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Contributions to a review of the *Dendrelaphis pictus* (GMELIN, 1789) complex – 2. the eastern forms
(Serpentes: Colubridae)

Beiträge zu einer Revision des
Dendrelaphis pictus (GMELIN, 1789) Komplexes – 2. die östlichen Formen
(Serpentes: Colubridae)

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KURZFASSUNG

Die südostasiatischen, indonesischen und philippinischen Formen der polytypischen Art *Dendrelaphis pictus* (GMELIN, 1789) werden mit Hilfe der Multivariationsanalyse untersucht. Mehrere phänetisch unterschiedliche Cluster sind erkennbar. Geografisch werden diese Cluster durch wichtige biogeographische Barrieren wie zum Beispiel der Isthmus von Kra, die Wallace Linie und die Weber Linie getrennt. Die indochinesischen und die Sunda-Populationen werden trotz morphologischer Unterschiede zwischen ihnen unter dem Namen *D. pictus* zusammengefaßt, da sie als nicht voneinander unabhängig betrachtet werden. Zwei weitere Cluster werden als eigenständige Arten betrachtet, da diese Populationen ohne Zweifel unabhängige evolutionäre Linien bilden. Der erste dieser Cluster umfaßt die Populationen der Philippinen und Sulawesis. Diese Populationen werden unter dem Namen *D. marenae* beschrieben. Diese Art unterscheidet sich von den bisher benannten Formen in der Färbung, der Größe der Vertebralschuppen, der Anzahl der Subcaudalia und der Schwanzlänge. Der zweite Cluster umfaßt die Populationen der Molukken, welche mit dem Namen *D. grismeri* belegt werden. Diese Art zeichnet sich durch die Anzahl der Ventralia, Subcaudalia und Temporalia sowie die Schwanzlänge aus.

ABSTRACT

The Southeast Asian, Indonesian and Philippine forms of the polytypic *Dendrelaphis pictus* (GMELIN, 1789) are reviewed using multivariate analyses. Several distinct phenetic clusters are discerned. Geographically, these clusters are separated by important biogeographic boundaries, such as the Isthmus of Kra, Wallace's line and Weber's line. The Indochinese and Sundaic populations, although morphologically distinct, are referred to the name *D. pictus* as these populations are assumed to be interdependent lineages. Two clusters are considered to represent distinct species as these population complexes undoubtedly represent separate evolutionary lineages. The first separate cluster comprises the populations from the Philippines and Sulawesi. This population complex is referred to the name *D. marenae*. This species differs from known forms in coloration, in the size of the vertebral scales, the number of subcaudals and the tail length. The second separate cluster comprises the Moluccan populations which are referred to the name *D. grismeri*. This species is characterized by the number of ventrals, subcaudals and temporals as well as tail length.

KEY WORDS

Reptilia: Squamata: Serpentes: Colubridae: *Dendrelaphis pictus*, *Dendrelaphis marenae* sp. nov., *Dendrelaphis grismeri* sp. nov., Philippines, Indonesia, Moluccas

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 China in the North (ZIEGLER & VOGEL 1999). Members of the genus *Dendrelaphis* are slender, diurnal species that are predominantly arboreal and feed mainly on lizards and amphibians.

Dendrelaphis pictus (GMELIN, 1789) has a wide range in Southeast Asia and is one of the most frequently encountered snakes in that area, as it is common in cultivated areas (e.g. LIM & LEE 1989; STUEBING & INGER 1999; CHAN-ARD et al. 2001; VAN ROOIJEN & VAN ROOIJEN 2007). Coincidentally, this species was described by both GMELIN (as *Coluber pictus*) and LACÉPÈDE (as *Coluber boiga*) in 1789. As dates of publication were unknown, the rule of priority could not subsequently offer a solution to the question of precedence of the names. The Commission on Zoological Nomenclature eventually ruled that relative precedence should be given to Gmelin's *Coluber pictus* (ICZN, Opinion 525, 1958). In the last revisions of the genus *Dendrelaphis*, *Dendrelaphis pictus* was regarded as a strongly polytypic species as evidenced by the number of subspecies and varieties recognized. For instance, MEISE & HENNING (1932) recognized the following seven subspecies: *D. pictus inornatus* BOULENGER, 1897, *D. pictus timorensis* SMITH, 1927, *D. pictus intermedius* (MERTENS, 1927), *D. pictus pictus* (GMELIN, 1789), *D. pictus cyanochloris* (WALL, 1921), *D. pictus andamanensis* (ANDERSON, 1871) and *D. pictus bifrenalis* (BOULENGER, 1890). MERTENS (1934) synonymized *D. pictus timorensis* with *D. pictus inornatus* and discussed the additional race *Dendrelaphis pictus* var. *striata* (COHN, 1905), which he regarded as a color variety.

Most of the aforementioned forms were subsequently elevated to species rank: *D. pictus inornatus* was elevated by HOW et al. (1996), who regarded *D. pictus intermedius* as a synonym and *D. pictus timorensis* as a subspecies of it. *Dendrelaphis cyanochloris* was elevated by SMITH (1940), albeit with some doubt (SMITH 1943). SMITH (1943) also synonymized *D. proarchus* WALL, 1909 and *D. pictus ngansonensis* BOURRET, 1935 with *D. pictus* while elevating *D. pictus bifrenalis* to specific status. ZIEGLER & VOGEL (1999) subsequently revalidated *D. pictus ngansonensis* BOURRET, 1935 and elevated it to species status. The status of *D. proarchus* is under investigation and will be treated in a later article. With the description of *D. hollinrakei* LAZELL, 2002 another species was added to this complex. The only currently recognized subspecies is *D. pictus andamanensis* which is endemic to the Andaman Islands, India. This taxon will also be discussed in this planned review.

This review was initiated to disentangle the intricate taxonomy of the *D. pictus* complex. In a previous part of this revision (VAN ROOIJEN & VOGEL 2008), a new species, *D. haasi*, was described that occurs sympatrically with *D. pictus* across Sundaland. All specimens of *D. haasi* had originally been referred to the binomen *D. pictus*, a fact that underscored the necessity to clarify the taxonomy of this complex. The present part focuses on the populations of *D. pictus* inhabiting Indochina, Sundaland, the Philippines and the Moluccas.

MATERIALS AND METHODS

Samples, selected characters and definitions

For this study, 217 "*Dendrelaphis pictus*" auctorum were examined. Locations and corresponding sample-sizes are given in Table 1. As multivariate analyses were restricted to specimens with complete tails, numbers of complete specimens are given separately.

For each examined specimen, 20 characters regarding color pattern, body proportions and scalation were recorded. These are listed in Table 2. Measurements on the eye-diameter, distance eye-nostril and width of the vertebral scale were measured with a slide calliper to the nearest 0.1 mm. For eye-diameter and distance eye-nostril, these measurements were made on the left and right side and subsequently averaged. Distance from centre of the eye to posterior border of the nostril was determined by measuring the distance from the posterior margin of the eye to the posterior margin of the nostril and subtracting the radius of the eye. 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 according to 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

Table 1: Sample-size according to locality of a total of 217 "*Dendrelaphis pictus*" auctorum examined. The number of specimens with complete tail is given in parentheses.

Tab. 1: Probengröße nach geographischer Verbreitung von insgesamt 217 untersuchten "*Dendrelaphis pictus*" auctorum. Die Anzahl der Exemplare mit komplettem Schwanz steht in Klammern.

Locality Fundort	Number of males Anzahl Männchen	Number of Females Anzahl Weibchen	Sex not determined Geschlecht unbestimmt
Myanmar	1 (0)	5 (2)	
Laos	4 (0)	4 (2)	
Vietnam	6 (6)	6 (5)	
Cambodia	3 (2)	2 (2)	
Thailand	5 (3)	6 (6)	
Peninsular Malaysia / Halbinsel Malaysia	2 (2)	3 (1)	
Java	5 (4)	9 (8)	5 (4)
Sumatra	3 (3)	4 (4)	4 (3)
Borneo	6 (6)	8 (6)	1 (1)
Bali	2 (2)	0	
Lombok	1 (1)	4 (4)	
Sulawesi	8 (7)	13 (9)	
Philippines (no exact locality / ohne Details)	2 (1)	8 (6)	
Philippines (Luzon)	13 (4)	31 (17)	
Philippines (Mindanao)	3 (3)	3 (1)	
Philippines (Sulu Archipelago)	3 (2)	1 (1)	
Philippines (Samar)	1 (0)	5 (4)	
Philippines (Panal Masbate)	1 (1)	3 (0)	
Philippines (Panay)	0	1 (1)	
Philippines (Balabac)	0	1 (1)	
Philippines (Palawan)	3 (2)	0	
Moluccas (Ceram)	0	6 (2)	
Moluccas (Boana)	2 (1)	0	
Moluccas (Manipa)	0	1 (1)	
Moluccas (Ambon, form 1)	3 (2)	3 (2)	
Moluccas (Ambon, form 2)	0	3 (3)	

last infralabial was defined as the last infralabial still covered completely by the last supralabial. The posteriormost temporal scales were defined as the scales of which more than half of the area lies in front of an imaginary line that runs from the apex of the last supralabial to the posterolateral corner of the parietal.

Primary Operational Taxonomic Units

Primary Operational Taxonomic Units (OTUs) corresponded with islands or countries as given in Table 1 with several exceptions. First of all, in case of very small sample-size, locations were grouped when not separated by known, major, biogeographic barriers. The following groupings were applied: Myanmar + Thailand, Laos + Vietnam, Balabac + Palawan, Panal + Masbate and the Moluccas (Ceram, Ambon, Manipa, Boana). However, three specimens from Ambon (Moluccas) did not correspond with other representatives of the Moluccan population-assemblage whereas the six other specimens from Ambon did. These three aberrant specimens closely resembled specimens from Sundaland. Therefore, these were assigned to a separate OTU ("Moluccas, form 2"). Finally, the three specimens from Peninsular Malaysia were assigned to their own OTU in order to explore its affinities with either Sundaic or Indochinese populations.

Size-adjustment of morphometric characters

For multivariate analyses, morphometric variables (EYED, EYEN, WVERT, TAIL) were adjusted to a common SVL of 60.0 cm to correct for potential ontogenetic variation between the samples from the various OTUs (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

Table 2: List of morphological and coloration characters analyzed in this study and their abbreviation.
Tab. 2: Liste der in dieser Arbeit untersuchten morphologischen und Färbungsmerkmale und ihre Abkürzungen.

Abbreviation /Abkürzung	Character / Merkmal
Morphometrics / Morphometrie	
EYED	Horizontal diameter of the eye / Horizontaler Augendurchmesser
EYEN	Distance from centre of the eye to posterior border of the nostril / Entfernung Augenmitte – hinterer Nasenlochrand
TAIL	Tail-length / Schwanzlänge
SVL	Snout-vent length / Kopf-Rumpf-Länge
WVERT	Maximum width of the vertebral scale at the position of the middle ventral scale / Größte Breite der vertebralen Schuppe auf Höhe der mittleren Bauchschiene
Scalation / Beschuppung	
VENT	Number of ventrals / Anzahl Ventralia
SUBC	Number of subcaudals / Anzahl Subcaudalia
DOR1	Number of dorsals one head-length behind the head / Anzahl Dorsalia eine Kopflänge hinter dem Kopf
DOR2	Number of dorsals at the position of the middle ventral / Anzahl Dorsalia-Längsreihen auf Höhe des mittleren Ventrale
DOR3	Number of dorsals 1 head-length before the vent / Anzahl Dorsalia-Längsreihen eine Kopflänge vor der Afteröffnung
SUBL	Number of infralabials touched by the first sublabial (left and right added) / Anzahl Infralabialia, die an das erste Sublabiale grenzen (Summe von rechter und linker Seite)
SL1	Number of supralabials (left and right added) / Anzahl Supralabialia (Summe von rechter und linker Seite)
SL2	Number of supralabials touching the eyes (left and right added) / Anzahl Supralabialia, die an das Auge grenzen (Summe von rechter und linker Seite)
LOR	Number of loreals (left and right added) / Anzahl Lorealia (Summe von rechter und linker Seite)
INFR	Number of infralabials (left and right added) / Anzahl Infralabialia (Summe von rechter und linker Seite)
TEMP	Number of temporals (left and right added) / Anzahl Temporalia (Summe von rechter und linker Seite)
POC	Number of postoculars (left and right added) / Anzahl Postocularia (Summe von rechter und linker Seite)
Coloration / Färbung	
STRIPE1	Ventrolateral stripe bright (1) or dull (0) / Ventrolateralstreifen leuchtend (1) oder matt (0)
STRIPE2	Black lines bordering the ventrolateral stripe clear (1) or rudimentary/absent (0) / Schwarze Linien begrenzen den Ventrolateralstreifen deutlich (1) oder andeutungsweise/gar nicht (0)
NECK	Black bars on neck (1: yes; 0: no) / Schwarze Streifen auf dem Hals (1: ja; 0: nein)

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. The adequacy of the procedure was assessed on the basis of the correlation between the adjusted variables and SVL (e.g. TURAN 1999).

Formation of secondary OTUs

The affinities between the primary OTUs of *D. pictus* were analysed on the basis of linear Principal Component Analysis (PCA; e.g. CRAMER 2003). In this step of the analysis PCA was preferred over Canonical Variate Analysis (CVA), because the results give a better impression of the overall similarity between groups and are less susceptible to bias due to small sample-size. A PCA was employed to reduce the dimensionality of the data-set in order to facilitate interpretation of multivariate patterns of affinities between OTUs. Variables exhibiting little or no geographic variation as well as qualitative variables were excluded from the analysis. The centroids (average scores on the principal components) of the primary OTUs were plotted in a two-dimensional graph. The primary OTUs were subsequently combined into secondary OTUs for further analysis in Canonical Variate Analysis. Combination of OTUs was based primarily on the patterns revealed by PCA. However, information on geological history and biogeography of specific regions as well as results of univariate analyses were taken into consideration to validate the formation of secondary OTUs.

Canonical Variate Analyses

The differences between the secondary OTUs were analysed by means of Canonical Variate Analysis (CVA). Individual object scores were plotted to illustrate the separation between the OTUs. Significance-levels were based on Wilk's Lambda.

Univariate analyses

Meristic variables were analysed using ANOVA unless the assumptions underlying this technique were violated. OTU and sex were used as factors. 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, EYEN, WVERT, TAIL) were analysed with ANCOVA (MAXWELL & DELANEY 1990; NORUSIS & SPSS 1993), using OTU and sex as factors and SVL as covariate. Qualitative variables were analysed using Chi-square. Analysis of sexual dimorphism within the recognized taxa was restricted to primary OTUs from which a sample of three or more was available for each sex.

Software

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

Taxonomic interpretation

The observed differences between OTUs were evaluated in the context of a General Lineage Species Concept (DE QUEIROZ 1998, 2005). Diagnosibility and geographic isolation (e.g. GRISMER 1999; MCGUIRE 2001; BURTON 2004) are used as criteria for independence.

Museum Abbreviations

BMNH: Natural History Museum, London, United Kingdom. MHNG: Muséum d'histoire naturelle de la Ville de Genève, Swizerland. MNHN: Muséum National d'Histoire Naturelle, Paris, France. NMW: Naturhistorisches Museum Wien, Austria. PSGV: Gernot VOGEL's private collection, Heidelberg, Germany. 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. ZSM: Zoologische Staatssammlung, München, Germany.

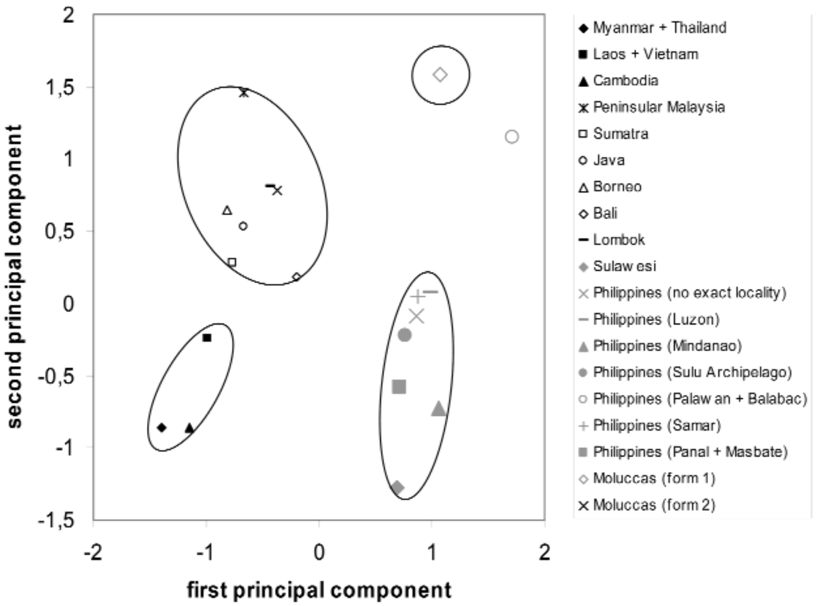

Fig. 1: Ordination of the centroids of the primary OTUs along the first two principal components. Secondary OTUs are demarcated with ellipses.

Abb.1: Ordination der Schwerpunkte der primären OTUs entlang der ersten und zweiten Hauptkomponente. Sekundäre OTUs werden durch Ellipsen angezeigt.

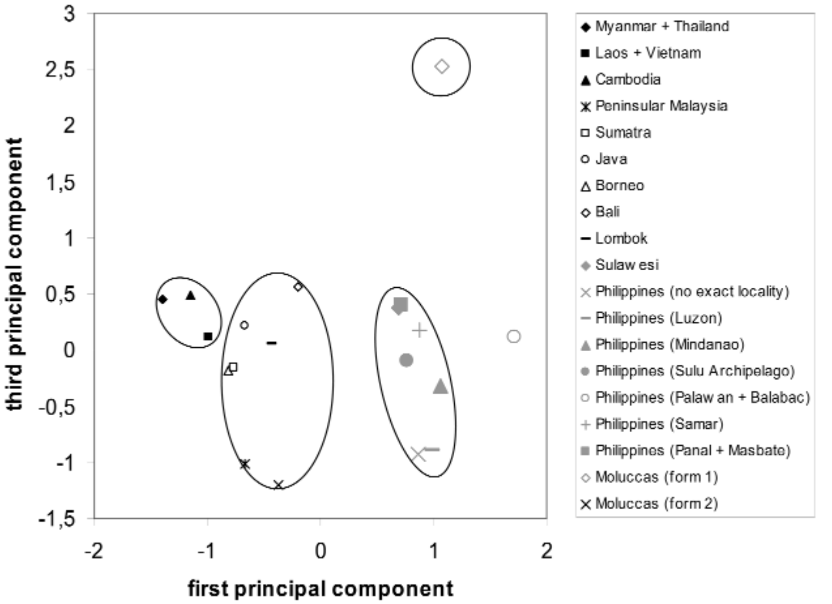

Fig. 2: Ordination of the centroids of the primary OTUs along the first and third principal components. Secondary OTUs are demarcated with ellipses.

Abb. 2: Ordination der Schwerpunkte der primären OTUs entlang der ersten und dritten Hauptkomponente. Sekundäre OTUs werden durch Ellipsen angezeigt..

RESULTS

Combination of primary OTUs

A plot of the first two Principal Components is shown in Fig. 1. As the third Principal Component still represented a substantial amount of information (Eigenvalue > 1), a plot of the first and third Principal Components is also provided (Fig. 2). On the basis of the patterns revealed by PCA, univariate analyses and biogeographic information, four secondary OTUs are formed (henceforth: OTUs 1 through 4). These are demarcated by ellipses in Figs. 1 and 2 and are discussed below. The specimens from Palawan and Balabac appear to occupy a unique position and can not be assigned unambiguously to one of the secondary OTUs. Given the small sample size from this population, these are not assigned to one of the four secondary OTUs. The three aberrant specimens from Ambon that had been assigned to a separate primary OTU (Moluccas, form2 in Figs. 1 and 2) indeed cluster with specimens from the Sundaic region. Two possible explanations can be put forward. First, these three specimens may actually originate from the Sunda region, their locality records being incorrect, a possibility that can certainly not be ruled out (e.g. SHEAR 1980; WÜSTER 1996) all the more since the three specimens have been collected by the same person. Secondly, two forms may coexist on Ambon, one form corresponding with the Sundaic populations. However, the latter scenario is extremely unlikely unless migration has taken place by means of anthropogenic agents. Thus, we assume erroneous registration of locality. The three specimens were consequently excluded from further analyses.

The first OTU comprises Thailand, Myanmar, Vietnam, Laos and Cambodia (henceforth: Indochinese region). This cluster is separated morphologically from the Sundaic cluster primarily on the basis of a short first sublabial, a slightly larger eye and a lower number of temporal scales ($p < 0.00001$ for all characters). In addition, a difference with regard to coloration was noted. In the Sundaic population the postocular stripe usually starts before the eye and breaks up into black bars on the neck. In the Indochinese population, the postocular stripe usually starts behind the eye and fades away in a continuous fashion on the neck. The morphological separation of the Indochinese population from the Sundaic population is noteworthy given the recent interconnection between mainland Southeast Asia and the Sundaic region (HOW & KITCHENER 1997; VORIS 2000; INGER & VORIS 2001). Interesting in this regard is that the specimens from Peninsular Malaysia correspond with the Sundaic cluster. Thus, a region of restricted or absent gene flow appears to exist between Peninsular Malaysia and Thailand. The most plausible explanation is that gene flow is restricted or inhibited at or near the Isthmus of Kra, which represents an important phytogeographical and zoogeographical transition zone between the Sundaic and Indochinese region (SMITH 1943; HUGHES et al. 2003; PAUWELS et al. 2003; WOODRUFF 2003). The position of this transition zone on the Thai-Malay Peninsula is probably associated with a change from wet seasonal evergreen dipterocarp rain forest to mixed moist deciduous forest. However, the origin of the different biotas of Sundaland and Indochina may lie in prolonged periods of isolation due to marine transgressions during the Miocene and the Pliocene (HUGHES et al. 2003; WOODRUFF 2003). The zoogeographic importance of the Isthmus of Kra is known to be also applicable to the genus *Dendrelaphis* as several species find their distributional limits on the Thai-Malay Peninsula (VOGEL 1990; VOGEL & VAN ROOIJEN 2007; VAN ROOIJEN & VOGEL 2008).

The second OTU comprises the Sundaic region and Lombok. These populations are jointly characterized by a bright ventrolateral line, a low number of subcaudals, narrow vertebral scales, a short tail and long first sublabial. The Greater Sunda Islands and mainland Southeast Asia have been interconnected relatively recently as a result of a lowering in sea-levels due to northern glaciation (HOW & KITCHENER 1997; VORIS 2000; INGER & VORIS 2001). The ensuing opportunities for faunal exchange account for the homogeneity of this cluster. The inclusion of Lombok in

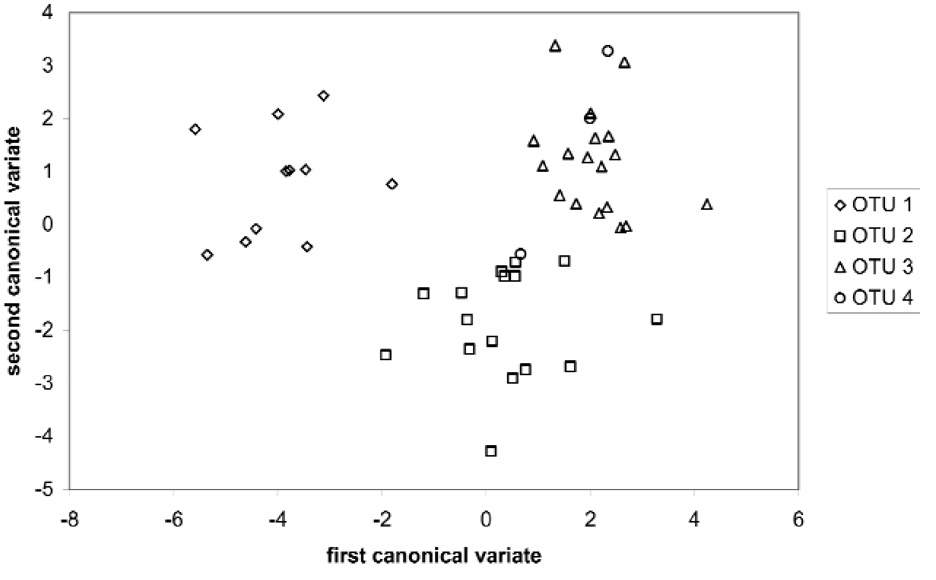

Fig. 3: Ordination of male *Dendrelaphis pictus* of the secondary OTUs along the first two canonical variates.
Abb. 3: Ordination der männlichen *Dendrelaphis pictus* der sekundären OTUs entlang der ersten beiden Diskriminanzfunktionen.

this group is noteworthy as this island is assumed to have remained separate from the Greater Sunda islands during the Pleistocene sea-level regressions. However, many Asian species actually terminate their distribution on Lombok (HOW & KITCHENER 1997).

The third OTU comprises the Philippines and Sulawesi. Univariate analyses demonstrate that specimens from the Philippines and Sulawesi are jointly characterized by having a faint ventrolateral line, wide vertebral scales, a long tail and correspondingly high number of subcaudals. In these characters, they differ strongly from the Sundaic population ($p<0.00001$ for all characters). Sulawesi and the Philippines have been isolated by marine barriers for vast geological time spans and remained isolated during Pleistocene sea level lowering (IN DEN BOSCH 1985; HOW & KITCHENER 1997; VORIS 2000; INGER & VORIS 2001). However, within the Philippine archipelago, groups of islands became connected during the Pleistocene sea level regressions, enabling faunal exchange (e.g. EVANS et al. 2003) relatively recently. In addition, the islands of the Philippine archipelago are now in close proximity to one another. Thus, chances of interisland dispersal within the archipelago may be appreciable. Due to their long isolation from surrounding land masses as well as their complex geography, levels of endemism on Sulawesi and in the Philippines are high (IN DEN BOSCH 1985; PETERSON 2000; INGER & VORIS 2001; JANSA et al. 2006). The phenetic similarity between the Philippine and Sulawesi populations of *D. pictus* is most notable. Sulawesi is biogeographically most closely related to Sundaland (IN DEN BOSCH 1985; HOW & KITCHENER, 1997). In addition, lowered sea levels during the Pleistocene substantially reduced the width of the Makassar strait, thus increasing the chance of dispersal between Sulawesi and Borneo. On the other hand, migration between the Philippines and Sulawesi may have been facilitated during the Miocene when the Philippines passed Sulawesi due to plate tectonics and a chain of volcanoes stretched the area between Sulawesi and the Philippines (INGER & VORIS 2001). Moreover, a systematic study of the Ranid genus *Limnonectes* (EVANS et al. 2003) and the

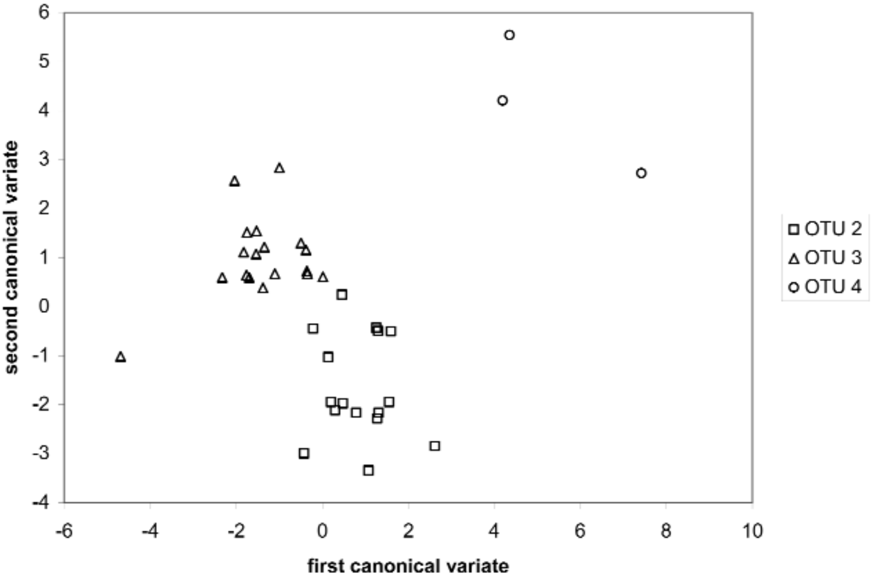

Fig. 4: Ordination of male *Dendrelaphis pictus* of the secondary OTUs 2-4 along the first two canonical variates.
Abb. 4: Ordination der männlichen *Dendrelaphis pictus* der sekundären OTUs 2-4 entlang der ersten beiden Diskriminanzfunktionen.

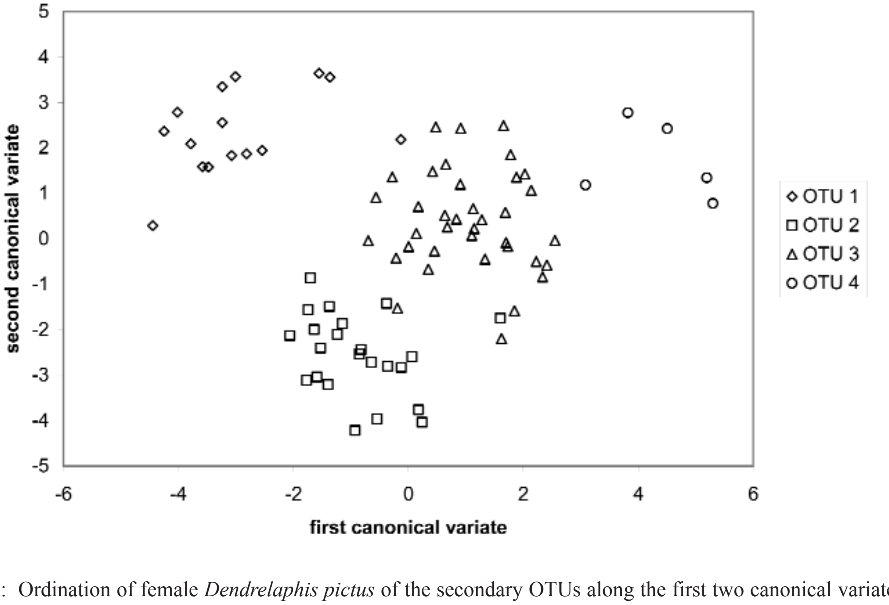

Fig. 5: Ordination of female *Dendrelaphis pictus* of the secondary OTUs along the first two canonical variates.
Abb. 5: Ordination der weiblichen *Dendrelaphis pictus* der sekundären OTUs entlang der ersten beiden Diskriminanzfunktionen.

Table 3: Descriptive statistics for each secondary OTU. Mean and range are shown in case of continuous quantitative variables (EYED-WVERT). Median and range are shown in case of discrete quantitative variables (VENT-POC). In case of qualitative variables (STRIPE1-NECK), the percentage of specimens possessing the indicated charateristic is shown. EYED, EYEN and TAIL represent the SVL-adjusted values.

Tab. 3: Deskriptive Statistiken für sekundäre OTUs. Angegeben sind Mittelwert und Variationsbreite für kontinuierliche quantitative Variablen (EYED-WVERT), Median und Variationsbreite für diskrete quantitative Variablen (VENT-POC). Bei qualitativen Variablen (STRIPE1-NECK), ist der Prozentanteil der Tiere gegeben, die die entsprechende Merkmalsausprägung aufweisen. EYED, EYEN und TAIL wurden für SVL = 60 cm korrigiert.

	Indochina (n = 42)	Sundaland (n = 57)	Philippines + Sulawesi[1)] (n = 96)	Moluccas (n = 15)
EYED (mm)	4.4 (4.0-5.0)	4.1 (3.2-4.7)	4.2 (3.7-4.9)	4.3 (4.0-4.7)
EYEN (mm)	6.1 (5.3-7.2)	6.5 (4.7-7.5)	6.3 (5.2-7.3)	6.4 (5.9-6.9)
TAIL (cm)	30.0 (24.5-33.5)	30.0 (27.0-34.0)	33.0 (30.0-36.5)	35.5 (34.0-38.5)
WVERT (mm)	2.6 (1.8-4.0)	2.5 (2.1-3.2)	3.2 (2.3-4.1)	2.5 (2.0-3.0)
VENT	174 (166-188)	169 (161-176)	173 (161-188)	183 (176-193)
SUBC	131 (113-145)	133 (117-148)	147 (136-158)	160 (151-174)
DOR1	15 (15-16)	15 (15-15)	15 (15-15)	16 (15-17)
DOR2	15 (15-15)	15 (13-15)	15 (15-15)	15 (15-15)
DOR3	11 (9-11)	11 (9-11)	11 (9-11)	11 (9-11)
SUBL	4 (4-7)	8 (4-10)	8 (4-11)	8 (5-9)
SL1	18 (16-20)	18 (16-19)	18 (16-20)	18 (18-18)
SL2	6 (4-6)	6 (4-6)	6 (4-6)	4 (4-6)
LOR	2 (2-2)	2 (2-3)	2 (0-4)	2 (2-2)
INFR	20 (19-23)	20 (18-24)	20 (18-23)	20 (20-24)
TEMP	9 (5-17)	11 (9-18)	12 (8-16)	16 (12-20)
POC	4 (3-6)	4 (3-6)	4 (2-6)	4 (4-6)
STRIPE1	0: 2.5% 1:97.5%	0: 4.5% 1: 95.5%	0: 91% 1: 9%	0; 0% 1: 100%
STRIPE2	0: 2.5% 1:97.5%	0: 3.5% 1: 96.5%	0: 92.5% 1: 7.5%	0; 0% 1: 100%
NECK	0: 88% 1:12%	0: 17.5% 1: 82.5%	0: 2.5% 1: 97.5%	0; 50% 1: 50%

[1)] The four specimens from Palawan and Balabac were excluded from this analysis as inclusion would have had a disproportionate influence on several of the statistics due to their deviant morphology.

Die vier Exemplare von Palawan and Balabac wurden von dieser Analyse ausgeschlossen, da ihre abweichende Morphologie verschiedene Statistiken überproportional stark beeinflußt hätte.

insect genus *Hydropsyche* (MEY 2003) have shown that migration between the Philippines and Sulawesi has occurred. In that regard, it is interesting to note that the population from Sulawesi is morphologically most similar to the population from Mindanao, the Philippine island nearest Sulawesi. However, this observation has to be treated with some reserve given the limited sample (n = 6) from Mindanao.

The fourth OTU comprises the Moluccan islands Ceram, Ambon, Manipa and Boana which are part of the Maluku group. Specimens from the Moluccan islands are characterized by a high number of temporal scales, ventrals and subcaudals, a very long tail, as well as a bright ventrolateral line, bordered by black lines. In these characters, this population is clearly separated from the Philippine and Sulawesi populations (p<0.00001 for all characters). The Moluccan insular populations constitute the eastern distributional limit of the *D. pictus* complex. Maluku is situated east of Weber's line which defines an important biogeographical transition zone between the faunas of Asia and Australia (HOW & KITCHENER 1997; DE LANG & VOGEL 2005). Zoogeographically, this region is more closely related to the Australo-Papuan fauna than to the Asian fauna and may be considered a unique biogeographic subregion in its own right as is also evident from the region's considerable level of endemism (e.g. HOW & KITCHENER 1997; NATUS 2005) which may rise in the near future as suggested by recent species-descriptions (e.g. ZUG 2004; EIDENMÜLLER & WICKER 2005).

Univariate analyses

Descriptive statistics for each secondary OTU are shown in Table 3.

Canonical Variate Analyses of secondary OTUs

The first Canonical Variate Analysis (CVA) was restricted to males. The object scores corresponding with the first two canonical variates ($p < 0.00001$ based on Wilks's Lambda) are shown in Fig. 3. OTUs 1, 2 and 3 are clearly separated. OTU 4, represented by three males, seems to overlap with OTUs 2 and 3. However, an analysis restricted to OTUs 2-4 demonstrates that it is actually strongly separated (Fig. 4).

The second CVA was restricted to females and a plot of the first two canonical variates ($p<0.00001$ based on Wilks's Lambda) is shown in Fig. 5.

Taxonomic interpretation

We refer OTU 2 (Sundaic region) to the name *Dendrelaphis pictus* (Gmelin, 1789) as the type locality of *D. pictus* was fixed as Java (Meise & Hennig 1932, invalid designation). A discussion of the type locality and the fixation of a neotype will follow in part 3 of this series on *D. pictus*. Although OTU 1 (Indochina) is separated morphologically from OTU 2, we also refer OTU 1 to *D. pictus* as gene flow across the Isthmus of Kra can not be ruled out on the basis of our data. Separate taxonomic status is given to both OTU 3 (Philippines + Sulawesi) and OTU 4 (Moluccas) which are therefore referred to with new names.

DESCRIPTION OF TAXA

Dendrelaphis marenae sp. nov. (Figs. 9-14 & 17)

Diagnosis – A species of *Dendrelaphis*, characterized by the combination of: (1) vertebral scales enlarged, equal to or larger than the dorsals of the first row; (2) 159-191 ventrals; (3) 136-167 divided subcaudals; (4) 15 dorsal scale rows at midbody; (5) anal shield divided; (6) 1 loreal scale; (7) 2 or 3 supralabials touching the eye; (8) 9 (rarely 10) supralabials; (9) a long first sublabial that touches 4 infralabials on average (range: 2-5); (10) 4 to 8 temporals; (11) 2 (rarely 1 or 3) postoculars; (12) maximum total length 131.0 cm; (13) very long tail, TAIL/TL 0.33-0.39; (14) a broad postocular stripe that starts on the postnasal or eye, covers the majority of the temporal region and extends onto the neck; (15) the presence of a light ventrolateral stripe and (16) black lines bordering the ventrolateral stripe absent or rudimentary.

Holotype – MNHN 1994.059: location Province Albay, island of Luzon, Philippines, Coll. Montamo-Ray, date 1880.

Paratypes – MNHN 5773 Albay, Lucon, Coll. Montano-Ray, date 1880; MNHN 1900.386 Manila, Coll. de Baer, date unknown, don. 10 November 1900; NMW 23661:5 Vingan, Luzon, Coll. Schadenberg, date unknown; NMW 23663:3 Zamboanga, Mindanao, Coll. Steindachner, date unknown, don. 1874; NMW 23668:6 N. Mindanao, Coll. Steindachner, date 1878; RMNH 40180 Menado, Celebes Coll. J. G. F. Riedel, date 1865; RMNH 40142 North Celebes, Coll. C. B. H. van Rosenberg, date 1864; RMNH 40145 Celebes, Coll. Van Delden, date 1836; SMF 70925 Luzon, Coll. Bregulla, date 18.4. 1966; SMF 74359 Panal Masbate, Coll. Gaulke, date 8.IV.1998; SMF 75151 Antique, Panay, Coll. Gaulke, date VI. 1996; SMF A4 Middle Luzon, Coll. v. Moellendorff, date 1888.

Additional material

Sulawesi: RMNH 838 (1)-(4) Menado, Celebes; RMNH 848 (1) Makassar; RMNH 40126 (1)-(5) Manado, Celebes; RMNH 40125 (1)-(5) N. Celebes; ZMA 21566 (1)-(2) Celebes.

Philippines: NMW 23662:1-2 Philippines, Moseley; NMW 23662:3 Philippines; NMW 23675:3,6,8,11 Philippines; RMNH 837 (1) - (3) Philippines.

Luzon: MNHN 1900.387-393 Manila; MNHN 1986.597 Manila; MNHN 1999. 8209-17 Manila; NMW 23661:1-4 Vingan,

Fig. 6: *Dendrelaphis pictus* (GMELIN, 1789) from Xepian, Laos. Photograph: Gernot VOGEL.
Abb. 6: *Dendrelaphis pictus* (GMELIN, 1789) von Xepian, Laos. Aufnahme: Gernot VOGEL.

Fig. 7: *Dendrelaphis pictus* (GMELIN, 1789) from Xepian, Laos. Photograph: Gernot VOGEL.
Abb. 7: *Dendrelaphis pictus* (GMELIN, 1789) von Xepian, Laos. Aufnahme: Gernot VOGEL.

Fig. 8: *Dendrelaphis pictus* (GMELIN, 1789) from Sarawak, Borneo. Photograph: Johan VAN ROOIJEN.
Abb. 8: *Dendrelaphis pictus* (GMELIN, 1789) von Sarawak, Borneo. Aufnahme: Johan VAN ROOIJEN.

Fig. 9: *Dendrelaphis marenae* sp. nov. from Cebu Island, Philippines. Photograph: Franz SEIDENSCHWARZ.
Abb. 9: *Dendrelaphis marenae* sp. nov. von der Insel Cebu, Philippinen. Aufnahme: Franz SEIDENSCHWARZ.

Table 4 (this and opposite page): Morphological and coloration characters of the paratypes of *Dendrelaphis marenae* sp. nov. Values of morphometric characters are unadjusted values. A - Collection number; B - Origin; C - Sex (*f* - female, *m* - male); D - Snout-vent length (cm); E - Tail-length (cm); F - Eye-diameter (mm); G - Ventrals; H - Subcaudals; I - Anal divided; K - Dorsal formula; L - Temporals; M - Supralabials; N - Supralabials touching the eye; O - Infralabials; P - Infralabials touched by first sublabial; R - Loreals; S - Postoculars; T - Vertebrals larger than dorsals of the first row; U - Clear ventrolateral stripe present; V - Number of black lines bordering the ventrolateral stripe; W - 'Postocular stripe' starts before the eye; X - Postocular stripe covers the majority of the temporal region and extends onto the neck; Y - Clear black bars on neck.

Tab. 4 (diese und gegenüberliegende Seite): Morphologische und Farbmerkmale der Paratypen von *Dendrelaphis marenae* sp. nov. Die Werte der morphometrischen Merkmale sind nicht angepaßt.

A B	MNHN 5773 Albay, Luzon	NMW 23661:5 Vingan, Luzon	MNHN 1900.386 Manila	RMNH 40180 Sulawesi	RMNH 40142 Sulawesi	RMNH 40145 Sulawesi
C	*f*	*f*	*f*	*f*	*f*	*m*
D	70.0	68.0	71.0	64.0	84.0	51.0
E	36.5	36.0	37.0	37.5	46.0	31.0
F	4.1/4.3	4.7/4.4	4.5/4.5	4.7/ 4.7	5.6/5.3	4.1/4.1
G	180	181	181	169	167	168
H	148	152	149	151	148	155
I	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
K	15-15-11	15-15-11	15-15-11	15-15-11	15-15-11	15-15-9
L	5/5	4/5	7/7	5/5	6/5	8/9
M	9/9	9/9	9/10	9/9	9/9	9/8
N	4,5,6/4,5,6	(4) 5,6/(4) 5,6	4,5,6/5,6	5,6/5,6	5,6/5,6	5,6/4,5
O	11/10	10/10	11/11	10/10	10/11	10/10
P	7-10/6-8	6-9/6-8	7-9/7-8	6-9/6-7	6-10/6-7	6-10/6-10
R	1/1	1/1	1/1	1/1	1/1	1/1
S	2/2	2/2	2/2	3/2	3/3	2/2
T	yes / ja	Yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
U	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
V	0	0	0	0	0	0
W	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
X	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
Y	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja

Luzon; SMF 18610-11 near Manila; SMF 18612, 18623, 18625-32, A1-6 middle Luzon; SMF 70936 Luzon.

Palawan: SMF 74465-66 Isumbo, Palawan; NMW 23661:6 Princesa Palawan; SMF 74356-58 Panal Masbate.

West Visayas: SMF 18636-41 Samar.

East Visayas: MNHN 5728 Mindanao; MNHN 1886.0144 Surigao, Philippines; SMF 74684 Mutia, Mindanao; ZMA 21568 Mindanao.

Sulu: SMF 74780-82 near Bongao, Bongao Isl. Sulu Archipel; SMF 74783 Bongao Hill, Bongao Isl. Sulu Archipel.

Description of the holotype (Figs. 12-14) – Adult female; SVL 62.0 cm; TAIL 34.0 cm; 171 ventral scales (1 preventral); 141 divided subcaudals; anal shield divided; dorsals in 15-15-11 rows; 9 supralabials (L+R), supralabials 5 and 6 touch the eye, the 4th just missing it (L), supralabials 4, 5 and 6 touch the eye (R); 10 infralabials (L+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 touches infralabials 6-10 (L), first sublabial touches infralabials 6-9 (R); 1 preocular, 2 postoculars (L+R); 1 loreal scale (L+R); 6 temporal scales (L+R); vertebral scales larger than dorsal scales of the first row; vertebral scales with concave posterior margin in first half of the body; eye-diameter 3.8 mm (L) and 3.9 mm (R); distance anterior border of the eye to posterior border of the nostril 4.1 mm (L), 4.2 mm (R); width of the snout measured at the position of the nostrils 3.5 mm; maximum width of the vertebral scale at the position of the middle ventral scale 3.8 mm; ground-color bluish grey with bronze parts of unshed skin; supralabials and throat yellow; venter anterior yellow getting yellowish-green posteriorly; a black postocural stripe starts on the eye, covers most of tem-

Table 4 (this and opposite page): Morphological and coloration characters of the paratypes of *Dendrelaphis marenae* sp. nov. Values of morphometric characters are unadjusted values.

Tab. 4 (diese und gegenüberliegende Seite): Morphologische und Farbmerkmale der Paratypen von *Dendrelaphis marenae* sp. nov. Die Werte der morphometrischen Merkmale sind nicht angepaßt. A - Sammlungsnummer; B - Herkunft; C - Geschlecht (*f* - Weibchen, *m* - Männchen); D - Kopf-Rumpf-Länge (cm); E - Schwanzlänge (cm); F - Augendurchmesser (mm); G - Ventralia; H - Subcaudalia; I - Anale geteilt; K - Dorsaliaformel; L - Temporalia; M - Supralabialia; N - Supralabialia mit Augenkontakt; O - Infralabialia; P - Infralabialia mit Kontakt zum ersten Sublabiale; R - Lorealia; S - Postocularia; T - Vertebralia breiter als die Dorsalia von Reihe 1; U - Ventrolateralstreifen deutlich; V - Anzahl schwarzer Linien, die den Ventrolateralstreifen begrenzen; W - 'Postokularstreifen' beginnt vor dem Auge; X - Postokularstreifen bedeckt den Großteil der Temporalregion und erstreckt sich bis zum Hals; Y - Schwarze Nackenstreifen deutlich.

A B	SMF 70925 Luzon	SMF A4 Middle Luzon	NMW 23668:6 N.Mindanao	NMW 23663:3 Zamboanga, Mindanao	SMF 74359 Panal Masbate	SMF 75151 Antique, Panay
C	*f*	*f*	*m*	*m*	*m*	*f*
D	73.5	64.0	56.5	31.0	54.0	70.0
E	37..5	32.5	34.0	18.0	30.0	37.5
F	4.7/4.6	4.7/4.5	3.9/3.9	3.0/2.9	4.0/3.9	5.0/4.9
G	180	170	167	162	172	180
H	138	148	157	142	149	149
I	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
K	15-15-11	15-15-11	15-15-11	15-15-9	15-15-9	15-15-11
L	4/4	7/8	7/7	6/6	6/5	6/6
M	9/9	9/8	9/9	9/9	9/9	9/9
N	4,5,6/4,5,6	5,6/4,5	(4) 5,6/(4) 5,6	(4) 5,6/(4) 5,6	4,5,6/4,5,6	4,5,6/4,5,6
O	10/11	10/10	11/10	10/10	10/10	10/10
P	6-10/6-10	6-9/6-7	7-10/6-8	6-9/6-9	6-7/6-8	7-9/6-10
R	1/1	1/1	1/1	1/1	1/1	1/1
S	1/1	2/2	2/3	2/2	2/2	2/2
T	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
U	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
V	0	1,5	0	0	0	0
W	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	no / nein
X	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
Y	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja

poral region and extends onto the neck where it breaks up into pronounced black bars; a yellowish ventrolateral stripe covers the first dorsal row and the lower half of the second dorsal row; the ventrolateral line is flanked above by a hardly visible black line. The specimen contains two eggs, and apparently had two more, judged from the shape of the body before the anal shield.

Description of the paratypes – A summary of the morphological and coloration characters of the paratypes is given in Table 4.

Etymology – This species is named in honour of Dr. Maren GAULKE, for her contributions to the knowledge of the herpetology of the Philippines. She collected some of the paratypes and several other specimens used in this study.

Sexual dimorphism – *D. marenae* exhibits a sexual dimorphism in the number of dorsal scale rows one head-length before the vent (DOR3). At this position, 65 out of 66 females possess 11 dorsal scale rows whereas 19 of the 34 males possess 9 dorsal scale rows ($p < 0.000001$). Furthermore, females tend to have less subcaudal scales (136-153 against 142-167; $p = 0.003$) and a correspondingly smaller relative tail-length (0.33-0.38 against 0.35-0.39; $p = 0.001$). Lastly, females are larger than males (see below).

Variation – In total, 100 specimens were examined of which 34 were males and 66 females. The largest specimen, a female from Sulawesi, measured 1,310 mm (SVL 875 mm, TAIL 435 mm). Two females from Luzon and Masbate had a longer SVL, but the tails were incomplete. The largest male, a specimen from Sulawesi, measured 1,025 mm (SVL 645 mm, TAIL 380 mm). The relative tail length is 0.33-0.39, based on 60 specimens. Fourty specimens had an incomplete tail.

Fig. 10: *Dendrelaphis marenae* sp. nov., from Mindoro Island, Philippines. Photograph: Ravan SCHNEIDER.
Abb. 10: *Dendrelaphis marenae* sp. nov., von der Insel Mindoro, Philippinen. Aufnahme: Ravan SCHNEIDER.

Fig. 11: *Dendrelaphis marenae* sp. nov., from Buton Island, Sulawesi, Indonesia. Photograph: Björn LARDNER.
Abb. 11: *Dendrelaphis marenae* sp. nov., von der Insel Buton bei Sulawesi, Indonesien.
Aufnahme: Björn LARDNER.

Fig. 12: MNHN 1994.059, Holotype of *Dendrelaphis marenae* sp. nov.
from Province Albay, Island of Luzon, Philippines. Photograph: Gernot VOGEL.

Abb. 12: MNHN 1994.059, Holotypus von *Dendrelaphis marenae* sp. nov.
aus der Provinz Albay auf der Insel Luzon, Philippinen. Aufnahme: Gernot VOGEL.

Fig. 13: Dorsal view of the head of MNHN 1994.059, Holotype of *Dendrelaphis marenae* sp. nov.
from Province Albay, Island of Luzon, Philippines. Photograph: Gernot VOGEL.

Abb. 13: Dorsalansicht des Kopfes von MNHN 1994.059, Holotypus von *Dendrelaphis marenae* sp. nov. aus
der Provinz Albay auf der Insel Luzon, Philippinen. Aufnahme: Gernot VOGEL.

The range of ventral scales is 161-188 for males, 162-191 for females. The range of subcaudals is 142-167 for males, 136-153 for females. If we exclude the population from Palawan, which needs further investigation (see below) we get: range of ventral scales is 161-188 for males, 162-183 for females. The range of subcaudals is 142-158 for males, 136-153 for females.

The subcaudals are divided in all cases. In the Philippine populations many tails were incomplete. This was also stated by LEVITON (1968). Anal shield divided; dorsals in 15-15-9 or 15-15-11 rows (see sexual dimorphism). Nine upper labials, rarely 10 (6 out of 200 cases), eye normally touched by upper labials 4 through 6, sometimes 4 just missing, rarely by 5 through 7. There are 18-23 infralabials (left and right added), normally 10 on each side. First infralabials touch at the mental groove; first sublabial touches 2-6 infralabials, mostly 4 or 5; one loreal scale, in one case 2, in two cases 0; one preocular scale (2 in 4 specimens), two postocular scales, rarely 1 (17 of 200 cases) or 3 (16 of 200 cases). There are 4-8 temporal scales, most commonly 6 (in 28 specimens). Vertebral scales usually larger than dorsal scales of the first row, equal in size in 11 of 200 specimens, smaller in 2 of 200. Relative eye size (EYED/EYEN) 0.8-1.2 with no obvious sexual dimorphism.

The color (in alcohol) is variable, depending in part on the initial preservation: bronze, brown, bluish or nearly black, below greenish. A light ventrolateral stripe is always present, but normally dull. A black stripe rarely borders the ventrolateral stripe and, when it does, usually only in the posterior part of the body. In a few specimens the ventrolateral stripe is bordered by one black stripe throughout the body and by two stripes in the posterior part of the body. A temporal streak starts on the postnasal, the loreal or the eye, covers most of the temporal region and extends onto the neck where it breaks up into pronounced black bars. The tongue is red.

The Inter-island variation in the number of ventrals is shown in Table 6. The average ventral count for the Sulawesi population is low in comparison with that for most insular populations the Philippines. However, the average number of ventrals as well as the range of the Sulawesi population (167 [161-172]; n = 21) are strikingly similar to those of the Mindanao population (168 [162-173]; n = 6). The same is true for the number of subcaudals (146 [136-158]; n = 15 versus 146 [136-157]; n = 4). In addition, the ranges of the ventral and subcaudal counts overlap strongly with those for other Philippine populations except Palawan. The population from Palawan Island differs strongly from the other populations with respect to the ventral and subcaudal counts. This is especially true for the ventrals in females in which the range overlaps only with that of specimens from Luzon ([181-191] against [167-184]). The subcaudal range of the two examined males with complete tail (162 and 167) does not overlap with the range obtained from males from other Philippine islands and Sulawesi (142-158). This population might warrant a taxonomic rank of its own and will be discussed again, when further material is available.

Distribution and natural history – *Dendrelaphis marenae* inhabits the Philippines and Sulawesi (Indonesia). It is known from the following Philippine Islands (LEVITON 1968):

Balabac, Bantayan, Basilan, Bohol, Busuanga, Calauit (GAULKE 1999), Camiguin, Candaraman, Catanduanes (ROSS & GONZALES 1992), Cebu, Culion, Kalotkot, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Samar, Siquijor, Siargao (ROSS & LAZELL 1990), Sulu-Archipel (Bongao).

Dendrelaphis pictus has additionally been recorded from the following Sulu Islands: Cagayan Sulu, Jolo, Lapac (GAULKE 1995). As we could not examine material from all these islands of the Sulu Archipelago and as Sulu Islands partly have a fauna similar to Borneo, we refrain from assigning these populations to *D. marenae* or *D. pictus* until material is available.

LEVITON (1968) found only frogs in the stomachs of specimens investigated. Based on this observation, he concluded that this species is partially terrestrial. He usually observed this species on lower bushes and trees. FERNER at al. (2001) encountered several specimens at night sleeping in stream-side vegetation. GAULKE (pers.

comm.) found it along roads and paths, in coconut plantations and at the edges of forests, and on clearances in forests.

On Mindoro this species is found at low elevations in gardens and plantations, where it is strictly arboreal. One specimen was found while consuming a frog in a bush. In captivity, house geckos and small skinks were consumed (LUTZ pers. comm.).

The biology on Sulawesi is summarized by DE LANG & VOGEL (2005). Specimens were found in the undergrowth of a primary and secondary forest, on the ground at a river bank while eating a frog, and in agricultural land on a small sawah dike. One specimen was even collected in the water of a wet rice field where it tried to hide. All were active during daytime. They moved astonishingly fast through the fields. When threatened these animals displayed a defensive behavior, which was primarily based on color. They enlarged the surface of the anterior body by laterally flattening the body and showing the blue interstitial skin. The Sulawesi specimens were not aggressive, but bit when approached from the front.

Comparison with *D. pictus* – The most prominent differences between *D. marenae* and *D. pictus* are as follows. The light ventrolateral line is rather faint in *D. marenae* whereas it is bright in *D. pictus* (Figs. 6-8, 17). In *D. pictus*, the ventrolateral line is bordered above and below by black lines. In *D. marenae*, these black lines are either absent or rudimentarily present. In *D. pictus*, the venter is off-white whereas it is yellowish in *D. marenae*. *Dendrelaphis marenae* has wide vertebral scales (Table 3), usually wider than the scales of the first dorsal row. In *D. pictus*, the vertebral scales are narrow, usually smaller than the scales of the first dorsal row. The body of *D. marenae* seems to be stouter than that one of *D. pictus*, but we did not verify this character. Finally, *D. marenae* has a substantially longer tail (average relative tail length 0.35 versus 0.33, Table 3) and correspondingly higher number of subcaudal scales (147 versus 133, Table 3).

Dendrelaphis grismeri sp. nov. (Figs. 15-16)

Diagnosis – A species of *Dendrelaphis*, characterized by the combination of: (1) vertebral scales enlarged, equal to or larger than the dorsals of the first row; (2) 176-193 ventrals; (3) 151-174 divided subcaudals; (4) 15 dorsal scale rows at midbody; (5) anal shield divided; (6) 1 loreal scale; (7) 2 or 3 supralabials touching the eye; (8) 9 supralabials; (9) a long first sublabial that touches 4 infralabials on average (range: 3-5); (10) 8 temporals on average (range: 6 to 10); (11) 2 to 3 postoculars; (12) maximum total length 148.0 cm; (13) very long tail, TAIL/TL 0.35-0.40; (14) a broad postocular stripe that starts on the postnasal or loreal, covers the majority of the temporal region and extends onto the neck; (15) the presence of a clear light ventrolateral stripe and (16) the presence of black lines bordering the ventrolateral stripe.

Holotype – RMNH 40176; location 'Wahaaij, côte N. O. de Céram' (Wahai, northeast coast of Seram); Coll. MOENS; Date 1862.

Paratypes – RMNH 851 (1-2): location Wahaaij, Cote N. O. de Céram, Coll. MOENS, date 1862; RMNH 5579 (1-2): location Boana, Coll. HOEDT, date 1863; RMNH 5621: location Manipa, Coll. HOEDT, date 1865; RMNH 40165 (1-2): location Ambon, Coll. F. KOPSTEIN, date 1922; ZMA 21564: location Ambon, Coll. ODIEN, date unknown; SMF 18594: location Moluccas (S. Ambon, Ema auf Leitimor), Coll. STRUBELL, date: 1890; RMNH 5418 (1-2): location Ceram, Coll. HOEDT, date unknown; MHNG 748.13: location Ambon, Coll. M. BEDOT & C. PICTET, date 1910.

Additional material – Moluccas (Ceram): RMNH 856; Moluccas (Ambon): ZMA 10532.

Description of the holotype (Figs. 15-16) – Subadult female; SVL 53.0 cm; TAIL 29.5 cm; 193 ventral scales (2 preventrals); 160 divided subcaudals; anal shield divided; dorsals in 15-15-11 rows; 9 supralabials (L+R), supralabials 5 and 6 touch the eye (L+R); 10 infralabials (L+R),

Fig. 14: Lateral view of the head of MNHN 1994.059, Holotype of *Dendrelaphis marenae* sp. nov. from Province Albay, island of Luzon, Philippines. Photograph: Gernot VOGEL.

Abb. 14: Lateralansicht des Kopfes von MNHN 1994.059, Holotypus von *Dendrelaphis marenae* sp. nov. aus der Provinz Albay auf der Insel Luzon, Philippinen. Aufnahme: Gernot VOGEL.

Fig. 15: RMNH 40176, Holotype of *Dendrelaphis grismeri* sp. nov. from Wahai, northeast coast of Seram, Indonesia. Photograph: Johan VAN ROOIJEN.

Abb. 15: RMNH 40176, Holotypus von *Dendrelaphis grismeri* sp. nov. von Wahai, Nordostküste von Seram, Indonesien. Aufnahme: Johan VAN ROOIJEN.

Fig. 16: Detail of RMNH 40176, Holotype of *Dendrelaphis grismeri* sp. nov. from Wahai, northeast coast of Seram, Indonesia. Photograph: Johan VAN ROOIJEN.

Abb. 16: Ausschnitt von RMNH 40176, Holotypus von *Dendrelaphis grismeri* sp. nov. von Wahai, Nordostküste von Seram, Indonesien. Aufnahme: Johan VAN ROOIJEN.

Fig. 17: Comparison of *Dendrelaphis marenae* sp. nov. (4 specimens on the right side) with *Dendrelaphis pictus* (3 specimens on the left side). Please note the difference in the ventrolateral stripe and the color of the belly. Photograph: Gernot VOGEL.

Abb. 17: Vergleich von *Dendrelaphis marenae* sp. nov. (4 Präparate rechts) mit *Dendrelaphis pictus* (3 Präparate links). Man beachte die Unterschiede beim Ventrolateralstreifen und bei der Bauchfärbung. Aufnahme: Gernot VOGEL.

Table 5 (this and opposite page): Morphological and coloration characters of the paratypes of *Dendrelaphis grismeri* sp. nov. Values of morphometric characters are unadjusted values. A - Collection number; B - Origin; C - Sex (*f* - female, *m* - male); D - Snout-vent length (cm); E - Tail-length (cm); F - Eye-diameter (mm); G - Ventrals; H - Subcaudals; I - Anal divided; K - Dorsal formula; L - Temporals; M - Supralabials; N - Supralabials touching the eye; O - Infralabials; P - Infralabials touched by first sublabial; R - Loreals; S - Postoculars; T - Vertebrals larger than dorsals of the first row; U - Clear ventrolateral stripe present; V - Number of black lines bordering the ventrolateral stripe; W - 'Postocular stripe' starts before the eye; X - Postocular stripe covers the majority of the temporal region and extends onto the neck; Y - Clear black bars on neck.

Tab. 5 (diese und gegenüberliegende Seite): Morphologische und Farbmerkmale der Paratypen von *Dendrelaphis grismeri* sp. nov. Die Werte der morphometrischen Merkmale sind nicht angepaßt.

A B	RMNH 851(1) Ceram	RMNH 851(2) Ceram	RMNH 5418(1) Ceram	RMNH 5418(2) Ceram	RMNH 5621 Manipa	RMNH 5579(1) Boana
C	*f*	*f*	*f*	*f*	*f*	*m*
D	77.5	31.5	68.0	30.0	55.0	59.0
E	-	17.0	-	-	31.5	35.0
F	5.2/5.0	3.0/3.0	4.9/4.7	3.0/3.1	4.0/4.0	4.6/4.6
G	193	193	189	192	183	176
H	-	159	-	-	151	154
I	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
K	16-15-11	16-15-11	16-15-11	17-15-11	15-15-11	15-15-11
L	7/7	9/10	8/9	6/7	6/6	8/8
M	9/9	9/9	9/9	9/9	9/9	9/9
N	5,6/5,6	5,6/5,6	4,5,6/4,5,6	5,6/5,6	5,6/5,6	5,6/4,5,6
O	10/10	10/10	10/11	10/11	10/11	10/10
P	6-8/6-9	6-9/6-9	6-9/6-9	6-9/7-10	6-9/6-10	6-8/6-8
R	1/1	1/1	1/1	1/1	1/1	1/1
S	2/2	2/3	2/2	2/2	2/2	2/2
T	yes / ja	equal / gleich	yes / ja	yes / ja	equal / gleich	equal / gleich
U	yes / ja	yes / ja	-	yes / ja	yes / ja	yes / ja
V	2	2	2	2	2	2
W	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
X	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
Y	yes / ja	yes / ja	no / nein	yes / ja	no / nein	no / nein

first infralabials in contact at the mental groove; first chinshield touches infralabials 1-5 (L+R); second chinshield touches infralabials 5 and 6 (L+R); first sublabial touches infralabials 6-10 (L), first sublabial touches infralabials 6-9 (R); 1 preocular (L+R); 2 postoculars (L), 3 postoculars (R); 1 loreal scale (L+R); 9 temporal scales (L+R); vertebral scales larger than dorsal scales of the first row; vertebral scales with concave posterior margin in first half of the body; eye-diameter 3.8 mm (L+R); distance anterior border of the eye to posterior border of the nostril 4.0 mm (L), 3.8 mm (R); width of the snout measured at the position of the nostrils 3.1 mm; maximum width of the vertebral scale at the position of the middle ventral scale 2.2 mm; background color olive-brown, based on color of unshed skin; supralabials and throat yellow; venter yellow; a black postocural stripe starts on the postnasal, covers the whole temporal region and extends onto the neck where it breaks up into pronounced black bars; a white ventrolateral stripe covers the upper half of the first dorsal row and the lower half of the second dorsal row; the ventrolateral line is flanked by black lines.

Description of the paratypes – A summary of the morphological and coloration characters of the paratypes is given in Table 5.

Etymology – This species is named in honour of Dr. L. Lee GRISMER (La Sierra University, La Siera, USA), for his major contributions to the knowledge of the herpetology of Southeast Asia and especially his investigations of the biodiversity of island herpetofaunas.

Sexual dimorphism – *D. grismeri*, like *D. pictus* and *D. marenae*, exhibits a sexual dimorphism in the number of dorsal

Table 5 (this and opposite page): Morphological and coloration characters of the paratypes of *Dendrelaphis grismeri* sp. nov. Values of morphometric characters are unadjusted values.

Tab. 5 (diese und gegenüberliegende Seite): Morphologische und Farbmerkmale der Paratypen von *Dendrelaphis grismeri* sp. nov. Die Werte der morphometrischen Merkmale sind nicht angepaßt. A - Sammlungsnummer; B - Herkunft; C - Geschlecht (*f* - Weibchen, *m* - Männchen); D - Kopf-Rumpf-Länge (cm); E - Schwanzlänge (cm); F - Augendurchmesser (mm); G - Ventralia; H - Subcaudalia; I - Anale geteilt; K - Dorsaliaformel; L - Temporalia; M - Supralabialia; N - Supralabialia mit Augenkontakt; O - Infralabialia; P - Infralabialia mit Kontakt zum ersten Sublabiale; R - Lorealia; S - Postocularia; T - Vertebralia breiter als die Dorsalia von Reihe 1; U - Ventrolateralstreifen deutlich; V - Anzahl schwarzer Linien, die den Ventrolateralstreifen begrenzen; W - 'Postokularstreifen' beginnt vor dem Auge; X - Postokularstreifen bedeckt den Großteil der Temporalregion und erstreckt sich bis zum Hals; Y - Schwarze Nackenstreifen deutlich.

A	RMNH 5579(2)	MHNG 748.13	RMNH 40165(1)	RMNH 40165(2)	ZMA 21564	SMF 18594
B	Boana	Ambon	Ambon	Ambon	Ambon	Ambon
C	*m*	*m*	*f*	*m*	*f*	*f*
D	59.0	66.0	67.0	62.0	58.5	93.0
E	-	42.5	-	-	37.0	55.0
F	4.2/4.4	4.9/4.8	5.0/4.9	4.4/4.4	4.1/4.1	5.4/5.4
G	177	178	181	181	181	183
H	131+	174	-	-	166	156
I	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
K	16-15-11	15-15-11	16-15-11	16-15-11	15-15-11	15-15-11
L	10/10	8/8	6/7	8/7	9/8	8/7
M	9/9	10/9	9/9	9/9	9/9	9/9
N	5,6/5,6	4,5,6/5,6	5,6/4,5,6	5,6/5,6	4,5,6/5,6	5,6/5,6
O	10/10	10/10	12/11	10/10	11/11	12/12
P	6-8/6-8	6-8/6-9	7-10/7,8	6-8/6-8	7-10/6-10	6-8/7,8
R	1/1	1/1	1/1	1/1	1/1	1/1
S	2/2	2/2	2/3	2/2	3/3	2/2
T	yes / ja	yes / ja	yes / ja	yes / ja	equal / gleich	equal / gleich
U	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
V	2	2	2	2	2	2
W	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	no / nein
X	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja	yes / ja
Y	no / nein	yes / ja	no / nein	no / nein	yes / ja	yes / ja

scale rows one head-length before the vent (DOR3). At this position, all 10 females possess 11 dorsal scale rows whereas 2 of the 4 males possess 9 dorsal scale rows. Sexual dimorphisms in other characters were not established though this may be due to the small sample of males and associated low statistical power.

Distribution and natural history – The examined specimens of *D. grismeri* originate from the Moluccan islands Ceram, Ambon, Boana and Manipa. BOULENGER (1894) provides an additional record from Ceram and a record from Misol. Both records are authentic beyond doubt given the high number of ventrals and subcaudals mentioned by BOULENGER (190, 158 and 185, 160 respectively). Nothing is known about its biology.

Comparison with *D. pictus* and *D. marenae* – The most prominent differences between *D. grismeri*, *D. marenae* and *D. pictus* are as follows. The light ventrolateral line is rather faint in *D. marenae* whereas it is bright in *D. pictus* and *D. grismeri*. *Dendrelaphis marenae* has wide vertebral scales (Table 3), usually wider than the scales of the first dorsal row. In *D. pictus* and *D. grismeri*, the vertebral scales are narrow, usually smaller than the scales of the first dorsal row. *Dendrelaphis grismeri* has a higher number of temporal scales (8 on average versus 6 and 6 respectively, Table 3). *Dendrelaphis grismeri* has a longer tail (relative tail length 0.37 on average versus 0.33 and 0.35 respectively, Table 3) and correspondingly higher subcaudal count (160 on average versus 133 and 147 respectively, Table 3). Finally, *D. grismeri* has a higher number of ventral scales (183 on average versus 169 and 173 respectively, Table 3).

DISCUSSION

The application of the single binomen *D. pictus* obviously does not do justice to the complex biological reality and evolutionary history of the clade to which it refers. The taxonomic arrangement presented here certainly is a more appropriate one though not devoid of uncertainties. Taxonomic interpretation of differences between allopatric populations is generally fraught with difficulties (e.g. FROST & HILLIS 1990; ZINK & MCKITRICK 1995; ALSTRÖM 2006). The current case is undoubtedly one of the more complicated given the large number of insular populations as well as the complex geological history of the area under investigation (INGER & VORIS 2001). In applying a General Lineage Species Concept (DE QUEIROZ 1998, 2005), independence of lineages is the key element in the evaluation. The applied criteria of geographic isolation and diagnosibility are merely indirect evidence for independence. Subsequently, type I as well as type II taxonomic errors (e.g. FROST & HILLIS 1990) can not be ruled out. For instance, in combining primary OTUs into secondary OTUs, the assumption is made that the primary OTUs constituting a secondary OTU evolve interdependently through sporadic gene flow as a result of chance dispersal. This assumption may not be valid in all cases. A point in case is the Sulawesi population which is grouped with the Philippine populations in a single secondary OTU. The strong geographic isolation of Sulawesi implies a slim chance of dispersal to or from the Philippines. On the other hand, the close phenetic resemblance between Sulawesi and Philippine populations, particularly Mindanao, does suggest relatively recent gene flow. Therefore, we refrain from assigning separate taxonomic status to the Sulawesi population although it might in fact represent an independent lineage. In a similar vein, the Indochinese population might in reality be reproductively and/or geographically fully isolated from the Sundaic population, thus constituting an independent lineage. Finally, the population from Palawan appears to be morphologically strongly distinct from the other Philippine populations and as such might also represent an independent lineage. However, due to the small sample size and associated uncertainties, this population is not given distinct status but is referred to the name *D. marenae*. Given the considerations mentioned above, the taxonomic arrangement presented here is probably conservative, entailing a higher chance of a type II error than a type I error.

In the context of this review, the description of *Dendrelaphis pictus* (GMELIN, 1789) was examined as a more or less mandatory part. The description was provided in Latin and is unfortunately overly concise. The translation is as follows: "*Colubrid snake with bluish dorsum, a white coloration laterally bordered by a black stripe*. *Pointed snout. 172* [ventrals]-*142* [subcaudals]". The "white coloration laterally bordered by a black stripe" very probably refers to the light ventrolateral line and adjoining black lines, which are invariably present in *D. pictus*. The "bluish dorsum" is not informative as the original coloration of conserved specimens often turns into blue. Finally, the number of ventrals and subcaudals, though relatively high, fall within the range of Sundaic *D. pictus* as recorded in this study (Table 3, results section). In addition, GMELIN (1789) certainly did not count ventrals according to the method of DOWLING (1951) which generally results in a slightly lower count. Thus, given this description, there is no reason to doubt that the name *D. pictus* is currently being applied to the species it originally referred to. Moreover, even if there had been doubt, the name *D. pictus* has been used unambiguously in so many herpetological works that any suggested nomenclatural change would probably be opposed by the regulations provided by the International Code of Zoological Nomenclature (ICZN, 1999).

With the conclusion of this study, the systematics of *Dendrelaphis* are still far from complete as well as far from unambiguous. For instance, SMITH (1943) synonymized the Indian taxon *D. proarchus* WALL, 1909 and *D. pictus ngansonensis* BOURRET, 1935 with *D. pictus* GMELIN, 1789 without providing a satisfacory foundation for his decision. *Dendrelaphis pictus*

Table 6: Variation of the ventral scale counts in *Dendrelaphis marenae* sp. nov. according to the faunal areas.
Tab. 6: Variationsbreite der Ventralia bei *Dendrelaphis marenae* sp. nov., nach Faunengebieten aufgetrennt.

-	Male / Männchen		Female / Weibchen	
	Leviton (1968) and this study / Leviton (1968) und diese Arbeit			
Faunal area / Faunengebiet	N	Range / Spannweite	N	Range / Spannweite
Luzon	26	170-181	49	167-184
Mindoro	1	177	1	179
Palawan	15	174-186	15	181-191
West Visayas	7	169-176	15	172-181
East Visayas	4	163-174	10	162-178
Mindanao	17	164-184	22	159-173
Sulu Isl.	4	165-172	2	174-178
without exact locality / Fundort nicht genau bekannt	2	172-172	8	170-180
Total Philippines / Philippinen insgesamt	76	163-186	122	159-191
Sulawesi	8	161-170	13	162-172
Dendrelaphis marenae sp. nov.	84	161-186	135	159-191

ngansonensis was later shown to be a full species (Ziegler & Vogel 1999) but the status of *D. proarchus* was never reinvestigated. Thus, the next part of this review will focus on several western, mainly Indian, taxa.

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APPENDIX

Examined specimens of *Dendrelaphis pictus*

Myanmar: MNHN 1893.398, NMW 23686:1, NMW 23686:2, ZSM 13/1993, NMW 23674, NMW 23676:2; Laos: MNHN 1896.650, MNHN 1896.651, MNHN 1963.750, MNHN 1962.283, MNHN 2004.0263, MNHN 2004.0253, MNHN 2004.0254, MNHN 2004.0251; Vietnam: MNHN 1948.82, MNHN 1901.505, MNHN 1909.21, MNHN 1885.288, MNHN 1885.288, MNHN 1920.207, PSGV 538L, PSGV 0578K, NMW 23660:1, NMW 23660:8, MNHN 1974.1320, MNHN 1974.1321; Cambodia: MNHN 1970.490-493, MNHN 1970.506; Thailand: RMNH 40174, RMNH 40175 (1) - (8), MNW 23673:1-2; Peninsular Malaysia: MNHN 1899.167, NMW 23684:2-3; Sumatra: ZMA 21558 (1)-(2), ZMA 21561, ZMA 21562, RMNH 844 (1)-(3), RMNH 11458 (1)-(2), ZMA 13332 (1)-(2); Borneo: NMW 23664:2, MNHN 1891.72, RMNH 866 (1)-(4), RMNH 8212 (1)-(3), RMNH 841 (1)-(3), RMNH 834 (1)-(2); Java: NMW 23675, NMW 23663:1, RMNH 8998, RMNH 40143, RMNH 9002, RMNH 36453, RMNH 36451, RMNH 36452, RMNH 36450, RMNH 35090, ZMA 10522 (1)-(4), ZMA 9442 (1)-(2), RMNH 40104, RMNH 9025 (1)-(3); Bali: ZMA 14454 (1)-(2); Lombok: ZMA 13688 (1)-(5).

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