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Lost and found: rediscovery and systematics of the Northeast Indian snake *Hebius pealii* (Sclater, 1891)

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Abstract

We report the rediscovery of the keelback snake *Hebius pealii* after 129 years from Arunachal Pradesh in Northeast India. We designate a lectotype for the species, and provide the first description of a female, of colour in life, and aspects of its natural history. Multilocus phylogenetic analyses of two mitochondrial (1071 bp *cytb*, 508 bp *16s*) and two nuclear (560 bp *bdnf*, 579 bp *cmos*) genes provides strong evidence for *Hebius pealii* being nested within the genus *Herpetoreas* instead of *Hebius*. We transfer this species to the genus *Herpetoreas*.

Key words

Eastern Himalaya, *Herpetoreas*, *Herpetoreas platyceps*, Natricinae, phylogeny, snakes.

Introduction

The natricine colubrid snake genus *Hebius* Thompson, 1913 is widespread across South Asia, mainland Southeast Asia and Sundaland (Guo *et al.,* 2014). It is one of the most speciose genera in the subfamily Natricinae, and 10 of the 44 currently recognised species (Uetz *et al.,* 2020) in this genus occur in India (Das & Das, 2017). Guo *et al*. (2014) reclassified the then widespread genus *Amphiesma* Duméril, Bibron, and Duméril, 1854 into three monophyletic genera, namely: *Hebius*, *Amphiesma* and *Herpetoreas* Günther, 1860. Guo *et al*. (2014) and most subsequent studies of natricine classification have mostly relied on molecular phylogenetic data to ascertain systematic relationships. In recent years taxon sampling for natricines in molecular phylogenetic studies has increased notably (Giri *et al.,* 2017, 2019; Lalronunga *et al.,* 2020, Takeuchi *et al.,* 2018, Zaher *et al.,* 2019).

Hebius pealii was first described by Sclater (1891a) as *Tropidonotus pealii* based on two male specimens collected by Samuel Edward Peal (1834–1897), a tea planter based in the upper Assam district of Sibsagar in erstwhile British India (Fig. 1). Of these two type specimens, one was kept in the Zoological Survey of India, Kolkata (ZSIK 4034) and the other in the Natural History Museum, London (BMNH 1946.1.13.43). This species has never been reported since then, either in the field or from additional voucher specimens (Smith 1943, Wallach *et al*. 2014, Whitaker & Captain, 2006). Between the time of Sclater's (1891a) description and Guo *et al*.'*s* (2014) study, *H. pealii* was classified in various natricine genera including *Amphiesma* (Das 1996, Wallach *et al.,* 2014), *Natrix* (Wall 1923, Smith 1943), *Paranatrix* (Mahendra 1984), and *Tropidonotus* (Sclater 1891b, Boulenger 1893). Natricinae as used here (and by e.g., Uetz *et al.,* 2020) is equivalent to Natricidae of Zaher *et al*. (2019) and Burbrink *et al*. (2020).

Recently, the first author (AD) with a team of researchers retraced the steps of the century-old iconic Abor Expedition (Annandale 1912) to Arunachal Pradesh and found a specimen of a keelback that we identified as *Hebius pealii* based on morphological comparison. In this paper we provide a detailed morphological comparison of this new material with the type specimens and provide

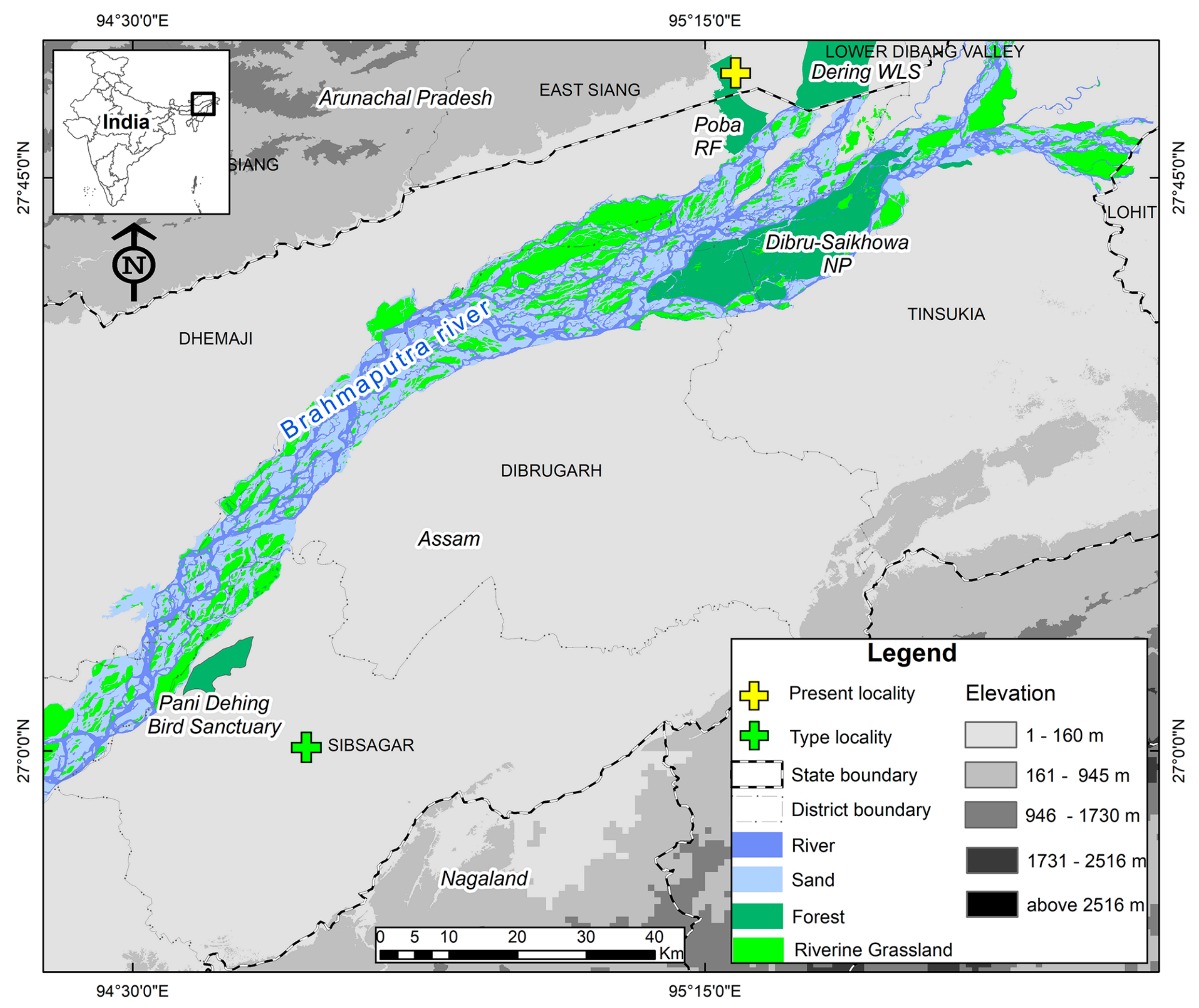

Fig. 1. Map of Upper Assam region showing type and newly reported (present) locality of *Herpetoreas pealii* in the upper Brahmaputra valley.

new data on the systematic relationships of *H. pealii* with other natricine snakes, as well as reporting new natural history observations of this poorly known snake.

Materials and Methods

Molecular systematics

Genomic DNA was extracted from liver tissue samples stored in absolute ethanol at –20°C, using the DNeasy (Qiagen™) blood and tissue kit. We generated DNA sequence data for one *Hebius pealii* from Poba Reserve Forest, Arunachal Pradesh, India (27°52′09.8″N 95°17′24.4″E, ca.123 m ASL elevation) and one *Herpetoreas* cf. *platyceps* from Chamoli District, Uttarakhand, India (30°28′04.8″N 79°20′21.8″E, ca. 3056 m ASL elevation). We amplified partial sequences of two nuclear (nu) and two mitochondrial (mt) genes. The mtDNA genes that were amplified are 16S rRNA (*16s*) and cytochrome b (*cytb*), and the nuDNA genes are oocyte maturation factor (*cmos*) and brain-derived neurotrophic factor (*bdnf*). See Table 1 in Deepak *et al.* (2020) for primer details. PCR amplifications were carried out in a S1000™ Thermal Cycler (Bio-Rad, USA). Amplified PCR products were run on a 2% agarose gel and viewed under an Essential V4 (UVITEC Cambridge, UK) gel documentation system. PCR products were Sanger sequenced in both directions at Medauxin Sequencing Services (Bangalore, India).

Contigs were assembled from bidirectional sequence chromatograms and edited in SNAPGENE Viewer (http://www.snapgene.com/products/snapgene_viewer). Protein-coding genes (*cytb*, *cmos* and *bdnf*) were checked for unexpected stop codons by translating nucleotide alignments to amino acids in MEGA7 (Kumar *et al.*, 2016). The new sequences generated in this study were concatenated with data for 118 other natricine snakes, most of which were used in Lalronunga *et al.*'*s* (2020) dataset, plus two sibynophiine snakes as an outgroup (Appendix 1). Sequences were aligned using clustalW in MEGA7 with default settings (Higgins *et al.*, 1994; Kumar *et al.*, 2016). A total of 2718 bp of concatenated dataset was used in this study, with alignments available online from

Table 1: Partitions and models of sequence evolution used in the Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses. In the second column, 1st, 2nd and 3rd refer to codon position.

Partitions	Sites	ML	BI
P1	*16s*, *cytb* 1st	GTR+G	GTR+I+G
P2	*bdnf* 1st, *bdnf* 2nd *cmos* 1st, *cmos* 2nd	GTR+G	K80+I
P3	*cmos* 3rd	GTR+G	HKY+G
P4	*cytb* 2nd	GTR+G	GTR+I+G
P5	*cytb* 3rd	GTR+G	GTR+G
P6	*bdnf* 3rd	GTR+G	K80+G

the Natural History Museum data portal (https://data.nhm.ac.uk/dataset/das_hebius_pealii). PARTITIONFINDER v2 (LANFEAR *et al.,* 2016) with default settings was used to find the best-fit partition scheme for the concatenated dataset and the best-fit model of sequence evolution for each partition. The best-fit scheme comprised six partitions, by gene and by codon position (Table 1).

Phylogenetic analyses were carried out using the CIPRES Science Gateway v3.3 platform (MILLER *et al.,* 2010). For Maximum Likelihood (ML) analysis carried out in RAXML version 1.8 (STAMATAKIS 2014) the data were partitioned by gene and codon as determined by PARTITIONFINDER. ML analysis in RAXML used the GTRGAMMA model of sequence evolution which is recommended over GTR+G+I because the 25 rate categories account for potentially invariant sites (STAMATAKIS 2006). Bayesian inference (BI) analysis was carried out using the program MRBAYES 3.2 (RONQUIST *et al.,* 2012), with default prior settings and with all six partitions assigned their optimum model as determined by PARTITIONFINDER (Table 1). Two separate runs were set up with four Markov chains each initiated from random trees and allowed to run for one million generations, sampling every 100 generations. Analyses were terminated when the standard deviation of split frequencies were less than 0.005, the first 25% of trees were discarded as "burn-in", and trees were constructed under 50% majority consensus rule. Support for internal branches in ML and BI trees was quantified using bootstrap (1000 replicates) and posterior probability, respectively.

Morphological analysis

We provide here morphological and meristic data from two specimens of *H. pealii*, the London type BMNH 1946.1.13.43 and the freshly collected specimen that was formalin fixed, washed and stored in ca. 70% ethanol (Appendix 2). The other type of *H. pealii* ZSIK 4034 is badly fragmented and unfit for external morphological comparisons. Given that *H. pealii* is poorly known and circumscribed, that we are in age of discovery of species-level diversity of Asian natricines, and that the systematics of Asian natricines is in a state of flux, designating a lectotype for *H. pealii* from the type series would help to provide stability. We here designate the best preserved of the types, BMNH 1946.1.13.43, as the lectotype of *Tropidonotus pealii* SCLATER, 1891a, thus rendering ZSIK 4034 as the only paralectotype. Catalogue numbers for voucher specimens bear the following prefixes: BMNH (The Natural History Museum, London, UK), ZSIK (Zoological Survey of India, Kolkata, India), WII-ADR (Wildlife Institute of India-Abhijit Das Reptile collection).

Total length, circumference, snout-vent length and tail length were measured with thread and a ruler to the nearest 1 mm. Other dimensions were recorded with dial callipers, to the nearest 0.1 mm. Bilateral scale counts separated by a comma are given in left, right order. Ventral scales were counted following DOWLING (1951a), and the scale reduction formulae compiled using a modified version of the method presented by DOWLING (1951b). Length and width of head scales were measured at the longest and the widest points of the respective scale(s). Eye diameter was measured horizontally.

Abbreviations. Snout-vent length (SVL), tail length (TaL), total length (TL), dorsal scale rows (DSR), ventrals (VEN), subcaudals (SC), supralabials (SL), infralabials (IL), head length from tip of snout to back of mandible (HL), maximum head width (HW).

Results

Molecular phylogeny

Both ML and BI phylogenetic analysis (Fig. 2a, b) recover *Hebius pealii* in a well-supported lineage along with *Herpetoreas* spp. *Hebius pealii* is sister to *Herpetoreas xenura* in both these analyses, though with poor support. The results are similar to those reported by GUO *et al*. (2014) and LALRONUNGA *et al*. (2020), in which the genera *Hebius*, *Amphiesma* and *Herpetoreas* are together paraphyletic but form three well-supported monophyletic lineages within the natricine tree. The newly sequenced individual of *Herpetoreas* cf. *platyceps* is sister to *H. platyceps* from Tibet, China. Given the consistency of the ML and BI phylogenetic results, and the high support for its position nested within species of *Herpetoreas*, we here transfer *Hebius pealii* to the genus *Herpetoreas*.

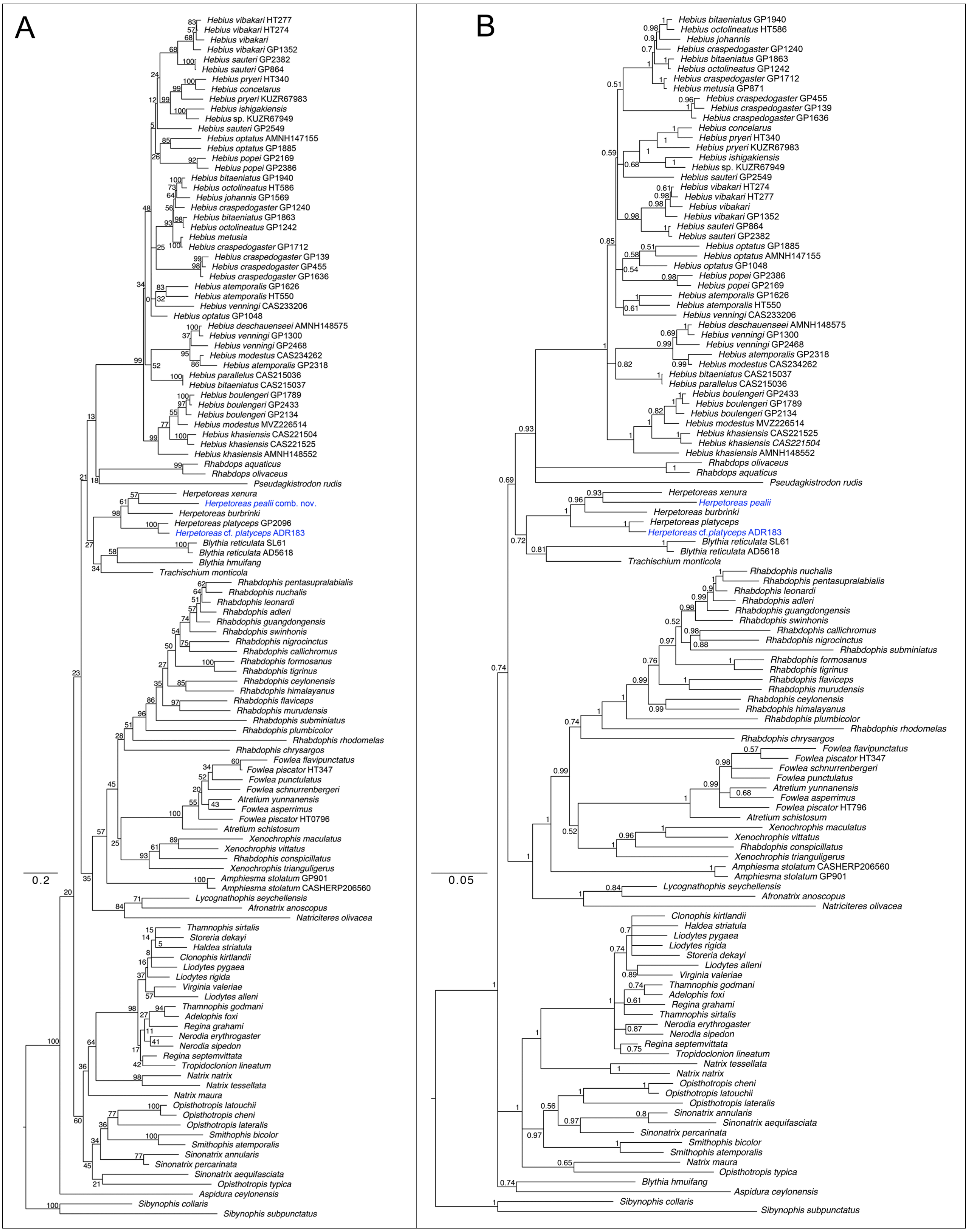

Fig. 2. Phylogenetic relationships of *Herpetoreas pealii*. A. ML phylogeny showing bootstrap support for internal branches. B. BI phylogeny showing posterior probability support values for internal branches. Individuals for which newly generated data are presented here highlighted in blue. Scale bar represents mean nucleotide substitutions per site.

Morphology

The new specimen of *Herpetoreas pealii* (WII-ADR547) collected from Arunachal Pradesh was accessioned into the WII biodiversity collection on 30 October 2018. This is the first record for Arunachal Pradesh State in India which is ca. 118 km northeast of the type locality in Sibsagar, Assam State (Fig. 1).

Systematics

Tropidonotus pealii – Sclater (1891a: 241); Sclater (1891b:41); Boulenger (1893: 214)

Natrix pealii – Wall (1923: 600)

Natrix peali [sic] – Smith (1943: 291)

Amphiesma peali [sic] – Malnate (1960: 50 & 52); Sharma (2007: 206 & 210)

Amphiesma pealii – Das *et al*. (1998:151); Das (2003: 473); Whitaker & Captain (2004: 25); Ahmed *et al*. (2009: 19); Das (2010: 42 &73); Purkayastha (2013: 59); Wallach *et al*. (2014: 32)

Hebius pealii – Das & Das (2017: 168); Das *et al*. (2019: 125); Purkayastha & David (2019: 86)

Herpetoreas pealii comb. nov.

(Figs. 3, 4, 5; Table 2)

Common name. Assam keelback (Uetz, 2020), Peal's Keelback (Whitaker & Captain, 2004; Das & Das, 2017), Bark Brown Keelback (Sharma, 2007)

Lectotype. (by present designation). BMNH 1946.1.13.43 adult male, from Sibsagar district (ca. 26°58′58.8″N 94°37′58.8″E), precise locality not known, Assam, India, collected by S. E Peal.

Paralectotype. ZSIK 4034, male (fide. Smith, 1943), Collection data as for lectotype.

Referred material. WII-ADR547, adult female, from Poba Reserved Forest (27°52′26.4″N 95°16′58.8″E, 147 m asl), Siang district, Arunachal Pradesh, India, collected by A. Das on 30 September 2018.

Diagnosis. A member of *Herpetoreas* that differs from other species of the genus in having fewer ventrals (136 and 142) than *H. sieboldii* (180), *H. platyceps* (174–217), *H. xenura* (158–165), and *H. burbrinki* (172). *Herpetoreas pealii* also has fewer subcaudals (69 and 77) than *H. platyceps* (86–107), *H. xenura* (82–105), and *H. burbrinki* (96). *Herpetoreas pealii* further differs from *H. platyceps* and *H. sieboldii*: in having nine (versus eight) supralabials and from *H. sieboldii* and *H. platyceps* in having laterally darkly blotched (verses immaculate) ventrals. *Herpetoreas pealii* differs from *H. xenura* in having paired (versus unpaired) subcaudals.

Description of female (WII-ADR547). We provide a detailed description of WII-ADR547 as the first description of a female *Herpetoreas pealii*. A comparison with the lectotype appears at the end of this section. See Table 2 for morphometric and meristic data. Good condition; ca. 15 mm longitudinal ventro-lateral incision on the body, ca. 180 mm from the tip of snout. Body generally oval in cross section (slightly wider than tall at midbody) with flattened venter and broadly rounded dorsum, widest at approximately midbody, tapering more posteriorly than anteriorly. Head broader than tall, notably wider than anterior of body. In dorsal view head ovate, sides convex, gently converging anteriorly. Front of snout not pointed, truncated. In lateral view top of head flat from back to just anterior of eye, sloping down gently anterior to this. Paired shields on top of head abutting along midline rather than overlapping.

In dorsal view rostral approximately three times broader than long, substantially shorter than distance between it and frontal; projects beyond tip of lower jaw; ventrally with transverse concavity, notched (C-shaped) at margin of mouth. Frontal hexagonal, lateral edges slightly diverging anteriorly; shorter and smaller than each parietal, longer than distance between it and snout tip. Prefrontals longer and broader than internasals. Each nasal divided into wider anterior and higher posterior parts, anterior parts are subquadrangular and posterior parts are subpentagonal. Quadrangular loreal (longer ventral than dorsal margin) smaller in size than anterior and posterior nasals on both sides. Single supraocular and preocular on each side, supraocular slightly larger than preocular, much longer than wide. Three postoculars on each side, uppermost largest, smaller than supraocular and preocular.

Subcircular external naris in front of a flap on lateral-facing surface, between anterior and posterior nasals, slightly closer to upper than lower edges. External naris more clearly visible anteriorly than dorsally.

Nine supralabials (SLs) on each side; SL 7 & 8 largest. SL 1 contacts rostral and anterior and posterior nasals on the right and only anterior nasal on the left. SL 2 contacts posterior nasal and loreal, SL 3 contacts loreal and preocular, SL 4 contacts eye and preocular, SLs 4–5 contact eye, SL 5 contacts eye and postocular, SL 6 contacts postocular, SL 7 contacts postocular and first lower temporal, SL 8 contacts first and second lower temporals, SL 9 contacts second lower temporals. Two lower and two upper temporals on each side; between the two lower temporals anterior one longer than high and posterior one subquadrangular in shape. Between the upper temporals, anterior one smaller than the posterior. Both upper temporals are longer than higH.

Eye lateral; pupil circular; longitudinal diameter slightly shorter than distance between eye and nostril. Parietals longer than wide; midline interparietal suture a little more than two thirds length of each parietal; frontal roughly two thirds the size of parietals; each parietal contacts frontal, supraocular, upper postocular, two upper temporals, plus three other scales. Posterior margin of each parietal spatula shaped.

Mental subtriangular, wider than long. Infralabials 10,10; first pair in midline contact; ninth pair smallest; fifth and sixth largest. Two pairs of genials; second pair largest, longer than broad, both anterior and posterior pair in long midline contact; Anterior genials contact infralabials (ILs) 1–5; posterior genials contact ILs 5–6. Anteriormost ventral separated from each posterior genial by two scales on the right and one scale on the left, separated from each posterior most infralabial by five scales. Teeth largely obscured by gingivae, but estimated as 12 or 13 marginals on each side of upper jaw.

All except the first row of body dorsal scales strongly, singly keeled. First row unkeeled at midbody, but feebly keeled towards posterior of body and tail. No apical

Fig. 3. First photographs in life of *Herpetoreas pealii* (WII-ADR547). **A**: animal in its natural habitat (photo by Dhritiman Mukherjee) and **B**: full body profile (photo by Abhijit Das).

pits. Middorsal scales not different from adjacent dorsal scale row. Exposed parts of dorsal body scales generally evenly sized on dorsum and along body except for those involved in dorsal scale row reductions. Dorsal scales closer to vent slightly smaller than at midbody; those at anterior of body smallest. Dorsal scale rows (DSR) 21 at level of first ventral, 19 by 6th ventral maintained until 79th ventral, loss of 4th row of dorsal scales at 80–81st ventral reducing to 17 DSR from 82nd maintained to the vent.

Two preventrals. Anal single, overlaps 3 small and 2 large scales on either side excluding anteriormost subcaudal. Tail base subtriangular in cross section, flattened ventrally. Subcaudals divided throughout except the first two that are undivided, terminal scale (scute) conical, longer than wide, pointed tip.

Bicoloured, dark brown above (with paler and darker spots), pale midventrally. On dorsum whitish spots (each generally on two dorsal scales) start from back of

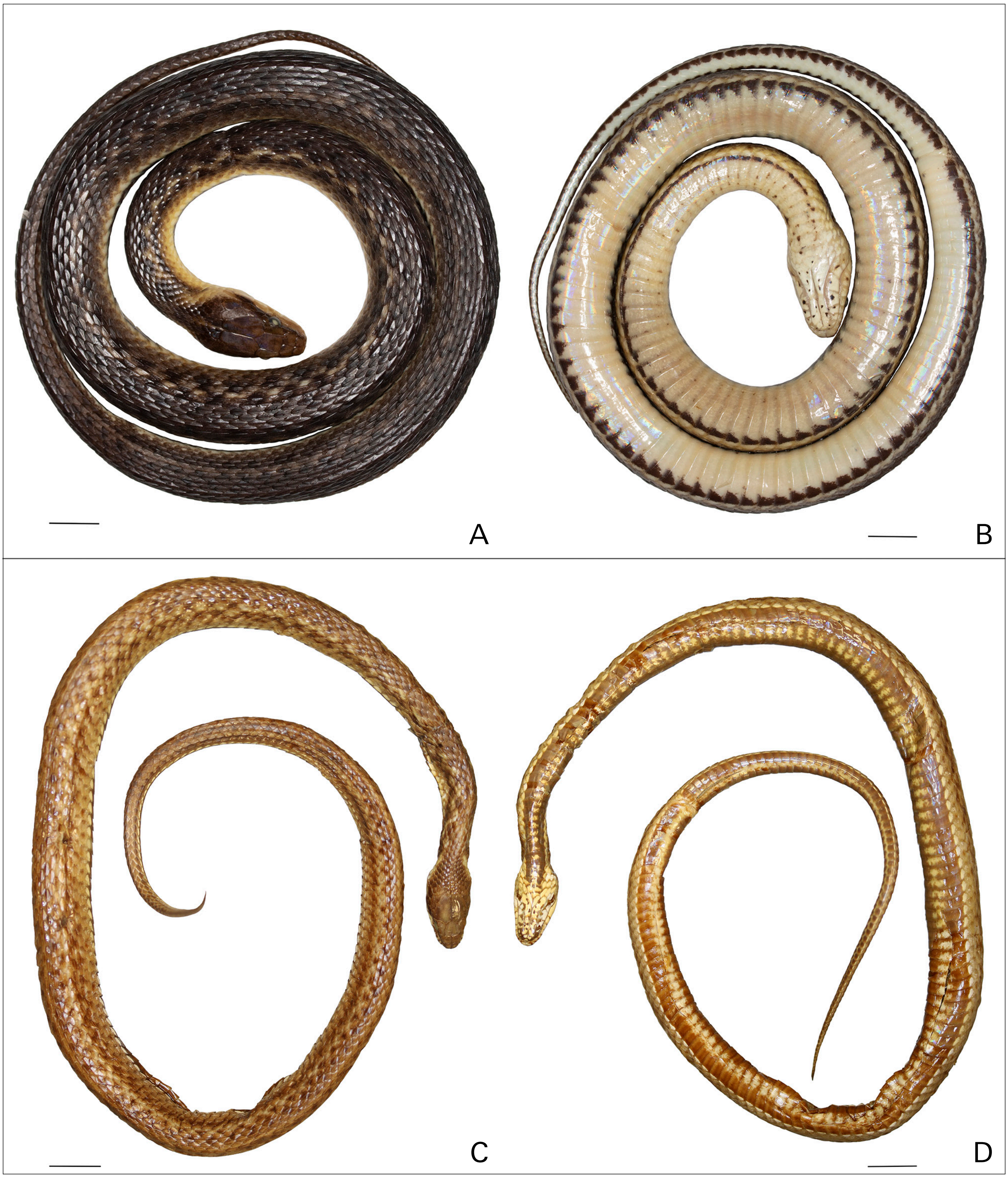

Fig. 4. Preserved specimens of *Herpetoreas pealii.* **A**: dorsal and **B**: ventral view of WII-ADR547 recently collected from Poba RF, Arunachal Pradesh, India, **C**: dorsal and **D**: ventral view of the lectotype BMNH 1946.1.13.43 from Sibsagar, Assam, India. Scale bar = 10 mm.

head and form two approximately symmetrical lines of spots that continue to end of body; placed on the 4th and 5th dorsal scale rows. Darker brown roundish spots on dorsum along the two sides of each pale spot often on 3–4 scales in an alternating, checkered pattern, placed on the 3rd and 4th dorsal scale rows below and on the 7th and 8th dorsal scale rows above. These darker spots are more prominent anteriorly and are reduced to dark lines from midbody to tail. Additional, less prominent darker spots occur on two or three scales on the dorsum above the upper row of darker spots, all forming checkered pattern on the dorsum. Tongue dark brown with pale tip.

Ventrals mostly pale with regular patches of brown, forming spots toward each lateral edge that are connected to form a continuous ventrolateral line. Small dark brown spots or speckles on the anterior to mid ventrals. Anals resemble ventrals, pale.

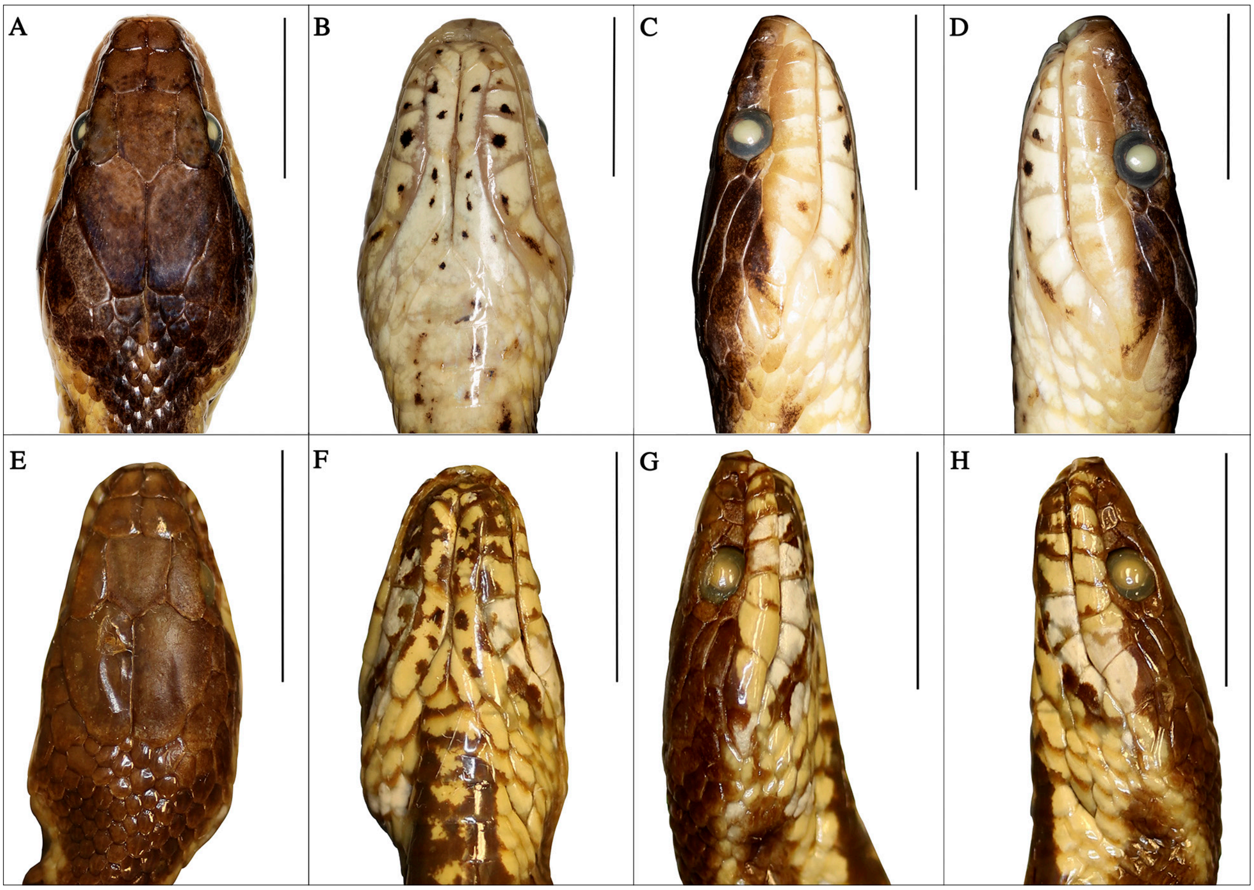

Fig. 5. Preserved specimens of *Herpetoreas pealii* showing head. **A**: dorsal, **B**: ventral, **C**: right lateral and **D**: left lateral views of WII-ADR547 recently collected from Poba RF, Arunachal Pradesh, India and **E**: dorsal, **F**: ventral, **G**: right lateral and **H**: left lateral views of the syntype BMNH 1946.1.13.43 from Sibsagar, Assam, India. Scale bar = 10 mm.

Head uniformly dark brown dorsally, paler than body dorsum with regular, fine, dark mottling. Dark of body dorsum extends onto upper lateral surface of head, loreal and preocular have equal proportion of pale and dark coloration; SLs mostly pale (as venter of body) with pale brown mottling, one dark spot on the seventh right SL. Postocular and temporals more darkly mottled than other lateral head scales, this dark mottling extends onto the SL 8 on either side as a short streak.

Underside of head generally pale, same colour as underside of body. Mental with two dark brown spots on anterolateral margins; one dark spot of varying size and shape on all ILs. Genials and preventrals mostly pale with isolated, small, irregular brown spots. Inside of mouth pale.

Comparison with the lectotype. The heads of the male lectotype BMNH 1946.1.13.43 and the new female WII-ADR547 specimen are illustrated in Figs. 4, 5. See Table 2 for variation in meristic and morphometric features. The lectotype is generally in good condition, with the following exceptions: the left parietal scale is slightly damaged, there are two distinct tag marks almost two head lengths behind the head on the dorsum, and two ventral longitudinal incisions on the body; the first starts from 31st ventral and the second starts from 75th ventral and ends six scales anterior to the anal scale. There is also a ventral incision on the anterior of the tail. The lectotype is somewhat fragile, a little distorted and soft at midbody and posteriorly.

The new specimen matches the lectotype with the following exceptions. In WII-ADR547 the frontal, prefrontal, internasal and supralabial scales are paler and there are fewer and smaller dark spots on the ILs and chin shields. On the body of WII-ADR547, a chain of paler scales gives rise to a dorsolateral series of paler spots that are contrasted with black spots most prominently anteriorly. These spots are barely visible anteriorly in BMNH 1946.1.13.43, though the dorsolateral lines are visible posteriorly. Laterally, WII-ADR547 is yellowish and this colouration runs at least two scale rows wide up to the level of the vent. The most prominent difference between the two specimens is their ventral colouration. The ventrals and subcaudals of BMNH 1946.1.13.43 are heavily spotted with brown except for a narrow midventral portion, whereas in WII-ADR547 the dark mottling is restricted to the far lateral edges of each ventral and subcaudal scale.

Habitat and natural history. On 30 September 2018, AD and colleagues surveyed Poba Reserve Forest, at the interstate boundary of Assam and Arunachal Pradesh states (elevation 120 m ASL). This forest is character-

Table 2: Morphometric and meristic characters of the two intact specimens of *Herpetoreas pealii*. * indicates lectotype. Bilateral scales given in right, left order

Voucher No	BMNH 1946.1.13.43*	WII-ADR547
Sex	Male	Female
DSR	19:19:17	19:19:17
Preventrals	3	2
Ventrals	142	136
Subcaudals	77	69
Anals	1	1
SLs	9,9	9,9
ILs	10,10	10,10
SLs contacting eye	4–5,4–5	4–5,4–5
ILs contacting anterior genial	1–5,1–5	1–5,1–5
IL contacting posterior genial	5–7,5–6	5–7,5–7
Preoculars	1,1	1,1
Postoculars	3,3	3,3
Temporals	2+2, 2+2	2+2, 2+2
SVL	334	511
TaL	117	150
HL	15.5	22.4
Head width	7.3	11.9
Head height	5.2	8.9
Eye to snout	4.1	6.1
Eye to nostril	2.7	3.7
Eye diameter	2.5	3.3
Parietal length	6.3	9.2
Frontal length	3.8	5.9
Prefrontal length	1.9	2.8
Internasal length	1.4	2.0
Body width immediately behind head	19	27
Body width midbody	30	43
Body width at last ventral	19	31
Midbody ventral scale width	9.5	12.7
Dorsal scales	keeled	keeled

Table 3: Comparison of select morphological characters of species in the genus *Herpetoreas*.

	H. sieboldii	*H. platyceps*	*H. xenura*	*H. burbrinki*	*H. pealii*
Maxillary teeth	17–21+2 with a diastema, last two enlarged	18–22 in continuous series, last 16 enlarged	22–23 gradually enlarged posteriorly. Last two teeth (large) after a small gap but without diastema	Not available	13–21 gradually enlarged posteriorly. Last two teeth after a small gap but without diastema
Hemipenes	Sulcus single, extends to tip, bilobate at tip	Sulcus single, extends to tip, single lobed rarely bilobate	Sulcus single, hemipenis bilobate at tip	Not available	Sulcus is single, bilobate
Source	Malnate (1966)	Malnate (1966)	This study	Guo *et al*. (2014)	Malnate (1960; this study)

ised by its flat terrain and numerous, small, slow-moving perennial streams and rivulets. Patches of habitat are more or less permanently waterlogged and marshy, supporting plants including *Lasia spinosa* and species of *Musa*, *Alpinia*, and *Tacca*. The forest has a three storied appearance with the > 30 m canopy composed of plant species including *Terminalia myriocarpa*, *Anthocephalus kadamba*, *Stereospermum* sp. and *Castanopsis* sp. Lianas and scandent shrubs contribute significantly to the structural and compositional diversity of this forest.

The *Herpetoreas pealii* individual was encountered while following one of the muddy bottomed streams in the forest interior, at around 10:30 H. It displayed a flight response comprised of multiple lashing movements 3–3.5 m in front of the field team, making the shallow water murky. After waiting for ca. 2 minutes the water cleared and part of the snake's distinctive black marked, pale belly coil was spotted under submerged leaflitter. When captured, the snake produced a typical natricine anal gland secretion odour but never attempted to bite while handling or during photography.

Conservation status. Poba Reserve Forest is one of the last remaining patches of low elevation tropical wet forest in the upper Brahmaputra valley but it has the lowest available protection status. The structure and composition of forests in this area have been highly modified as a result of past logging events and other forms of extraction (Page 2019), and Poba Reserve Forest is fragmented by a National highway and a village road. During two days of post monsoon fieldwork in September 2018, slow loris (*Nycticebus bengalensis*) and at least 20 herpetofaunal species were also seen, perhaps signifying that better protection measures are required for this area. We strongly encourage additional faunal and floral surveys.

The newly reported locality for *H. pealii* is to the North of the Brahmaputra, and the only other known, type locality is to the South (Fig. 1) of this major river. The type locality "Sibsagar" is a district headquarter within Assam State and has been developed into a city since the type specimens of *H. pealii* were collected. In addition, the majority of the surrounding areas are under tea plantation and agriculture, and it is unknown whether *H. pealii* remains extant here in some small remnant forest patches. Pani Dihing Wildlife Sanctuary (Fig. 1: area ca. 33 km^2) is perhaps the closest area of remaining natural habitat, and so might be a priority target for discovery of extant populations of *H. pealii* South of the Brahmaputra.

Although the new specimen reported here is clearly referable to *H. pealii*, the lectotype has more pronounced dark markings on the venter (though the two specimens are of different sex), and the Brahmaputra River is a known major biogeographic barrier (Pawar *et al.,* 2007), such that an assessment of intraspecific genetic variation would help to ascertain whether extant populations either side can be treated as a single conservation management unit. Although it is of obvious concern that an extant population of *H. pealii* is known only from one disturbed forest, there is likely insufficient information to categorise the species beyond Data Deficient based on criteria for the Red List of Threatened Species (IUCN Standards and Petitions Committee 2019).

Discussion

With the transfer of *Hebius pealii* into the genus *Herpetoreas*, now there are 43 nominal species of *Hebius* globally, with nine species occurring in India. *Hebius* still remains one the most species rich genera of natricine snakes, including almost 17% of the subfamily's species diversity. However, it might be noted that many species currently classified in *Hebius* have yet to be sampled in phylogenetic studies. Additionally, although the type species of *Hebius* (*H. vibakari*) has been sampled in molecular phylogenetic studies, there are no DNA sequence data yet available for the type species of *Herpetoreas*, *H. sieboldii*. There is limited information available on the dental and hemipenial anatomy of some species of this genus (see Table 3) though none for *H. burbrinki*. Thus, further genus-level changes to the classification of Asian natricines might be required. The genus name *Hebius* established by Thompson (1913) is assumed to be masculine, given its "-us" ending (e.g. Winston, 1999). Therefore, some of the species that have been transferred into this genus require name changes as follows: *Hebius atemporalis*, *H. bitaeniatus*, *H. celebicus*, *H. concelarus*, *H. frenatus*, *H. ishigakiensis*, *H. khasiensis*, *H. metusia*, *H. modestus*, *H. nicobariensis*, *H. octolineatus*, *H. optatus*, *H. parallelus*, *H. sanguineus*, *H. sarawacensis*, *H. taronensis* and *H. viperinus*.

Herpetoreas occurs along the southern margin of the Himalaya, into Northeast India and adjacent China. Of the five species of *Herpetoreas* currently recognised, three (*H. burbinki*, *H. platyceps*, *H. sieboldii*) are known only from subtropical to temperate regions above elevations of 1200 m (up to 3056 m). The Northeast Indian *Herpetoreas xenura* and *H. pealii* on the other hand are found from as low as 30 m up to low and middle elevations (up to 1170 m). *Herpetoreas pealii* so far is known only from lowland evergreen forest, which is known to be generally highly threatened. Extensive changes in land use, mainly from the expansion of tea plantations and agriculture, have resulted in the dramatic transformation of the once contiguous upper Brahmaputra Valley forests into many small, isolated fragments (Sharma *et al.,* 2012).

In addition to new fieldwork to look for *H. pealii* close to its type locality, searches in other lowland evergreen forest patches close to Poba RF are warranted, such as Dibru Saikhowa National Park in Assam and D'Ering Wildlife Sanctuary in Arunachal Pradesh (Fig. 1).

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Appendix 1

GenBank sequences and new sequences used in this study. "—" indicates no data.

Species	Voucher number	*cytb*	*16S*	*cmos*	*bdnf*
Adelophis foxi	LSUMZ 40846, LSUMZ H08272	AF420069	—	—	KF258601
Afronatrix anoscopus	ROM 19842 (ATOL A111)	AF420073	—	AF471123	EU402622
Amphiesma stolatum	CAS HERP 206560	AF471030	MK193918	AF471097	—
Amphiesma stolatum	GP901	JQ687432	—	JQ687450	—
Aspidura ceylonensis	RS-145	KC347477	KC347361	KC347400	—
Atretium schistosum	RS-R	KC347487	—	KC347383	—
Atretium yunnanensis	GP842	GQ281787	—	JQ687448	—
Blythia hmuifang	MZMU 715	MN993853	MT003010	MN993861	—
Blythia reticulata	PUCZM/X/SL61	MN993856	MT003013	MN993864	—
Blythia reticulata	AD5618	—	MT003015	MN993890	—
Clonophis kirtlandii	LSUMZ H08189	KF258647	—	—	KF258596
Haldea striatula	LSUMZ:H18238	KF258657	—	—	KF258606
Hebius atemporalis	GP2318	KJ685695	—	KJ685645	—
Hebius atemporalis	GP1626	KJ685680	—	KJ685630	—
Hebius atemporalis	HT0550	LC325320	—	LC325766	—
Hebius bitaeniatus	GP1940	KJ685688	—	KJ685648	—
Hebius bitaeniatus	GP1863	KJ685686	—	KJ685636	—
Hebius bitaeniatus	CAS 215037	KJ685667	—	KJ685616	—
Hebius boulengeri	GP2433	KJ685699	—	KJ685649	—
Hebius boulengeri	GP2134	KJ685691	—	KJ685641	—
Hebius boulengeri	GP1789	KJ685684	—	KJ685634	—
Hebius concelarus	KUZ: R20253 & KUZ:R18557	AB989268	—	AB989271	—
Hebius craspedogaster	GP455	KJ685704	—	KJ685654	—
Hebius craspedogaster	GP1712	KJ685682	—	KJ685632	—
Hebius craspedogaster	GP1636	KJ685681	—	KJ685631	—
Hebius craspedogaster	GP1240	KJ685672	—	KJ685622	—

Appendix 1 continued.

Hebius craspedogaster	GP139	JQ687429	—	JQ687437	—
Hebius deschauenseei	AMNH 148575	KJ685665	—	KJ685614	—
Hebius ishigakiensis	KUZ:R48405	AB989284	—	AB989287	—
Hebius johannis	GP1569	KJ685678	—	KJ685628	—
Hebius khasiensis	CAS 221525	KJ685669	—	KJ685618	—
Hebius khasiensis	CAS 221504	KJ685668	—	KJ685617	—
Hebius khasiensis	AMNH 148552	KJ685663	—	KJ685612	—
Hebius metusia	GP871	KJ685707	—	KJ685657	—
Hebius modestus	CAS 234262	KJ685671	—	KJ685620	—
Hebius modestus	MVZ 226514	KJ685709	—	KJ685659	—
Hebius octolineatus	GP1242	KJ685673	—	KJ685623	—
Hebius octolineatus	HT0586	LC325321	—	LC325767	—
Hebius optatus	GP1885	KJ685687	—	KJ685637	—
Hebius optatus	GP1048	—	—	KJ685621	—
Hebius optatus	AMNH 147155	KJ685662	—	KJ685611	—
Hebius parallelus	CAS 215036	KJ685666	—	KJ685615	—
Hebius popei	GP2386	KJ685697	—	KJ685647	—
Hebius popei	GP2169	KJ685692	—	KJ685642	—
Hebius pryeri	KUZ: R67983	AB989102	—	AB989105	—
Hebius pryeri	HT0340	LC325312	—	LC325758	—
Hebius sauteri	GP864	KJ685706	—	KJ685656	—
Hebius sauteri	GP2549	KJ685701	—	KJ685651	—
Hebius sauteri	GP2382	KJ685696	—	KJ685646	—
Hebius sp.	KUZ: R67949	AB989298	—	AB989301	—
Hebius venningi	CAS:233206	KJ685670	—	KJ685619	—
Hebius venningi	GP2468	KJ685700	—	KJ685650	—
Hebius venningi	GP1300	KJ685675	—	KJ685625	—
Hebius vibakari	GP1352	KJ685677	—	KJ685627	—
Hebius vibakari	KUZ: R21587	AB989302	—	AB989305	—
Hebius vibakari	HT0274	LC325309	—	LC325755	—
Hebius vibakari	HT0277	LC325310	—	LC325756	—
Herpetoreas burbrinki	YBU 071128/GP600	GQ281781	—	JQ687443	—
Herpetoreas cf. *platyceps*	WII-ADR183	MT571587	MT578065	—	MT571589
Herpetoreas pealii	WII-ADR547	MT571586	MT578066	MT571590	MT571588
Herpetoreas platyceps	GP2096	KJ685690	—	KJ685640	—
Herpetoreas xenura	PUCZM/X/SL1	MN993850	MT003007	MN993858	—
Liodytes alleni	LSUMZ:H08565	KF258653	—	—	KF258602
Liodytes pygaea	LSUMZ 42686, SJA 7787	KF258654	—	—	KF258603
Liodytes rigida	LSUMZ:H20703	KF258659	—	—	KF258608
Lycognathophis seychellensis	–	—	—	FJ404294	—
Natriciteres olivacea	CAS:220640	AF471058	—	AF471146	—
Natrix maura	0145M	—	KY762065	KY762081	—
Natrix natrix	ROM 26841 & 42	KX694876	—	KX694827	JQ599036
Natrix tessellata	ROM 23418	AY866531	—	—	—
Nerodia erythrogaster	SJA 6512, UTA R-59349, JDM 1004	AF402912	—	JN090137	KT884157
Nerodia sipedon	ROM 22671, MEA 503	KX694873	KX694654	KX694812	KX694741
Opisthotropis cheni	GP383	GQ281779	MK194106	JQ687441	—
Opisthotropis lateralis	GP646	GQ281782	MK194251	JQ687445	—
Opisthotropis latouchii	GP647	GQ281783	MK194254	JQ687446	—
Opisthotropis typica	HT0794	LC325343	—	LC325789	—
Pseudagkistrodon rudis	GP384	GQ281780	KX694651	JQ687442	KX694735
Regina grahami	H08535, MEA 505	KF258650	—	—	KF258599
Regina septemvittata	LSUMZ 40101	KF258646	—	—	KF258595
Rhabdophis conspicillatus	HT0791	LC325342	—	LC325788	—
Rhabdophis adleri	WJC 20090801	KF800931	—	KF800921	—
Rhabdophis callichromus	HT0674	LC325325	—	LC325771	—
Rhabdophis ceylonensis	RS-D, HT0785	KC347474	KC347344	KC347384	—
Rhabdophis chrysargos	MSNG 54962	HG763866	—	—	—
Rhabdophis flaviceps	HT0809	LC325355	—	LC325801	—
Rhabdophis formosanus	HT0033	LC325304	—	LC325750	—
Rhabdophis guangdongensis	SYS r000018	KF800930	—	KF800920	—

Appendix 1 continued.

Rhabdophis himalayanus	HT0847	LC325299	—	LC325746	—
Rhabdophis leonardi	HT0851	LC325300	—	LC325747	—
Rhabdophis murudensis	HT0788	LC325341	—	LC325787	—
Rhabdophis nigrocinctus	HT0253	LC325307	—	LC325753	—
Rhabdophis nuchalis	GP251	GQ281786	—	JQ687438	—
Rhabdophis pentasupralabialis	HT0700	LC325332	—	LC325778	—
Rhabdophis plumbicolor	HT0782	LC325336	MK350253	LC325782	—
Rhabdophis rhodomelas	ADM 0003	KX660528	KX660258	KX660399	—
Rhabdophis subminiatus	GP57	GQ281777	—	—	—
Rhabdophis swinhonis	HT0717	LC325334	—	LC325780	—
Rhabdophis tigrinus	HT0098	LC325305	—	LC325751	—
Rhabdops aquaticus	NCBS-AU163	MF352835	MF352830	MF352833	—
Rhabdops olivaceus	NCBS-AU164	MF352838	MF352831	MF352834	—
Sibynophis collaris	–	JN211315.1	JN211315.2	—	—
Sibynophis subpunctatus	RAP0491	KC347471	KC347373	KC347411	—
Sinonatrix aequifasciata	GP357	JQ687430	—	JQ687440	—
Sinonatrix annularis	MNHN 1999.9016	—	AF544807	AF544712	—
Sinonatrix percarinata	ROM 35669	KX694872	KX694667	KX694819	—
Smithophis atemporalis	BNHS 2366	MK350262	MK350255	MK350265	—
Smithophis bicolor	BNHS 2369	MK350261	MK350254	MK350264	—
Storeria dekayi	ROM 41891	KX694874	KX694669	KX694821	KF258593
Thamnophis godmani	MZFC:10202	AF420135	—	AF471165	—
Thamnophis sirtalis	ROM 26937	—	KX694670	—	KX694767
Trachischium monticola	GP1487	JQ687435	—	JQ687453	—
Tropidoclonion lineatum	H13044	KF258655	—	—	KF258604
Virginia valeriae	RAP 0572	KR814700	KR814654	KR814673	KF258605
Xenochrophis asperrimus	RS-J	KC347480	KC347376	KC347413	—
Xenochrophis flavipunctatus	CUB MZ R 1998.12.11.16	—	AF544809	AF544714	—
Xenochrophis maculatus	HT0720	LC325335	—	LC325781	—
Xenochrophis piscator	HT0347	LC325317	—	LC325763	—
Xenochrophis piscator	HT0796	LC325345	—	LC325791	—
Xenochrophis punctulatus	CAS HERP 206594	AF471079	—	AF471106	—
Xenochrophis schnurrenbergeri	JP337	KY379922	—	—	—
Xenochrophis trianguligerus	HT0795	LC325344	—	LC325790	—
Xenochrophis vittatus	FMNH 257460, HT0615	EF395895	EF395846	EF395920	—

Appendix 2

Comparative specimens examined.

Herpetoreas sieboldii (holotype) BMNH 1946.1.13.16

Herpetoreas xenura BMNH 1940.3.4.8, BMNH 1956.1.12.79

Herpetoreas platyceps (holotype) ZSIK 7482

Herpetoreas cf. *platyceps* WII-ADR 183

Herpetoreas pealii ZSIK 4034 (paralectotype), BMNH 1946.1.13.43(lectotype), WII-ADR547

Hebius clerki (holotype) BMNH 1946.1.13.50

Hebius khasiensis (holotype) BMNH 1946.1.13.63

Hebius modestus (holotype) BMNH 1946.1.13.41

Hebius parallelus (holotype) BMNH 1946.1.13.53