Contributions to Zoology, 77 (1) 33-43 (2008)

An investigation into the taxonomy of *Dendrelaphis tristis* (Daudin, 1803): revalidation of *Dipsas schokari* (Kuhl, 1820) (Serpentes, Colubridae)

Johan van Rooijen[1], Gernot Vogel[2]
[1]*Tulpentuin 313, 2272 EH, Voorburg, The Netherlands, j1.van.rooijen@hetnet.nl*
[2]*Society for Southeast Asian Herpetology, Im Sand 3, D-69115 Heidelberg, Germany, Gernot.Vogel@t-online.de*

Key words: *Dendrelaphis*, *Dendrelaphis tristis*, *Dipsas schokari*, taxonomy, India, Western Ghats, Sri Lanka

Abstract

The taxonomic status of the colubrid snake *Dendrelaphis tristis* (Daudin, 1803) was investigated on the basis of morphological data taken from 64 museum specimens. Univariate and multivariate analyses of these data reveal that *Dendrelaphis tristis* is composed of two species. One of these species agrees with the description of *Dipsas schokari* Kuhl, 1820 which is revalidated in the combination *Dendrelaphis schokari* (Kuhl, 1820). The syntypes of *D. schokari* have been lost and a type for *D. tristis* has never been deposited in a collection. Neotypes are designated and described for both species in order to stabilize the names. *D. schokari* differs from *D. tristis* in having a lower number of ventrals and subcaudals, a larger eye, a shorter vertebral stripe and the absence of a bright interparietal spot. *D. tristis* and *D. schokari* exhibit a partially overlapping distribution. *D. tristis* ranges from Sri Lanka northward through most of India to Myanmar whereas the distribution of *D. schokari* is restricted to Sri Lanka and South-west India (Western Ghats). Although the two species coexist on Sri Lanka and in South-west India, these species presumably do not occur syntopically as suggested by their distribution patterns and morphology.

Contents

Introduction ... 33
Material and methods ... 34
Results ... 35
Statistical analyses ... 35
Nomenclature ... 37
Taxonomy ... 38
Discussion ... 41
Acknowledgements ... 42
References ... 42

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 and 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 (1921a), Meise and Henning (1932), Mertens (1934) and Smith (1943) have in turn revised the systematics of this genus and have in turn disagreed with one another. As such, it is not surprising that the systematics of this genus have remained ambiguous as well as incomplete, a fact that was underlined by the recent descriptions of two wide-spread as well as rather common Southeast Asian species, *Dendrelaphis kopsteini* Vogel and Van Rooijen, 2007 and *Dendrelaphis haasi* Van Rooijen and Vogel, 2008.

Dendrelaphis tristis (Daudin, 1803), as hitherto defined, inhabits Sri Lanka, India, Pakistan, Bangladesh and Myanmar (Ziegler and Vogel, 1999). Daudin described *D. tristis* on the basis of a plate and some additional information provided by Russell (1796). A type was not deposited in a collection as was ususal at that time. *D. tristis* superficially resembles *D. pictus* (Gmelin, 1789). Consequently, Meise and Henning (1932) doubted the validity of its specific status. This illustrates the rather crude approach to the systematics of this genus at that time. *D. tristis* actually differs in many aspects from *D. pictus*. For instance, *D. tristis* has a substantially more stocky build, smaller vertebral scales and a conspicuous vertebral stripe which is absent in *D. pictus*. The names *D. tristis* and *D. pictus* in fact refer to separate clades each composed of two or more species (this report; Van Rooijen and Vogel, 2008; Vogel and Van Rooijen, in prep).

We initially examined a dozen specimens referred to *D. tristis* in the context of a taxonomic revision of the genus and noticed that the distribution of the number of ventral scales was bimodal. Examination of additional specimens and further research demonstrated the two superimposed distributions correspond with other differences in morphology as well as differences in coloration. This dichotomy of forms could not be attributed to sexual dimorphism and thus corresponds with two distinct taxa. In this paper, univariate and multivariate statistical techniques are used to illustrate and confirm these findings.

Material and methods

Sixty four museum specimens were examined for this study. In this sample the two forms were represented with 26 and 38 specimens. For each examined specimen, 21 characters including aspects of colour pattern, body proportions and scalation were recorded (Table 1). Eye-diameter and distance eye-nostril 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 last infralabial still covered completely by the last supralabial. The posterior most temporal scales 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. The length of the vertebral stripe was expressed as the number of the ventral scale opposite which the stripe ends, divided by the total number of ventral scales (% VS, Thorpe, 1975).

For multivariate analyses, morphometric variables (EYED, EYEN, TAIL) were adjusted to a common SVL of 62.5 cm to correct for potential ontogenetic variation between the samples of the two 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_{mean} is the overall mean snout-vent length; β 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).

Specimens were initially assigned to one of either species on the basis of the characters VENT, SUBC, EYED and ISPOT. The initial grouping was subse-

Table 1. List of morphometric, meristic and coloration characters used in this study 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
	SVL	Snout-vent length
Scalation	VENT	Number of ventrals
	SUBC	Number of subcaudals
	DOR1	Number of dorsals 1 head-length behind the head
	DOR2	Number of dorsals at the position of the middle ventral
	DOR3	Number of dorsals 1 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)
	TSTRIPE	Postocular stripe absent (0), rudimentary (1), present (2)
	VSTRIPE	Length of the vertebral stripe expressed as % VS
	LSTRIPE	Ventrolateral stripe absent (0), present (1)

quently validated by means of TwoStep Cluster analysis (SPSS, 2001; Bacher *et al*., 2004) using log-likelihood as distance measure and BIC as clustering criterion. This technique automatically determines the most plausible number of clusters and assigns each specimen to one of the resulting clusters. In order to illustrate the separation of the two species, a Principal Components Analysis (PCA, e.g. Wüster *et al*., 2001; Cramer, 2003) was performed on the characters VENT, SUBC, TAIL and EYED and the object scores corresponding with the first two principal components were plotted. Only specimens with a complete tail were included, reducing the sample by 25 specimens. Subsequently, VENT was plotted against EYED in order to include specimens with incomplete tails.

Confirmatory analyses of the differences between the two species were carried out univariately. Meristic variables were analysed with ANOVA unless the assumptions underlying this technique were violated. Species and sex were included as factors. In cases where the assumptions were violated, the nonparametric Mann Whitney U test was used. Morphometric variables (EYED, EYEN, TAIL) were analysed with ANCOVA (e.g. Maxwell and Delaney, 1990), using species and sex as factors and SVL as covariate. Qualitative variables were analysed using a χ^2 test.

For analysis of geographical variation, localities were grouped into the following operational taxonomic units (OTU's). OTU 1: Sri Lanka; OTU 2: Western Ghats, India; OTU 3: Eastern Ghats, India; OTU 4: Northeast India + Myanmar. Analysis of geographic variation was restricted to quantitative variables that did not violate the assumptions of ANOVA or ANCOVA. The analyses were carried out as described above with OTU as additional factor.

All statistical analyses were carried out with the software SPSS (2006; SPSS for Windows. Release 14.0.2. Chicago: SPSS Inc.).

Museum abbreviations: BMNH: Natural History Museum, London, United Kindom. 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 Netherlands.

Results

Statistical analyses

TwoStep Cluster analysis split the sample into two clusters and validated the initial assignment of specimens to the two species (henceforth: species A and

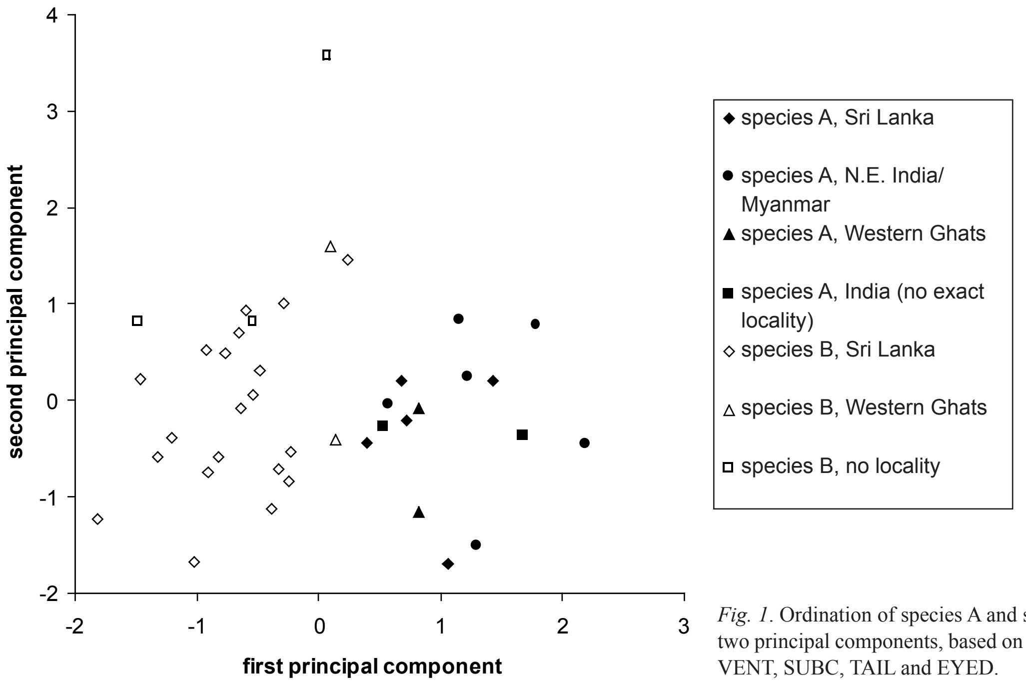

Fig. 1. Ordination of species A and species B along the first two principal components, based on a PCA of the characters VENT, SUBC, TAIL and EYED.

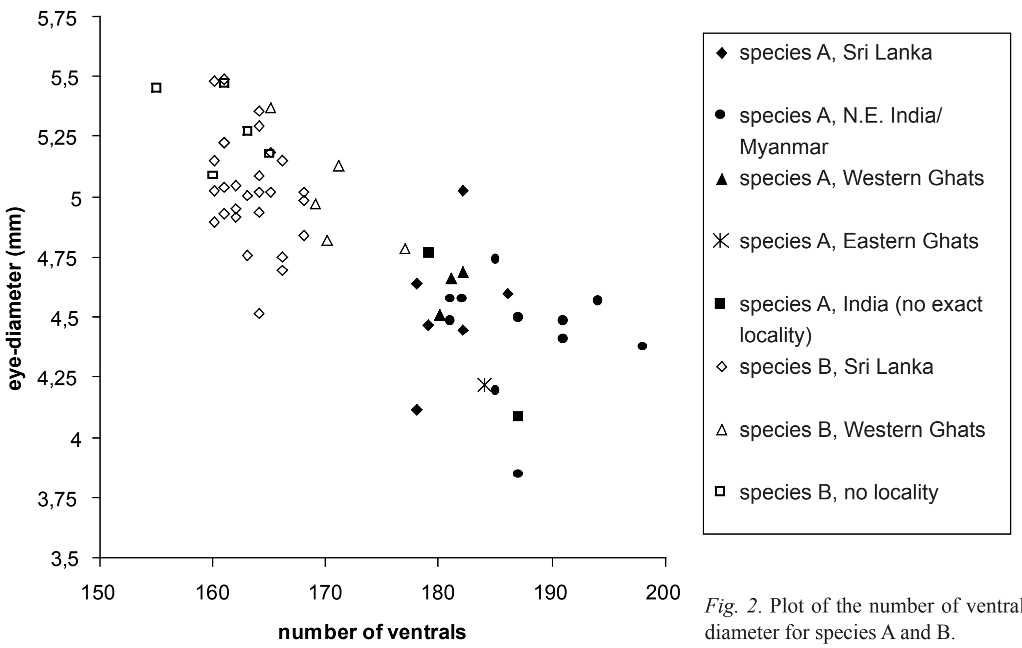

Fig. 2. Plot of the number of ventral scales against the eye-diameter for species A and B.

species B). The results of a PCA are shown in Figure 1. A plot of the number of ventral scales against eye-diameter is shown in Figure 2. Both figures demonstrate a clear separation between the two species.

The most prominent results of univariate confirmatory analyses are summarized in Table 2. Species A has a higher number of ventral scales, a higher average number of subcaudal scales and a smaller average eye-diameter. The relation between SVL and eye-diameter for the two species is depicted in Figure 3. With regard to coloration, a conspicuous character of species A is a bright interparietal spot which is absent in species B. However, several specimens constituted exceptions to this rule. In one specimen of species A (from Bombay, India) and two specimens of species B (from Sri Lanka), an interparietal spot was present but in a rudimentary (i.e. barely visible) form. Finally, species A has a substantially shorter vertebral stripe than species B.

Sexual dimorphism in the diagnostic characters was not detected in either species, a finding that is largely in line with results regarding several congeneric species (How *et al*., 1996; Vogel and Van Rooijen, 2007; Van Rooijen and Vogel, 2008).

Eye-diameter, number of ventrals and number of subcaudals were subjected to analysis of geographical variation. This analysis was restricted to OTU's from which both species had been sampled, thus excluding

Table 2. Descriptive statistics with regard to the most diagnostic characters of species A and B. Eye-diameter is SVL-adjusted (see Materials and Methods). Significance-levels are provided in the last column.

Character	Species A (n = 26)	Species B (n = 38)	Significance of the difference
Eye-diameter (mm)	4.5 (3.9-5.0)	5.1 (4.5-5.5)	P < 0.000001
Ventrals	184 (178-198)	164 (155-177)[a]	P < 0.000001
Subcaudals	130 (121-136)	118 (105-127)	P < 0.000001
Interparietal spot	Bright: 96% Rudimentary: 4% Absent: 0%	Bright: 0% Rudimentary: 5% Absent: 95%	P < 0.000001
Length vertebral stripe (%VS)	9 (0-15)	26 (0-36)	P = 0.000001

[a] The range of ventral scales of species B is influenced strongly by an outlier with an exceptionally high ventral count. When this specimen is excluded the range is (155-171)

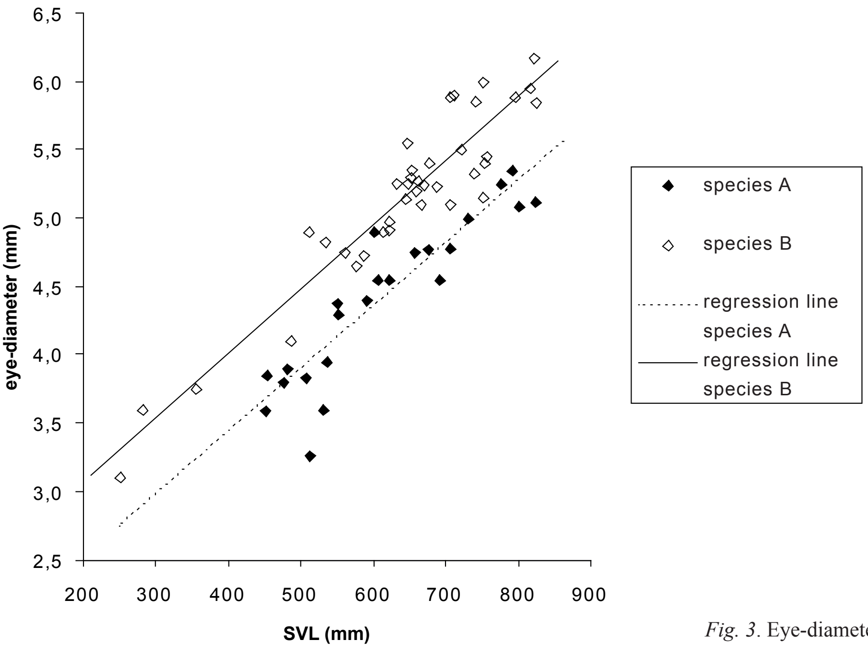

Fig. 3. Eye-diameter relative to SVL in species A and B.

OTU 3 and OTU 4. Only the number of ventral scales was found to exhibit significant geographic variation ($P = 0.01$), although this variation is negligible in the context of interspecific differences ($P < 0.000001$). With regard to this character, the two species were found to differ slightly in their patterns of geographic variation based on a significant interaction OTU x species ($P = 0.02$).

Nomenclature

The analyses demonstrate unequivocally that two species are currently referred to the binomial *Dendrelaphis tristis*. *Dendrelaphis tristis* was described by Daudin (1803) on the basis of information on a single specimen published by Russell (1796). Daudin did not deposit a type-specimen in a collection as was usual at that time. He mentioned 181 ventrals and 130 subcaudals, enlarged vertebral scales and a whitish-grey first dorsal scale row. The enlarged vertebral scales and the light first dorsal row are consistent with both species but the high ventral and subcaudal counts are only consistent with species A. Therefore, we refer species A to the name *Dendrelaphis tristis* (Daudin, 1803). The next available name according to the rule of priority is *Dipsas schokari* Kuhl, 1820. This name was synonymized with *D. tristis* by Boulenger (1894). Kuhl also did not assign a type-specimen, nor a type locality, but he provided ventral and subcaudal counts for five syntypes. The range of ventrals and subcaudals (168-183 and 111-131 respectively) given by Kuhl indicate that both species were included in his type-series. In his general description Kuhl mentioned a vertebral stripe, a light ventrolateral line, a postocular stripe and 5-6 temporal scales. These characters are also consistent with both species. Despite the fact that Kuhl's name *Dipsas schokari* refers to both taxa and a type-specimen was not designated explicitly, the name is available according to the International Code of Zoological Nomenclature (ICZN, 1999). The fifth syntype mentioned by Kuhl agrees beyond doubt with species B. In Figure 4, the number of ventrals and subcaudals of the specimens examined for this study are plotted together with those of Daudin's type of *D. tristis* and Kuhl's fifth syntype of *D. schokari*. Figure 4 shows that Daudin's type is situated within the area occupied by species A whereas Kuhl's 5th syntype is positioned within the area occupied by species B. Indeed, Daudin's type differs significantly from species B as the ventral and subcaudal counts differ more than 2.5 standard deviations from the respective means of species B. In a similar vein, Kuhl's 5th syntype differs significantly from species A as its ventral count is situated further than 3 standard deviations from the mean of species A. As such, there is no doubt that *Dendrelaphis tristis* (Daudin, 1803) is the correct name for species A whereas

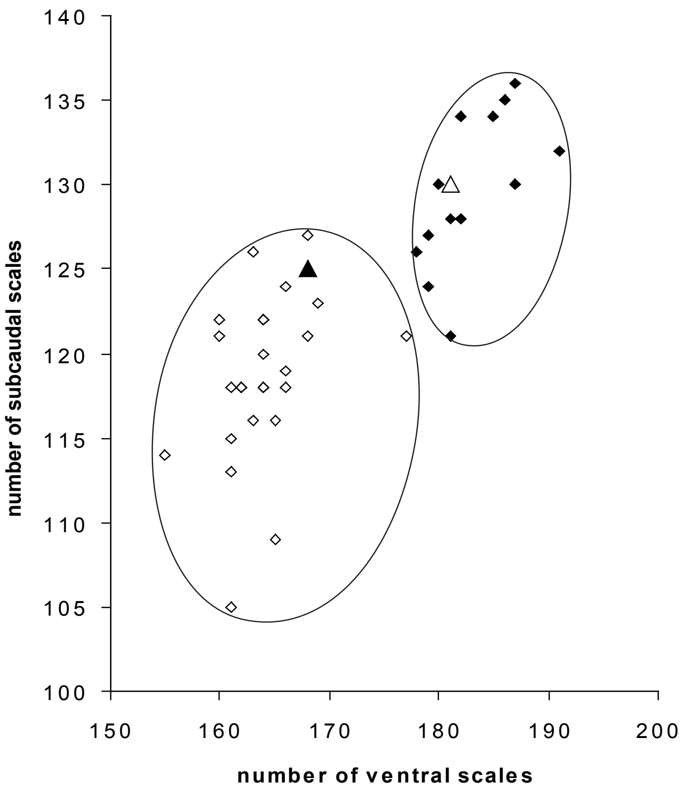

Fig. 4. Plot of the number of ventrals against the number of subcaudals for species A and species B. Ventral and subcaudal counts of the holotype of *D. tristis* and the 5[th] syntype of *D. schokari* are included.

Dipsas schokari Kuhl, 1820, in the combination *Dendrelaphis schokari* (Kuhl, 1820), should be adopted for species B.

An excellent overview of the life and work of Heinrich Kuhl is provided by Klaver (2007). Heinrich Kuhl (1797-1821) studied natural sciences at the University of Groningen, The Netherlands from 1816 to 1819. In 1820 Kuhl was employed by the Dutch government and was sent to Java to study the natural history of this island. After reaching Java he died within a year.

Kuhl described *Dipsas schokari* while he studied at the University of Groningen. The types mentioned by Kuhl were part of his personal collection. He donated this collection to the museum of natural history of the University of Groningen when he departed to Java. Unfortunately, the collection of the museum of natural history of the University of Groningen was destroyed in a fire in 1906. The syntypes of *Dendrelaphis schokari* should be considered lost. In order to stabilize the names *D. tristis* and *D. schokari* as well as designate a type locality for the latter, we designate RMNH 842 as the neotype of *Dendrelaphis schokari* (Kuhl, 1820) and SMF 58442 as the neotype of *Dendrelaphis tristis* (Daudin, 1803) on the basis of article 75 of the ICZN. The type locality of *Dendrelaphis schokari* becomes Ceylon (now: Sri Lanka). The type locality of *Dendrelaphis tristis* becomes Calcutta, India.

Taxonomy

Dendrelaphis schokari (Kuhl, 1820) n. comb. (Figs. 5-8)

Dipsas schokari Kuhl, 1820
Dendrophis helena Werner, 1893

Remarks. The synonymy-list is restricted to references in which data on numbers of ventral scales and subcaudal scales are given as these characters are diagnostic. Two currently recognized synonyms of *D. tristis*, *Leptophis mankas* (Bell, 1826) and *Dendrophis maniar* (Boie, 1827) can not be referred to either *D. tristis* or *D. schokari* and will be subjected to further research.

Material examined. 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; India (Malabar Coast): MNHN 244; India (Kottayam, Travancore): BMNH 1924.10.13.15, BMNH 1924.10.13.14; India (Punkanaad, Travancore): BMNH 1924.10.13.12, BMNH 1924.10.13.13; unknown locality: RMNH 7081 (1), RMNH 7081 (2), RMNH 7081 (3), RMNH 7081 (4), RMNH 7081 (5).

Neotype. RMNH 842; collector: Frank, 1853, locality: "Ceylon", now Sri Lanka. (Figs. 5,6)
Type locality (by designation of a neotype). "Ceylon", now Sri Lanka.

Diagnosis. A species of *Dendrelaphis*, characterized by the combination of: (1) vertebral scales enlarged but smaller than the dorsals of the first row; (2) 155-177 ventrals; (3) 105-127 divided subcaudals; (4) 15 dorsal scale rows at midbody; (5) anal shield divided; (6) 1 loreal scale; (7) 2 supralabials touching the eye; (8) a short first sublabial that touches 2 infralabials; (9) 4 to 7 temporal scales; (10) 2 to 3 postoculars; (11) maximum total length 119.0 cm; (12) TAIL/TL 0.30-0.34; (13) an interparietal spot is absent (rarely rudimentarily present); (14) the presence of a light ventrolateral stripe; (15) the presence, in most specimens, of a vertebral stripe.

Description of the neotype. Adult female; SVL 51.0 cm; TAIL 22.5 cm; 161 ventrals (2 preventrals); 113 subcaudals, all divided; anal shield divided; 1 loreal scale (L+R); 9 infralabials (L+R); first infralabials touch at the mental groove; first sublabial touches infralabials 6 and 7 (L+R); 9 supralabials (L+R), supralabials 5 and 6 touch the eye (L+R); 2 postoculars (L+R); temporal formula: 2+2 (L+R); dorsal formula: 15-15-11; vertebral scales enlarged but smaller than the scales of the first dorsal row; width of the dorsal scale at the position of the middle ventral 2.1 mm; eye-diameter 4.9 mm (L+R); distance anterior border

Fig. 5. Dendrelaphis schokari, Sri Lanka, neotype RMNH 842.

Fig. 6. Dendrelaphis schokari, Sri Lanka, neotype RMNH 842, left side of the head.

Fig. 7. Dendrelaphis schokari, living specimen from Sri Lanka. Photograph by Ruchira Somaweera.

Fig. 8. Dendrelaphis schokari, living specimen from Sri Lanka. Photograph by Ruchira Somaweera.

of eye to posterior border of nostril 4.5 mm (L+R); a dark postocular stripe starts behind the eye, covers only the lower quarter of the temporal region and ends at the edge of the jaw; a vertebral stripe, formed by yellow spots on the vertebral scales, starts behind the head and is no longer visible after the level of the 34th ventral scale; an interparietal spot is absent; a faint light ventrolateral line is present, not bordered by black lines; ground color brown, based on the color of unshed skin; supralabials and throat yellow; ventrals yellow anteriorly, yellowish-green posteriorly.

Variation and comparison with *Dendrelaphis tristis* (Daudin, 1803). Descriptive statistics with regard to *D. tristis* and *D. schokari* are provided in Table 3.

Sexual dimorphism. *D. schokari* exhibits sexual dimorphism in the number of dorsal scale rows one head-length before the anal shield ($P < 0.00001$, χ^2 test). All male specimens have 9 dorsal scale rows at this position whereas 75% of the female specimens have 11 dorsal scale rows at this position.

Distribution. The examined specimens of *D. schokari* originated from Sri Lanka and the Western Ghats (South-West India), areas that have been shown to be biogeographically closely related (Das, 1995).

Dendrelaphis tristis (Daudin, 1803) (Figs. 9-11)

Coluber tristis Daudin, 1803
Dipsas schokari Kuhl, 1820 (part.)
Dendrophis scandens Boie, 1827
Dendrophis chairecacos Boie, 1827
Dendrophis boii Cantor, 1839

Material examined. Sri Lanka: BMNH 1955.1.9.80, BMNH 93.10.6.1, BMNH 1972.2183, ZMA 21563, SMF 18671, SMF 32367; India (Bengals): RMNH 843 (1), RMNH 843 (2), RMNH 843 (3), RMNH 843 (4), RMNH 843 (5); India (Calcutta): NMW 23686:6, NMW 23686:7, SMF 58442, SMF 58071; India (Darjeeling): BMNH 72.4.17.342, BMNH 1909.3.9.12; India (Bombay): ZMA 14120(2), BMNH 69.8.28.126, ZMA 14120(1); India (Madras): SMF 18634, SMF 18595; India (no exact locality): BMNH 52.10.4.18, MHNG 1553.8; Bengals/Myanmar: NMW 23669:5, NMW 23669:3.

Neotype. SMF 58442 collector: H. Schetty, locality: Calcutta, India. (Figs. 9,10)

Type locality (by designation of a neotype). “Calcutta, India” (original type locality: “Hyderabad”).

Diagnosis. A species of *Dendrelaphis*, characterized by the combination of: (1) vertebral scales enlarged but smaller than the dorsals of the first row; (2) 178-198 ventrals; (3) 121-136 divided subcaudals; (4) 15 (rarely 13) dorsal scale rows at midbody; (5) anal shield divided; (6) 1 loreal scale; (7) 2 supralabials touching the eye; (8) a short first sublabial that touches 2 infralabials; (9) 5 to 8 temporal scales; (10) 2 postoculars; (11) maximum total length 115.0 cm; (12) TAIL/TL 0.30-0.33; (13) a bright (rarely rudimentary) interparietal spot; (14) the presence of a light ventrolateral stripe; (15) the presence, in most specimens, of a vertebral stripe.

Description of the neotype. Adult male; SVL 45.0 cm; TAIL 21.5 cm; 185 ventrals (2 preventrals); 134 subcaudals, all divided; anal shield divided; 1 loreal scale (L+R); 11 infralabials (L+R); first infralabials touch at the mental groove; first sublabial touches infralabials 6 and 7 (L+R); 9 supralabials (L+R), supralabials 5 and 6 touch the eye (L+R); 2 postoculars (L+R); temporal formula: 2+2+2 (L), 2+1+2 (R); dorsal formula: 15-15-9; vertebral scales enlarged but smaller than the scales of the first dorsal row; width of the dorsal scale at the position of the middle ventral 1.9 mm; eye-diameter 3.8 mm (L), 3.9 mm (R); distance anterior border of eye to posterior border of nostril 3.2 mm (L+R); a postocular stripe starts behind the eye and covers approximately 30% of the temporal region; a vertebral stripe, formed by a light colour of the vertebral scales and edges of adjoining dorsal scale rows, starts behind the head and is no longer visible after the level of the 17th ventral scale; an interparietal spot is present; a light ventrolateral line is present, bordered above by a thin dark line; ground color brown; supralabials, throat and ventral scales off-white.

Variation and comparison with *Dendrelaphis schokari*. Descriptive statistics with regard to *D. tristis* and *D. schokari* are provided in Table 3.

Sexual dimorphism. Like *D. schokari*, *D. tristis* exhibits sexual dimorphism in the number of dorsal scale rows one head-length before the anal shield ($P = 0.0003$, χ^2 test). 85% of the females have 11 dorsal scale rows at this position whereas 90% of males have 9 dorsal scale rows at this position.

Distribution. The examined specimens of *D. tristis* originated from Sri Lanka, Western Ghats (Bombay), Eastern Ghats (Madras), Northeast India and Myanmar. Daudin’s type originated from Central India (Hyderabad). Boulenger (1894) provides a record from North-West India (Sind). His record is unambiguous given the mentioned ventral and subcaudal counts (185 and 127 respectively). According to Shrestha (2001), *D. tristis* also occurs in Nepal. Unfortunately, Shrestha did not provide diagnostic data on his record. Howev-

Fig. 9. Dendrelaphis tristis, Calcutta, neotype SMF 58442.

Fig. 10. Dendrelaphis tristis, Calcutta, neotype SMF 58442, left side of the head.

Fig. 11. Dendrelaphis tristis, Bombay, ZMA 14120(2), note the interparietal spot on top of the head.

Table 3. Descriptive statistics for *D. tristis* and *D. schokari*. Mean and range are shown in case of continuous quantitative variables (EYED-VSTRIPE). Median and range are shown in case of discrete quantitative variables (VENT-POC). In case of qualitative variables (VERT-LSTRIPE), the percentage of specimens possessing the indicated charateristic is shown. EYED, EYEN and TAIL are SVL-adjusted values.

Character	*D. tristis* (n = 26)	*D. schokari* (n = 38)
EYED (mm)	4.5 (3.9-5.0)	5.1 (4.5-5.5)
EYEN (mm)	6.7 (5.7-7.7)	7.1 (6.4-7.9)
TAIL (cm)	29.0 (27.0-31.0)	28.5 (26.0-32.5)
VSTRIPE (% VS)	9 (0-15)	26 (0-36)
VENT	184 (178-198)	164 (155-177)
SUBC	130 (121-136)	118 (105-127)
DOR1	15 (15-15)	15 (15-15)
DOR2	15 (13-15)	15 (15-15)
DOR3	11 (9-11)	9 (9-11)
SUBL	4 (4-4)	4 (4-4)
SL1	18 (16-19)	18 (18-20)
SL2	4 (4-4)	4 (4-4)
LOR	2 (2-2)	2 (2-2)
INFR	20 (18-22)	20 (18-22)
TEMP	12 (10-15)	12 (8-14)
POC	4 (4-4)	4 (4-5)
VERT	0: 100%	0: 100%
	1: 0%	1: 0%
ISPOT	0: 0%	0: 95%
	1: 4%	1: 5%
	2: 96%	2: 0%
TSTRIPE	0: 20%	0: 10%
	1: 25%	1: 5%
	2: 55%	2: 85%
LSTRIPE	0: 0%	0: 0%
	1: 100%	1: 100%

er, the occurrence of *D. tristis* in Nepal is plausible given the verified presence of this species in North-East India. In summary, *D. tristis* ranges from Sri Lanka northward through most of India to Myanmar whereas the distribution of *D. schokari* is restricted to Sri Lanka and South-west India (Western Ghats) As such, *D. schokari* appears to have a limited distribution in comparison with *D. tristis*. This is in agreement with data provided by Boulenger (1894) and Wall (1909, 1921a, 1921b). These authors mention high ventral and subcaudal counts, consistent with *D. tristis*, for specimens from northern regions and mention both high and low ventral and subcaudal counts, consistent with a combination of *D. tristis* and *D. schokari*, for specimens from southern regions.

Discussion

The close phenetic similarity between *D. schokari* and *D. tristis* indicates that these taxa are sister species, although a phylogenetic analysis should corroborate this. The interparietal spot, bright in *D. tristis* and rudimentary in some specimens of *D. schokari*, in particular suggests a close relationship. This conspicuous character is absent in all congeneric species and presumably represents an apomorphy within these two species. Although sympatric on Sri Lanka and the Western Ghats, these species probably do not occur syntopically. The fact that the distribution of *D. schokari* is restricted to Sri Lanka and the Western Ghats suggests that it is an inhabitant of tropical forest. The wide distribution of *D. tristis* in India on the other hand suggests an adaptation to relatively dry and open habitat. The difference in eye-size points in the same direction: the comparatively large eye of *D. schokari* presumably represents an adaptation to the lower light intensity prevalent in tropical forest habitat. *D. schokari* may have evolved allopatrically on Sri Lanka. The connections between Sri Lanka and India that came into existence due to Pleistocene lowering of sea levels (e.g. Voris, 2000; Pethiyagoda, 2005) could have enabled *D. schokari* to disperse into South India, at the same time enabling *D. tristis* to invade Sri Lanka from India.

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). Recent species descriptions suggest that biodiversity as well as levels of endemism harboured by these areas may be substantially higher than currently known (e.g. Pethiyagoda, 2005; Mendis Wickramasinghe *et al*., 2007; Mukherjee and Bhupathy, 2007). The resurrection of *D. schokari* from synonymy highlights the unique biological status of this area. Furthermore, it stresses the shortcomings in our current understanding of *Dendrelaphis*-systematics, as previously noted (Vogel and Van Rooijen, 2007; Van Rooijen and Vogel, 2008). The systematics of *Dendrelaphis* are still far from complete. For instance, *Leptophis mankas* (Bell, 1826) might represent a valid name as indicated in the results-section. Its status will be subjected to further research. One reason for the unsatisfactory status of *Dendrelaphis*-systematics lies in the fact that most prior taxonomic arrangements were based on rather crude as well as subjective judgements. For example, Meise and Henning (1932) recognized eight species and many subspecies but their criteria remained largely implicit. Since the last major revisions of the genus, the advent of computer-technology and associated development of advanced multivariate techniques have greatly improved possibilities for sophisticated and objective taxonomic analysis. Application of such new techniques will considerably refine the taxonomic dissection of this genus. In addition, the application of species concepts that, more than the biological species concept, reflect evolutionary history (e.g. Frost and Hillis, 1990; Zink and McKitrick, 1995; De Queiroz, 1998) may be expected to have a substantial impact on the systematics of this genus, especially with regard to allopatric populations.

Acknowledgements

We are grateful to Patrick David (Paris, France) for his critical reading of this manuscript and his constructive comments that greatly improved the draft of this paper. We thank Annemarie Ohler and Alain Dubois (Paris, France), Colin J. McCarthy (London, United Kingdom), Franz Tiedemann and Richard Gemel (Vienna, Austria), Koos van Egmond, Caroline Pepermans and Pim Arntzen (Leiden, The Netherlands), Ronald Vonk and Dik Iliohan (Amsterdam, The Netherlands), Gunther Köhler and Monika Laudahn (Frankfurt am Main, Germany), Uwe Fritz and Edgar Lehr (Dresden, Germany) and Andreas Schmitz (Genève, Swizerland) for their assistance in sending us or letting us examine preserved specimens. We thank Ruchira Somaweera (Kandy, Sri Lanka) for providing pictures of living specimens of *Dendrelaphis schokari*. Furthermore, the critical and constructive comments of Pim Arntzen and two anonymous reviewers contributed to the honing of the final text and we wish to thank them here. Last but not least, we are grateful to Hein van Grouw (Leiden, The Netherlands) for providing information on the work and collection of Heinrich Kuhl.

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.

Bell T. 1826. On Leptophina, a group of Serpents comprising the Genus *Dryinus* of Merrem, and a newly formed Genus proposed to be named *Leptophis*. *The Zoological Journal* 2: 322-329.

Boie F. 1827. Bemerkungen über Merrem's Versuch eines Systems der Amphibien. Marburg. 1820. Erste Lieferung: Ophidier. *Isis von Oken*, 20 (10), col. 508-566.

Boulenger GA. 1894. *Catalogue of the Snakes in the British Museum (Natural History).Volume II, Containing the Conclusion of the Colubridae Aglyphae*. London: Taylor and Francis.

Cantor T. 1839. Spicilegium Serpentium Indicorum. *Proceedings of the Zoological Society of London* 7: 53.

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 FM. 1803. *Histoire Naturelle, génerale et particulière des Reptiles*. Paris: F Dupart. V. 6: 430-431.

De Queiroz K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH, eds., *Endless Forms: Species and Speciation*. Oxford: Oxford University Press, 57-75.

Dowling HG. 1951. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1: 97-99.

Frost DR, Hillis DM. 1990. Species in concept and practice: herpetological applications. *Herpetologica* 46(1): 87-104.

Gmelin JF. 1789. *Carola a Linné Systema Naturae*. Leipzig: G. E. Beer. 1(3): 1033-1516.

How RA, Schmitt LH, Maharadatunkamsi 1996. Geographical variation in the genus *Dendrelaphis* (Serpentes: Colubridae) within the islands of south-eastern Indonesia. *Journal of Zoology*, London 238: 351-363.

International Commission on Zoological Nomenclature 1999. *International Code of Zoological Nomenclature*, Fourth Edition adopted by the International Union of Biological Sciences. The International Trust for Zoological Nomenclature, London, 306 pp.

Ishwar NM, Chellam R, Kumar A. 2001. Distribution of forest floor reptiles in the rainforest of Kalakad-Mundanthurai Tiger Reserve, South India. *Current Science* 80(3): 413-418.

Klaver C. 2007. *Inseparable friends in life and death. The life and work of Heinrich Kuhl (1797-1821) and Johan Conrad van Hasselt (1797-1823), students of prof. Theodorus van Swinderen*. Groningen: Barkhuis.

Kuhl H. 1820. *Beiträge zur Zoologie und vergleichenden Anatomie*. *Erste Abtheilung. Beiträge zur Zoologie*. Frankfurt am Main: Verlag der Hermannschen Buchhandlung.

Maxwell SE, Delaney HD. 1990. *Designing experiments and analyzing data*. California: Wadsworth Inc.

Meise W, Henning W. 1932. Die Schlangengattung *Dendrophis*. *Zoologischer Anzeiger* 99(11/12): 273-297.

Mendis Wickramasinghe LJ, Roshan Rodrigo, Nihal Dayawansa, Jayantha ULD. 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(2): 187-204.

Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB. 2005. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Monterrey, Mexico: Cemex, Conservation International and 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(1): 21-26.

Peters JA. 1964. *Dictionary of herpetology: a brief and meaningful definition of words and terms used in herpetology*. New York: Hafner Publ. Co.

Pethiyagoda R. 2005. Exploring Sri Lanka's biodiversity. *The Raffles Bulletin of Zoology* Supplement 12: 1-4.

Russell P. 1796. *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*. London: Nicol, p. 36, plate xxxi.

Shrestha TK. 2001. *Herpetology of Nepal: a study of Amphibians and Reptiles of Trans-Himalayan Region of Asia*. Kathmandu: Shrestha.

Smith MA. 1943. *The fauna of British India, Ceylon and Burma. Reptilia and Amphibia. Vol. 3 Serpentes*. London: Taylor and Francis.

SPSS Inc. 2001. *The SPSS TwoStep Cluster Component, a scalable component enabling more efficient customer segmentation*. White paper – technical report, Chicago.

Thorpe RS. 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 RS. 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*, London 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. 2008. A review of the *Dendrelaphis pictus* complex (Serpentes: Colubridae) - I: Description of a sympatric species. *Amphibia-Reptilia* 29: 101-115.

Vogel G, Van Rooijen J. 2007. A new species of *Dendrelaphis* (Serpentes: Colubridae) from Southeast Asia. *Zootaxa* 1394: 25-45.

Voris HK. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153-1167.

Wall F. 1909. Notes on snakes from the neighbourhood of Darjeeling. *Journal of the Bombay natural History Society* 19: 337-357.

Wall F01921. Remarks on the Indian Species of *Dendrophis* and *Dendrelaphis*. *Records of the Indian Museum* 22: 151-162.

Wall F. 1921. *Ophidia Taprobanica or the snakes of Ceylon*. Colombo: Cottle.

Werner F. 1893. Herpetologische Nova. *Zoologischer Anzeiger* 16 (414): 81-82.

Wüster W, Yrausquin JL, Mijares-Urrutia A. 2001. A new species of Indigo Snake from North-Western Venezuela (Serpentes: Colubridae; *Drymarchon*). *Herpetological Journal* 11: 157-165.

Ziegler T, Vogel G. 1999. On the knowledge and specific status of *Dendrelaphis ngansonensis* (Bourret, 1935) (Reptilia: Serpentes: Colubridae). *Russian Journal of Herpetology* 6(3): 199-208.

Zink RM, McKitrick MC. 1995. The debate over species concepts and its implications for ornithology. *The Auk* 112(3): 701-719.

Received: 14 November 2007
Accepted: 8 February 2008