

## A revised taxonomy of the Australo-Papuan species of the colubrid genus *Dendrelaphis* (Serpentes: Colubridae)

JOHAN VAN ROOIJEN<sup>1</sup>, GERNOT VOGEL<sup>2</sup> & RUCHIRA SOMAWEERA<sup>3</sup>

<sup>1</sup>) Netherlands Centre for Biodiversity Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands

<sup>2</sup>) Society for Southeast Asian Herpetology, Im Sand 3, 69115 Heidelberg, Germany

<sup>3</sup>) Biologic Environmental Survey, 50B, Angove Street, North Perth, WA 6006, Australia

Corresponding author: JOHAN VAN ROOIJEN, e-mail: j1.van.rooijen@hetnet.nl

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**Abstract.** This study investigates the taxonomy of an Australo-Papuan species group within the colubrid snake genus *Dendrelaphis*, which is characterised by the combination of 13 dorsal scale rows at midbody and enlarged vertebral scales. Members of this group inhabit the southeastern Moluccas, Palau Islands, New Guinea, Solomon Islands, and the northern and eastern parts of Australia. The taxonomy of this group has been reviewed several times in the past, resulting in a sequence of completely different sets of species as well as groupings into higher-order taxa. The capricious succession of taxonomic interpretations can be attributed to a lack of objectivity in most previous studies. This study attempts to clarify the taxonomy of this group by applying multivariate techniques to a set of morphological data taken from 171 museum specimens covering the entire geographic range. In addition, all extant type specimens of this species group were examined. The results provide evidence for the validity of nine species: 1) *D. calligaster* (GÜNTHER, 1867) which inhabits New Guinea and adjacent islands, the Solomon Islands as well as Australia (Cape York Peninsula); 2) *D. gastrostictus* (BOULENGER, 1894) from mainland New Guinea; 3) *D. keiensis* (MERTENS, 1926) from the Moluccan islands of Babar, Timor-Laut, and Kei-Dulah; 4) *D. lineolatus* (JAQUINOT & GUICHENOT, 1853) from mainland New Guinea and several adjacent islands; 5) *D. lorentzii* (VAN LIDTH DE JEUDE, 1911) from mainland New Guinea, Normanby Island, and Salawati Island; 6) *D. macrops* (GÜNTHER, 1877) from mainland New Guinea, Daru Island, Numfoor Island, and Duke of York Island; 7) *D. papuensis* BOULENGER, 1895 from the Trobriand Islands; 8) *D. punctulatus* (GRAY, 1826) from northern and eastern Australia as well as several of the Torres Strait Islands; and 9) *D. striolatus* (PETERS, 1867) from the Palau Islands. The presented taxonomy entails revalidating *D. keiensis*, *D. lineolatus*, and *D. macrops*, synonymising *D. salomonis* with *D. calligaster*, and elevating to specific status *D. punctulatus striolatus*. Neotypes are designated for *Dendrophis punctulatus* var. *atrostriata* MEYER, 1874 and *Dendrophis punctulatus* var. *fasciata* MEYER, 1874, which are considered synonyms of *D. lineolatus*.

**Key words.** Bronze back snakes, Palau, Australia, New Guinea, Solomon Islands.

### Introduction

The colubrid snakes of the genus *Dendrelaphis* BOULENGER, 1890 are widely distributed in South and Southeast Asia, ranging from Pakistan to the east coast of Australia (ZIEGLER & VOGEL 1999). Members of this genus are slender, diurnal species that are predominantly arboreal and feed mainly on lizards and frogs (e.g., WALL 1921, SHINE 1991, VAN ROOIJEN & VAN ROOIJEN 2007, FEARN & TREMBATH 2010). BOULENGER (1894), WALL (1921), MEISE & HENNIG (1932), MERTENS (1934), SMITH (1943), and LEVITON (1968) have in turn revised the systematics of this genus. Lately however, a comprehensive revision of the taxonomy of the Asian members of this genus has led to the description of ten new species, the revalidation of five more taxa, and the elevation to specific status of five former subspecies (VAN

ROOIJEN & VOGEL 2008a, b, c, 2009, 2010, 2012, VOGEL & VAN ROOIJEN 2007, 2008, 2011a, b, c, VOGEL et al. 2012).

This study deals with the taxonomy of a principally Australo-Papuan group within *Dendrelaphis*, which is characterized by having 13 dorsal scale rows at midbody and enlarged vertebral scales. All Australian and New Guinean species of *Dendrelaphis* belong to this group, and its members can be found as far west as the Moluccan Kei- and Babar Islands, north to the islands of Palau, and east to the Solomon Islands. As such, this group principally inhabits islands of the Sahul Shelf, which has repeatedly been exposed as dry land during the Pleistocene (e.g., VORIS 2000). A map of the area inhabited by this group, as well as locations relevant in this study, are illustrated in Figure 1.

The taxonomy of this group has been, and still is, rather confused. Between 1826 and 1932, 28 species and subspe-

cies were described. Many were subsequently considered to be synonyms, with only seven taxa being currently considered valid. The large number of synonyms can in part be attributed to the fact that different researchers were unaware of each other's work. This is illustrated, for example, by the application of the same name in two different species descriptions: *Dendrophis olivacea* GRAY, 1842 and *Dendrophis olivacea* MACLEAY, 1878. In their comprehensive review of the genus *Dendrelaphis*, MEISE & HENNIG (1932) recognized three species that were subdivided into nine subspecies: *D. calligaster* [*D. c. calligaster* (GÜNTHER, 1867), *D. c. schlenkeri* (OGILBY, 1898), *D. c. papuensis* (BOULENGER, 1895b), *D. c. salomonis* (GÜNTHER, 1872), *D. c. distinguendus* MEISE & HENNIG, 1932, *D. c. keiensis* MERTENS, 1926], *D. punctulatus* (GRAY, 1826), and *D. lineolatus* [*D. l. lineolatus* (JAQUINOT & GUICHENOT, 1853), *D. l. striolatus* (PETERS, 1867)]. MERTENS (1934) subsequently merged *D. punctulatus* and *D. lineolatus* into one species: *D. punctulatus* [*D. p. punctulatus*, *D. p. lineolatus*, and *D. p. striolatus*]. COGGER et al. (1983) then reduced the number of recognized taxa substantially by synonymising *D. schlenkeri*, *D. papuensis*, *D. salomonis*, *D. c. distinguendus*, *D. c. keiensis*, and *D. lineolatus* with *D. calligaster*. Consequently, only three taxa were considered valid at that point in time:

*D. calligaster*, *D. punctulatus punctulatus*, and *D. punctulatus striolatus*. However, COGGER et al. (l.c.) emphasized that the status of many of the synonyms of *D. calligaster* were uncertain. MCDOWELL (1984) subsequently revised the taxonomy of the New Guinean members of this group on the basis of hemipenial morphology as well as several other character states. He arrived at a quite different set of species as well as a different classification into higher-order taxa: the *D. punctulatus* group [comprising *D. gastrostictus* (BOULENGER, 1894), *D. calligaster*, *D. punctulatus*, *D. salomonis*], the *D. papuensis* group [*D. papuensis*], and the *D. lorentzii* group [*D. lorentzii* (VAN LIDTH DE JEUDE, 1911)]. Finally, WELLS & WELLINGTON (1985) presented yet another arrangement by revalidating various taxa, which we will not list here. In conclusion, the sequence of taxonomic classifications of this group, as perceived by subsequent authors, must today almost appear as a succession of haphazard selections out of the pool of nominal species. That said, some arrangements certainly afforded a more solid scientific basis than others. For instance, WELLS & WELLINGTON (1985) provided no justification whatsoever for their taxonomic arrangement. It appears to have been based on belief much rather than any form of scientific endeavour and as a consequence has generally been regarded



Figure 1. Map of the region inhabited by the studied species group.

as controversial at best (e.g., WÜSTER et al. 2001). McDOWELL (1984) on the other hand, based his taxonomic revision on a study of morphology, and although he did not provide quantitative data and accompanying analyses, one may expect his arrangement to be largely in line with biological reality.

Unsurprisingly, the conflicting taxonomic interpretation of this group has translated into confusion about the identity of specific populations (O'SHEA 1996). For instance, the population assemblage from the Palau Islands was referred to as *Dendrelaphis* sp. by CROMBIE & PREGILL (1999). In a similar vein, ALLISON & BIGILALE (2001), BUDEN et al. (2001), and AUSTIN et al. (2008) were unable to identify specimens from New Ireland, Phonpei, and New Guinea, respectively.

The present study attempts to improve the taxonomic interpretation of this group by providing a more solid underpinning based on multivariate analyses applied to a broad set of morphological characters.

### Material and methods

For this study, 171 museum specimens were examined (listed in the appendix). Localities and corresponding sample sizes are summarized in Table 1. Type specimens (onomatophores) of 24 of the 28 relevant nominal taxa were located and examined. The type specimens of 20 nominal taxa were directly examined by us while four nominal taxa were studied using photographs provided by museums. Type specimens of the four remaining nominal taxa no longer exist.

For most examined specimens, a set of 22 characters was recorded (Tab. 2). Eye diameter, eye–nostril distance, length of the frontal scale, snout width, and width of the vertebral scale were measured with sliding callipers to the nearest 0.1 mm. Measurements of (horizontal) eye diameter and eye–nostril distance were taken on the left and right side and averaged. Eye–nostril distance was measured from the anterior border of the eye to the posterior border of the nostril. Snout width was measured level with the position of the nostrils, just touching the prenasals with the callipers. Width of the vertebral scale was measured at the level of the middle ventral scale. Snout–vent length was measured from the tip of the snout to the posterior margin of the cloacal scute by marking the length on a piece of string and measuring this to the nearest 5 mm. Tail length was measured to the nearest 5 mm by straightening the tail against a ruler. The number of ventrals was counted following DOWLING (1951). Subcaudals were counted down one side, starting with the first scale that touched neighbouring member of its pair; the terminal scute was excluded. The first sublabial was defined as the scale that started between the posterior chin shield and the infralabials and bordered the infralabials (see PETERS 1964, Fig. 7, LILLYWHITE 2008). The last infralabial was defined as the infralabial still completely overlapped by the last supralabial. The posterior-most temporal scales were defined as the scales with more

Table 1. Locations and corresponding sample sizes.

Location	Sample size
western New Guinea	25
Papua New Guinea	18
New Guinea, unspecified	4
Misool Island	3
Salawati Island	2
Yapen Island	2
Aru Islands	1
Daru Island	5
Numfoor Island	2
Trobriand Islands	5
Fergusson Island	4
Solomons: Bougainville Island	11
Solomons: Guadalcanal Island	5
Solomons: unspecified	2
New Britain	3
Fiji (erroneous)	1
Australia	26
Torres Strait Islands	4
Babar Island	2
Kei-Dulah	1
Palau: unspecified	4
Palau: Babeldaob	7
Palau: Ngercheu (Carp Isl.)	2
Palau: Ulebsechel	1
Palau: Malakal	3
Palau: Ngeaur	4
Palau: Ngerekebesang	2
Palau: Ulong: West Ulong	3
Palau: Ulong: East Ulong	1
Palau: Ngesebus	1
Palau: Ngerchaol	3
Palau: Ngeanges	1
Palau: Ngeruktabel	5
Palau: Koror	2
Palau: Ngerukeuid Islands (Isls. 24)	1
Palau: Ngermalk Island	1

than half of their area anterior to an imaginary line from the apex of the last supralabial to the posterolateral corner of the parietal. The scales behind the parietals were defined as those scales (not being temporal scales) that touch the posterior edges of the parietal scales. Characters pertaining to head scalation were measured on the left and right sides and added. Sexes were identified by making an incision in the base of the tail (if not pre-existing) to establish the presence or absence of hemipenes. In some specimens however, the hemipenes had been everted before conservation. In a few cases, the sex was not identified (small juveniles, damaged specimens, some type specimens).

Table 2. List of characters used in this study and their abbreviations.

Abbreviation	Character
EYED	diameter of the eye
EYEN	distance eye-nostril
LFRNT	length of the frontal shield
WSNT	width of the snout
WVRT	width of the vertebral scale
TAIL	tail length
SVL	snout-vent length
SEX	sex
VENT	number of ventrals
SUBC	number of subcaudals
DOR1	number of dorsal scale rows at the level of the middle ventral
DOR2	number of dorsal scale rows one head length anterior to the tail
SUBL1	number of infralabials in contact with the first sublabial
SUBL2	infralabials in contact with the first chinshield
SUBL3	infralabials in contact with the second chinshield
SUPR1	number of supralabials
SUPR2	number of supralabials entering the orbit of the eye
LOR	number of loreals
INFR	number of infralabials
TEMP	number of temporals
POC	number of postoculars
PARSC	number of scales behind the parietals

Tail length (TAIL) and the number of subcaudals (SUBC) were not recorded in specimens with damaged tails. In addition, for some type specimens and some damaged specimens, a more limited set of characters was recorded. Consequently, 104 specimens could be included in multivariate analyses with TAIL and SUBC, while 140 specimens could be included without TAIL and SUBC. In most univariate analyses, all 171 specimens could be included.

Variables that exhibited negligible variation (DOR1, SUBL1, SUBL2, LOR, POC) were excluded from analysis.

Based upon obvious differences in colouration and/or morphology, the sample was divided into *a priori*-Operational Taxonomic Units (OTUs) representing putative species. A justification of the definition of OTUs is provided in the Results section. Homogeneity of the *a priori*-OTUs was examined by carrying out a Principal Component Analysis (PCA) followed by ordination of specimens along the first two Principal Components (PCs) and visual inspection of the resulting pattern. In addition, multivariate analyses of covariance (MANCOVA) were run using isolated (sub-) populations and sex as groups, and SVL as a covariate. In the case of the Palauan population aggregate, a regression analysis was performed to assess the relation between PC scores and geographic coordinates. Coordinates were obtained from CROMBIE & PREGILL (1999).

The morphological separation of the OTUs was illustrated primarily by applying Canonical Variate Analyses

(CVAs) and subsequent ordination of specimens along the first two Canonical Variates (CVs).

Before their inclusion in the aforementioned CVAs or PCAs, variables representing morphometric characters (EYED-TAIL) were adjusted to a common SVL (following, e.g., THORPE 1975, 1983b, HOW et al. 1996, TURAN 1999) in order to correct for between-sample differences in ontogenetic composition (see THORPE 1983a). 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 (68.0 cm.); and  $\beta$  is the within-OTU coefficient of the linear regression of  $X$  against SVL. An obvious drawback of this approach is that interspecific size-differences, which turned out to be considerable in the studied species group, are neglected. Therefore, these were assessed separately. The potential significance of sexual composition in the context of interspecific variation was investigated by running a MANCOVA with sex and OTU as factors and SVL as covariate.

Univariate comparisons between OTUs were carried out either with ANCOVA (quantitative variables) using unadjusted variables, or with a  $\chi^2$ -test (qualitative variables).

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

## Results

### Establishment of a priori-OTUs

Nine a priori-OTUs were delimited on the basis of obvious differences in colouration, size, and/or morphology. Prior to the sections dealing with taxonomic evaluations and nomenclature, the definitive species names are applied in this paper as to facilitate cross-referencing between the various sections.

*Dendrelaphis striolatus* (PETERS, 1867). A representative of the genus endemic to the remote Palau islands. Easily distinguished on the basis of the oblique black bars on the neck (Fig. 12). As it represents an extensive population aggregate, homogeneity of this OTU was assessed using PCA of all characters except SUBC and TAIL (in order to maximize sample size by including specimens with incomplete tails). The results are summarized in Figure 2A. Some geographic variation is in evidence, as specimens representing different insular populations occupy slightly different positions in morphospace. Moreover, in spite of not being immediately apparent in the figure, specimens from

more southwestern Palauan islands are situated farther to the right, i.e., have higher PC1 scores on average. This was borne out by a linear regression analysis of latitude, longitude (independent variables), and PC1 score (dependent variable) ( $p = 0.005$ ). As such, the geographical variation in *D. striolatus* appears to be, at least in part, clinal. This is remarkable insofar as these populations are isolated by oceanic barriers. Although geographic variation is in evidence, there is no strong evidence for discrete transitions between diagnosably different populations. The Palauan population assemblage was therefore treated as a single OTU in subsequent CVA's.

*Dendrelaphis lineolatus* (JAQUINOT & GUICHENOT, 1853). A large species from New Guinea and adjacent islands with a highly conspicuous colouration (Fig. 7). The head is black dorsally and contrasts sharply with the white supralabials and chin. The tail is black, and the neck bears black V-shaped markings. The venter exhibits black round dots. This pattern may be more or less pronounced. No noteworthy within-OTU heterogeneity was detected.

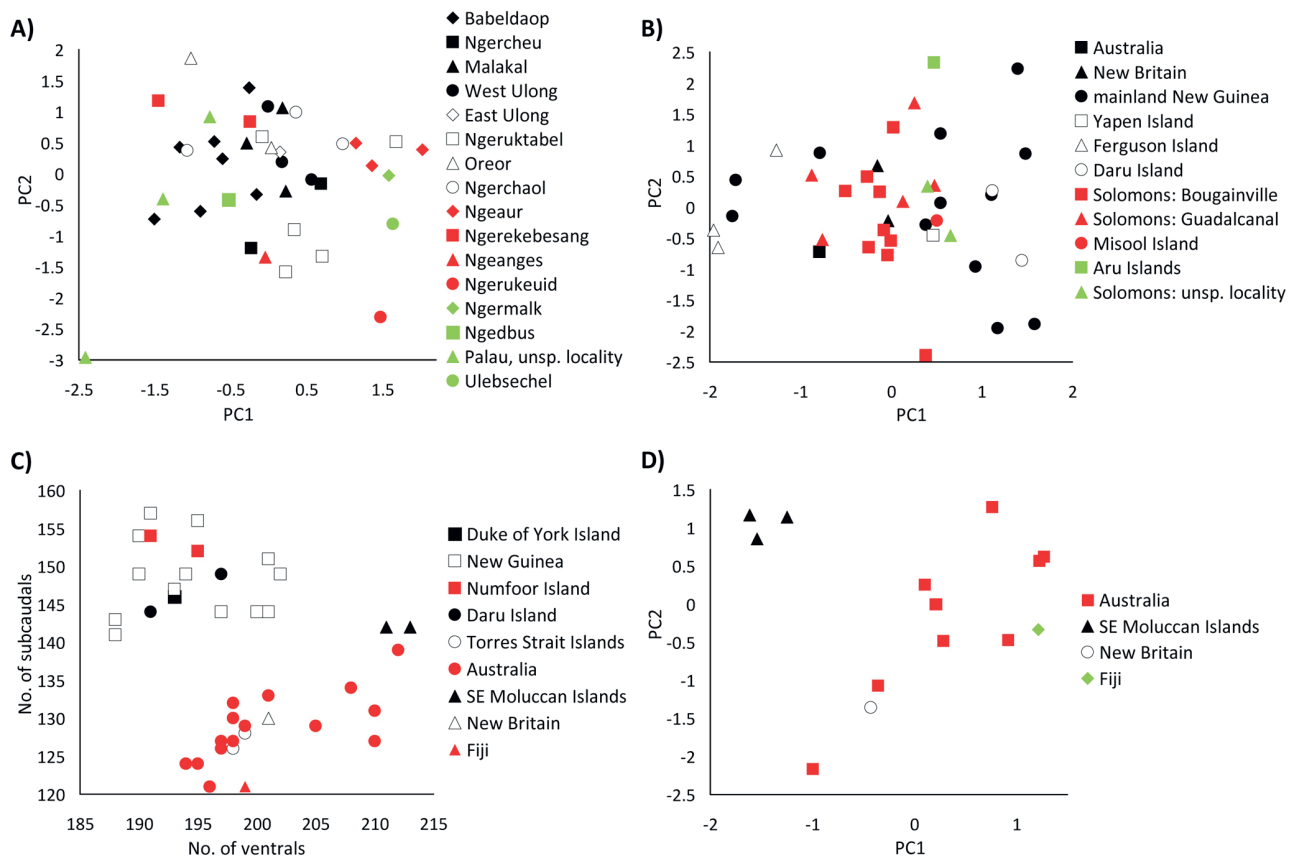


Figure 2. A, B. Ordination of specimens of *D. striolatus* (A), *D. calligaster* (B) along the first two Principal Components based on a PCA of the characters EYED, EYEN, LFRNT, WSNT, WVRT, VENT, SUPR1, SUPR2, INFR, TEMP, PARSC; C) plot of ventrals against subcaudals for *D. punctulatus* / *D. macrops* / *D. keiensis*, a clear separation of *D. macrops* (top left cluster) is visible; D) ordination of specimens of *D. punctulatus* / *D. keiensis* along the first two Principal Components based on a PCA of the characters EYED, EYEN, LFRNT, WSNT, WVRT, VENT, SUPR1, SUPR2, INFR, TEMP, PARSC, *D. keiensis* (top left cluster) is separated from *D. punctulatus*.



*Dendrelaphis macrops* (GÜNTHER, 1877), *D. punctulatus* (GRAY, 1826), and *D. keiensis* (MERTENS, 1926). These are superficially similar species, all growing to a fairly large size and exhibiting a uniform colouration (Figs. 6, 9, 11). They are clearly distinct, however, on the basis of morphology. Figure 2C shows a plot of their ventral and subcaudal counts. One cluster representing specimens from New Guinea and adjacent islands is clearly separated from other specimens on account of its lower number of ventrals and higher number of subcaudals. This cluster is referred to the OTU *D. macrops*. Within this OTU, some clinal variation seems to occur in New Guinea. Whereas specimens from the northern parts of New Guinea usually have 9 supralabials (82%,  $n = 11$ ), with supralabials 5 and 6 bordering the eye, specimens from the southern side of New Guinea (Western Province including the nearby Daru Island) usually possess 8 supralabials (86%,  $n = 7$ ) with supralabials 4 and 5 bordering the eye ( $P = 0.001$ ). The second cluster in Figure 2C represents specimens from mainland Australia, several of the adjacent Torres Strait islands, New Britain, Fiji, as well as the remote southeast Moluccan islands of Babar and Kei-Dulah. Specimens from the latter islands were originally described as a distinct taxon, *D. c. keiensis*. Figure 2C shows that those specimens have high ventral and subcaudal counts in comparison to Australian specimens. Heterogeneity of the second cluster was examined further with a PCA of all characters except SUBC and TAIL (in order to maximize sample-size by including specimens with incomplete tails). The results are summarized in Figure 2D. Evidently, the southeast Moluccan specimens are morphologically distinct. Accordingly, these were assigned to the separate OTU *D. keiensis*. The remaining specimens were assigned to the OTU *D. punctulatus*. The distribution of *D. punctulatus* appears to be remarkably disjunctive. While most specimens included in this study had been collected in Australia, one specimen originated from New Britain and another from “Viti Inseln” (= Fiji Islands, ~3000 km distant from Australia). Both are situated in or very close to the morphospace occupied by the Australian specimens (Fig. 2C, Fig. 2D). The limited data available for the Fijian specimen (RMNH.RENA.4017), “Godeffroy, 1877, coll. number 558”, imply that it was obtained from the Godeffroy Museum. Although the Godeffroy Museum has indeed collected Fijian material, it has also collected in Australia and New Britain (EVENHUIS 2007). As such, erroneous locality data cannot be ruled out, particularly since locality data of other specimens obtained from the Godeffroy Museum have been questioned as well (BAUER & WATKINS-COLWELL 2001). Moreover, this otherwise rather common snake has not been recorded from Fiji since (ALLISON 1996, MORRISON 2005). Consequently, the locality of this specimen should be considered erroneous. The presence of *D. punctulatus* on New Britain needs further verification. FOUFOPOULOS & RICHARDS (2007) recorded this species from New Britain, but this record is unfortunately not very meaningful, as the superficially similar *D. macrops* has been masquerading under the name *D. punctulatus*. Furthermore, as the specimen mentioned

by FOUFOPOULOS & RICHARDS (2007) was not collected, its identity cannot be re-assessed.

*Dendrelaphis gastrostictus* (BOULENGER, 1894). A small New Guinean species characterized by very large eyes and a highly conspicuous ventral colouration consisting of small speckles interspersed with large, irregularly shaped spots (Fig. 5). No morphological heterogeneity was observed within this OTU.

*Dendrelaphis lorentzii* (VAN LIDTH DE JEUDE, 1911). A small New Guinean species characterized by very small eyes, uniformly coloured venter, and black spots on the dorsum of the head (Fig. 8). Specimens from north of the central mountains appear to possess more ventrals than specimens from south of the central mountains. A specimen from Salawati Island had a ventral count of 179, a specimen from North New Guinea 173. Furthermore, McDOWELL (1984) documented 181 ventrals in a specimen from the Huon Peninsula. Three specimens from southern areas exhibited a ventral range of 161–168. McDOWELL reported a range of 156–173 for specimens from southern New Guinea.

*Dendrelaphis calligaster* (GÜNTHER, 1867) and *D. papuensis* BOULENGER, 1895. Similar species, both of medium size, moderately large eyes, and a postocular stripe (Figs. 4, 10). *D. papuensis*, an endemic from the Trobriand Islands, was treated as an OTU distinct from the widely distributed *D. calligaster* on account of its substantially lower number of subcaudals (124 [120–126] vs. 145 [130–156];  $p < 0.0001$ ), smaller relative tail length (0.29 [0.28–0.30] vs. 0.35 [0.33–0.37];  $p < 0.0001$ ), and fewer infralabials bordering the second chinshield ( $p < 0.0001$ ). The homogeneity of *D. calligaster* was further examined using PCA. The ordination of *D. calligaster* specimens along the first two PCs suggests geographic variation (Fig. 2B). For instance, specimens from Daru Island, Bougainville, and Fergusson Island are situated at different positions along the first PC. This notion was supported by MANCOVAs of which one included all specimens (TAIL and SUBC excluded;  $p = 0.004$ ) and another all variables (specimens with missing tail tips excluded;  $p = 0.02$ ). As such, inter-population divergence has occurred although apparently not to a large extent. Also noteworthy is the comparatively large variation within the mainland New Guinea population. Indeed, the PC scores of most other populations fall within the region of the morphospace occupied by the latter.

#### Morphological divergence of OTUs: Canonical Variate Analysis

A MANCOVA with sex and OTU as factors and SVL as covariate demonstrated that intersexual differences were negligible in the context of interspecific differences ( $p = 0.5$  vs.  $p = 8 \times 10^{-62}$ ). Therefore, no distinction was made between males and females in the CVA-based plots that were used to visualise morphological differences between OTUs. This allowed for halving the otherwise rather large number of groups.

The first CVA included all OTUs, with TAIL and SUBC included (thus specimens with incomplete tails excluded). The first two CVs were highly significant ( $p < 0.00001$ ; Fig. 3A). *D. lorentzii*, *D. calligaster*, and *D. gastrostictus* are mutually separated as well as separated from the other OTUs. Furthermore, *D. lineolatus*, *D. macrops*, and *D. striolatus* are clearly separated from *D. papuensis*, *D. punctulatus*, and *D. keiensis*. The subsequent CVAs therefore focussed on three subsets of OTUs (Figs. 3B–D). In each CVA, the first two CVs were highly significant ( $p < 0.00001$ ). In the CVA underlying Figure 3D, the characters TAIL and SUBC were excluded as to maximize the sample size of *D. papuensis* and *D. keiensis*. The plots reveal a clear morphological separation of all a priori-OTUs.

#### Taxonomic evaluation

The results of this study provide compelling evidence for the existence of at least nine species within this group, as each of the a priori-OTUs was morphologically distinct from all others. The known distribution of the nine recognized species is summarized in Fig. 13. *Dendrelaphis*

*macrops*, *D. calligaster*, *D. lorentzii*, *D. gastrostictus*, and *D. lineolatus* occur on New Guinea as well as some of its neighbouring islands. Obviously, New Guinea is a huge land mass and specimens examined for this study originate from widely spaced localities. However, in this study, *D. macrops*, *D. lineolatus*, *D. gastrostictus*, and *D. calligaster* were all recorded from the Vogelkop Peninsula, West Papua. In addition, McDOWELL (1984) documented *D. lorentzii*, *D. gastrostictus*, *D. calligaster*, and either *D. macrops* or *D. lineolatus* (as *D. punctulatus*) from the Huon Peninsula, eastern Papua New Guinea. As such, these five species may be assumed to occur sympatrically and therefore be mutually isolated by intrinsic reproductive barriers. In contrast, *D. papuensis*, *D. keiensis*, and *D. striolatus* do not coexist with congeners whereas *D. punctulatus* only co-occurs with *D. calligaster* (in Australia and possibly New Britain). These four species are strongly isolated from other species by extrinsic reproductive barriers (ocean). Moreover, given their level of morphological divergence, the presence of intrinsic reproductive barriers is likely. In conclusion, the combination of mutual morphological divergence and either sympatric occurrence or geographic isolation strongly supports the

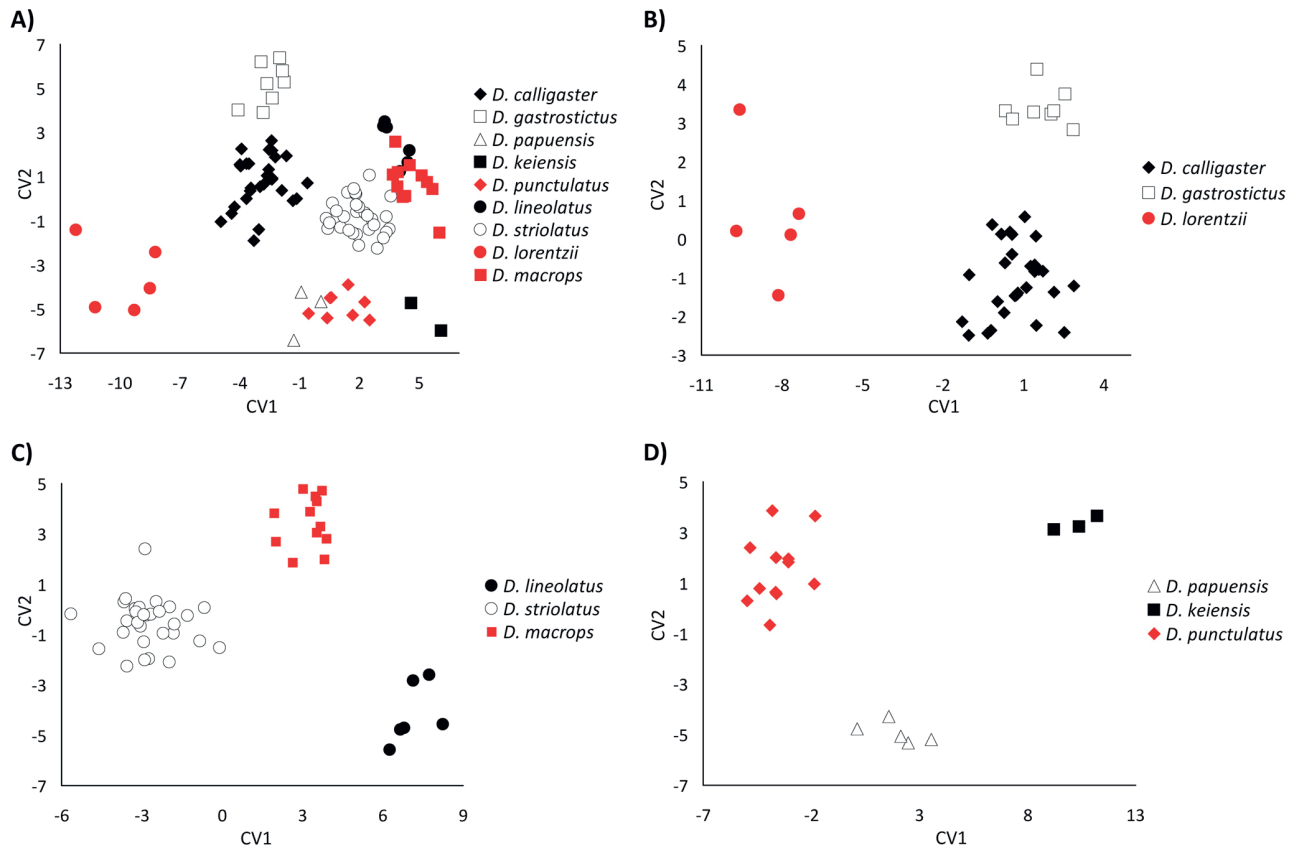


Figure 3. A–C. Ordination of specimens along the first two Canonical Variates based on CVAs of the characters EYED, EYEN, LFRNT, WSNT, WVRT, TAIL, VENT, SUBC, SUPR1, SUPR2, INFR, TEMP, PARSC; D) ordination of specimens along the first two Canonical Variates based on a CVA of the characters EYED, EYEN, LFRNT, WSNT, WVRT, VENT, SUPR1, SUPR2, INFR, TEMP, PARSC.

view that the nine a priori-OTUs represent independent lineages in the sense outlined by DE QUEIROZ (1998).

Less obvious is the interpretation of geographic variation within two of the recognized species, *D. striolatus* and *D. calligaster*. As discussed above, the insular subpopulations of *D. striolatus* exhibit some degree of morphological differentiation and are separated by oceanic barriers. However, due to the relatively small distances between the various Palauan islands, infrequent gene flow through dispersal events is likely. Moreover, the observed morphological variation seems to be clinal in nature, at least in part. As such, prominent phenotypic transitions are not in evidence. Therefore, the Palauan population aggregate is assumed to represent a single meta-population lineage. Given that most Palauan islands were physically connected in a single landmass during the Pleistocene (CROMBIE & PREGILL 1999), the various populations probably are of vicariate origin. As such, the observed clinal variation may be a relic phenomenon. As for *D. calligaster*, the chance of dispersal between some insular populations is much lower because the across-sea distances are greater in many cases. That said, many islands inhabited by this species have never been connected by land bridges, indicating that transmarine dispersal has occurred commonly in this species. Still, as differentiation of populations is in evidence, *D. calligaster* might in reality represent a species complex. This suspicion is strengthened by observations discussed by BOULENGER (1894) and SCHMIDT (1932). The former included populations that were not covered in this study and noted considerable variation, while the latter mentioned a dichotomy in the number of ventral scales within several Solomon populations. Also, McDOWELL (1984), using different characters, considered the Solomon Island populations to be specifically distinct from *D. calligaster*. Nevertheless, we consider the evidence for lineage separation revealed in this study too meagre for supporting this concept. Examination of more material from other localities is needed to underpin a possible division of this species.

#### Univariate comparisons between recognized species

A selection of univariate statistical comparisons between species is provided herein. Comparisons are limited to those that outline deviations from past and current taxonomic notions as well as to those that concern species that can be confused. Ranges of values of various characters are given in the taxonomic section.

*Dendrelaphis gastrostictus* is most similar to *D. calligaster*. It differs from the latter in having substantially larger eyes ( $p < 0.0001$ ), fewer ventrals ( $p < 0.0001$ ), a longer tail ( $p < 0.0001$ ), and more subcaudals ( $p = 0.005$ ) on average. In addition, McDOWELL (1984) noted a major difference in maxillary teeth: 30–41 in *D. gastrostictus* versus 19–25 in *D. calligaster*. KINGHORN (1921) mentioned 21 maxillary teeth in a *D. calligaster* (a syntype of *D. schlenckeri*). Finally, the venter of *D. gastrostictus* exhibits small dark speckles interspersed with large, irregularly shaped spots

(Fig. 5C), a pattern absent in all other species in the group. Some populations of *D. calligaster* have small speckles on the venter, but these are not interspersed with large spots.

*Dendrelaphis lorentzii* can be easily distinguished by its conspicuous black spots on the dorsum of the head (Fig. 8). While it is most similar to *D. gastrostictus* and *D. calligaster*, it differs from the former by having substantially smaller eyes ( $p = 0.0001$ ), a narrower snout ( $p = 0.01$ ), a shorter frontal scale ( $p = 0.002$ ), fewer subcaudals ( $p = 0.0001$ ), and a shorter tail ( $p = 0.004$ ) on average. Furthermore, McDOWELL (1984) recorded 23 maxillary teeth in one specimen of *D. lorentzii* and 30–41 in *D. gastrostictus*. It differs from *D. calligaster* by having smaller eyes ( $p = 0.002$ ), a narrower snout ( $p = 0.004$ ), a shorter frontal scale ( $p = 0.02$ ), fewer ventral scales ( $p = 0.001$ ), and fewer subcaudals ( $p < 0.0001$ ) on average.

*Dendrelaphis papuensis* is most similar to *D. calligaster*. It differs from the latter by having fewer subcaudals ( $p < 0.0001$ ), a shorter tail ( $p < 0.0001$ ), a longer frontal scale ( $p = 0.005$ ), and fewer infralabials bordering the second chinshield ( $p < 0.0001$ ).

*Dendrelaphis keiensis* was originally described as a subspecies of *D. calligaster* and later synonymised with the latter. It differs by having more ventral scales ( $p < 0.0001$ ), more supralabials ( $p = 0.0003$ ), a narrower snout ( $p = 0.01$ ), a shorter eye–nostril distance ( $p = 0.01$ ), and a shorter tail ( $p = 0.0001$ ). It exhibits some similarities with *D. punctulatus* (see also Fig. 2C) from which it differs predominantly by having more ventral ( $p = 0.002$ ), subcaudal ( $p = 0.0003$ ), and temporal scales ( $p < 0.0001$ ). In addition, supralabials 5 and 6 usually border the eye (83%,  $n = 3$ ) in *D. keiensis* whereas supralabials 4 and 5 usually border the eye in *D. punctulatus* (94%,  $n = 32$ ).

*Dendrelaphis macrops*, *D. lineolatus*, and *D. striolatus* have been treated as either synonyms or subspecies of *D. punctulatus*. As far as colouration is concerned, *D. macrops* is nearly indistinguishable from *D. punctulatus*. However, it differs from the latter in various morphological characters, most importantly its fewer ventrals ( $p < 0.0001$ ), more temporals ( $p < 0.0001$ ), more subcaudals ( $p < 0.0001$ ), a longer tail ( $p = 0.003$ ), and larger eyes ( $p = 0.0001$ ).

*Dendrelaphis lineolatus* differs from *D. punctulatus* by its highly characteristic colouration, which consists of a black dorsum and white underside of the head, a black tail, oblique black bars on the neck, and large black round spots on the posterior edges of the ventrals in the anterior part of the body (Fig. 7). Morphologically it differs from the latter by a broad set of morphological characters: fewer ventrals ( $p < 0.0001$ ), more temporals ( $p = 0.005$ ), more subcaudals ( $p < 0.0001$ ), a longer tail ( $p = 0.0001$ ), larger eyes ( $p < 0.0001$ ), more supralabials ( $p < 0.0001$ ), and different supralabials that enter the orbit of the eye (usually Nos. 4, 5, 6 in *D. lineolatus* (91%,  $n = 11$ ) vs. 4 and 5 in *D. punctulatus* (94%,  $n = 32$ );  $p < 0.0001$ ).

*Dendrelaphis striolatus* differs from *D. punctulatus* by having more supralabials ( $p < 0.0001$ ), more temporals ( $p < 0.0001$ ), larger eyes ( $p < 0.0001$ ), fewer ventrals



Table 3. Mean snout–vent lengths (cm) by species and sex.

Species	Males	Females
<i>D. lorentzii</i>	49.5 (n=3)	49.5 (n=2)
<i>D. calligaster</i>	63.0 (n=20)	73.5 (n=21)
<i>D. papuensis</i>	71.5 (n=1)	73.5 (n=3)
<i>D. gastrostictus</i>	60.5 (n=4)	55.0 (n=5)
<i>D. keiensis</i>	–	75.5 (n=3)
<i>D. striolatus</i>	60.5 (n=18)	70.0 (n=22)
<i>D. punctulatus</i>	81.0 (n=5)	80.0 (n=5)
<i>D. macrops</i>	85.5 (n=4)	100.0 (n=9)
<i>D. lineolatus</i>	89.5 (n=5)	96.0 (n=4)

( $p < 0.0001$ ), a longer tail ( $p < 0.0001$ ), and by usually having black bars on the neck (Fig. 12). Finally, *D. striolatus* differs from all other species of the studied group by exhibiting a sexual dimorphism in the reduction of the number of dorsal scale rows towards the tail. Most females have 11 dorsal scale rows anterior to the tail whereas most males have 9 dorsal scale rows anterior to the tail ( $p = 0.0001$ ).

The most prominent differences between *D. macrops* and *D. lineolatus* relate to their colouration. Whereas *D. macrops* is uniformly coloured (Fig. 9), *D. lineolatus* exhibits a highly conspicuous colouration (Fig. 7). Morphologically, *D. macrops* differs from *D. lineolatus* predominantly by having more ventral scales ( $p < 0.0001$ ) and fewer supralabials entering the orbit of the eye (usually 2 in *D. macrops* (93%,  $n = 14$ ) vs. usually 3 in *D. lineolatus* (91%,  $n = 11$ );  $p < 0.0001$ ). There are smaller differences in the length of the frontal scale ( $p = 0.03$ ), the width of the snout ( $p = 0.05$ ), and the tail length ( $p = 0.02$ ).

MEISE & HENNIG (1932) regarded *D. striolatus* as a subspecies of *D. lineolatus*. *D. striolatus* differs from *D. lineolatus* by having fewer subcaudals ( $p < 0.0001$ ), fewer ventrals ( $p = 0.001$ ), fewer supralabials entering the orbit of the eye ( $p < 0.0001$ ), and broader vertebral scales ( $p = 0.0001$ ). In addition, it lacks the black dorsum of the head, black tail, and black spots on the venter that are typical for *D. lineolatus*. It differs from *D. macrops* by having fewer ventrals and subcaudals (both  $p < 0.0001$ ), broader vertebral scales ( $p = 0.001$ ), and black bars on the neck. Finally, *D. striolatus* differs from both species by exhibiting a sexual dimorphism in the reduction of the number of dorsal scale rows towards the tail. Most females have 11 dorsal scale rows anterior to the tail whereas most males have 9 dorsal scale rows anterior to the tail ( $p = 0.0001$ ).

As discussed in the methodology section, interspecific size differences were eliminated in CVA and PCA and are automatically eliminated in (M)ANCOVA. However, size differences are in fact substantial and should therefore be considered. Table 3 gives the median SVL per species and by sex. The median (middle) value was chosen because it is not influenced by outliers such as juveniles and exceptionally large specimens and therefore gives a more solid indication of length than, for instance, mean or maximum

values. If one ignores the complicating fact that a smaller sample size will result in a less accurate median value, a trichotomy is in evidence: 1) *D. lorentzii* is a very small species, 2) *D. calligaster*, *D. papuensis*, *D. gastrostictus*, *D. keiensis*, and *D. striolatus* appear to be of intermediate size, and 3) *D. punctulatus*, *D. macrops* and *D. lineolatus* are fairly large species. In order to obtain a good impression of size differences, the differences in length can be translated into differences in body volume. For instance, the third group (*D. punctulatus*, *D. macrops*, *D. lineolatus*) is roughly 1.32 times as long as the second group (*D. calligaster*, *D. papuensis*, *D. gastrostictus*, *D. keiensis*, *D. striolatus*), which translates into a  $(1.32)^3 = 2.3$  times larger body volume, assuming identical body proportions. The second group in turn is approximately 2.5 times as large as the first (*D. lorentzii*).

#### Issues pertaining to nomenclature and type specimens

Because the majority of the type material could be located and examined, either directly or through photographs provided by the curators of the respective collections, most of the 28 available names could unequivocally be linked to the nine species recognised in this study. Some noteworthy issues concerning nomenclature and type specimens are discussed below.

Regrettably, the types of *Dendrophis punctulatus* var. *atrostriata* MEYER, 1874a, *D. p.* var. *fasciata* MEYER, 1874a, and *D. calligaster distinguendus* MEISE & HENNIG, 1932 were destroyed during World War II (OBST 1977). The syntypes of *Dendrophis olivacea* MACLEAY, 1878 are presumed lost, too (COGGER 1983).

MEYER provided very little information on the types of *Dendrophis punctulatus* var. *atrostriata* and *D. p.* var. *fasciata*. To make things worse, his localities were often erroneous (e.g., LEVITON 1968). However, supposing his localities were correct in this instance, *D. p.* var. *fasciata* is undoubtedly a synonym of *D. lineolatus*, as it originated from New Guinea and MEYER clearly described a dorsal pattern of oblique black bars. Two species, *D. striolatus* and *D. lineolatus*, exhibit oblique black bars, but only *D. lineolatus* inhabits New Guinea and surrounding islands. For *D. p.* var. *atrostriata*, MEYER did not mention oblique black bars, but did state that the black dorsum of the head contrasted sharply with the lighter underside. This character state also agrees with *D. lineolatus*. Given that the oblique black bars are prominent in some specimens of *D. lineolatus* but faint in others, *D. p.* var. *atrostriata* probably corresponds with *D. lineolatus* as well. This would agree with MEISE & HENNIG (1932) who examined the types when these were still in existence and synonymised this taxon with *D. lineolatus*. As such, following MEISE & HENNIG's judgement seems the most appropriate choice in this case. MEYER gave Jobi (present-day Yapen) and Mysore (present-day Superiori) as cotype localities of *D. p.* var. *atrostriata*. To settle any nomenclatorial confusion, we here designate a specimen of *D. lineolatus* that was collected on Jobi, RMNH.

RENA.42938, as the neotype of *D. p.* var. *atrostriata* MEYER, 1874a. The type locality of *D. p.* var. *fasciata*, “Passim”, is somewhat problematic as its exact location is uncertain (ZUG 2004). However, in his writings (e.g., MEYER 1874b), MEYER clearly indicated that it was located on the west coast of Geelvink Bay (= Cenderawasih Bay). For the same reasons, we here designate RMNH.RENA.47093, from “Aitinjo, Vogelkop”, as the neotype of *D. p.* var. *fasciata* MEYER, 1874a. Descriptions of the neotypes are provided in the taxonomic section.

The status of *Dendrophis calligaster distinguendus* MEISE & HENNIG, 1932, from Neumecklenburg (today: New Ireland), is unclear as the ventral counts and number of supralabials given by these authors do not agree with those of *D. calligaster* as found in this study. In the number of ventral scales and the supralabials entering the orbit of the eye, it seems to be more similar to *D. keiensis*. However, the latter inhabits a geographically distant region (S.E. Moluccas), which makes a close relationship unlikely. Therefore, we provisionally follow COGGER et al. (1983) in regarding *D. c. distinguendus* as a synonym of *D. calligaster*.

Finally, MACLEAY's (1878) description of *Dendrophis olivacea* is sufficiently detailed to unambiguously synonymise this name with *D. punctulatus*.

Three available names, *Dendrophis breviceps* MACLEAY, 1877, *D. macrops* GÜNTHER, 1877, and *D. papuae* OGILBY, 1891, were found to refer to a single species. In order to apply the rule of priority, the year of publication does not suffice in this case, as the two oldest names were published in the same year. The description of *D. breviceps* was published in the Proceedings of the Linnean Society of New South Wales, 1<sup>st</sup> Ser., Vol. ii, Part 1. The exact date of publication of this work is unknown. However, FLETCHER (1895) established July 1877 as the date of registration by librarians of the Public Library (Sydney) and the Royal Society of New South Wales. The description of *D. macrops* was published in the Proceedings of the Scientific Meetings of the Zoological Society of London for the year 1877, Part I. DUNCAN (1937) established June 1877 as the publication date. Thus, the name *D. macrops* precedes *D. breviceps*, and was adopted for this taxon.

There has been some confusion regarding the authorship of *Dendrophis lineolatus* because it was described by DUMÉRIL (1854) as well as JACQUINOT & GUICHENOT (1853). MEISE & HENNIG (1932) and MERTENS (1934) attributed the name to JACQUINOT & GUICHENOT (1853), whereas COGGER et al. (1983) and McDOWELL (1984) attributed it to DUMÉRIL (1854). In their description of *D. lineolata*, JACQUINOT & GUICHENOT (1853) stated that this species name had been “established” by DUMÉRIL. However, the establishment of this name by DUMÉRIL was based on a manuscript that was not published before the “Erpétologie Générale” by DUMÉRIL, BIBRON & DUMÉRIL in 1854. As such, according to the code, the manuscript does not constitute a published work until 1854. Consequently, the description by JACQUINOT & GUICHENOT (1853) takes priority.

In his description of *Dendrophis bilorealis*, MACLEAY (1884) stated that he had two specimens at his disposal

and that the data in the description were taken from one of these. The two specimens mentioned by MACLEAY should be considered syntypes. COGGER (1979) mentioned even a series of three type specimens: AM B5942, AM R31906 (MM R561), AM R31907 (MM R562). In a later work however, COGGER et al. (1983), stated that AM B5942 were the holotype. In his description of *D. bilorealis*, MACLEAY outlined that there were “two loreals placed exactly above one another”. For this study, AM R31906 and AM R31907 were examined, and AM R31907 was found to possess two loreal shields on the left side of the head, one above the other. The same appears to the case in AM R31906, although this was difficult to ascertain as the specimen has a misshapen head. The presence of a twinned loreal shield is an extremely rare condition, never seen by us in the hundreds of specimens examined in the context of a comprehensive revision of the taxonomy of the genus *Dendrelaphis*. Therefore, we assume that AM R31906 (MM R561) and AM R31907 (MM R562) are the syntypes of *D. bilorealis* MACLEAY, 1884. We regard the twinned loreal shield as an anomaly and do not hesitate to place *D. bilorealis* in the synonymy of *D. punctulatus* in line with COGGER (1979) and COGGER et al. (1983).

In his description of *Dendrelaphis schlenckeri*, OGILBY (1898) mentioned that “5 specimens are in the collection”. He did not designate a holotype. However, the editor of the publication (T. STEEL) wrote in a note following OGILBY's description that he had deposited “the type” (R2380) in the Australian Museum. However, in accordance with the ICZN article 73.1.3, only the original author can designate a holotype. Consequently, the five specimens mentioned by OGILBY should be regarded as syntypes of *D. schlenckeri*. Mister T. STEEL furthermore indicated that he intended to send a specimen to the BMNH. According to a note in the catalogue of the Australian Museum, he actually took several specimens to the BMNH (KINGHORN 1921). Indeed, for this study, three specimens (BMNH 1946.1.6.7–9) were examined, which were furnished with the notes “*Dendrelaphis schlenckeri* Ogilby Fife Bay British New Guinea. T. Steel, 1898” (on the jar) and “these specimens are the co-types detailed in the original description” (inside the jar). As for the remaining type specimens, SHEA & SADLER (1999) list three specimens present in the collection of the Australian Museum (R2380, R6514–15), two of which were examined for this study. Therefore, there are six candidates for the five syntypes. R2380 is certainly one of the syntypes. One of the candidate specimens (BM 1946.1.6.7) is incomplete (head missing). It is not unlikely that OGILBY disregarded this specimen in his description and therefore mentioned only five specimens.

## Taxonomy

Species accounts are provided in this section. The types of the recognized species are re-described, because their original descriptions offer little detail. In addition, descriptions of the neotypes of *Dendrophis punctulatus* var. *atrostriata* MEYER, 1874a, and *D. p.* var. *fasciata* MEYER, 1874a are given.

As with all identification keys, the key provided below is based on only a few characters as to make identification straightforward. As a consequence, however, specimens exhibiting unusual characters may not key out correctly. In cases of doubt, the taxonomy section should be consulted as it offers more detailed information on morphology and colouration.

1. Head speckled; eye very small (diameter significantly smaller than distance eye–nostril) (Figs. 8A–D) ..... *D. lorentzii*
  - Head not speckled, eye moderately large or large (diameter equal to, or larger than, distance eye–nostril)..... 2
2. Oblique black bars on the neck (more or less pronounced, Figs. 7C, E; 12A, C) ..... 3
  - No black bars on neck ..... 4
3. Head dorsally blackish, ventrally whitish; tail black; large round spots on edges of ventrals in anterior part of the body (Figs. 7A–F) ..... *D. lineolatus*
  - Colour of head and tail correspond with ground-colour, venter uniform ..... *D. striolatus*
4. Postocular stripe present (Figs. 4A–D, 5A–B, 10A–B) 5
  - Postocular stripe absent (Figs. 6C, 9B, 11A–B) ..... 7
5. Venter with small, dark speckles interspersed with large, irregularly shaped, dark spots (Fig. 5C); eye very large (diameter significantly larger than eye–nostril distance, Fig. 5B) ..... *D. gastrostictus*
  - Venter immaculate or with dark speckles, not interspersed with large, irregularly shaped, dark spots; eye moderately large (diameter equal to eye–nostril distance) ..... 6
6. 120–126 subcaudals ..... *D. papuensis*
  - 134–156 subcaudals ..... *D. calligaster*
7. More than 203 ventral scales, more than 10 temporal scales ..... *D. keiensis*
  - Fewer than 203 ventral scales or fewer than 10 temporal scales ..... 8
8. Fewer than 140 subcaudals ..... *D. punctulatus*
  - More than 140 subcaudals ..... *D. macrops*

***Dendrelaphis calligaster* (GÜNTHER, 1867)**

*Dendrophis calligaster* GÜNTHER, 1867: 53. Fig. 4.

*Dendrophis salomonis* GÜNTHER, 1872. Type data: syntypes, BMNH 1946.1.6.11 and BMNH 1946.1.5.97, from Solomon Islands.

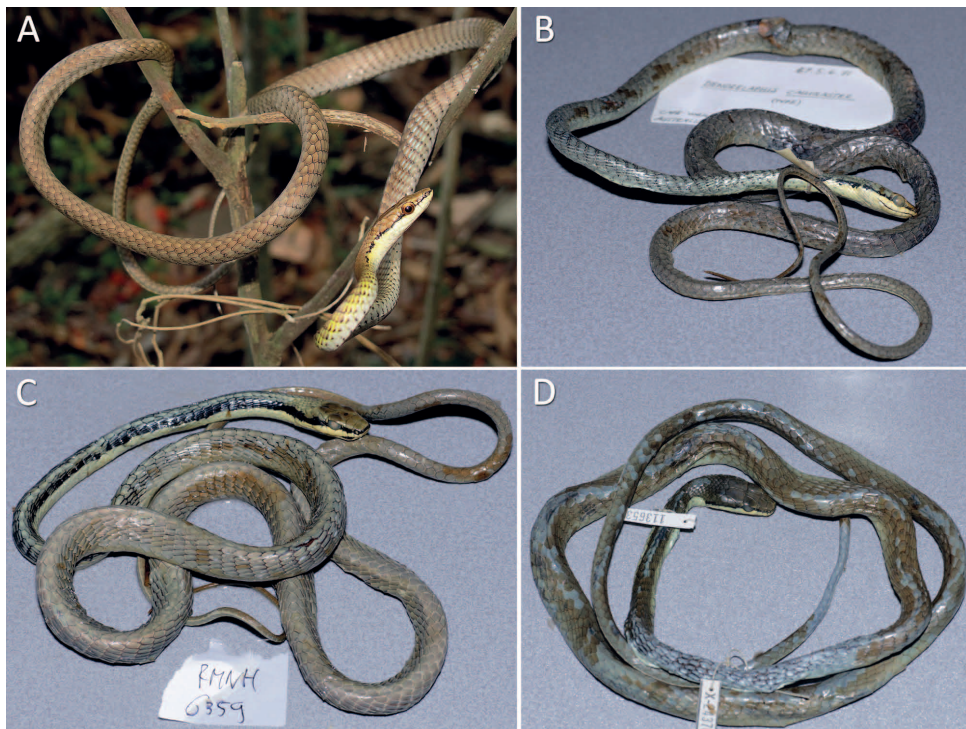


Figure 4. *D. calligaster*. A) Portland road, Queensland, Australia (photograph by BRAD MARYAN); B) Cape York, Australia (BMNH 1867.5.6.71, holotype); C) West Papua (RMNH.RENA.6359 (1)); D) Solomons: Bougainville (CAS 113653).



*Dendrophis aruensis* DORIA, 1874. Type data: 3 syntypes, MCG C. E. 30594, from Wokan, Aru Islands, Indonesia.

*Dendrophis katowensis* MACLEAY, 1877. Type data: syntypes, AM R31916–17, from Mawatta, Binaturi River (as Katow), Papua New Guinea.

*Dendrophis darnleyensis* MACLEAY, 1877. Type data: syntypes, AM R31914–15, from Darnley Island, Torres Strait, Queensland, Australia.

*Dendrophis meeki* BOULENGER, 1895a. Type data: syntypes BMNH 1946.1.23.30–33 from Fergusson Island, Papua New Guinea.

*Dendrelaphis schlenkeri* OGILBY, 1898. Type data: syntypes, AM R2380, R6514–15, from Fife Bay, Papua New Guinea, and BMNH 1946.1.6.8–9, from Dinawa, British New Guinea.

*Dendrophis calligaster distinguendus* MEISE & HENNIG, 1932. Type data: holotype, from Muliamia, east coast of Neumecklenburg, Papua New Guinea; destroyed (OBST 1977).

Type. BMNH 1867.5.6.71 from Cape York, Australia (Holotype).

Description of holotype. Unsexed specimen, body slender; pupil round; vertebral scales strongly enlarged, hexagonal in shape; snout–vent length 56.5 cm; tail length 29.5 cm; ventral scales 176; subcaudal scales 139; anal scute divided; dorsal scale rows 13–13–11; loreal fused with prefrontal on both sides; supralabials 8; supralabials entering the orbit of the eye 4, 5; infralabials 10 (L) / 9 (R); infralabials touching first chinshield 1–5; infralabials touching second chinshield 5, 6; postoculars 2; temporal shields 2:2:2; scales bordering the posterior edges of the parietal scales 4; eye-diameter 4.0 mm (L) / 4.2 mm (R); eye–nostril distance 3.4 mm; snout width 4.1 mm; width of the vertebral scale at the level of middle ventral 3 mm; length of frontal scale 4.7 mm; ground-colour olive-brown. A thin black temporal stripe starts on the rostral shield, passes through the nostril, and covers the lower margins of the postnasal, loreal, preocular, and the upper edges of supralabials 2, 3 and 4. Behind the eye, it covers the lower half of the lower postocular and the lower margin of the temporal region. It extends onto the neck, although not as a continuous stripe. Supralabials and throat yellowish; venter yellowish, becoming darker posteriorly. Venter with numerous small black spots.

Species description. Venter immaculate or with small speckles (not interspersed with large, irregularly shaped spots); a black temporal stripe is present in most specimens (see below, geographic variation); 8 supralabials (rarely 9); supralabials 4, 5 enter the orbit of the eye (rarely 5, 6 or 4, 5, 6); 6–17 temporal scales; 167–193 ventrals; 134–156 subcaudals; relative tail length (tail length divided by total length) 0.33–0.37; eye moderately large (diameter roughly equal to eye–nostril distance); maximum total length 137.5 cm.

Sexual dimorphism. On average, females have a slightly broader snout than males ( $p = 0.01$ ; based on 22 males, 22 females).

Geographic variation. There is significant geographic variation in *D. calligaster* with regard to its colouration. Populations from West Papua, Misool Island, and Yapen Island exhibit a very prominent postocular stripe that ex-

tends far onto the body. In populations from Papua New Guinea, Waigeo Island, the Aru Islands, and Daru Island, the postocular stripe is still very clear, but extends much less far onto the body. In populations from Bougainville, Fergusson, and Australia, it is faint, and in specimens from New Britain, it is nearly absent, although scales in the temporal region and on the neck have black edges. There is also variation in the colouration of the venter. In Australian specimens and specimens from Bougainville and Guadalcanal and Daru, the venter exhibits small dark spots. These spots are absent or nearly absent in other populations. Morphological variation in *D. calligaster* (Fig. 2B) deserves further exploration; see also Discussion.

Distribution. *Dendrelaphis calligaster* is a widespread species. Specimens included in this study originated from New Guinea (West Papua and Papua New Guinea), Daru Island, Misool Island, Yapen Island, Aru Islands, Fergusson Island, New Britain, Bougainville (Solomons), Guadalcanal (Solomons), Darnley Island, and Australia. In Australia, it inhabits the northern and eastern Cape York Peninsula (CAMERON & COGGER 1992). Furthermore, it is known from Waigeo Island (HAMIDY & MULYADI 2007) and Murray Island, Torres Strait (COGGER 2000). It probably inhabits many more islands.

#### *Dendrelaphis gastrostictus* (BOULENGER, 1894)

*Dendrophis gastrostictus* BOULENGER, 1894: 86, pl. 3: fig. 4. Fig. 5.

*Dendrophis nouhuysii* VAN LIDTH DE JEUDE, 1911. Type data: syntypes, RMNH.RENA.4709 A–E, from Noord Rivier, New Guinea.

Type. BMNH 1946.1.23.20 from N. W. New Guinea (Holotype).

Description of holotype. Male; body slender, eye large, pupil round, vertebral scales strongly enlarged, hexagonal in shape; SVL 68.0 cm; tail length 42.0 cm (tail tip missing); ventral scales 162; subcaudal scales 147+ (tail tip missing); anal scute divided; dorsal scale rows 14–13–11; supralabials 8; supralabials entering the orbit of the eye 4, 5; infralabials 8 (L) / 10 (R); infralabials touching first chinshield 1–4 (L) / 1–5 (R); infralabials touching second chinshield 4, 5, 6 (L) / 5, 6 (R); postoculars 3; temporal shields 2:2; scales bordering the posterior edges of the parietal scales 5; eye diameter 5.3 mm (L) / 5.1 mm (R); eye–nostril distance 4.0 mm (L) / 4.2 mm (R); snout width 4.6 mm; width of the vertebral scale at the level of the middle ventral 3.1 mm; length of frontal scale 5.8 mm; ground-colour light brown; head and neck dorsally dark brown; a black temporal stripe starts at the nostril, passes through the eye, covers the lower postocular and lower third of the temporal region, and extends onto the neck; supralabials and throat light yellow; venter light yellow, becoming darker posteriorly and covered with numerous small black spots interspersed with large, irregularly shaped spots; tail dark.

Species description. Venter with small speckles interspersed with large, irregularly shaped spots; a black tem-



poral stripe that extends onto the neck; no black bars on the neck; 8 or 9 supralabials; supralabials 4, 5 or 4, 5, 6 enter the orbit of the eye; 8–14 temporal scales; 162–174 ventrals; 139–165 subcaudals; relative tail length 0.37–0.40; eye very large (diameter substantially larger than eye–nostril distance); maximum total length 115 cm.

Sexual dimorphism. No sexual dimorphism was noted among 5 females and 4 males.

Geographic variation. No geographic variation was noted.

Distribution. *Dendrelaphis gastrostictus* inhabits mainland New Guinea (West Papua, Papua, and Papua New Guinea).

***Dendrelaphis keiensis* (MERTENS, 1926)**

*Dendrophis calligastra keiensis* MERTENS, 1926: 277. Fig. 6.

Type. SMF 18662 from Kei-Dulah, Indonesia (Holotype).

Description of holotype. Female; body slender; pupil round; vertebral scales strongly enlarged, hexagonal in shape; SVL 95.2 cm; tail length 40.0 cm (tail tip possibly missing); ventral scales 213; subcaudal scales 142 (tail tip possibly missing); anal scute divided; dorsal scale rows 13–13–11; supralabials 8 (L) / 9 (R); supralabials entering the orbit of the eye 4, 5 (L) / 5, 6 (R); infralabials 10; infralabials touching first chinshield 1–5; infralabials touching second chinshield 5, 6; postoculars 2; temporal shields 2:2:2;

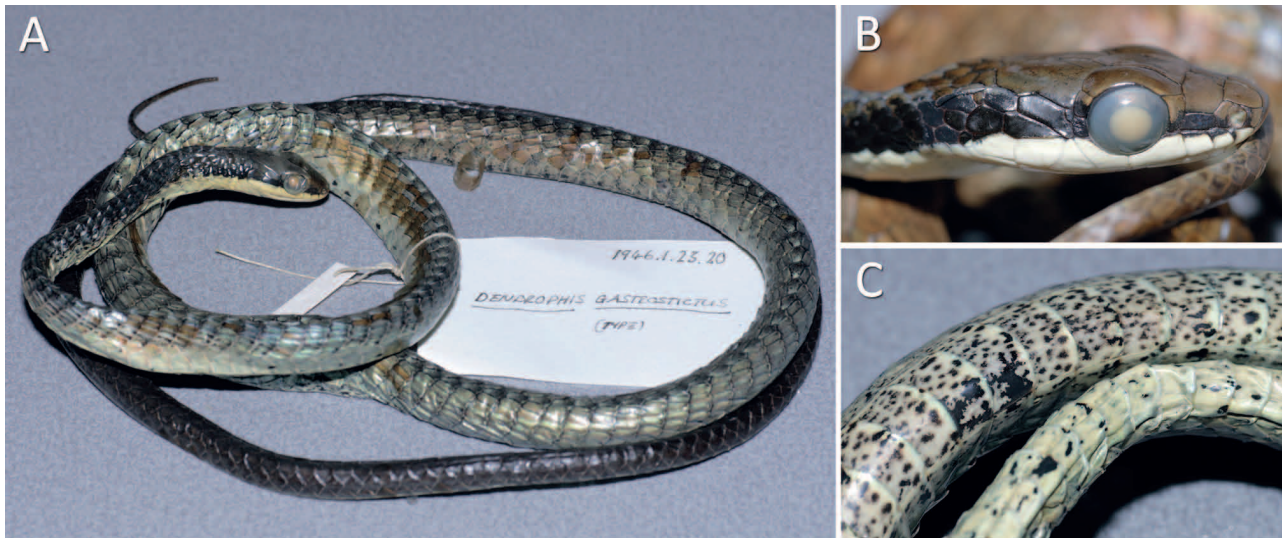


Figure 5. *D. gastrostictus*. A) New Guinea (BMNH 1946.1.23.20, holotype); B) western New Guinea (RMNH.RENA.42731); C) New Guinea (BMNH 1946.1.23.20, holotype, view of the venter).

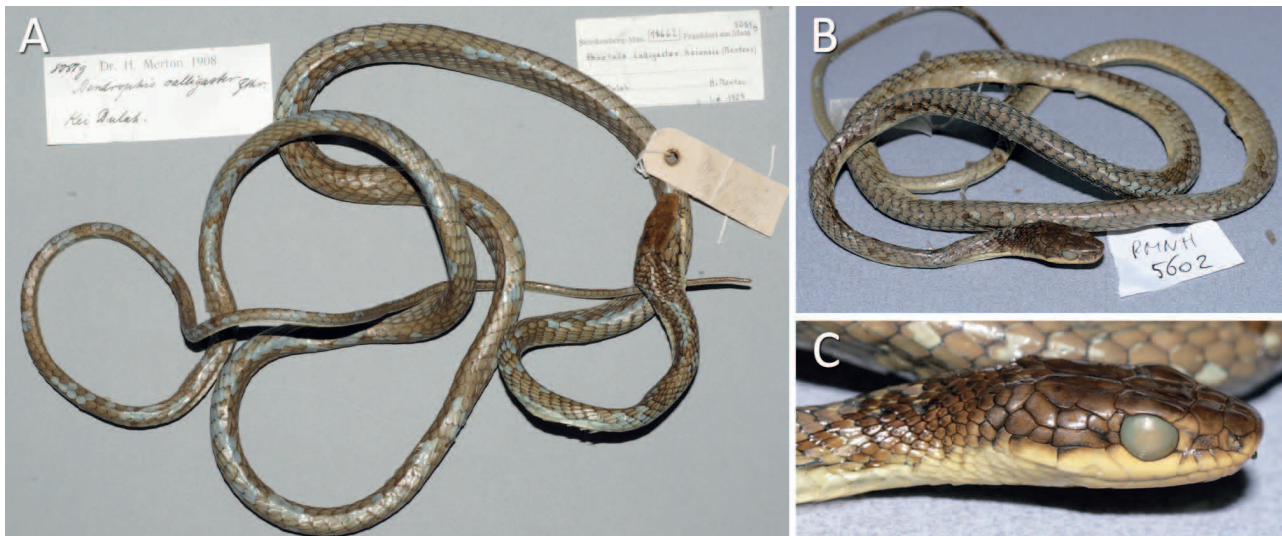


Figure 6. *D. keiensis*. A) Kei-Dulah (SMF 18662, holotype); B, C) Babar Island (RMNH.RENA.5602).

scales bordering the posterior edges of the parietal scales 6; eye diameter 5.4 mm; eye–nostril distance 5.0 mm (L) / 5.3 mm (R); snout width 6.4 mm; width of the vertebral scale at the level of the middle ventral 3.9 mm; length of the frontal scale 7.1 mm; ground-colour olive-brown; temporal stripe absent although the edges of supralabials 2, 3, 4, 8, 9, lower edges of lower temporals, and lower postocular shield are dark; supralabials and throat light yellow; venter light yellow, becoming darker posteriorly; venter immaculate; a thin whitish line runs along the edges of the ventral scales.

Species description. Venter immaculate; no temporal stripe; 8–10 supralabials; supralabials 5, 6 usually enter the orbit of the eye (4, 5 on one side in one of three specimens); 12–13 temporals; 211–213 ventrals; 142 subcaudals; relative tail length 0.29–0.30; eye moderately large (diameter roughly equal to eye–nostril distance); maximum total length 135.5 cm.

Sexual dimorphism. Because the three examined specimens were all females, sexual dimorphism could not be studied.

Geographic variation. Due to the small sample size ( $n = 3$ ), geographic variation could not be studied.

Distribution. *Dendrelaphis keiensis* inhabits the south-east Moluccan islands of Babar and Kei-Dulah (Kai-Dulah). BOULENGER (1894) mentioned a specimen from Timor-Laut (Tanimbar) with 211 ventral scales. As Timor-Laut is situated between Babar Island and Kei-Dulah and the number of ventral scales agrees with the geographical range of *D. keiensis* (211–213), this species undoubtedly occurs on Timor-Laut as well. It presumably inhabits various other southeast Moluccan islands. Indeed, ISKANDAR & COLIJN (2001) mention several other Moluccan islands for this species. However, these authors did not provide verifiable data in the form of references or voucher numbers.

#### *Dendrelaphis lineolatus* (JAQUINOT & GUICHENOT, 1853)

*Dendrophis lineolata* JACQUINOT, H. & GUICHENOT 1853: 20. Fig. 7.

*Dendrophis elegans* OGILBY, 1891. Type data: holotype: AM R1089, Fly River, Papua New Guinea

*Dendrophis punctulatus* var. *atrostriata* MEYER, 1874a. Type data: neotype RMNH.RENA.42938, Jobi

*Dendrophis punctulatus* var. *fasciata* MEYER, 1874a. Type data: neotype RMNH.RENA.47093, from Aitinjo, Vogelkop

Type. MNHN 5081 from Nouvelle Guinée (holotype).

Description of holotype. Specimen from New Guinea; unsexed; body slender, eye very large, pupil round, vertebral scales strongly enlarged, with convex posterior margins; ventral scales 180; anal scute divided; 13 dorsal scale rows at midbody; supralabials 10 (L) / 9 (R); supralabials entering the orbit of the eye 5, 6, 7 (L) / 4, 5, 6 (R); infralabials 9 (L); infralabials touching first chinshield 1–5; infralabials touching second chinshield 5, 6; postoculars 2; temporal shields 2:2:2 (L) / 2:3:2 (R); ground-colour ol-

ive; head dorsally black including upper edges of the supralabials; lower parts of the supralabials as well as throat yellow, contrasting sharply with dark upper side of head; posterior part of body and tail black; faint presence of narrow, oblique, black bars on anterior part of the body; venter yellow anteriorly, nearly black posteriorly; with large semicircular black spots on posterolateral or posteromedial edges of many of the ventrals in the anterior part of the body. Vertebral scales in anterior part of the body with a black posteromedial spot; many of the dorsal scales in the anterior part of the body with a black upper margin or black posterior tip.

Description of the neotype of *Dendrophis punctulatus* var. *atrostriata* MEYER, 1874 (RMNH.RENA.42938). Male from Jobi, collected by ROSENBERG; body slender, eye large, pupil round, vertebral scales strongly enlarged, with convex posterior margins; SVL 89.5 cm; tail length 43.0 cm; ventral scales 187; subcaudal scales 144; anal shield divided; dorsal scale rows 13–13–11; supralabials 9; supralabials entering the orbit of the eye 4, 5, 6; infralabials 10; infralabials touching first chinshield 1–5 (L) / 1–6 (R); infralabials touching second chinshield 5, 6 (L) / 6, 7 (R); postoculars 2; temporal shields 2:2 (L) / 1:1:2 (R); scales bordering the posterior edges of the parietal scales 5; eye diameter 5.7 mm (L) / 5.8 mm (R); eye–nostril distance 4.8 mm (L) / 5.1 mm (R); snout width 6.8 mm; width of the vertebral scale at the level of the middle ventral 3.7 mm; length of frontal scale 6.9 mm; ground-colour brown; head dorsally black, including upper edges of the supralabials; lower parts of supralabials as well as throat dirty white, contrasting sharply with dark upper side of head; neck, posterior part of the body and tail black; narrow, oblique, black bars on anterior part of the body; venter dirty white anteriorly, nearly black posteriorly; large black spots on posterolateral or posteromedial edges of many of the ventrals in the anterior part of the body.

Description of the neotype of *Dendrophis punctulatus* var. *fasciata* MEYER, 1874 (RMNH.RENA.47093). Female from Aitinjo, Vogelkop; body slender, eye large, pupil round, vertebral scales strongly enlarged, with convex posterior margins; SVL 92.0 cm; tail length 49.5 cm; ventral scales 179; subcaudal scales 147; anal scute divided; dorsal scale rows 13–13–11; supralabials 9; supralabials entering the orbit of the eye 4, 5, 6; infralabials 10; infralabials touching first chinshield 1–6; infralabials touching second chinshield 6, 7; postoculars 2; temporal shields 2:2 (L) / 1:2:1 (R); scales bordering the posterior edges of the parietal scales 6; eye diameter 6.4 mm; eye–nostril distance 5.1 mm (L) / 5.5 mm (R); snout width 7.2 mm; width of the vertebral scale at the level of the middle ventral 4.8 mm; length of frontal scale 7.4 mm; ground-colour brown; head dorsally black, including upper edges of supralabials; lower parts of supralabials as well as throat dirty white, contrasting sharply with dark upper side of head; neck, posterior part of the body and tail black; faint indication of narrow oblique black bars on anterior part of the body; venter dirty white anteriorly, nearly black posteriorly; large black spots on posterolateral or postero-



medial edges of many of the ventrals in the anterior part of the body.

Species description. Head dorsally black; tail black; more or less pronounced oblique black bars on neck present; round, black dots on outer edges of ventrals in anterior part of the body; 9 supralabials; supralabials 4, 5, 6 enter the orbit of the eye (rarely 5, 6 or 5, 6, 7); 8–13 temporal scales; 179–193 ventrals; 144–151 subcaudals; relative tail length 0.32–0.35; eye diameter larger than eye–nostril distance; maximum total length 170 cm.

Sexual dimorphism. No sexual dimorphism was noted among 4 females and 5 males.

Geographic variation. No geographic variation was noted.

Distribution. *Dendrelaphis lineolatus* inhabits New Guinea (West Papua, Papua, and Papua New Guinea), Misool Island, Salawati Island, and Yapen Island.

***Dendrelaphis lorentzii*** (VAN LIDTH DE JEUDE, 1911)

*Dendrophis lorentzii* VAN LIDTH DE JEUDE, 1911: 274. Fig. 8.

Type. RMNH.RENA.4710 from Sabang, New Guinea (holotype).

Description of the holotype. Male; body slender; pupil round; vertebral scales strongly enlarged, hexagonal in shape; SVL 47.0 cm; tail length 28.0 cm; ventral scales 161; subcaudal scales 131; anal scute divided; dorsal scale rows 13–13–11; supralabials 8; supralabials entering the orbit of the eye 4, 5; infralabials 10; infralabials touching first chinshield 1–5; infralabials touching second chinshield 5, 6; postoculars 2 (L) / 3 (R); temporal shields 2:2:2; scales bordering the posterior edges of the parietal scales 6; eye diameter 3.3 mm (L) / 3.2 mm (R); eye–nostril distance 3.8 mm (L) / 3.5 mm (R); snout width 3.1 mm; width of the vertebral scale at the level of the middle ventral 2.6 mm;



Figure 7. *D. lineolatus*. A) Western New Guinea (RMNH.RENA.47097); B) Wewak, East Sepik Province, New Guinea (photograph by FRED KRAUS); C) juvenile, Wewak, East Sepik Province, New Guinea (photograph by FRED KRAUS); D) western New Guinea (RMNH.RENA.47093, ventral view); E) western New Guinea (RMNH.RENA.47097, dorsal view of the neck); F) Yapen Island (RMNH.RENA.42938).



length of frontal scale 4.4 mm; ground-colour light brown; dorsum of head with conspicuous black spots on the frontal, supraoculars, and parietals; supraoculars, frontal, and prefrontals with narrow black edges anteriorly; a rudimentary temporal stripe in the form of black edges on the supralabials, loreal, lower postocular, and lower temporals. A short black stripe behind the jaw and another behind the suture of the parietals; supralabials and throat light yellow; venter immaculate, light yellow, becoming darker posteriorly.

**Species description.** Head speckled; venter immaculate; 8 supralabials (rarely 9); supralabials 4, 5 enter the orbit of the eye (rarely 4, 5, 6); 10–12 temporal scales; 161–179 ventrals (156–181 according to McDOWELL (1984) who examined more material); 119–132 subcaudals (McDOWELL (1984) counted 134 in a specimen); relative tail length 0.32–0.37; eye very small (diameter significantly smaller than distance eye–nostril); maximum total length 79 cm.

**Sexual dimorphism.** No sexual dimorphism was noted among two males and two females.

**Geographic variation.** As discussed in the results section, specimens from north of the central mountains appear to exhibit a higher ventral count than specimens from south of the central mountains.

**Distribution.** McDOWELL (1984) suspected a disjunctive distribution in New Guinea. He examined 12 specimens from the southern parts of the island and a single specimen

from the Huon Peninsula (northeastern New Guinea). In this study, specimens from Salawati Island (northwestern New Guinea) and north New Guinea were examined and a photograph of a specimen from Normanby Island (extreme eastern New Guinea) was obtained (Fig. 8B). As a consequence, it has now been recorded from various, widely separated locations. This species may in fact be widely distributed, but rather uncommon and therefore undersampled.

***Dendrelaphis macrops* (GÜNTHER, 1877)**

*Dendrophis macrops* GÜNTHER, 1877: 131. Fig. 9

*Dendrophis breviceps* MACLEAY, 1877. Type data: syntypes, AM R31911–13, from Mawatta, Binaturi River (as Katow), Papua New Guinea.

*Dendrophis papuae* OGILBY, 1891. Type data: holotype, AM R1088 from Fly River, Papua New Guinea

Type. BMNH 1946.1.23.42 from Duke of York Island, Papua New Guinea (holotype).

**Description of holotype.** Male from Duke of York Island; body slender, eye very large, pupil round, vertebral scales strongly enlarged, hexagonal in shape; SVL 78.5 cm; tail length 36.0 cm; ventral scales 193; subcaudal scales 146; anal scute divided; dorsal scale rows 13–13–9; supralabials 9 (L) / 8 (R); supralabials entering the orbit of the eye 5, 6 (L) / 4, 5 (R); infralabials 10; infralabials touching first chinshield

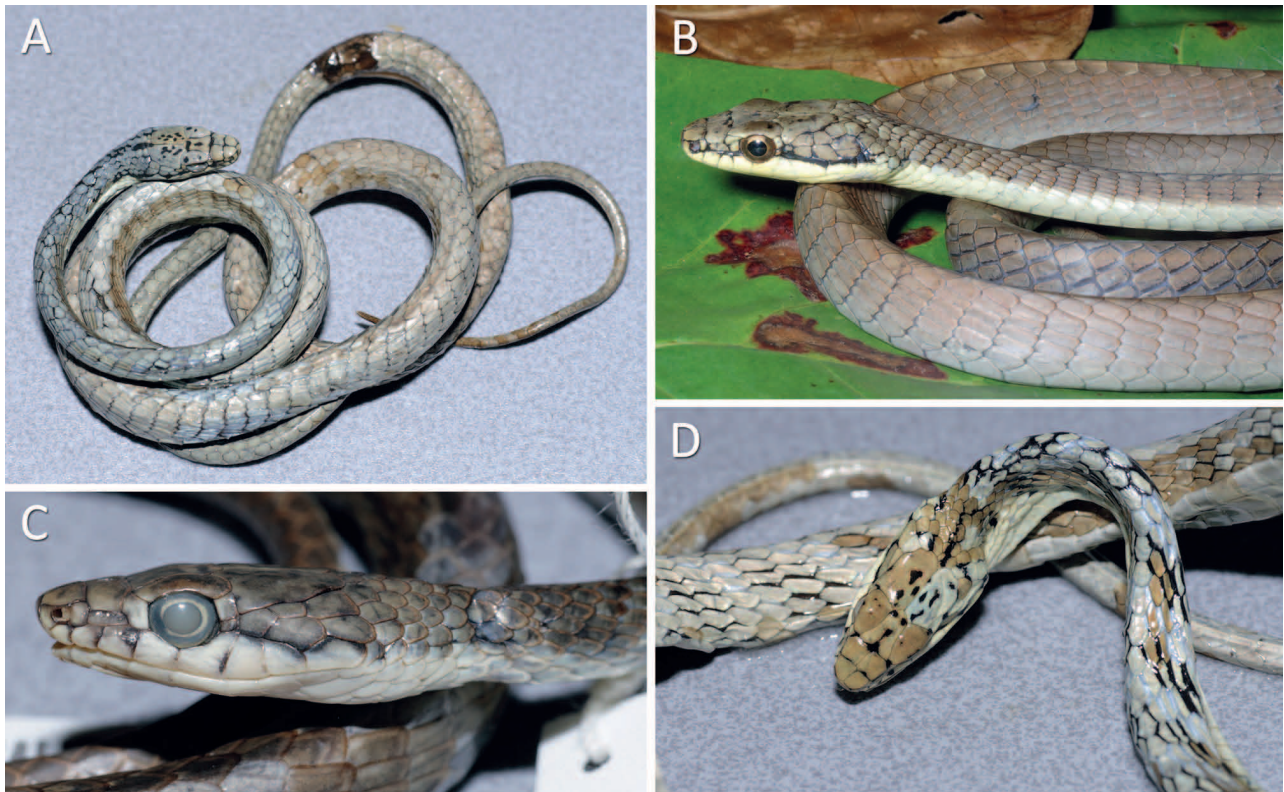


Figure 8. *D. lorentzii*. A) Papua (RMNH.RENA.4710, holotype); B) Normanby Island (photograph by FRED KRAUS); C) southern Papua New Guinea (CAS 127375); D) western New Guinea (RMNH.RENA.4986, dorsal view of head).



1–5; infralabials touching second chinshield 5, 6; postoculars 2; temporal shields 2:2:2:2 (L) / 2:2:2 (R); scales bordering the posterior edges of the parietal scales 6; eye diameter 6.2 mm (L) / 6.0 mm (R); eye–nostril distance 4.8 mm (L) / 4.6 mm (R); snout width 5.5 mm; width of the vertebral scale at the level of the middle ventral 2.8 mm; length of frontal scale 7.2 mm; dorsum of head light brown anteriorly, dark brown posteriorly; supralabials and throat yellow; venter yellow anteriorly and becoming darker posteriorly; a thin yellowish line runs along the lateral edges of the ventrals; venter otherwise immaculate; no temporal stripe; no black bars on the neck; subcaudals with black edges medially.

Species description. Uniformly coloured dorsally, no postocular stripe, venter without spots; no black bars on the neck; 8 or 9 supralabials (rarely 7); supralabials 4, 5 or 5, 6 enter the orbit of the eye (rarely 4, 5, 6); 8–14 temporal scales; 188–202 ventrals; 141–157 subcaudals; relative tail length 0.31–0.35; eye diameter larger than eye–nostril distance; maximum total length 164 cm.

Sexual dimorphism. No sexual dimorphism was noted among 9 females and 4 males.

Geographic variation. Specimens from the northern parts of New Guinea usually have 9 supralabials (82%), with supralabials 5 and 6 bordering the eye, whereas specimens from the southern side of New Guinea (Western Province including the nearby Daru Island) usually possess 8 supralabials (86%) with supralabials 4 and 5 bordering the eye ( $p = 0.001$ ).

Distribution. *Dendrelaphis macrops* inhabits New Guinea (West Papua, Papua, and Papua New Guinea), Daru Island, Numfoor Island, and Duke of York Island.

***Dendrelaphis papuensis* BOULENGER, 1895b**

*Dendrelaphis papuensis* BOULENGER, 1895b: 409. Fig. 10

Types. BMNH 1946.1.6.57–61, from Trobriand Islands (5 syntypes).

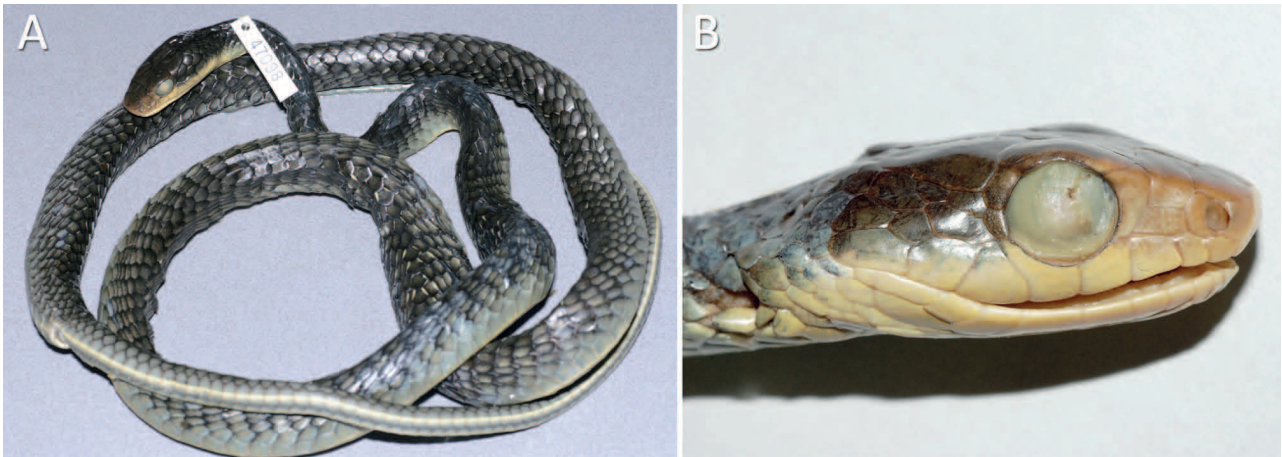


Figure 9. *D. macrops*. A) West Papua (RMNH.RENA.47098); B) Duke of York Island (BM 1946.1.23.42, holotype).

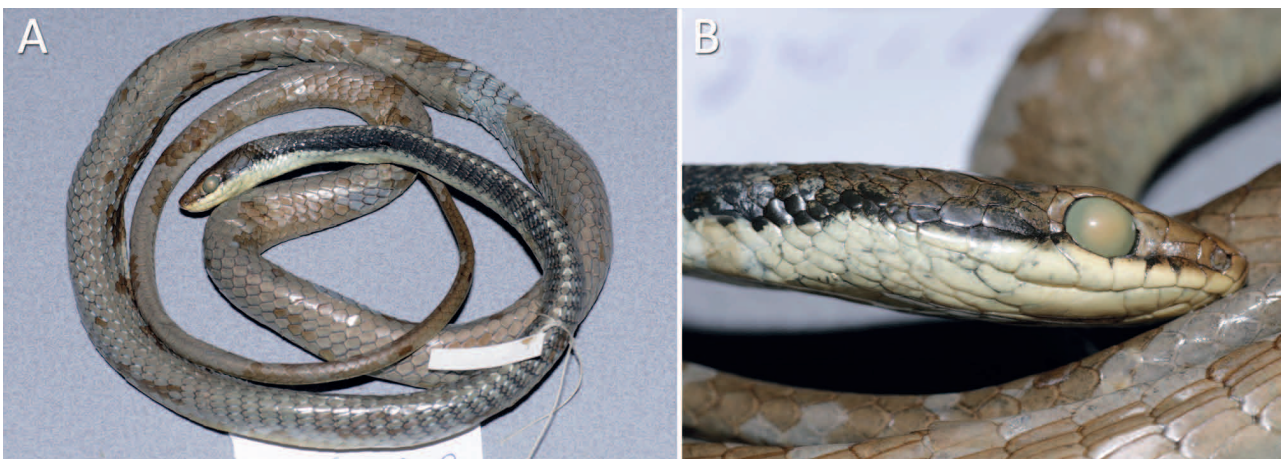


Figure 10. *D. papuensis*. A) Trobriand Islands (BMNH 1946.1.6.58, syntype); B) Trobriand Islands (BMNH 1946.1.6.61, syntype).

Description of the syntypes. See the species description below which is based on the five syntypes.

Species description. Ground-colour olive-brown; supralabials and throat white or yellowish, venter immaculate, olive-brown; a black temporal stripe covers less than half of the temporal region and extends onto the neck where it covers all dorsals except the first row and the vertebrals; no black bars on the neck; 13 dorsal scale rows at midbody, vertebral scales strongly enlarged, hexagonal in shape or nearly pentagonal due to their convex posterior margins; 8 supralabials; supralabials 4, 5 enter the orbit of the eye; usually 10 infralabials (rarely 9 or 11); 2 postoculars; 12 temporal scales; 4–7 scales border the posterior edges of the parietals; 185–190 ventrals; 120–126 subcaudals; relative tail length 0.28–0.30; eye moderately large (diameter roughly equal to eye–nostril distance); minimum recorded total length 33.5 cm, maximum 123.5 cm.

Sexual dimorphism. No sexual dimorphism was noted among 3 females and 1 male (the sex of one juvenile was not identified).

Distribution. *Dendrelaphis papuensis* inhabits the Trobriand Islands. Unfortunately, the exact origin of the syntypes of *D. papuensis* is unknown. They were probably collected on Kiriwina Island, which is by far the largest island in the group. According to McDOWELL (1984), this taxon also inhabits the eastern part of mainland New Guinea. We found no evidence in support of such a distribution and conservatively consider *D. papuensis* a Trobriand Islands endemic.

### *Dendrelaphis punctulatus* (GRAY, 1826)

*Leptophis punctulatus* GRAY, 1826: 432. Fig. 11

*Dendrophis (Ahetula) olivacea* GRAY, 1842. Type data: syntypes, BMNH 1946.1.23.37, BMNH 1946.1.23.41, BMNH 1964.1514, from Port Essington, N. T., Australia, and N coast of Australia.

*Dendrophis prasinus* GIRARD, 1858. Type data: holotype USNM 5535, from New Holland [Australia].

*Dendrophis fuscus* JAN, 1863. Type data: holotype MNHN 7234, from Australia.

*Dendrophis gracilis* MACLEAY, 1875. Type data: syntypes, AM R31908–10, from Cleveland Bay, Townsville, Queensland, Australia.

*Dendrophis olivacea* MACLEAY, 1878. [non *Dendrophis (Ahetula) olivacea* GRAY, 1842]. Type data: syntypes, presumed lost (COGGER et al. 1983), from Port Darwin, N. T., Australia.

*Dendrophis bilorealis* MACLEAY, 1884. Type data: syntypes AM R31906–07, Herbert River, Queensland, Australia.

Type. BMNH 1946.1.23.34 from Australia (holotype).

Description of the holotype. Unsexed specimen, body slender, eye large, pupil round, vertebral scales strongly enlarged, roughly triangular in shape, with convex posterior edges; due to the fact that the specimen is in bad condition, the junction of body and tail could not be determined accurately. Consequently, some measurements and scale counts (SVL, tail length, subcaudals) could not be taken; ventral scales at least 213; anal scute divided; dorsal scale rows 15–13–? (damaged); supralabials 8; supralabials entering the orbit of the eye 4, 5; infralabials 9; infralabials touching first chinshield 1–5; infralabials touching second chinshield 5, 6; postoculars 2; temporal shields 2:1:2 (L) / 2:2:1 (R); scales bordering the posterior edges of the parietal scales 4; eye diameter 4.2 mm; eye–nostril distance 4.8 mm (L) / 4.7 mm (R); snout width 5.5 mm; length of frontal scale 6.1 mm; ground-colour light brown; head dorsally light brown; supralabials, throat and venter pale yellow, immaculate.

Species description. Usually uniformly coloured dorsally although the colouration highly varies (see CAMERON & COGGER 1992, COGGER 2000, WILSON & SWAN 2010), ranging from black (e.g., in mid-eastern Queensland),

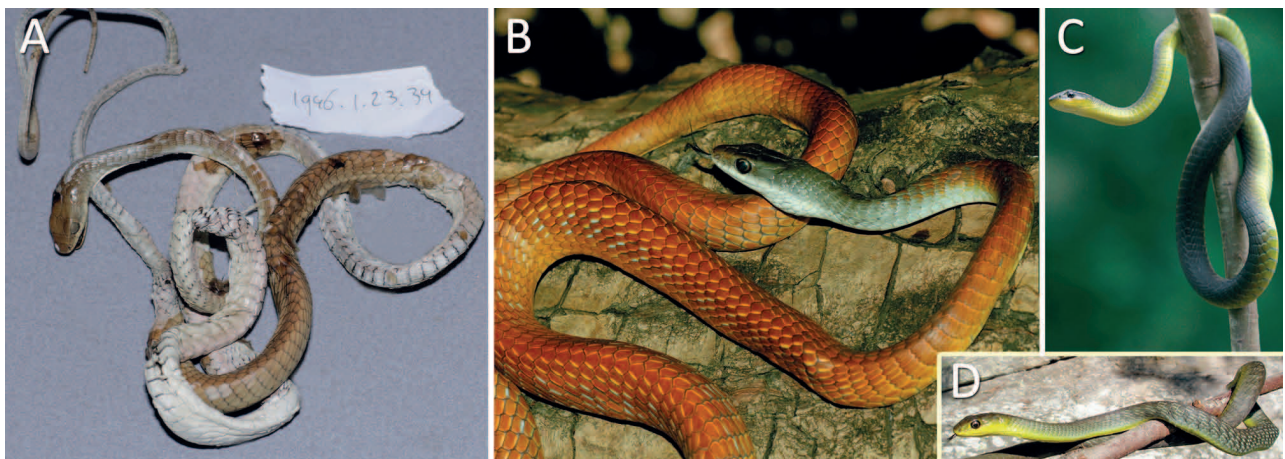


Figure 11. *D. punctulatus*. A) Australia (BMNH 1946.1.23.34, holotype); B) Darwin, Australia (photograph by RUCHIRA SOMAWEERA); C) Smiths Lake, New South Wales, Australia (photograph by RUCHIRA SOMAWEERA); D) Royal National Park, Sydney, Australia (Photo: RUCHIRA SOMAWEERA).



yellow or light orange with a pale bluish grey head and neck (northern Australia) to dull green, olive-green, bluish green or blue (eastern Australia); venter immaculate or with small speckles that become more dense posteriorly; no postocular stripe; no black bars on the neck; 8 supralabials (rarely 7); supralabials 4, 5 enter orbit of eye; 5–10 temporal scales; 197–213 ventrals; 121–139 subcaudals; relative tail length 0.28–0.32; eye diameter equal to, or smaller than, eye–nostril distance; maximum total length recorded in this study 148 cm, but 2 meters according to COGGER (2000).

**Sexual dimorphism.** Males have a slightly shorter frontal scale and eye–nostril distance on average than females ( $p = 0.01$ ;  $p = 0.03$  based on 5 females and 5 males). This finding agrees with results obtained by CAMILLERI & SHINE (1990) who established intersexual differences in head morphology in this species. FEARN & TREMBATH (2010) demonstrated that females grow larger than males.

**Geographic variation.** There is considerable geographic variation in colouration, as is apparent in the species description above. Geographical variation in morphology could not be studied satisfactorily as many of the examined specimens were not furnished with detailed locality data. STORR et al. (1986) provided rather different ventral and subcaudal counts (211–234 and 131–146 respectively) than found in this study. Their values are based on specimens in the Western Australian Museum collection, almost all from Western Australia or the Northern Territory. The discrepancy between their data and those found in this study may indicate a pronounced geographic variation in ventral and subcaudal counts.

**Distribution.** Coast and adjacent areas of northern and eastern Australia (COGGER et al. 1983, CAMERON & COGGER 1992). There are several records from New Guinea (MCDOWELL 1984, ALLISON 2006, AUSTIN et al. 2008), but these probably refer to *D. macrops*, which has long been masquerading under the name *D. punctulatus*.

**Natural History.** See FEARN & TREMBATH (2010).

### *Dendrelaphis striolatus* (PETERS, 1867)

*Dendrophis striolatus* PETERS, 1867: 25. Fig. 12

**Type.** ZMB 5450 from Palau (unspecified locality) (holotype).

**Description of the type.** Male; body slender, eye large, pupil round, vertebral scales strongly enlarged, hexagonal in shape; SVL 59.9 cm; tail 28.5 cm; 173 ventrals; 131 subcaudals; dorsal scales in 13–13–9 rows; supralabials 9 (L) / 8 (R); supralabials 5, 6 (L) / 4, 5 (R) enter orbit of eye; infralabials 9 (L) / 10 (R); infralabials 1–5 touch first chinshield, 5, 6 touch second chinshield; 2 postoculars; temporal scales 2–2; scales bordering posterior edges of parietal scales 7; eye diameter 4.3 mm (L) / 4.5 mm (R); eye–nostril distance 3.5 mm (L); 3.7 mm (R); snout width 4.1 mm; width of vertebral at the level of the middle ventral 3.1 mm; length of frontal scale 5.2 mm; ground-colour brown; no temporal stripe; no oblique black bars on the neck; supralabials and throat whitish; venter immaculate, whitish anteriorly, becoming darker posteriorly.

**Remarks.** The holotype of *D. striolatus* is somewhat atypical in lacking the black bars on the neck that are otherwise one of the diagnostic characteristics of this species. However, although rare, the lack of colour pattern was also seen in a specimen from Babeldaop (CAS 123977) and has also been recorded by CROMBIE & PREGILL (1999).

**Species description.** Oblique black bars on neck (rarely absent), no postocular stripe, venter immaculate; 9 supralabials (rarely 8); supralabials 5, 6 enter the orbit of the eye (rarely 5, 6 or 4, 5, 6); 7–16 temporal scales; 171–187 ventrals; 133–147 subcaudals; relative tail length 0.32–0.36; eye diameter larger than eye–nostril distance; maximum total length 133.5 cm.

**Sexual dimorphism.** *D. striolatus* exhibits sexual dimorphism in the reduction of the number of dorsal scale rows towards the tail. Most females have 11 dorsal scale rows anterior to the tail whereas most males have 9 dor-

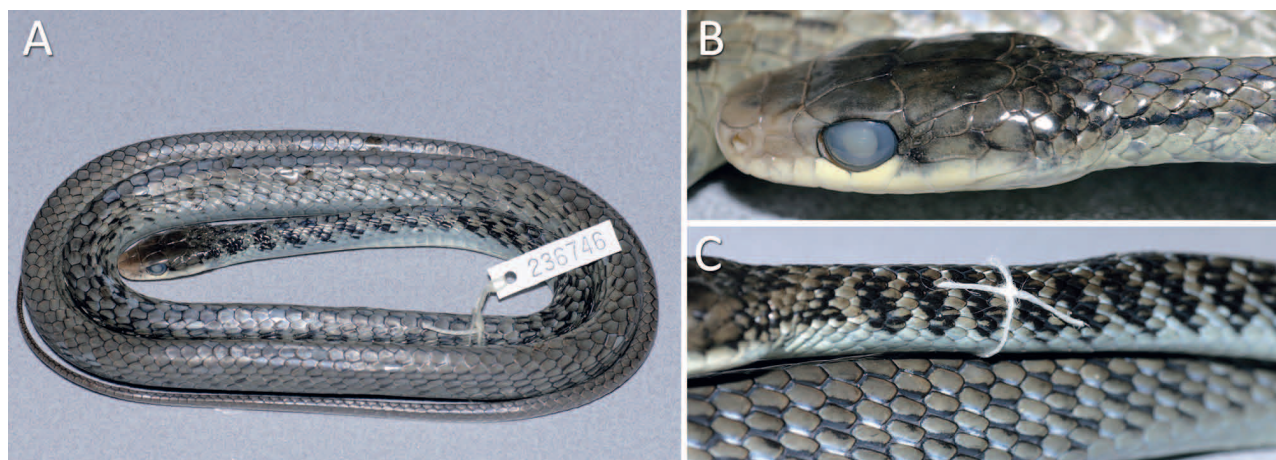


Figure 12. *D. striolatus*. A) Palau: Ngerekebesang Island (CAS 236746); B) Palau: Ngeaur Island (CAS 236475); C) Palau: Malakal (CAS 249064).

sal scale rows anterior to the tail ( $p = 0.0001$ ; based on 22 females and 18 males).

Geographic variation. Some clinal variation was noted (see Results).

Distribution. Palauan Islands (see Tab. 1 for more detailed localities)

### Discussion

This study has revealed the existence of at least nine species within the Australasian group of *Dendrelaphis*. The derived taxonomy and corresponding nomenclature entail revalidating *D. keiensis*, *D. lineolatus*, and *D. macrops*, elevating *D. punctulatus striolatus* to specific status, and synonymising *D. salomonis* with *D. calligaster*. Although the presented taxonomy undoubtedly constitutes an improvement of our understanding of the Australasian members of *Dendrelaphis*, it is still far from being conclusive. Examination of more material from more geographical locations would probably reveal the existence of additional species. As discussed in the Results section above, observations presented by BOULENGER (1894), SCHMIDT (1932) and McDOWELL (1984) indicate that some Solomon Islands populations of *D. calligaster* deserve further study. In a similar vein, the status of *Dendrophis calligastera distinguendus*, MEISE & HENNIG, 1932 is unclear. In spite of morphological dif-

ferences, we have followed COGGER et al. (1983) in placing this name in the synonymy of *D. calligaster*. Finally, the observed geographical variation in New Guinean *D. calligaster* and *D. macrops* deserve more detailed investigation. In conclusion, the taxonomic arrangement arrived at in this study should be seen as a working hypothesis (e.g., PAPA 2008) that can be used as a basis for further research. We are fairly confident that the presented taxonomy is conservative, i.e., does not contain type-I taxonomic errors (recognizing more species than exist), but may be flawed by type-II taxonomic errors (failing to recognize species) (FROST & HILLIS 1990). Thus, further research should focus on each species separately or on subsets of similar species by including more material from more locations.

Presumably, the group treated in this study is monophyletic. The combination of characters that defines this group, i.e., 13 dorsal scale rows and enlarged vertebral scales, is not found in species occurring directly to the west of Australasia (VOGEL & VAN ROOIJEN 2008, VAN ROOIJEN & VOGEL 2012). The centre of evolution of this group appears to be New Guinea, which is inhabited by five members: *D. calligaster*, *D. gastrostictus*, *D. lineolatus*, *D. lorentzii*, and *D. macrops*. Australia harbours two species, *D. calligaster* and *D. punctulatus*, whereas the remote Palau Islands and southeastern Moluccan Islands as well as Trobriand Islands and the Solomons are each inhabited by one species (*D. striolatus*, *D. keiensis*, *D. papuensis*, and

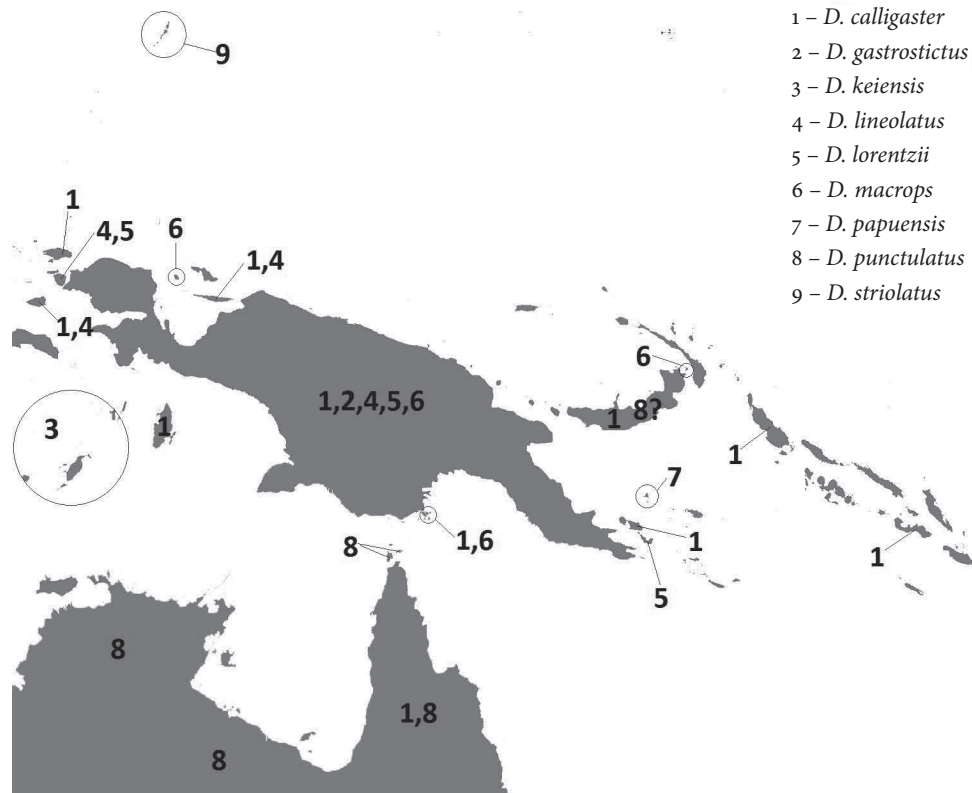


Figure 13. Currently known distribution of the nine recognized species.



*D. calligaster*, respectively). Species richness thus appears to decline with increasing distance to New Guinea. Ancestors of *D. keiensis* and *D. striolatus* have probably reached the Moluccan and Palauan islands by across-sea dispersal, as these islands were not connected to New Guinea during the Pleistocene (VORIS 2000). The same holds true for the Solomon populations of *D. calligaster*. The distributional pattern observed in this group is in line with general patterns. Herpetofaunal species richness in general declines with increasing distance from New Guinea, which has been the major source of colonists for Pacific island groups (ALLISON 1996).

### Acknowledgements

Special thanks go to ESTHER DONDORP (RMNH) for all her efforts and friendliness. Many thanks are due to GLENN SHEA for a very thorough review of an earlier version of this paper as well as for providing morphological data on several specimens of *D. macrops* and *D. punctulatus*. We are also very grateful to JENS VINDUM (CAS), PATRICK CAMPBELL, and TRACY HEATH (BMNH), ROSS SADLER (AM), ANNEMARIE OHLER, and ALAIN DUBOIS (MNH), FRANZ TIEDEMANN and RICHARD GEMEL (NMW), GUNTHER KÖHLER and MONIKA LAUDAHN (SMF), D. RÖDDER and W. BÖHME (ZFMK), and MARK-OLIVER ROEDEL and FRANK TILLACK (ZMB) for allowing us to examine specimens from their collections. Thank you, FRANK TILLACK, RAFFAEL ERNST, MARKUS AUER, NED GILMORE, PATRICK DAVID, PETER UETZ, MARIANNE VAN DER WAL, and J. C. HERREMANS for providing valuable information and literature. GEORGE ZUG and GIULIANO DORIA provided photographs of museum specimens, while FRED KRAUS and BRAD MARYAN supported us with fine photographs of live specimens. PATRICK DAVID also shared his invaluable knowledge on Latin and the correct usage of binomens. We are furthermore grateful to JODI ROWLEY, SAMANTHA TESORIERO, and PETERA HANKE for their assistance in studying museum specimens.

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## Appendix

Specimens examined for this study

Museum abbreviations follow SABAJ PÉREZ (2013)

*Dendrelaphis calligaster* (GÜNTHER, 1867) – New Guinea: AM R31916–17 (MM MR563–64), Katow (Binaturi River) (syntypes *D. katowensis* MACLEAY, 1877); AM R2380, Fife Bay (syntype *D. schlenckeri* OGILBY, 1898); BMNH 1946.1.6.7–9, Dinawa, Brit. New Guinea (syntypes *D. schlenckeri* OGILBY, 1898); RMNH. RENA.42741, Papua, Manokwari; RMNH.RENA.6359 (1)–(2), FakFak; RMNH.RENA.40163 (B), Aitinjo, Vogelkop; RMNH. RENA.47089, Vogelkop; RMNH.RENA.47090, Kamboaja, Vogelkop; CAS 116014, Kundiawa; CAS 127376, Wipim; CAS 132205, Binaturi River; CAS 127367, Abam, Oriomo river; NMW 23710:1, Haveri, Brit. New Guinea; CAS 100070, Nivi; Yapen Island: RMNH.RENA.42862, Seroei; Aru Island: RMNH.RENA.509; Daru Island: CAS 127368; CAS 132203; Misool: RMNH. RENA.42940; New Britain: BMNH 98.3.3.24; BMNH. 1931.10.5.1; Solomons: Bougainville Island: CAS 113650–56; CAS 113658–61;



Solomons Guadalcanal Island: CAS 49962–63; CAS 49913–15; Australia: BMNH 1867.5.6.71, Cape York (holotype *D. calligaster* GÜNTHER, 1867); Darnley Island: AM R31914–15 (MM R565–66) (syntypes *D. darnleyensis* MACLEAY, 1877; Fergusson Island, British New Guinea: BMNH 1946.1.23.30–33 (syntypes *D. meeki* BOULENGER, 1895); Solomons: unspecified locality: BMNH 1946.1.6.11, BMNH 1946.1.5.97 (syntypes *D. salomonis* GÜNTHER, 1872)

*Dendrelaphis gastrostictus* (BOULENGER, 1894) – New Guinea: BMNH 1946.1.23.20 (holotype *D. gastrostictus* BOULENGER, 1894); RMNH.RENA.4709, Noord Rivier (syntype *D. nouhuysii* VAN LIDTH DE JEUDE, 1911); RMNH.RENA.4987(1)–(2), S. New Guinea; RMNH.RENA.40164, Hollandia; RMNH.RENA.42841–2, Ajamara, Vogelkop; RMNH.RENA.42873, Aifat, Vogelkop; RMNH.RENA.42731, Papua, Kauh

*Dendrelaphis keiensis* (MERTENS, 1826) – Babar Island: RMNH.RENA.5602 (1)–(2); Kei-Dulah: SMF 18662 (holotype *D. calligastera keiensis* MERTENS, 1826)

*Dendrelaphis lineolatus* (JAQUINOT & GUICHENOT, 1853) – New Guinea: MNHN 5081, New Guinea (type *D. lineolatus* JAQUINOT & GUICHENOT, 1853); MNHN 5186, New Guinea; AM R1089, Papua New Guinea (holotype *D. elegans* OGILBY, 1891); RMNH.RENA.40163 (A), Aitinjo, Vogelkop; RMNH.RENA.47093 (neotype *D. punctulatus* var. *fasciata* MEYER, 1874a), Aitimo, Vogelkop; RMNH.RENA.47097, Alkmaar, Nieuw guinea; ZMA 16606, Korime Rivier; ZMA 6607, Jeko, Humboldt Baai; Misool Island: RMNH.RENA.47127; Salawati Island: RMNH.RENA.42869; Yapen Island: RMNH.RENA.42938 (neotype *D. punctulatus* var. *atrostriata* MEYER, 1874a); Misool: RMNH.RENA.42941

*Dendrelaphis lorentzii* (VAN LIDTH DE JEUDE, 1911) – New Guinea: RMNH.RENA.4710, Sabang (type *D. lorentzii* VAN LIDTH DE JEUDE, 1911); RMNH.RENA.4986, Bivak Island, S. New Guinea; CAS 127375, Balimo; RMNH.RENA.42868, Salawati; RMNH 16598, North New Guinea

*Dendrelaphis macrops* (GÜNTHER, 1877) – New Guinea: MNHN 5117; AM R31911–13 (MM R581–83), Katow (Binaturi River), Papua New Guinea (syntypes *D. breviceps* MACLEAY, 1877); AM R1088 (holotype *Dendrophis papuae* OGILBY, 1891); RMNH.RENA.47098, Kamboeaja, Vogelkop; RMNH.RENA.42874, Hollandia; RMNH.RENA.42844–46, Ajamara, Vogelkop, Papua; RMNH.RENA.42975, Papua, Kouk aan de Digoel; CAS 116015, New Guinea, Sepik Distr., SW Angoram; R31239, Maiwara, Madang Province; R86865, Madang, Madang Province; R115493, Usaki River; R121224, Nagada Harbour, Madang, Madang Province; R24290, Lake Murray, Western Province; R121185, Wipim, Western Province; Numfoor Island: RMNH.RENA.42931, RMNH.RENA.42934, Papua, Mefoor; Duke Of York Island: BMNH 1946.1.23.42 (holotype *D. macrops* GÜNTHER, 1877); Daru Island: CAS 121091, CAS 139563, CAS 121227

*Dendrelaphis papuensis* Boulenger, 1895 – Trobriand Islands: BMNH 1946.1.6.57–61 (syntypes *D. papuensis* BOULENGER, 1895)

*Dendrelaphis punctulatus* (GRAY, 1826) – Australia: BMNH 1946.1.23.34 (type *Leptophis punctulatus* GRAY, 1826); BMNH 1964.1514, N. C. Australia; BMNH 1946.1.23.37; 1946.1.23.41 (syntypes *D. olivacea* GRAY, 1842); MNHN 7234 (holotype *D. fuscus* JAN, 1863); AM R31908–10 (MM R569–71), Townsville, Queensland (syntypes *D. gracilis* MACLEAY, 1875); AM R31906–07 (MM R561–62), Herbert River, Queensland (possible syntypes *D. bilorealis* MACLEAY, 1884); ZMA 13947 (1)–(2); RMNH.RENA.4022, Queensland; RMNH.RENA.4221–22, Queensland; MNHN 976; MNHN 1896\_318; MNHN 1897\_494; MNHN 1898\_376; MNHN 5626; MNHN 6075; RMNH.RENA.23347, East Australia; R105126, Mapoon Mission House, Weipa, Qld; R91659, 5 km N Pennefather River Mouth, Weipa, Qld; R82532, Regeneration Nursery, Weipa, Qld; R91623, Weipa district, Qld; R91633, 24 km N Wei-

pa on Sunrise Creek Road, Qld; R128184, Batavia Downs, Wenlock River, Qld; R17649, Silver Plains, Qld; R119697, Healy Creek, Walwa Plains, Qld; New Britain: ZFMK 35859; VITI INSELN: RMNH.RENA.4017; Torres Strait Islands: R4496, Murray Island; R47509, Prince of Wales Island; R55930, Prince of Wales Island; R64222, Moa Island

*Dendrelaphis striolatus* (PETERS, 1867) – Palau: Babeldaob: CAS 236956; CAS 249358; CAS 237340; CAS 123977; CAS 122473–75; Palau: Ngercheu: CAS 237947; CAS 238085; Palau: Ulebsechel: CAS 248922; Palau: Malakal: CAS 249064–65; CAS 238078; Palau: Angaur: CAS 236653; CAS 248822; CAS 236475–76; Palau: Ngerekebesang: CAS 236746; CAS 236747; Palau: Ulong: West Ulong: CAS 249007–8; CAS 249211; Palau: Ulong: EAST Ulong: CAS 248873; Palau: Ngeesebus: CAS 238143; Palau: Ngerchaol: CAS 237879; CAS 236365; CAS 236374; Palau: Ngeanges: CAS 236973; Palau: Ngeruktabel: CAS 248993; CAS 236347–49; CAS 249112; Palau: koror: CAS 98664; CAS 19013; Palau: Ngerukeuid Islands (ISL. 24): CAS 237309; Palau: Ngermalk Island: CAS 236439; Palau: unspecified locality: RMNH.RENA.4016 (A)–(B); ZFMK 35860; ZMB 5450 (holotype *D. striolatus* PETERS, 1867).