51	AB989268 <i>Hebius conclarus</i>	0.192	0.192	0.192	0.154	0.192	0.154	0.192	0.154	0.154	0.192	0.192	0.231	0.154	0.192	0.154	0.192	0.192	0.192	0.192

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
52	OK315821 <i>Hebius leucomystax</i>	0.231	0.231	0.231	0.269	0.231	0.269	0.269	0.269	0.269	0.231	0.192	0.231	0.269	0.269	0.192	0.308	0.231	0.308
53	AB989102 <i>Hebius pryori</i>	0.231	0.231	0.231	0.192	0.231	0.192	0.231	0.192	0.192	0.231	0.231	0.269	0.192	0.269	0.192	0.231	0.231	0.231
54	KJ685694 <i>Amphiesma stolatium</i>	0.154	0.192	0.192	0.154	0.192	0.231	0.231	0.154	0.231	0.269	0.269	0.269	0.231	0.192	0.269	0.269	0.269	0.269
55	OK315803 <i>Amphiesma monticola</i>	0.231	0.231	0.231	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.231	0.269	0.231	0.308	0.231
56	OK315814 <i>Sahyadriophis beddomei</i>	0.346	0.308	0.308	0.346	0.385	0.346	0.346	0.346	0.346	0.385	0.385	0.385	0.385	0.346	0.346	0.385	0.308	0.308
57	OK326949 <i>Amphiesmoides ornaticeps</i>	0.500	0.385	0.385	0.423	0.462	0.423	0.423	0.346	0.423	0.462	0.500	0.462	0.423	0.423	0.500	0.462	0.462	0.462

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malhate, 1961 as outgroup.

No.	Species	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	
1	OK315830 <i>Herpetoreas davidi</i> sp. nov																					
2	ON204025 <i>Herpetoreas murlen</i>																					
3	MZ358098 <i>Herpetoreas burbrinki</i>																					
4	GQ281781 <i>Herpetoreas burbrinki</i>																					
5	MW111464 <i>Herpetoreas platyceps</i>																					
6	MT571587 <i>Herpetoreas</i> cf. <i>sieboldii</i>																					
7	MT571586 <i>Herpetoreas pealii</i>																					
8	MN993850 <i>Herpetoreas xenura</i>																					
9	MN993852 <i>Herpetoreas xenura</i>																					
10	MN993851 <i>Herpetoreas xenura</i>																					
11	MN993891 <i>Herpetoreas xenura</i>																					
12	MW111476 <i>Herpetoreas tpser</i>																					
13	OM313293 <i>Herpetoreas tpser</i>																					
14	OM313292 <i>Herpetoreas tpser</i>																					
15	MK201567 <i>Herpetoreas tpser</i>																					
16	MK253674 <i>Hebius andreae</i>																					
17	OK315812 <i>Hebius annamensis</i>																					
18	KJ685671 <i>Hebius modestum</i>																					
19	KJ685684 <i>Hebius boulengeri</i>																					
20	KJ685700 <i>Hebius deschauenseei</i>																					
21	MH778702 <i>Hebius chapaensis</i>																					
22	MN788503 <i>Hebius khasiensis</i>																					
23	KJ685668 <i>Hebius khasiensis</i>																					
24	KJ685683 <i>Hebius</i> cf. <i>ruthveni</i>																					
25	OQ085073 <i>Hebius youjiangensis</i>																					
26	KJ685711 <i>Hebius clerki</i>																					
27	AF402905 <i>Hebius maximus</i>																					
28	KJ685687 <i>Hebius optatum</i>																					
29	MZ570490 <i>Hebius weixiensis</i>																					

**Appendix 4** (continued). Uncorrected p-distance estimated using Cytb gene sequence among the genera *Hebius* Thompson, 1913, *Herpetoreas* Günther, 1860, *Amphiesma* Duméril, Bibron & Duméril, 1854, and *Sahyadriophis* Patel, Thackeray, Campbell & Mirza, 2023, with *Amphiesmoides* Malnate, 1961 as outgroup.

No.	Species	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	
30	OK315813 <i>Hebius atemporalis</i>																					
31	KJ685673 <i>Hebius johannis</i>																					
32	OK315824 <i>Hebius terrakarenorum</i>																					
33	MZ570485 <i>Hebius septemlineatus</i>																					
34	AB989302 <i>Hebius vibakari</i>																					
35	KJ685678 <i>Hebius octolineatus</i>																					
36	KJ685682 <i>Hebius metusia</i>																					
37	KJ685688 <i>Hebius</i> sp.																					
38	MH532291 <i>Hebius yambianensis</i>	0.077																				
39	OK315816 <i>Hebius bitaeniatas</i>	0.154	0.154																			
40	KJ685689 <i>Hebius craspedogaster</i>	0.192	0.192	0.115																		
41	MK340763 <i>Hebius sangzhiensis</i>	0.038	0.115	0.115	0.154																	
42	OK315825 <i>Hebius groundwateri</i>	0.115	0.115	0.115	0.154	0.077	0.154															
43	KJ685670 <i>Hebius yenningsi</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038														
44	OR389974 <i>Hebius yenningsi</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038	0.000													
45	OR389975 <i>Hebius yenningsi</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038	0.000	0.231												
46	KJ685701 <i>Hebius sauteri</i>	0.115	0.038	0.192	0.231	0.154	0.154	0.077	0.115	0.115	0.192											
47	AB989296 <i>Hebius ishigakiensis</i>	0.115	0.038	0.192	0.231	0.154	0.154	0.154	0.115	0.115	0.192	0.077										
48	KJ685692 <i>Hebius popei</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038	0.000	0.000	0.231	0.115	0.115									
49	KJ685679 <i>Hebius taronensis</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038	0.000	0.000	0.231	0.115	0.115	0.000								
50	OK315829 <i>Hebius nigriventer</i>	0.154	0.154	0.154	0.192	0.115	0.192	0.038	0.000	0.000	0.231	0.115	0.115	0.000								
51	AB989268 <i>Hebius concealarus</i>	0.192	0.115	0.192	0.154	0.154	0.192	0.154	0.115	0.115	0.269	0.154	0.077	0.115	0.115							
52	OK315821 <i>Hebius leucomystax</i>	0.308	0.308	0.154	0.269	0.269	0.308	0.269	0.308	0.308	0.231	0.346	0.346	0.308	0.308	0.346						
53	AB989102 <i>Hebius pryeri</i>	0.231	0.154	0.154	0.269	0.192	0.269	0.154	0.115	0.115	0.231	0.154	0.115	0.115	0.115	0.115	0.308					
54	KJ685694 <i>Amphiesma stollatum</i>	0.269	0.192	0.308	0.231	0.269	0.192	0.269	0.231	0.231	0.269	0.231	0.154	0.231	0.231	0.154	0.385	0.231				
55	OK315803 <i>Amphiesma monticola</i>	0.231	0.308	0.308	0.269	0.231	0.269	0.231	0.269	0.269	0.385	0.269	0.346	0.269	0.346	0.308	0.385	0.385	0.308			
56	OK315814 <i>Sahyadriophis beddomei</i>	0.308	0.385	0.423	0.462	0.308	0.385	0.308	0.346	0.346	0.385	0.346	0.423	0.346	0.346	0.462	0.423	0.462	0.423	0.308		
57	OK326949 <i>Amphiesmoides ornaticeps</i>	0.462	0.462	0.538	0.577	0.500	0.462	0.500	0.462	0.462	0.538	0.500	0.423	0.462	0.462	0.500	0.577	0.538	0.500	0.577	0.538	



**Appendix 5** (continued on next four pages). Literature used for the revised distribution of *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890).

No.	Species	Number in map	Verified by molecular	Verified by morphology	Location	Sources
1	<i>Herpetoreas davidi</i> sp. nov.	1	yes	yes	Daung Stream, Rakhine Yoma Elephant Sanctuary, Rakhine, Myanmar (type locality)	our data
2	<i>Herpetoreas davidi</i> sp. nov.	2	no	yes	Kyat Stream, Rakhine Yoma Elephant Sanctuary, Rakhine, Myanmar	our data
3	<i>Herpetoreas xenura</i>	1	no	yes	Cherrapunji, East Khasi Hills, Meghalaya, India (type locality)	Wall 1907; Ren <i>et al.</i> 2022
4	<i>Herpetoreas xenura</i>	2	no	yes	Tura, West Garo Hills, Meghalaya, India	Mathew 1995; Ren <i>et al.</i> 2022
5	<i>Herpetoreas xenura</i>	3	no	yes	Umroi, Meghalaya, India	Muansanga <i>et al.</i> 2021
6	<i>Herpetoreas xenura</i>	4	no	yes	Narpuh RF, Jaintia Hills, Meghalaya, India	Mathew & Meetei 2004; Ren <i>et al.</i> 2022
7	<i>Herpetoreas xenura</i>	5	yes	no	Menam Mikir Punjee, Assam, India	Lalronunga <i>et al.</i> 2020
8	<i>Herpetoreas xenura</i>	6	no	yes	Kohima, Nagaland, India	Romer 1945; NHMUK 1956.1.12.79
9	<i>Herpetoreas xenura</i>	7	no	yes	Naga Hills, Nagaland, India	Romer 1945; Ren <i>et al.</i> 2022
10	<i>Herpetoreas xenura</i>	8	no	yes	North Hlimes, Kolasib Dist., Mizoram, India	Muansanga <i>et al.</i> 2021
11	<i>Herpetoreas xenura</i>	9	no	yes	Sihphir, Aizawl Dist., Mizoram, India	Muansanga <i>et al.</i> 2021
12	<i>Herpetoreas xenura</i>	10	no	yes	Reiek Community Reserved Forest, Mamit, Mizoram, India	Hmar <i>et al.</i> 2020
13	<i>Herpetoreas xenura</i>	11	no	yes	Dampa Tiger Reserve, Mamit Dist., Mizoram, India	Malsawmdawngliana <i>et al.</i> 2022
14	<i>Herpetoreas xenura</i>	12	no	yes	Pala Lake Area, Mizoram, India	Pawar & Birand 2001; Ren <i>et al.</i> 2022
15	<i>Herpetoreas xenura</i>	13	no	yes	Tripura, India	Samuel Lalronunga unpubl. data
16	<i>Herpetoreas xenura</i>	14	no	yes	Kaptai NP, Rangamati, Bangladesh	Reza 2010; Ren <i>et al.</i> 2022
17	<i>Herpetoreas xenura</i>	15	no	yes	Bandarban, Koekradong, Bangladesh	Ahsan <i>et al.</i> 2009; Ren <i>et al.</i> 2022

**Appendix 5** (continued). Literature used for the revised distribution of *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890).

No.	Species	Number in map	Verified by molecular	Verified by morphology	Location	Sources
18	<i>Herpetoreas xenura</i>	16	no	yes	Bilkhawthlir, Kolasib Dist., Mizoram, India	our data
19	<i>Herpetoreas xenura</i>	17	no	yes	Sawlung, Aizawl Dist., Mizoram, India	our data
20	<i>Herpetoreas xenura</i>	18	no	yes	Kawnpui, Kolasib Dist., Mizoram, India	our data
21	<i>Herpetoreas xenura</i>	19	no	yes	Dampa Tiger Reserve, Mamit Dist., Mizoram, India	our data
22	<i>Herpetoreas xenura</i>	20	no	yes	Tamdil national Wetland, Saitual Dist., Mizoram, India	our data
23	<i>Herpetoreas xenura</i>	21	no	yes	Saitual, Saitual Dist., Mizoram, India	our data
24	<i>Herpetoreas xenura</i>	22	no	yes	Hmuifang Community Reserved Forest, Aizawl Dist., Mizoram, India	our data
25	<i>Herpetoreas xenura</i>	23	no	yes	Thenzawl, Serchhip Dist., Mizoram, India	our data
26	<i>Herpetoreas xenura</i>	24	no	yes	Lunglei, Lunglei Dist., Mizoram, India	our data
27	<i>Herpetoreas xenura</i>	Not shown	no	yes	Mizoram University Campus, Aizawl Dist., Mizoram, India	our data
28	<i>Herpetoreas xenura</i>	Not shown	no	yes	Luangmual, Aizawl Dist., Mizoram, India	our data
29	<i>Herpetoreas xenura</i>	Not shown	no	yes	Durtlang, Aizawl Dist., Mizoram, India	our data
30	<i>Herpetoreas xenura</i>	Not shown	no	yes	Chandmari West, Aizawl Dist., Mizoram, India	our data
31	<i>Herpetoreas xenura</i>	Not shown	no	yes	Ramrikawn, Aizawl Dist., Mizoram, India	our data
32	<i>Herpetoreas xenura</i>	Not shown	no	yes	Tanhri, Aizawl Dist., Mizoram, India	our data
33	<i>Herpetoreas xenura</i>	Not shown	no	yes	Sihhmui, Aizawl Dist., Mizoram, India	our data

**Appendix 5** (continued). Literature used for the revised distribution of *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890).

No.	Species	Number in map	Verified by molecular	Verified by morphology	Location	Sources
34	<i>Herpetoreas xenura</i>	Not shown	no	yes	Mission venghlang, Aizawl Dist., Mizoram, India	our data
35	<i>Herpetoreas xenura</i>	Not shown	no	yes	Tuirial, Aizawl Dist., Mizoram, India	our data
36	<i>Herpetoreas xenura</i>	Not shown	no	yes	Seling, Aizawl Dist., Mizoram, India	our data
37	<i>Herpetoreas xenura</i>	Not shown	no	yes	College veng, Aizawl Dist., Mizoram, India	our data
38	<i>Hebius khasiensis</i>	1	no	yes	Khasi Hills, Meghalaya, India (type locality)	David <i>et al.</i> 2013; our data
39	<i>Hebius khasiensis</i>	2	no	yes	Dibang, Arunachal Pradesh, India	David <i>et al.</i> 2013; our data
40	<i>Hebius khasiensis</i>	3	no	yes	Namdapha Tiger Reserve, Changlang, Arunachal Pradesh	<a href="https://www.inaturalist.org/observations/29628011">https://www.inaturalist.org/observations/29628011</a>
41	<i>Hebius khasiensis</i>	4	no	yes	Changlang, Arunachal Pradesh, India	David <i>et al.</i> 2013; our data
42	<i>Hebius khasiensis</i>	5	no	yes	Zunheboto, Nagaland, India	David <i>et al.</i> 2013; our data
43	<i>Hebius khasiensis</i>	6	no	yes	Kohima, Nagaland, India	David <i>et al.</i> 2013; our data
44	<i>Hebius khasiensis</i>	7	no	yes	Reiek Community RF, Mizoram, India	Hmar <i>et al.</i> 2020
45	<i>Hebius khasiensis</i>	8	no	yes	Dampa Tiger Reserve, Mizoram, India	Malsawmdawngliana <i>et al.</i> 2022
46	<i>Hebius khasiensis</i>	9	yes	yes	Putao, Kachin, Myanmar	David <i>et al.</i> 2013; our data
47	<i>Hebius khasiensis</i>	10	no	yes	Hutung, Bhamo, Kachin, Myanmar (type locality of <i>Natrix gilhodes</i> )	David <i>et al.</i> 2013; our data
48	<i>Hebius khasiensis</i>	11	no	yes	Bhamo, Kachin, Myanmar	<a href="https://www.inaturalist.org/observations/119392371">https://www.inaturalist.org/observations/119392371</a>
49	<i>Hebius khasiensis</i>	12	no	yes	Nat Ma Taung, Chin, Myanmar	David <i>et al.</i> 2013; our data
50	<i>Hebius khasiensis</i>	13	no	yes	Mindat, Chin, Myanmar	<a href="https://www.inaturalist.org/observations/144728979">https://www.inaturalist.org/observations/144728979</a>
51	<i>Hebius khasiensis</i>	14	no	yes	Karen Hills, Shan, Myanmar	David <i>et al.</i> 2013; our data

**Appendix 5** (continued). Literature used for the revised distribution of *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890).

No.	Species	Number in map	Verified by molecular	Verified by morphology	Location	Sources
52	<i>Hebius khasiensis</i>	15	no	yes	Medog, Nyingchi, Tibet, China	David <i>et al.</i> 2013; Che <i>et al.</i> 2020
53	<i>Hebius khasiensis</i>	16	no	yes	Htamanthi WS., Sagaing, Myanmar	our data
54	<i>Hebius khasiensis</i>	17	yes	yes	Yingjiang, Yunnan, China	Yang & Rao 2008; Wu <i>et al.</i> 2023
55	<i>Hebius khasiensis</i>	18	no	yes	Ruili, Dehong, Yunnan, China	David <i>et al.</i> 2013; our data
56	<i>Hebius khasiensis</i>	19	no	yes	Longling, Baoshan, Yunnan, China	Yang & Rao 2008
57	<i>Hebius khasiensis</i>	20	no	yes	Menglian, Puer, Yunnan, China	Yang & Rao 2008
58	<i>Hebius khasiensis</i>	21	no	yes	Xichuangbanna, Yunnan, China	David <i>et al.</i> 2013; our data
59	<i>Hebius khasiensis</i>	22	no	yes	Boun Tay, Phongsaly, Laos	David <i>et al.</i> 2013; our data
60	<i>Hebius khasiensis</i>	23	no	yes	Doi Tung Mt., Chiang Rai, Thailand	<a href="https://www.inaturalist.org/observations/128635317">https://www.inaturalist.org/observations/128635317</a>
61	<i>Hebius khasiensis</i>	24	no	yes	Doi Luang NP, Chiang Rai, Thailand	<a href="https://www.inaturalist.org/observations/86044420">https://www.inaturalist.org/observations/86044420</a>
62	<i>Hebius khasiensis</i>	25	no	yes	Chae Son NP, Lampang, Thailand	Chan-ard <i>et al.</i> 2015
63	<i>Hebius khasiensis</i>	26	no	yes	Doi Phu Kha NP, Nan, Thailand	<a href="https://www.inaturalist.org/observations/165474307">https://www.inaturalist.org/observations/165474307</a>
64	<i>Hebius khasiensis</i>	27	no	yes	Doi Suthep-Pui NP, Chiang Mai, Thailand	Chan-ard <i>et al.</i> 2015
65	<i>Hebius khasiensis</i>	28	no	yes	Doi Inthanon NP, Chiang Mai, Thailand	our data; <a href="https://www.inaturalist.org/observations/123678122">https://www.inaturalist.org/observations/123678122</a>
66	<i>Hebius khasiensis</i>	29	no	yes	Mae Tho NP, Chiang Mai, Thailand	Chan-ard <i>et al.</i> 2015; our data
67	<i>Hebius khasiensis</i>	30	no	yes	Huai Nam Dang NP, Mae Hong Son, Thailand	Chan-ard <i>et al.</i> 2015; our data
68	<i>Hebius khasiensis</i>	31	no	yes	Lan Sang NP, Tak, Thailand	Chan-ard <i>et al.</i> 2015; our data
69	<i>Hebius khasiensis</i>	32	no	yes	Namtok Pha Charoen NP, Tak, Thailand	Chan-ard <i>et al.</i> 2015; our data
70	<i>Hebius khasiensis</i>	33	no	yes	Khlong Wang Chao NP, Kamphaeng Phet, Thailand	Chan-ard <i>et al.</i> 2015; our data



**Appendix 5** (continued). Literature used for the revised distribution of *Herpetoreas davidi* sp. nov., *H. xenura* (Wall, 1907), and *Hebius khasiensis* (Boulenger, 1890).

No.	Species	Number in map	Verified by molecular	Verified by morphology	Location	Sources
71	<i>Hebius khasiensis</i>	34	no	yes	Umphang WS, Tak, Thailand	David <i>et al.</i> 2013; our data
72	<i>Hebius khasiensis</i>	35	no	yes	Phu Suan Sai NP, Loei, Thailand	<a href="https://www.inaturalist.org/observations/53232442">https://www.inaturalist.org/observations/53232442</a>
73	<i>Hebius khasiensis</i>	36	no	yes	Phu Luang WS, Loei, Thailand	our data; <a href="https://www.inaturalist.org/observations/105954833">https://www.inaturalist.org/observations/105954833</a>
74	<i>Hebius khasiensis</i>	37	no	yes	Phu Suan Sai NP, Loei, Thailand	<a href="https://www.inaturalist.org/observations/53232442">https://www.inaturalist.org/observations/53232442</a>
75	<i>Hebius khasiensis</i>	38	no	yes	Nam Nao NP, Phetchabun, Thailand	<a href="https://www.inaturalist.org/observations/37859050">https://www.inaturalist.org/observations/37859050</a>