



A new Indian species of *Rhinophis* Hemprich, 1820 closely related to *R. sanguineus* Beddome, 1863 (Serpentes: Uropeltidae)

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Abstract

A new species of the uropeltid (shieldtail snake) genus *Rhinophis* is described based on a type series of seven specimens from the Wayanad region of the Western Ghats of peninsular India. The holotype was collected before 1880 but had been misidentified as the phenotypically similar and parapatric (possibly partly sympatric) *R. sanguineus*. *Rhinophis karinthandani* sp. nov. is diagnosed by a combination of 15 dorsal scale rows at midbody, 4–8 pairs of subcaudal scales, colour pattern (uniformly dark above, whitish below with extensive dark mottling), and by its distinct mitochondrial DNA sequences (e.g. >7.6% uncorrected p-distance for *nd4*). Phylogenetic analysis of mitochondrial DNA sequence data indicates that the new species is most closely related to *R. sanguineus* among currently recognised species, with this pair most closely related to the partly sympatric *R. melanoleucus*. The new species description brings the number of currently recognised species in the genus to 24, six of which are endemic to India and 18 endemic to Sri Lanka. A new key to the identification of Indian species of *Rhinophis* is provided.

Key words: identification key, *Rhinophis microlepis*, shieldtail, snakes, Wayanad, Western Ghats

Introduction

Uropeltids, or shieldtails, are typically small (total length < 600 mm) fossorial snakes endemic to Sri Lanka and peninsular India. The approximately 60 currently recognised species are classified into seven or eight genera (Pyrone *et al.* 2016; Cyriac & Kodandaramaiah 2017). All uropeltid genera occur in India, with only one genus occurring also in Sri Lanka, *Rhinophis* Hemprich, 1820 (e.g. Pyrone *et al.* 2016). Eighteen of the 23 currently recognised species of *Rhinophis* are endemic to Sri Lanka, and no species occur in both Sri Lanka and India (Cyriac *et al.* 2020; Pyrone *et al.* 2016; Wickramasinghe *et al.* 2017; 2020; Gower 2020). Following the recent description of *R. melanoleucus* Cyriac, Narayanan, Sampaio, Umesh & Gower, 2020, there are five currently recognised Indian species of *Rhinophis* (Cyriac *et al.* 2020). The description of *R. melanoleucus* prompted us to more closely examine historical and recent specimens of Indian (especially Wayanad region) *Rhinophis* in collections and in the field and using DNA sequence data. Here we present new molecular phylogenetic data for *Rhinophis*, describe a new Indian species, and provide an updated key to the Indian species of the genus.

Materials and methods

Comparative material of Indian *Rhinophis* is reported in Appendix 1. Taxonomy and taxon spellings follow McDiar-mid *et al.* (1999) and Pyron *et al.* (2016). Catalogue numbers of reported specimens bear the following institutional prefixes: BMNH (Natural History Museum, London, UK), BNHS (Bombay Natural History Society, Mumbai, India), BUB (Bangalore University, Bengaluru, India), CAS (California Academy of Sciences, San Francisco, USA), MCZ (Museum of Comparative Zoology, Harvard University, USA), MNHN (Muséum national d'Histoire naturelle, Paris, France), ZMB (Museum für Naturkunde, Berlin, Germany), ZSI/WGRC (Western Ghats Regional Centre of the Zoological Survey of India, Kozhikode). Vouchers reported with a VP prefix are field numbers of specimens destined to be deposited in BNHS, Centre for Ecological Sciences (Indian Institute of Science, Bengaluru, India) or ZSI/WGRC. We have examined type specimens of all currently recognised species of *Rhinophis* except *R. goweri* Aengals & Ganesh, 2013, for which we rely on the original description (Aengals & Ganesh 2013) and examination of BNHS 3465.

Ventral scale counts were recorded following Gower & Ablett (2006). Scale row reductions were recorded following Dowling (1951). All measures were taken with dial calipers to the nearest 0.1 mm, except for total length and circumference, which were taken to 1 mm using a ruler and a piece of thread plus ruler, respectively. Snout-vent length was calculated by subtracting tail length from total length. Bilateral measures were taken on the right side of each specimen, unless that side was damaged. Sex was determined by observing everted hemipenes, by examining urogenital systems *in situ* through small ventral incisions in the body wall, or by inference from numbers of subcaudals.

We generated DNA sequence data for 10 available specimens of Indian *Rhinophis* spp. (Appendix 2). Genomic DNA was extracted from ethanol-preserved muscle or liver samples using Qiagen's DNeasy kit (Qiagen, Valencia, CA). DNA sequence data for parts of the following three mitochondrial (mt) genes were amplified and sequenced: 12s rRNA (*12s*, primers 12Sa-L1091 and 12Sb-H1478: Kocher *et al.* 1989), 16s rRNA (*16s*, primers 16Sar-L and 16Sbr-H: Palumbi *et al.* 1996) and NADH dehydrogenase subunit 4 (*nd4*, primers ND4 and Leu: Arévalo *et al.* 1994). Sequences were edited manually in Geneious Prime (Biomatters). The newly generated sequence data were combined with the data for all species of *Rhinophis*, *Plectrurus* and *Pseudoplectrurus* that were analysed by Cyriac & Kodandaramaiah (2017) and Jins *et al.* (2018; see Appendix 2).

Alignments for each individual marker were carried out using Clustal Omega v. 1.2.3 (Sievers *et al.* 2011; Sievers and Higgins 2018) implemented in Geneious with default settings. Ambiguously aligned positions in *12s* and *16s* alignments were removed using Gblocks v. 0.91b (Castresana 2000) via an online server (<http://phylogeny.lirmm.fr/>, Dereeper *et al.* 2008) using the 'less stringent' options. The final concatenated alignment used in analyses included 43 specimens and 1524 nucleotide positions (351 bp [base pairs] of *12s*, 475 bp of *16s*, 698 bp of *nd4*). Newly generated sequences have been deposited in GenBank (Appendix 2) and the analysed alignment is available from the Natural History Museum's Data Portal (data.nhm.ac.uk: <https://doi.org/10.5519/0066595>).

Pairwise uncorrected distances (p-distances) were calculated using MEGA version X (Kumar *et al.* 2018; Stecher *et al.* 2020). The concatenated dataset was analysed with PartitionFinder v. 2.1.1 (Lanfear *et al.* 2016; Guindon *et al.* 2010), applying the corrected Akaike Information Criterion (AICc) to find the best-fitting partition scheme and available models of nucleotide substitution to be implemented in subsequent phylogenetic analyses. The best partition scheme comprised four different models that were best fitting for four partitions: TRN+I+G: *nd4* 2nd codon and *12s*; GTR+I+G: *16s*; HKY+I: *nd4* 3rd codon; GTR+G: *nd4* 1st codon.

Phylogenetic relationships for the concatenated dataset were inferred using Bayesian Inference (BI) and Maximum Likelihood (ML). BI analysis was performed in MrBayes v. 3.2.6 (Ronquist *et al.* 2012), conducting two independent runs for 1×10^6 generations, sampling every 100 generations, resulting in 10,000 trees. The first 25% of trees were discarded as burn-in and the remaining trees used to determine posterior probability values for internal branches. Runs were checked using Tracer v. 1.7.1 (Rambaut *et al.* 2018) to verify convergence of the runs and that effective sample sizes (ESS) were all >200. ML analysis was performed using Garli v. 2.01 (Zwickl 2006). The best tree was estimated from 10 independent runs, and bootstrap support for internal branches was assessed with 1000 replicates. Bootstrap support values were added to the best tree with the DendroPy v. 4.4.0 (Sukumaran and Holder, 2010) SumTrees v. 4.4.0 (Sukumaran and Holder, 2020) Python libraries. Analyses for PartitionFinder, MrBayes and Garli were carried out in the Cipres Science Gateway v. 3.1 (Miller *et al.* 2010). Trees were rooted with *Plectrurus* + *Pseudoplectrurus*, based on phylogenetic results reported by Cyriac & Kodandaramaiah (2017) and Jins *et al.* (2018).

Results

The 10 Indian *Rhinophis* individuals sampled from Wayanad (Kerala) and Karnataka constitute a near-maximally (BI posterior probability 1, ML bootstrap 99) supported clade comprising three main clades, two strongly supported (posterior probability 1, bootstrap 99–100) lineages, and one strongly supported under BI (posterior probability 1) but not under ML (bootstrap 57) analysis (Fig. 1). The two specimens of *R. melanoleucus* (Wayanad) form one lineage, sister to the other two main lineages of Wayanad (and Karnataka) *Rhinophis*. The other two lineages comprise eight specimens that can be referred on the basis of morphology separately to *R. sanguineus* Beddome, 1863 (four specimens: Wayanad), to a dehydrated roadkill specimen (*Rhinophis* sp.: Karnataka), and to a new species described here (three specimens: Wayanad). The results of the phylogenetic analyses agree with those of Jins *et al.* (2018) in that the Indian *R. travancoricus* is more closely related to the Sri Lankan clade than to other sampled Indian *Rhinophis*.

Uncorrected p-distances for the three genes are available from the Natural History Museum's Data Portal (data.nhm.ac.uk: <https://doi.org/10.5519/0066595>). Values for within and between *R. melanoleucus*, *R. sanguineus*, *R. sp.* and the new species are summarized in Table 1.

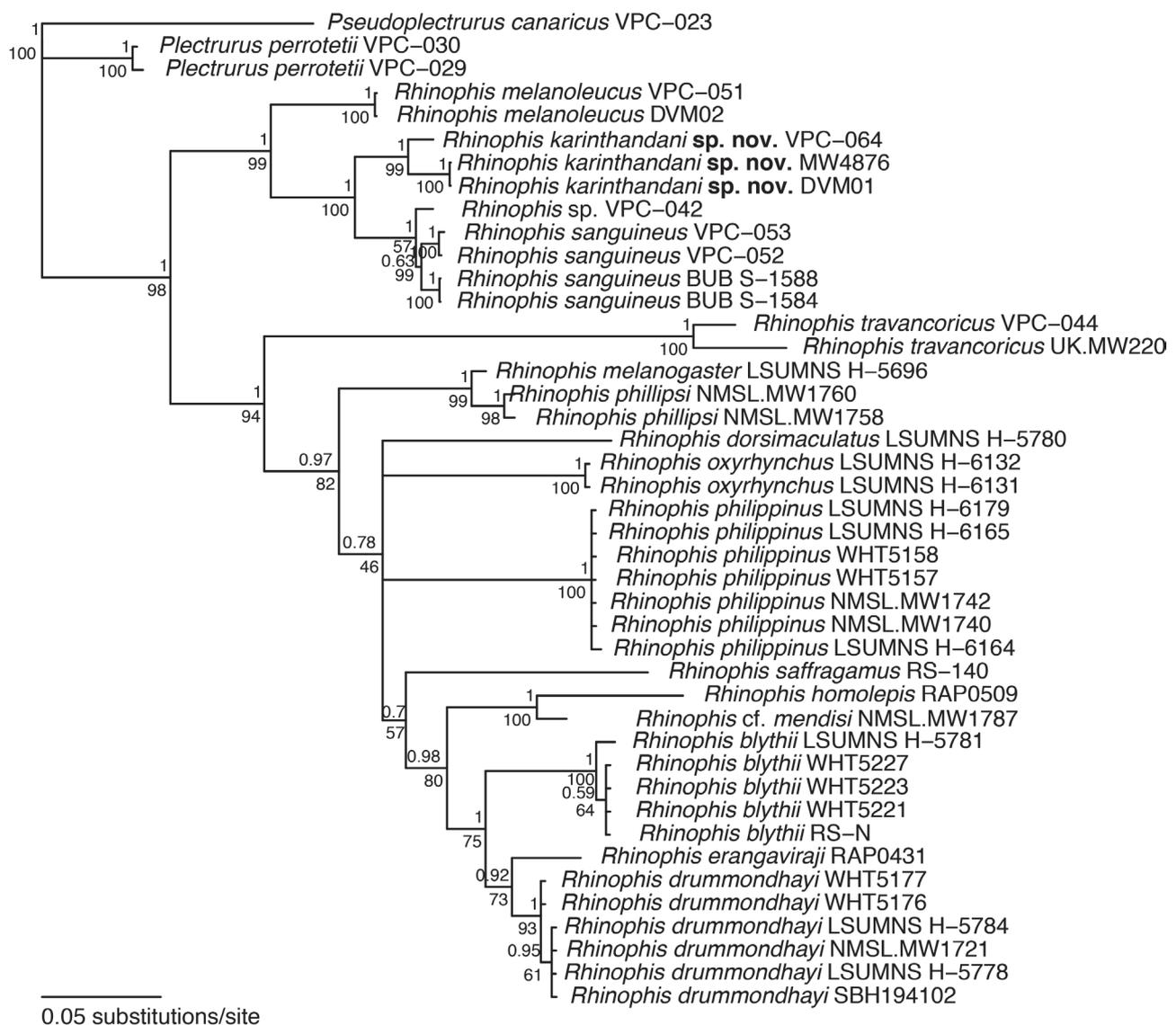


FIGURE 1. Bayesian Inference phylogeny of *Rhinophis*, based on *12s*, *16s* and *nd4* mitochondrial DNA sequence data. Numbers at internal branches are Bayesian posterior probabilities (above, given to two decimal places) and maximum likelihood bootstrap values (below). See Appendix 2 for specimen details. Scale bar indicates substitutions per site.

Rhinophis karinthandani sp. nov.

Figs. 1–3, 6–9, Tables 1–3, Appendices 1–4

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Chresonymy

Rhinophis sanguineus Beddome, 1863; Cyriac *et al.* 2020, in part (see Appendix 1)

Holotype (Fig. 2). BMNH 79.7.4.2, female, “Manantoddy, Wynad, 2,000 ft” [= Mananthavady, Wayanad district], Kerala, India (Fig. 3). Mananthavady today is a small town, the centre of which (according to GoogleEarth) is at 11.8035° N, 76.005° E and an elevation of ca. 760 m. We can find no collection date associated with this specimen, but it was accessioned into the collection of the Natural History Museum, London in July 1879.

Paratypes (n = 6). The paratypes were collected on different dates between 2013–2019. Five are from Lakkidi, Wayanad district, Kerala, India (11.514944° N, 76.038242° E; 835 m): BNHS 3540, female; BNHS 3542, male; BNHS 3544, female; BNHS 3545, male; BNHS 3546, female. The other paratype is ZSI/WGRC/V-3143 from Chandanathodu, Mananthavady, Wayanad district, Kerala, India (11.844758° N, 75.807739° E; 824 m).

Referred specimens (n = 9). BMNH 79.7.4.3, female, same data as for holotype, lacks head and anterior end of body. BMNH 74.4.29.109, Wynad [Wayanad district, Kerala, India], ZMB 10358, Wayanad, India. MNHN 1895.75, “Sri Lanka” (presumably in error). BNHS 3153, Anakkampoil, Wayanad district, Kerala (listed as *R. sanguineus* by Cyriac *et al.* 2020). BNHS 3541 and 3543, Lakkidi, Wayanad district, Kerala, India. BNHS 3605 and 3606, near Pookode, Wayanad district, Kerala, India. These nine specimens are considered referred rather than type specimens because they are damaged (BMNH 79.7.4.3, BNHS 3541 and 3543), are associated with imprecise or probably incorrect locality data, or because they have not been compared in as much detail with the holotype.

Diagnosis. *Rhinophis karinthandani* sp. nov. differs from all other species of *Rhinophis* except *R. fergusonianus* Boulenger, 1896, *R. melanoleucus*, and *R. sanguineus* in having 15 dorsal scale rows at (or just behind) midbody (versus 17 or 19 in other congeners). *Rhinophis karinthandani* sp. nov. differs from *R. fergusonianus* and *R. melanoleucus* in having a reduction from 17 to 15 dorsal scale rows that occurs anterior to the 80th ventral (versus posterior to the 90th ventral in *R. fergusonianus* and posterior to the 99th ventral in *R. melanoleucus*: Cyriac *et al.* 2020), and in having dark spots or speckles ventrally (versus dark blotches). *Rhinophis karinthandani* sp. nov. differs from *R. melanoleucus* also in having fewer ventrals (< 206 versus > 217) and fewer subcaudals (in males: 4–5 versus 6–7). The new species is most similar superficially to the parapatric (possibly partly sympatric) *R. sanguineus*, but the two species can be distinguished on the basis of the former having fewer subcaudals (left-right means of 4–5 in females and 6.5–8 in males versus 5–7 and 8.5–10.5, respectively), having a reduction from 19 to 17 dorsal scale rows that occurs anterior to the 34th ventral (mean 28th ventral [n = 18 sides]; versus posterior to the 26th ventral, mean 34 [n = 28]) and a reduction from 17 to 15 dorsal scale rows that occurs anteriorly to the 78th ventral (mean 68th ventral [n = 18 sides]; versus posterior to the 67th ventral, mean 79th [n = 28]) (Appendix 4; Cyriac *et al.* 2020), in mitochondrial DNA sequences (e.g. >7.6% uncorrected p-distance for *nd4*: Table 1), and in colour pattern. In terms of colour pattern, both species have a dark dorsum and generally pale venter, but *R. karinthandani* sp. nov. has an extensively darkly mottled or speckled or spotted venter, except for a narrow (approximately one scale wide, generally across second and third and/or third and fourth dorsal scale rows), longitudinal, ventrolateral pale line along each side, immediately below the dark dorsum (and sometimes other, subparallel pale lines further ventrally), whereas *R. sanguineus* has a less mottled venter with the paler colour below the darker dorsum being much more extensive than a narrow regular line. In life, the paler venter of *R. karinthandani* sp. nov. is whitish (to pale pinkish more anteriorly), but in *R. sanguineus* is a vivid red (paler in smaller specimens, see Discussion). The colour pattern differences in preservation hold well for almost all specimens we have identified, although in *R. sanguineus* specimen VPRS0918093, many of the mostly pale scales in the broad pale areas below the darker dorsum have small blackish dots. At least in life, the dorsal colour of *R. sanguineus* appears to be darker, more blackish than in *R. karinthandani* sp. nov. Photographs of the type specimens of *R. sanguineus* and its junior synonym *R. microlepis* are presented in Figs. 4 and 5.

Identification. The new uropeltid species is referred to *Rhinophis* because it has an eye that lies within an ocular scale (eye distinct from adjacent scales in *Platyplectrurus* Günther, 1868), has a clearly discrete tail ‘shield’ comprising a single, enlarged terminal scute (absent in *Melanophidium*, *Brachyophidium*, *Platyplectrurus*, *Plectrurus* and *Teretrurus*), lacks a mental groove (present in *Melanophidium*), lacks supra- or postoculars or temporals (at least one of which is present in *Brachyophidium*, *Platyplectrurus*, *Plectrurus* and *Teretrurus*), and lacks midline



FIGURE 2. Photographs of the holotype (BMNH 79.7.4.2) of *Rhinophis karinthandani* **sp. nov.** Upper row: head in dorsal, right lateral, ventral and left lateral views; central two rows whole specimen in approximately dorsolateral (upper) and ventrolateral (lower) views; lower row: tail in dorsal, right lateral, ventral, dorsal and left lateral views. Scale bar increments in mm. Photographs by Kevin Webb (NHM, London).

contact between the nasals (present in *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Pseudoplectrurus* Boulenger, 1890, *Teretrurus*, and almost all *Uropeltis* [those *Uropeltis* that lack nasal-nasal contact have small terminal scutes and > 15 dorsal scales rows at, or just behind, midbody]).

TABLE 1. Uncorrected p-distances (%) for intra- and interspecific comparisons for three closely related species of Indian *Rhinophis*, for three mitochondrial genes. Values in parentheses in first column are number of pairwise comparisons; values in last three columns are means, with ranges in parentheses.

	<i>nd4</i>	<i>12s</i>	<i>16s</i>
Within <i>R. melanoleucus</i> (1)	0	0	0.2
Within <i>R. sanguineus</i> (6)	2.0 (0–2.9)	0.5 (0–0.9)	0.2 (0–0.4)
Within <i>R. karinthandani</i> sp. nov. (3)	2.4 (0–3.7)	1.3 (0–2.0)	0.7 (0–1.0)
<i>R. melanoleucus</i> — <i>R. sanguineus</i> (8)	11.8 (11.5–12.1)	4.9 (4.8–5.1)	3.2 (3.0–3.4)
<i>R. melanoleucus</i> — <i>R. karinthandani</i> sp. nov. (6)	12.6 (12.5–12.8)	4.4 (4.3–4.6)	3.2 (3.0–3.4)
<i>R. melanoleucus</i> — <i>R. sp.</i> (2)	11.6 (11.6)	4.3 (4.3)	3.0 (2.9–3.1)
<i>R. sanguineus</i> — <i>R. sp.</i> (4)	2.8 (2.8)	1.2 (1.1–1.4)	0.2 (0–0.2)
<i>R. sanguineus</i> — <i>R. karinthandani</i> sp. nov. (12)	8.8 (8.2–9.6)	4.1 (3.4–4.6)	2.0 (1.9–2.1)
<i>R. karinthandani</i> sp. nov. — <i>R. sp.</i> (3)	8.3 (7.7–8.6)	4.0 (3.4–4.3)	1.7 (1.5–1.8)

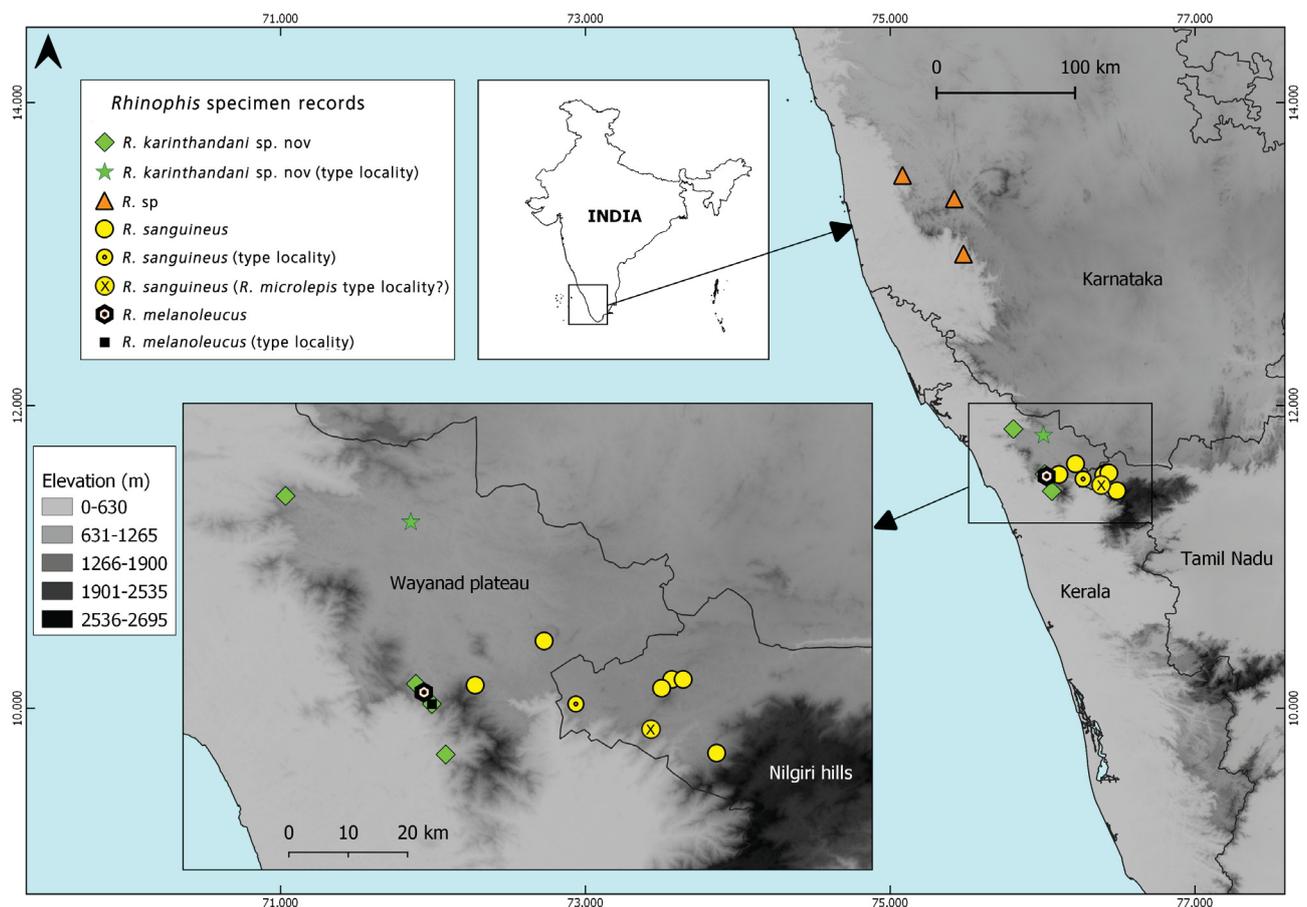


FIGURE 3. Map showing specimen record locations of *Rhinophis* from the Wayanad plateau region and from Karnataka. See Appendix 3 for underlying distribution data.

Description of holotype (Fig. 2). See Table 2 for morphometric and meristic data. Good condition; longitudinal right-of-ventral incision 25 mm extending anteriorly from ca. 45 mm from tail tip. Head small, snout pointed. Rostral pointed, longer than wide, without dorsal crest but with narrow, rounded dorsal ridge; in lateral view with slightly convex ventral and (more strongly) dorsal margins; widest at level of anterior upper corner of first supralabials.

Rostral many (ca. 4) times longer (in dorsal view) than rostral-frontal gap. Frontal irregularly hexagonal, longer than wide, lateral (ocular) margins converging posteriorly; lateral (ocular) margin shortest, posterolateral edges longest. Frontal shorter, wider than rostral. Nasals separated from each other by posterior half of rostral. External naris small, subcircular, slightly countersunk within small depression, located at anteroventral corner of nasal. Nasal contacts first and second supralabials. Prefrontals in contact with each other along midline (left overlapping right) for longer distance than portion of rostral posterior to nasals. Prefrontals wider than long, shorter than frontal. Supralabials four, first smallest, making the least contribution to margin of mouth; fourth largest. Ocular contacts third and fourth supralabials. Eye distinct, diameter approximately 0.3 times the length of ocular, located near anteroventral corner of ocular (very close to lower edge, closer to this edge than to anterior of ocular), only very slightly (at most) bulging slightly from ocular surface, pupil subcircular. Paired parietals longer than wide, approximately as long and as wide as frontal, posteriorly broadly rounded, angle between posteromedial and posterolateral edges approximately 90°. Parietals in longer midline contact than between opposite prefrontals, left overlapping right. Each parietal contacts four scales other than head shields. No mental groove; mental pentagonal, wider than long, smaller than infralabials, contacting first infralabials but not first ventral; three pairs of infralabials on left, two on right (first two 'fused'). On left, second infralabial largest, first smallest. First and second ventrals longer than wide, third and fourth approximately as long as wide, fifth and subsequent ventrals wider than long.

TABLE 2. Meristic and metric data for holotype (*) and paratypes of *Rhinophis karinthandani* sp. nov. Measures given in mm. SL4 = fourth supralabial; hyphen (-) indicates shortest distance between two points. Paired scale counts given in left, right order.

	BMNH 79.7.4.2*	BNHS 3540	BNHS 3542	BNHS 3544	BNHS 3545	BNHS 3546	ZSI/WGRC V-3143
Sex	F	F	M	F	M	F	—
Total length	245	228	163	252	233	287	201
Tail length	6.3	7.0	6.0	7.8	12.0	7.0	4.8
Midbody width	5.9	4.6	4.6	6.0	5.2	5.3	4.8
Midbody circumference	18	—	—	—	—	—	15
Snout tip-posterior edge SL4 (head length)	6.3	5.5	4.7	5.3	5.7	6.2	5.7
Head width at posterior edge SL4	4.5	3.6	3.7	3.3	3.5	4.1	3.6
Maximum rostral length	2.3	2.2	2.1	2.2	2.1	2.2	2.2
Rostral-frontal	0.6	—	—	—	—	—	0.5
Frontal length	2.0	1.9	1.7	2.0	1.9	1.8	2.0
Frontal width	2.0	1.7	1.5	1.8	2.0	1.9	2.0
Snout tip-eye	—	2.9	2.6	2.9	3.0	3.1	3.0
Tail shield width at base	5.4	4.8	4.0	4.8	4.5	5.5	5.0
Tail shield height at base	6.2	—	—	—	—	—	5.8
Tail shield middorsal length	6.3	—	—	—	—	—	6.0
Tail shield midventral length	1.2	—	—	—	—	—	1.3
Ventral scales	195	203	197	194	198	205	197
Subcaudal scales (number unpaired)	5,5 (0)	5,5 (0)	8,8 (1)	5,5 (0)	7,7 (1)	5,5 (0)	4,4 (0)
Supralabial scales	4,4	4,4	4,4	4,4	4,4	4,4	4,4
Infralabial scales	3,2	3,3	3,3	3,3	3,3	3,3	3,3
Scales surrounding terminal scute	14	12	13	11	11	13	12

Body cylindrical. Body scales generally evenly sized on dorsum and along body except for those involved in dorsal scale row reductions. Midline ventral scales between mental and anal of even size though anteriormost ones gradually narrow. At midbody, exposed part of ventrals approximately 1.5 times wider than scales in first dorsal row. Ventrals 195. Dorsal scale rows 19 anteriorly, reducing to 17 by level with 28th ventral and to 15 rows by 65th ventral, maintained thereafter until close to the vent; scale row reduction formula:



FIGURE 4. BMNH 1946.1.16.54 (formerly BMNH 64.3.9.2) lectotype of *Rhinophis sanguineus*. Upper row head (left, ventral, dorsal, right views) and tail (right, dorsal, ventral, left views); middle and lower rows whole animal in approximately dorsal and ventral views. Scale bar increments in mm. Photographs by Harry Taylor (NHM, London).

3 + 4 (28) 3 + 4 (49), +4 (58), 3 + 4 (65)
 19 ----- 17 ----- 15
 3 + 4 (28) 3 + 4 (45), +4 (54), 3 + 4 (62)

Dorsal scale rows (i.e., excluding subcaudals) approximately 15 at level of first subcaudals. Head and body scales macroscopically smooth. Paired anal scales (right overlying left) considerably larger than posteriormost ventrals and subcaudals. Distal margin of each anal overlaps two (left) and three (right) small scales in addition to anteriormost subcaudals. Five subcaudals on each side. Some scales at posterior end of specimen bear very low, short parallel ridges, towards posterior edges—on small scales overlapped by anals, on lower three or four dorsal scale rows of posterior of body and of tail, and on subcaudals. Tail ‘shield’ large, forming tip of tail, visible from below

and especially clearly from above, flattened to slightly concave on anterior end of upper surface, domed posteriorly, longer than wide in dorsal view, wider than depth of tail (at base of shield), larger than head (longer than distance between snout tip and back of parietals), base surrounded by 14 scales (including last subcaudals). Shield surface roughened, bearing narrow, discontinuous ridges (longer, more continuous stretches located laterally towards shield base), receding and somewhat converging towards tip; evenly spaced, subparallel, approximately straight; without projections or ridges close to midline immediately anterodorsal to shield apex.

Colour in alcohol. Rostrum pale brown. Head shields brown; supralabials paler towards lower edges. Infralabials mostly pale brown with pale edges. Dorsal surface of body brown with small, isolated, pale, off-white flecks; scales darker brown at bases. Ventral surface of body brown and (slightly less in area) pale off-white; mostly irregular though with some irregular and mostly intermittent longitudinal lines. Most notably, a mostly continuous, narrow (< 1 scale wide) pale, off-white line across dorsal scale rows 3–4 posteriorly and between rows 4–5 or 5–6 anteriorly. Dorsal scale rows ventromedial to this line typically with brown centre and pale, off-white upper and lower margins. Anal shields brown with translucent narrow edges. Subcaudals and lower tail dorsal scale rows brown and pale, off-white, similar to the ventral surface of the body though with a darker brown. Tail shield mostly matt brown with pale orange anterolateral strip on each side.



FIGURE 5. BMNH 1946.1.16.76 (formerly BMNH 74.4.29.110) holotype of *Rhinophis microlepis*. Upper row head (dorsal, left, ventral, right views) and tail (dorsal, left, ventral, right views); lower row whole specimen in two views. Scale bar increments in mm. Photographs by Harry Taylor (NHM, London).

Paratypes (Fig. 6). Variation in some meristic and morphometric characters are reported in Table 2 and Appendix 4. Paratypes generally in moderate to good condition. All paratypes female except BNHS 3542 and 3545. The number, form and arrangement of head shields are as in the holotype with the following exceptions. In all paratypes, except BNHS 3546, rostral with slightly blunt tip in dorsal view; more prominently arched in lateral view in BNHS 3542 and 3545. In BNHS 3546, rostral widest at the level of naris. Rostral length three times longer than the rostral-frontal gap in BNHS 3540. Shape and size of frontal differs slightly from that of holotype in some specimens; approximately pentagonal in BNHS 3546, slightly subtriangular in BNHS 3540. Frontal wider than long in BNHS 3546, longer than rostral in BNHS 3540 and approximately as long as wide in BNHS 3542. Paired parietals vary in shape, being subpentagonal and relatively shorter in BNHS 3540 and 3545, and as long as wide in BNHS 3544. Three infralabials on both sides in all paratypes, as on left of holotype.



FIGURE 6. BNHS paratypes of *Rhinophis karinthandani* **sp. nov.** Heads and tails shown in (from left to right) dorsal, ventral, right lateral and left lateral views. A. BNHS 3540; B. BNHS 3542; C. BNHS 3544; D. BNHS 3545; E. BNHS 3546. Scale bars 10 mm.

Ventrals 194–205; in BNHS 3544 ventrals 182 and 183 are divided (paired). Subcaudals 4–5 in females, 7–8 in males. Number of anteriormost ventrals that are longer than wide 1–5 in BNHS 3540, 1–3 in BNHS 3542. Dorsal scales in paratypes reduce from 19 to 17 rows by between ventral 20–31, and reduce from 17 to 15 rows by between ventral 48–77 (Appendix 4). Scales on the underside of the posteriormost part of the body and the tail bear short parallel ridges that vary in extent, absent in small male BNHS 3542, occurring only on anal scales in female BNHS 3540, less prominent on underside of tail in female BNHS 3544, most prominent on anals and adjacent scales in male BNHS 3545. All paratypes similar to holotype in colour pattern except that the subcaudal region is entirely

whitish without black markings in BNHS 3545, and the extent of darker and paler areas on the tail shield and lateral surfaces of the tail vary (though tail shield more dark than pale in all specimens). BNHS 3544 has notably more dark (blackish) scales ventrally.

Variation in referred specimens. See Table 3 and Appendix 4 for variation in scalation and some morphometric features.

Colour in life. The darker head, dorsal and ventral body markings are dark brown to dark grey or black. The paler colours on the lateral and ventral surfaces of the body are off-white, to slightly pale pinkish anteriorly where underlying tissues are infused with oxygenated blood. The underside of the tail, and the tail shield, has some bright orange to yellow-orange patches. See Fig. 7 for examples of live animals.



FIGURE 7. Photographs of live *Rhinophis karinthandani* sp. nov. (A–D) and *R. sanguineus* (E–F). **A, B.** dorsal and ventral views of BNHS 3541; **C, D.** dorsal and ventral views of BNHS 3542; **E, F.** dorsal and ventral views of VPRS0918093.

Sexual dimorphism. As in some other species of *Rhinophis* (e.g. Wickramasinghe *et al.* 2017, 2020; Gower 2020), including *R. sanguineus* (Wall 1919), females tend to have fewer subcaudals (and shorter tails) and more ventrals. The number of ventrals is broadly overlapping between the sexes, but the subcaudal counts are not, being

a mean (of left and right counts) of 4–5 in females and 6.5–8 in males (Fig. 8). Cyriac *et al.* (2020) reported that the ridges on the scales on the underside of the tail were more prominent in males than in females of *R. melanoleucus*; the most prominent ridges in *R. karinthandani* **sp. nov.** are also seen in males, though it should be noted that they are absent in the smallest male paratype (BNHS 3542).

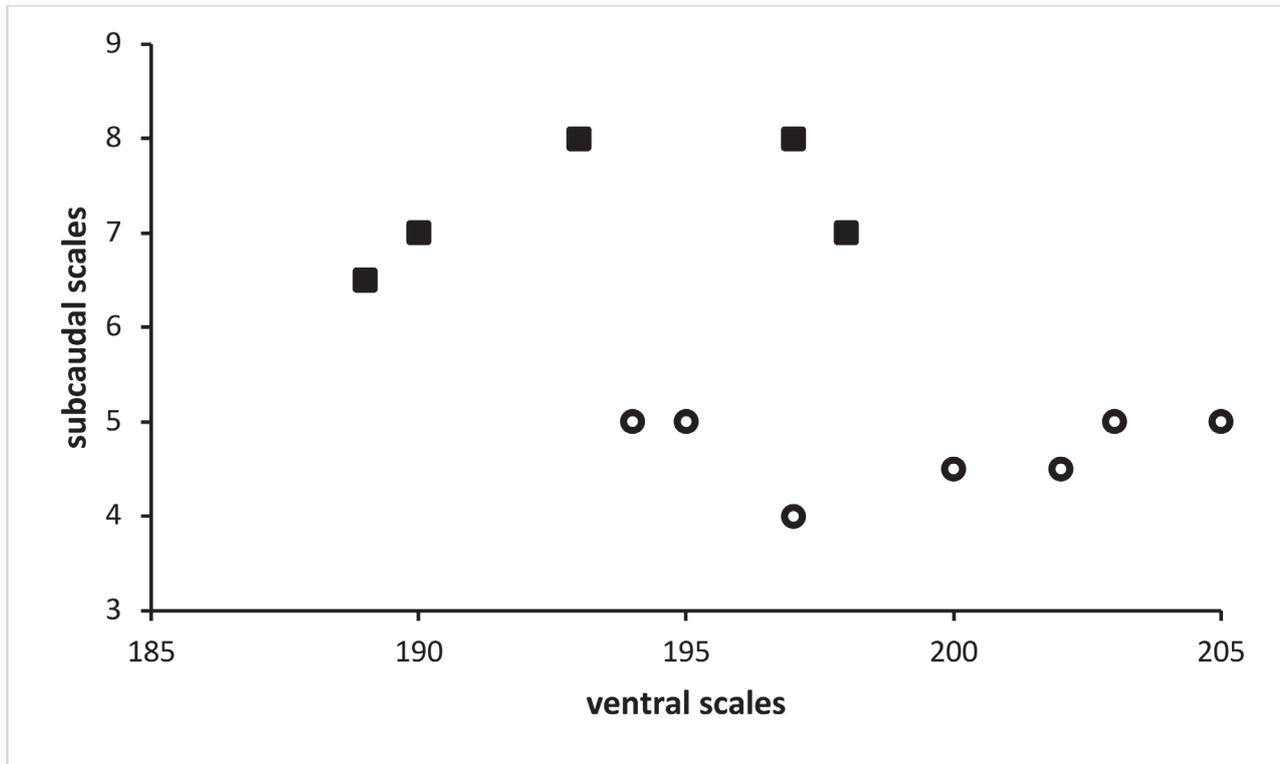


FIGURE 8. Plot showing bimodal distribution of numbers of ventral versus subcaudal scales in female (circles) and male (squares) *Rhinophis karinthandani* **sp. nov.**

Etymology. The species is named in honour of Karinthandan, a member of the Paniya (also Paniyar, Paniyan) tribe indigenous primarily to the tri-state region of Kerala-Karnataka-Tamil Nadu. Karinthandan is believed to have been a chieftain (= moopan) who was murdered in the 1700s by colonial British after he showed them the Thamarassery churam mountain pass between the Adivaram (foothills) and Wayanad plateau. Legend has it that Karinthandan’s spirit is today chained to a banyan tree at Lakkidi (a paratype locality of the new species), which has become a place of worship. In addition, Karinthandan in Malayalam is from “kari” meaning black and “thandan” (thandu) meaning stem or backbone, which also seems appropriate given the blackish dorsal colour of the newly described species. For nomenclatural purposes, the species epithet is considered a noun in apposition.

Distribution, habitat, natural history and conservation status. *Rhinophis karinthandani* **sp. nov.** is known only from the Wayanad region of Kerala (Fig. 3), though it might perhaps occur in nearby Karnataka and Tamil Nadu states. The historical specimens are not associated with habitat or other field data. The paratypes were collected from evergreen forest and adjoining coffee plantations between 820–900 m elevation that receive annual rainfall of ca. 5,000 mm. Here *R. karinthandani* **sp. nov.** is not rare. The paratypes and other individuals (not collected) in the same area were found during or immediately after rains, except BNHS 3540 which was found on the surface during a sunny day at 15:15 hrs. BNHS 3541 and 3542 were found at 14:00 hrs while digging soil to a depth of ca. 30 cm, under canopy. BNHS 3543 and 3544 were found at 11:00 hrs, dead on the road after excavations of soil for road extension works. BNHS 3545 and BNHS 3546 were found at 10:30 and 21:30 hrs, respectively, moving on the road surface close to a stream, after heavy rains. In addition to the paratypes, nine other individuals were encountered in the period April 2017–Dec 2019. Most were seen moving on the surface, but three individuals were found beneath decaying logs in an undisturbed forest patch, and one small individual (ca. 80–100 mm) was encountered under a stone. Referred specimens BNHS 3605 and 3606 were collected in October 2005 by digging in shaded, moist soil on the edge of low intensity plantations. None of the individuals attempted to bite when handled.

TABLE 3. Meristic and metric data for referred specimens of *Rhinophis karinthandani* **sp. nov.** and the holotype of *R. microlepis* (a synonym of *R. sanguineus*). Measures given in mm. SL4 = fourth supralabial; DSR1 = first dorsal scale row; hyphen (-) indicates shortest distance between two points. See Cyriac *et al.* (2020) for comparative data on types of *R. fergusonianus*, *R. melanoleucus* and *R. sanguineus*. Paired scale counts given in left, right order.

	<i>R. microlepis</i>							
	BNHS 3541	BNHS 3605	BNHS 3606	BNHS 3153	BMNH 79.7.4.3	ZMB 10358	MNHN 1895.75	BMNH 74.4.29.110
Sex	F	F	M	—	F	M	F	M
Total length	173	211	211	198	—	257	280	158
Tail length	6	5.2	5.9	7.4	6.8	10.3	6.7	4.2
Midbody width	4.6	5.2	5.9	—	6.2	7.0	6.6	4.2
Midbody circumference	—	17	20	—	—	22	23	14
Snout tip-posterior edge SL4 (head length)	—	5.6	6.0	—	—	6.4	6.3	5.0
Head width at posterior edge SL4	—	3.5	3.5	—	—	4.8	4.3	3.2
Maximum rostral length	—	2.2	2.2	1.9	—	2.3	2.2	1.6
Rostral-frontal	—	0.5	0.5	0.6	—	0.6	0.7	0.3
Frontal length	—	2.1	2.2	1.8	—	2.0	2.0	2.1
Frontal width	—	1.9	1.9	1.7	—	2.0	2.0	1.6
Snout tip-eye	—	3.1	3.2	—	—	3.3	3.3	2.5
Ventral scale width at midbody	—	2.0	2.2	—	—	2.8	2.8	1.5
DSR1 scale width at midbody	—	1.6	1.6	—	—	1.9	1.9	1.0
Tail shield width at base	4.0	4.8	5.2	4.7	5.6	5.8	5.8	3.4
Tail shield height at base	—	5.6	5.7	5.0	6.2	6.5	6.7	4.0
Tail shield middorsal length	—	5.8	6.1	5.2	6.4	6.4	6.4	4.2
Tail shield midventral length	—	1.5	1.6	1.4	1.4	1.3	1.5	0.9
Ventral scales	200	190	189	190	—	193	202	213
Subcaudal scales (number unpaired)	5,4 (1)	7,7(1)	7,6 (0)	7,7 (1)	4,5 (1)	8,8 (1)	4,5 (0)	10,11 (0)
Supralabial scales	—	4,4	4,4	4,4	—	4,4	4,4	4,4
Infralabial scales	—	3,3	3,3	3,3	—	3,3	3,3	3,3
Scales surrounding terminal scute	11	12	13	11	12	15	14	16

Although seemingly locally abundant, and tolerant of at least low intensity agriculture, better information on the distribution and/or ecology of *R. karinthandani* **sp. nov.** is probably needed for the species to qualify for anything other than Data Deficient status under IUCN Red List criteria. It occurs sympatrically with other uropeltids including at least *R. melanoleucus*, *Uropeltis* cf. *nilgherriensis*, *Teretrurus* cf. *hewstoni*, *Melanophidium bilineatum* and *M. wynaudense*. *Rhinophis karinthandani* **sp. nov.** has been seen by us in microsympatry with *M. wynaudense* at Lakkidi and Vythiri, and with *R. melanoleucus* at least at Lakkidi. We do not have direct evidence of sympatry of *R. sanguineus* and *R. karinthandani* **sp. nov.**, although this is possible given the close proximity of some specimen records (Fig. 3). The R.H. Beddome specimens BMNH 74.4.29.108 and 109 (*R. sanguineus* and *R. karinthandani* **sp. nov.**, respectively) were stored in the same jar, accessioned into the collection on the same day, and are both listed as from Wayanad, but it is not clear if they were collected from the same exact locality.

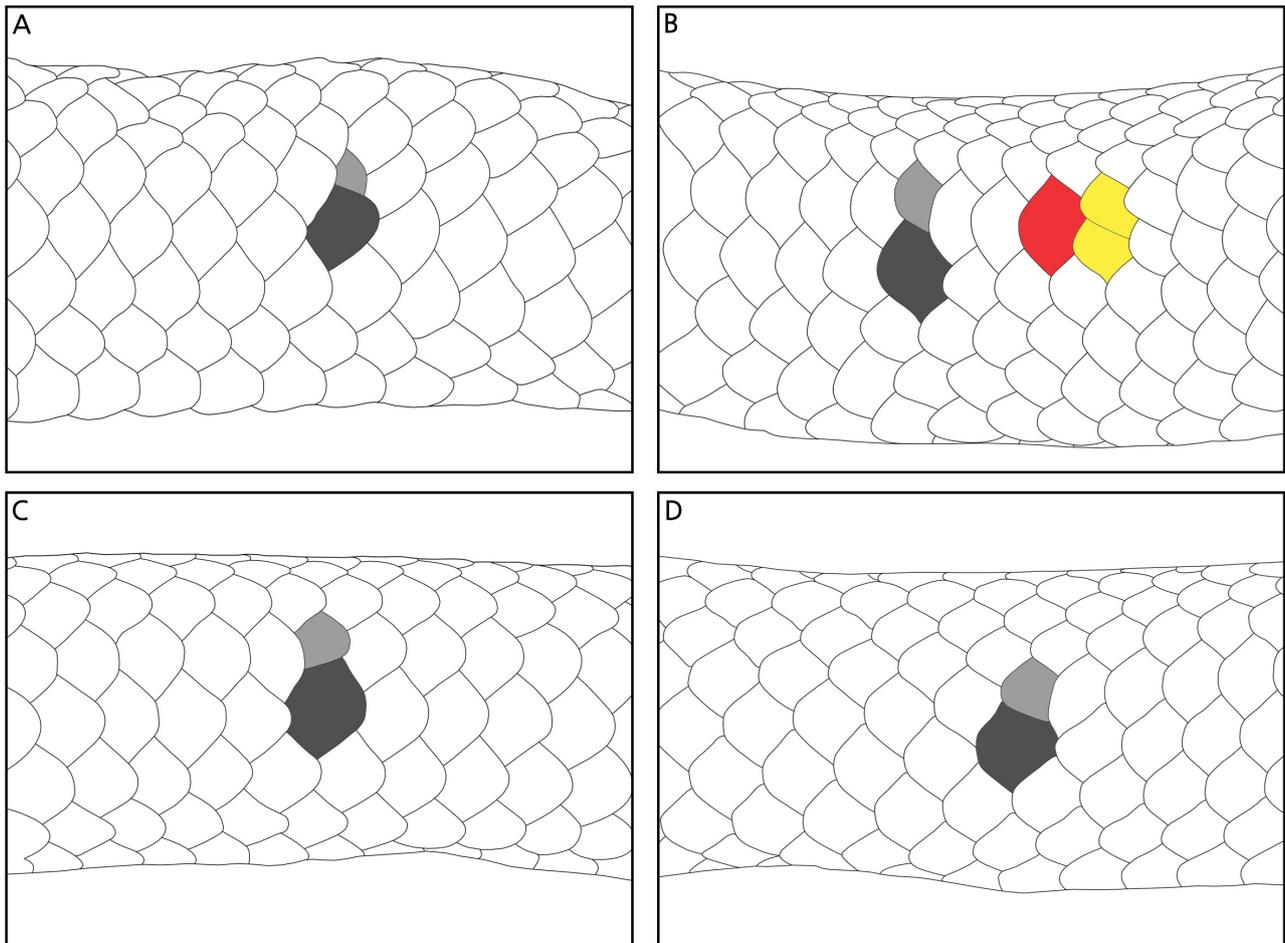


FIGURE 9. Lateral views of bodies showing dorsal scale row irregularities in *Rhinophis karinthandani* **sp. nov.** (A and B) and *R. melanoleucus* (C and D). Anomalously large dark grey scales and small pale gray scales are not involved in scale row reductions. Red and yellow scales indicate typical scale row reduction. **A.** Right side of BNHS 3545 level with 49th ventral; **B.** Left side of BNHS 3541 level with 29th ventral; **C & D.** left and right side, respectively of BNHS 3538 level with 74th and 72nd ventral, respectively.

Key to the Indian species of *Rhinophis*

This is an updated version of the key presented by Cyriac *et al.* (2020), revised with the addition of *R. karinthandani* **sp. nov.** We have removed the relative rostral length character used in Cyriac *et al.*'s (2020) key because we are less convinced of its diagnostic value and because it can be difficult to measure. All six species are endemic to India and are the only members of this genus known to occur in India.

- | | | |
|---|--|---|
| 1 | Number of dorsal scale rows just behind midbody 17 | 2 |
| - | Number of dorsal scale rows just behind midbody 15 | 3 |
| 2 | Ventral shields fewer than 160 | <i>R. travancoricus</i> |
| - | Ventral shields more than 180 | <i>R. goweri</i> |
| 3 | Ventral surface with dark blotches in irregular, staggered, transverse half-bands | 4 |
| - | Ventral surface with irregular dark speckles or spots | 5 |
| 4 | Only known specimen a female with 195 ventral and 5,5 subcaudal shields (from Cardamom Hills of Western Ghats, South of Palghat Gap) | <i>R. fergusonianus</i> |
| - | Ventral shields more than 215; subcaudals 6 or more pairs (from Wayanad region of Western Ghats, North of Palghat Gap) | <i>R. melanoleucus</i> |
| 5 | Subcaudals 5 (more typically 6)–11 (5–7 females; 8–11 males); venter background colour bright red in life (paler, more orange-yellow in smaller specimens) | <i>R. sanguineus</i> |
| - | Subcaudals 4–8 (4–5 females; 6–8 males); venter background colour whitish (to pale pink anteriorly) in life | <i>R. karinthandani</i> sp. nov. |

Discussion

It is possible that beyond the listing of some *R. karinhandani* **sp. nov.** specimens as *R. sanguineus* by Cyriac *et al.* (2020), some other accounts of *R. sanguineus* have confused the two species. For example, Smith (1943) reported *R. sanguineus* as having 182–218 ventrals. However, this is impossible to check because Smith did not report the specimens that this range was based on, or their sex or localities. Although sample sizes are not yet large, a further difference between *R. sanguineus* and *R. karinhandani* **sp. nov.** might be maximum size—we examined seven specimens of the former > 289 mm total length in preservation, whereas all specimens we examined of the latter were < 288 mm. The same is true for numbers of ventrals—none of the specimens of *R. karinhandani* **sp. nov.** that we examined has > 205 ventrals, but four *R. sanguineus* do, and Wall (1919) reported ventral counts of 200–218 for 35 specimens of the latter species. Wall's (1919) specimens of *R. sanguineus* were from approximately 15 km to the East-Southeast of the type locality for the species (Cherambadi), and approximately 50 km to the Southeast of the type locality of *R. karinhandani* **sp. nov.** (Fig. 3).

Beddome (1886), Smith (1943) and Pyron *et al.* (2016) report *R. sanguineus* as having a bright red ventral colour in life, as did Beddome (1863) in his description of the species. However, Wall (1919) reported that this was not true of young specimens of this species, though he did not specify at which size this change occurred. Beddome (1863) described the ventral colour of *R. microlepis* Beddome, 1863 as “yellowish white, with dark mottlings”. In terms of scalation, the holotype of *R. microlepis* resembles *R. sanguineus* much more than *R. karinhandani* **sp. nov.** (in having 10,11 subcaudals, 213 ventrals, and a posteriormost reduction from 17 to 15 dorsal scale rows not until level with the 80th ventral), and also in colour pattern in preservation (broader unmottled region of pale colour immediately beneath the dark dorsum). The holotype of *R. microlepis* is small (total length 158 mm), and thus it is our interpretation that if Beddome's observation of a yellowish white venter was made in life, then this is because this specimen had not yet attained the ‘adult’ red colour reported by Wall (1919), and not because this specimen is not conspecific with *R. sanguineus*. Beddome (1886) was apparently of the same opinion, listing *R. microlepis* in the synonymy of *R. sanguineus* with the comment that the former was based on a “young specimen”. Beddome (1863) reported the type locality of *R. microlepis* as “Mr Minchin's Estate in the Wynaud”. One of us (VPC) has discovered that Minchin (T.W. Minchin) was an Australian gold miner in Devala (currently in Nilgiri District, Tamil Nadu) during the early Malabar region gold rush in the 1860s, who established the Wynaad Prospecting Company (see Clarke 1881: 542). VPC has visited the sites of some 19th Century gold mines in Wayanad; these are in the vicinity of Vythiri and Meppadi. Devala is ca. 13 km from Cherambadi, the type locality of *R. sanguineus*, and is ca. 30 km from Meppadi and ca. 40 km from Vythiri in Wayanad (Fig. 3), we consider it possible that Minchin's estate was somewhere between these places.

Three records of *Rhinophis* from Karnataka (Fig. 3) require further comment. Cyriac & Kodandaramaiah (2017) presented DNA sequence data (to which we have added a *12s* sequence here) for a dried, roadkill specimen (VPC-042) from Seegodu, Karnataka identified as *Rhinophis* sp., and molecular analyses indicate that this sample is much more similar to *R. sanguineus* than to *R. karinhandani* **sp. nov.** (Fig. 1, Table 1). Confidently generating colour pattern and scalation data for this specimen is challenging. However, from photographs, a recently encountered fresh specimen from this same locality has a colour pattern more similar to that of *R. karinhandani* **sp. nov.** than *R. sanguineus*, in having a whitish rather than red venter with lots of black spotting and the paler colour forming a narrow, longitudinal line immediately below the dark dorsum. Ganesh *et al.* (2013) reported and figured a *Rhinophis* from Karnataka that they identified as *R. sanguineus*. However, that small (125 mm total length), probably male specimen, from Agumbe, had only 181 ventrals (7 subcaudals) and did not have a bright red venter (S.R. Ganesh pers. comm.). BNHS 3604 from near Neria also has a colour pattern more like that of *R. karinhandani* **sp. nov.** than *R. sanguineus*, and is a male with only 181 ventrals. Although we are convinced of the specific distinctiveness and coherence of *R. sanguineus*, *R. melanoleucus*, and *R. karinhandani* **sp. nov.**, we are currently unable to identify these three Karnataka records to species level. This difficulty also impacts our ability to confidently identify some museum specimens that lack locality data. Two examples examined during this study are MCZ 3854b (“Madras”: probably the large historical administrative region of Madras Presidency) and MNHN 1897.246 (“Sri Lanka”: probably in error), both females based on relative tail length. The former (445 mm total length; 197 ventrals; 7 subcaudals) is very heavily spotted to mottled ventrally but lacks narrow, pale, longitudinal lines; the latter (337 mm; 196 ventrals; 7 subcaudals) has narrow pale lines at midbody but not posteriorly. These might simply be slightly aber-

rantly coloured *R. sanguineus*, but this can hopefully be clarified following examination of more *Rhinophis* from peninsular India. Adding nuclear DNA sequence data might also be useful.

Many of the *Rhinophis* specimens examined for this study have isolated or short-series of irregularities in their dorsal row scalation on the anterior half of the body (Appendix 4). Even in specimens where these minor fluctuations in numbers of dorsal scale rows do not occur, there is in a similar position typically a single, much smaller scale on row 3 or 4 on one or both sides, with a much larger scale alongside it on the adjacent lower row (row 2 or 3) (Fig. 9). For example, this occurs on both sides of *R. melanoleucus* paratypes BNHS 3537 and BNHS 3538, between level with the 65–80th ventral, but in *R. karinthandani* **sp. nov.** specimens BNHS 3541 and BNHS 3545 this occurs only on one side, level with the 29th ventral (right side) and 47th ventral (left side), respectively. In addition to the *R. melanoleucus* and *R. karinthandani* **sp. nov.** specimens reported here, many specimens of other *Rhinophis* examined for this study have a brief scale reduction in a similar position, for as few as one scale in length, for example *R. sanguineus* BMNH 74.4.29.695. Gower (2020) reported similar scalation patterns in the Sri Lankan *R. mendisi* Gower, 2020. We have not investigated whether this corresponds with any particular underlying structure and/or the extent to which variation in this feature might represent taxonomically useful data, but it might be worthwhile examining it in more detail.

The Wayanad region is a hotspot of Indian *Rhinophis* diversity, with at least three species occurring here, *R. karinthandani* **sp. nov.**, *R. melanoleucus* and *R. sanguineus*. It remains to be seen whether this apparent hotspot is real or an artefact of sampling effort to date. Including material from Karnataka reported here and by Cyriac & Kodandaramaiah (2017), this assemblage is monophyletic, and comprises three of the four species of *Rhinophis* (all of which are Indian) with 15 rather than 17 or 19 dorsal scale rows along the posterior half of the body. Thus, we hypothesise that the as yet unsampled *R. fergusonianus* (which also has 15 dorsal scale rows posteriorly, but is not known from Wayanad) is also a member of this lineage. The molecular phylogenetic analyses also support the hypothesis that Sri Lankan uropeltids (all *Rhinophis*) are monophyletic, with Indian *Rhinophis* paraphyletic with respect to the Sri Lankan clade; consistent with the island lineage resulting from a single dispersal event from India (Cadle *et al.* 1990; Bossuyt *et al.* 2004; Pyron *et al.* 2013, 2016; Cyriac & Kodandaramaiah 2017).

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APPENDIX 1. Material examined of Indian *Rhinophis*

Specimen numbers with a VP and MW prefix are field tags on specimens due to be permanently deposited in BNHS (Mumbai), NCBS (Bangalore), Centre for Ecological Sciences (Indian Institute of Science, Bengaluru, India) and/or ZSI (Kozhikode and/or Pune). Information in square brackets are modern interpretations of historical locality data.

Rhinophis fergusonianus

BMNH 1946.1.16.77 (formerly BMNH 95.7.29.1) holotype, Cardamom Hills, “Travancore” [probably Kerala].

Rhinophis goweri

BNHS 3465, near Solakkadu, Kolli Hills, Namakkal district, Tamil Nadu.

***Rhinophis karinthandani* sp. nov.**

BMNH 79.7.4.2, holotype, Manantoddy, Wynad, 2,000 ft [= Mananthavady, Wayanad district, Kerala].

BNHS 3540, BNHS 3542, 3544, 3545 and 3546, paratypes, Lakkidi, Wayanad district, Kerala.

ZSI/WGRC/V-3143, paratype, Chandanathodu near Mananthawady, Wayanad district, Kerala.

BNHS 3541 and 3543, Lakkidi, Wayanad district, Kerala.

BMNH 79.7.4.3, Manantoddy, Wynad, 2,000 ft [= Mananthavady, Wayanad district, Kerala][originally in same jar as holotype BMNH 79.7.4.2]; lacks head and anterior end of body.

BMNH 74.4.29.109, Wynad [Wayanad district, Kerala].

BNHS 3605 and BNHS 3606, near Pookode, Wayanad district, Kerala. One of these is from nr. Pozhutana and one from Sugandhagiri.

BNHS 3153, Anakkampoil, Wayanad district, Kerala; listed as *R. sanguineus* in Cyriac *et al.* (2000).

ZMB 10358, Wayanad, India; listed as *R. sanguineus* in Cyriac *et al.* (2000).

MNHN 1895.75, "Sri Lanka" [presumably in error]; listed as *R. sanguineus* in Cyriac *et al.* (2000).

Rhinophis melanoleucus

BNHS 3534, holotype, Wayanad Wild resort, Lakkidi, Wayanad district, Kerala.

BNHS 3537 and BNHS 3538, paratypes, Lakkidi, Wayanad district, Kerala.

BNHS 3535, BNHS 3536 and ZSI/WGRC/IR/V/3101, paratypes, Kerala Veterinary and Animal Sciences University, Pookode, Wayanad district, Kerala.

ZSI/WGRC/IR/V/3100, paratype, Vythiri road, Pookode, Wayanad district, Kerala (female), Kerala.

BNHS 3539, Wayanad Wild resort, Lakkidi, Wayanad district, Kerala.

Rhinophis sanguineus

BMNH 1946.1.16.54 (formerly BMNH 64.3.9.2) lectotype (see Pyron *et al.* 2016), Cherambady [Cherambadi, Nilgiris district, Tamil Nadu].

BMNH 1946.1.16.76 (formerly BMNH 74.4.29.110) holotype of *R. microlepis*, Wayanad district, Kerala.

BMNH 74.2.29.695–697, Wynad [Wayanad district, Kerala].

BMNH 68.4.3.38, Nilgherries [possibly Wayanad district, Kerala or Nilgiris district, Tamil Nadu].

BMNH 1922.5.25.6, Nellacolla [Nellacotta?, Nilgiris district, Tamil Nadu].

BMNH 74.4.29.108, Wynad [Wayanad district, Kerala].

BMNH 66.12.15.3, Wynad, Madras Presidency [possibly Wayanad district, Kerala or Nilgiris district, Tamil Nadu].

ZMB 5536, Cherambady [Cherambadi, Nilgiris district, Tamil Nadu].

VPRS0918092 and VPRS0918093, Meppadi, Wayanad district, Kerala.

BUB S-2, BUB S-4, BUB S-15, BUB S-1584, BUB S-1588, Regional Agricultural Research Station (RARS), Ambalavayal, Wayanad district, Kerala.

MNHN 1897.246, "Sri Lanka" [probably in error]. See Discussion for comments on colour pattern and identification of this specimen.

MCZ 3865 and MCZ 3854b, "Madras" [probably the historical administrative region of Madras Presidency, which included parts of present-day Wayanad]. See Discussion for comments on colour pattern and identification of MCZ 3854b.

Rhinophis travancoricus

BMNH 92.10.5.2, holotype, 6 miles along Trivandrum-Vambayam road, Thiruvananthapuram district, Kerala.

BMNH 1903.4.7.1–2 and BMNH 99.11.16.1, Trivandrum, Thiruvananthapuram district, Kerala.

BMNH 94.3.15.1, Piermed [Peermade, Peermedu], Idukki district, Kerala.

CAS 244341, Sakrapani Mukku, near Kulithurai river, Kanyakumari district, Tamil Nadu.

CAS 39620, Trivandrum, Thiruvananthapuram district, Kerala.

MW219 and MW221, Palod, Thiruvananthapuram district, Kerala.

MW 2180, MW 2182, MW 2183 and MW 2184, Maramalai, Kanyakumari district, Tamil Nadu.

VPRT1115073, near Konni, Pathanamthitta district, Kerala.

APPENDIX 2. GenBank accession numbers for sequences of uropeltids used in phylogenetic analyses. All sequences were previously published except for those accession codes in bold text. Species identifications follow those reported on GenBank and/or in papers in which data were reported, except for: * (listed as *R. blythii* in LSMNS catalogue but identified by Jins *et al.* 2018 as *R. drummondhayi* on basis of DNA data), and ** (following Gower 2020; listed as *R. homolepis* in previous studies). Abbreviations not listed in the Materials and Methods or by Pyron *et al.* (2016) or Cyriac & Kodandaramaiah (2017) as follows: KA: Kamataka; KL: Kerala; LSUMNS: Louisiana State University Museum of Natural Science; NMSL: National Museum, Sri Lanka, Colombo field tag; NP: National Park; UK: University of Kerala field tag; WHT: World Heritage Trust specimens housed in NMSL. VP: V.P. Cyriac field tag. Blank cell indicates lack of data. In the Sample column, numbers in parentheses indicate voucher code where this is known to differ from tissue code.

Taxon	Sample	Country	Locality	I2s	I6s	nd4
<i>Plectrurus perroteti</i>	VPC-029	India	Silent Valley NP, KL	MF775133	MF775173	MF775256
<i>Plectrurus perroteti</i>	VPC-030	India	Silent Valley NP, KL	MF775134	MF775174	-
<i>Pseudoplectrurus canaricus</i>	VPC-023	India	Kudremukh NP, KA	MF775135	MF775175	MF775257
<i>Rhinophis travancoricus</i>	UK.MW220(219)	India	nr. Palod, KL	AY701010	AY701041	-
<i>Rhinophis travancoricus</i>	VPC-044	India	Konni, Pathanamthitta, KL	MF775136	MF775177	MF775259
<i>Rhinophis</i> sp.	VPC-042 (VPRS1015065)	India	Seegodu, Chickmangalore, KA	MT911831	MF775176	MF775258
<i>Rhinophis sanguineus</i>	VPC-052 (VPRS0918092)	India	Elimbilerimala, Mepadi, Wayanad, KL	MT911834	MT911845	MT911852
<i>Rhinophis sanguineus</i>	VPC-053 (VPRS0918093)	India	Elimbilerimala, Mepadi, Wayanad, KL	MT911835	MT911843	MT911853
<i>Rhinophis sanguineus</i>	BUB S-1584	India	Ambalavayal, Wayanad, KL	MT911832	MT911842	MT911850
<i>Rhinophis sanguineus</i>	BUB S-1588	India	Ambalavayal, Wayanad, KL	MT911833	MT911844	MT911851
<i>Rhinophis melanoleucus</i>	DVM02	India	Lakkidi, Wayanad, KL	MT911829	MT911840	MT911849
<i>Rhinophis melanoleucus</i>	VPC-051 (VPRS0918091)	India	Lakkidi, Wayanad, KL	MT911830	MT911841	MT911848
<i>Rhinophis karinthandani</i> sp. nov.	DVM01(BNHS 3540)	India	Lakkidi, Wayanad, KL	MT911836	MT911846	MT911855
<i>Rhinophis karinthandani</i> sp. nov.	MW4876 (BNHS 3605)	India	nr. Pookode, Wayaand, KL	MT911837	MT911839	MT911856
<i>Rhinophis karinthandani</i> sp. nov.	VPC-064 (ZSI/WGRC/V-3143)	India	Chandhanathodu, Periya, Wayanad, KL	MT911838	MT911847	MT911854
<i>Rhinophis blythii</i>	LSUMNS H-5781	Sri Lanka	Talawakella	AY701018	AY701049	-
<i>Rhinophis blythii</i>	RS-N	Sri Lanka		KC347332	KC347370	KC347517
<i>Rhinophis blythii</i>	WHT5221	Sri Lanka	nr. Dickoya	AY701019	AY701050	-
<i>Rhinophis blythii</i>	WHT5223	Sri Lanka	nr. Dickoya	AY701020	AY701051	-
<i>Rhinophis blythii</i>	WHT5227	Sri Lanka	nr. Dickoya	AY701021	AY701052	-
<i>Rhinophis dorsimaculatus</i>	LSUMNS H-5780	Sri Lanka	Marrichekkadi	AY701009	AY701040	-
<i>Rhinophis drummondhayi</i> *	LSUMNS H-5784	Sri Lanka	Talawekalla	AY700995	AY701026	-
<i>Rhinophis drummondhayi</i>	WHT5176	Sri Lanka	Madulsima	AY700997	AY701028	-

.....continued on the next page

APPENDIX 2. (Continued)

Taxon	Sample	Country	Locality	I2s	I6s	nd4
<i>Rhinophis drummondhayi</i>	WHT 5177	Sri Lanka	Madulsima	AY700998	AY701029	-
<i>Rhinophis drummondhayi</i>	LSUMNS H-5778	Sri Lanka	Above Namunkula	AY700996	AY701027	-
<i>Rhinophis drummondhayi</i>	NMSL.MW1721(1718)	Sri Lanka	nr. Passara	AY700994	AY701025	-
<i>Rhinophis drummondhayi</i>	SBH194102	Sri Lanka		Z46447	Z46477	-
<i>Rhinophis erangaviraji</i>	RAP0431	Sri Lanka		KC347333	KC347371	KC347503
<i>Rhinophis cf. mendisi**</i>	NMSL.MW1787(1785)	Sri Lanka	nr. Rakwana	AY701015	AY701046	-
<i>Rhinophis homolepis</i>	RAP0509	Sri Lanka		KC347334	KC347372	KC347522
<i>Rhinophis melanogaster</i>	LSUMNS H-5696	Sri Lanka		AF512739	AF512739	-
<i>Rhinophis oxyrhynchus</i>	LSUMNS H-6131	Sri Lanka		AY701013	AY701044	-
<i>Rhinophis oxyrhynchus</i>	LSUMNS H-6132	Sri Lanka	Polonnaruwa	AY701014	AY701045	-
<i>Rhinophis philippinus</i>	WHT5157	Sri Lanka	Kalugaltenna	AY701006	AY701037	-
<i>Rhinophis philippinus</i>	WHT5158	Sri Lanka	Kalugaltenna	AY701007	AY701038	-
<i>Rhinophis philippinus</i>	LSUMNS H-6164	Sri Lanka	Palatenne	AY701016	AY701047	-
<i>Rhinophis philippinus</i>	LSUMNS H-6165	Sri Lanka	Palatenne	AY701017	AY701048	-
<i>Rhinophis philippinus</i>	LSUMNS H-6179	Sri Lanka		AF512740	AF512740	-
<i>Rhinophis philippinus</i>	NMSL.MW1740(1739)	Sri Lanka	nr. Rattota	GQ200594	GQ200594	GQ200594
<i>Rhinophis philippinus</i>	NMSL.MW1742(1741)	Sri Lanka	nr. Rattota	AY701005	AY701036	-
<i>Rhinophis phillipsi</i>	NMSL.MW1758(1757)	Sri Lanka	Moussakanda	AY701012	AY701043	-
<i>Rhinophis phillipsi</i>	NMSL.MW1760(1759)	Sri Lanka	nr. Gammaduwa	AY701011	AY701042	-
<i>Rhinophis saffragamus</i>	RS-140	Sri Lanka		KC347331	KC347369	KC347492

BNHS 3544†

3+4(29) 4+5(50), +4(65), 3+4(71)
 19-----17-----15
 4+5(25) 4+5(46), +4(64), 3+4(66)

BNHS 3545†

4+5(31) 4+5(51), +4(52), 3+4(53), +4(55), 3+4(77)
 19-----17-----15
 4+5(27) 4+5(70), +5(72), 3+4(74)

BNHS 3546†

3+4(31) 4+5(56), +4(62) 3+4(73)
 19-----17-----15
 3+4(29) 3+4(65)

ZSI/WGRC/V-3143†

3+4(26) 3+4(52), +5(59), 3+4(67)
 19-----17-----15
 3+4(28) 3+4(50), +4(59), 3+4(65)

BMNH 74.4.29.109

3 + 4 (36) 3 + 4 (83)
 19-----17-----15
 3 + 4 (33) 3 + 4 (81)

BNHS 3541

4+5 (26) 3+4(47), +5(61), 3+4(70)
 19-----17-----15
 3+4(25) 4+5(46), +5(53), 3+4(65)

(B) *Rhinophis sanguineus* (see Cyriac *et al.* 2020 for holotype data)

BMNH 74.4.29.110 (holotype of *R. microlepis*)

3 + 4 (31) 3 + 4 (62), +3 (63), 3 + 4 (81)
 19-----17-----15
 4 + 5 (27) 3 + 4 (56), +3 (58), 3 + 4 (80)

BMNH 66.12.13.3

4 + 5 (36) 3 + 4 (76)
 19-----17-----15
 4 + 5 (33) 3 + 4 (74)

BMNH 74.4.29.108

3 + 4 (34) 3 + 4 (55), +4 (64), -4 (66)
 19-----17-----15
 2 + 3 (33) 3 + 4 (53), +4 (55), 3 + 4 (65)

BMNH 68.4.3.38

4 + 5 (34) 3 + 4 (73)
 19-----17-----15
 4 + 5 (31) 3 + 4 (75)

BMNH 74.4.29.695

4 + 5 (29) 4 + 5 (57), +5 (58), 4 + 5 (61), + 5 (62), 3 + 4 (78)
19-----17-----15
4 + 5 (27) 4 + 5 (53), +5 (57), 4 + 5 (58), + 5 (60), 3 + 4 (76)

BMNH 74.4.29.696

3 + 4 (39) 3 + 4 (86), +4 (89), 3 + 4 (90)
19-----17-----15
4 + 5 (27) 3 + 4 (80)

BMNH 74.4.29.697

4 + 5 (38) 3 + 4 (60), +4 (61), 3 + 4 (77), + 4 (79), - 4 (83)
19-----17-----15
4 + 5 (27) 4 + 5 (56), +5 (58), 3 + 4 (80)

BMNH 1922.5.25.6

3 + 4 (39) 4 + 5 (83)
19-----17-----15
4 + 5 (38) 4 + 5 (79)

BUB S-2

4 + 5 (40) 4 + 5 (87)
19-----17-----15
4 + 5 (37) 4 + 5 (85)

BUB S-4

3 + 4 (34) 3 + 4 (71)
19-----17-----15
4 + 5 (32) 4 + 5 (68)

BUB S-15

4 + 5 (34) 4 + 5 (76)
19-----17-----15
3 + 4 (37) 3 + 4 (76)

VPRS0918092

3+4 (38) 3+4 (73)
19-----17-----15
3+4 (34) 3+4 (73)

VPRS0918093

3+4 (35) 3+4 (58), +4 (61), 4+5 (64), +4 (67), 3+4 (70)
19-----17-----15
3+4 (40) 3+4 (74)