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Systematic Assessment of *Hebius beddomei* (Günther, 1864) (Serpentes: Colubridae: Natricinae) with Description of a New Genus and a New Allied Species from the Western Ghats, India †

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† urn:lsid:zoobank.org:act:1E518A20-B9C5-4135-A460-AAC7E8C552D4; urn:lsid:zoobank.org:act:D3F8E8D8-9815-4709-895A-AE3762291D68; urn:lsid:zoobank.org:pub:2D8E9650-0A2D-4CC5-BFCA-695043256A59.

Abstract: *Hebius beddomei* (Günther, 1864) is an endemic natricine colubrid snake species from the biodiverse Western Ghats, India. A recent molecular phylogeny provided evidence for the paraphyly of the genus *Hebius*, with *Hebius beddomei* recovered as sister to a clade containing *Fowlea* and *Atretium*. Freshly collected specimens and existing museum material allowed us to elucidate the generic status of the species and identify two distinct populations, one of which is described as a new species. A new genus, *Sahyadriophis* gen. nov., is proposed to accommodate *Sahyadriophis beddomei* gen. et. comb. nov., and *Sahyadriophis uttaraghati* gen. et. sp. nov. is described as a new species from the northern part of the range. The discovery of a new Oligocene divergent lineage, *Sahyadriophis* gen. nov., highlights the role of the Western Ghats as a source of relic lineages.

Keywords: biodiversity hotspot; integrated taxonomy; molecular phylogeny; natricinae; keelback; Sahyadri

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1. Introduction

Natricine colubrid snakes are represented by 264 species in 38 genera, with their greatest diversity in Asia [1,2]. Most species are either aquatic or semi-aquatic and are integral to aquatic and associated habitats [2–4]. Twenty-two genera have thus far been reported from Asia. Deepak et al. [2,5] presented a robust, multilocus molecular phylogeny of natricine snakes which enhanced our understanding of the group. The work further presented evidence for a reassessment of the generic status of several species, one of which is the Western Ghats-endemic *Hebius beddomei* (Günther, 1864).

Beddome described *Hebius beddomei* as *Spilotes vittatus* in 1863. A year later in 1864, Günther described the same species as *Tropidonotus beddomei*. Boulenger [6,7] in his compilation on the reptilian fauna of the region realized the name *Spilotes vittatus* was then preoccupied and hence proposed the name *Tropidonotus beddomei* be substituted for the species. Smith [3] referred most natricine snakes to the genus *Natrix* Laurenti, 1768, including *N. beddomei*, and the species was later referred to two genera by subsequent revisers, viz. *Rhabdophis* Fitzinger, 1843, and *Amphiesma* Duméril, Bibron and Duméril, 1854. Guo et al. [8] partitioned the genus *Amphiesma* and, based on its morphology and distribution, transferred *Amphiesma beddomei* to the genus *Hebius* Thompson, 1913. In a recent phylogeny of natricine snakes, the genus *Hebius* was recovered as paraphyletic and *Hebius beddomei* was recovered as sister to the genera *Fowlea* Theobald, 1868, *Xenochrophis* Günther, 1864 and *Atretium* Cope, 1861 [2]. The species is distributed nearly completely throughout the Ghats,

ranging from Tamhini in Pune District, Maharashtra, to Agasthyamalai range in Tamil Nadu [3,9–11]. We assessed the systematic status of the species in a discussion based on freshly collected specimens and existing museum material. Molecular data and scalation and skull osteological data were employed to evaluate the status of the species distributed in most parts of the Western Ghats.

2. Materials and Methods

The present study is based on eleven specimens catalogued in the collections of the Bombay Natural History Society (BNHS), Mumbai; lectotype housed in the collections of the Natural History Museum (NHMUK), London; two freshly collected specimens, one each from Amboli, Maharashtra, and Kalakkad Mundanthurai Tiger Reserve, Tamil Nadu; and two live individuals examined from Amboli, Maharashtra. The freshly collected specimens were caught, photographed, and later euthanized using standard euthanasia protocol for reptiles [12]. Morphological data for related species were compared with the relevant literature [3,8,13–20] and material was examined (see Appendix A) from the natural history museums listed below. Ventral scales were counted according to Dowling [21]. The number of dorsal scale rows were counted at the 10th ventral, midbody, and at 10th ventral before the vent, respectively. The dorsal scale reduction formula follows Dowling [22], with modifications proposed by Das et al. [23] and Mirza et al. [24]. Subcaudal counts reported here do not include the terminal scute. The number of supralabials in contact with the eye is given in brackets next to the number of supralabials. Values for symmetric head characters are given in right-to-left order. The description style follows Patel et al. [25,26] and Mirza et al. [24] with some modifications. Scalation and other comparable characters are described as ventral scales (V); subcaudal scales (SC); dorsal rows of scales (D); supralabial scales (SL); loreal scales (L); preocular scales (PreO); postocular scales (PostO,); temporal scales (T); infralabial scales (IL); snout–vent length (SVL); tail length (TaL); and total length (TL). Measurements were taken with the help of a digital caliper to the nearest 0.1 mm, and those for snout–vent Length (SVL) and tail length (TaL) were taken with the aid of a piece of string, which was then measured using a scale. The number of scales bordering the posterior border of the Parietals were counted (STP, scales touching parietals); these exclude the temporal scales.

The hemipenis of the freshly euthanized male holotype was everted by palpation of the organ until it was everted to the maximum extent, after which the organ was separated by making an incision around its circumference at the cloacal region and was immersed in warm water (50 °C) for about 5 min to soften the tissue. Then, it was slowly everted using a blunt pair of forceps, gently pushing the organ from the distal to proximal end. After eversion, the organ was inflated with 4% formaldehyde and tied at the base with a thread. Later it was stained in 1% alizarin red solution for 30 min. Observations were made using a stereomicroscope (Omano OM2360-BL). Descriptions of hemipenial morphology and terminology follow Smith [3], Dowling and Savage [27], and Zaher [28]. Distribution data for the species are based on the literature, personal observations, and photographs from colleagues. The species were identified based largely on number of supralabials and subcaudals.

Abbreviations of institutions where comparative material was examined: BNHS—Bombay Natural History Society, Mumbai, India; FMNH—Field Museum of Natural History, Chicago, USA; MNHN—Muséum national d'Histoire naturelle, Paris, France; NCBS—Collection Facility of the National Centre for Biological Sciences, Bangalore, India; NHMUK—Natural History Museum, London, U.K.; ZMUC—Natural History Museum of Denmark, University of Copenhagen, Denmark; ZSIK—Zoological Survey of India, Kolkata; and ZAM—Zeeshan Mirza field series.

Micro-CT scans of the skulls were generated for the freshly collected specimens using a Bruker® Skyscan 1272 (Bruker BioSpin Corporation, Billerica, MA, USA). The head of the specimen was scanned for 210 min at resolution of 5.4 µm, recording data for every 0.4° rotation for 360° with (AL) a 1 mm filter. The source voltage for the scan was 65 kV

and the source current was 153 uA. Volume rendering was performed with CTVox (Bruker BioSpin Corporation, Billerica, MA, USA) and images were edited in Adobe Photoshop CS6. Osteological descriptions are based on volume renders retrieved from CTVox following terminology of the skull described by Heatwole [29]. Measurements of the skull were taken as follows: skull length (SkL) measured from the anterior border of the nasal to the posterior border of the posterior border of the exoccipital, skull width (SkW) measured at the widest portion of the parietal, parietal anterior width (PaW) measured at the posterior border of the frontals, parietal posterior width (PpW) measured at the borders on the parietal and the supraoccipital; measurements of lengths, heights, and/or widths of other bones were taken at their broadest positions.

Genomic DNA was isolated from the preserved tissues of the holotype of the new species described in the present study and a specimen from Tamil Nadu using QIAGEN DNeasy kits, following protocols directed by the manufacturer. A fragment of the mitochondrial cytochrome b (cyt b) and three nuclear Oocyte Maturation Factor mos (c-mos) and recombination activating gene (RAG1) genes were amplified using primers used by Pyron et al. [30] and Mirza et al. [24] (Supplementary Table S1). A 22.4 µL reaction was set for a bi-directional Polymerase Chain Reaction (PCR), containing 10 µL of Thermo Scientific DreamTaq PCR Master Mix, 10 µL of molecular grade water, 0.2 µL of each 10 µM primer and 2 µL template DNA, carried out with an Applied Biosystems ProFlex PCR System. The thermo-cycle profile used for amplification was as follows: 95 °C for 3 min, (denaturation temperature 95 °C for 30 sec, annealing temperature 48 °C for 45 sec for cyt b, 56 °C for c-mos and 58 °C for RAG1 elongation temperature 72 °C for 1 min) × 36 cycles, 72 °C for 10 min, hold at 4 °C. The PCR product was cleaned using a QIAquick PCR Purification Kit and sequenced with an Applied Biosystems 3730 DNA Analyzer. In addition to this, sequences analyzed by Deepak et al. [2] of Natricinae available on GenBank® were downloaded for inferring molecular phylogeny, and the sequences were concatenated using SequenceMatrix [31]. Sequences were aligned in MegaX [32] using ClustalW [33] with the default settings. The aligned dataset was subject to Maximum Likelihood (ML) phylogenetics on the IQ-TREE (http://iqtree.cibiv.univie.ac.at/, accessed on 1 May 2023) online portal [34]. A sequence substitution model was selected using the auto parameter with provision for FreeRate heterogeneity, and the analysis was run with an ultrafast bootstrap option for 1000 iterations to assess clade support. The uncorrected pairwise *p*-distance (% sequence divergence) was calculated in MegaX with pairwise deletions of missing data and gaps. The sequences used in the phylogenetic analysis are listed in Supplementary Table S2, and the sequence evolution model for individual analysis is presented in Supplementary Table S3.

3. Results

3.1. Molecular Data

Concatenated molecular data comprised mitochondrial 16S rRNA (514bp), cytochrome b (1117bp), NADH subunit 4 (696bp) and nuclear brain-derived neurotrophic factor (683bp), oocyte maturation factor mos (585bp), neurotrophin 3 (595bp), and recombination activating gene (1008bp) summing to 5198bp. The relationship recovered in the present analysis is comparable to that of Deepak et al. [2], as the same dataset was used for the present study with additional sequences for the focal species. *Hebius beddomei* and the new species described here were recovered as sister to a clade of Asian natricines containing *Xenochrophis*, *Fowlea*, and *Atretium*, though with poor support (Figure 1, ML bootstrap support 56, Supplementary Figure S1). Samples of the species from southern India representing *H. beddomei* sensu stricto and a sample of the species from the northern part of the range are 5% divergent for the cyt b gene and are here described as a new species along with a new genus to contain the species. See the systematics section for morphological details.

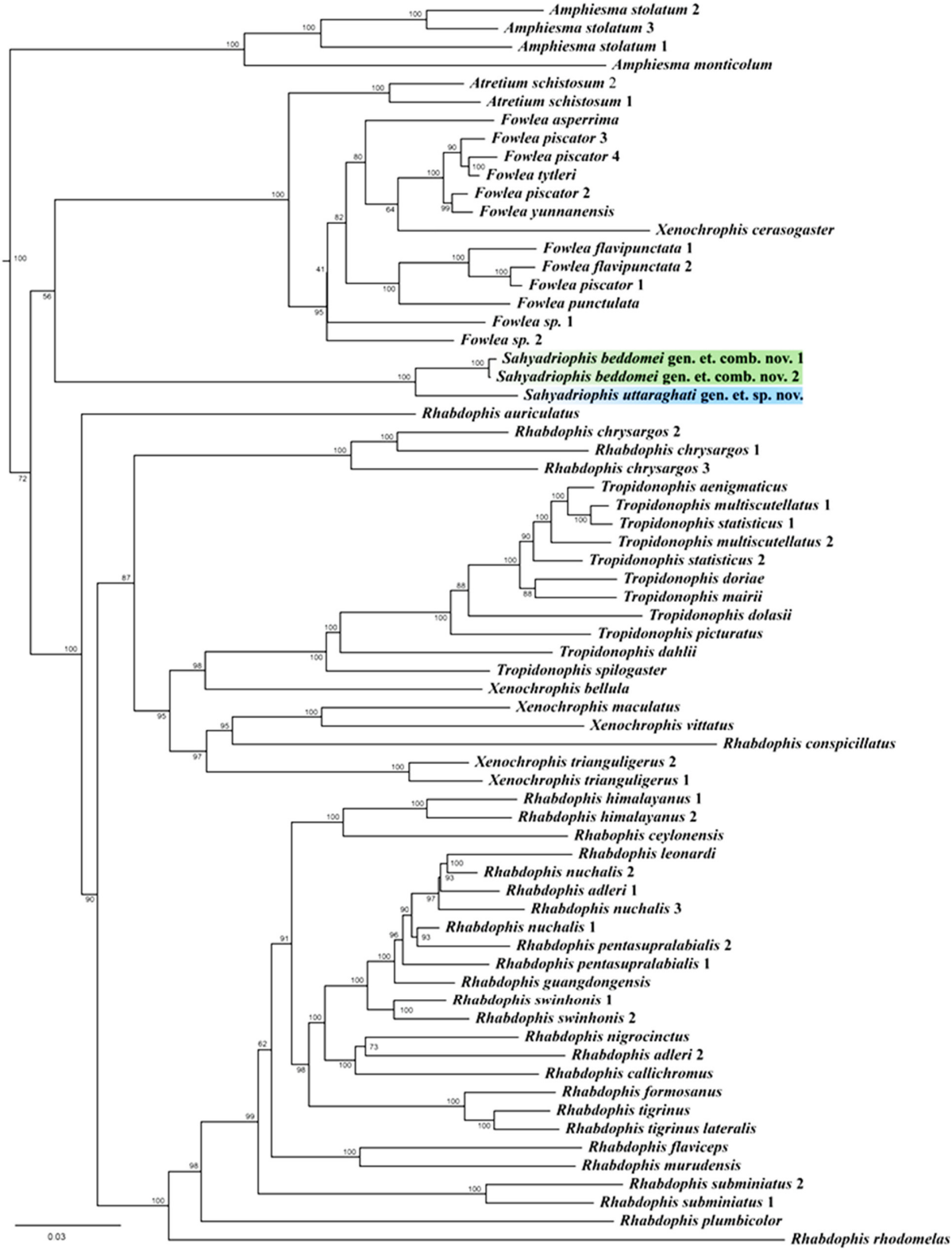

Figure 1. Maximum likelihood phylogeny of natricine colubrid snakes based on a concatenated dataset comprising of mitochondrial 16S rRNA (514bp), cytochrome b (1117bp), NADH subunit 4 (696bp) and nuclear brain-derived neurotrophic factor (683bp), oocyte maturation factor mos (585bp), neurotrophin 3 (595bp), and recombination activating gene (1008bp) summing up to 5198bp reconstructed with IQ-TREE. The new genus and its species are marked in shades of green and blue. Numbers at nodes show ML bootstrap support. The tree has been pruned to display focal taxa; see Figure S1 for the complete tree.

3.2. Systematics

***Sahyadriophis* gen. nov.**

Spilotes Beddome, 1863: 43 (in part)
Tropidonotus Günther, 1864: (in part)
Rhabdophis Wall, 1923: 605 (in part)
Natrix Smith, 1943: 306 (in part)
Amphiesma Whitaler and Captain, 2004: 242 (in part); Wallach et al., 2014: 28 (in part)
Hebius Guo et al., 2014: 437; Deepak et al., 2022 (in part)
LSID: urn:lsid:zoobank.org:act:1E518A20-B9C5-4135-A460-AAC7E8C552D4
(Figure 2)

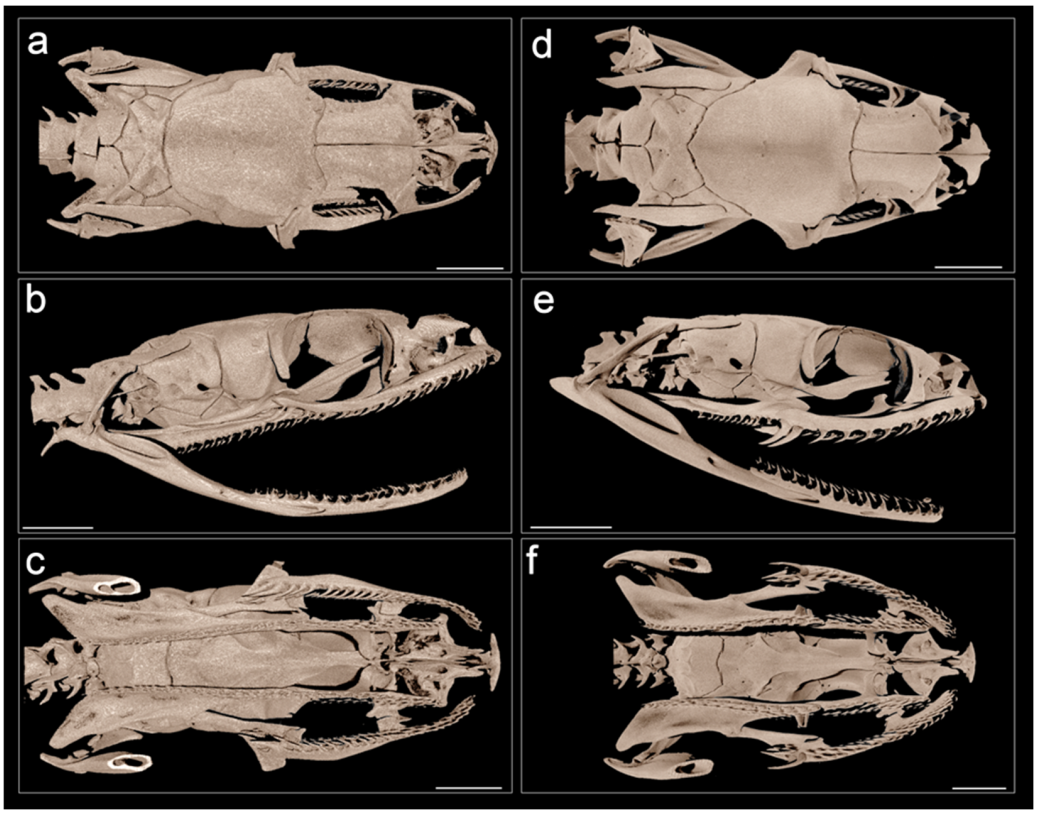

Figure 2. MicroCT scans of the head of *Sahyadriophis* gen. nov., (**a**–**c**) *Sahyadriophis uttaraghati* gen. et. sp. nov. ♂NCBS NRC-AA-0024, (**d**–**f**) *Sahyadriophis beddomei* gen. et. comb. nov. ♀ NCBS NRC-AA-4503. Skull dorsal view (**a**,**d**), lateral view (**b**,**e**), ventral view without the mandibles (**c**,**f**). Scale bar 2 mm.

Type species. *Sahyadriophis uttaraghati* gen. et. sp. nov.

Species included. *Sahyadriophis beddomei* gen. et. comb. nov. and *Sahyadriophis uttaraghati* gen. et. sp. nov.

Diagnosis. Medium-sized snakes in relation to family members measuring SVL 215–495 mm with 19 dorsal keeled scale rows at mid-body. Head distinct from neck. Nuchal groove and glands absent. Pupil rounded. Nostrils in nasals, a pair or internasals. Paired internasals and prefrontals. Posterior maxillary teeth longest and present after a distinct diastema, 18–26 functional maxillary teeth, 10–15 palatine teeth and 22–25 ptyerogoid teeth. Scales at the sacral region bear dentate keels in males.

Etymology. The generic name is a combination of two words: '*Sahyadri*', a Sanskrit word for the Western Ghats, and the Greek word '*ophis*' for snakes. The name is masculine in gender.

Description. Natricine snakes with a head distinct from neck. Head scales complete and typical of members of the family Colubridae. One pair of internasals, prefrontals,

parietals; single frontal, single preocular (rarely two), single loreal. Nasal divided, and the nostrils situated medially, oriented laterally. Two to three postoculars and one anterior temporal. Eye large. Supralabials 8 or 9 (rarely 7), 3–5 or 4–6th in contact with orbit. Dorsal scales in 19:19:17 rows, keeled, the reduction from 19 to 17 occurs between ventrals 74 to 81. Scales on the sacral region of males bear dentate keels. Ventrals 140–153; subcaudals 62–83, paired. Anal divided. The skull of *Sahyadriophis* gen. nov. is typical of a natricine snake as described by Andjelković et al. [35]; however, with a few differences. The skull is well built and calcified evenly, with a few exceptions. The skull of the female is more robust compared to that of the male and so are individual bones of the skull. The male's skull is more compact and elongated (SkW/SkL 0.51), with only the postorbital bone protruding distinctly, whereas the skull of the female is much wider (SkW/SkL 0.51). The female skull is triangular anteriorly with a constriction in its girth towards the posterior part of the parietal; the posterior part of the skull is the widest. The parietal in the male is dorsally flat with distinct lateral ridges, which slope downwards; the female lacks these ridges. The teeth in the female are much larger than those of the male.

The parietal covers 40.8% of the skull length in the female and 38.3% in the male. The maxillary bone is more compactly placed in the male along the skull but displaced outward in the female. The maxilla accounts for about 58% of the skull length in both sexes. The palatine occupies about 34% of the female and 38% of the male, whereas the pterygoid is about 57% and 53% in females and males, respectively. The pterygoid-palatine bones run parallel to the longitudinal axis of the skull and do not converge or diverge abruptly posteriorly. Posterior maxillary teeth are longest and follow a distinct diastema, 18–26 functional maxillary teeth, 10–15 palatine, and 22–26 pterygoid. Overall in a shade of brown to dark grey with irregularly placed black and white markings which diffuse towards the posterior part of the body. Ventrally white in the anterior that gradually turns cream and yellow posteriorly. The head may bear a light-colored bar on the nape and a downward directed post-ocular stripe which is white or lighter colored and edged with black. Juveniles are dark brown to black with more pronounced markings; the nape bears either a light bar or a blotch which fades away as the animal grows.

Comparison. Here, we compare the new genus with other Natricine genera distributed in South and Southeast Asia. *Sahyadriophis* gen. nov., differs from most natricine genera in bearing 19 dorsal scale rows at mid-body (vs. 13–15 in *Trachischium* Günther, 1858, 13 in *Blythia* Theobold, 1868, 17 in *Rhabdops* Boulenger, 1893, 15–17 in *Aspidura* Wagler, 1830 and *Hydrablabes* Boulenger, 1891, 23 in *Pseudagkistrodon* Van Denburgh, 1909), nuchal groves or glands absent (vs. present in *Rhabdophis*), a pair of internasals (vs. single internasal in *Atretium*; internasals fused in *Opisthotropis* Günther, 1872, *Smithophis* Giri, Gower, Das, Lalremsanga, Lalronunga, Captain, and Deepak, 2019, *Aspidura*; 3–4 internasals in *Pseudagkistrodon*), a pair of prefrontals (vs. fused in *Smithophis* and *Isanophis* David, Pauwels, Nguyen and Vogel, 2015, some species of *Opisthotropis*), posterior maxillary teeth abruptly enlarged (vs. teeth gradually increasing in size from anterior to posterior in *Xenochrophis* and *Fowlea*), dorsal scales keeled throughout (vs. keels only on posterior part of the body in *Trimerodytes* Cope, 1895, dorsal scales smooth in *Rhabdops* and *Iguanognathus* Boulenger, 1898), teeth pointed and curved (vs. teeth crowns spatulated in *Iguanognathus*), maxillary teeth 18–26 (vs. 38–46 in *Amphiesmoides* Malnate, 1961), ventrals 140–152 (vs. 157–168 in *Amphiesmoides*), subcaudals 62–83 (vs. 114–131 in *Amphiesmoides*), single anterior temporal (vs. two anterior temporals in *Atretium*), and pterygoid-palatine bones run parallel to the plane of the skull and do not converge or diverge posteriorly abruptly (vs. pterygoid-palatine bones converge posteriorly in *Amphiesma* and *Fowlea*).

The new genus closely resembles *Amphiesma*, *Hebius* and *Herpetoreas* Günther, 1860 in sharing several morphological characteristics. However, it differs from these in having substantial differences in dentition, hemipenial morphology and some characteristics in lepidosis, which are as follows: the new genus differs from *Amphiesma* in having the nasal in broad contact with supralabials I and II (vs. nasal in broad contact with only supralabial I), adult males having scales on the sacral region with dentate keels (vs. such dentate scales

absent), sulcus spermaticus extends to the base or tip of inner right side of lobe (vs. sulcus spermaticus extends to the middle of crotch), not well-developed apical naked area (vs. well-developed apical naked area), and pterygoid-palatine bones run parallel to the plane of the skull and do not converge or diverge posteriorly abruptly (vs. pterygoid-palatine bones converge posteriorly).

The new genus differs from *Hebius* in having a maxillary diastema between the posterior enlarged teeth and normal functional teeth (vs. maxillary diastema absent), adult males having scales on the sacral region with dentate keels (vs. such dentate scales absent), single basal hook weakly developed (vs. single basal hook well developed and distinctly larger in size), apical naked area not well developed and not visible (vs. apical naked area well developed, protruding and visible from the asulcate surface) and both these genera have disjunct distribution.

The new genus differs from *Herpetoreas* in subcaudals 62–83, all divided (vs. 69–111, divided or single), anal scale divided (vs. anal scale divided or single), anterior temporal single (vs. anterior temporals 1–3), adult males with scales on the sacral region with dentate keels (vs. such dentate scales absent in most species, except in *Herpetoreas xenura* (Wall, 1907)), weakly developed single basal hook (vs. well-developed single basal hook and distinctly larger in size) and both these genera have disjunct distribution.

***Sahyadriophis uttaraghati* gen. et. sp. nov.**

Rhabdophis beddomei Wall, 1923: 605 (in part)
Natrix beddomei Smith, 1943: 306 (in part)
Amphiesma beddomei Whitaler and Captain, 2004: 242 (in part); Wallach et al., 2014: 28 (in part)
LSID: urn:lsid:zoobank.org:act:D3F8E8D8-9815-4709-895A-AE3762291D68
(Figures 4 and 5; Table 1)

Holotype. adult ♂NCBS NRC-AA-0024 collected from Amboli (15.96472° N 74.00357° E; ca. 690 m a.s.l), Maharashtra, India by Hemant Ogale on 3 May 2018.

Paratypes. adult ♀BNHS 3196 collected from Mahabaleshwar, Satara District, Maharashtra, India, by Sudhir Sawant on 1 May 2002; juvenile ♂BNHS 3198 collected from Amboli, Maharashtra, India, by V. Giri, V. Hegde and S. Kehimkar on 13 June 2002.

Referred material. an unsexed specimen BNHS 1578 and an adult ♀BNHS 1579 from Mahabaleshwar, Satara District, Maharashtra.

Diagnosis. A medium sized snake ranging from SVL 365 to 425mm with 19 keeled dorsal scales at mid-body; nine supralabials; ventrals 145–148 ♂, 151–153 ♀and subcaudals 78–83 ♂, 74–76 ♀; maxilla with 26 teeth, 14 or 15 pterygoid and 23–24 palatine teeth; pterygoid-palatine oriented nearly parallel to the head and converges to a small degree posteriorly; TaL/TL 0.27–0.30 ♂.

Comparison. The new species, *Sahyadriophis uttaraghati* gen. et. sp. nov. differs from *Sahyadriophis beddomei* gen. et. comb. nov. as follows: the new species has nine supralabials (vs. seven–eight, rarely nine in *S. beddomei* gen. et. comb. nov.), 74–83 subcaudal scales (vs. 62–76 in *S. beddomei* comb. nov.) (Figure 3a), 26 functional maxillary teeth (vs. 18 functional maxillary teeth in *S. beddomei* gen. et. comb. nov.), Tal/TL 0.22–0.26 (Figure 3b), adult males having scales on the sacral region with prominent dentate keels (vs. adult males having scales on the sacral region with feebly developed dentate keels in *S. beddomei* gen. et. comb. nov.). See Table 1 for a summary of morphological characteristics.

Etymology. The specific epithet is a combination of two Sanskrit words: '*uttara*' for north and '*ghati*' meaning dweller of the mountains/Ghats. The combination refers to the northern distribution of the new species.

Description of male holotype NCBS NRC-AA-0024 (Figure 4). The specimen is in good condition, preserved in a coil with its head situated outside of the coil. The specimen bears one longitudinal incision at mid-length of the body; hemipenes are everted and preserved separately (Figure 4a,b).

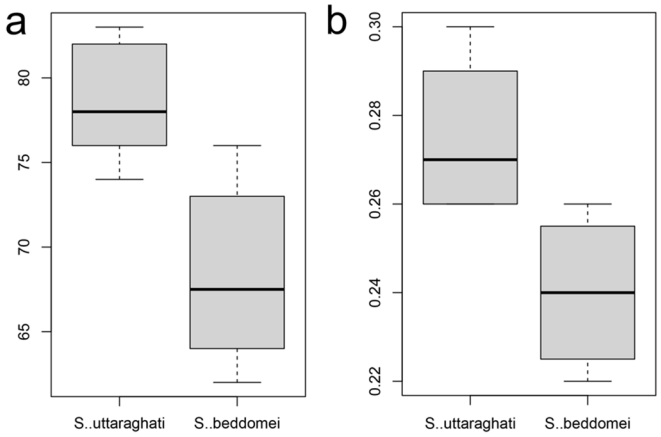

Figure 3. (**a**) Boxplots showing subcaudal range of *Sahyadriophis* spp.; (**b**) boxplot showing TaL/TL rations in *Sahyadriophis* spp.

Table 1. Scale counts, measurements (mm) and collection details of snake specimens of *Sahyadriophis uttaraghati* gen. et. sp. nov. R/L.

Specimen No	NCBS NRC-AA-0024 (Holotype)	BNHS 3198 (Paratype)	BNHS 3196 (Paratype)	BNHS 1578	BNHS 1579	ZAM 01	ZAM 02
Locality	Amboli	Amboli	Mahabaleshwar	Mahabaleshwar	Mahabaleshwar	Amboli	Amboli
Sex	♂	♂	♀	ND	♀	♂	♀
TL	510	295	570	-	-	370	460
SVL	365	215	425	-	-	260	345
TaL	145	80	145	-	-	110	115
TaL/TL	0.29	0.27	0.26			0.30	0.25
D	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17
V	146	148	151	-	-	145	153
A	Divided	Divided	Damaged	Divided	-	Divided	Divided
SC	78	82	74	-	-	83	76
SL	9/9	9/9	9/9	-/-	-/9	9/9	9/9
L	1/1	1/1	1/1	1/-	-/1	1/1	1/1
IL	10/9	10/10	9/8	8/8	10/9	9/10	10/10
PreO	1/1	1/1	1/1	1/1	1/1	1/1	1/1
PostO	3/3	3/3	3/3	2/2	2/2	3/3	3/3
T	1 + 2/1 + 2	1 + 2/1 + 2	1 + 2/1 + 2	1 + 2/1 + 2	1 + 1/1 + 1	1 + 2/1 + 2	1 + 2/1 + 2

Short head, measuring 15.8 mm from snout tip to the constriction at neck, comprising 3.10% of total length; high, 4.5 mm, with a blunt snout in lateral view; upper jaw visible from ventral side. Head broader (8.8 mm) than neck (5.8 mm). Snout gradually tapering to blunt, squarish tip in dorsal view (Figure 5a). Rostral subhexagonal, slightly visible when viewed from top; wider (3.0 mm) than deep (1.7 mm). Nostrils small, elliptical shaped, present in the anterior border of the posterior nasal. Paired internasals, slightly longer (1.9 mm) than wide (1.8 mm); smaller than prefrontals. Prefrontals, wider (2.2 mm) than long (1.9 mm). Frontal bell shaped, 3.3 mm at the widest anterior border, median length 4.6 mm. Parietals 5.9 mm long, 3.5 mm at its widest anterior and 1.8 mm at its posterior border. Temporals 1 + 2 on both sides, subequal in size, anterior ones larger than the posterior ones. Seven nuchal scales, unequal on size, bordering parietals. Supraocular larger than preocular; preocular large, deeper (2.0 mm) than wide (1.1 mm). Loreal longer (1.3 mm) than high (1.0 mm). Three postoculars, upper one larger. Eye circular, 3.0 mm diameter with an elliptic pupil. Nine supralabials; fourth, fifth and sixth in contact with orbit (Figure 5c,d). Supralabials increase in size gradually, seventh and eighth larger than the rest. First supralabial, not the second supralabial, contacts only rostral and nasal. Second supralabial in contact with nasal, loreal and first and third supralabials. Fifth

supralabials wider than high. Third supralabial in contact with preocular, second and forth supralabials and loreal. Sixth supralabial as high as the fourth supralabial.

Figure 4. *Sahyadriophis uttaraghati* gen. et. sp. nov. holotype ♂NCBS NRC-AA-0024, (**a**) dorsal view, (**b**) ventral view. Scale bar 20 mm.

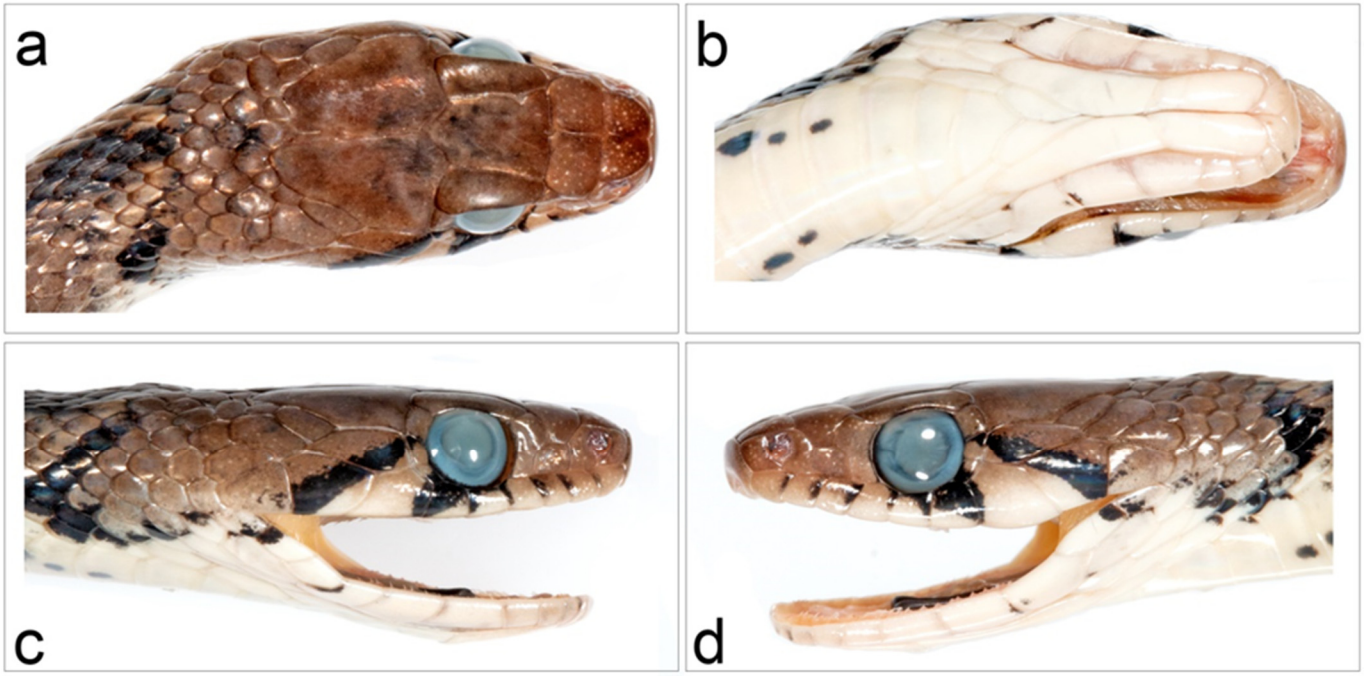

Figure 5. *Sahyadriophis uttaraghati* gen. et. sp. nov. holotype ♂NCBS NRC-AA-0024 showing head, (**a**) dorsal view, (**b**) ventral view, (**c**) right lateral view, (**d**) left lateral view.

Mental short, triangluar. Infralabials 10 on the right side and 9 on the left side, first long, II to IV infralabials short and thin, fifth onwards larger (Figure 5b). Seventh infralabial broadest on both sides, fifth on the right side and seventh on the left side longest. First seven infralabials in contact with the genials. Anterior genials almost thrice as long (4.1 mm) as wide (1.5 mm); posterior genials larger than the anterior ones, 6.3 mm long and 1.8 mm wide and in contact anteriorly (Figure 5b).

Body rounded; ventral surface flattened. Dorsal scales in 19-19-17 rows. Dorsal scale reduction formula is presented in Table 2.

Table 2. Scale reduction for representatives of *Sahydriophis* gen. nov.

Species	Voucher Number	Sex	Scale Reduction
Sahyadriophis uttaraghati gen. et. sp. nov.	NCBS NRC-AA-0024	♂	$19(10)\frac{3+4(74)}{3+4(75)}17(136)$
	BNHS 3196	♀	$19(10)\frac{3+4(81)}{4+5(79)}17(141)$
Sahyadriophis beddomei gen. et. comb. nov.	BNHS 1588	♀	$19(10)\frac{2+3(77)}{3+4(79)}17(133)$
	BNHS 1583	♂	$19(10)\frac{3+4(75)}{3+4(74)}17(135)$

The first lateral reduction in the number of DSR is observed after the 10th ventral is at 50% of the ventrals, whereas the third and fourth DSR are involved in reduction from 19 to 17 at ventral 75. Dorsal scales imbricate, regularly arranged, vertebral scales not enlarged, costal scales slightly enlarged. All body scales keeled, lacking apical pit. The dorsal scales on the ischiadic, anal and tail base regions are smaller, coarsely keeled, with 1–3 peaks on each scale (Figure 6a,b). Ventral scales 146 excluding two preventrals. Anal shield divided, slightly larger than last ventral scale. Subcaudals paired, 78. Tail terminates in a sharp, tapering apical spine. Total length 510 mm, tail length 145 mm, tail/total length ratio 0.28.

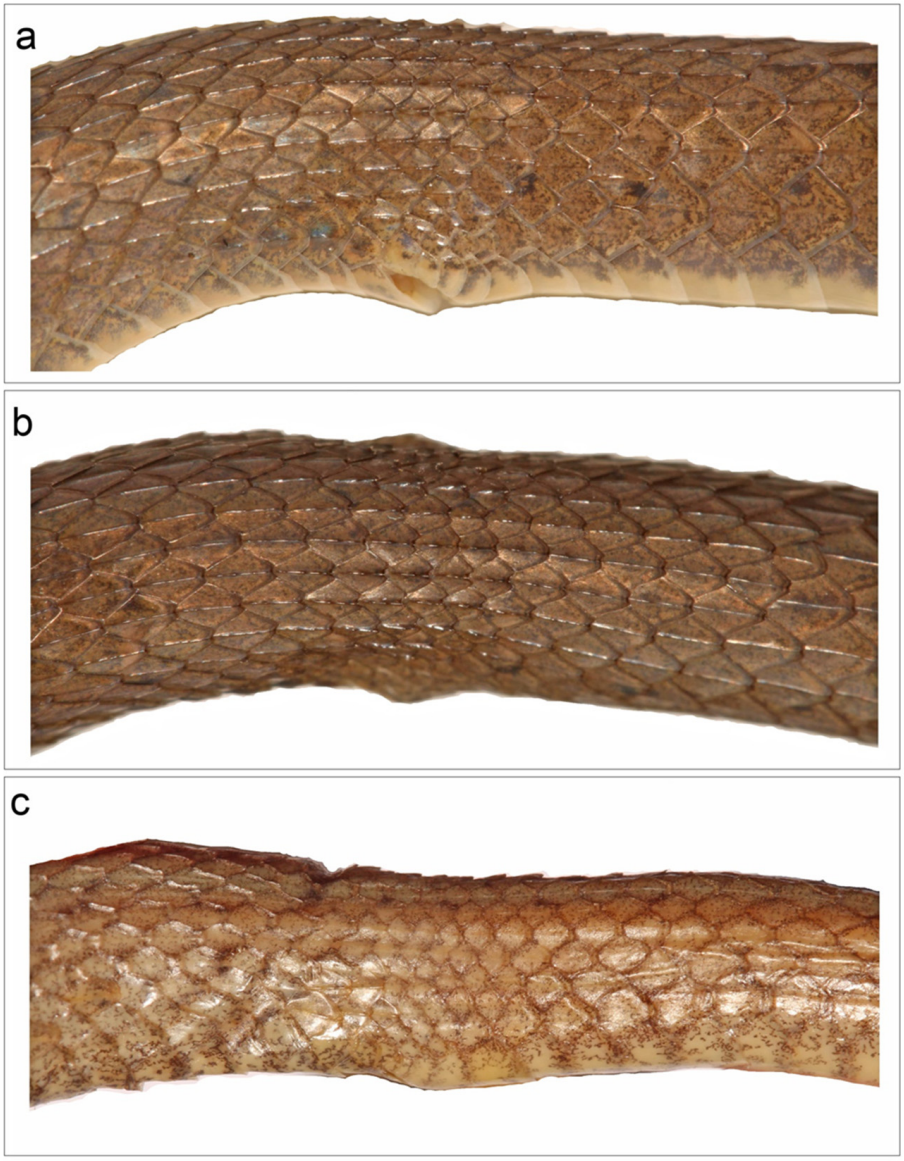

Figure 6. Sacral region of *Sahyadriophis* gen. nov., (**a**,**b**) *Sahyadriophis uttaraghati* gen. et. sp. nov. holotype ♂NCBS NRC-AA-0024, (**c**) *Sahyadriophis beddomei* gen. et. comb. nov. ♂BNHS 1583.

Hemipenial morphology (Figure 7, everted organ N = 2). The hemipenial description is based on the right hemipenis. The hemipenis is fully everted and expanded. The organ is thin and short, shallowly bilobed, noncalyculate and semicapitate; lobes extend to about 1/6 of the hemipenis, the left lobe slightly longer. The organ is ornamented throughout with spines and spinules; the spines are larger in size near the base and gradually decrease in size distally, more densely packed on the asulcul side; the apical naked area on crotch is weakly developed and not protruding; a basal hook is present at the hemipenial base, which is slightly larger than the adjacent spines; sulcus spermaticus single, deep, extending to the base of inner right lobe where it takes a centripetal position; sulcate lip poorly developed and not raised, not covered with spines; hemipenial base is almost nude, with few spinnules.

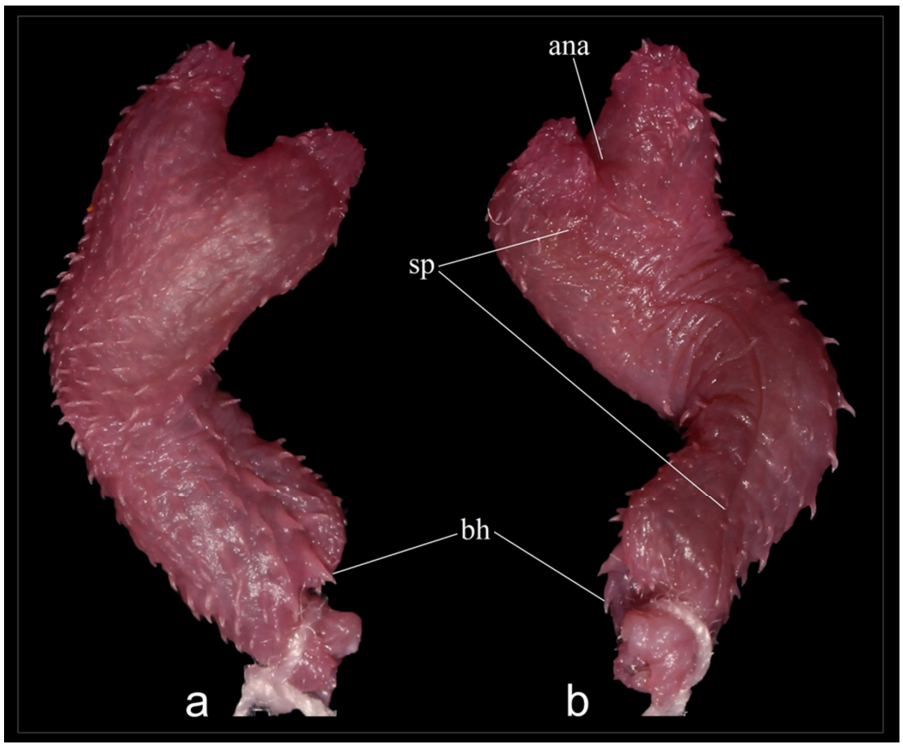

Figure 7. Hemipenis of *Sahyadriophis uttaraghati* gen. et. sp. nov. holotype ♂NCBS NRC-AA-0024, (**a**) asulcul view, (**b**) sulcate view. Legends are as following, ana: apical naked area; sp: sulcus spermaticus; bh: basal hook.

Variation. A summary of the variation observed in the type series and examined specimens is presented in Table 1. Nasal and loreal united on the left side in BNHS 1579 (Figure 8b).

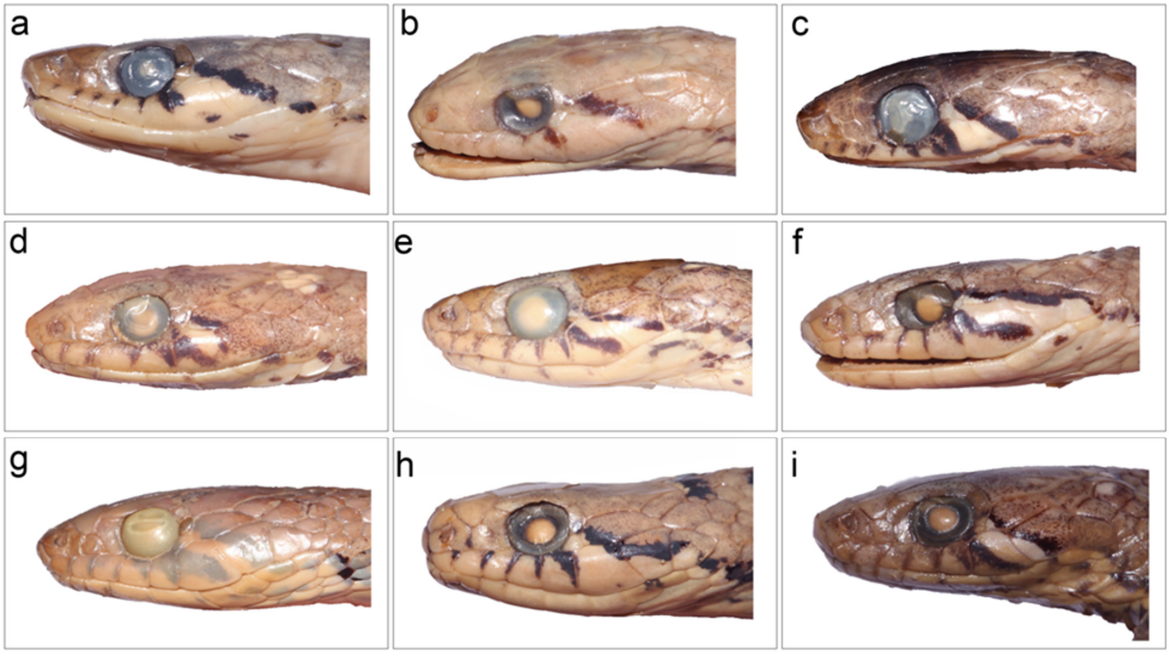

Figure 8. Lateral view of head showing scalation of *Sahyadriophis* gen. nov., (**a**–**c**) *Sahyadriophis uttaraghati* gen. et. sp. nov., (**d**–**i**) *Sahyadriophis beddomei* gen. et. comb. nov.; (**a**) BNHS 3196, (**b**) BNHS 1579, (**c**) BNHS 3198, (**d**) BNHS 1580, (**e**) BNHS 1583, (**f**) BNHS 1585, (**g**) BNHS 1588, (**h**) BNHS 1589, (**i**) BNHS 1592.

Coloration (Figure 9a). Overall, a shade of brown to dark grey with irregularly placed black and white markings which diffuse towards the posterior part of the body. Ventrally white in the anterior that gradually turns cream and yellow posteriorly. The head may bear a light-colored bar on the nape and a downwardly directed post-ocular stripe which is white or lighter colored edged with black.

Figure 9. Images of *Sahyadriophis* gen. nov. in life, (**a**) *Sahyadriophis uttaraghati* gen. et. sp. nov. holotype ♂NCBS NRC-AA-0024, (**b**) juvenile *Sahyadriophis beddomei* gen. et. comb. nov. (uncollected) from Madikeri, (**c**) adult male *Sahyadriophis beddomei* gen. et. comb. nov. Periyar Tiger Reserve, Kerala; photos by Harshil Patel (**a**), Zeeshan A. Mirza (**b**,**c**).

Natural history and distribution. The holotype was observed actively moving during the day in a dried streambed. The species appears to be largely diurnal and has been observed feeding on *Indirana* sp. and eggs of *Nyctibatrachus*. The species appears to be common and widespread across the Western Ghats of Maharashtra: Tamhini in Pune district (Shinde et al., 2020 [9]), Mahabaleshwar, Satara District, Amboli, Sindhudurg District; Goa: Cotigao Wildlife Sanctuary (Wall, 1923 [36]; Smith, 1943 [3]; Whitaker and Captain, 2004 [11]).

***Sahyadriophis beddomei* (Günther, 1864) gen. et. comb. nov.**

Spilotes vittatus Beddome, 1863: XX
Tropidonotus beddomei Günther, 1864: 269; Boulenger 1890: 344, 1893: 252
Rhabdophis beddomei Wall, 1923: 605 (in part)
Natrix beddomei Smith, 1943: 306 (in part)
Amphiesma beddomei Whitaler and Captain, 2004: 242 (in part); Wallach et al., 2014: 28 (in part), Deepak et al., 2022: 8
Hebius beddomei Guo et al., 2014: 437; Deepak et al., 2022: 7
(Figure 10; Table 3)
Lectotype. NHMUK 1946.1.15.32 'Nilgherries, India'.
Material examined. 3♀ BNHS 1589, BNHS 1588 and BNHS 1585 Paralai, Anamalai; 1♂ BNHS 1583, 1♀ BNHS 1580 Peermade, Travancore; 1♂ BNHS 1592 Nelliampathy Hills;

1♂ BNHS 1598 Kalsa Hills, Mysore; 1♀ NCBS NRC-AA-4503 Kalakad Mundanthurai Tiger Reserve, Tamil Nadu.

Diagnosis. A medium-sized natricid ranging from SVL 177 to 495 with 19 keeled dorsal scales at mid-body; eight supralabials (rarely seven or nine); ventrals 140–145 ♂, 143–152 ♀ and subcaudals 71–76 ♂, 62–68 ♀; maxilla with 18 teeth, 12 pterygoid and 20–22 palatine teeth; pterygoid-palatine oriented nearly parallel to the head and does not converge or diverge posteriorly; TaL/TL 0.22–0.26 ♂. Additional morphological characteristics of the species are provided in Table 3.

Table 3. Scale counts, measurements (mm) and collection details of snake specimens of *Sahyadriophis beddomei* gen. et. comb. nov. R/L. Values with '*' indicated damaged.

Specimen No	NHMUK 1946.1.15.32 (Lectotype)	BNHS 1589	BNHS 1588	BNHS 1592	BNHS 1585	BNHS 1583	BNHS 1580	BNHS 1598	NCBS NRC-AA-0024
Locality	Nilgherries, India	Paralai, Anamalai	Paralai, Anamalai	Nelliampathy Hills	Paralai, Anamalai	Peermade, Travancore	Peermade, Travancore	Kalsa Hills, Mysore	Kalakad Mundan-thurai TR
Sex	??	♀	♀	♂	♀	♂	♀	♂	♀
TL	233	645	560	465	585	515	470	460	425 *
SVL	177	495	420	345	455	405	360	340	397
TaL	56	150	140	120	130	110	110	120	28 *
TaL/TL	0.24	0.23	0.25	0.26	0.22	0.22	0.24	0.26	-
D	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	19:19:17	-:19:17	19:19:17
V	143	152	143	140	144	145	146	141	140
A	Divided	Divided	Divided	Divided	Divided	Divided	Divided	Divided	Divided
SC	67	63	68	71	65	76	62	75	14 *
SL	9/9	8/8	8/8	8/8	8/8	8/8	8/7	8/8	8/8
L	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
IL	10/10	9/10	10/9	9/10	9/9	10/10	9/8	9/9	9/10
PreO	1/1	1/1	1/1	1/1	1/1	2/2	1/1	1/1	1/1
PostO	3/3	2/2	3/3	3/3	2/2	3/3	3/3	3/3	3/3
T	1 + 2/1 + 2	1 + 2/1 + 2	1 + 1/1 + 2	1 + 1/1 + 1	1 + 1 */1 + 2	1 + 1/1 + 1	1 + 1/1 + 1	1 + 1/1 + 1	1 + 1/1 + 1

Description of lectotype NHMUK 1946.1.15.32. The lectotype is a juvenile, the specimen is in decent condition, slightly dehydrated (Figure 10). Head short, measuring 10.6 mm from snout tip to the constriction at neck, comprising 4.54% of total length, with a blunt snout in lateral view; upper jaw visible from ventral side. Head broader (6.4 mm) than neck. Snout gradually tapering to blunt, squarish tip in dorsal view (Figure 10d). Rostral subhexagonal, slightly visible when viewed from top; wider than deep. Nostrils small, elliptical shaped, present in the anterior border of the posterior nasal. Paired internasals, smaller than prefrontals. Prefrontals, wider than long. Frontal bell-shaped. Parietals longer than wide. Temporals 1 + 2 on both sides, subequal in size, anterior ones larger than the posterior ones. Four nuchal scales, unequal in size, bordering parietals. Supraocular larger than preocular; preocular large, deeper than wide. Loreal almost as long as high. Three postoculars, upper one larger. Eye circular, 2.2 mm diameter with an elliptic pupil. Nine supralabials; fourth, fifth and sixth in contact with orbit (Figure 10e,f). Supralabials increase in size gradually; seventh and eighth larger than the rest. First supralabial, apart from second supralabial, contacts only rostral and nasal. Second supralabial in contact with nasal, loreal and first and third supralabials. Fifth supralabials wider than high. Third supralabial in contact with preocular, second and fourth supralabials and loreal. Sixth supralabial as high as the fourth supralabial.

Mental short, triangular. Ten infralabials on each side, first long, II to IV infralabials short and thin, fifth onwards larger (Figure 10g). First seven infralabials in contact with the genials. Anterior genials almost thrice as long as wide; posterior genials larger than the anterior ones, in contact anteriorly (Figure 10g).

Body rounded, compressed, ventral surface flattened. Dorsal scales in 19-19-17 rows. Dorsal scales imbricate, regularly arranged, vertebral scales not enlarged, coastal scales slightly enlarged. All body scales keeled, lacking apical pit. The dorsal scales on the ischiadic, anal and tail base regions are smaller. Ventral scales 143 in number, excluding

two preventrals. Anal shield divided, slightly larger than last ventral scale. Subcaudals paired, 67 in number. Tail terminates in a sharp, tapering apical spine. Total length 177 mm, tail length 56 mm, tail/total length ratio 0.24.

Distribution. The species is known from Madikeri District in southern Karnataka southwards. The species appears to be distributed in the southern part of the central Western Ghats all the way to the southern Western Ghats [3,36]. The known distribution range and localities of genus *Sahyadriophis* gen. nov. are presented in Figure 11 and Appendix B.

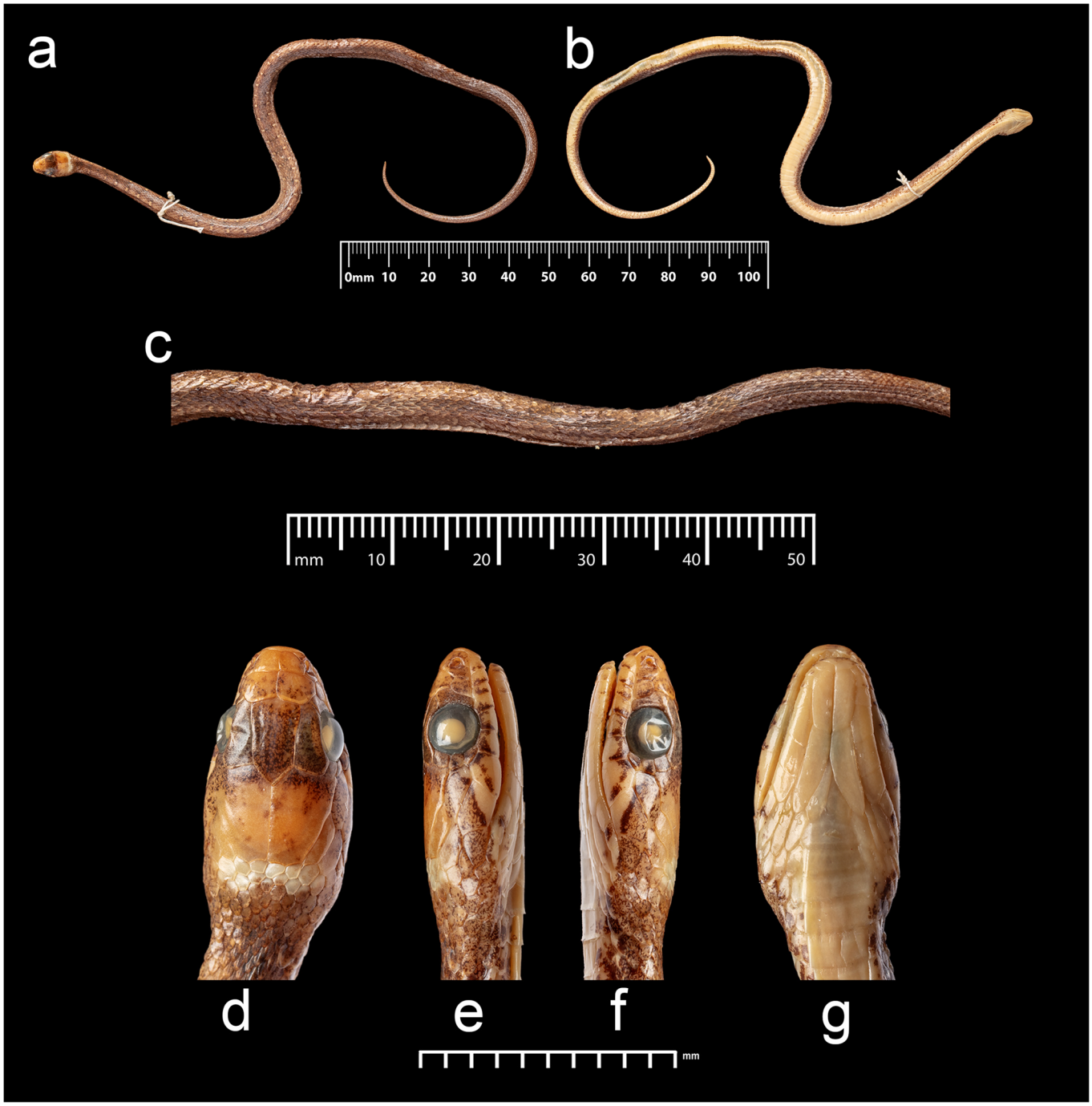

Figure 10. Lectotype NHMUK 1946.1.15.32 of *Sahyadriophis beddomei* gen. et. comb. nov., (**a**) dorsal view, (**b**) ventral view, (**c**) lateral view of body, (**d**) head dorsal, (**e**) head right lateral, (**f**) head left lateral, (**g**) head ventral view.

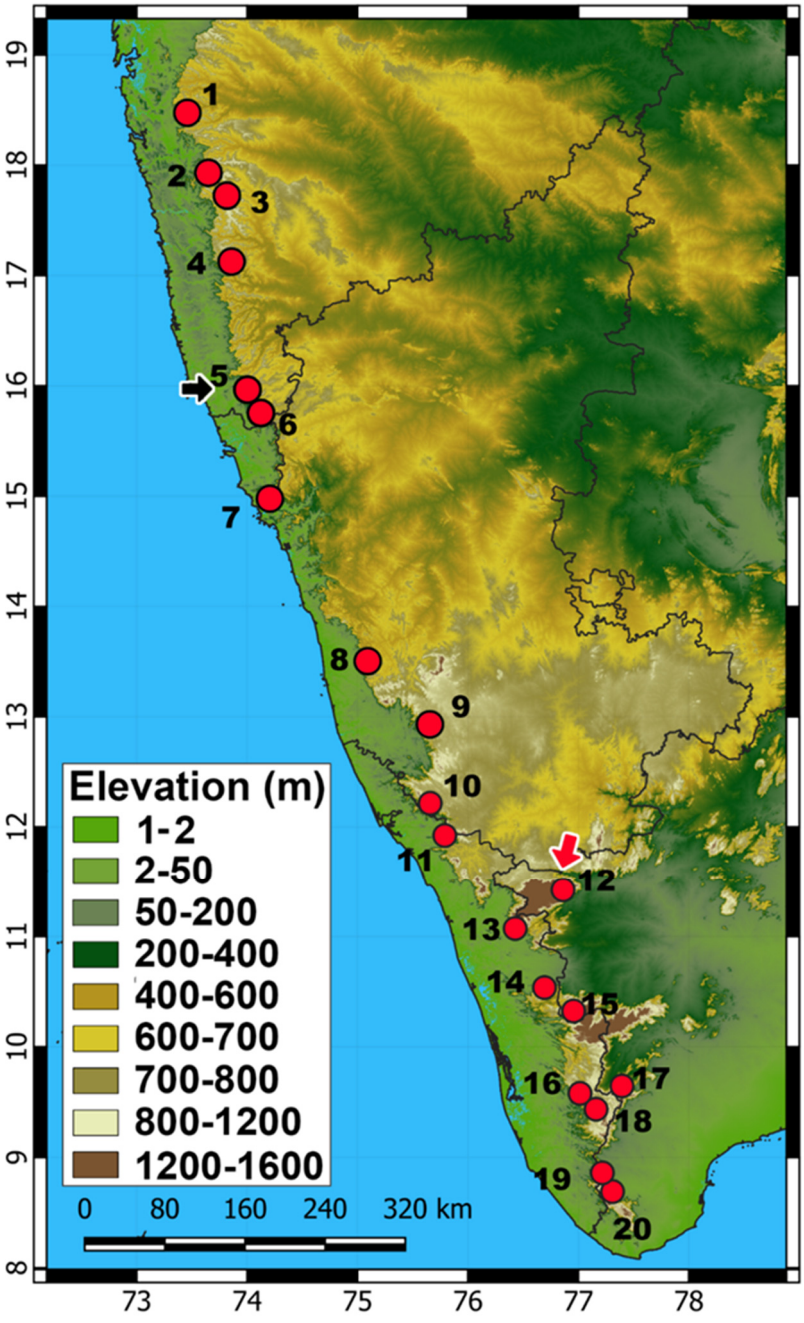

Figure 11. Elevation map of peninsular India showing the distribution of *Sahyadriophis* gen. nov., black and white edged arrow indicates type locality of *Sahyadriophis uttaraghati* gen. et. sp. nov., red and white edged arrow indicates type locality of *Sahyadriophis beddomei* gen. et. comb. nov.; Localities: 1. Tamahini, 2. Mahabaleshwar, 3. Kaas, 4. Chandoli NP, 5. Amboli, 6. Tillari, 7. Cotigao WLS, 8. Agumbe, 9. Kadumane, 10. Honey Valley, 11. Arlam WLS, 12. Nilgiri, 13. Silent Valley NP, 14. Nelliampathy, 15. Valparai, 16. Peermade, 17. Meghamalai, 18. Periyar, 19. Shendurney WLS, 20. Kalakad Mundanthurai TR.

4. Discussion

Recent molecular phylogeny studies on natricine snakes [2,5,20,37] have shed light on the systematics of the members of the group. This has led to several taxonomic changes and further work remains. The present work only goes a small way in resolving the species that were assigned to the genus *Amphiesma* in the past. Discovery of a new Western Ghats-endemic genus highlights the potential for discovery of more distinct linages. Despite the fact that the *Sahyadriophis beddomei sensu lato* is a common snake throughout its range and

is represented by numerous specimens across natural history museums, it remains largely unstudied. The new species is not just genetically distinct, but is also morphologically distinct. This highlights the need for dedicated attention to snake systematics through an integrated approach for a more widespread taxa, as in the present case.

Sahyadriophis gen. nov. appears to be basal to the clade containing *Xenochrophis*, *Fowlea* and *Atretium* and is shown to have shared a common ancestor with them during the late Oligocene to early Miocene [2]. Given that the support of the relationship recovered is poor to moderate, we refrain from proposing any biogeographic hypothesis in this scenario until further sampling of *Amphiesma s. l.* is complete. *Proahaetulla* Mallik, Achyuthan, Ganesh, Pal, Vijayakumar and Shanker, 2019, is another lineage of an ancient serpent discovered in the Western Ghats with which *Sahyadriophis* gen. nov. shares the same time of diversification [38].

The new species is currently known from the northern and parts of the central Western Ghats, whereas *Sahyadriophis beddomei* gen. et. comb. nov. is settled in the remaining part of the Western Ghats. Further sampling would be necessary to define their exact ranges and to identify possible biogeographic barriers. Based on IUCN criteria for conservation, we propose to treat both the species as data deficient pending additional data on their distribution and biology. Examination of additional material and molecular data from across the Western Ghats would be necessary to define the distribution of the two species of the new genus.

The Western Ghats are a known biodiversity hotspot [39], and despite continued herpetological explorations, new species are discovered even now [40–44]. Description of the new genus and the species merely adds to our understanding of the biodiversity of this region, which remains not entirely well documented.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/taxonomy3030024/s1, Figure S1: Complete phylogeny tree; Table S1: Primers used for amplification and sequencing; Table S2: GenBank accession numbers and voucher numbers; Table S3: Sequence evolution model.

Author Contributions: Conceptualization, H.P., T.T. and Z.A.M.; methodology, H.P. and Z.A.M.; data curation, H.P., P.D.C. and Z.A.M.; formal analysis, H.P. and Z.A.M.; writing—original draft preparation, H.P. and Z.A.M.; writing—review and editing, T.T. and P.D.C. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All data are presented in this article and in GenBank (https://www.ncbi.nlm.nih.gov).

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

Appendix A. Comparative Material Examined

Amphiesma stolatum ZAM 124, Pakke Tiger Reserve, Arunachal Pradesh; ZAM 200, Ratnagiri, Maharashtra, India; CT scan of FMNH 169627, Chieng Mai Prov., Thailand

Amphiesma monticola: BNHS 1596, Wayanad, Malabar; BNHS 1597, Peermade, Travancore.

Aspidura ceylonensis: BNHS 1750, Uva Patnas.

Atretium schistosum: BNHS 1671, Cannanore, Kerala; BNHS 2945, BNHS 2962, Avadi, Madras.

Fowlea piscator: BNHS 1337, Kurduwadi, Solapur; BNHS 1382, Deolali, Nashik; BNHS 1418, Arunachal, Cachar dist., India; CT scan of FMNH 179132, Chiang Mai, Thailand

Hebius venningi: BNHS, 1317, BNHS, 1318, BNHS, 1319, BNHS 1320, Haka Chin Hills.

Herpetoreas platyceps: BNHS 1555, Ghora Galli, Punjab; BNHS 1562, Gonda, UP; BNHS 1565, Gangtok, Sikkim; BNHS 1576, Kurseong, Darjeeling; BNHS 2742, Nainital; BNHS 3087, Dhanaulti, Tehri, UP.

Herpetoreas xenura: BNHS 3212, Aizawal Tourist Lodge, Mizoram; BNHS 3213, Palak Stream, S. Mizoram.

Rhabdops aquaticus: BNHS 3194, Near Mula Mutha River, Manjari Budruk, Pune, Maharashtra.

Rhabdophis himalayanus NHMUK 1946.1.23.75 and NHMUK 1946.1.14.27, Nepal; ZMUC R-60956, Assam, India

Rhabdophis bindi NCBS-AG732, Trishna Wildlife Sanctuary, Tripura, India

Smithophis arunachalensis ZSIK 23875, Namdapha Camp, Changlang District, Arunachal Pradesh

Smithophis atemporalis: BNHS 3530, Model Veng, Aizawl, India; BNHS 3531, Luangmual, Aizawl, India.

Smithophis bicolor: BNHS 1730, BNHS 1731, Shillong, Assam; BNHS 1732, Tura Garo Hills.

Xenochrophis cerasogaster: BNHS 1658, BNHS 1665, BNHS 1667, BNHS 1670, Fyzabad, UP

Appendix B. Distribution of *Sahydriophis* gen. nov. Across the Western Ghats. See Figure 11 for Locality Codes

Locality	Latitude (°N)	Longitude (°E)	Locality Code
Tamil Nadu, Kalakad Mundanthurai Tiger Reserve	8.68834	77.30947	20
Kerala, Silent Valley National Park	11.07064	76.42817	13
Karnataka, Honey Valley	12.21454	75.6581	10
Kerala, Arlam WLS	11.92198	75.7904	11
Kerala, Peryar TR	9.434325	77.16058	18
Kerala, Shendurney WLS	8.857829	77.21752	19
Tamil Nadu, Valparai	10.32338	76.9569	15
Tamil Nadu, Kotagiri	11.42177	76.86173	12
Tamil Nadu, Meghamalai	9.644689	77.39547	17
Kerala, Peermade	9.577265	77.01508	16
Kerala, Nelliampathy	10.53539	76.69361	14
Karnataka, Kadumane Estate	12.92978	75.65515	9
Karnataka, Agumbe	13.50323	75.09244	8
Mahatashtra, Tillari	15.75335	74.12523	6
Mahatashtra, Amboli	15.96472	74.00357	5
Goa, Cotigao WLS	14.97603	74.20619	7
Maharashtra, Chandoli NP	17.12611	73.85931	4
Maharashtra, Mahabaleshwar	17.93127	73.64934	2
Maharashtra, Tamahini	18.47575	73.45891	1
Maharashtra, Kaas	17.72497	73.81708	3

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