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A NEW SPECIES OF *Dendrelaphis* BOULENGER, 1890 (REPTILIA: COLUBRIDAE) FROM THE WET ZONE OF SRI LANKA WITH A REDESCRIPTION OF *Dendrelaphis bifrenalis* (BOULENGER, 1890)

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Abstract

Examination of the *Dendrelaphis bifrenalis* populations on Sri Lanka showed that there are two populations that are morphologically different from each other. One population is distributed only in the wet zone forests (hereafter treated as wet zone population), while the other population occurs widely in the dry zone and intermediate zones (hereafter dry zone population). The type series of *D. bifrenalis* consist of 3 specimens from which the specimen representing the dry zone population was chosen as lectotype, and the wet zone population is described here as a new species. It clearly differs from *D. bifrenalis* by having a shorter snout, orbit diameter 103–114% of eye–nostril length (*vs* 77–95%), and larger eye, orbit diameter 21–23% of head length (*vs* 17–20%). Furthermore it differs by having a temporal stripe stopping just beyond the neck (*vs* continues behind neck), the absence of black transverse dorsolateral bars on the anterior 1/4th of body (*vs* prominent), a narrow and pointed snout (*vs* broad and flat), a divided nasal (*vs* single), and a ventrolateral stripe continuing up to the tail (*vs* stopping at the level of the anal plate). This morphological differentiation is supported by the divergence in the mitochondrial NADH dehydrogenase subunit 4 (*ND*4) region separating clearly with the divergence of 1.70±0.35%. Also, here we resurrect *D. effrenis* (Werner, 1909) as a valid species, and *D. sinharajensis* as a junior synonym of it. The holotype of *D. sinharajensis* was chosen as the neotype of *D. effrenis* to stabilize nomenclature, and to make it an objective synonym. The third and fourth known specimens of this rare species are reported. A key of the species of the genus *Dendrelaphis* in Sri Lanka is provided.

***Key words*:** Holotype, island biogeography, lectotype, neotype, syntype, systematic, taxonomy.

Introduction

The bronzebacks, or the arboreal colubrid snake genus *Dendrelaphis* Boulenger, 1890 in Sri Lanka has been studied extensively for the last two centuries (Boulenger 1894, Wall 1921, Meise & Henning 1932, Smith 1943, Deraniyagala 1955, Leviton 1970, De Silva 1980 etc.). However, most of the taxonomic issues remained unsolved until Vogel & van Rooijen (e.g. 2008, 2011a) and van Rooijen & Vogel (e.g. 2008a, 2012) reviewed the genus.

The first *Dendrelaphis* species recorded from Sri Lanka was *Dendrelaphis tristis* (Daudin, 1803) which was considered to be a widespread species in Sri Lanka and India, until van Rooijen & Vogel (2008b, 2009) restricted it to the dry zone of the island and South India, while resurrecting *D. schokari* (Kuhl, 1820) for the population in the wet zone. *D. caudolineolatus* (Günther, 1869) is endemic to Sri Lanka.

D. bifrenalis (Boulenger, 1890) was considered to be widespread in Sri Lanka and India, until Vogel & van Rooijen (2011b) restricted it to Sri Lanka. *D. oliveri* (Taylor, 1950), is only known from its holotype and no new records have been published for the last 70 years. The last species to be described from the island was *D. sinharajensis* Wickramasinghe, 2016. In addition to the above six species, another species, *D. effrenis* (Werner, 1909) was described from Sri Lanka, based on a single specimen collected from Colombo (Sri Lanka). Smith (1943) referred it to the synonymy of *D. caudolineolatus*, and it is currently regarded as a subjective synonym of *D. caudolineatus* (Gray, 1834), a Malayan member of the genus.

Dendrelaphis bifrenalis is the smallest among the Sri Lankan *Dendrelaphis*, and can be easily distinguished from its congeners by the presence of a red tongue and two loreal scales (De Silva 1980). Boulenger (1890) described this species based on three syntypes. However, after a critical comparison of the *Dendrelaphis bifrenalis* populations (live and museum specimens, see Appendix I) in Sri Lanka, we realized that there are two populations which are morphologically different from each other. One population is distributed only in the wet zone forests (hereafter treated as wet zone population), while the other population occurs widely in the dry zone and intermediate zones (hereafter dry zone population). The wet zone population is described here as a new species.

Material and Methods

***Data collection*.** Specimens were examined in the collections of the Natural History Museum, London, UK (BMNH); the National Wildlife Research and Training Centre, Department of Wildlife Conservation, Girithale, Sri Lanka (DWC); Field Museum of Natural History, Chicago, USA (FMNH); Muséum d'histoire naturelle, Genève [Geneva], Switzerland (MHNG); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museum für Tierkunde, Dresden, Germany (MTKD); National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL); Naturhistorisches Museum Wien, Vienna, Austria (NMW); National Museum of Natural History, Leiden, The Netherlands (RMNH); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany (SMF); and Smithsonian Institution National Museum of Natural History, Washington, D.C., USA (USNM). Museum acronyms follow Uetz *et al*. (2019).

Morphometric and meristic data for species comparisons were obtained from examined specimens (see Appendix I). Sex was determined by ventral tail incision of adult specimens followed by the checking for presence or absence of hemipenes. Natural history data were taken from our own field observations during the last ten years, as well as published literature.

***Morphometric and meristic data*.** The following characters were measured with a digital caliper (±0.1 mm): eye diameter (ED, horizontal diameter of eye); eye–nostril length (EN, distance between anterior most point of eye and middle of nostril); snout length (ES, distance between anterior most point of eye and snout); nostril diameter (ND, horizontal diameter of nostril); internarial distance (IN, least distance between nostrils); mandible–posterior eye distance (MPE, distance between posterior edge of mandible and posterior most edge of eye); interorbital width (IO, least distance between upper margins of orbits); head length (HL, distance between posterior edge of mandible and tip of snout); head width (HW, maximum width of head); snout–vent length (SVL, measured from tip of snout to anterior margin of vent); tail length (TAL, measured from anterior margin of vent to tail tip). Meristic characters were taken as follows: supralabials and infralabials (SUP and INF, first labial scale to last labial scale bordering gape); costal scales

(counted around the body from one side of ventrals to the other in three positions, on one head length behind neck, at mid body and at one head length prior to anal plate); when counting the number of ventral scales, we counted according to the method described by Dowling (1951). We counted paired subcaudal scales from the first scale under the tail meeting its opposite subcaudal scale, to the scale before the tip of the tail.

***Morphometric analyses*.** We conducted a principal component analysis (PCA) to examine patterns of morphometric variation of *Dendrelaphis bifrenalis*. A series of components, exceeding 80% of eigenvalues as a whole, were taken into account when inspecting the ordination. The principal axis method was used to extract the components followed by an orthogonal rotation. Both sexes were included in this analysis, using the following six measurements normalized to the percentages of TAL/SVL, EN/ED, ED/HL, EN/HL, HL/SVL, and HL/TAL. Prior to the ordination, those measurements were standardized by scaling them to a standard deviation of 1.0, and mean of 0.0. In each PCA, the majority of variation was captured by the first component (Table 1). Because the first three components together accounted for a large amount of variance (80%), we used only the first three principal components for the analysis. All analyses were performed in the statistical software environment R, v2.15.0 (R Development Core Team, 2012).

Table1. Loadings for the first four principal components (PC) of morphometric characters in *Dendrelaphis bifrenalis* and the new species. See text for definitions of character abbreviations.

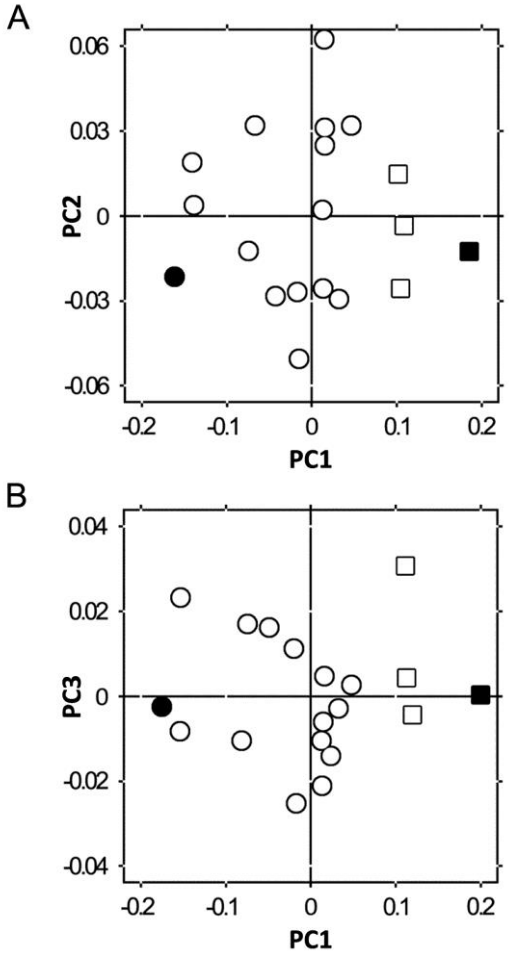
Character	PC1	PC2	PC3	PC4
TL/SVL	0.0168	0.9913	0.0780	0.0899
ED/EN	0.9814	-0.0098	-0.1081	0.0193
ED/HL	0.1889	-0.0282	0.5978	-0.2459
EN/HL	-0.0233	-0.0260	0.6902	-0.3052
HL/SVL	0.0112	-0.0132	0.2012	0.4726
HL/TL	0.0173	-0.1244	0.3287	0.7839
Eigenvalue	0.0082	0.0010	0.0002	0.0001
Proportion of variance	86.63	10.383	1.7913	1.1943

***DNA based species delimitation*.** From live specimens a 20µl sample of blood or 2mm sample of tail clip was extracted to Queens's analysis buffer (Seutin *et al*. 1991). A sample of muscle, liver or skin tissue was extracted to 80% ethanol from museum specimens following the guidelines of the respective institute. Genomic DNA was extracted using the DNeasy Tissue Kit (Qiagen) (Fernando *et al*. 2016). The fourth subunits of mitochondrial nicotinamide adenine dinucleotide dehydrogenase (*ND*4) was amplified by polymerase chain reaction (PCR) and sequenced using Sanger sequencing. *ND*4 was sequenced using primers CACCTATGACT ACCAAAAGCTCATGTCGAAGC and CATT ACTTTTACTTGGATTTGCACCA (Forstner *et al*. 1995). The thermo cycling profile was as below: denaturation at 94°C for 4min, an initial boost of denaturation at 94°C for 60s, annealing at 42°C for 60s and extension at 68°C for 90s, followed by 39 cycles of denaturation at 94°C for 30s, annealing at 48°C for 30s, extension at 72°C for 60s, and a final extension step of 72°C for 15min (modified after Figueroa *et al*. 2016). Molecular work was done at the Laboratory for Molecular Ecology and Evolution at the Department of Zoology, University of Colombo. The Sequencing services of Macrogen (South Korea) was used for sequencing. To increase the coverage of species, we used *ND*4 sequences of selected *Dendrelaphis* species available at the NCBI Genbank. The samples used and their accession numbers are given in Table 2. As for the outgroup, sequences of *Chrysopelea ornata* (Shaw, 1802) and *C. taprobanica* Smith, 1943 from Sri Lanka were used (after Figueroa *et al*. 2016: see Table 3). We used Geneious version 7.1.6 (Kears *et al*. 2012) to examine the trace files for quality, to edit sequences and multiple align sequences across taxa using ClustalW algorithm (Larkin *et al*. 2007). We examined appropriate models of evolution and the best way to partition gene regions using PartitionFinder ver. 1.1.0 (Lanfear *et al*. 2012). Phylogenetic trees were built through Maximum likelihood (ML) approach using RAxML ver. 8.1.22 (Stamatakis 2014) and Bayesian approach using MrBayes ver. 3.2.5 (Ronquist & Huelsenbeck 2003). For ML, we conducted tree searches rapid bootstrap of 10000 replicates and thereafter a thorough ML search of 10 runs using a separate GTR evolutionary model for each partition. Invariant sites were not included in the model. We conducted a Bayesian analysis by running the MCMC chain for 20,000,000 generations, sampling every 100 steps, with 25% of the samples discarded as burnin. We assessed the convergence using the standard deviation of split frequencies below 0.01 and checking for stationarity using Tracer ver. 1.6 (Rambaut *et al*.

2014). The number of base substitutions per site was conducted using the Maximum Composite Likelihood model (Tamura *et al*. 2004). The analysis involved 18 nucleotide sequences. Codon positions included were 1st+2nd+3rd+ Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 620 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar *et al*. 2016). The obtained sequences will be deposited in NCBI GenBank.

Results

***Morphometric analyses*.** We retained the first three components for the inspection of PCA, which entailed over 98% of the whole eigenvalues (Table 1, Fig. 1: the eigenvalues were allocated 86.6%, 10.4%, and 1.8% on component 1, 2, and 3 respectively. The multivariate PCA plots separated *Dendrelaphis bifrenalis* and the new species into two morphometrically distinct clusters (Fig. 1). The first axis was highly correlated with several measurements, where ED/EN (loading value: 0.98) among the six measurements. The second axis was characterized by TL/SVL (0.99).



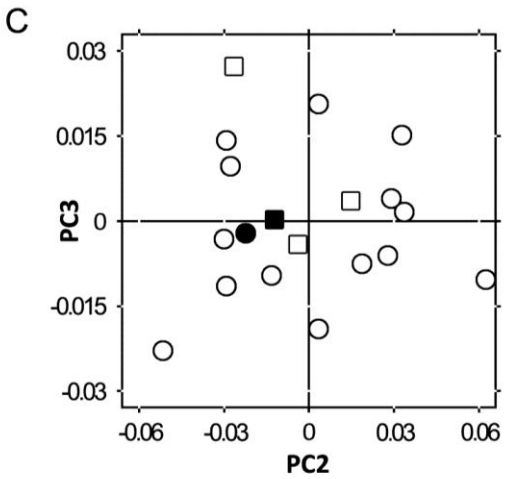


Figure 1. Morphometric analysis of *Dendrelaphis bifrenalis* (circles), *D. wickrorum* sp. nov. (squares): (A) PC1 *vs*. PC2; (B) PC1 *vs*. PC3; (C) PC2 *vs*. PC3; The filled symbol represents the examined lectotype and holotype respectively.

The third axis was ED/HL (0.60). All the specimens of the new species are distinctively distributed along the first, second, and third axis from fifteen *D. bifrenalis* specimens. According to this multivariate trait distribution, the new species is characterized by relatively shorter eye-nostril length (EN), larger eye (ED), and shorter tail (TL) compared to *D. bifrenalis*.

***Phylogenetic analysis*.** We studied sequences of 14 specimens of *Dendrelaphis* from Sri Lanka, India and Southeast Asia (Table 2). The final alignment used for the phylogenetic analysis comprised 620 bp segment of the mitochondrial *ND*4 region, about 170 variable sites were observed within the cluster (all data given for ingroup only). The partitioned ML and Bayesian trees showed similar topologies. In both analyses, there were several short internodes, however, the clades relevant to the *Dendrelaphis* species in question were well supported (Fig. 2). The monophyly of the genus was strongly supported as well (Bootstrap value of 95% and Bayesian posterior probability of 1). The sequence of *D. sinharajensis* was poor due to the degraded nature of the tissue sample. Therefore we removed it from all trees.

The new species separated well and placed as the sister node to *D. bifrenalis* (100% bootstrap support and Bayesian posterior probability of 1: Fig. 2). Together the *D. bifrenalis*-new species clade was sister to widespread East Indian-Southeast Asian bronzebacks. The remaining members of *Dendrelaphis* that were included in the analysis

and are found in Sri Lanka formed weakly supported clades. The general topology of the phylogenetic relationships resulting from our analyses was consistent with results reported in previous studies (Figueroa *et al*. 2016). The numbers of base substitutions per site between sequences are shown in Table 3. The observed *p*-distances among members of *D. bifrenalis* complex varied from 1.31% to 2.10% of substitutions with 1.7% (± 0.35) divergence.

Table 2. Voucher and GenBank data on the *Dendrelaphis* and *Chrysopelea* specimens used in this study. GenBank accession numbers are given; NP, national park; FR, forest reserve; R, resort; "—" = unknown.

Species	GenBank AN	Voucher ID	Locality	Reference
D. subocularis	KX660623.1	LSUHC7429	—	Figueroa *et al*. 2016
D. tristis	KC347493.1	RAP0492	Bundala NP, Sri Lanka	Pyron *et al*. 2013
D. schokari	KC347497.1	RAP047	Hiyare Forest, Sri Lanka	Pyron *et al*. 2013
D. pictus	KX660582.1	CAS210338	—	Figueroa *et al*. 2016
D. marenae	KX660640.1	KU324549	—	Figueroa *et al*. 2016
D. haasi	KX660622.1	LSUHC10042	—	Figueroa *et al*. 2016
D. cyanochloris	KX660621.1	LSUHC6768	—	Figueroa *et al*. 2016
D. striatus	KX660625.1	LSUHC4792	—	Figueroa *et al*. 2016
D. striatus	KX660624.1	LSUHC10012	—	Figueroa *et al*. 2016
D. bifrenalis	D03ND4_ND4	not collected	Waahalkada, Sri Lanka	this study
D. bifrenalis	D04ND4_ND4	not collected	Nilgala, Sri Lanka	this study
D. wickrorum sp.nov.	D01ND4_ND4	not collected	Ambagaspitiya, Sri Lanka	this study
D. wickrorum sp.nov.	KC347509.1	RAP0455	Kanneliya FR, Sri Lanka	Pyron *et al*. 2013
D. caudolineolatus	KC347518.1	RAP0508	Rambukpitiya, Sri Lanka	Pyron *et al*. 2013
C. taprobanica	KC347508.1	RAP0538	Kandalama R, Sri Lanka	Pyron *et al*. 2013
C. ornata	KC347496.1	RAP0433	Kanneliya FR, Sri Lanka	Pyron *et al*. 2013

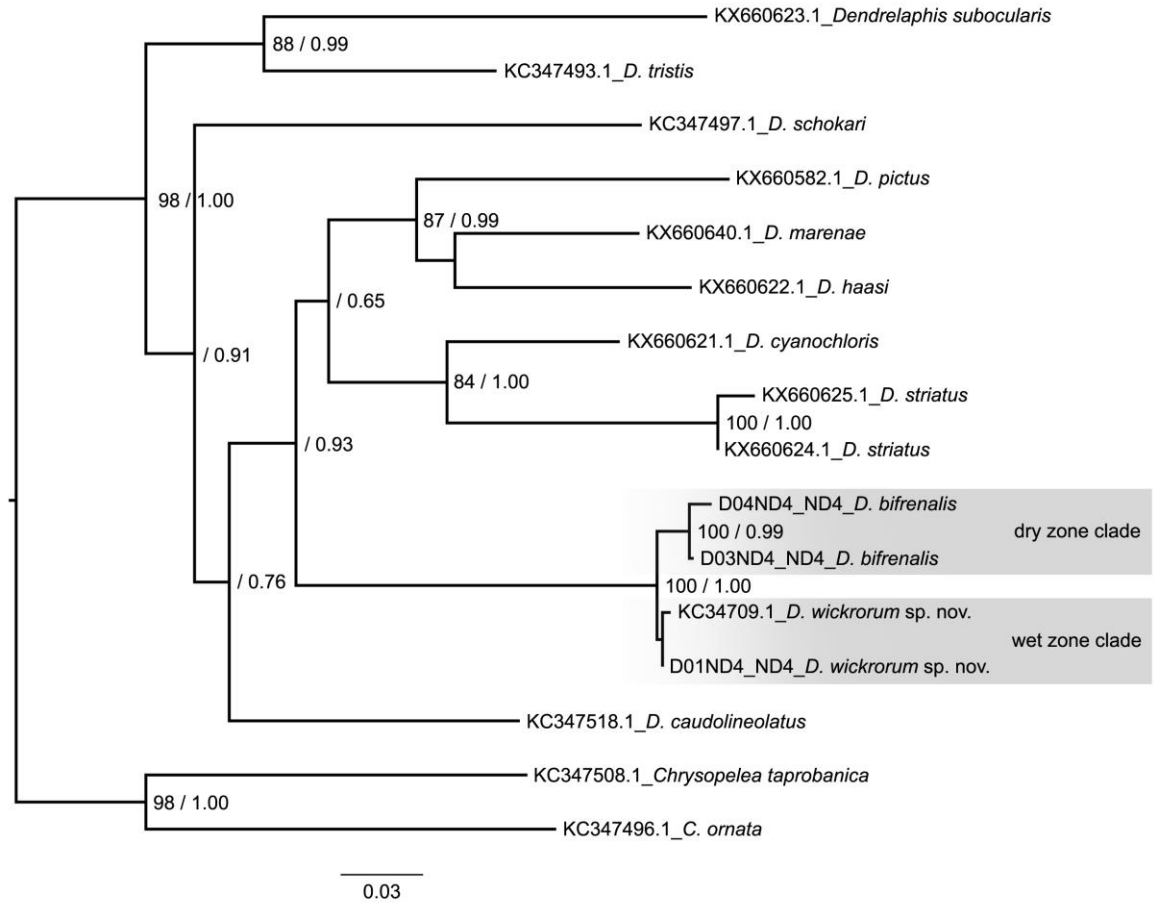


Figure 2. Phylogenetic affinities of *D. bifrenalis* and *D. wickrorum* sp. nov. using maximum likelihood (ML) analyses of the mitochondrial *ND*4 region. The topology of ML and Bayesian analyses were similar. Values on top of the node indicate ML bootstrap support >80% and Bayesian posterior probabilities >0.80 respectively.

Table 3. Estimates of similarity values and pairwise evolutionary distances of the members of *Dendrelaphis* and *Chrysopelea*. See Table 2 for details of the studied samples.

		Species	GenBank AN	Pair-wise Genetic Distance															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Similarity %	1	*D. wickrorum*	D01ND4_ND4		0.013	0.018	0.147	0.168	0.158	0.156	0.185	0.148	0.134	0.169	0.158	0.003	0.169	0.179	0.189
	2	*D. bifrenalis*	D03ND4_ND4	93.8		0.008	0.155	0.169	0.162	0.161	0.187	0.158	0.135	0.173	0.161	0.016	0.171	0.185	0.198
	3	*D. bifrenalis*	D04ND4_ND4	96.5	95.0		0.160	0.173	0.166	0.164	0.190	0.160	0.139	0.177	0.164	0.021	0.174	0.187	0.198
	4	*D. marenae*	KX660640.1	85.0	80.6	82.6		0.163	0.137	0.129	0.168	0.108	0.134	0.127	0.156	0.147	0.161	0.181	0.182
	5	*D. schokari*	KC347497.1	82.9	79.1	81.1	83.3		0.169	0.166	0.177	0.166	0.156	0.173	0.153	0.171	0.156	0.168	0.181
	6	*D. striatus*	KX660625.1	83.9	79.8	82.1	85.7	82.3		0.014	0.176	0.153	0.124	0.148	0.155	0.158	0.168	0.179	0.187
	7	*D. striatus*	KX660624.1	84.1	80.0	82.3	86.5	82.6	98.6		0.171	0.148	0.113	0.137	0.148	0.156	0.161	0.174	0.189
	8	*D. subocularis*	KX660623.1	81.7	77.7	79.8	83.2	81.7	82.1	82.6		0.181	0.168	0.205	0.168	0.185	0.155	0.202	0.208
	9	*D. haasi*	KX660622.1	84.7	80.1	82.7	88.9	83.0	84.2	84.7	81.7		0.124	0.127	0.156	0.148	0.148	0.177	0.169
	10	*D. cyanochloris*	KX660621.1	86.8	82.4	84.8	86.7	84.1	87.4	88.5	83.2	87.1		0.134	0.148	0.134	0.145	0.174	0.166
	11	*D. pictus*	KX660582.1	82.9	78.9	80.7	87.3	82.1	84.7	85.7	79.7	87.1	86.5		0.147	0.173	0.173	0.184	0.181
	12	*D. caudolineolatus*	KC347518.1	84.4	79.2	82.0	83.5	83.6	83.5	84.1	82.7	83.5	84.7	84.5		0.158	0.155	0.182	0.189
	13	*D. wickrorum*	KC347509.1	99.4	93.8	96.2	85.3	82.9	84.1	84.2	82.0	85.0	87.0	82.9	84.1		0.169	0.176	0.189
	14	*D. tristis*	KC347493.1	82.9	79.1	80.9	83.3	83.5	82.6	83.2	84.7	84.4	85.0	82.6	83.8	83.2		0.173	0.169
	15	*C. taprobanica*	KC347508.1	82.0	77.6	80.0	81.7	82.7	81.5	82.0	80.0	81.7	82.6	80.9	81.1	82.4	82.4		0.153
	16	*C. ornata*	KC347496.1	81.7	76.7	79.4	82.3	81.7	81.4	81.2	79.8	83.2	83.6	82.4	80.9	82.0	83.2	84.2	

Taxonomy

In the original description of *Dendrophis bifrenalis*, Boulenger (1890: 80) clearly mentioned his description was based on three specimens (hence syntypes), and provided meristic characters as a range, except for one measurement. Among the three syntypes, we noticed that there are two morphospecies (mentioned as A and B in Table 4), after a critical comparison of the types, other museum specimens, and live specimens we were convinced that the latter (morph B) is morphologically distinct enough to be regarded as a separate species. Therefore, in order to stabilize the name with a recognized type specimen and to solve the taxonomical problem, we designate the specimen measured (intentionally used to write the description) by Boulenger (1890), BMNH 1946.1.6.4 as the lectotype of *Dendrophis bifrenalis*.

Table 4. Specimen composition of the syntypes of *Dendrophis bifrenalis*: based on the type series as recorded at BMNH, and as identified by Günther (1858), Boulenger (1890, 1894), and personal examination.

specimen (syntype)		**1**	**2**	**3**
present catalogue no. BMNH		1946.1.6.4	1946.1.10.19	1946.1.10.20
morpho-species recognized		A (dry zone)	A (dry zone)	B (wet zone)
personal examination	Sex	female	male	male
	stage	adult	subadult	juvenile
	ventrals	171	damaged	159
	subcaudals	144	damaged	150
	total length	102.5 cm	damaged	27.7 cm
	tail length	37.9 cm	damaged	10.3 cm
Günther (1858) listed as *Dendrophis picta* var. *C* [vouchers]	condition:	adult: bad state	half-grown	young
	presented by:	R. Templeton, Esq.	A. Paul, Esq.	from Mr. Cuming's collection
Boulenger (1890) listed as *Dendrophis bifrenalis* [types]	ventrals		154 – 171	
	subcaudals		144 – 155	
	total length	3 feet 3 inches (=99.1 cm)	not given	
	tail length	14.5 inches (=36.8 cm)		
Boulenger (1894) listed as *Dendrophis bifrenalis* [types]	presented by:	not mentioned	A. Paul, Esq.	not mentioned
	ventrals	171	155	154
	subcaudals	144	?	155
	total length	1,030 mm	not given	
	tail length	380 mm	not given	
location		Ceylon (=Sri Lanka)		

Dendrelaphis bifrenalis (Boulenger, 1890)
(Figs. 1–5, 8, 9B, 10; Tables 1–4, 6, 7)

Dendrophis bifrenalis Boulenger, 1890

Lectotype (designated herein). Adult female, BMNH 1946.1.6.4, SVL 646.0 mm, collected from Ceylon (=Sri Lanka), by A. Paul (*fide* Boulenger 1894) [presented by R. Templeton (*fide* Günther 1858), see discussion]

Other specimens (*n*=12). BMNH 1946.1.10.19, damaged, collected from Ceylon, by A. Paul (paralectotype); see Appendix I for other specimen data; Tables 5, 6 for morphometric and meristic data.

Description of lectotype. Adult female (BMNH 1946.1.6.4), SVL 646.0 mm; tail length 379.0 mm; head elongate (HL 3.8% of SVL), twice as long as wide (HW 42.5% of HL), slightly flattened, distinct from neck; snout elongate (ES 27.5% of HL), moderate, blunt in dorsal view, pointed in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 78.1% of HW); internasals pentagonal; nostrils rather large; nasal undivided, elongate, in anterior contact with rostral and internasal dorsally, 1st and 2nd supralabials ventrally, anterior loreal posteriorly; prefrontal rather large, broader than long, and subpentagonal; frontal large, subpentagonal, shorten posteriorly, and length more or less equal to width; supraoculars wide, elongated, posteriorly wider and rounded; parietals large, butterfly wing-like in shape, shorten, rounded posteriorly, bordered by frontal, supraoculars, upper postocular

anteriorly, anterior and upper posterior temporals, and five dorso-nuchal scales posteriorly; two loreal scales; anterior loreal broader and larger than posterior loreal, in contact with internasal and prefrontal dorsally, and 2nd & 3rd supralabials ventrally; posterior loreal narrow and more elongate than anterior loreal, in contact with prefrontal and preocular dorsally and 3rd & 4th supralabials ventrally; one preocular (both sides), vertically elongated, pentagonal, in contact with prefrontal and posterior loreal anteriorly, supraocular and frontal (slightly in contact) dorsally, and 4th & 5th supralabials ventrally; eye large (ED 16.6% of HL), round, shorter than eye–nostril length (ED 77.3% of EN, ED 60.3% of ES), pupil rounded; two postoculars, upper postocular larger, quadrangular, in contact with supraocular and parietal broad, in narrow contact with lower postocular and upper anterior temporal; lower postocular crescent in contact with 6th supralabial ventrally, anterior temporal posteriorly; temporals 2+2+2; anterior and posterior temporals elongated, hexagonal; anterior temporals smaller than posterior temporals, in contact with parietal dorsally, 7th & 8th supralabials ventrally; posterior temporals in contact with parietal dorsally, 8th & 9th supralabials ventrally.

Supralabials 9 (on both sides), 5th–9th larger in size, 6th–9th being the largest; 1st supralabial in contact with rostral anteriorly, nasal dorsally, 2nd supralabial with nasal and anterior loreal dorsally, 3rd supralabial with anterior and posterior loreals dorsally, 4th supralabial with posterior loreal and preocular dorsally, 5th supralabial with preocular and orbit dorsally, 6th supralabial with orbit and the lower postocular dorsally, 7th supralabial with upper & lower anterior temporals dorsally, 8th supralabial with lower anterior and posterior temporals dorsally, and 9th supralabial with lower posterior temporals dorsally and body scales posteriorly.

Mental of moderate size, triangular, wider than length; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shield posteriorly; eleven infralabials, 1st–6th in contact with anterior chin shield, 6th infralabial in narrow contact with posterior chin shield, 7th infralabial in contact with posterior chin shield and gular scales; two anterior chin shields in broad contact, and two posterior chin shields in narrow contact; posterior chin shields slightly longer than anterior chin shields; posterior chin shields bordered posteriorly by eight gular scales.

Body robust, elongate and subcylindrical; costals in 15-15-11 rows, all smooth and bluntly pointed; 171 ventrals; anal plate divided. Tail comparatively long (TL 58.7% of SVL), robust and thick, 144 paired subcaudals.

Variation. See Table 6.

Colouration. Over 160 years in preservative (Fig. 3), dorsally dark bluish black; a white colour longitudinal ventro-lateral line starts from anterior body up to the level of vent; dorsal head blue; black transverse ventro-lateral cross bars on the anterior part of the body; a black band (two-scale wide) from posterior nasal across the eye beyond the neck, afterwards connect with black transverse ventro-lateral cross bars (bands); ventral side creamy yellow.

In life (based on Figures 5, 8, 9B and observations), dorsally dark bluish green; a cream colour longitudinal ventro-lateral line starts from anterior body up to the level of vent; dorsal head greenish blue; black transverse ventro-lateral cross bars on the anterior part of the body, in between cross bars luminous blue, brown and gray colour; a black band from posterior nasal across the eye beyond the neck, afterwards connect with black transverse ventro-lateral cross bars; vertebral column usually orange or light brown, distinct on the anterior part of the body; ventral side light greenish yellow, throat white.

Dendrelaphis wickrorum sp. nov.
(Figs. 1, 2, 6–8, 9A, 10; Tables 1–7)

Holotype. Adult male, BMNH 1905.3.25.98, SVL 368.0 mm, collected from Punduloya, 4,000 ft, Ceylon (= Pundaluoya, Sri Lanka, 7˚00'47" N, 80˚39'47" E; alt. 1,060 m a.s.l.), Nuwara Eliya District, Central Province, Sri Lanka. Collector and the date unknown.

Paratypes (*n*=4). Adult female, DWC 2020.05.03, SVL 708.0 mm, collected from Pinwatta-Panadura (6˚41'23" N, 79˚55'24" E; alt. 15 m a.s.l.), Kalutara District, Western Province, Sri Lanka; Adult male, DWC 2020.05.04, SVL 489.0 mm, collected from Kuda-Waskaduwa (6˚37'11" N, 79˚56'51" E; alt. 15 m a.s.l.), Kalutara District, Western Province, Sri Lanka, by L.J.M. Wickramasinghe on 20 October 2006; Subadult male, USNM 267765, SVL 285.0 mm, collected from Labugama (6˚50'49" N, 80˚11'35" E; alt. 140 m a.s.l.), Colombo District, Western Province, Sri Lanka, by A. de Silva, on

Plate 30

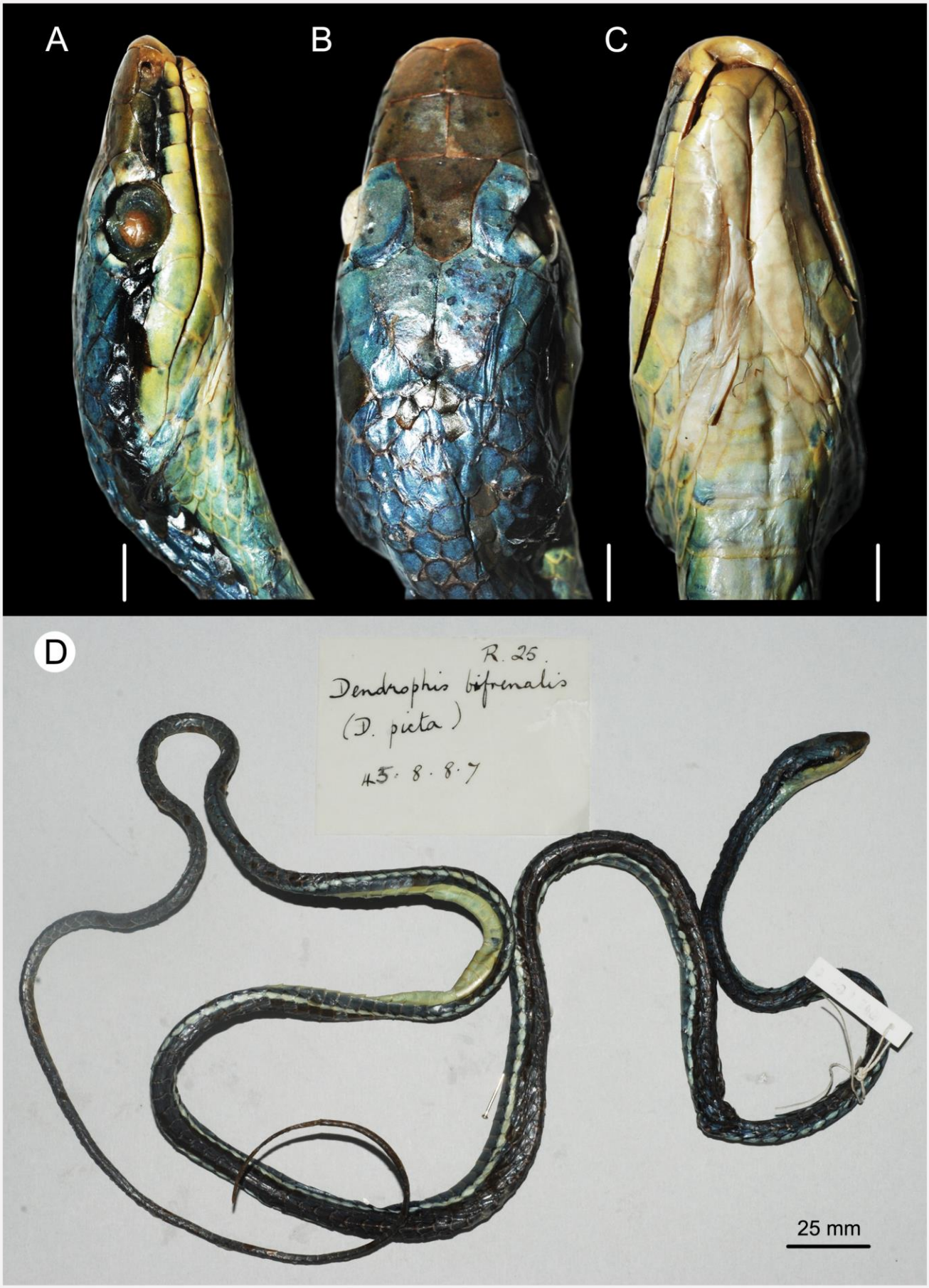


Figure 3. *Dendrelaphis bifrenalis* lectotype, female (BMNH 1946.1.6.4) from Ceylon [=Sri Lanka, probably from dry zone of Sri Lanka]; head in **(A)** lateral view, **(B)** dorsal view, **(C)** ventral view (scale: 3 mm); and **(D)** the full body of the lectotype (SVL 646.0 mm).

Plate 31

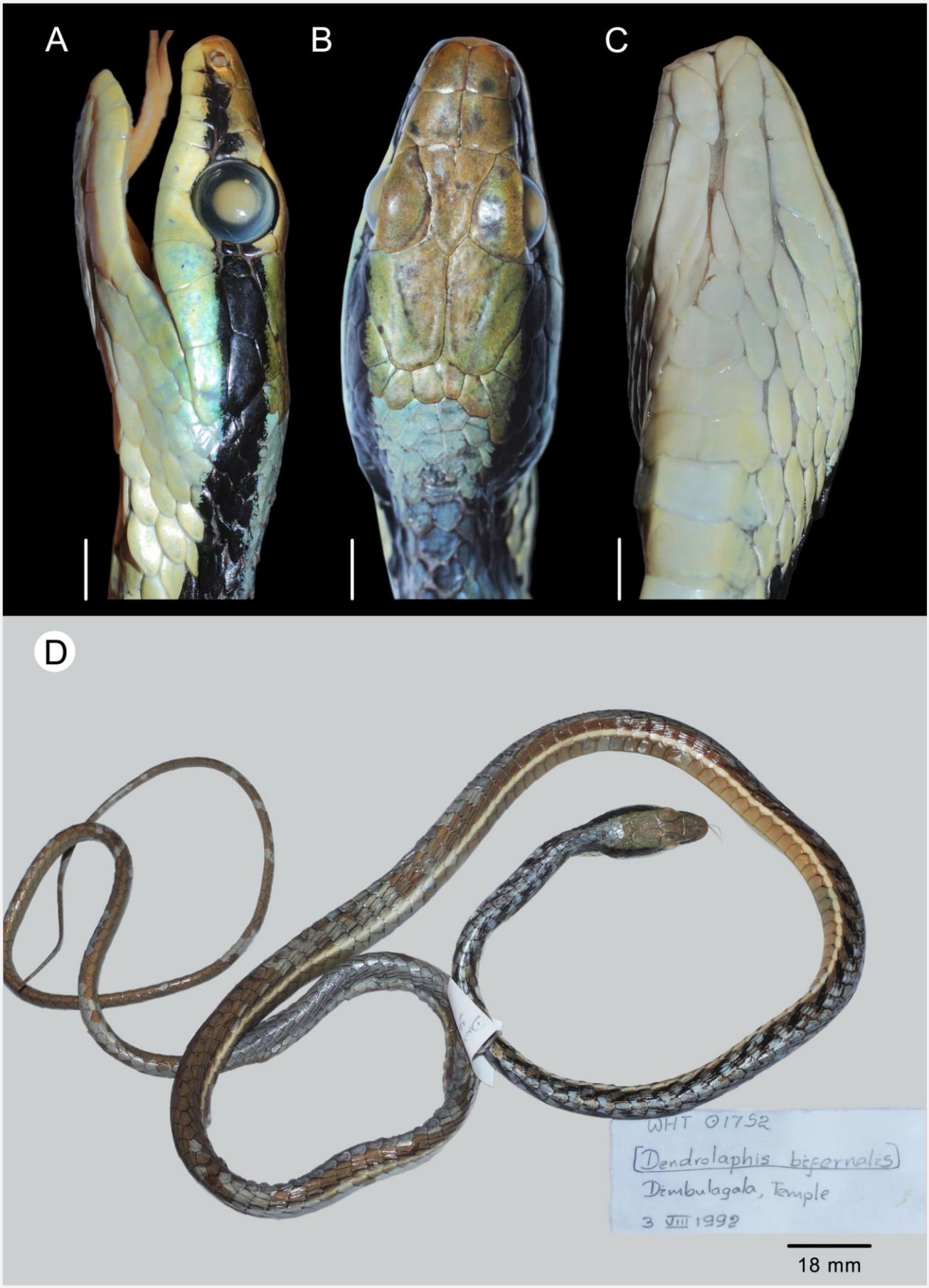


Figure 4. *Dendrelaphis bifrenalis* adult male (WHT 1752A) from Dimbulagala Temple, Polonnaruwa District, dry zone of Sri Lanka; head in **(A)** lateral view, **(B)** dorsal view, **(C)** ventral view (scale: 3 mm); and **(D)** the full body of the specimen (SVL 620.0 mm).

Plate 32

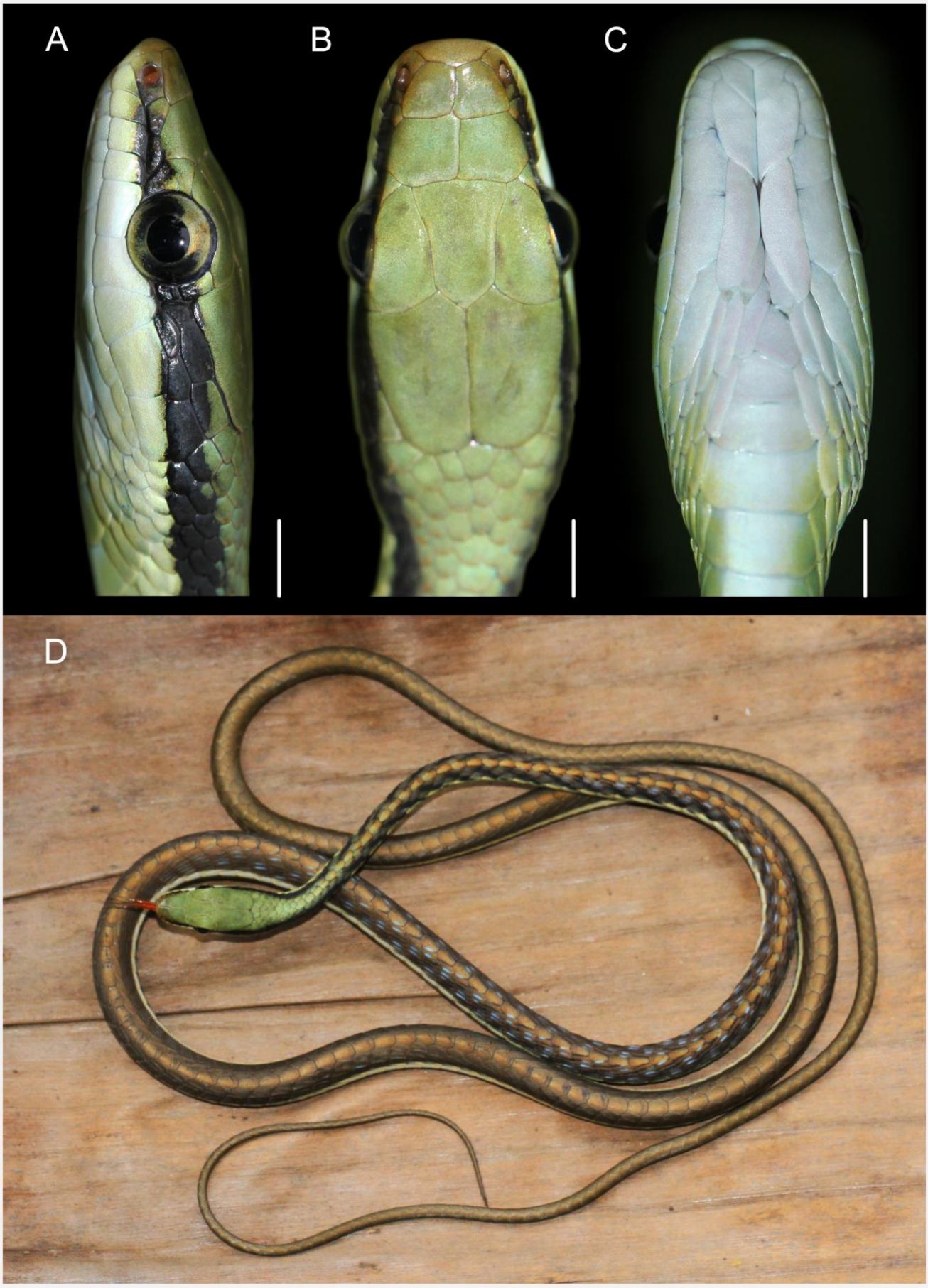


Figure 5. A subadult male of *Dendrelaphis bifrenalis* (not collected) from Wahalkada, near Padaviya, North Central Province, Sri Lanka; head in **(A)** lateral view, **(B)** dorsal view, **(C)** ventral view (scale: 2 mm); and **(D)** the full body of the individual (SVL, 470.0 mm).

December 1976; Juvenile male, BMNH 1946.1.10.20, SVL 174.0 mm, collected from Ceylon, by Mr. Hugh Cuming (paralectotype of *D. bifrenalis*), collecting data unknown; see Tables 4 for morphometric and meristic characters.

Diagnosis. The following combination of characters distinguishes the new species from *Dendrelaphis bifrenalis*: shorter snout: ED 103–114% of EN (*vs* 77–95%), larger eye: ED 21–23% of HL (*vs* 17–20%), presence of a temporal stripe stopping just beyond the neck (*vs* continues behind neck), absence of black transverse dorsolateral bars on the anterior 1/4th of body (*vs* prominent), presence of a ventro-lateral stripe continuing up to the tail (*vs* stopping at the level of anal plate) and narrow and pointed snout (*vs* broad and flat). Furthermore a divided nasal (*vs* single) distinguishes the new species; the differences are shown in Figs. 8 & 9, and summarized in Tables 6 & 7.

Description of holotype. Adult male, SVL 368.0 mm; tail length 222.0 mm; head elongate (HL 3.7% of SVL), twice as long as wide (HW 46.3% of HL), slightly flattened, distinct from neck; snout elongate (ES 28.7% of HL), moderate, rounded in dorsal and lateral profiles, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, concave posteriorly; interorbital width broad (IO 73.0% of HW); internasals pentagonal; nostrils rather large; nasal divided, elongate, in anterior contact with rostral and internasal dorsally, 1st and 2nd supralabials ventrally, anterior loreal and prefrontal (slightly touched) posteriorly; prefrontal rather large, broader than long, and subpentagonal; frontal large, subpentagonal, elongate posteriorly and longer than its width; supraoculars wide, elongated, subrectangular, posteriorly wider and pointed; parietals large, butterfly wing-like in shape, elongated, bordered by frontal, supraoculars, upper postocular anteriorly, anterior and posterior temporals, and six dorso-nuchal scales posteriorly; two loreal scales; anterior loreal smaller than posterior loreal, in contact with prefrontal dorsally and 2nd & 3rd supralabial ventrally; posterior loreal broad and more elongate than anterior loreal, in contact with prefrontal and preocular dorsally and 3rd–5th supralabials ventrally; one preocular (both sides), vertically elongated, pentagonal, in contact with prefrontal and posterior loreal anteriorly, supraocular dorsally, and 5th supralabial ventrally; eye large (ED 23.5% of HL), oval, greater than eye–nostril length (ED 114.3% of EN, ED 82.0% of ES), pupil rounded; two postoculars, upper postocular larger, quadrangular, vertically elongated, in contact with supraocular, parietal and anterior temporal broadly; lower postocular crescent in contact with 7th supralabial ventrally, anterior temporal posteriorly; temporals 1+1+2, anterior temporal shorten, posterior temporals elongated, hexagonal; anterior temporal in contact with parietal dorsally, 8th & 9th supralabials ventrally; posterior temporals larger and similar in size, in contact with parietal dorsally, 9th–10th supralabials ventrally.

Supralabials 10 (9 on left sides), 6th–10th larger in size, 9th being the largest; 1st supralabial in contact with rostral anteriorly, nasals dorsally, 2nd supralabial with posterior nasal and anterior loreal dorsally, 3rd supralabial with anterior and posterior loreals dorsally, 4th supralabial with posterior loreal dorsally, 5th supralabial with posterior loreal and preocular dorsally, 6th supralabial with orbit dorsally, 7th supralabial with orbit and the lower postocular dorsally, 8th supralabial with anterior temporal dorsally, 9th supralabial with anterior and posterior temporals dorsally, and 10th supralabial with posterior temporals dorsally and body scales posteriorly.

Mental of moderate size, triangular, wider than long; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shield posteriorly; ten infralabials, 1st–5th in contact with first chin shield, 5th infralabial in broad contact with posterior chin shield, 6th infralabial in contact with posterior chin shield and gular scales; two smaller anterior chin shields in broad contact, and two elongated posterior chin shields in broad contact; posterior chin shields bordered posteriorly by eight gular scales.

Body robust, elongate and subcylindrical; costals in 15-15-9 rows, smooth and bluntly pointed, anterior costals with a single apical pit at the tip; 162 ventrals; anal plate divided. Tail comparatively long (TL 60.3% of SVL), robust and thick, 150 paired subcaudals.

Variation. See Table 5.

Colouration. In preservative (Fig. 6), dorsally brownish green; a yellow colour longitudinal ventro-lateral line starts from anterior body continues until tail; dorsal head pale grayish green; a black stripe (one scale

wide) from posterior nasal across the eye until the neck, disappeared afterwards; some faint ventro-lateral cross stripes are visible [not prominent as in *D. bifrenalis*, which are cross bands]; ventral side brownish yellow.

In life (Figs. 7, 8, 9A), dorsally olive green; a yellow colour longitudinal ventro-lateral line starts from anterior body continues until tail; dorsal head dark olive green; a black stripe (mostly one scale wide) from posterior nasal across eye until the neck, disappeared afterwards; rarely ventro-lateral cross stripes are visible, but never prominent as in *D. bifrenalis*; ventral side creamy yellow.

Etymology. The specific epithet is a noun in the genitive case, honoring Mr. L.J. Mendis Wickramasinghe and his wife Mrs. Nethu Wickramasinghe for their remarkable contributions to the field of herpetology in Sri Lanka. Especially, Mendis Wickramasinghe's enormous effort in popularizing snake conservation among the general public is highly commendable. We shorten their modern name to the stem "Wickr" and formed in case of plural adding the suffix [-*orum*].

Suggested vernacular names are වික්‍රමසිංහලාගේ හාල්දණ්ඩා and Wickramasinghes' Bronze-back in Sinhala and English respectively.

Comparison. *Dendrelaphis wickrorum* sp. nov. is most similar to *D. bifrenalis* (in Sri Lanka) and *D. girii* Vogel & van Rooijen, 2011b (in India), the diagnostic characters are listed in the diagnosis and Table 6. The new species is distinguished from all the Sri Lankan and Indian *Dendrelaphis* by having two loreal scales (*vs* absent or single), except for *D. bifrenalis* (see Table 7). It further differs from *D. caudolineolatus* by having 9 or 10 supralabials 5^{th}–6^{th} or 6^{th}–7^{th} touching the eye (*vs* 8 and 4^{th}–5^{th} touching the eye), costals in 15 rows at mid body (*vs* 13), 157–162 ventrals (*vs* 149); from *D. sinharajensis* by having temporal stripe and ventrolateral stripe (*vs* absent), 9 or 10 supralabials (*vs* 8), costals in 15 rows at mid body (*vs* 13), 157–162 ventrals (*vs* 174); from *D. oliveri* by having 5^{th}–6^{th} or 6^{th}–7^{th} supralabials touching the eye (*vs* 4^{th}–6^{th}), 157–162 ventrals (*vs* 173), 150–157 subcaudals (*vs* 134), temporal stripe stops beyond the neck (*vs* until tail base); from *D. schokari* by having 150–157 subcaudals (*vs* 105–127); and from *D. tristis* by having 157–162 ventrals (*vs* 178–198), no interparietal bright spot (*vs* present).

Table 5. Selected Morphometric (in mm), meristric, and morphological characters of the holotype and paratypes of *Dendrelaphis wickrorum* sp. nov.; "—" = not measured.

Character	*D. wickrorum* sp. nov.				
	males				female
	holotype BMNH 1905.3.25.98	paratype BMNH 1946.1.10.20	paratype USNM 267765	paratype DWC 2020.05.04	paratype DWC 2020.05.03
snout–vent length (SVL)	368.0	172.0	285.0	489.0	708.0
tail length (TL)	222.0	104.0	179.0	298.0	396.0
relative TL (TL/SVL)%	60.33%	60.46%	62.80%	60.94%	60.0%
head length (HL)	13.65	11.24	12.40	18.04	23.45
head width (HW)	6.34	4.84	—	7.28	11.36
internarial distance (IN)	2.39	2.05	—	3.09	3.93
interorbital width (IO)	4.57	4.11	—	6.07	7.56
eye–nostril length (EN)	2.80	2.34	2.61	3.77	4.94
eye–snout length (ES)	3.92	2.55	—	5.71	7.75
eye diameter (ED)	3.20	2.41	2.69	3.91	5.00
relative ED/EN %	114.28%	102.99%	103.06	103.71%	101.21%
relative ED/HL%	23.44%	21.44%	21.69%	21.67%	21.32%
costals	15-15-9	15-15-9	15-15-9	15-15-10	15-15-11
ventrals	162	162	163	174	167
subcaudals	150	154	157	154	137
supralabials (SUP)	10	9	9	9	9
SUP at mid orbit position	6, 7	5, 6	5, 6	5, 6	5, 6
infralabials	11	10	10	10	12
Location	Pundaluoya	unknown	Labugama	Waskaduwa	Pinwatta

Plate 33

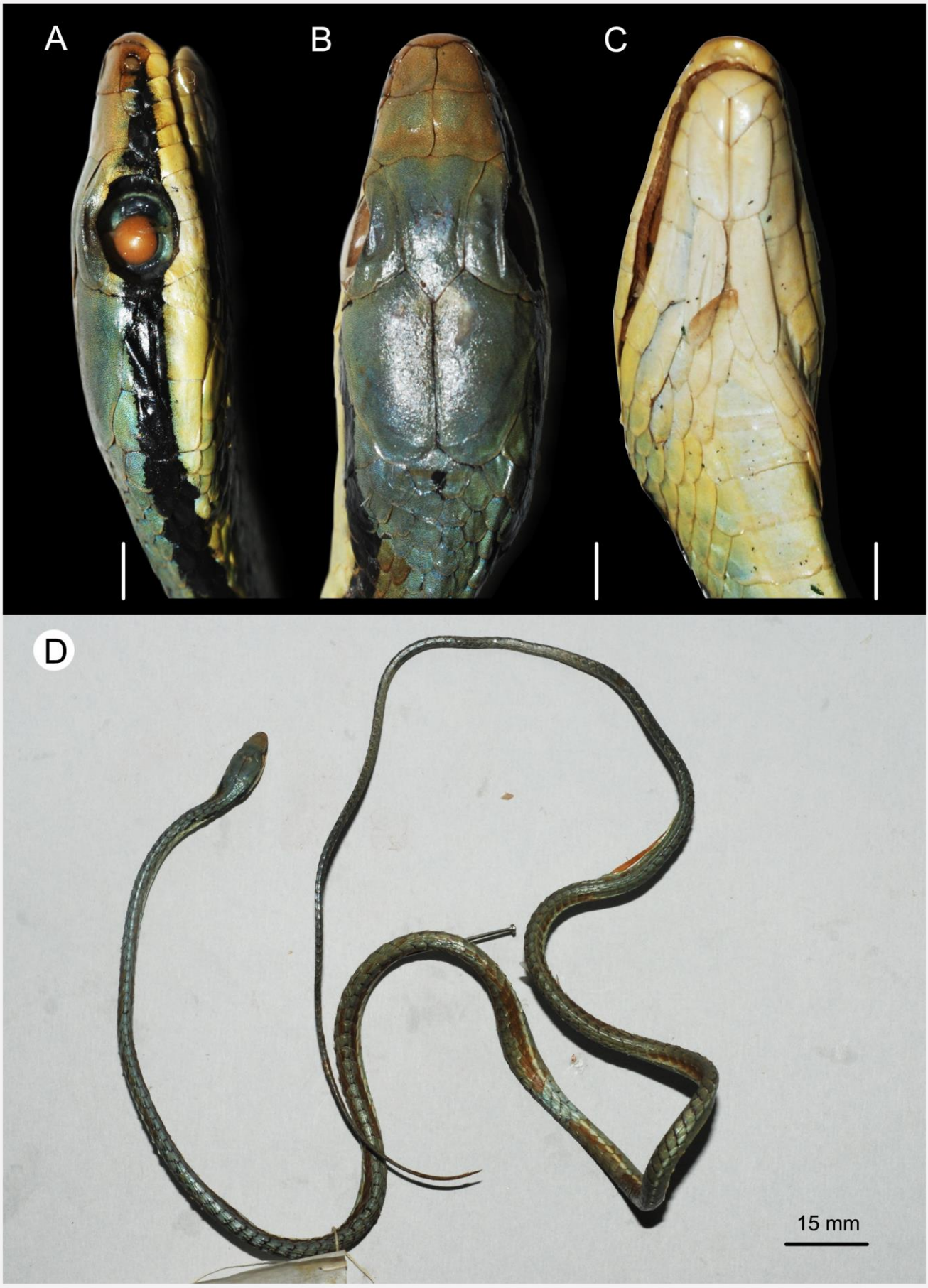


Figure 6. *Dendrelaphis wickrorum* sp. nov., an adult male, holotype (BMNH 1905.3.25.98) from Pundaluoya, Central Province, Sri Lanka (submontane wet zone); head in **(A)** lateral view, **(B)** dorsal view, **(C)** ventral view (Scale: 1.5 mm); and **(D)** the full body of the specimen (SVL 368.0 mm).

Plate 34

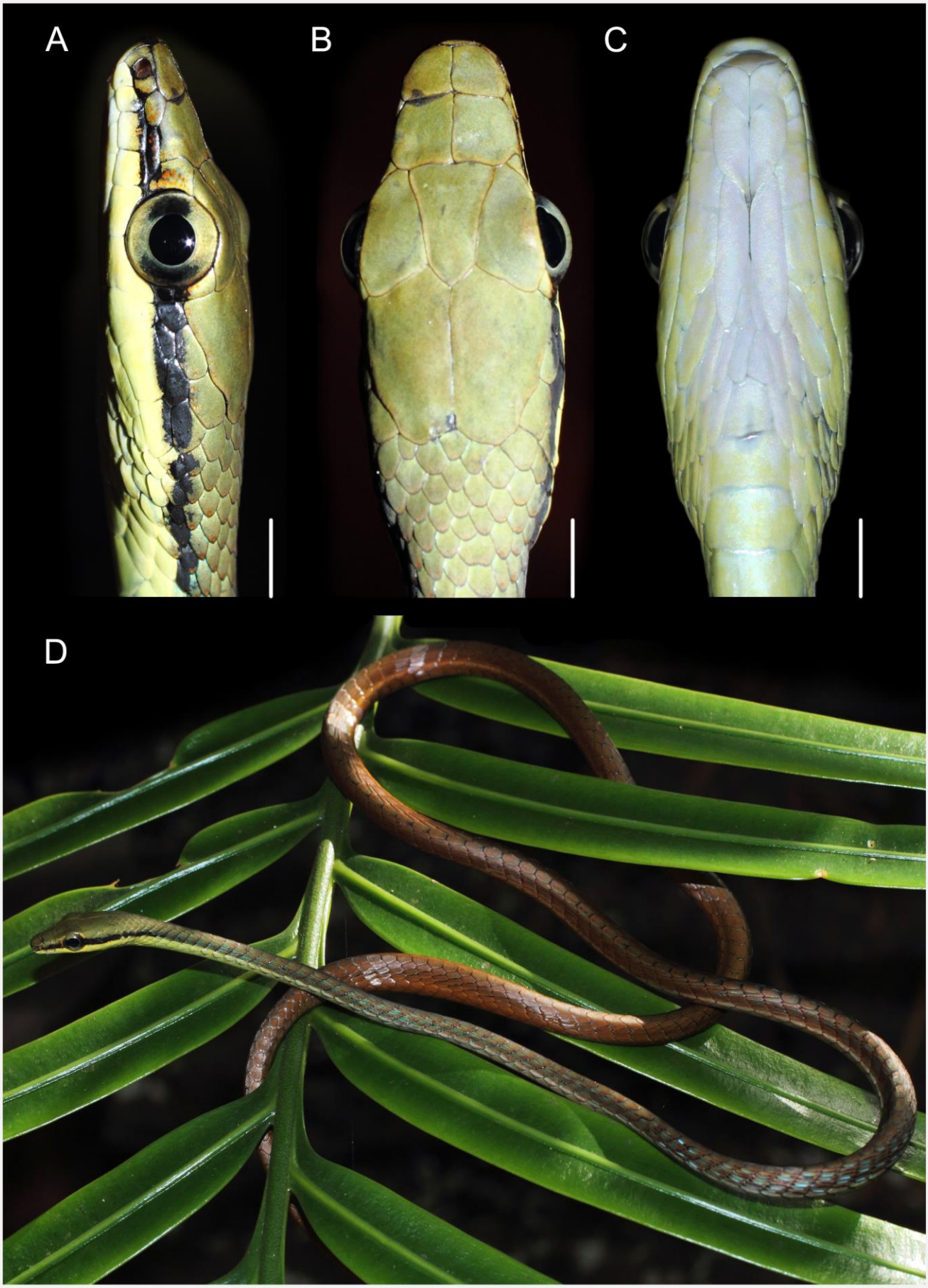


Figure 7. An adult male of *Dendrelaphis wickrorum* sp. nov. (not collected) from Athwalthota forest, Matugama, Kalutara District, Sri Lanka; head in **(A)** lateral view, **(B)** dorsal view, **(C)** ventral view (scale: 2 mm); and **(D)** the full body of the individual (SVL, 350.0 mm).

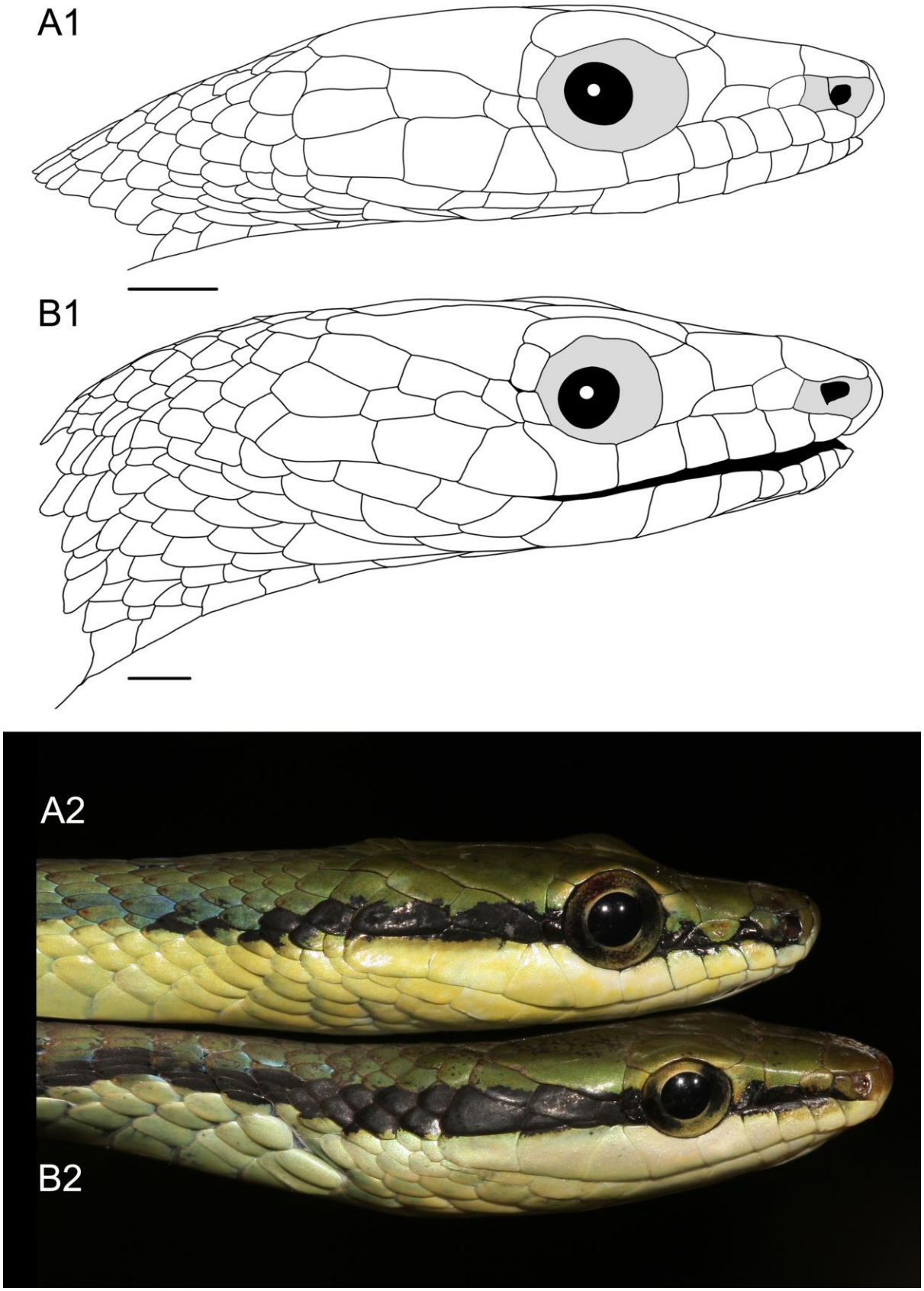


Figure 8. Head in lateral view **(A1)** holotype male of *Dendrelaphis wickrorum* sp. nov. (BMNH 1905.3.25.98) from Pundaluoya (wet zone) and **(B1)** lectotype female of *D. bifrenalis* (BMNH 1946.1.6.4) from dry zone; **(A2)** paratype female of *D. wickrorum* sp. nov. (DWC 2020.05.03) from Pinwatta (wet zone) and **(B2)** female *D. bifrenalis* (DWC 2020.05.06) from Girithale (dry zone); scale: 2 mm. Illustration and Photo © L.J.M. Wickramasinghe.

Table 6. Selected Morphometric (in mm), meristric, and morphological characters of the species of the *Dendrelaphis bifrenalis* complex including data of onomatophores; "—" = not measured.

Character	*D. bifrenalis*		*D. girii*		*D. wickrorum* sp. nov.	
	males (*n*=6)	females (*n*=8)	male (*n*=1)	females (*n*=4)	males (*n*=4)	female (*n*=1)
snout–vent length	379–620	344–646	653.0	465–743	173–489	708
tail length (TL)	261–370	201–395	373.0	271–334	103–298	396
relative TL of SVL	0.58–0.64	0.58–0.61	0.57	0.58–0.59	0.60–0.63	0.60
head length (HL)	15.6–24.3	14.1–27.4	23.1	17.6–26.3	11.2–18.0	23.4
head width	6.5–8.9	9.2–11.4	—	—	4.8–7.3	11.4
eye–nostril length (EN)	3.1–5.0	3.1–5.9	5.0	3.8–6.1	2.3–3.8	4.9
eye–snout length	3.9–6.5	4.2–7.7	—	—	2.5–5.7	7.7
eye diameter (ED)	2.9–4.3	2.8–4.9	4.4	3.2–4.9	2.4–3.9	5.0
relative ED of EN %	86–97%	77–95%	86%	77–95%	103–114%	101%
relative ED of HL%	18–20%	17–19%	18%	17–20%	21–23%	21%
costals	15-15-9	15-15-11	15-15-11	15-15-11	15–15-9	15-15-11
ventrals	153–173	161–173	169	166–173	162–174	167
subcaudals	140–166	139–154	147	140–145	150–157	137
supralabials	9	9	9	8, 9	9, 10	9
infralabials	10	10	10	9, 10	10, 11	12
nasal plate	undivided		divided		divided	
snout shape	wide, flat		wide, flat		narrow, pointed	
% of temporal region covered by temporal stripe	60–80%		15–25%		40–60%	
transverse dorsolateral bars	present		absent		absent	
ventro-lateral line	up to vent		absent		up to tail	
Distribution	Mostly in dry zone Sri Lanka		south and western parts of India		wet zone Sri Lanka	

Table 7. Selected diagnostic characters of the *Dendrelaphis* species occur in Sri Lanka; "—" = not evaluated.

Character	*bifrenalis* (*n*=13)	*caudolineolatus* (*n*=2)	*effrenis* (*n*=3)	*oliveri* (*n*=1)	*schokari* (*n*=23)	*tristis* (*n*=7)	*wickrorum* (*n*=7)
maximum SVL in mm	708	650	672	756	1,190	1,310	489
relative (TL/SVL)%	58–64	36	38–48	33	44–56	48–64	60–63
relative (ED/EN) %	86–97	100	109	—	69–70	65–68	101–114
loreal absent (0) one (1) two (2)	2	1	0	0	1	1	2
snout narrow (0), wide (1)	1	1	0	0	0	1	0
nasal single (1), divided (2)	1	2	1	2	2	2	2
interparietal spot absent (0), present (1)	0	0	0	0	0	1	0
parietal stripe absent (0), present (1)	0	0	1	0	0	0	0
ventro-lateral line absent (0), upto vent (1), upto tail (2)	1	0	0	1	2	2	2
cross bands on dorsum absent (0), present (1)	0	1	1	0	0	0	0
temporal stripe absent (0), present (1)	1	1	0	1	1	1	1
costals at midbody	15	13	13	15	15	15	15
ventrals	153–173	149–164	174–175	173	155–177	178–198	162–174
subcaudals	137–166	119–128	129–139	134	105–127	121–136	150–157
SUP touching the eye	5, 6	4, 5	4, 5	4–6	5, 6	5, 6	5, 6
INF touching chin shields	1–5	1–4	1–5	1–5	—		1–5
temporals	2+2	1+1, 1+2	1+2, 2+3	1+1	2+2	2+1	1+1
anal plate single (1), divided (2)	2	2	1	2	2	2	2
maxillary teeth	24–25	29–32	—	—	—	—	24–25

Plate 35

Figure 9. Adult females of **(A)** *Dendrelaphis wickrorum* sp. nov. (paratype, DWC 2020.05.03, SVL 708.0 mm) collected from Pinwatta - Panadura (wet zone); and **(B)** *D. bifrenalis* (DWC 2020.05.06, SVL 602.0 mm) collected from Girithale (dry zone) in Sri Lanka. Photo © L.J.M. Wickramasinghe. **(A1, B1)** different individuals, not collected.

Discussion

In his book of "The Catalogue of Colubrine Snakes", Günther (1858: 148) listed three specimens of *Dendrophis picta* var *C* from Ceylon (=Sri Lanka), see Table 4. Ferguson (1877: 20) too mentioned possibly the same three specimens as *Dendrophis picta* var *C*. Neither Boulenger (1890) nor any other author provided precise locality data for the syntypes of *Dendrelaphis bifrenalis*, except to say they came from Ceylon (=Sri Lanka). According to Günther (1858) the largest syntype was presented by R. Templeton but the collector was not mentioned, so therefore remains untraceable.

Robert Templeton (1802–1892), a naturalist, artist, and entomologist, worked in Sri Lanka as a surgeon in the Royal Artillery of the British Army from 1839 to 1851, until he was recalled in 1852 due to the Crimean War (Nash *et al*. 1980, Pethiyagoda 2007, Beolens *et al*. 2011). During a twelve-year stay in Sri Lanka, Templeton worked mainly on Lepidoptera, Coleoptera and Hymenoptera. From 1848 until 1951 he collaborated with Edgar Leopold Layard (1824–1900), a British diplomat and a naturalist mainly interested in ornithology (Mennell 1892). In addition to massive collections of insects, snails, annelids, birds, and mammals, both Templeton and Layard collected few reptiles. There is one specimen of *D. bifrenalis* in London (BMNH 1894.9.11.20) collected by E.L. Layard himself, but without a precise locality (only Ceylon). Among the species described based on Templeton's collections throughout the country, for example the Common Acacia Blue butterfly, *Surendra quercetorum* (Moore, 1857) is a species restricted to the dry and intermediate zones. In addition, the type of *Oligodon templetonii* Günther, 1862 (currently a synonym of *Oligodon calamarius* (Linnaeus, 1758) and *Mytilia templetonii* Gray, 1858 (currently a synonym of *Rhinophis blythii* Kelaart, 1853) were collected by R. Templeton himself, probably in the vicinity of Kandy, as the latter species is restricted to the Kandian mid hills. Among the species, which are based on specimens collected by either Layard or Templeton, most are distributed in the vicinity of Kandy (alt. 500 m a.s.l.). Interestingly the specimen, NMW 23724 collected from Kandy is very close to the morphology of the lectotype of *D. bifrenalis* as well as to Layard's specimen. In addition to the above three specimens, based on live specimens we observed that the Kandyan population represent the true *D. bifrenalis* along with the populations in dry and intermediate zones (see Fig. 10). Therefore we have to conclude that the lectotype of *D. bifrenalis* was probably collected from either dry zone or surrounding Kandy. In contrast *D. wickrorum* is restricted to the rest of the southwestern wet zone to a high elevations (alt. 1,000 m a.s.l.), mostly in forests. Therefore, in the map (Fig. 10) we only plotted vouchered or personally observed specimens.

D. bifrenalis and *D. wickrorum* sp. nov. are clearly separated species based on morphology, morphometry, and molecular data, the distribution patterns of this species pair is not in accordance with the currently identified biogeographic zonation based on vegetation types and climate of the island. This phenomenon is similar to that which has been observed for *D. schokari* and *D. tristis*. *D. bifrenalis* is sympatric with *D. tristis* in the dry and intermediate zones. In contrast, *D. wickrorum* is sympatric with *D. sinharajensis*, *D. schokari* and *D. caudolineolatus* in the wet zone. Previous studies of the biogeographic patterns of less vagile groups in Peninsula India and Sri Lanka (Bossuyt *et al*. 2004, Lajmi *et al*. 2019, Mallik *et al*. 2019) suggested vicariance coupled with allopatry as the main model for speciation in Sri Lanka. Our analysis supports a climate induced allopatric speciation model as the likely cause for the divergence of *D. wickrorum* sp. nov. from *D. bifrenalis* complex (a hypothesis also valid for *D. schokari* and *D. tristis*). The darker, wet, tropical rainforest of the wet zone of Sri Lanka might have favored the dark larger eyes in these diurnal visual predators of the sub-canopy and the understory (personal observations and Pyron *et al*. 2013).

Wall (1921) examined five specimens of *Dendrelaphis bifrenalis* (*sensu lato*) from Sri Lanka, collected from Punagalla (Central Province), Yatiyantota and Balangoda (Sabaragamuwa Province), and Galle (Southern Province). Probably his specimens from Yatiyantota and Galle represent the new species, and the specimens from Balangoda and Punagalla, which are located on the transitional zone between wet and intermediate zones, might be either *D. bifrenalis* or *D. wickrorum* sp. nov., as we observed several live specimens of *D. bifrenalis* from the dry and intermediate valleys towards the dry zone in the central highlands as

well as the Knuckles massif. According to Wall (1921), *D. bifrenalis* was never recorded above 1,000 feet elevation (=300 m a.s.l.). However the holotype of *D. wickrorum* sp. nov. (BMNH 1905.3.25.98) was collected from an elevation of 4,000 feet (=1,060 m a.s.l.), the highest elevation record for this species.

Taylor (1950) mentioned a single specimen (EHT-HMS No. 30745 in it) found in Trincomalee, and he noticed "The eye is large but its diameter is distinctly less than its distance from the nostril", an obvious representation of *D. bifrenalis* (in similarity with the specimen of *D. bifrenalis* found in Waahalhada 50 km away).

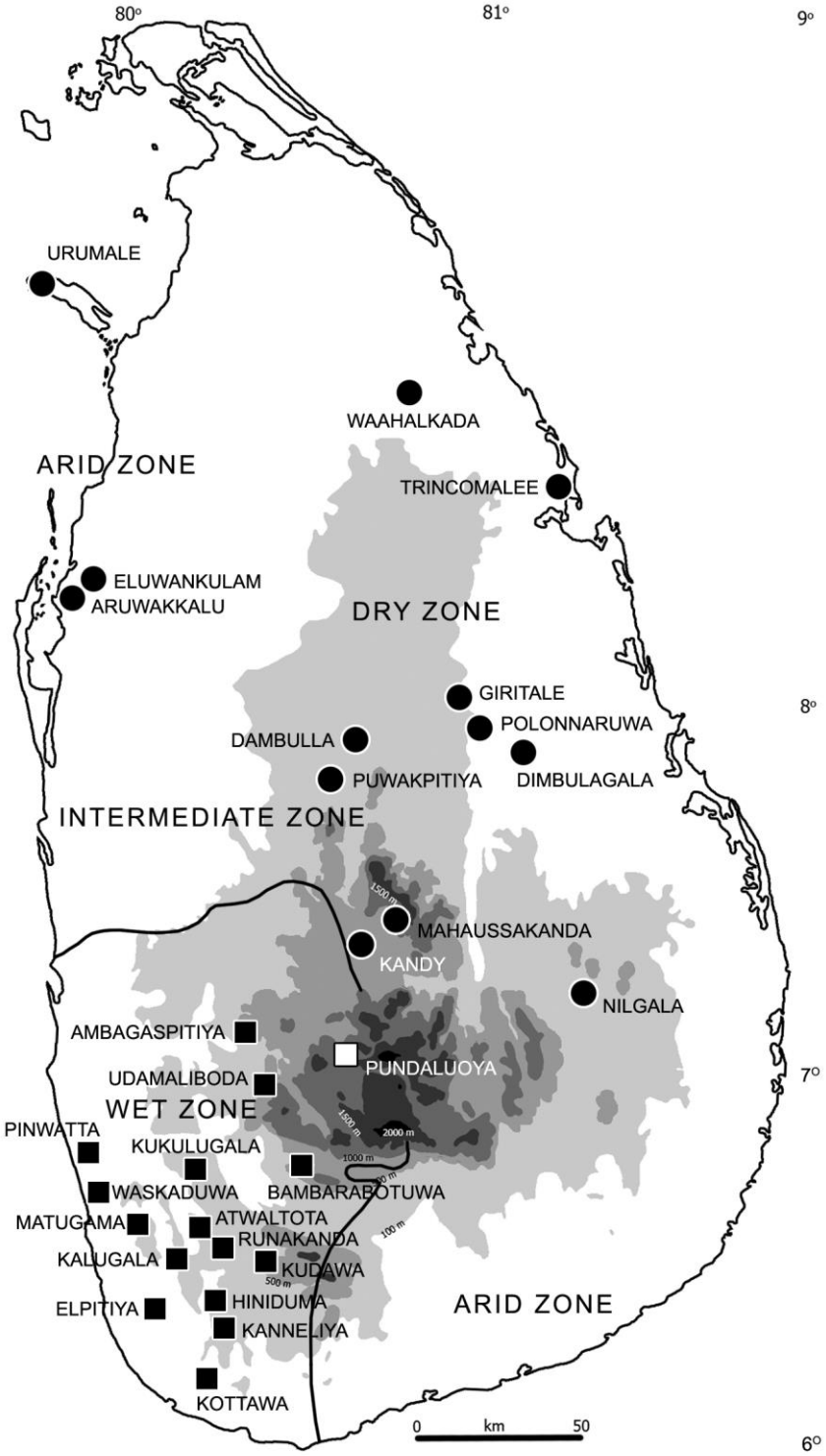


Figure 10. Current distribution map of *Dendrelaphis bifrenalis* (filled circles) and *D. wickrorum* sp. nov. (filled squares) in Sri Lanka; holotype locality of *D. wickrorum* sp. nov. marked with a white square, the lectotype locality of *D. bifrenalis* is unknown [possibly around Kandy].

Deraniyagala (1955) further extended the distribution of *D. bifrenalis* from Vavuniya (Northern Province), Mullativu and Trincomalee (Eastern Province), most probably those specimens represent *D. bifrenalis*. He recorded *D. bifrenalis* (*sensu lato*) from Veyangoda (Western Province), probably the new species (in similarity with the live specimen of *D. wickrorum* sp. nov. found 10 km from Ambagaspitiya, Western Province).

Based on recent publications, the records of *D. bifrenalis* from Nilgala, Uva Province (Karunarathna & Amarasinghe 2011, Karunarathna *et al*. 2013) and Eluwankulam, North Western Province (Kumarasinghe *et al*. 2013) are confirmed with the species identity as *D. bifrenalis*, but the following records of *D. bifrenalis*, here we assign for *D. wickrorum* sp. nov. as one of us (AATA) personally observed and recorded the characters of the same specimens published there in: Kukulugala forest, Sabaragamuwa Province (Karunarathna & Amarasinghe 2010); Kalugala Forest Reserve, Western Province (Botejue & Wattavidanage 2012); Udamaliboda forest, Sabaragamuwa Province (Peabotuwage *et al*. 2012) and Beraliya-Mukalana forest, Southern Province (Karunarathna & Amarasinghe 2012).

The phylogenetic analysis based on the mitochondrial *ND*4 region grouped individuals identified as the members of *D. bifrenalis* complex together as a well separated monophyletic group. Similarly, all individuals of *D. bifrenalis* and *D. wickrorum* sp. nov. form well separated distinct groups sister to each other (Fig. 2). We observed concordance between morphometric and phylogenetic divergence across these two species (Figs. 1 & 2), hence we conclude that they are phenotypically and phylogenetically distinct lineages and true taxonomic entities.

Similar to other studies of recently diverged colubrids (Figueroa *et al*. 2016, Mallik *et al*. 2019, Jiang *et al*. 2020), the *D. bifrenalis* complex might have diversified rapidly as implied by the short internodes throughout much of the tree (this study and in Pyron *et al*. 2013, Jiang *et al*. 2020). Nevertheless, we can draw conclusions based on strong nodal support values regarding the placement of the proposed new species (see Mallik *et al*. 2019, Jiang *et al*. 2020). Our analysis did not include the probable mainland congener of *D. bifrenalis* complex in Sri Lanka (*D. girii*), due to the absence of sequences in the global databases and its restricted range. The isolated nature of the *D. bifrenalis* clade in Sri Lankan *Dendrelaphis* suggesting that there is a good possibility that *D. girii* will cluster with that clade. Our phylogeny further suffers from the absence of two Sri Lankan endemic taxa, *D. oliveri* and *D. sinharajensis* in the analysis. It is high time for a comprehensive phylogenetic study for this divergent, ecologically complex genus, to understand not just the phylogenetic affinities of its members, but also its colonization patterns across Southern and Southeastern Asia.

Among the Sri Lankan *Dendrelaphis*, *D. oliveri* is the rarest species. It is only known from a single specimen (holotype). The type locality is 12 miles north of Trincomalee, Ceylon (=Sri Lanka). *D. effrenis* was also described based on a single specimen collected much earlier (in 1909) than *D. oliveri*, from Colombo, Sri Lanka. The original description of *D. effrenis* was written in German by Werner (1909) and is comprehensive enough to distinguish it from other species. Wall (1921) provided an English description, but considered this species could be an aberrant specimen of *D. caudolineolatus*. Smith (1943) synonymised Werner's species with *D. caudolineolatus* without any discussion, and subsequent authors followed that taxonomic treatment. However, according to the original description, *D. effrenis* is clearly distinguishable from *Dendrelaphis caudolineolatus* by having no loreal (*vs* present), three postoculars (*vs* two), a combination of a red neck and conspicuous red/white cross bars (*vs* oblique black stripes on anterior bronze body, that meets mid dorsally forming a 'V' shape), a throat with black blotches (*vs* blotching absent). Furthermore, *D. effrenis* is clearly distinguishable by any of the species in a group of Malayan bronzebacks, *D. caudolineatus* complex, which has similar colour patterns, by having no black longitudinal dorsal stripes (*vs* present), no ventrolateral stripe (*vs* present), and 129 subcaudals (*vs* 101–113). The English translation of the German description by Werner (1909) is given in Appendix II.

Wickramasinghe (2016) described *Dendrelaphis sinharajensis* from Sinharaja forest (alt. 285 m a.s.l.), Sri Lanka, based on a single specimen (NMSL 2016.06.01). A comparison of the holotype and the original description of *D. sinharajensis* with the original description of *D. effrenis* revealed that both

names were created for the same species. There is only individual variation as follows: the SVL 672 mm, ventrals 174, temporals 1+3, and 138 subcaudals in *D. sinharajensis* (*vs* SVL 640 mm, ventrals 175, temporals 2+2, subcaudals 129 in *D. effrenis*). According to the curator of the ZMH collection, the holotype of *D. effrenis*, collected by John Hagenbeck from Colombo, Ceylon is missing, misplaced or has been destroyed during the World War II (Pers. comm. Jakob Hallermann, Universität Hamburg - Zoologisches Museum). However, the original description of *D. effrenis* is comprehensive enough (Appendix II) to distinguish it from the other valid species of the genus *Dendrelaphis*. Therefore here we revalidate *D. effrenis* as a distinct species of the genus *Dendrelaphis*. Furthermore, according to the Article 23 of the ICZN (1999), we synonymise *D. sinharajensis* with *D. effrenis*. To fix the taxonomy of *D. effrenis*, we choose the holotype of *D. sinharajensis* described by Wickramasinghe (2016), as the neotype for *Dendrophis effrenis* Werner, 1909.

During field surveys we found the third and fourth specimen of *D. effrenis* (not collected) from Kudawa, Sinharaja forest (6˚26'09" N, 80˚25'10" E; alt. 350 m a.s.l.), and Athwalthota, Mathugama (6˚31'13" N, 80˚16'53" E; alt. 50 m a.s.l.), Sabaragamuwa Province, Sri Lanka (Fig. 11). The type locality of the species is given as Colombo (Werner 1909). It may have been collected from one of several patches of rainforests near Colombo (e.g. Dombagaskanda, Waga Forest Reserve etc.) as this species may have been widely distributed in the lowland rainforests (alt. 50–350 m a.s.l.) during its time of description. The possibility also exists that the location of the specimen was erroneously assigned disregarding the climatic and biogeographic heterogeneity of the island.

An identification key for the *Dendrelaphis* species in Sri Lanka is given below.

1. (a) Midbody scale in 13 rows 2
   (b) Midbody scale in 15 rows 3

2. (a) Loreal present, 149 ventrals, 119–128 subcaudals, and temporal stripe present ..... *D. caudolineolatus*
   (b) Loreal absent, 174–175 ventrals, 129–139 subcaudals, and temporal stripe absent ..... *D. effrenis*

3. (a) Loreal present 4
   (b) Loreal absent ..... *D. oliveri*

4. (a) Single loreal scale 5
   (b) Two loreal scales 6

5. (a) 155–177 ventrals, interparietal spot absent ..... *D. schokari*
   (b) 178–198 ventrals, interparietal spot present ..... *D. tristis*

6. (a) temporal stripe continues behind neck, prominent black transverse dorsolateral bars on the anterior 1/4th of body, ventro-lateral stripe stopping at the level of anal plate, wide and flat snout, eye small and eye diameter < eye–nostril distance ..... *D. bifrenalis*
   (b) temporal stripe stopping just beyond the neck, no black transverse dorsolateral bars on the anterior 1/4th of body, ventro-lateral stripe continuing up to the tail, narrow and rounded snout, eye large and eye diameter > eye–nostril distance ..... *D. wickrorum* sp. nov.

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Plate 36

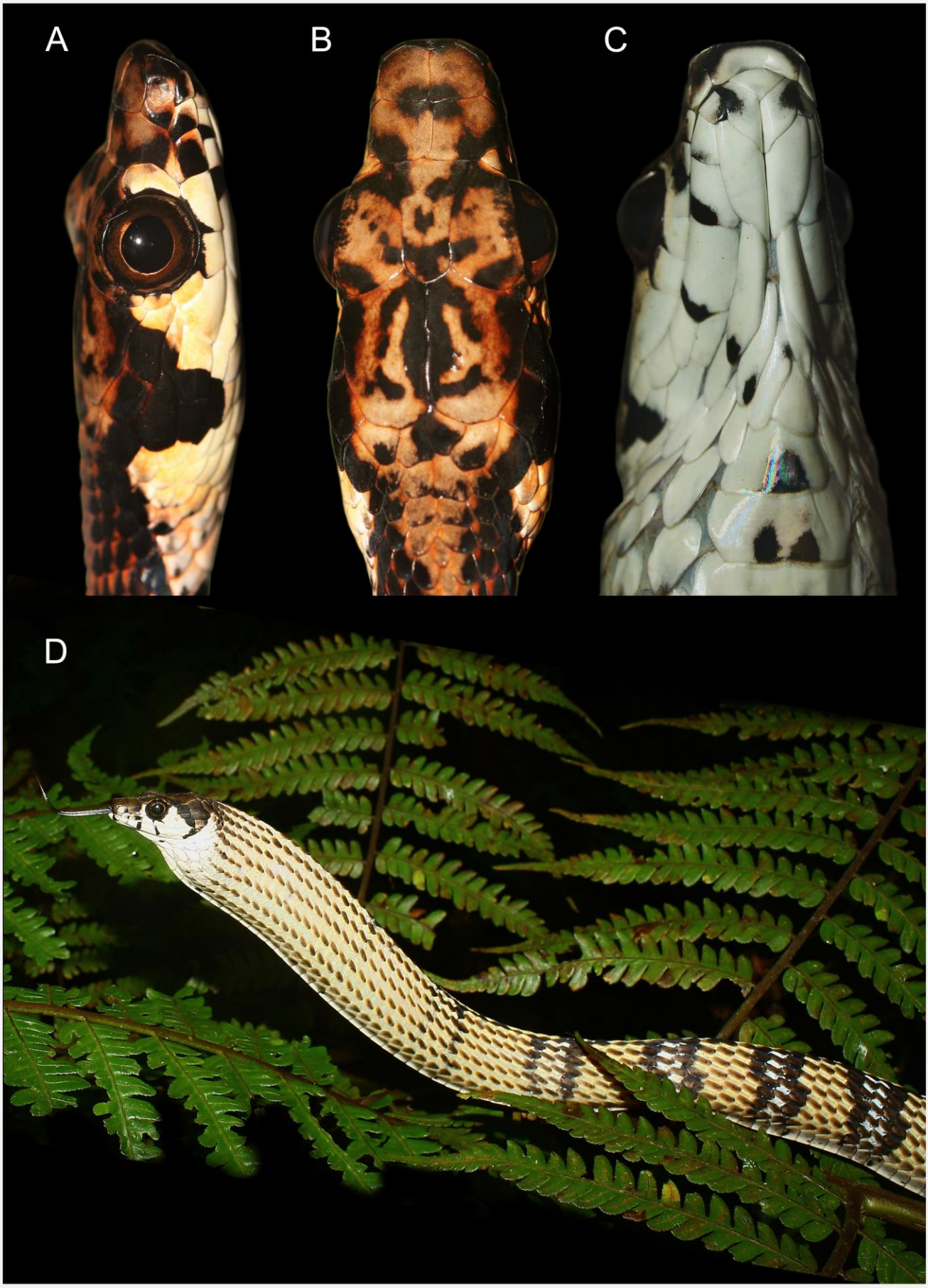

Figure 11. *Dendrelaphis effrenis* (Werner, 1909) male (not collected), head in **(A)** lateral view, **(B)** dorsal view from Kudawa, Sinharaja Forest, Ratnapura District, Sri Lanka; female (not collected), head in **(C)** ventral view and **(D)** the anterior body, from Athwalthota Forest, Matugama, Kalutara District, Sri Lanka.

and nicely illustrate the line drawing. Also, we wish to thank Nuwan Madushanka, Dushmantha Kulathunga, Tharidu Ranasinghe, Rev. Hatangala Medanananda Thero, Mithun Chanaka, and Vishwa Sachith for the support in the field; Divanka Randula and Himesh Jayasinghe assisted in taking the photographs. Tharindu Premachandra, Shynika Lasanthi and Sanjaya Weerakkody at the Department of Zoology, UOC assisted in the genetic and phylogenetic analysis. Part of the funding for the fieldwork was provided by the Wildlife Conservation Society of Galle (WCSG). We also thank J. Supriatna and the staff of the Research Center for Climate Change, University of Indonesia, and the members of the Avian Evolution Node and the Laboratory for Molecular Ecology and Evolution, University of Colombo for their support.

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Appendix I. Other specimens examined

***D. bifrenalis* (13 ex.): Sri Lanka:** BMNH 1946.1.6.4 (lectotype designated herein), 1946.1.10.19 (paralectotype of *D. bifrenalis*), 94.9.11.20, MHNG 762.75, 743.36, FMNH 142366; Kandy: NMW 23724; Polonnaruwa: NMSL uncat. (WHT 1752-A), SMF 25483; Mahaussakanda: DWC 2020.05.02; Maha-Waskaduwa: DWC 2020.05.05; Girithale: DWC 2020.05.06; Aruwakkalu, Puttalam: DWC 2020.05.07.

***D. caudolineolatus* (2 ex.): Sri Lanka:** BMNH 1946.1.23.21 & 1858.2.17.19 (syntypes).

***D. effrenis* (1 ex.): Sri Lanka:** NMSL 2016.06.01 (neotype designated herein, holotype of *D. sinharajensis*).

***D. girii* (6 ex.): India:** Karnataka: BNHS 3494 (holotype), 3495 (paratype); Tamil Nadu: BNHS 3273 (paratype); Maharashtra: 3423, 3491, 3493 (paratypes).

***D. oliveri* (1 ex.): Sri Lanka:** FMNH 123726 (holotype).

***D. schokari* (23 ex.): Sri Lanka:** RMNH 842 (neotype designated by van Rooijen & Vogel 2008), 7066a–b, NMW23669:1–2, 24382:2–4, MNHN-RA 1890.0065, BMNH 1969.2781, SMF 18672, 32366, 62074, 62076, 70285, MHNG 762.73, 1198.50–51, 1198.53, 1198.55, MTKD 10440, 10646, 15438.

***D. tristis* (7 ex.): India:** SMF 58442 (neotype designated by van Rooijen & Vogel 2008); **Sri Lanka:** BMNH 1955.1.9.80, 93.10.6.1, 1972.2.18.3, ZMA 21563, SMF 18671, 32367.

Appendix II. English translation of the original description of *Dendrophis effrenis* Werner, 1909.

Dendrophis effrenis n. sp.

Colombo, Ceylon (leg. JOHN HAGENBECK 1904).

Dor. 13, V. 175, Anal divided, Sc. 129/129 + 1.

Rostral twice as wide as long. Internasals as long as prefrontals. Frontal 1.66 times as long as wide, longer as its distance from tip of snout, as long as parietals. No loreal, 1 preocular, 3 postoculars, temporals 2+2, 4 infralabials in contact with the anterior chin shields, which are shorter than the posteriors. Eye large, but its diameter only as long as its distance from posterior margin of the hole in the nose.

Colouration (in formalin): Upper side blackish gray, neck scales with narrower and wider red bands, so that in the anterior part of the body 7 dark bands can be seen separate by wide spaces. Rostral dorsal with dark margins; 1st and 2nd supralabials dark; a broad dark band from the eye to the corner of the mouth and a little bit beyond it. Lower labials partially spotted black, throat just as well. Ventrals with dark dots.

Total length 884 mm, tail 244 mm.

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