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A NEW SPECIES OF *DENDRELAPHIS* (SERPENTES: COLUBRIDAE) FROM JAVA, INDONESIA

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***ABSTRACT.* –** A new species of the colubrid snake genus *Dendrelaphis* Boulenger, 1890, *Dendrelaphis underwoodi*, new species, is described herein. *Dendrelaphis underwoodi* is endemic to Java, Indonesia. Univariate and multivariate analyses of the differences between *D. underwoodi* and the congeneric taxa *D. cyanochloris* (Wall, 1921), *D. formosus* (Boie, 1827), *D. humayuni* Tiwara & Biswas, 1973, *D. kopsteini* Vogel & Van Rooijen, 2007, and *D. pictus* (Gmelin, 1789) demonstrate that *D. underwoodi* constitutes a distinct insular lineage. The available data on the three known specimens suggest that *D. underwoodi* is an inhabitant of hilly or mountainous habitat. An updated key to the *Dendrelaphis* species of the Sunda region is provided.

***KEY WORDS.* –** *Dendrelaphis underwoodi*, new species, *Dendrelaphis cyanochloris*, *Dendrelaphis formosus*, *Dendrelaphis humayuni*, *Dendrelaphis kopsteini*, *Dendrelaphis pictus*; Indonesia: Java.

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 on lizards and amphibians. Boulenger (1894), Wall, (1921), Meise & Henning (1932), Mertens (1934) and Smith (1943) have successively revised the systematics of this genus, each author disagreeing with the taxonomic arrangements of his predecessors. Consequently, it is not surprising that the systematics of this genus have remained ambiguous as well as incomplete. This was underlined by a recent investigation into the taxonomy of *D. cyanochloris* (Wall, 1921) and *D. formosus* (Boie, 1827) which clarified their indentity and status and resulted in the description of a new species, *Dendrelaphis kopsteini* Vogel & Van Rooijen, 2007. Pending phylogenetic analysis, the group which comprises *D. cyanochloris*, *D. formosus*, *D. kopsteini* and *D. humayuni* Tiwara & Biswas, 1973, was informally named the *D. formosus* group. It was phenetically defined by Vogel & Van Rooijen (2007) as follows: eye moderate to very large; vertebral scales strongly enlarged, larger than the scales of the first dorsal row; 15 dorsal scale rows at midbody; a single loreal scale; no light ventrolateral stripe. The study of the *D. formosus* group revealed the existence of a possible fifth member of this group. This member was represented by three specimens from Java that had originally been identified as *D. formosus* according to the museum labels. They were tentatively re-identified as *D.* cf. *cyanochloris* by Vogel & Van Rooijen (2007) but appeared to represent an independent lineage based on multivariate analysis. In this article, this species is described and compared with several congeneric species.

MATERIALS AND METHODS

Although the three known specimens of *D. underwoodi*, new species, had originally been identified as *D. formosus*, they are phenotypically most similar to *D. cyanochloris*. Therefore, *D. cyanochloris* was considered the primary candidate for comparisons. Given the history of taxonomic confusion regarding *D. cyanochloris*, *D. formosus* and *D. kopsteini* (Vogel & Van Rooijen, 2007), the latter two species were included in the analysis. *Dendrelaphis humayuni* was included as it is presumed to be related to *D. cyanochloris*, *D. formosus* and *D. kopsteini* (Vogel & Van Rooijen, 2007).

Table 1. List of morphometric, meristic and colouration characters used in this study and their abbreviations.

Abbreviation	Character
Morphometrical characters	
EYED	horizontal diameter of the eye
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)
Colouration	
STR1	presence or absence of three lateral black stripes on the posterior half of the body
STR2	presence or absence of a light ventrolateral stripe
STR3	presence or absence of a single black stripe on the lower half of the third dorsal row
TSTR1	postocular stripe runs onto the neck or ends at the rear of the jaw
TSTR2	postocular stripe covers complete temporal region or only part of the temporal region

Finally, *D. pictus* (Gmelin, 1789) was included as *D. cyanochloris* was originally described as a subspecies of *D. pictus. Dendrelaphis formosus* and *D. pictus* inhabit most of the Sunda region and occur sympatrically with *D. underwoodi* on Java. In order to preclude potential bias due to geographic variation, only Javanese specimens of the former species were included in the analysis. *Dendrelaphis cyanochloris* does not occur on Java or any of the major islands of the Sunda region. Therefore, *D. underwoodi* was compared with *D. cyanochloris* from mainland Southeast Asia and from two islands off the coast of Peninsular Malaysia (Pulau Tioman and Pulau Pinang). *Dendrelaphis kopsteini* does not inhabit Java either. Specimens from Thailand, Peninsular Malaysia, Singapore and Sumatra were used in the analysis. *Dendrelaphis humayuni* is endemic to the Nicobar islands.

For statistical comparisons 22 specimens of *D. cyanochloris*, 21 *D. formosus*, 3 *D. humayuni*, 12 *D. kopsteini* and 16 *D. pictus* were examined. In addition, the individual data of 8 *D. humayuni* were taken from Tiwari & Biswas (1973). For each examined specimen, 20 characters bearing on colour pattern, body proportions and scalation were recorded. These are listed in Table 1. Colour pattern characters focused on the postocular stripe and on striping patterns alongside the body. All colour pattern characters were coded as polarized (1, 0) variables. 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, excluding the terminal scute. 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.

Analyses of the differences between the species were first carried out univariately. Meristic variables were log-transformed before analysis and were analysed using ANOVA unless the assumptions underlying this technique were violated. The normality-assumption was tested using the Kolmogorov-Smirnov test and the homogeneity of variance was tested using Levene's test. In cases where the assumptions were violated, the nonparametric Mann Whitney U test was used. Morphometric variables (EYED, TAIL) were analysed with ANCOVA, using species as factor and SVL as covariate. Qualitative variables were analysed using Chi-square.

In a relatively late stage of this study, it was noted that *D. underwoodi* has a more compact build than its congeneric species. As *D. underwoodi* can only be confused with *D. cyanochloris*, this character was quantified for 15 specimens of *D. cyanochloris* that were still available for examination and for the 3 types of *D. underwoodi*. The stockiness of these species was determined by establishing the relationship between head-length and SVL. Thus, the analysis was aimed at establishing whether, at the same head-length, the two species differ in body-length. Differences between the regression lines were tested with ANCOVA, using SVL as dependent variable, head-length as covariate and species as factor. This analysis will be treated separately as it was restricted to a univariate comparison of *D. underwoodi* and *D. cyanochloris*.

For multivariate analyses, morphometric variables (EYED, TAIL) were adjusted to a common SVL of 66.0 cm to correct for potential ontogenetic variation between the samples of the various 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. Homoscedasticity and linearity were verified by visually inspecting the plot of residuals versus predicted values. Normality of residuals was verified by Kolmogorov-Smirnov tests. The adequacy of the procedure was assessed by testing the significance of the correlation between the adjusted variables and SVL (e.g. Turan, 1999). Linear discriminant analysis was used to analyse quantitative variables and was consequently restricted to morphological variables. The data on *D. humayuni* taken from Tiwari & Biswas (1973) represented a limited selection of the variables taken from the examined specimens. Therefore, *D. humayuni* was excluded from linear discriminant analysis. Nonlinear canonical correlation analysis (OVERALS) was used for the simultaneous analysis of quantitative and qualitative variables. Thus, aspects regarding colouration were included in this analysis. In nonlinear canonical correlation analysis the correlation between species, as a multiple nominal variable, and the independent variables was maximized. This specific application can be regarded as a nonlinear version of discriminant analysis (Michailidis & De Leeuw, 1998; Meulman et al., 2001).

All statistical analyses were carried out with the software SPSS (2003; SPSS for Windows. Release 11.5.2.1. Standard Version. SPSS Inc., Chicago).

Museum abbreviations: BMNH: Natural History Museum, London, Great Britain. LSUHC: La Sierra University Herpetological Collection, La Sierra University, Riverside, California, United States. MNHN: Muséum National d'Histoire Naturelle, Paris, France. NMW: Naturhistorisches Museum Wien, Austria. PSGV: Gernot Vogel's private collection, Heidelberg, Germany. QSMI: Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand. 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. ZMB: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany. ZMH: Zoologisches Institut und Museum, Universität Hamburg, Hamburg, Germany. ZSM: Zoologische Staatssammlung, München, Germany.

TAXONOMY

Dendrelaphis underwoodi, new species

(Figs. 1–4)

***Material examined*. – Holotype**. RMNH 7447 (82), adult female, "Radjamandala, West Java, 335 meters", now Rajamandala, Province of Jawa Barat, Java, Indonesia, coll. J. Semmelink.

Paratypes. RMNH 6880, female, "Goenoeng Simpai, 2,100 feet, West Java", now Gunung Simpai, coll. C. P. J. De Haas.; RMNH 40100, male, "Tjiladjang, 900 meters, West Java", now Cilayang, Province of Jawa Barat, Java, Indonesia, coll. C. P. J. De Haas.

***Diagnosis*. –** A species of *Dendrelaphis* characterized by the combination of the following characters: 1) 15 dorsal scale rows at midbody; 2) one loreal scale; 3) 6–7 temporal scales; 4) supralabials 4, 5, and 6 touch the eye (4th with posterior corner); 5) a short first sublabial that touches infralabials 6 and 7; 6) vertebral scales strongly enlarged, larger than the scales of the first dorsal row; 7) 183–189 ventrals; 8) 126–133 subcaudals; 9) a divided anal shield; 10) a relatively compact build, SVL/head-length 23.5–28.5; 11) a black postocular stripe that starts on the loreal, covers the whole temporal region and extends onto the neck where it is broken up into more or less pronounced oblique black bars; 12) the presence of a narrow black stripe in the posterior half of the body, covering the lower half of the third dorsal row; and 13) the absence of a light ventrolateral stripe.

***Etymology*. –** This species is named after Prof. Garth Underwood (British Museum of Natural History), who investigated this group but did not publish his results (Tiwari

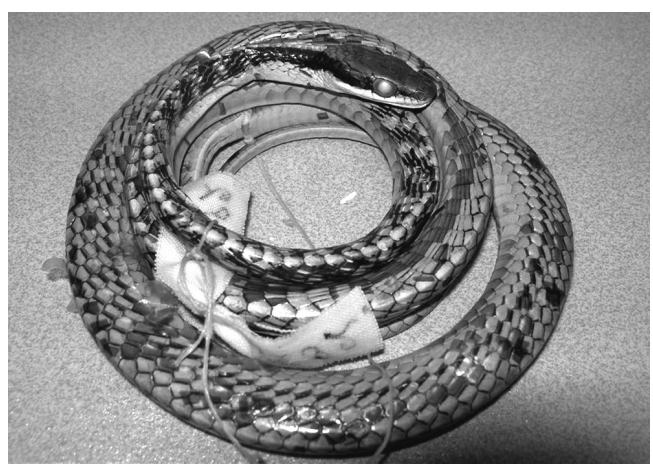

Fig. 1. *Dendrelaphis underwoodi*, new species, RMNH 7447 (82), holotype.

& Biswas, 1973). He helped us in several ways, as he was so kind as to write down his observations and left them with the specimens in the Natural History Museum of London. In addition, one of the authors (GV) had the opportunity to meet Prof. Underwood once in the Natural History Museum and wishes to express the deep impression this great herpetologist made on him. Suggested English name: Underwood's Bronzeback snake.

***Description of the holotype*. –** Adult female; SVL 60.0 cm; TAIL 30.0 cm; Head-length: 22.9 mm; 189 ventrals (2 preventrals); 131 divided subcaudals; anal plate divided; dorsals 15-15-11; vertebrals larger than first row of dorsals, hexagonal in shape and with straight posterior margin; one loreal (L+R); one preocular (L+R); two postoculars (L+R); one supraocular (L+R); nine supralabials (L+R); supralabials 4,5 and 6 touch the eye (4th with posterior corner) (L+R); 10 infralabials (L), 11 infralabials (R); first infralabials touch at the mental groove; first chinshield touches infralabials 1–5 (L+R); second chinshield touches infralabials 5 and 6 (L+R); first sublabial short, touches infralabials 6 and 7 (L+R); temporals 2+2+2 (L+R); eye small, 4.9 mm in diameter (L and R averaged); pupil round; distance from anterior border eye to posterior border nostril 4.5 mm (L+R averaged).

Background colour of the preserved specimen olive-brown, based on unshed skin; head in background colour dorsally; supralabials and underside of chin light yellow; venter light-green; a black temporal stripe starts on the loreal, covers the whole temporal region and extends onto the neck where it is broken up into black oblique bars which fade posteriorly; some dorsals in the anterior part of the body have blueish spots which are not covered by neighbouring dorals; a narrow black stripe covers the lower half of the third dorsal row in the posterior half of the body. A light ventrolateral stripe is absent. The specimen was gravid at the time of collection as eggs are clearly noticeable.

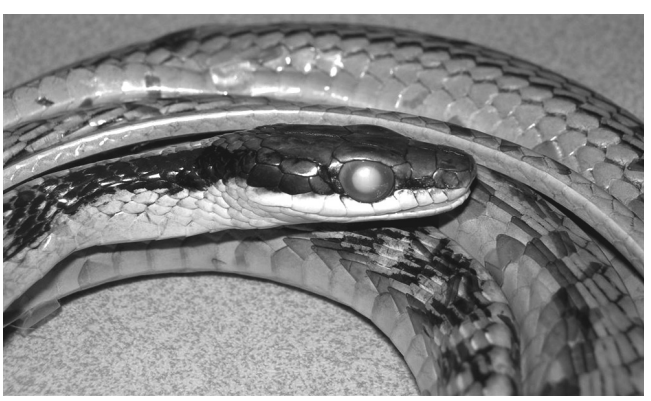

Fig. 2. *Dendrelaphis underwoodi*, new species, RMNH 7447 (82), holotype, right side of the head.

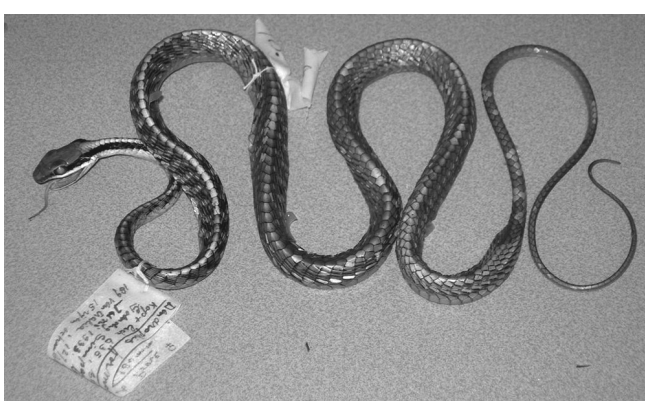

Fig. 3. *Dendrelaphis underwoodi*, new species, RMNH 6880, paratype.

***Description and variation*. –** The smallest specimen has a total length of 55 cm. The largest specimen, a gravid female, has a total length of 90 cm. TAIL/TL 0.31 to 0.33; ventrals 183–189; two preventrals; subcaudals 126–133, all divided; anal shield divided; dorsal formula 15-15-11; one loreal; vertebrals strongly enlarged, larger than the scales of the first dorsal row; first chinshield touches infralabials 1–5; second chinshield touches infralabials 5 and 6; first sublabial touches infralabials 6 and 7; nine supralabials, supralabials 4,5 and 6 touch the eye (4th with posterior corner); infralabials 10–11; postoculars 2–3; temporal formula 2+2+2/2+2+2 in two specimens, 3+2+2/3+2+1 in one specimen; eye small, 3.5–4.9 mm when unadjusted, 4.7–5.2 mm when adjusted to a SVL of 66.0 cm; diameter eye / distance (anterior border of) eye to (posterior border of) nostril 1.1-1.2.

Background colour of preserved specimens olive or olive-brown, based on unshed skin; head in background colour dorsally; underside of chin and supralabials light yellow; venter light green; a black temporal stripe starts on the loreal, covers the whole temporal region and extends onto the neck where it is broken up into black oblique bars which fade posteriorly; The black oblique bars are pronounced in the holotype but less pronounced in the paratypes; some dorsals in the anterior part of the body have blueish spots which are not covered by neighbouring dorals; a narrow black stripe covers the lower half of the third dorsal row in the posterior half of the body. A light ventrolateral stripe is absent. A summary of the morphological and colouration characters of the types is given in Table 2.

***Sexual dimorphism*. –** The three known specimens represent too little variation to allow for statistical generalization of differences between the sexes.

***Range*. –** *Dendrelaphis underwoodi* is endemic to Java, Indonesia. The three known specimens have all been

Fig. 4. *Dendrelaphis underwoodi*, new species, RMNH 40100, paratype.

Table 2. Morphological and colouration characters of the types of *Dendrelaphis underwoodi*, new species. Values of morphometric variables are unadjusted.

Collection number	RMNH 7447 (82) holotype	RMNH 6880 paratype	RMNH 40100 paratype
Sex	F	F	M
Snout-vent length (cm)	60.0	61.0	37.5
Tail-length (cm)	30.0	28.0	17.5
Head-length (mm)	22.9	21.5	16.0
Eye-diameter (mm)	4.9	4.5	3.5
Distance eye-nostril (mm)	4.5	4.0	2.9
Ventrals	189	186	183
Subcaudals	131	126	133
Anal shield divided	yes	yes	yes
Dorsal formula	15–15–11	15–15–11	15–15–11
Temporal formula	2+2+2/2+2+2	2+2+2/2+2+2	3+2+2/3+2+1
Supralabials	9/9	9/9	9/9
Supralabials touching the eye	4,5,6/4,5,6	4,5,6/4,5,6	4,5,6/4,5,6
Infralabials	10/11	10/10	11/11
Infralabials touched by first chinshield	1–5/1–5	1–5/1–5	1–5/1–5
Infralabials touched by second chinshield	5,6/5,6	5,6/5,6	5,6/5,6
Infralabials touched by first sublabial	6,7/6,7	6,7/6,7	6,7/6,7
Loreals	1/1	1/1	1/1
Postoculars	2/2	2/2	3/3
Vertebrals larger than dorsals of the first row	yes	yes	yes
Light ventrolateral stripe present	no	no	no
Black lateral stripe in posterior half of the body	yes	yes	yes
Postocular stripe covers whole temporal region	yes	yes	yes
Postocular stripe extends onto the neck	yes	yes	yes

collected in West Java (Cilayang and Rajamandala, both locations in Province of Jawa Barat; Gunung Simpai).

***Biology*. –** *Dendrelaphis underwoodi* appears to be a rare species as only three specimens were found in the extensive material of the examined museum collections. It may be an inhabitant of mountainous areas as the types were collected at altitudes of 900, 640 and 335 metres respectively. Nothing else is known about its biology.

Key to the species of the genus *Dendrelaphis* inhabiting the Sunda region[1]

1. Thirteen dorsal scale rows at midbody ..... *D. caudolineatus*
– Fifteen dorsal scale rows at midbody 2
2. A bright, white or yellow, ventrolateral stripe is present ..... *D. pictus*
– No light ventrolateral stripe 3
3. The temporal stripe covers only the lower part of the temporal region 4
– The temporal stripe covers the whole temporal region 5
4. Temporal stripe ends at the corner of the jaw; in life, neck red when inflated; eye large; two supralabials touch the eye; first sublabial touches two infralabials ..... *D. kopsteini*
– The temporal stripe extends onto the neck where it breaks up into black bars; in life, neck not red when inflated; eye small ..... *D. humayuni*
5. In life, neck yellow when inflated; black oblique bars laterally on the body; less than 170 ventrals ..... *D. striatus*
– In life, neck not yellow when inflated; more than 170 ventrals 6
6. Three black lateral stripes present on the posterior third of the body; eye very large, head bulges behind the snout to accomodate the large eye; first sublabial touches more than two infralabials ..... *D. formosus*
– Three black lateral stripes absent; eye small, head nearly flat 7
7. A single black lateral stripe in posterior half of the body, covering the lower half of the third dorsal row; subcaudals 126–133; ventrals 183–189; first sublabial touches two infralabials; compact build (SVL/head-length 23.5–28.5) ..... *D. underwoodi,* new species
– Black lateral stripe absent; subcaudals 137-156; ventrals 189-206; slender build (SVL/head-length 31.0–36.0) ..... *D. cyanochloris*

[1] The Sunda region encompasses Peninsular Malaysia, Singapore, Sumatra, Java, Borneo and surrounding smaller islands. *D. humayuni* is endemic to the Nicobar Islands which are not part of the Sunda region. However, *D. humayuni* is included in the key as it is a member of the *D. formosus* group as defined by Vogel & Van Rooijen (2007).

Table 3. Descriptive statistics for the species of the genus *Dendrelaphis* treated in this study, with regard to the examined characters. Mean and range are shown in case of continuous quantitative variables (EYED, TAIL). Median and range are shown in case of discrete quantitative variables (VENT-LOR). In case of polarized variables (STR1-TSTR2), the percentage of specimens possessing the indicated character is shown. EYED and TAIL represent the SVL-adjusted values. TLMAX represents the maximum recorded total length.

	D. underwoodi **(n = 3)**	***D. cyanochloris*** **(n = 22)**	***D. formosus*** **(n = 21)**	***D. humayuni*** **(n = 11)**	***D. kopsteini*** **(n = 12)**	***D. pictus*** **(n = 16)**
EYED (mm)	4.9 (4.7–5.2)	4.7 (4.4–5.2)	6.0 (5.6–6.6)	4.4 (3.9–5.0)	5.7 (5.2–6.1)	4.6 (4.2–5.0)
TAIL (cm)	31.0 (30.0–32.5)	30.0 (28.0–32.0)	33.5 (31.0–39.0)	33.0 (31.0–34.5)	34.0 (32.0–37.0)	33.0 (31.5–35.0)
VENT	186 (183–189)	200 (189–206)	181 (176–194)	176 (170–178)[1]	176 (163–182)	168 (161–176)
SUBC	131 (126–133)	143 (137–156)	148 (142–162)[3]	142 (137–148)[2]	148 (138–154)	134 (126–141)
SUBL	4 (4–4)	4 (4–10)	8 (5–10)		4 (4–4)	8 (4–10)
SPL1	18 (18–18)	18 (16–18)	18 (17–18)		18 (16–19)	18 (18–18)
SPL2	6 (6–6)	6 (4–6)	6 (4–6)		4 (4–4)	5 (4–6)
POC	4 (4–6)	4 (4–4)	4 (4–9)		4 (4–4)	4 (4–6)
INFR	21 (20–22)	20 (18–22)	20 (19–22)		20 (19–21)	20 (18–21)
TEMP	12 (12–13)	12 (8–14)	12 (8–13)	17 (15–17)	12 (10–16)	12 (9–16)
DOR1	15 (15–15)	15 (15–16)	15 (15–15)	15 (15–15)	15 (15–15)	15 (15–15)
DOR2	15 (15–15)	15 (13–15)	15 (13–15)	15 (13–15)	15 (15–15)	15 (15–15)
DOR3	11 (11–11)	11 (11–11)	11 (11–11)	9 (9–11)	11 (11–11)	11 (9–11)
LOR	2 (2–2)	2 (2–2)	2 (2–2)		2 (2–2)	2 (2–2)
STR1 (%)	0	0	100	0	0	0
STR2 (%)	0	0	0	0	0	100
STR3 (%)	100	0	0	0	0	0
TSTR1 (%)	100	100	100	100	0	100
TSTR2 (%)	100	100	100	0	0	50
TLMAX (cm)	90.0	143.0	147.0	123.0	142.5	105.5

[1] The ventral range is based on Vijayakumar & David (2006) and differs little from the range obtained in this study (171–178).
[2] Vijayakumar & David (2006) extended the subcaudal range of *D. humayuni* to (106–148). However, the extremely low minimum is suspect and may have been taken from a specimen with incomplete tail.
[3] The subcaudal value of 162 is from an outlier with an extremely long tail. When this specimen is excluded, the subcaudal range is (142–151)

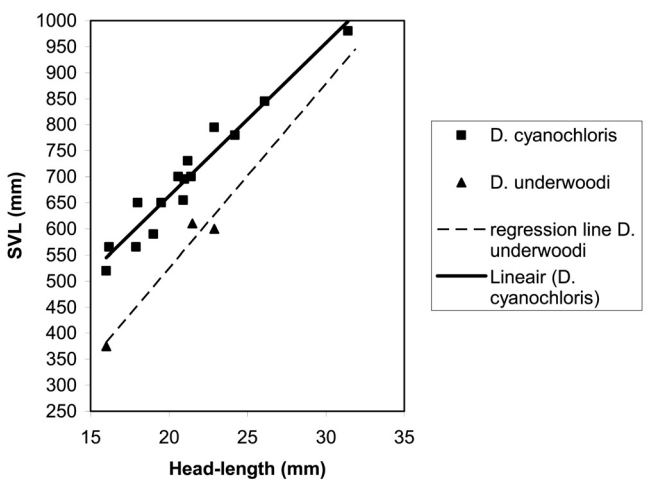

Fig. 5. Relation between head-length and SVL for *Dendrelaphis underwoodi*, new species, and *D. cyanochloris*.

DISCUSSION

Statistical analyses were aimed at the comparison of *D. underwoodi* with *D. cyanochloris*, *D. formosus*, *D. kopsteini*, *D. humayuni* and *D. pictus*. Descriptive statistics for each species are shown in Table 3 and the results of the univariate statistical tests are presented in Table 4. Figure 5 shows the relationship between head-length and SVL for *D. underwoodi* and *D. cyanochloris*. The difference in regression lines was found to be highly significant ($p = 0.00001$). Thus, at the same head-length, *D. underwoodi* has a substantially shorter body than *D. cyanochloris*. Linear discriminant analysis was restricted to morphological variables. Head-length was excluded as this character was only measured for *D. underwoodi* and *D. cyanochloris*. In the first analysis, *D. underwoodi* was compared with *D. cyanochloris* and *D. formosus*. Both canonical variates were highly significant based on Wilk's lambda ($p \leq 0.00001$). In the second analysis, *D. underwoodi* was compared with *D. kopsteini* and *D. pictus* and both canonical variates were again highly significant ($p < 0.00001$). Plots of the object scores are shown in Figs. 6 and 7. The results of the discriminant analyses demonstrate

Table 4**.** Univariate significance-levels of the differences between *Dendrelaphis underwoodi*, new species, the other members of the *D. formosus* group and *D. pictus.*

	D. underwoodi* / *D. cyanochloris	***D. underwoodi* / *D. formosus***	***D. underwoodi* / *D. humayuni***	***D. underwoodi* / *D. kopsteini***	***D. underwoodi* / *D. pictus***
EYED	–	P < 0.00001	–	P = 0.003	P = 0.02
TAIL	–	–	–	–	P = 0.04
VENT	P = 0.00003	–	P = 0.00006	P = 0.01	P < 0.00001
SUBC	P = 0.0003	P < 0.00001	P = 0.0003	P = 0.0002	–
SUBL	–	P = 0.001	–	–	P = 0.01
SPL1	–	–	–	–	–
SPL2	–	–	–	P = 0.0001	–
POC	–	–	–	–	–
INFR	–	–	–	–	–
TEMP	–	–	P = 0.005	–	–
DOR1	–	–	–	–	–
DOR2	–	–	–	–	–
DOR3	–	–	–	–	–
LOR	–		–	–	–
STR1	–	P = 0.0005	–	–	–
STR2	–	–	–	–	P = 0.00001
STR3	P < 0.00001	P = 0.0005	P = 0.005	P = 0.0001	P = 0.00001
TSTR1	–	–	–	P = 0.001	–
TSTR2	–	–	P = 0.005	P = 0.001	–

a clear morphological separation of *D. underwoodi* from the other species. Nonlinear discriminant analysis was applied to morphological as well as colouration characters and to all species simultaneously. A plot of the object scores is depicted in Fig. 8 and shows the close (phenetic) association between *D. underwoodi* and *D. cyanochloris*.

The analyses show that *D. underwoodi* differs significantly from the other species in several aspects of its morphology and colouration. The eye is smaller than in *D. formosus* and *D. kopsteini* and larger than in *D. pictus*. The tail is shorter than that of *D. pictus*. The ventral count is lower than in *D. cyanochloris* and higher than in *D. humayuni*, *D. kopsteini* and *D. pictus*. The subcaudal count is lower than in *D. cyanochloris*, *D. formosus*, *D. humayuni* and *D. kopsteini*. The number of infralabials touched by the first sublabial is lower than in *D. formosus* and *D. pictus*. The number of supralabials touching the eyes is higher than in *D. kopsteini.*

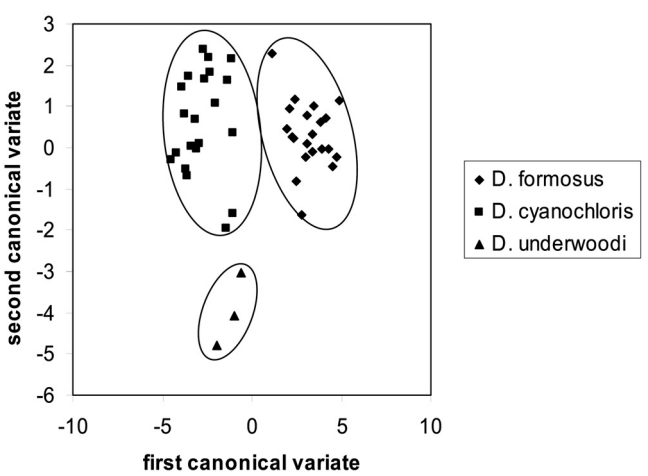

Fig. 6. Ordination of *Dendrelaphis underwoodi*, new species, *D. cyanochloris* and *D. formosus* along the canonical variates, based on linear discriminant analysis of morphological characters.

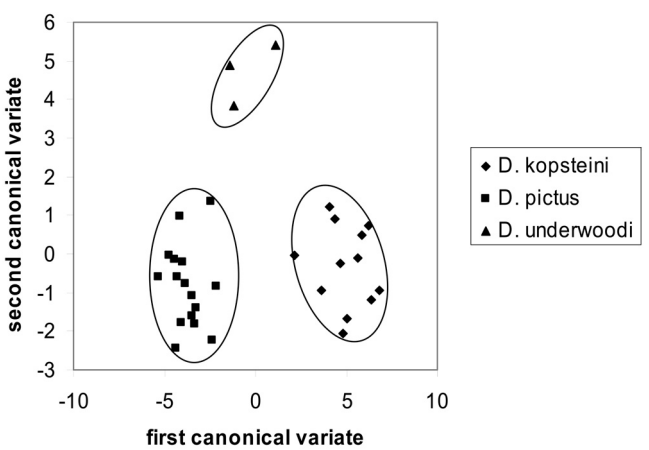

Fig. 7. Ordination of *Dendrelaphis underwoodi*, new species, *D. kopsteini* and *D. pictus* along the canonical variates, based on linear discriminant analysis of morphological characters.

Dendrelaphis underwoodi has a more compact build than *D. cyanochloris*. *Dendrelaphis underwoodi* lacks the three black lateral stripes that are invariably present on the posterior half of the body of *D. formosus*. *Dendrelaphis underwoodi* lacks the light ventrolateral stripe, which is characteristic for *D. pictus*. *Dendrelaphis underwoodi* has a postocular stripe that covers the whole temporal region and extends onto the neck. On the contrary, the postocular stripe covers only the lower part of the temporal region in *D. kopsteini* and *D. humayuni*. In addition, the postocular stripe ends at the rear of the jaw in *D. kopsteini*. Finally, *D. underwoodi* has a single black lateral stripe in the posterior half of the body, occupying the lower half of the third dorsal row, which is absent in the other species. The total length of *D. underwoodi* was not tested statistically as such a test would be sensistive to differences in growth stage distributions between the samples. However, *D. underwoodi* does seem to be substantially smaller than *D. cyanochloris*, *D. formosus* and *D. kopsteini*. The two largest specimens of *D. underwoodi* are both 90 cm long. One of these, the holotype, is a gravid female. The second is a female that appears to have been collected just after egg-laying as the rear part of the body is conspicuously stretched. As such, both specimens represent adult females. Females of *D. cyanochloris*, *D. formosus* and *D. kopsteini* attain a total length of over 140 cm.

The univariate and multivariate comparisons demonstrate that *D. underwoodi* is diagnosibly different from its congeneric species primarily on the basis of the combination of its compact build, ventral range, subcaudal range and presence of a narrow black lateral stripe in the posterior part of the body. On the basis on the General Lineage Species Concept (De Queiroz, 1998), applying diagnosibility and geographic isolation as criteria for independence (e.g. Grismer, 1999), the population represented by the three type-specimens is considered to constitute a distinct species.

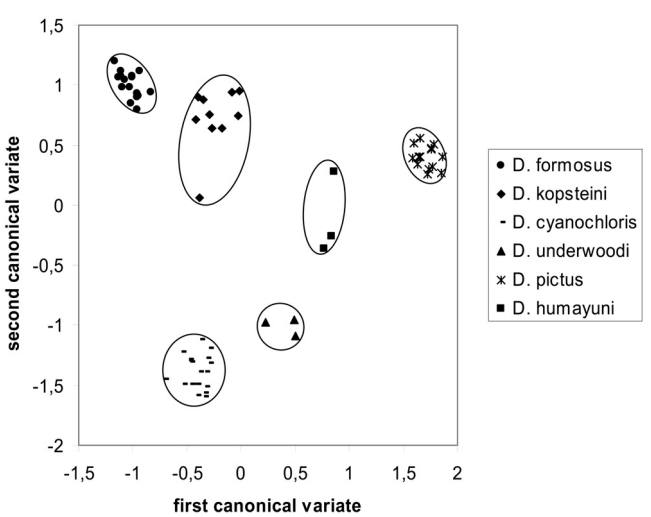

Fig. 8. Ordination of *Dendrelaphis underwoodi*, new species, *D. cyanochloris*, *D. formosus*, *D. humayuni*, *D. kopsteini* and *D. pictus* along the first two canonical variates, based on nonlinear discriminant analysis of morphological and colouration characters.

The morphology and colouration of *D. underwoodi* suggest that it may be a sister taxon of *D. cyanochloris*, although phylogenetic analysis will have to corroborate this. *Dendrelaphis cyanochloris* inhabits mainland Southeast Asia. Vogel & Van Rooijen (2007) doubted the records of *D. cyanochloris* from Pulau Tioman, Peninsular Malaysia (e.g. Hien et al., 2001; Van Rooijen & Van Rooijen, 2002), consequently limiting the most southern part of its range to Peninsular Thailand. For this study, several specimens from Pulau Tioman and Pulau Pinang were examined and these were found not to differ from the mainland population of *D. cyanochloris*. As such, *D. cyanochloris* ranges from India to Peninsular Malaysia (Pulau Tioman and Pulau Pinang). Consequently, according to the currently known distributions, the population of *D. underwoodi* is separated from *D. cyanochloris* by 1,000 kilometers "as the crow flies".

The statistical analyses demonstrate that eye size is a taxonomically important character (see also Vogel & Van Rooijen, 2007). As such, eye size appears to have been an important axis of differentiation in *Dendrelaphis*. Assuming a relationship between eye size and light intensity in the preferred habitat of a species, the differences in eye size probably reflect differences in occupied niches. Indeed, *D. pictus* is an inhabitant of cultivated areas (high light intensity) and has a correspondingly small eye whereas *D. formosus*, an inhabitant of dense primary rainforest (low light intensity), has a very large eye.

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Dendrelaphis formosus. Java: SMF 32346, SMF 32347, SMF 32348, MNHN 1975.70, SMF 18667, RMNH 877, RMNH 9005 (1), RMNH 9005 (2), RMNH 40098, RMNH 40105, RMNH 40099, MNHN 7307, MNHN 469, RMNH 40102, RMNH 36443, RMNH 36446, RMNH 40101, RMNH 36444, RMNH 36447, RMNH 36445, ZMB 7151.

Dendrelaphis humayuni. Nicobar Islands: BMNH 1940.3.4.28, NMW 23686:3, NMW 23686:4.

Dendrelaphis kopsteini. Peninsular Malaysia: MNHN 1962.1051, ZMH R08445 (former PSGV 269), RMNH 40117 (former PSGV 777), MNHN 1962.1052, BMNH 1912.2.22.12, BMNH 1933.12.5.10, BMNH 1971.1872; Singapore: MNHN 1893.147; Peninsular Thailand: MNHN 1997.6579, QSMI Q531 (former PSGV 45); Sumatra: ZSM 277/1909, ZMB 32192.

Dendrelaphis pictus. Java: RMNH 36451, RMNH 36452, RMNH 36450, RMNH 35090, RMNH 40104, ZMA 10522 (1), ZMA 10522 (2), ZMA 10522 (3), ZMA 10522 (4), ZMA 9442 (1), ZMA 9442 (2), RMNH 9025 (1), RMNH 9025 (2), RMNH 9025 (3), RMNH 36451, RMNH 36452.