# A multivariate investigation into the population systematics of *Dendrelaphis tristis* (Daudin, 1803) and *Dendrelaphis schokari* (Kuhl, 1820): revalidation of *Dendrophis chairecacos* Boie, 1827 (Serpentes: Colubridae)

# Johan Van Rooijen<sup>1</sup> & Gernot Vogel<sup>2</sup>

<sup>1</sup>Zoological Museum Amsterdam, The Netherlands <sup>2</sup>Society for Southeast Asian Herpetology, Heidelberg, Germany

The population systematics of the closely related colubrid snakes *Dendrelaphis tristis* (Daudin, 1803) and *Dendrelaphis schokari* (Kuhl, 1820) were investigated on the basis of morphological data taken from 82 museum specimens. Multivariate and univariate analyses of these data reveal the existence of a third species that occurs sympatrically with *D. tristis* in south India. This hitherto unrecognized species agrees with the description of *Dendrophis chairecacos* Boie, 1827 which is consequently revalidated under the combination *Dendrelaphis chairecacos* (Boie, 1827). A neotype is designated to objectively define this taxon. *Dendrelaphis chairecacos* inhabits south India and *D. schokari* inhabits Sri Lanka. *D. tristis* occurs sympatrically with both species, ranging from Sri Lanka through most of India to Nepal. A key to the three species is provided. Observed differences in head morphology are probably correlates of niche partitioning between *D. tristis* on the one hand and *D. chairecacos* and *D. schokari* on the other hand. The revalidation of *D. chairecacos* strengthens the notion that Sri Lanka and the Western Ghats are faunally more distinct than previously recognized.

Key words: Dendrelaphis chairecacos, multivariate analysis, taxonomy, India, Western Ghats, Eastern Ghats, Sri Lanka

# INTRODUCTION

The colubrid snakes of the genus *Dendrelaphis* Boulenger, 1890 are widely distributed, ranging from Pakistan in the west to the northern and eastern coast of Australia in the east and south and to southern China in the north (Ziegler & Vogel, 1999). Members of the genus *Dendrelaphis* are slender, diurnal species that are predominantly arboreal and feed mainly on lizards and amphibians.

Boulenger (1894), Wall (1921), Meise & Henning (1932), Mertens (1934) and Smith (1943) have in turn worked on the systematics of this genus. However, their cumulative effort did not result in an unambiguous and complete taxonomy of this genus, a fact underlined by recent descriptions and revalidations of several species (Vogel & Van Rooijen, 2007, 2008; Van Rooijen & Vogel, 2008a,b,c).

Dendrelaphis tristis (Daudin, 1803) ranges from Sri Lanka through most of India to Nepal. Within this vast range, it is one of the most commonly encountered, and consequently best known, snakes. Ironically though, Dendrelaphis tristis was recently shown to be composed of two species (Van Rooijen & Vogel, 2008b). The name Dipsas schokari Kuhl, 1820 was revalidated under the combination Dendrelaphis schokari (Kuhl, 1820) to represent the second species. Dendrelaphis schokari was found to occur sympatrically with D. tristis in Sri Lanka and in southwest India. However, the occurrence of D. schokari in southwest India was based on just five specimens. Subsequent examination of further material from south India cast doubt on the taxonomic status of the population from south India as it appeared to differ in its morphology and coloration from its Sri Lankan counterpart. In this paper, multivariate techniques are applied to investigate the population systematics of *D. tristis* and *D. schokari* with particular focus on the southern Indian populations.

# MATERIALS AND METHODS

Eighty-two museum specimens were examined for this study. For each specimen examined, 22 characters including aspects of colour pattern, body proportions and scalation were recorded (Table 1). Eye diameter and eyenostril distance were measured with a slide calliper to the nearest 0.1 mm. These measurements were made on the left and right side and were subsequently averaged. Snout-vent length and tail length were measured by marking the length on a piece of string and subsequently measuring the position of the mark to the nearest 0.5 cm. Snout-vent length was measured to the posterior margin of the anal plate. The number of ventrals was counted following Dowling (1951). Subcaudals were counted on one side, the terminal scute was excluded. The first sublabial was defined as the scale that starts between the posterior chin shield and the infralabials and that borders the infralabials (see Peters, 1964, fig. 7). The last infralabial was defined as the infralabial still covered completely by the last supralabial. The posteriormost temporal scales

Correspondence: Johan Van Rooijen, Tulpentuin 313, 2272 EH, Voorburg, The Netherlands. E-mail: j1.van.rooijen@hetnet.nl

Table 1. List of morphometr	ic, scalation and coloration characters	s used in this stud	ly and their abbreviations
-----------------------------	---	---------------------	----------------------------

Abbreviation	Character
Morphometrics	
EYED	Horizontal diameter of the eye
EYEN	Distance from centre of the eye to posterior border of the nostril
TAIL	Tail length
WVERT	Width of the vertebral scale at the position of the middle ventral
SVL	Snout-vent length
Scalation	
VENT	Number of ventrals
SUBC	Number of subcaudals
DOR1	Number of dorsal scale rows one head length behind the head
DOR2	Number of dorsal scale rows at the position of the middle ventral
DOR3	Number of dorsal scale rows one head length before the tail
SUBL	Number of infralabials touched by the first sublabial (L+R)
SL1	Number of supralabials (L+R)
SL2	Number of supralabials touching the eyes (L+R)
LOR	Number of loreals (L+R)
INFR	Number of infralabials (L+R)
TEMP	Number of temporals (L+R)
POC	Number of postoculars (L+R)
VERT	Vertebral scales smaller than (0) or larger than (1) scales of the first dorsal row
Coloration	
ISPOT	Interparietal spot absent (0), rudimentary (1), present (2)
VSTRIPE	Vertebral stripe absent (0), rudimentary (1), present (2)
TSTRIPE	Postocular stripe absent (0), rudimentary (1), present (2)
LSTRIPE	Ventrolateral stripe absent (0), present (1)

were defined as the scales of which more than half of the area lies in front of an imaginary line that runs from the apex of the last supralabial to the posterolateral corner of the parietal.

For multivariate analyses, morphometric variables (EYED, EYEN, TAIL, WVERT) were adjusted to a common SVL of 62.5 cm to correct for potential ontogenetic variation between the samples of the species (e.g. Thorpe, 1975, 1983; How et al., 1996; Turan, 1999). The following allometric equation was applied:  $X_{_{adj}}$  = X –  $\beta(SVL$  –  $SVL_{mean}$ ) where  $X_{adj}$  is the adjusted value of the morphometric variable; X is the original value; SVL is the snout-vent length; SVL<sub>mean</sub> is the overall mean snoutvent length;  $\beta$  is the coefficient of the linear regression of X against SVL. Linearity of the relation between SVL and each morphometric variable was checked by visual inspection of the scatter plot. The adequacy of the procedure was assessed by testing the significance of the correlation between the adjusted variables and SVL (e.g. Turan, 1999).

Three multivariate techniques were applied in order to demonstrate the presence of a hitherto unrecognized species on the Indian subcontinent. TAIL and SUBC were excluded from multivariate analyses as 26 specimens had incomplete tails. First, specimens from the Indian subcontinent were subjected to a twostep cluster analysis (SPSS, 2001; Bacher et al., 2004). This technique automatically determines the most plausible number of clusters and assigns each specimen to one of the resulting clusters. The clusters were additionally visualized by running a principal components analysis (PCA) and plotting the resulting factor scores. Subsequently, operational taxonomic units (OTUs) were formed. These were used as *a priori* groups in a canonical variate analysis (CVA, e.g. Cramer, 2003). The object scores corresponding with the first two canonical variates were plotted in order to illustrate the separation of the OTUs.

Confirmatory analyses of the differences between the species were carried out univariately. Meristic variables were analysed with ANOVA. Species and sex were included as factors. Morphometric variables were analysed with ANCOVA (e.g. Maxwell & Delaney, 1990), using species and sex as factors and SVL as covariate. Qualitative variables were analysed using a  $\chi^2$  test.

All statistical analyses were carried out with the software package SPSS for Windows Release 14.0.2 (SPSS Inc., Chicago).

Museum abbreviations: BNHS: Bombay Natural History Society, Mumbai, India. BMNH: Natural History Museum, London, UK. CAS: Collection of the California Academy of Sciences, USA. FMNH: Field Museum of Natural History, Chicago, USA. MHNG: Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Swizerland. MNHN: Muséum National d'Histoire Naturelle, Paris, France. MTKD: Museum für Tierkunde, Dresden, Germany. NMW: Naturhistorisches Museum Wien, Austria. RMNH: National Museum of Natural History, Leiden, The Netherlands. SMF: Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany. ZMA: Zoological Museum Amsterdam, The



**Fig. 1.** Ordination of specimens from the Western and Eastern Ghats along the first two principal components, based on a PCA of the characters VENT, EYED, EYEN, WVERT, TEMP and IL.

Netherlands. ZSI: Collection of the Zoological Survey of India, Calcutta, India.

## RESULTS

### Statistical analyses

The sample was divided into three preliminary OTUs corresponding to *D. tristis*, *D. schokari* and the putative third taxon, which was identified on the basis of its low ventral count and wanting vertebral stripe. Within these OTUs ANCOVAs were run to determine whether the morphometric characters exhibited either intersexual or geographical differences. No significant effects were found. Therefore, adjustment of morphometric characters was carried out at the level of these preliminary OTUs.

A twostep cluster analysis of the characters VENT, EYED, EYEN, WVERT, TEMP and IL split specimens from the Western and Eastern Ghats into two clusters. A PCA was run on the same characters to illustrate the separation of these clusters (Fig. 1). One of the clusters corresponds with *D. tristis*. The other (cluster 2 in Fig. 1) corresponds with specimens previously referred to as *D. schokari* (Van Rooijen & Vogel, 2008b). In order to facilitate crossreference with the taxonomy section, this second cluster is already denoted as *D. chairecacos* at this stage of the analysis.

Final operational taxonomic units (OTUs) were formed for analysis in CVA. Four specimens of *D. tristis* were excluded as these were from unknown locations. The OTUs, and corresponding sample sizes, are given in Table 2.

All OTUs, as given in Table 2, were included as *a priori* groups in a CVA of the characters VENT, EYED, EYEN, WVERT, TEMP and IL. Ordination of the OTUs along the first two canonical variates is shown in Figure 2. *Dendrelaphis chairecacos* is clearly separated from both

*D. tristis* and *D. schokari*. In addition, *D. tristis* is shown to occur sympatrically with *D. schokari* in Sri Lanka and with *D. chairecacos* in south India (Kerala and Tamil Nadu). This holds true at a much more local level than distinguished in the CVA: two *D. tristis* and two *D. chairecacos* originated from Madras, Tamil Nadu and one *D. tristis* and five *D. chairecacos* originated from Travancore, Kerala.

Univariate comparisons between *D. chairecacos*, *D. tristis* and *D. schokari* are provided in Table 3. In comparison with *D. schokari*, *D. chairecacos* has a higher number of ventrals and subcaudals and wider vertebral scales. In addition, *D. chairecacos* lacks a vertebral stripe whereas a vertebral stripe was present in all but one of the 33 examined *D. schokari*. In comparison with *D. tristis*, *D. chairecacos* has a lower number of ventral scales, a larger eye, a larger eye–nostril distance and wider vertebral scales. Furthermore, most *D. tristis* exhibit a vertebral stripe which is wanting in *D. chairecacos*.

A remark with regard to the coloration of *D. tristis* is in place here. Although *D. tristis* appears to be fairly homogeneous morphologically, a geographic variation was noted with regard to its coloration. In most of its range, *D. tristis* is characterized by a pronounced interparietal spot and vertebral stripe. However, in the population from Gujarat and Maharashtra, a dichotomy appears to exist. In a large proportion of the specimens, the interparietal spot and vertebral stripe were found to be either absent or rudimentarily present. In the others, they were pronounced. This is in agreement with observations made by Wall (1913).

#### Taxonomic evaluation

The morphological differences between *D. chairecacos* and *D. tristis* and especially their sympatric occurrence leave no room for doubt that these forms represent distinct lineages that are genetically isolated by intrinsic reproductive barriers. As such, *D. chairecacos* and *D. tristis* would be considered separate species under any concept of species. Previously, however, *D. chairecacos* was referred to as *D. schokari* on the basis of its comparatively large eye and low ventral count (Van Rooijen &

Table2.Operationaltaxonomicunitsandcorresponding sample sizes.

		Sample size
OTU		unknown)
D. schokari	Sri Lanka	17/16
D. tristis	Bengal, India	6/5/2
D. tristis	Nepal	2/0
D. tristis	Gujarat, India	2/2
D. tristis	Madhya Pradesh, India	0/1
D. tristis	Maharashtra, India	3/4
D. tristis	Sri Lanka	3/3
D. tristis	Kerala/Tamil Nadu, Indi	a 0/3
D. chairecacos	Kerala/Tamil Nadu, Indi	a 4/5

Table 3. Descriptive statistics with regard to the most diagnostic characters of D. chairecacos, D. tristis and D.
schokari. EYED, EYEN and WVERT are SVL-adjusted (see Materials and Methods). Significance levels pertaining to
the differences between D. chairecacos on the one hand and D. tristis and D. schokari on the other hand are provided
in the last two columns.

	D. chairecacos n=9	D. tristis n=40	D. schokari n=33	D. chairecacos/ D. tristis	D. chairecacos/ D. schokari
VENT	175 (165–177)	185 (178–198)	163 (155–168)	< 0.0000001	< 0.0000001
SUBC	125 (121–132)	129 (117–136)	118 (105–127)	_	0.01
EYED	5.0 (4.8–5.5)	4.5 (3.8–5.0)	5.1 (4.6–5.5)	0.00001	_
EYEN	7.4 (6.9–8.0)	6.6 (5.9–7.7)	7.1 (6.4–7.9)	0.00002	_
WVERT	2.9 (2.6–3.5)	2.5 (1.9–3.4)	2.6(1.9–3.3)	0.01	0.004
VSTRIPE	Present: 0% Rudimentary:0% Absent: 100%	Present: 60% Rudimentary: 10% Absent: 20%	Present: 97% Rudimentary:0% Absent: 3%	0.0003	0.000001
ISPOT	Bright: 11% Rudimentary: 11% Absent: 78%	Bright: 77% Rudimentary: 10% Absent: 13%	Bright: 0% Rudimentary: 5% Absent: 95%	0.001	_

Vogel, 2008b). The distinguishing aspects of D. chairecacos were not noticed due to the fact that few specimens had been examined. However, Van Rooijen & Vogel (2008b) do mention an outlier that has now turned out to be a *D. chairecacos*. For the present study more material was included and the analyses show unequivocally that D. chairecacos differs substantially from D. schokari. In particular its higher ventral count and the absence of a vertebral stripe are distinguishing characters. Dendrelaphis schokari inhabits Sri Lanka whereas D. chairecacos inhabits south India. Therefore, these forms are genetically isolated at least by extrinsic reproductive boundaries. Thus, within the framework of a lineage-based concept (De Queiroz, 1998, 1999), D. chairecacos would be considered a distinct species. Whether D. chairecacos is a distinct species according to the biological species concept cannot be determined as D. chairecacos and D. schokari are distributed allopatricaly. As a consequence, the presence of intrinsic

reproductive barriers cannot be established directly. However, the existence of intrinsic reproductive barriers between *D. chairecacos* and *D. schokari* is plausible on the basis of morphological differences. After all, *D. chairecacos* differs as much from *D. schokari* as it does from *D. tristis* (Fig. 2) and it is reproductively isolated from the latter.

#### Nomenclature

*D. chairecacos* was described by Boie (1827) on the basis of a plate and some accompanying information published by Russell (1807; species XXVI, "Cumberi muken", pp. 30–31). The specimen depicted by Russell should be regarded as the holotype of *D. chairecacos* (ICZN, 1999, article 73). Russell did not provide an unambiguous type locality. He states: "The specimen was received from Mr John of Tranquebar". As such, the geographic origin of the specimen itself is uncertain. Russell deposited his snake skin collection in the Natural History Museum in







Fig. 3. Dendrelaphis chairecacos (Boie, 1827), neotype BMNH 1924.10.13.15.

London (Hawgood, 1994). However, Boulenger (1894) did not locate the type of *D. chairecacos* in BMNH. Boulenger (1894) does mention a specimen of *D. tristis*. However, its ventral and subcaudal counts (184 and 140 respectively) do not agree with the data on the type of *D. chairecacos* given by Russell (176 and 127), nor do they agree with the counts pertaining to Russell's type of *D. tristis* (180 and 130). In order to define this taxon objectively, as well as designate an unambiguous type locality, we designate BMNH 1924.10.13.15 as a neotype of *D. chairecacos* (Boie, 1827) on the basis of article 75 of the International Code of Zoological Nomenclature (ICZN, 1999). The type locality thus becomes Kottayam, Travancore (South India).

## Taxonomy

Dendrelaphis chairecacos (Boie, 1827) n. comb. (Fig. 3)

Dendrophis chairecacos Boie, 1827

*Material examined*. India (Malabar Coast): MNHN 244; India (Kottayam, Travancore): BMNH 1924.10.13.15, BMNH 1924.10.13.14; India (Travancore): CAS 17223; India (Punkanaad, Travancore): BMNH 1924.10.13.12, BMNH 1924.10.13.13; South India: CAS 17221; India (Madras): SMF 18595, CAS 12258.

*Neotype*. BMNH 1924.10.13.15; Kottayam, Travancore; collector Abercromby (Fig. 3).

*Type locality* (by designation of a neotype). Kottayam, Travancore.

*Diagnosis*. A species of *Dendrelaphis*, characterized by the combination of: 1) vertebral scales enlarged but smaller than the dorsals of the first row; 2) 165–177 ventrals; 3) 121–132 divided subcaudals; 4) 15 dorsal scale rows at midbody; 5) anal shield divided; 6) one loreal scale; 7) two supralabials touching the eye; 8) a short first sublabial that touches two infralabials; 9) 5 to 6 temporal scales; 10) 2 to 3 postoculars; 11) maximum total

length 113.5 cm; 12) TAIL/TL 0.30-0.33; 13) an interparietal spot may be present; 14) the presence of a light ventrolateral stripe; 15) the absence of a vertebral stripe. Description of the neotype (BMNH 1924.10.13.15; Kottayam, Travancore/Abercromby). Adult male; SVL 48.5 cm; tail broken; 170 ventral scales, two preventrals; anal shield divided; dorsal scales in 15-15-9 rows; nine supralabials, supralabials 5 and 6 touch the eye (L+R); 10 infralabials (L), nine infralabials (R); one preocular (L+R); two postoculars (L+R); one loreal (L+R); temporals 2:2:2 (L+R); first sublabial touched by infralabials 6,7 (L), first sublabial touched by infralabials 5,6 (R); vertebral scales distinctly enlarged but smaller than the dorsals of the first row; eye diameter 4.0 mm (L), 4.2 mm (R); distance anterior border of the eye to posterior border of the nostril 4.0 mm (L), 3.9 mm (R); snout width 3.7 mm; width of the vertebral scale at the position of the middle ventral 2.3 mm; postocular stripe rudimentarily present along the lower edge of the temporal region; oblique black bars laterally on the neck; a light ventrolateral stripe is present, bordered above by a black line; no vertebral stripe; no interparietal spot.

Variation and comparison with Dendrelaphis tristis (Daudin, 1803) and Dendrelaphis schokari (Kuhl, 1820). Descriptive statistics with regard to D. chairecacos, D. tristis and D. schokari are provided in Table 4.

Sexual dimorphism. Like D. tristis and D. schokari, D. chairecacos exhibits sexual dimorphism in the number of dorsal scale rows one head-length before the anal shield (P=0.02,  $\chi^2$  test). Four male specimens have nine dorsal scale rows at this position whereas four out of five female specimens have 11 dorsal scale rows at this position.

*Distribution*. The specimens of *D. chairecacos* examined originated from the southern Indian states of Kerala and Tamil Nadu.

#### J. Van Rooijen & G. Vogel

**Table 4.** Descriptive statistics for *D. chairecacos, D. tristis* and *D. schokari*. Mean and range are shown for continuous quantitative variables (EYED–WVERT). Median and range are shown for discrete quantitative variables (VENT–POC). In the case of qualitative variables (VERT–LSTRIPE), the percentage of specimens possessing the indicated charateristic is shown. EYED, EYEN, TAIL and WVERT are SVL-adjusted values.

Character	D. chairecacos (n=9)	D. tristis (n=40)	D. schokari (n=33)
EYED (mm)	5.0 (4.8–5.5)	4.5 (3.8–5.0)	5.1 (4.6–5.5)
EYEN (mm)	7.4 (6.9–8.0)	6.6 (5.9–7.7)	7.1 (6.4–7.9)
TAIL (cm)	29.5 (28.5–31.0)	29.0 (27.0-31.0)	28.5 (26.0–32.5)
WVERT	2.9 (2.6–3.5)	2.5 (1.9–3.4)	2.6(1.9–3.3)
VENT	175 (165–177)	185 (178–198)	163 (155–168)
SUBC	125 (121–132)	129 (117–136)	118 (105–127)
DOR1	15 (15–15)	15 (15–15)	15 (15–15)
DOR2	15 (13–15)	15 (13–15)	15 (15–15)
DOR3	11 (9–11)	11 (9–11)	9(9–11)
SUBL	4 (4-4)	4 (4-4)	4 (4-4)
SL1	18 (16–20)	18(16–19)	18 (18–20)
SL2	4 (4-4)	4 (4-4)	4 (4-4)
LOR	2(2-2)	2 (2-2)	2 (2-2)
INFR	20(18–21)	20(18–22)	20(18–22)
TEMP	12(11–13)	12(10–15)	12 (8–14)
POC	4 (4–5)	4 (4-4)	4 (4–5)
VERT	0:100%	0:100%	0:100%
	1:0%	1:0%	1:0%
ISPOT	0:88%	0:13%	0:95%
	1:11%	1:10%	1:5%
	2:11%	2:77%	2:0%
VSTRIPE	0:100%	0:20%	0:3%
	1:0%	1:10%	1:0%
	2:0%	2:60%	2:97%
TSTRIPE	0:28%	0:16%	0:0%
	1:57%	1:6%	1:0%
	2:15%	2:78%	2:100%
LSTRIPE	0:0%	0:0%	0:0%
	1:100%	1:100%	1:100%

# DISCUSSION

Below, a key is provided to the species hitherto referred to as *D. tristis*. Morphometric characters could not be included as statistical adjustments are needed to enable comparisons (see Materials and Methods).

– vertebral stripe present; interparietal spot absent (rarely rudimentarily present); 155–168 ventrals ... *D. schokari* (Sri Lanka)

- vertebral stripe absent, interparietal spot rarely present; 165–177 ventrals ... *D. chairecacos* (S. India)

- vertebral stripe and interparietal spot usually present; 178–198 ventrals ... *D. tristis* (Sri Lanka, India, Nepal)

Although tentative in the absence of a phylogenetic analysis, *D. tristis*, *D. schokari* and *D. chairecacos* probably constitute a clade of closely related species. The three species are phenetically very similar and share a combination of characters that sets them apart from other *Dendrelaphis* species: a comparatively stocky build, small vertebral scales and an interparietal spot (varying strongly in occurrence and distinctness). The sympatric occurence of *D. tristis* with *D. schokari* in Sri Lanka and with *D. chairecacos* in southern India poses the intriguing question of which niche differences allow the co-occurence of such similar species. The established differences in head morphology between *D. tristis* on the one hand and *D. schokari* and *D. chairecacos* on the other hand may offer a partial answer. For instance, the comparatively large eye in *D. schokari* and *D. chairecacos* is a likely correlate of niche differentiation as it may be linked to smaller prey, which would need higher visual resolving power for detection (e.g. Kassam et al., 2003).

The Western Ghats and Sri Lanka together have been designated as one of the biodiversity hotspots of the world (Mittermeier et al., 2005) and are known to host a high level of endemism among reptiles (e.g. Das, 1996; Ishwar et al., 2001; Mittermeier et al., 2005; Gunawardene et al., 2007). Recent species descriptions suggest that biodiversity as well as the level of endemism harboured by this area may be substantially higher than currently known (e.g. Pethiyagoda, 2005; Mendis Wickramasinghe et al., 2007; Mukherjee & Bhupathy, 2007). The resurrec-

tion of *D. schokari* and *D. chairecacos* from synonymy underscores the unique biological status of this area. Furthermore, it adds to the notion that the faunas of Sri Lanka and the Western Ghats are more distinct than previously recognized (e.g. Bossuyt et al., 2004).

# ACKNOWLEDGEMENTS

We are grateful to Colin J. McCarthy (London) and Frank Tillack (Berlin) for their comments, which significantly improved this manuscript. We thank Varad Giri (BNHS, Mumbai, India), Jens V. Vindum and Alan E. Leviton (CAS, San Francisco, USA), Annemarie Ohler and Alain Dubois (MNHN, Paris, France), Colin J. McCarthy (BMNH, London, United Kingdom), Franz Tiedemann and Richard Gemel (NMW, Vienna, Austria), Koos van Egmond and Caroline Pepermans (RMNH, Leiden, The Netherlands), Ronald Vonk and Dik Iliohan (ZMA, Amsterdam, The Netherlands), Gunther Köhler and Monika Laudahn (SMF, Frankfurt am Main, Germany), Harold Voris (FMNH, Chicago, USA), Uwe Fritz and Edgar Lehr (MTKD, Dresden, Germany) and B.H.C. Murphy (ZSI, Kolkata, India) for making preserved specimens available for examination. GV wants to thank the following people for their help in the field: Mittal Gala, S.R. Chandramouli, Sunjeev P. (Sunny), Vineith Torule, Divya, A.S. Pradeep and a special thank-you to S.R. Ganesh.

## REFERENCES

- Bacher, J., Wenzig, K. & Vogler, M. (2004). SPSS TwoStep Cluster – A First Evaluation. Arbeits- und Diskussionspapiere 2004-2, 2., korr. Aufl. Erlangen-Nürnberg: Friedrich-Alexander Universität.
- Boie, F. (1827). Bemerkungen über Merrem's Versuch eines Systems der Amphibien. Marburg. 1820. Erste Lieferung: Ophidier. *Isis von Oken*, 20, col. 508–566.
- Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L., Schneider, C.J., Oommen, O.V. & Milinkovitch, M.C. (2004). Local endemism within the Western Ghats–Sri Lanka biodiversity hotspot. <u>Science</u> 306, 479.
- Boulenger, G.A. (1890). The Fauna of British India, including Ceylon and Burma. XVIII. Reptilia and Batrachia. London: Taylor & Francis.
- Boulenger, G.A. (1894). Catalogue of the Snakes in the British Museum (Natural History). Volume II., Containing the Conclusion of the Colubridae Aglyphae. London: Taylor & Francis.
- Cramer, D. (2003). Advanced Quantitative Data Analysis. Philadelphia: Open University Press.
- Das, I. (1995). *Biogeography of the Reptiles of South Asia*. Malabar, Florida: Krieger Publishing Company.
- Daudin, F.M. (1803). *Histoire Naturelle, Génerale et Particulière des Reptiles, V. 6.* Paris: F. Dupart.
- De Queiroz, K. (1998). The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In *Endless Forms: Species and Speciation*, 57–75. Howard, D.J. & Berlocher, S.H. (eds).

Oxford: Oxford University Press.

- De Queiroz, K. (1999). The general lineage concept of species and the defining properties of the species category. In *Species: New Interdisciplinary Essays*, 49–89. Wilson, R.A. (ed.). Cambridge, Massachusetts: MIT Press.
- Dowling, H.G. (1951). A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1, 97–99.
- Gunawardene, N.R., Daniels, A.E.D., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., Karunakaran, P.V., Nayak, K.G., Prasad, S., Puyravaud, P., Ramesh, B.R., Subramanian, K.A. & Vasanthy, G. (2007). A brief overview of the Western Ghats–Sri Lanka biosiversity hotspot. *Current Science* 93, 1567–1572.
- Hawgood, B.J. (1994). The life and viper of DR Patrick Russell MD FRS (1727–1805): physician and naturalist. *Toxicon* 32, 1295–1304.
- How, R.A., Schmitt, L.H. & Maharadatunkamsi (1996). Geographical variation in the genus *Dendrelaphis* (Serpentes: Colubridae) within the islands of southeastern Indonesia. *Journal of Zoology* 238, 351–363.
- International Commission on Zoological Nomenclature (1999). International Code of Zoological Nomenclature, 4<sup>th</sup> edn adopted by the International Union of Biological Sciences. London: The International Trust for Zoological Nomenclature.
- Ishwar, N.M., Chellam, R. & Kumar, A. (2001). Distribution of forest floor reptiles in the rainforest of Kalakad-Mundanthurai Tiger Reserve, South India. *Current Science* 80, 413–418.
- Kassam, D.D., Adams, D.C., Ambali, A.J.D. & Yamaoka, K. (2003). Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. <u>Animal Biology</u> 53, 59– 70.
- Kuhl, H. (1820). Beiträge zur Zoologie und Vergleichenden Anatomie. Erste Abtheilung. Beiträge zur Zoologie.
  Frankfurt am Main: Verlag der Hermannschen Buchhandlung.
- Maxwell, S.E. & Delaney, H.D. (1990). Designing Experiments and Analyzing Data. California: Wadsworth Inc.
- Meise, W. & Henning, W. (1932). Die Schlangengattung Dendrophis. Zoologischer Anzeiger 99, 273–297.
- Mendis Wickramasinghe, L.J., Rodrigo, R., Dayawansa, N. & Jayantha, U.L.D. (2007). Two new species of *Lankascincus* (Squamata: Scincidae) from Sripada Sanctuary (Peak Wilderness), in Sri Lanka. *Zootaxa* 1612, 1–24.
- Mertens, R. (1934). Die Schlangengattung *Dendrelaphis* Boulenger in systematischer und zoogeographischer Beziehung. *Archiv für Naturgeschichte, Berlin (N. F.)* 3, 187–204.
- Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & da Fonseca, G.A.B. (2005). *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Monterrey, Mexico: Cemex, Conservation International & Agrupacion Sierra Madre.

Mukherjee, D. & Bhupathy, S. (2007). A new species of

wolf snake (Serpentes: Colubridae: *Lycodon*) from Anaikatti Hills, Western Ghats, Tamil Nadu, India. *Russian Journal of Herpetology* 14, 21–26.

- Peters, J.A. (1964). Dictionary of Herpetology: A Brief and Meaningful Definition of Words and Terms used in Herpetology. New York: Hafner.
- Pethiyagoda, R. (2005). Exploring Sri Lanka's biodiversity. *The Raffles Bulletin of Zoology* Supplement 12, 1–4.
- Russell, P. (1801, 1802, 1807). An Account of Indian Serpents, Collected on the Coast of Coromandel; Containing Descriptions and Drawings of Each Species; Together with Experiments and Remarks on their Several Poisons, Vol. 2, parts 1,2,3. London: G. & W. Nicol.
- Smith, M.A. (1943). The Fauna of British India, Ceylon and Burma. Reptilia and Amphibia. Vol. 3 Serpentes. London: Taylor & Francis.
- SPSS Inc. (2001). The SPSS TwoStep Cluster Component, a Scalable Component Enabling More Efficient Customer Segmentation. White paper – technical report. Chicago: SPSS Inc.
- Thorpe, R.S. (1975). Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snakes *Natrix natrix* (L.). *Biological Journal of the Linnean Society* 7, 27–43.
- Thorpe, R.S. (1983). A biometric study of the effects of growth on the analysis of geographic variation: tooth number in green geckos (Reptilia: *Phelsuma*). *Journal of Zoology* 201, 13–26.
- Turan, C. (1999). A note on the examination of morphometric differentiation among fish populations: the Truss system. *Turkish Journal of Zoology* 23, 259– 263.

- Van Rooijen, J. & Vogel, G. (2008a). A review of the *Dendrelaphis pictus* complex (Serpentes: Colubridae) I: Description of a sympatric species. <u>Amphibia–Reptilia</u> 29, 101–115.
- Van Rooijen, J. & Vogel, G. (2008b). An investigation into the taxonomy of *Dendrelaphis tristis* (Daudin, 1803): revalidation of *Dipsas schokari* (Kuhl, 1820) (Serpentes, Colubridae). *Contributions to Zoology* 77, 33–43.
- Van Rooijen, J. & Vogel, G. (2008c). A new species of Dendrelaphis (Serpentes: Colubridae) from Java, Indonesia. The Raffles Bulletin of Zoology 56, 189–197
- Vogel, G. & Van Rooijen, J. (2007). A new species of Dendrelaphis (Serpentes: Colubridae) from southeast Asia. Zootaxa 1394, 25–45.
- Vogel, G. & Van Rooijen, J. (2008). A review of the *Dendrelaphis pictus* complex (Serpentes: Colubridae) 2: The eastern forms. *Herpetozoa* 21, 3–29.
- Wall, F. (1913). A popular treatise on the common Indian snakes. *Journal of the Bombay Natural History Society* 19(4), 779.
- Wall, F. (1921). Remarks on the Indian species of Dendrophis and Dendrelaphis. Records of the Indian Museum 22, 151–162.
- Ziegler, T. & Vogel, G. (1999). On the knowledge and specific status of *Dendrelaphis ngansonensis* (Bourret, 1935) (Reptilia: Serpentes: Colubridae). *Russian Journal of Herpetology* 6, 199–208.

Accepted: 17 September 2009

# APPENDIX

### Other material examined

Dendrelaphis schokari (Sri Lanka): NMW 23669:2, NMW 24382:2, NMW 24382:3, NMW 24382:4, MNHN 1890.0065, NMW 23669:1, RMNH 842, RMNH 7066 (1), RMNH 7066 (2), BMNH 1933.12.6.12, BMNH 1969.2781; SMF 62076, SMF 62074, SMF 18672, MHNG 1198.52, MTKD D 10646, MTKD D 10440, MTKD D 15438, MHNG 1199.57, MHNG 1198.54, SMF 70286, MHNG 762.73, MHNG 1198.51, MHNG 1198.55, MHNG 1198.53, MHNG 1198.50, SMF 32366, SMF 70285.

*Dendrelaphis schokari* (unknown locality): RMNH 7081 (1), RMNH 7081 (2), RMNH 7081 (3), RMNH 7081 (4), RMNH 7081 (5).

*Dendrelaphis tristis* (Sri Lanka): BMNH 1955.1.9.80, BMNH 93.10.6.1, BMNH 1972.2183, ZMA 21563, SMF 18671, SMF 32367.

*Dendrelaphis tristis* (India, Bengal): RMNH 843 (1), RMNH 843 (2), RMNH 843 (3), RMNH 843 (4), RMNH 843 (5), NMW 23686:6, NMW 23686:7, SMF 58442, SMF 58071, BMNH 72.4.17.342, BMNH 1909.3.9.12, BNHS 998,

#### BNHS 1003.

Dendrelaphis tristis (India, Gujarat): BNHS 992, BNHS 995, BNHS 996, ZSI 23069.

*Dendrelaphis tristis* (India, Maharashtra): ZMA 14120(2), BMNH 69.8.28.126, ZMA 14120(1), BNHS 991, BNHS 994, BNHS 997, BNHS 2882.

Dendrelaphis tristis (India, Madhya Pradesh): FMNH 60646.

Dendrelaphis tristis (Nepal): FMNH 152583, FMNH 62428.

*Dendrelaphis tristis* (India, Kerala (Travancore: Trivandum)): CAS 14921.

Dendrelaphis tristis (India, Tamil Nadu (Madras)): CAS 15982, SMF 18634.

*Dendrelaphis tristis* (India, no exact locality): BMNH 52.10.4.18, MHNG 1553.8.

*Dendrelaphis tristis* (Bengal/Myanmar): NMW 23669:5, NMW 23669:3.