

Population affinities of the asiatic cobra (*Naja naja*) species complex in south-east Asia: reliability and random resampling

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The population systematics of the cobras of the genus *Naja* in southern Thailand, Malaysia and Indonesia are investigated, using multivariate analysis of a large number of morphological characters. These populations are found to constitute three distinct groups: a northern form, which occurs in Thailand and northern Peninsular Malaysia; an equatorial form, which occurs in southern Thailand, Peninsular Malaysia, Sumatra and Borneo; and a southern form, which occurs on Java and the Lesser Sunda Islands. The first two forms are sympatric in northern Peninsular Malaysia and southern Thailand, and therefore constitute separate species. This is of importance for the treatment of snakebite in the region. The distribution of the three forms can be related both to present ecological conditions and to Pleistocene geological and climatic events. The reliability of the results is demonstrated by the relationship between character number and congruence of patterns of geographic variation, investigated by random resampling. The pattern of geographic variation within two of the three main forms is investigated and related to current ecological conditions and Pleistocene events.

KEY WORDS:—*Naja* – population systematics – multivariate morphometrics – geographic variation – congruence – random resampling – sympatry – snakebite – south-east Asia – biogeography.

CONTENTS

Introduction	392
Materials and methods.	394
Materials	394
Characters	394
Selection of operational taxonomic units	394
Multivariate techniques	395
Results	396
Population affinities in south-east Asia	396
Reliability of the results	396
Patterns of within-group geographic variation	397
Discussion	398
Population affinities	398
Reliability of the pattern of geographic variation	400
Sympatry between the northern and the equatorial form	401
Nomenclature.	403
Within-group variation	404
Acknowledgements	405
References.	405
Appendix 1	407
Appendix 2	408

INTRODUCTION

In Asia, the cobras of the genus *Naja* constitute a widespread group, ranging from the Caspian Sea to China, Indonesia and the Philippines. The taxonomy of these snakes has always been the subject of considerable confusion and controversy.

Most authorities dealing with the systematics of the group have considered all Asiatic populations as subspecies of a single species, *Naja naja* (L.). The confusion regarding the taxonomy of these snakes is particularly acute in the south-eastern part of their range, that is, southern Thailand, Malaysia and Indonesia. De Rooij (1917) and de Haas (1950) recognized no less than three subspecies from Sumatra and Borneo, and two from Java and Sulawesi. More recently, many herpetologists, such as Klemmer (1963), Leviton (1968) and Golay (1983), have recognized four subspecies from this area (Fig. 1): *N. n. kaouthia* Lesson 1831 (type locality: Bengal), which ranges from India to northern Peninsular Malaysia; *N. n. sputatrix* Boie 1827 (type locality: Java), from Peninsular Malaysia, Java, Sulawesi (formerly Celebes), Bangka, Belitung, the Lesser Sunda Islands and the Riau Archipelago; *N. n. sumatrana* Müller 1890 (type locality: Solok, south-western Sumatra), from Sumatra; and *N. n. miolepis* Boulenger 1896 (type locality: Sarawak), from Borneo and Palawan.

Deraniyagala (1960, 1961) accorded specific status to *N. kaouthia* on the basis of sympatry with *N. naja* in Bengal, and to *N. sputatrix* on the basis of a few ill-defined and poorly substantiated characters, his taxonomy in the area under consideration here being as follows: *N. kaouthia kaouthia* in Thailand and northern Malaysia, *N. sputatrix sputatrix* on Sumatra and Java, *N. s. malayae* in Peninsular Malaysia, *N. s. miolepis* on Borneo and *N. s. celebensis* on Sulawesi. At the same time, he suggested the existence of a wide zone of introgression between *N. kaouthia* and *N. sputatrix malayae* in Peninsular Malaysia, thus contradicting his earlier statement that the two forms are separate species. Deraniyagala's contributions have had little influence on later workers.

More recently, Viravan *et al.* (1986) and Warrell (1986) have also suggested specific status for *N. kaouthia*, and Warrell (1986 and personal communication) and Theakston (personal communication) have noted the occurrence in central and northern Thailand of a heterogeneous group of spitting cobras which they provisionally assigned to *N. n. sputatrix*.

All these classifications are based on few specimens and a very small number of scalation and colour pattern characters. Indeed, some workers based their conclusions on unpublished information, without ever examining any specimens themselves. Not surprisingly, the resulting taxa are generally poorly defined, and their geographic distribution is frequently incoherent—especially that of the conventional *N. n. sputatrix* (Fig. 1).

Underwood (1967) emphasized the desirability of using a large number of characters, including aspects of the internal anatomy, in snake classification in general, and Thorpe (1979, 1980) and Rossman, Rossman & Keith (1982) have demonstrated the usefulness of a large character set from various body systems, coupled with the use of modern methods of multivariate analysis, in intraspecific and intrageneric taxonomy. The superiority of these quantitative methods over the naming of conventional subspecies in the investigation of patterns of geographic variation is discussed in Thorpe (1980, 1987a).

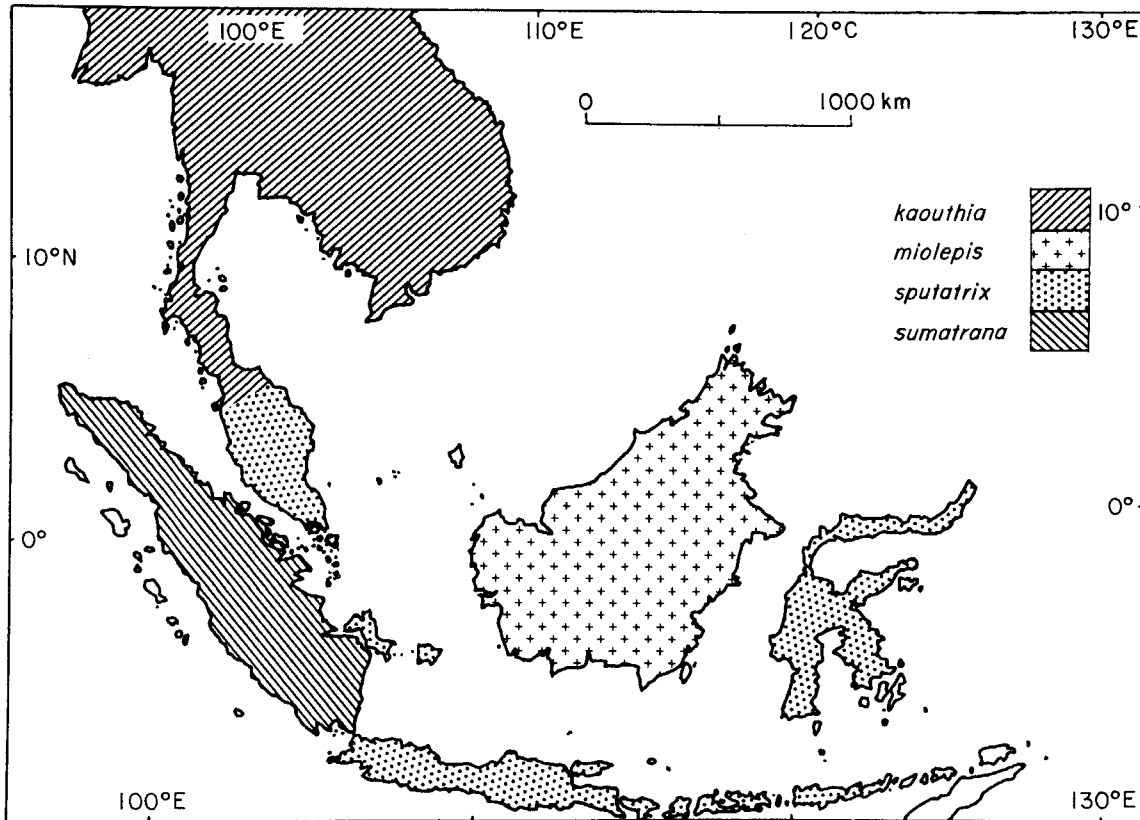


Figure 1. Distribution of the four conventional subspecies of *Naja naja* in south-east Asia, according to Klemmer (1963).

The only multivariate study on the cobras of south-east Asia (Wüster & Thorpe, 1987) showed that the populations from Peninsular Malaysia grouped with those from Sumatra, whereas the populations from Java and Komodo formed a separate cluster, as did the samples from southern Thailand and northern Malaysia. The taxon *N. n. sputatrix*, as conventionally defined, was thus shown to be heterogeneous.

One of the advantages of numerical taxonomic techniques is that the reliability of the results can be assessed quantitatively. The degree of congruence between patterns of geographic variation based on different character systems and different numbers of characters indicates the reliability of a set of results. The relationship between congruence and character number is particularly important in studies in which all available specimens have to be used. If damaged specimens, in which some characters are unrecordable, are to be included in an analysis, the missing characters have to be omitted from the analysis. If there are many such specimens, the total number of usable characters can be drastically reduced. This makes an understanding of the effects of a reduction in character numbers extremely important.

As has been amply demonstrated in the case of the *Echis carinatus* complex, where the use of heterologous antivenoms resulted in poor response to treatment (Warrell *et al.*, 1974), and greatly increased mortality rates (Hughes, 1976), a sound understanding of the taxonomy and distribution of venomous snakes is extremely important for the treatment of their bites. Since *Naja* bites represent a considerable public health problem in many parts of south-east Asia (Sawai *et al.*,

1972; Warrell, 1986), the confusion presently surrounding the systematics of the group is particularly regrettable. There is substantial evidence that the Asiatic *Naja* may pose the same problems as the *Echis carinatus* group, as it has already been demonstrated that antivenom raised against the venom of cobras from southern Malaysia (*N. n. sputatrix* in the conventional classification) fails to neutralize the venoms of cobras from Thailand, India and Sri Lanka (Warrell, 1986). Thus, the systematics of this group have important implications for the treatment of bites in the area under consideration.

This study attempts to elucidate the population affinities within the Asiatic *Naja* species complex in the south-eastern part of its range (southern Thailand, Malaysia and Indonesia), using quantitative methods and recently developed random resampling procedures.

MATERIALS AND METHODS

Materials

In view of the difficulties involved in the acquisition and maintenance of large numbers of live specimens of highly venomous snake species, only preserved material was used in this study. For this reason, only morphological characters were recorded; no attempts were made to include ecological, physiological, biochemical or genetic data in this study. All available preserved specimens from the region in question were examined.

Characters

Many of the characters used by Thorpe (1975) were found to be useful in the analysis of geographic variation in the *Naja naja* complex. Other characters were identified on the basis of a preliminary examination of samples from various parts of the range of the group.

In order to record the positions of various features of colour pattern and internal anatomy along the body or tail, the ventral and subcaudal scales were numbered from the head according to the Dowling (1951) method, and the position of a character was recorded as the number of the ventral or subcaudal scale opposite which it was situated. This was then converted to % Ventral Scale (%VS) or % Caudal Scale (%CS) position, in order to compensate for differences in ventral or subcaudal scale counts. Similarly, the degree of encroachment of certain features of the ventral pattern onto the sides of the neck was measured in terms of the number of dorsal scale rows involved. This was then converted into % Dorsal Scale row (%DS).

The snout-vent length and the tail length were measured to the nearest mm with a piece of string. Scale, fang and head dimensions were recorded to the nearest 0.01 mm with digital calipers. All linear characters were regressed to a common snout-vent length using the pooled within-group regression coefficient for each character. The characters used in this study are numbered and listed in Appendix 1.

Selection of operational taxonomic units

In many regions, the localities of museum specimens were scattered over a wide area; in these cases, it was necessary to pool specimens from several localities into

one Operational Taxonomic Unit (OTU). These were defined on the basis of collecting gaps and potential physiographic barriers. The OTUs used in this study are listed in Appendix 2. Unfortunately, no specimens from Sulawesi were available for examination.

In order to avoid the formation of compound localities with geographic variation within them, which would obscure the very pattern of geographic variation to be elucidated, each proposed compound locality OTU was checked for within-group geographic variation by single-linkage cluster analysis of cases. If a proposed OTU appeared to be heterogeneous, it was split into two or more OTUs, one for each apparent phenotype. For a more detailed discussion of locality pooling, see Thorpe (1979).

Multivariate techniques

In order to investigate the population affinities in the entire region, the male specimens of all size classes from 21 of the 24 defined OTUs were subjected to a canonical variate analysis (CVA), using 54 characters showing geographic variation (nos. 1-29, 32-53, 55, 57, 61; see Appendix 1). This technique maximizes the separation of the groups relative to the within-group correlation between characters. Only male specimens were used because sexual dimorphism occurs in a wide range of characters and female specimens were not available from many areas of interest.

The resulting pattern of geographic variation was tested by principal coordinate analysis of the sample means of the 12 OTUs containing five or more male specimens. Only characters exhibiting significant geographic variation were included. In the case of character pairs with a high degree of within-group correlation ($r > 0.8$), only the character exhibiting a higher degree of between-group variation relative to the within-group variation was included. A total of 65 characters was found to be suitable for principal coordinate analysis (all except nos. 55-56, 58-61 & 64; see Appendix 1).

The stability of the pattern of geographic variation was then tested by comparing completely independent subsets of n characters randomly selected from the total character set. This was carried out using a series of interconnected FORTRAN programs. For every given value of n , a set of $2n$ characters was randomly selected from the full character set, and randomly divided into two sets of n characters. A principal coordinate analysis was then run on each of these two independent sets. The congruence in the pattern of geographic variation between these ordinations, based on the first three principal coordinates, was computed as Gower's (1971) rotational fit, R^2 . This procedure was repeated 20 times for each value of n . Values of n used in this study were 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 17, 20, 22, 25, 28 and 32. The mean congruence between independent datasets was calculated for each value of n across 20 cycles. This method for analysing the reliability of patterns of geographic variation was discussed in more detail in Thorpe (1987b). The congruence between the ordination of each subset of n characters and the ordination resulting from a principal coordinate analysis run on the entire set of 65 characters was also computed.

In order to investigate the patterns of geographic variation within the equatorial and the southern cluster, further CVAs were performed on these two

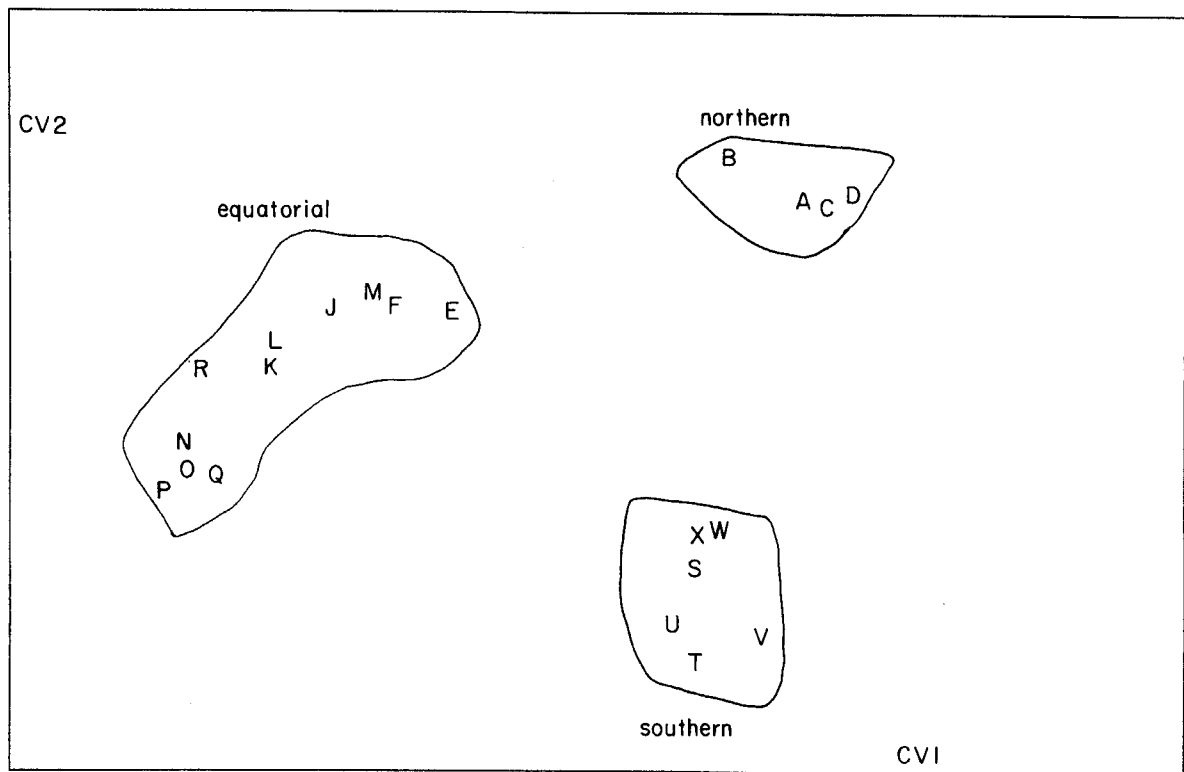


Figure 2. Ordination of the south-east Asian *Naja* samples along the first two canonical variants, based on 136 male specimens. The letters correspond to the sample means of the OTUs listed in Appendix 2. The lines around them indicate the extent of scatter of individual specimens.

groups. The characters used were nos. 1–25, 27–29, 32–51, 55, and 57 for the equatorial form, and 1–57 and 61 for the southern form (see Appendix 1).

RESULTS

Population affinities in south-east Asia

The first CVA indicates clearly that the populations cluster into three distinct morphological groups, between which there is no overlap (Fig. 2). The geographical distribution of these three forms is as follows (Fig. 3):

(1) A northern form, which is distributed from Bangkok south to northern Peninsular Malaysia. Specimens of this form from central Thailand, Burma and north-east India have also been seen.

(2) An equatorial form, which occurs in Peninsular Malaysia, extreme southern Thailand, and on Sumatra, Borneo, Bangka, Belitung and the Riau and Lingga islands. It overlaps with the northern form in northern Malaysia and southern Thailand.

(3) A southern form, which occurs on Java, Bali, Lombok, Sumbawa, Komodo, Flores and Alor.

This pattern of geographic variation was confirmed by the subsequent principal coordinate analysis.

Reliability of the results

The plot of the mean congruence (R^2) between the independent character sets against character number is shown in Fig. 4. The curvilinear relationship between

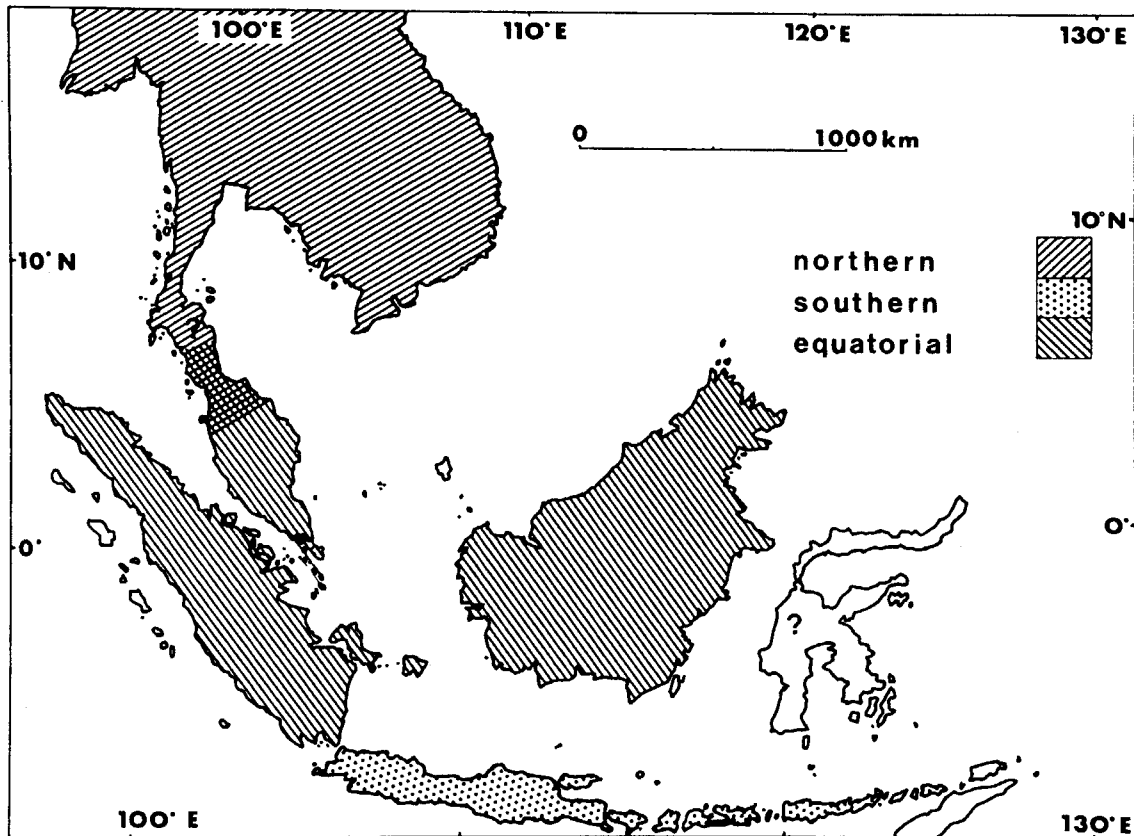


Figure 3. Distribution of the three main evolutionary groups of *Naja* in south-east Asia.

congruence and character number is asymptotic, and is defined by the formula:

$$R^2 = a + b(e^{-cn})$$

where the asymptote $a = 0.165$, $b = 0.699$ and $c = 0.078$.

In the case of the comparison of subsets with the full character set, a congruence value of $R^2 < 0.2$ is reached when 15 characters are used, and when 28 or 32 characters, that is approximately half the complete dataset, are used, the mean congruence is excellent ($R^2 < 0.1$).

Patterns of within-group geographic variation

The pattern of geographic variation within two of the three primary clusters was investigated by further CVAs. Within-cluster geographic variation in the northern form was not investigated, since its range extends beyond the geographic limits covered in this study.

The equatorial form consists of three moderately distinct groups: one from Sumatra and Peninsular Malaysia, one from Borneo and one from the islands of Bangka and Belitung (Fig. 5).

Similarly, three subgroups can be identified in the southern form (Fig. 5): the sample from West Java is isolated from all the other populations. The second subgroup is formed by samples from Central and East Java and the island of Sumbawa, and the third subgroup by the samples from the islands of Komodo and Flores.

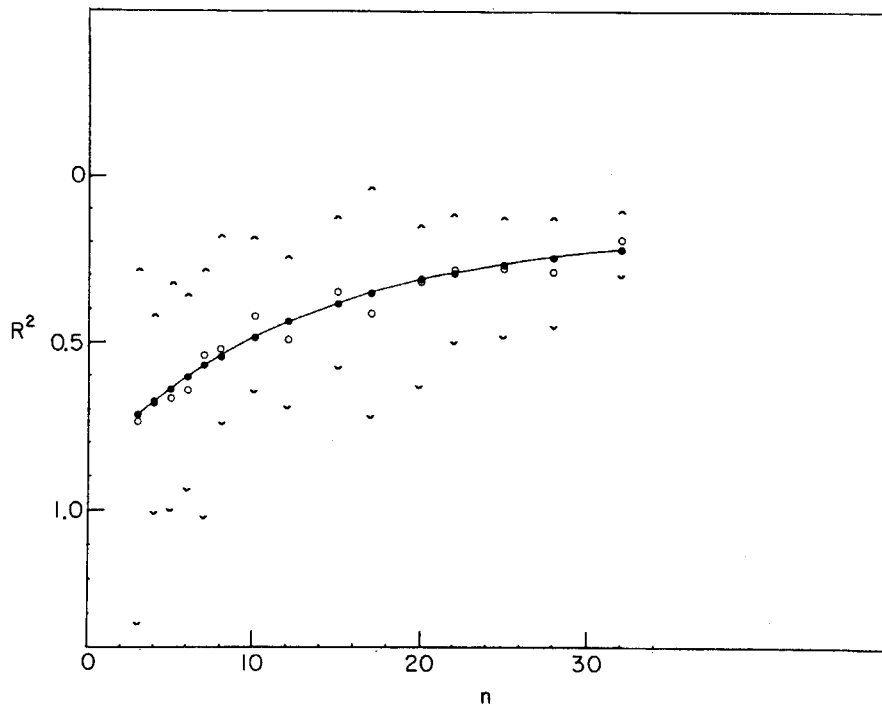


Figure 4. Plot of congruence (R^2) against character number (n) for independent character sets. Solid circles represent the mean values of R^2 predicted by the formula, hollow circles represent actual mean values, and the maximum and minimum values for each value of n are indicated.

DISCUSSION

Population affinities

The first point to note is that the distribution of the three clusters identified by the CVA forms a geographically coherent, latitude-related pattern (Fig. 3), which also reflects ecological and climatic factors. This contrasts with the disjunct and geographically incoherent distribution pattern suggested by the conventional classification.

The second point to note is the almost total failure of the conventional taxonomic arrangement to represent the population affinities within this region. Of the four original subspecies of *Naja naja*, only *kaouthia* was found to represent a valid taxon, and even here, the nature of the contact zone with the Malayan form had not been represented accurately. *N. n. miolepis* and *N. n. sumatrana* were found to form a single cluster, together with the samples of *N. n. sputatrix* from Peninsular Malaysia, the Riau Archipelago and the islands of Bangka and Belitung. On the other hand, the specimens from Java and the Lesser Sunda Islands, supposedly in the same subspecies as the Malay specimens, form a completely separate cluster. This confirms the results of Wüster & Thorpe (1987), who pointed out that *N. n. sputatrix*, as interpreted in the conventional classification, does not form a homogeneous taxon.

When analysing current distribution patterns, it is essential to consider the geological and ecological history of the region concerned. In that part of south-east Asia, which is today fragmented into a number of islands, the most important historical factor to be taken into consideration is the pattern of sea level changes during the Pleistocene and Quaternary glaciations. During glacial maxima, enough water was locked up in the ice caps to cause a world-wide fall of sea levels

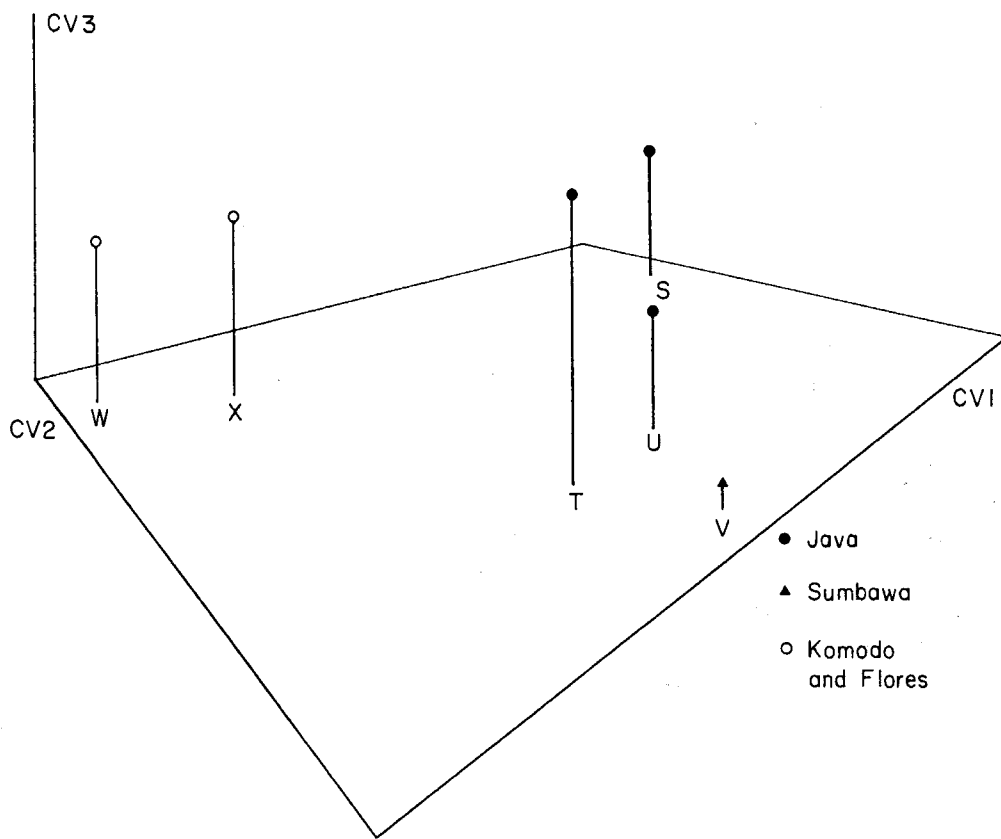
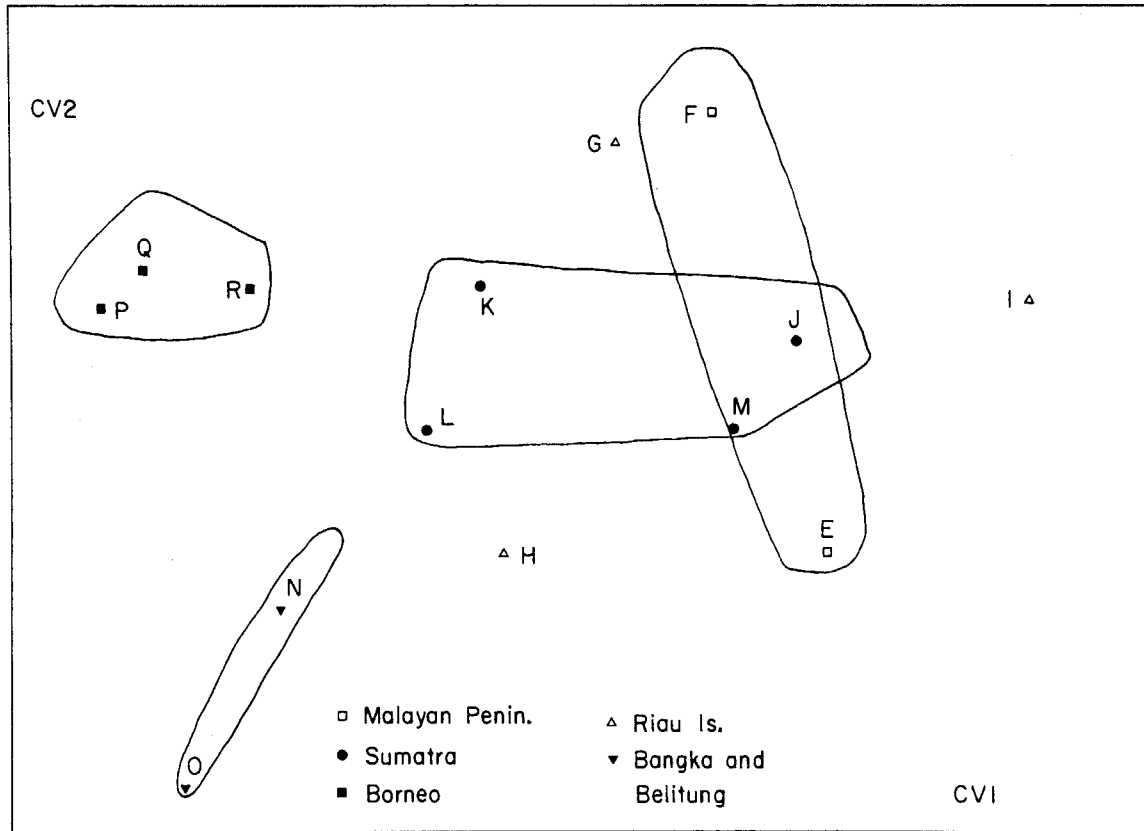


Figure 5. Ordination of the samples within the equatorial form (top) and the southern form (bottom) along, respectively, the first two and the first three canonical variants, based on, respectively, 66 and 41 male specimens. Letters and scatter as in Figure 2.

of 120–200 m. The result of this was that the entire Sunda Shelf area formed a single landmass, allowing free passage of faunal elements from mainland south-east Asia into the area of present-day western Indonesia, and between the different islands in the latter area (Heaney, 1985; Morley & Flenley, 1987).

The distribution of the equatorial form corresponds largely to the areas currently endowed with an aseasonal or slightly seasonal climate, and covered by evergreen or semi-evergreen forest (see Whitmore (1975) for descriptions and maps of the climatic and vegetational zones in south-east Asia).

However, in parts of Borneo and Sumatra, the equatorial form occurs in more seasonal habitats. One possible explanation for this distribution pattern is that this form may be able to exist on its own in a seasonal climate, outside the evergreen rainforest, but is outcompeted in those areas by the northern form where this is present. It is unlikely that habitat alone has played a critical role in determining the range of the equatorial form, since it occurs in a wide variety of habitats in its area of distribution (Lim, 1982).

The southern limit of the northern form does not correspond to any geographical or environmental boundary. It is possible that the destruction of the tropical rainforests by man, which has created a choice of more open habitats in large parts of Peninsular Malaysia, has allowed the northern form to penetrate south of the areas with a seasonal climate. If this hypothesis is correct, this form is able to coexist with or outcompete the equatorial form in non-rainforest habitats (such as rice paddies and rubber and oil palm plantations). The southern limit of the distribution of the northern form would thus represent the present extent of a recently-begun, and ongoing, range expansion, made possible by man-made ecological changes. Obviously, a detailed study of the habitat requirements of the two species, and their patterns of habitat use in the area of sympatry, would be needed to test this hypothesis.

The southern form occupies primarily seasonal, and even semi-arid, environments, although it also occurs in the few aseasonal rainforest areas still existing in West Java.

Reliability of the pattern of geographic variation

The relationships of congruence and character number both between independent sets of characters and between subsets and the entire character set indicate that the pattern of geographic variation described here is highly reliable; since the characters used relate to five different character systems, this suggests that the distinctness of the three forms is due to a separate evolutionary history rather than to current ecological conditions. The mathematical model describing the relationship of congruence between completely independent character sets and the number of characters used is the same as that found in Thorpe's analyses of simple (Thorpe, 1985) and complex (Thorpe, 1987b) patterns of geographic variation in the European natricine snake *Natrix natrix*. The R^2 values for a given number of characters are in all cases smaller than those found by Thorpe (1987b) in three-dimensional ordinations. Similarly, the asymptote of R^2 found in this study ($a=0.165$) is better than that found by Thorpe (1987b) in the case of *Natrix natrix* ($a=0.203$). In the case of comparisons with the entire character set, the mean R^2 for half the character set ($n=32$, $R^2=0.056$) is again better than the value found by Thorpe for half of his character set ($n=40$, $R^2=0.08$).

The greater stability of the pattern of geographic variation stems from the greater distinctness of the groupings, which is due to the higher taxonomic level involved. Thorpe (1987b) discussed intraspecific geographic variation, whereas the complex under investigation in this study is polyspecific. It is therefore not surprising that the pattern of geographic variation within this complex is more robust.

The low number of characters needed to achieve a good degree of congruence between independent sets is encouraging in view of the frequency of specimens with unrecordable characters. Since some OTUs from poorly sampled localities include only very few specimens, it is frequently necessary to exclude some characters from an analysis in order to accommodate those samples, which may be important from a biogeographical point of view. If a slight reduction in the number of characters resulted in a significant loss of reliability, the value of those OTUs would be greatly reduced.

Sympatry between the northern and the equatorial form

It is clear from the CVA (Fig. 2) that there is no evidence of introgression between the northern and the equatorial form. No locality of actual sympatry has been found on the basis of museum specimens examined by the authors. However, there is a broad zone of range overlap between the two taxa (Fig. 6): of the material that we have examined, the northernmost specimen of the equatorial form originates from Khao Chong, Trang Province, Thailand (7°30'N), whereas the southernmost specimen of the northern form originates from Kulim, Kedah State, Malaysia (5°20'N). The ranges of the two forms therefore overlap by at least 250 km.

Since the two forms can be easily distinguished on the basis of several diagnostic characters, such as the presence or absence of a hood mark, and several scalation characters (see Table 1), literature records can provide further information on the nature of the contact zone between the two taxa. Two specimens from Na Pradoo, Pattani Province, Thailand, which were described by Taylor (1965) as *N. n. kaouthia* var. A, actually belong to the equatorial form. We have seen a specimen of the northern form from the same area, indicating sympatry in that area. Duckett (1987) states that he caught cobras with monocellate hood-marks—which identify them with absolute certainty as belonging to the northern form—at Taiping and Ipoh, Perak, Malaysia (4°50' and 4°30'N). We have examined a specimen of the equatorial form from Taiping, again indicating sympatry.

Reid (1964) mentions both the northern form, with a monocellate hood-mark (not *N. n. leucodira*, as stated by Reid), and another, less common, yellow or light brown form, without a hood mark, from Penang and adjoining Kedah State. The latter probably represents the equatorial form, which is usually light brown in northern Malaysia and southern Thailand, unlike the populations from central and southern Malaysia, which are generally black. Tumwipat & Nutphand (1982) report uniform yellow spitting cobras from as far north as Nakhon Si Thammarat and Surat Thani Provinces in Thailand (approx. 9°N). If both the Ipoh and the Surat Thani records are correct, the ranges of the two forms overlap by at least 500 km. These records are plotted out in Fig. 6.

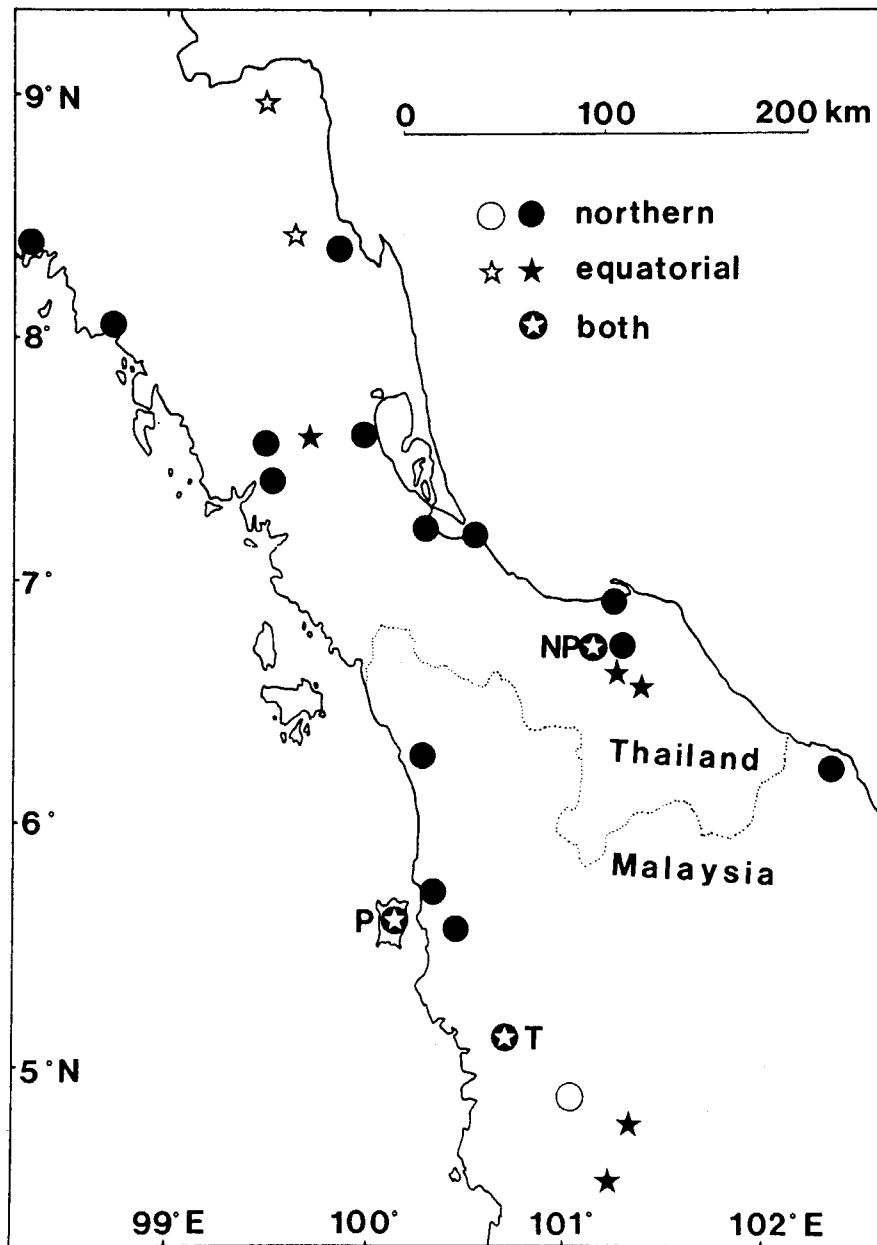


Figure 6. Locality records of the northern and equatorial forms in southern Thailand and northern Malaysia. Solid symbols represent specimens examined by the authors, outline symbols represent literature records. Localities with sympatry are discussed in the text (NP=Na Pradoo, P=Penang, T=Taiping).

TABLE 1. Distinguishing characters of the northern and equatorial forms in southern Thailand and Peninsular Malaysia. Exceptional values are shown in parentheses

	Northern	Equatorial
Dorsal scale rows at the level of the 10th ventral	(27) 28–31 (34)	(21) 23–25 (27)
Dorsal scale rows at 20% and 40% VS length	(19) 21–23	17–19
Dorsal scale rows at 80% VS length	15–17	13–14 (15)
No. of pterygoid teeth	(10) 11–14 (15)	(15) 16–19 (20)
Hood mark	Nearly always present	Never present

In conclusion, it can be said that the evidence for sympatry between the northern and the equatorial form is conclusive, and the two forms should be considered as separate species.

The discovery of an area of sympatry between the northern and the equatorial forms is extremely important with respect to the problem of antivenom treatment of snakebite patients. Warrell (1986) states that an antivenom against the venom of cobras from southern Malaysia failed to neutralize the venom of Thai cobras *in vitro*. This means that in some areas of southern Thailand and northern Peninsular Malaysia, there are two sympatric species of *Naja*, the bites of which require different antivenoms. To our knowledge, no polyvalent antivenom for both these species is available at present. Physicians treating cases of cobra-bite in this area should therefore take great care to correctly identify the offending reptile so that the correct antivenom can be given. The distinguishing characters of the two forms in Thailand and Malaysia are given in Table 1.

It should also be noted in this context that the northern form is a non-spitting cobra, whereas both the equatorial and the southern forms are spitting cobras, with fangs fully adapted for that purpose.

Nomenclature

Since the relationships of the forms discussed here with the forms of *Naja* occurring in other parts of Asia have not yet been investigated, it would not be appropriate to propose any definitive changes in the nomenclature of these forms at this stage.

Although the northern, monocellate form known conventionally as *N. n. kaouthia* was found to form a well differentiated taxon, it is not yet clear whether it actually forms a separate species from the Indian cobra, *N. naja naja*. Sympatry between monocellate and binocellate cobras has been reported by Bannerman & Pocha (1905), Sights (1949) and Deraniyagala (1960).

The oldest available name for the equatorial form as it stands is *N. naja sumatrana*. Since this form occurs sympatrically with the northern form in southern Thailand and Malaysia (see below), and is therefore distinct at species level, it should, at least for the time being, be referred to as *Naja sumatrana*.

The taxonomic rank, and therefore the nomenclature, of the southern form are difficult to resolve, since, being restricted to an island range, it does not enter into contact with either of the two other forms, so that there are no areas of hybridization or sympatry which would help clarify its taxonomic status. The taxonomic distance of this form from the equatorial form (measured as the Mahalanobis D-squared distance) is approximately equal to that from the northern form, and of the same magnitude as that between those two non-conspecific forms; for this reason, we provisionally suggest that it should be treated as a separate species, for which the correct name is *Naja sputatrix*. However, the discovery of populations morphologically intermediate between this form and others with earlier available names in parts of Asia that have not so far been investigated (e.g. Sulawesi) would invalidate that argument. If the Sulawesi populations were found to be intermediate between the southern and the equatorial form, the latter would have to be considered as a subspecies of the

former. The populations from central and northern Thailand 'informally' referred to *N. n. sputatrix* by Warrell (1986 and personal communication) are currently the subject of further investigations (Wüster & Thorpe, unpublished). Preliminary results indicate that at least some of these populations are morphologically close to the Javan *Naja* populations.

The status of the *Naja* populations of Sulawesi will have to remain unsolved for the time being. We have not been able to trace a single preserved specimen of cobra from that island in any natural history collection we have contacted. In the only description of a *Naja* specimen from Sulawesi that we have been able to find, Kopstein (1936) suggests, on the basis of ventral, subcaudal and dorsal scale counts, that the Sulawesi population is close to the *Naja* populations of the Lesser Sunda islands. Although compatible with that hypothesis, Kopstein's description is not precise enough to allow any further comments about the affinities of the specimen.

Within-group variation

The northern form ranges over a wide area of eastern Asia, from northern India to Indo-China and northern Malaysia. Since only the southernmost part of that range has been included in this study, it was not considered useful to investigate the intraspecific geographic variation in this form within this limited area.

Within the equatorial form, there are three fairly distinct groups (Fig. 5). One consists of the populations from Peninsular Malaysia and Sumatra, which cluster together; the samples from Borneo form the second group, and those from the islands of Bangka and Belitung the third. The samples from the Riau and Lingga Islands appear to fit in with the first group; however, only three of the islands were sampled, and in each case only one specimen was available, which makes any conclusions regarding these populations tentative at best. The populations on these small islands were probably isolated from those on Sumatra and in Malaysia when sea levels rose at the end of the Pleistocene. The founder effect resulting from the small population sizes of these isolates may account for the great morphological diversity in this small area (*cf.* Fig. 5).

One effect of the large contiguous landmass of the Sunda Shelf during the Pleistocene was a more continental climate in this presently tropical area. This resulted in areas of semi-evergreen forest and other drier ecosystems in parts of Pleistocene Sundaland which are now covered by evergreen rainforest (Morley & Flenley, 1987).

The differentiation between the three main groups could be due to these climatic changes: during times when parts of the Sunda Shelf had a more seasonal climate than at present, the equatorial form would have been relegated to refugia where the climate remained aseasonal or slightly seasonal. The results of this study suggest the existence of at least two refugia: one in the east, on Borneo, which is postulated by Morley & Flenley (1987), and one in the west, probably somewhere on Sumatra, since, according to those two authors, at least parts of Peninsular Malaysia had a seasonal climate during the Pleistocene.

The southern form exhibits a very clear pattern of geographic differentiation (Fig. 5), which relates partly to current ecological conditions, and partly to Pleistocene and Quaternary events.

The taxonomic isolation of the western population can be related to current

ecological conditions: the western parts of Java have mostly humid, aseasonal or slightly seasonal climate and a rainforest-type vegetation cover, whereas central and eastern Java, and the islands of the Lesser Sunda chain, have a seasonal or strongly seasonal climate (Whitmore, 1975).

The populations from the eastern two-thirds of Java and the Lesser Sunda Islands form two clusters. The populations from central and eastern Java and Sumbawa group together and exhibit clear clinal variation along the third canonical variate. This is despite the presence of deep trenches between the islands of Bali and Lombok, which would have remained submerged throughout the Pleistocene and Quaternary. It is regrettable that no male specimens from Bali and Lombok were available, since they would have furnished more information about the pattern of geographic variation in this area.

The samples from Komodo and Flores are morphologically similar to each other, and are taxonomically isolated from the Sumbawan and Javan populations. This may reflect the existence of a deep trench between Komodo and Sumbawa, and the broad connection that existed between Komodo and Flores during the times of low sea-levels (Auffenberg, 1980).

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APPENDIX 1. LIST OF CHARACTERS USED

1. No. of ventral scales
2. No. of subcaudal scale pairs (undivided subcaudals count as 1 pair)
3. Percentage of undivided subcaudal scales
4. No. of cuneate scales
5. No. of posterior temporal scales
6. No. of temporal and nuchal scales contacting parietal scales
7. Adjusted length of frontal shield
8. Adjusted width of frontal shield
9. Adjusted distance from frontal shield to rostral shield
10. Adjusted mean of lengths of supraocular shields
11. Adjusted length of suture between prefrontal shields
12. Adjusted length of suture between parietal shields
13. Adjusted mean of lengths of parietal shields
14. No. of dorsal scale rows at the level of the 10th ventral scale
15. No. of dorsal scale-rows at 20% VS length
16. No. of dorsal scale rows at 40% VS length
17. No. of dorsal scale rows at 60% VS length
18. No. of dorsal scale rows at 80% VS length
19. No. of dorsal scale rows at the level of the last ventral scale
20. Proportion of tail in %CS lengths with 2 dorsal scale rows
21. %CS position of reduction from 6 to 4 dorsal scale rows on tail
22. %CS position of reduction from 8 to 6 dorsal scale rows on tail
23. %CS position of reduction from 10 to 8 dorsal scale rows on tail
24. %VS position of anterior edge of thyroid
25. %VS position of posterior tip of heart
26. %VS position of systemic junction
27. %VS position of anterior tip of liver
28. %VS position of posterior tip of liver
29. %VS position of anterior edge of pancreas
30. %VS position of cystic duct-gut junction
31. %VS length of cystic duct
32. %VS position of anterior tip of right testis
33. %VS position of posterior tip of right testis
34. %VS position of anterior tip of left testis
35. %VS position of posterior tip of left testis
36. %VS position of anterior tip of right kidney
37. %VS position of posterior tip of right kidney
38. %VS position of anterior tip of left kidney
39. %VS position of posterior tip of left kidney
40. No. of renal arteries (total of both sides)
41. Adjusted total length of fang
42. Adjusted length of fang discharge orifice
43. Adjusted distance from proximal end of fang discharge orifice to fang tip
44. No. of palatine teeth
45. No. of pterygoid teeth
46. No. of dentary teeth
47. Adjusted snout-vent length

48. Adjusted tail length
49. Adjusted head width between supraoculars
50. Adjusted head length from snout tip to end of interparietal suture
51. Adjusted head length from snout tip to posterior end of lower jaw
52. Adjusted head depth across supraoculars
53. Adjusted head depth from mouth edge to top of supraoculars
54. Adjusted width of widest ventral scale
55. %VS position of last ventral involved in formation of light throat area
56. %DS encroachment of light throat area onto dorsal scales
57. No. of lateral spots on throat
58. %VS position of largest pair of lateral throat spots
59. %VS length of largest pair of lateral spots on throat
60. %DS encroachment of largest pair of lateral throat spots onto neck
61. %VS length of ventral band after throat
62. Presence/absence of contact between posterior chin shields
63. Presence/absence of hood mark
64. Presence/absence of a connection between the hood mark and the throat
65. Presence/absence of a median throat spot
66. Presence/absence of cross-banding
67. No. of supralabials with conspicuous dark posterior edges
68. No. of supralabials with inconspicuous dark posterior edges
69. No. of supralabials without dark posterior edges
70. Darkness of throat (0 = no pigment, 5 = 100% pigmented)
71. Presence/absence of speckling on dorsal scales
72. No. of dark bands across venter

APPENDIX 2. OPERATIONAL TAXONOMIC UNITS AND SAMPLE SIZES (N) OF *NAJA* USED
IN THIS STUDY

- A. Bangkok, Thailand. $N=13$
- B. Phuket Island, Thailand. $N=6$
- C. Southern Thailand, northern form. $N=4$
- D. Northern Peninsular Malaysia, northern form. $N=5$
- E. Northern Peninsular Malaysia and Southern Thailand, equatorial form.
 $N=5$
- F. Central and southern Malaysia. $N=21$
- G. Pulau Balan, Riau Archipelago. $N=1$
- H. Pulau Penuba, Riau Archipelago. $N=1$
- I. Pulau Karimon, Riau Archipelago. $N=1$
- J. Medan, Sumatra. $N=15$
- K. Padang, Sumatra. $N=6$
- L. Bengkulu, Sumatra. $N=2$
- M. Palembang, Sumatra. $N=1$
- N. Bangka Island, Indonesia. $N=2$
- O. Belitung Island, Indonesia. $N=1$
- P. Western Sarawak, Borneo. $N=4$
- Q. Sabah, Borneo. $N=7$
- R. Balikpapan, Borneo. $N=3$
- S. Western Java. $N=21$

- T. Central Java. $N=4$
- U. Eastern Java. $N=6$
- V. Sumbawa Island, Indonesia. $N=2$
- W. Komodo Island, Indonesia. $N=5$
- X. Flores Island, Indonesia. $N=3$