On the discovery and origin of a Javan population of the Indochinese colubrid snake *Dendrelaphis subocularis* (Boulenger, 1888): a multivariate study

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Abstract

The colubrid snake *Dendrelaphis subocularis* is distributed throughout Indochina, the southern limit of its range corresponding with the Isthmus of Kra, an important biogeographic barrier that separates the Indochinese biota from the Sundaic biota. This study presents five museum specimens that represent a hitherto unknown population that inhabits the Sundaic island Java. Thus, the distribution of *Dendrelaphis subocularis* is disjunct, with the Javan population being isolated by 2000 kilometres from the nearest mainland population. Principal Components Analysis was applied to morphological data taken from the five Javan specimens as well as from 26 museum specimens of Indochinese origin. Regression analysis of the spatial pattern of the resulting scores indicated that: 1) the Javan population exhibits negligible morphological differentiation, and 2) a phenetic cline exists from which the Javan population does not appreciably deviate in spite of its isolated status. These findings suggest a vicariant origin of the Javan population entailing climatic changes and formation of land bridges during Pleistocene glaciations. The Javan and Indochinese populations represent independent sister lineages, and are therefore valid species within the framework of a lineage-based species concept. However, to conform to current taxonomic practice, the Javan population is not named separately due to the fact that it is not diagnosable.

Contents

Introduction

The colubrid snake *Dendrelaphis subocularis* (Boulenger, 1888) is widespread in Indochina, the southern-most locality record corresponding with the Isthmus of Kra (Boulenger, 1894; Wall, 1921; Smith, 1930, 1943; Taylor, 1965; Vogel, 1990; Cox *et al*., 1998; Zug *et al*., 1998; Grismer *et al*., 2007). The Isthmus of Kra represents an important phytogeographical and zoogeographical transition zone between the Indochinese and Sundaic regions (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 applicable to the genus *Dendrelaphis*. The Sundaic species *D. haasi* Van Rooijen and Vogel, 2008 and *D. kopsteini* Vogel and Van Rooijen, 2007 have their northern distributional limits on the Thai-Malay Peninsula. In addition, Indochinese and Sundaic populations of the widely distributed *Dendrelaphis pictus* have been shown to be morphologically distinct (Vogel and Van Rooijen, 2008). Given the known distribution of *D. subocularis* and biogeographic importance of the Isthmus of Kra, we were quite surprised to find several museum specimens that had been collected on Java. All had been erroneously identified as *D. pictus* (Gmelin, 1789). These specimens thus represent a population that is isolated by 2000 km from the nearest population on mainland Southeast Asia and that is separated from the latter by the Isthmus of Kra as well as a sea barrier.

In this study, multivariate analyses of morphological data were used to determine the degree of morphological divergence between the Javan population and

the mainland Asia population. The results are evaluated in the light of a vicariance-hypothesis and the taxonomic status of the Javan population is discussed within the framework of a lineage-based species concept (*e.g.* De Queiroz, 1998, 2005).

Material and methods

The following material was examined for this study (museum abbreviations follow Leviton *et al.* (1985)): Java: RMNH 6681 (46), RMNH 6681 (60), RMNH 6681 (106), RMNH 40107, NMW 23675:7; Vietnam: MNHN 1908.55; BMNH 1921.4.1.15; Myanmar: CAS 215552, CAS 214124, CAS 215512, CAS 215721, CAS 233045, CAS 214028, CAS 240762, BMNH 1946.1.6.10; Thailand: FMNH 180040, FMNH 180039, FMNH 180037, FMNH 180035, FMNH 180042, FMNH 180038, FMNH 180036, FMNH 178541, FMNH 169419, BMNH 1974.5184, BMNH 1938,8.7.53, BMNH 1938,8.7.52, BMNH 1914.5.11.3, BMNH 1974.5185; China: CIB 9061, KIZ 75I305.

For each examined specimen, 19 characters pertaining to body proportions and scalation were recorded (Table 1). In addition, longitude and latitude were determined for inclusion in an analysis of geographic variation. The coordinates were taken directly from the field notes or were obtained by translating locations to coordinates. EYED, EYEN, HL and WSNT were measured with a slide calliper to the nearest 0.1 mm. EYED and EYEN represent the average of left and right measurements. HL was measured from the back of the upper jaw to the tip of the snout. WSNT was measured between the prenasals. SVL was measured to the posterior margin of the anal plate by marking the length on a piece of string and subsequently measuring the position of the mark to the nearest 0.5 cm. TAIL was measured to the nearest 0.5 cm by straightening the tail against a ruler. VENT was determined following Dowling's method (1951). SUBC was counted on one side, the terminal scute was excluded. The last infralabial was defined as the infralabial still covered completely by the last supralabial. 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 posterior most temporal scales were defined as the scales of which more than half of the area lies in front of an imaginary line that runs from the apex of the last supralabial to the posterola-

Table 1. List of characters used in this study and their abbreviations.

abbreviation	character
EYED	horizontal diameter of the eye
EYEN	distance from anterior border of the eye to posterior border of the nostril
TAIL	tail-length
HL	length of the head
WSNT	width of the snout
SVL	snout-vent length
SEX	sex
VENT	number of ventrals
SUBC	number of subcaudals
DOR1	number of dorsal scale rows 1 head-length behind the head
DOR2	number of dorsal scale rows at the position of the middle ventral
DOR3	number of dorsal scale rows 1 head-length before the tail
SUBL	number of infralabials in contact with the first sublabial
SL1	number of supralabials
SL2	number of supralabials touching the eye
LOR	number of loreals
INFR	number of infralabials
TEMP	number of temporals
POC	number of postoculars
PARSC	number of scales bordering the posterior edge of the parietal scales

teral corner of the parietal.

Specimens were allocated to two Operational Taxonomic Units (OTU's): Indochina and Java. The characters EYED, EYEN, TAIL, HL, WSNT, VENT, SUBC, INFR, TEMP and PARSC were subjected to a Principal Components Analysis (PCA, *e.g.* Cramer, 2003). Other characters were excluded as they exhibited limited variation. Only specimens with complete tails were included, reducing the sample to 26 specimens. Morphometric variables (EYED-WSNT) were first adjusted to a common SVL of 46.5 cm to correct for potential ontogenetic variation between the population samples (*e.g.* Thorpe, 1975, 1983; How *et al.*, 1996; Turan, 1999). The following allometric equation was applied: $X_{adj} = X - \beta(SVL - SVL_{mean})$ where X_{adj} is the adjusted value of the morphometric variable; X is the original value; SVL is the snout-vent length; SVL_{mean} is the overall mean snout-vent length; β is the coefficient of the linear regression of X against SVL. The object scores corresponding with those principal components (PC's) having eigenvalues > 1, were subjected to a linear regression analysis. Longitude, latitude, SEX and OTU (the latter two in the form of dummy-variables) were included as

independent variables. The objective of this analysis was to determine whether a discrete morphological transition from Indochina to Java was in evidence, possibly superimposed on a geographic cline. Additionally, the PC-scores were plotted against longitude and latitude in order to illustrate potential morphological clines as well as transitions and to check for deviations from linearity. All statistical analyses were carried out with the software SPSS (2006, SPSS for Windows 14.0.2., Chicago: SPSS Inc.).

Fig. 1. RMNH 6681(46), *Dendrelaphis subocularis*; Goenoeng Simpai, W. Java, 2100 ft.; Febr. 1932; C.P.J. de Haas.

Fig. 2. RMNH 40107, *Dendrelaphis subocularis*, Boie and Macklot, Java. Note the single, broad, supralabial bordering the eye (indicated by an arrow).

Table 2. Locations and a selection of measurements with respect to the 5 museum specimens of *D. subocularis* collected on Java.

location	RMNH 6681 (46) Goenoeng Simpai, Java	RMNH 6681 (60) Goenoeng Simpai, Java	RMNH 6681 (106) Goenoeng Simpai, Java	RMNH 40107 Java	NMW 23675:7 Tasikmalaya, Java
SEX	f	m	f	f	m
TAIL	22.5	16.5	12.0	23.5	-
SVL	60.0	46.0	34.0	60.5	37.5
VENT	171	162	165	161	160
SUBC	91	95	99	97	-
DOR2	15	15	15	15	15
SL1	8	8	8	8	8
SL2	1	1	1	1	1

Results

Table 2 provides locations and a selection of measurements pertaining to the museum specimens collected on Java. Characteristic for *D. subocularis*, and unique within its genus, is the fact that a single, very broad, supralabial invariably borders the eye. The name subocularis ('beneath the eye') was derived from this conspicuous character. In addition, a low number of subcaudals (74-105) is highly characteristic for this species (Meise and Henning, 1932). The combination of these two characters leaves no room for misidentifications. As the Javan specimens exhibit this diagnostic combination of characters (see SL2 and SUBC in Table 2), the population they represent is at the least closely related to *D. subocularis*. Illustrations of two Javan specimens are provided in Figs 1-2.

The first 3 PC's had eigenvalues > 1 and were thus used in further analyses. Together, these PC's represented 65% of the information that was present in the original variables. Component loadings (correlations between the original variables and the PC's) are giv-

en in Table 3. Figs 3-4 depict the scores on PC1 against longitude and latitude respectively. A morphological cline is in evidence. This is borne out by regression analysis. Both longitude (P<0.0001) and latitude (P<0.0001) explain a significant amount of variation in PC1-scores. Together, these independent variables explain 74% of the variation in PC1-scores. Inclusion of OTU and sex in the regression model did not have added value (P>0.2 for both). Thus, there is

Table 3. Component loadings.

	PC1	PC2	PC3
EYED	.69	-.42	.26
EYEN	.52	.03	.58
TAIL	-.76	-.19	.38
HL	.28	-.62	-.41
WSNT	.47	.05	.39
VENT	-.34	.56	-.42
SUBC	-.78	.11	.30
INFR	-.03	.70	.37
TEMP	.46	.64	.15
PARSC	.51	.55	-.46
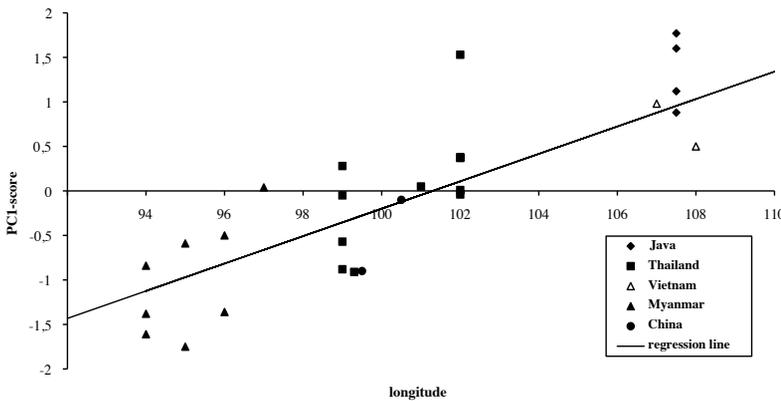
Fig. 3. PC1-scores in relation to longitude. The depicted regression line was fitted on the basis of Indochinese specimens.
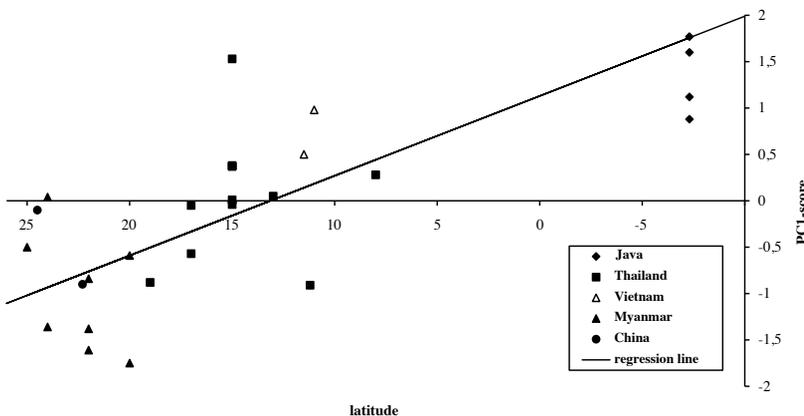
Fig. 4. PC1-scores in relation to latitude. The depicted regression line was fitted on the basis of Indochinese specimens.

no evidence of a superimposed morphological transition from Indochina to Java, despite the obvious absence of gene flow. With regard to PC2 scores, geographic coordinates did not explain a significant amount of variation. Some sexual dimorphism (P=0.01) as well as a barely significant (P=0.05) effect of OTU was established. As for PC3-scores, none of the independent variables explained a significant amount of variation.

Discussion

The first question that needs to be addressed is whether the locality data of the five Javanese specimens might have been incorrect, the specimens in fact originating from Indochina. This is extremely unlikely. The five specimens have been collected independently by three scientists. In addition, one was collected by Boie and Macklot and three by De Haas, scientists who are known to have collected extensively on Java but never in Indochina. Finally, three specimens (collected by De Haas) were individually provided with detailed locality data as well as original field numbers. Thus, we can safely assume that the examined material indeed originated from Java.

Three hypotheses regarding the origin of this population can be put forward. The first entails a vicariant event during the Pleistocene. During Pleistocene glaciations, Sundaic islands became united to a single landmass which in turn became connected to the Asian mainland (How and Kitchener, 1997; Voris, 2000; Inger and Voris, 2001; Sathiamurthy and Voris, 2006). Fig. 5 (Sathiamurthy and Voris, 2006) shows the map of Southeast Asia, illustrating the depth contours of 80 meters below present level. During the past 17,000 years, sea levels have been at or below that level for a period of roughly 5000 years (Voris, 2000). At that sea level, Java was amply connected to mainland Asia.

In addition to the formation of land bridges, major climatic changes occurred, entailing lower temperatures, decreased rainfall and increased seasonality. A corridor of low rainfall and seasonality that ran from the mainland to eastern Java probably came into existence (Heaney, 1991). This corridor may have provided habitats that enabled *D. subocularis* to expand its range southward to Java. When sea levels rose in geologically recent times, the Javan population would have become isolated and changes in climate and vegetation may have eliminated other populations south of the Isthmus of Kra. A similar scenario has been put forward

with regard to the viperid snake *Daboia russelii* (Shaw and Nodder, 1797). *Daboia russelii* is widespread in South Asia. It does not occur south of the Isthmus of Kra, with the notable exception of populations on Java and several of the lesser Sunda Islands. Wüster *et al*. (1992) studied the population systematics of this species on the basis of multivariate analyses of morphological data. The Javan population was shown to cluster with the mainland Asia populations. Given the limited phenetic divergence of the Javan population from the mainland population, Wüster *et al*. (1992) concluded that a founder effect (Mayr, 1954) had probably not occurred. Consequently, a vicariant origin of the Javan population was assumed.

The second hypothesis as to the origin of the Javan population entails a sweepstake dispersal event. For most species inhabiting the larger Sunda Islands and their off shore islands, a vicariant origin of the constituent populations is considerably more likely than a dispersal origin, as the latter would require a succession of rare events (*e.g.* Zink *et al*., 2000). In the case of *D. subocularis* however, an over-water sweepstake dispersal event is not necessarily less likely than diffusion dispersal from Indochina to Java across Pleistocene land bridges followed by the extinction of the intermediate
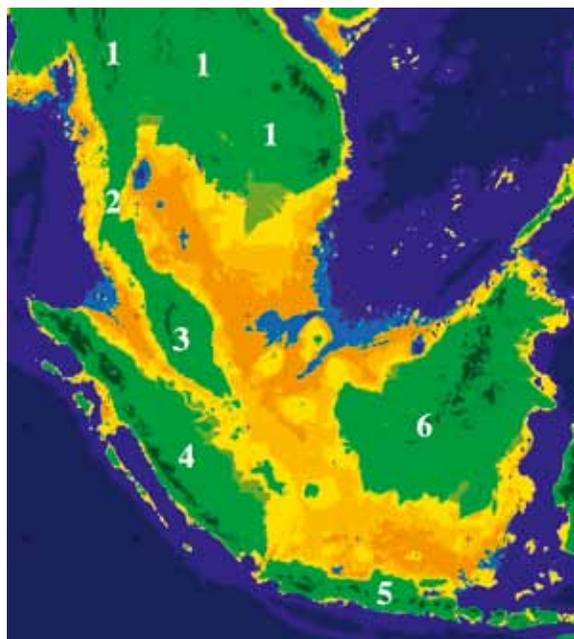
Fig. 5. Map of Southeast Asia (Sathiamurthy and Voris, 2006). Green parts represent currently exposed areas. Yellow parts represent areas that were exposed when sea levels were 80 meters below present level. 1) Indochina; 2) Isthmus of Kra; 3) Peninsular Malaysia; 4) Sumatra; 5) Java; 6) Borneo.

populations on Sumatra and Peninsular Malaysia (*e.g.* Ronquist, 1997).

The final hypothesis entails colonization of Java by a human vector. Colonization by accidental human transport is considered unlikely, although it can not be ruled out. One specimen was collected by Boie and Macklot whose joint stay on Java lasted from 1826 to 1827 (Husson and Holthuis, 1955; Holthuis, 1995). Thus, the population already inhabited Java in a time when human transport over long distances was still uncommon. Furthermore, *D. subocularis* is not known to be an inhabitant of cultivated areas. As a consequence, it is rather unlikely to end up in a human vector in the first place. Finally, a founder effect associated with human introduction followed by adaptation due to local selection pressures (not counteracted by gene flow) may be expected to result in substantial differentiation (*e.g.* Mayr, 1954), even in a limited number of generations (*e.g.* Losos *et al*., 1997; Herrel *et al*., 2008). Obviously, this also holds true for a sweepstake dispersal event. The results of this study demonstrate that the Javan population of *D. subocularis* exhibits no appreciable phenetic divergence from its mainland sister population. Moreover, the phenetic properties of the Javan population correspond with an extension of a mainland cline. These findings support a vicariance-hypothesis according to which *D. subocularis* has in the recent past inhabited the region between the Isthmus of Kra and Java. The existing evidence for a Pleistocene corridor of favourable climatic conditions (Heaney, 1991) adds to the likelihood of a vicariant origin. Thus, *D. subocularis* has probably migrated southward during Pleistocene sea level regressions using a corridor of suitable habitat that came into existence due to climatic changes. When sea levels rose and climate changed, the population that inhabited the region between the Isthmus of Kra and Java was eliminated. For some reason, a relict population survived on Java.

In the above scenario, *D. subocularis* is assumed to have expanded its range southward to Java in stead of northward to Indochina. This assumption is based on the following arguments. First, *D. subocularis* is widely distributed in Indochina. Second, three species from west Asia (*D. tristis* (Daudin, 1803), *D. schokari* (Kuhl, 1820) and *D. chairecacos* (Boie, 1827)) appear to be closely related to *D. subocularis*. These species share a suite of characters with *D. subocularis*, namely a stocky build, a vertebral stripe and narrow vertebral scales. As such, the four species constitute a distinct group within *Dendrelaphis*. Indeed, *D. subocularis* was in the past considered a subspecies of *D. tristis* (Meise and Hen-

ning, 1932). Thus, the cradle of *D. subocularis* is undoubtedly situated in mainland Asia.

Of course, one cannot rule out the possibility that *D. subocularis* in fact does inhabit the region between the Isthmus of Kra and Java. After all, absence of evidence does not equal evidence of absence. Indeed, the Javan population was also hitherto unknown due to the fact that the existing museum specimens had been identified incorrectly. However, the occurrence of *D. subocularis* in the region between the Isthmus of Kra and Java is very unlikely for several reasons. First, *D. subocularis* is actually one of the most easily identified members of its genus. The fact that the Javan specimens have been misidentified as *D. pictus* is actually hard to grasp. Furthermore, an extensive set of recent surveys (see Grismer and Khang Aun, 2008 for review), particularly in West Malaysia, has not produced a specimen of *D. subocularis*. Finally, in the context of a revision of the taxonomy of the genus *Dendrelaphis* (Vogel and Van Rooijen, 2007, 2008; Van Rooijen and Vogel, 2008a, b, c, 2009), the authors have examined, and re-identified, more than 700 Southeast Asian specimens from 20 museum collections. The efforts did not yield a *D. subocularis* from Sundaland apart from the Javan specimens.

The taxonomic status of the Indochinese and Javan sister populations of *D. subocularis* are here evaluated in the light of a General Lineage Species Concept (GLSC, De Queiroz, 1998, 2005). According to this concept, species are equivalent to segments of independently evolving lineages. Given the unequivocal genetic isolation of the Javan population of *D. subocularis*, it undoubtedly represents an independent lineage. Consequently, it could legitimately be named and described within the framework of a GLSC. However, most taxonomists are reluctant to name nondiagnosable lineages. McGuire and Heang (2001) and McGuire *et al*. (2007), in their study of allopatric populations of the agamid genus *Draco*, explicitly discussed the issue of nondiagnosable lineages within the context of a GLSC. They refrained from recognizing nondiagnosable lineages as species, so as to avoid taxonomic arrangements that could be conceived as controversial and whose usefulness for future users might be questionable. The approach of those authors is followed here. Thus, the Javan sister lineage of *D. subocularis* is not named separately.

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