Herpetologica, 48(1), 1992, 69–85

ASIATIC COBRAS: POPULATION SYSTEMATICS OF THE *NAJA NAJA* SPECIES COMPLEX (SERPENTES: ELAPIDAE) IN INDIA AND CENTRAL ASIA

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ABSTRACT: The population systematics of the cobras of the genus *Naja* in the Indian subcontinent and in central Asia were investigated using multivariate analysis of morphometric characters recorded from preserved material. The cobras from this region, formerly thought to belong to a single species, comprise three well-differentiated species: *N. naja* occurs throughout India, as well as in Pakistan, Nepal, and Bangladesh; *N. oxiana* is found in Soviet central Asia, northeastern Iran, Afghanistan, northern Pakistan, and northwestern India; *N. kaouthia* is found from Delhi east to Assam, and south to Vietnam and northern Malaysia. The pattern of intraspecific geographic variation in *N. naja* is investigated and discussed with reference to previously described subspecies, which are not recognized.

Key words: Serpentes; *Naja*; Population systematics; Taxonomy; Geographic variation; Subspecies; Sympatry; Congruence; India; Multivariate analysis

THE Asiatic cobras of the genus *Naja* constitute a complex and widespread group of venomous snakes. The systematics of these animals have been controversial for many years. All populations of the complex have been thought to belong to a single species, *N. naja*, by most workers (e.g., Boulenger, 1896; Golay, 1985; Klemmer, 1963; Leviton, 1968). However, as part of a complete revision of the Asiatic cobra complex, we have recently shown that two taxa found in Indonesia and on the Malayan Peninsula are full species, *N. sumatrana* and *N. sputatrix* (Wüster and Thorpe, 1989), and the two endemic Philippine taxa, *samarensis* and *philippinensis*, probably also constitute full species (Wüster and Thorpe, 1990).

In central Asia and the Indian subcontinent, the systematics of the group have been less confused than elsewhere. Three subspecies of *Naja naja* have been recognized in this region by most recent workers (Golay, 1985; Harding and Welch, 1980; Klemmer, 1963; Leviton, 1968; Whitaker, 1978). The populations from Pakistan, India and Sri Lanka, with a spectacle-shaped hood mark, are normally assigned to *N. n. naja* (Linnaeus), 1758; the populations with a monocellate hood mark, from northeastern India, Burma, Thailand, Indochina and northern Malaysia, are generally assigned to *N. n. kaouthia* Lesson, 1831; and the populations without a hood mark from Soviet central Asia, Iran, Afghanistan, and northern Pakistan are assigned to *N. n. oxiana* (Eichwald), 1831. The frequent absence of hood marks in specimens from the northern and western parts of India has often caused them to be assigned to *N. n. oxiana*, but the occurrence of this subspecies in parts of India other than Kashmir is not universally accepted (e.g., Joger, 1984).

Deraniyagala (1945, 1960, 1961) reviewed the systematics of Asiatic cobras and raised both *oxiana* and *kaouthia* to the rank of full species, restricted the type locality of *Naja naja* to Sri Lanka, and described five subspecies of *N. naja* from the Indian subcontinent: *N. n. madrasiensis* from southern India, *N. n. gangetica* from the northeast, *N. n. indusi* from the Punjab, *N. n. karachiensis* from southern Pakistan and northwestern India, and *N. n. bombaya* from Maharashtra and neighboring areas. His work has been largely ignored by subsequent workers, although Soderberg (1973) and Warrell (1986) followed him in treating *kaouthia* as a full species.

In this paper, the population affinities of the cobras of the Indian subcontinent and central Asia are investigated, using multivariate analysis of morphological characters. Populations of monocellate cobras from Burma, Thailand, Malaysia, and Indochina, which are normally assigned to *N. n. kaouthia*, are also discussed.

Materials and Methods

The material used in this study consisted of preserved museum specimens. Consequently, only morphological characters were recorded, and we made no attempt to record biochemical, physiological, behavioral, or ecological data. All available museum material from the Indian subcontinent and central Asia was examined. Specimens with a monocellate hood mark from other parts of Asia, which are generally assigned to *N. n. kaouthia*, were also included in this study. The specimens examined are listed in Appendix I. The institutional codes used to refer to specimens follow Leviton et al. (1985), with the following exceptions: SAM refers to Sherman A. Minton, personal collection, and UMZC refers to the University Museum of Zoology, Cambridge, England.

Characters

In order to assess the overall phenotype of the specimens, we used as many characters as possible, from several different body systems. The characters recorded from the specimens used in this study related to the following body systems: scalation, color pattern, visceral topography, dentition, and body proportions. Many of these characters were defined by Thorpe (1975). Others were identified on the basis of literature descriptions, and some new characters were defined after the examination of specimens from a number of localities throughout Asia.

The ventral and subcaudal scales were numbered using the method of Dowling (1951). The position of a character along the body was recorded as the number of the ventral or subcaudal scale opposite which it was situated. In order to compensate for variation in the number of ventral and subcaudal scales, this was then transformed to percent ventral scale (% VS) or percent caudal scale (% CS) position (Thorpe, 1975). The encroachment of color pattern features onto the neck, or their width, was measured as the number of dorsal scale rows involved. This was then expressed as a percentage of the total number of dorsal scale rows at that level (% DS). See also Wüster and Thorpe (1989) for a description of this procedure.

Characters relating to certain obvious color pattern features, particularly the hood mark, could not be used, as the relevant feature is absent in many populations. Categorical characters, such as the presence or absence of a hood mark, are unsuitable for use in studies using advanced techniques of multivariate analysis, such as canonical variate analysis. The same applies to characters such as the presence or absence of a small, solid tooth on the maxilla behind the fang, which has been used by Bogert (1943) as a taxonomic character in distinguishing between various Asiatic cobra populations.

The snout–vent length and the tail length were measured to the nearest 1 mm with a string; other linear dimensions were measured to the nearest 0.01 mm with digital calipers. All characters were recorded by the senior author, in order to eliminate problems due to interobserver variation. The characters used in this study, and their numbers, are listed in Appendix II.

Construction of Operational Taxonomic Units (OTUs)

Because the localities of the museum specimens used in this study were widely scattered, it was necessary to pool specimens from more than one locality into single OTUs in order to maximize sample sizes. When specimens are pooled in this way, it is important to avoid forming OTUs which contain a significant amount of geographic variation within them, and, more importantly, it is important to ensure that only a single species is included in any one OTU in situations where the presence of two sympatric species is a possibility. The presence of two species is not always self-evident from a superficial examination of specimens (e.g., Thorpe and McCarthy, 1978).

OTUs were initially established on the basis of hypothesized physiographic bar-

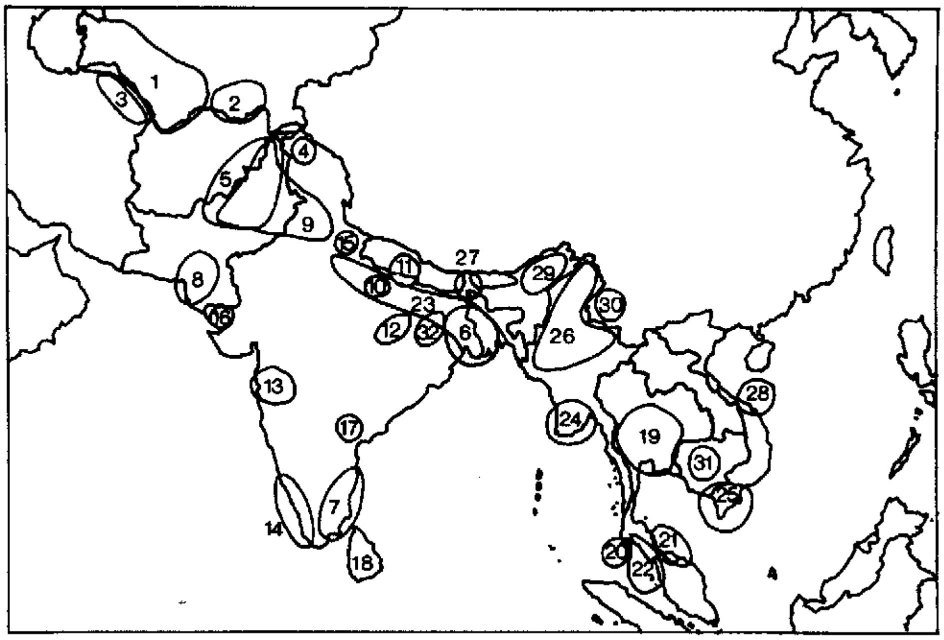

FIG. 1.—Localities of the OTUs used in this study. Overlapping OTUs are the result of sympatry between distinct taxa.

riers and collecting gaps. All of these proposed OTU's were then checked for heterogeneity by means of principal components analyses, which were run on the individual specimens, using meristic characters only. All characters were standardized to zero mean and unit standard deviation, and the analyses were run on a correlation matrix. Separate analyses were run for male and female specimens in order to avoid any difficulties due to sexual dimorphism. If a two-dimensional plot of the scores of each specimen along the first two principal components revealed either geographic variation or the existence of two sympatric, phenetically distinct forms, it was split into a separate OTU for each phenotype. In all cases, the aim was to maintain maximum homogeneity, and the proposed OTU was split if there was any sign of heterogeneity. The OTUs used in this study are mapped in Fig. 1, and listed, with sample sizes, in Table 1. See Thorpe (1979) for a more detailed discussion of locality pooling.

Multivariate Techniques

In this study, we used a mixture of meristic and other characters, which are not influenced by growth, and linear measurements, which are. In such cases, it is necessary to remove the effect of body size from the linear measurements by regressing them against the snout–vent length (SVL). The pooled within-OTU regression coefficient of each linear measurement against the SVL was obtained by analysis of covariance, and all linear measurements were regressed to the mean SVL of all specimens examined (665 mm) before further analysis.

The multivariate technique used in the investigation of the population affinities of these snakes was canonical variate analysis (CVA). This technique maximizes the separation between groups relative to the within-group variance, taking into account the within-group correlation between characters. The use of this technique in population systematics is demonstrated, reviewed, and discussed in Thorpe (1976, 1980, 1983, 1987*a*).

Because far more male than female specimens were available in this study, only the results of analyses of male specimens will be presented here. The female specimens were subjected to the same analyses (except for differences in OTU composition), and the same results were obtained.

Seven CVAs were run. The first, CVA 1 was run on all available OTUs from the Indian subcontinent and central Asia, as well as the monocellate populations from

TABLE 1.—List of OTUs used in the CVAs in this study, with sample sizes (n) for both sexes. The number of specimens included in the CVAs is less than the number of specimens listed in Appendix I, because some of these specimens were in too bad a state to be included. M = males, F = females.

OTU Number	Locality		n	
			M	F
Central Asian taxon.				
1.	Turkmenia and Uzbekistan, U.S.S.R.		7	7
2.	Tadzhikistan, U.S.S.R.		8	5
3.	Northeastern Iran.		5	1
4.	Gilgit, Kashmir.		3	0
5.	Northern Pakistan, eastern Afghanistan.		3	6
		Total	26	19
Spectacled taxon.				
6.	West Bengal and Bangladesh.		8	5
7.	Tamil Nadu State, India.		9	2
8.	Sind Province, Pakistan.		12	7
9.	Northern Pakistan and northwestern India.		10	6
10.	Kanpur and Lucknow, Uttar Pradesh, India.		4	2
11.	Devanandpur, Nepal.		2	1
12.	Mungeli and Ambikapur, Madhya Pradesh, India.		3	0
13.	Maharashtra State, India.		9	1
14.	Kerala State, India.		4	2
15.	Mussoorie, Uttar Pradesh, India.		1	0
16.	Bhuj, Gujarat, India.		1	0
17.	Hyderabad, Andhra Pradesh, India.		1	0
18.	Sri Lanka.		13	12
		Total	77	38
Monocellate taxon.				
19.	Central Thailand.		18	18
20.	Phuket Island, Thailand.		6	0
21.	Eastern slope of Malayan Peninsula.		4	5
22.	Western slope of Malayan Peninsula.		5	6
23.	Northern India and Bangladesh.		17	15
24.	Rangoon area, southern Burma.		6	2
25.	Southern Vietnam.		2	3
26.	Northern Burma.		5	5
27.	Sikkim area, India.		4	0
28.	Hue area, Vietnam.		3	0
29.	Assam, India.		0	3
30.	Yongde, Yunnan, China.		0	1
31.	Central Cambodia.		0	1
		Total	70	59
Uncertain affinities.				
32.	Bihar State, India.		0	2
		Total	0	2

Indochina and parts of the Malayan Peninsula (Fig. 1). The characters used were 1–33 and 38–50.

Because the interrelationships between the taxa are hypermultivariate (Thorpe, 1976), all groups could not separate along the first two canonical variates. A further analysis, CVA 2, was therefore run on all OTUs except OTUs 1–5, and using characters 1–32 and 34–50, in order to clarify the relationships between the remaining OTUs.

Further CVAs were run in order to elucidate the pattern of geographic variation in the spectacled cobra. In particular, we wished to investigate the degree of congruence between patterns of variation in different character systems, because this can help establish whether a pattern of variation is due to the effects of separate ancestry (phylogenesis) or current ecological selection pressures (ecogenesis). These used all OTUs of the spectacled cobra (OTUs 6–18). CVA 3 used all characters available in these OTUs (Characters 1–32, 34–50). CVA 4 was run on scalation characters 1–16. CVA 5 was run on internal anatomy characters 17–29. CVA 6 was run on body and scale proportions characters 38–50. CVA 7 was run on dentition characters 30–31 and 51–53, but did not use OTUs 15 and 17, in which some of the characters concerned were not recorded.

Because CVA 4 showed a clear pattern of geographic variation, the scores of individual specimens along the first canonical variate were used to visualize the pattern of geographic variation by means of a three-dimensional surface plot, generated by the SURFER package (Anon., 1990).

Results

All Indian and Central Asian Populations

CVA 1 (Fig. 2A) divides the cobras of the Indian subcontinent and central Asia into two phenetically highly distinct groups. One group includes the cobra populations from Soviet central Asia and Iran, and some of those from northern Pakistan and adjoining Afghanistan. These lack a hood mark, and are also characterized by very high ventral and subcaudal scale counts. Juvenile specimens of this form appear very washed-out, and display a conspicuous pattern of cross-bands. This taxon will be referred to as the central Asian taxon.

The remaining group consists of all the OTUs representing populations with hood marks. Within this group, the populations with a monocellate hood mark are largely separated from the populations with a spectacled hood mark in CVA 1, but this separation is not complete.

CVA 2 (Fig. 2B), which excludes the central Asian taxon, completely separates the monocellate and the spectacled populations along the first canonical variate. The spectacled form includes most of the populations from India, Pakistan, Nepal, and Bangladesh; these possess medium to high ventral and subcaudal scale counts. This taxon will be referred to as the spectacled taxon.

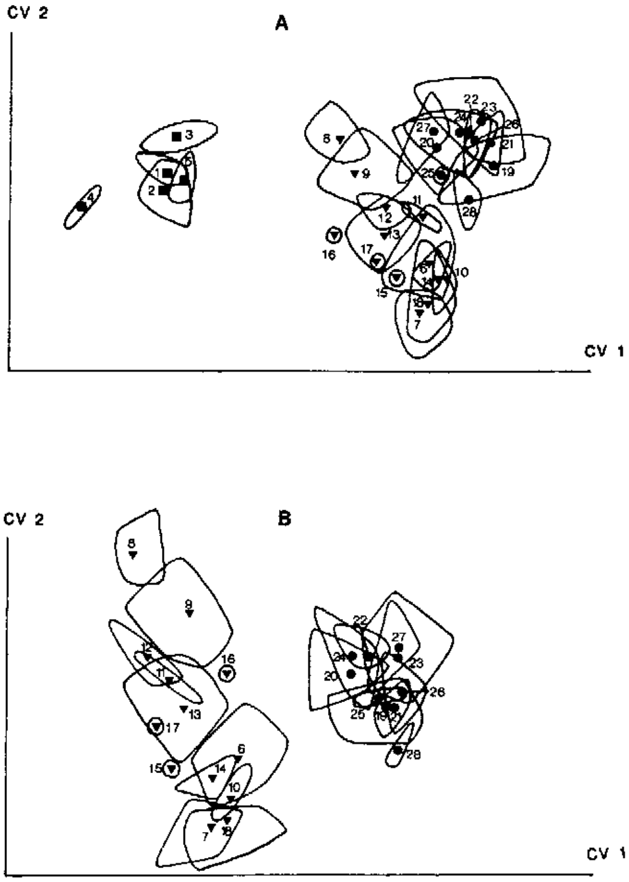

FIG. 2.—Systematics of the cobras of central Asia and the Indian subcontinent. (A) Ordination of all OTUs from central Asia, the Indian subcontinent, and the monocellate OTUs from Indochina, along the first two canonical variates of CVA 1. Symbols represent OTU means, solid lines the scatter of individual specimens. Three clearly distinct taxa are evident. Squares indicate the central Asian taxon, triangles the Indian spectacled taxon, and circles the monocellate taxon. CV 1 and CV 2 represent respectively 49.0% and 14.5% of the total dispersion. (B) Ordination of the spectacled OTUs and the monocellate OTUs from Indochina along the first two canonical variates, showing clear separation between the two taxa. CV 1 and CV 2 represent respectively 35.5% and 21.5% of the total dispersion. Refer to Fig. 1 for the geographic position of the OTUs.

The monocellate form includes some of the populations from northeastern India, and those from Burma, Thailand, Indochina, and northern Malaysia. These have a monocellate or, more rarely, mask-shaped hood mark, and possess medium to high ventral scale counts and medium subcaudal scale counts. This taxon will be referred to as the monocellate taxon.

There are extensive areas of sympatry

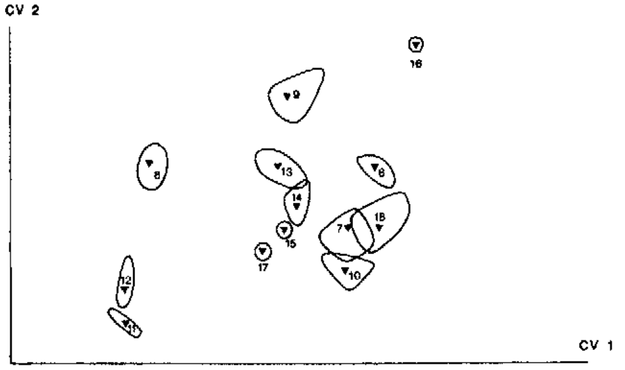

FIG. 3.—Geographic variation in the Indian spectacled cobra (*N. naja*): ordination of the OTUs along the first two canonical variates of CVA 3. Legend as in Fig. 2. The OTUs from northwestern India (nos. 8, 9, 16) have higher scores along the second canonical variate. CV 1 and CV 2 represent respectively 45.3% and 19.2% of the total dispersion.

between the spectacled taxon and the central Asian taxon, and between the spectacled taxon and the monocellate taxon.

Geographic Variation in the Spectacled Cobra

CVA 3 (Fig. 3), run on the entire character set, does not reveal a distinct pattern of geographic variation within the spectacled cobra. The OTUs from the northwestern part of the range of the taxon have a higher score along the second canonical variate, but the pattern is not very distinct. CVA 4, run on the scalation characters, reveals a clear pattern of geographic variation, the populations from the northwest having low scores along the first canonical variate, those from the east and south having higher scores (Fig. 4A). This is visualized in the three-dimensional surface plot (Fig. 5), which shows a clear northwest–southeast cline in the first canonical variate scores of individual specimens across the range of the spectacled cobra. CVAs 5, 6, and 7, run on characters relating to the internal anatomy, body proportions, and dentition, respectively, do not reveal a distinct pattern of geographic variation in those character systems (Fig. 4B–D).

DISCUSSION

Population Affinities throughout India and Central Asia

Relationships between the spectacled taxon and the central Asian taxon.—CVA 1 shows unambiguously that the cobras

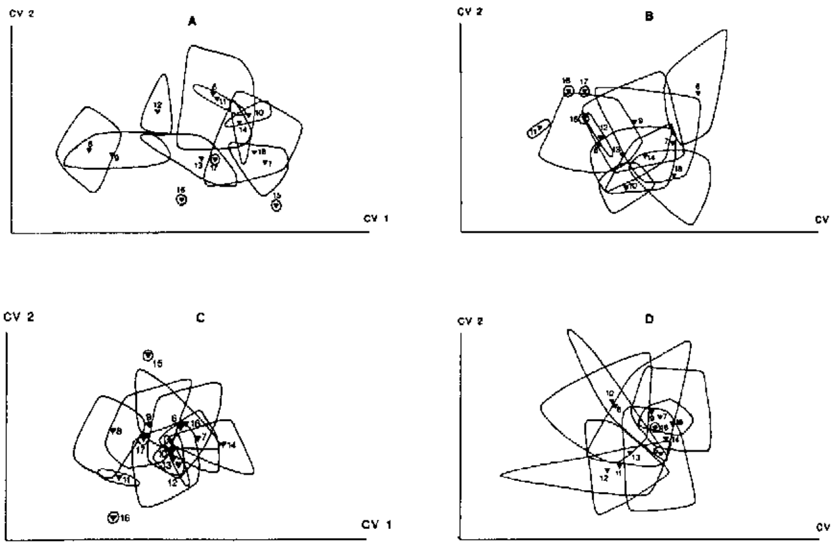

FIG. 4.—Geographic variation and congruence between character systems in the Indian spectacled cobra (*Naja naja*). Legend as in Fig. 2. Refer to Fig. 1 for the geographic origin of the OTUs. (A) Scalation.—Ordination of the OTUs along the first two canonical variates of CVA 4. Note the separation between the northwestern OTUs (nos. 8 and 9) and the remaining OTUs. CV 1 and CV 2 represent respectively 62.6% and 10.9% of the total dispersion. (B) Internal anatomy.—Ordination of the OTUs along the first two canonical variates of CVA 5. Note the absence of any clear pattern of differentiation. CV 1 and CV 2 represent respectively 37.5% and 19.2% of the total dispersion. (C) Body and scale proportions.—Ordination of the OTUs along the first two canonical variates of CVA 6. Note the absence of any clear pattern of differentiation. CV 1 and CV 2 represent respectively 38.4% and 16.6% of the total dispersion. (D) Dentition.—Ordination of the OTUs along the first two canonical variates of CVA 7. Note the absence of any clear pattern of differentiation. CV 1 and CV 2 represent respectively 35.2% and 26.7% of the total dispersion.

from central Asia and the Indian subcontinent, as well as the monocellate populations from Indochina, comprise three well-differentiated taxa.

The central Asian taxon is highly distinct from both the spectacled and the monocellate taxa. There is ample evidence for sympatry between the central Asian and the spectacled taxa in several localities. We have examined specimens of both taxa from Multan, Pakistan (BNHM 2228 and 2229), and from the Chitral Valley, northern Pakistan (BNHM 2224, BMNH 1910.1.4.7–9).

The occurrence of the spectacled taxon in the Chitral valley suggests that this taxon occurs in Afghanistan: the Chitral valley drains into the Kabul River valley at Jalalabad, in Nangarhar province, Afghanistan. In view of the mountains surrounding the Chitral valley in its Pakistani part, the only way the species could have penetrated the valley is through Nangarhar and Konarha provinces in Afghanistan. Dispersal of the species can be assumed in this case, because these high altitude valleys would have been too cold to support populations of cobras during Pleistocene cold phases. The spectacled cobra may therefore still occur in extreme eastern Afghanistan, a country from which it has not been recorded before.

There is some evidence that the two species occur sympatrically in parts of northeastern Baluchistan; we have seen specimens of the spectacled form from Duki (SMF 63060, 63063, 63065), whereas the central Asian taxon has been found at Quetta (RMNH 4029) and Sibi (AMNH 88469; SAM 709), and has been reported from the Suleiman Range (Joger, 1984; Minton, 1966).

Several literature reports indicate sympatry between what is usually referred to as *N. n. naja* (spectacled cobra) and *N. n. oxiana* (central Asian taxon). However, the literature concerning these two forms needs to be interpreted carefully, because the frequent absence of a hood mark in some populations of the spectacled taxon has confused some authors. It is necessary to consider characters such as scalation and the presence of banding in juveniles before

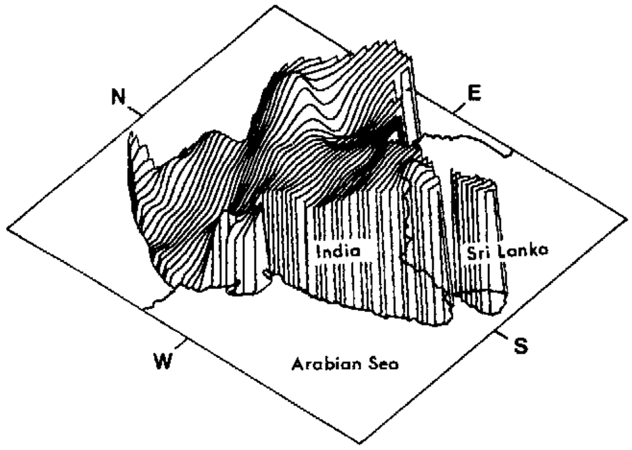

FIG. 5.—Constant-x three-dimensional surface plot of the scores of individual specimens along the first canonical variate of CVA 4, seen from the SW, at a vertical angle of 45°. Note the clear NW–SE cline in first canonical variate scores.

the identity of the specimens discussed can be taken for granted.

Khan (1977) noted sympatry between the spectacled cobra and the central Asian cobra at Ahmed Nagar (Jhang Sadar District, Punjab, Pakistan) and, in a later paper (Khan, 1983), in parts of the Punjab and the North-West Frontier Province. His descriptions of the two forms indicate that these records are reliable.

To summarize, there is clear evidence that the spectacled and the central Asian cobra occur sympatrically in many parts of northern Pakistan. The available locality records for both species are mapped in Fig. 6.

Because the two forms are clearly distinct and yet sympatric, they represent two distinct species. The type specimen of *N. naja* (Linnaeus), 1758 is a spectacled cobra. The type locality of this taxon is usually given as India, but was restricted to Sri Lanka by Deraniyagala (1945). The Indian spectacled taxon should therefore be referred to as *Naja naja*. The oldest available name for the central Asian cobra is *Tomyris oxiana* Eichwald, 1831 (Type locality: Transcaspia; i.e., Soviet Central Asia). The correct designation for this species is therefore *Naja oxiana*.

The eastern limit of the range of *N. oxiana* is poorly known. Joger (1984, p. 100) mapped Gilgit as the most easterly locality and did not mention the occurrence of this

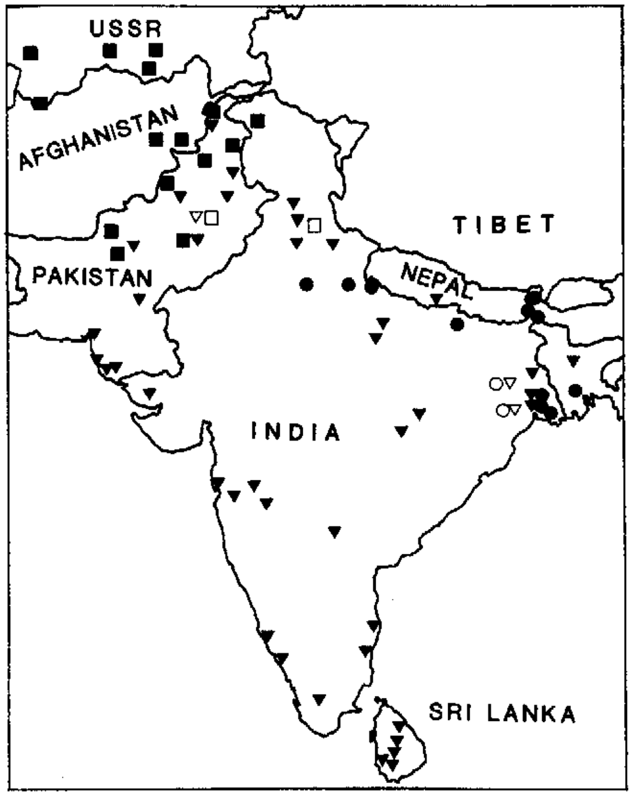

FIG. 6.—Locality records of the three species of cobras occurring in India. Squares indicate the central Asian cobra, triangles the Indian spectacled cobra, circles the monocellate cobra. Solid symbols represent specimens examined by the authors, hollow symbols literature reports considered to be reliable. Note the considerable area of sympatry between the spectacled and the central Asian Cobras in Pakistan and northwestern India, and between the spectacled and the monocellate cobras in northern and northeastern India.

species in India, except in the disputed territories of northern Kashmir. However, Murthy and Sharma (1976) and Murthy et al. (1979) reported specimens from the Punch Valley, northwest of Jammu, in India, and Mahajan and Agrawal (1976) described a specimen from the Simla Hills, in Himachal Pradesh. In each case, the presence of crossbands on what were immature specimens is a reliable indicator that these specimens were indeed *N. oxiana*.

As was mentioned above, not all locality records for *N. oxiana* in the literature are necessarily trustworthy. Some Indian workers have assigned all cobra specimens without a hood mark to the taxon *oxiana*. Many of the OTUs of *N. naja* included in CVA 1 contain specimens without hood marks: these include OTUs 8, 9, 10, 11, 12, 13, and 16. The mere absence of a hood mark does not, therefore, identify a cobra from northwestern India as *N. oxiana*.

In many areas, especially in southern Pakistan, spectacled cobras undergo pronounced ontogenetic color change: young specimens are gray, with or without a spectacled hood mark; as they grow older, they darken until they have a more or less uniformly black dorsum. This ontogenetic change has led several workers to assume that the adults belong to a different taxon than the young. For instance, Sundersingh (1960) assigned a young specimen from Pilani, Rajasthan, to *N. n. naja*, whereas two adults from the same locality, which were brown or black, were assigned to *N. n. oxiana*. Similarly, Biswas and Sanyal (1977) assigned a number of uniformly brown specimens from Rajasthan to *N. n. oxiana*. The scale counts given by these authors correspond to those of *N. naja* sensu stricto in northern India.

In this context, it is worth noting that adult *N. oxiana* are generally more or less uniformly medium or light brown; we have not seen a specimen that we would describe as darker than medium brown (after preservation), and certainly none that is black. Conversely, most adult specimens of the spectacled cobra from southern Pakistan (and the single specimen that we have seen from Gujarat) have a more or less uniformly black dorsum. Also, most *N. oxiana* retain at least a trace of the conspicuous juvenile banding pattern until at least early adulthood.

One of the characteristic features of most populations of Asiatic *Naja* is the presence of one or several small scales, which are situated between the edge of the mouth, and between the 4th and 5th infralabials, sometimes also between the 5th and 6th. It has been stated (e.g., Khan, 1977) that, unlike *N. naja*, *N. oxiana* lacks a cuneate scale. This is generally true in the case of the populations from Soviet central Asia and Iran, but most of the specimens from Pakistan, Afghanistan, and India that we have examined had a cuneate on each side.

Another source of confusion regarding the central Asian cobra concerns the number of maxillary teeth: *N. oxiana* consis-

TABLE 2.—Distinguishing characters of *Naja naja* and *N. oxiana* in their zone of sympatry in northwestern India and Pakistan. Specimens from other parts of the ranges of the two species are easier to distinguish due to additional scalation differences (lack of a cuneate in northern populations of *N. oxiana*; 29 or more scale rows around the hood in southern and eastern populations of *N. naja*, versus 23–27 in *N. oxiana*). M = males, F = females.

	Naja naja	*Naja oxiana*
Ventral scales	M: 184–193; F: 182–196	M: 199–207; F: 191–210
Subcaudal scales	M: 58–67 F: 53–63	M: 66–71 F: 62–70
Maxillary teeth	0 (very rarely 1)	1
Juvenile pattern	Speckled or uniform, one or two ventral bands, often hood mark and lateral throat spots	Conspicuously banded, both ventrally and dorsally, along most of body length, no hood mark or lateral throat spots

tently has one solid maxillary tooth. The erroneous statement by Bogert (1943) that this species has two solid maxillary teeth is based on a misinterpretation of Eichwald's (1831) original description of the species. Deraniyagala (1960) erroneously stated that this species has "no solid tooth behind the poison fang". All specimens of this species that we have examined had a single solid maxillary tooth. Table 2 lists characters that can be used to distinguish between *N. oxiana* and *N. naja*.

The sympatry between *N. naja* and *N. oxiana* in northern India and Pakistan is important from the point of view of snakebite treatment and antivenin usage. Karlsson and Eaker (1972) reported major differences between the neurotoxins of *N. oxiana* and other species of Asiatic *Naja*, which suggests that their antigenic qualities may differ. Kankonkar et al. (1972) reported that Indian (Haffkine) polyvalent antivenin neutralizes the venom of "acellate" cobras, which he assigned to *N. n. oxiana*. It is, however, possible that the specimens from which the venom was obtained were patternless specimens of *N. naja*, which, as was discussed above, are often confused with *N. oxiana*. A study comparing the venoms of known *N. oxiana* and *N. naja*, and assessing the efficacy of commercially available antivenins against the former, is urgently needed.

Relationships between the spectacled taxon and the monocellate taxon.—The status of the monocellate cobra is similar to that of the central Asian cobra. CVA 2 has shown that the monocellate and the spectacled taxa are clearly morphologically distinct. Again, there is evidence for widespread sympatry between the two forms. It is also clear that the populations of monocellate cobras from Indochina and northern Malaysia are part of the same taxon as the monocellate cobras from northern India.

We have examined specimens of both monocellate and spectacled cobras from a wide range of localities in northern India. The specimens of the spectacled cobra originated from as far east as the Madhupur Jungle, in Tangail District, Bangladesh (SMF 70323), the Gayshpur Colony, Nadia District, West Bengal (FMNH 165086), and from Tangrah (ZMH R 03115–6), Serampore (ZMUC R 65313), and Howrah (FMNH 161466), near Calcutta, West Bengal. In the Gangetic plain, we have seen spectacled specimens from Kanpur (FMNH 171332, 171767, 191886–7; USNM 193293), Lucknow (MCZ 75611), and Mussoorie, Uttar Pradesh (FMNH 25498), and from Devanandpur, southern Nepal (MHNG 1328.14–16) (these were erroneously described as *N. n. kaouthia* by Kramer, 1977). There are monocellate specimens from localities much further west. We have seen specimens from Howrah (BNHM 2244, 2296), and several other localities in the Calcutta area, in Bengal; we have also seen specimens from further west, namely from Bettiah in Bihar (BMNH 1940.3.7.33), from Sonaripur (BMNH 1940.3.7.34), and Rampur (BNHM 2251), in Uttar Pradesh, and even from Sonipat, Haryana, northwest of Delhi

TABLE 3.—Distinguishing characters of *Naja naja* and *N. kaouthia* in northern and northeastern India. Specimens from other parts of the ranges of the two species may differ with respect to the characters listed.

	Naja naja	*Naja kaouthia*
Hood mark	Spectacle-shaped or absent	Monocellate or mask-shaped, never totally absent
Scale rows at level of 10th Ventral	Usually >29	Usually 29 or less
Scale rows at 20% and 40% VS length	Usually 23	Usually 21
Throat pattern	Often indistinct, lateral spots usually encroach on second dorsal scale row	Usually distinct, lateral spots usually encroach on lowest dorsal scale row only

(UF 20521). The localities for these specimens, as well as records taken from the literature, are mapped in Fig. 6.

Data from the literature can be used with confidence to establish the distributions of these two taxa: previous workers have always distinguished them by the type of hood mark, which is a reliable diagnostic character. There are a number of literature reports which indicate sympatry between spectacled and monocellate cobras. Fayrer (1874) reported both monocellate and spectacled cobras from Calcutta and Puruliya, Bengal. Bannerman and Pocha (1905) noted the occurrence of both forms at Medinipur (formerly Midnapore) in West Bengal. Sights (1949) also reported both monocellate and spectacled cobras to be fairly common in three localities in the Medinipur area. Table 3 shows distinguishing characters between the two species.

There have also been reports of habitat differences between the two forms: Fayrer (1874), Murthy (1986), Sights (1949), and Whitaker (1978) all noted that where the two species occur sympatrically, the monocellate cobra is found in wetter areas than the spectacled cobra.

In conclusion, there is unequivocal evidence that the monocellate and the spectacled cobras occur sympatrically in much of northeastern India, and that they are highly distinct morphologically. This demonstrates that they are reproductively isolated under natural conditions, and therefore are separate species.

Although these two species are undoubtedly separate species, there is a report of fertile matings between two captive sibling "reported hybrids" between the two forms (Campbell and Quinn, 1975). The photos of the two specimens do not allow a definitive identification of the two snakes. The authors reported that the parents were also sibling hybrids. This report suggests that the reproductive isolation between the two species may be weak. Nevertheless, the widespread sympatry between the two species, together with the consistent morphological differences between them, demonstrate that they are reproductively isolated in the wild, although the occasional appearance of hybrids cannot be excluded. Pre-copulatory reproductive isolating mechanisms can break down in unnatural conditions, and in such cases, fertile hybrids can result from interspecific matings: see Aird et al. (1989) for an example in the genus *Crotalus*. The captive hybridization between the two taxa cannot, therefore, be taken as evidence of conspecificity. The oldest available name for the monocellate cobra is *Naja kaouthia* Lesson 1831 (type locality: Bengal).

There do not appear to be any problems with regard to antivenin efficacy in the case of *N. naja* and *N. kaouthia*; Kankonkar et al. (1972) reported that Indian (Haffkine) polyvalent antivenin neutralizes the venoms of both species.

Summary.—The cobras of the Indian subcontinent and central Asia fall into three distinct species, the distribution of which is mapped in Fig. 7: (1) the central Asian cobra, *N. oxiana* (Eichwald, 1831), from Soviet central Asia, northeastern Iran, Afghanistan, northern Pakistan, and extreme

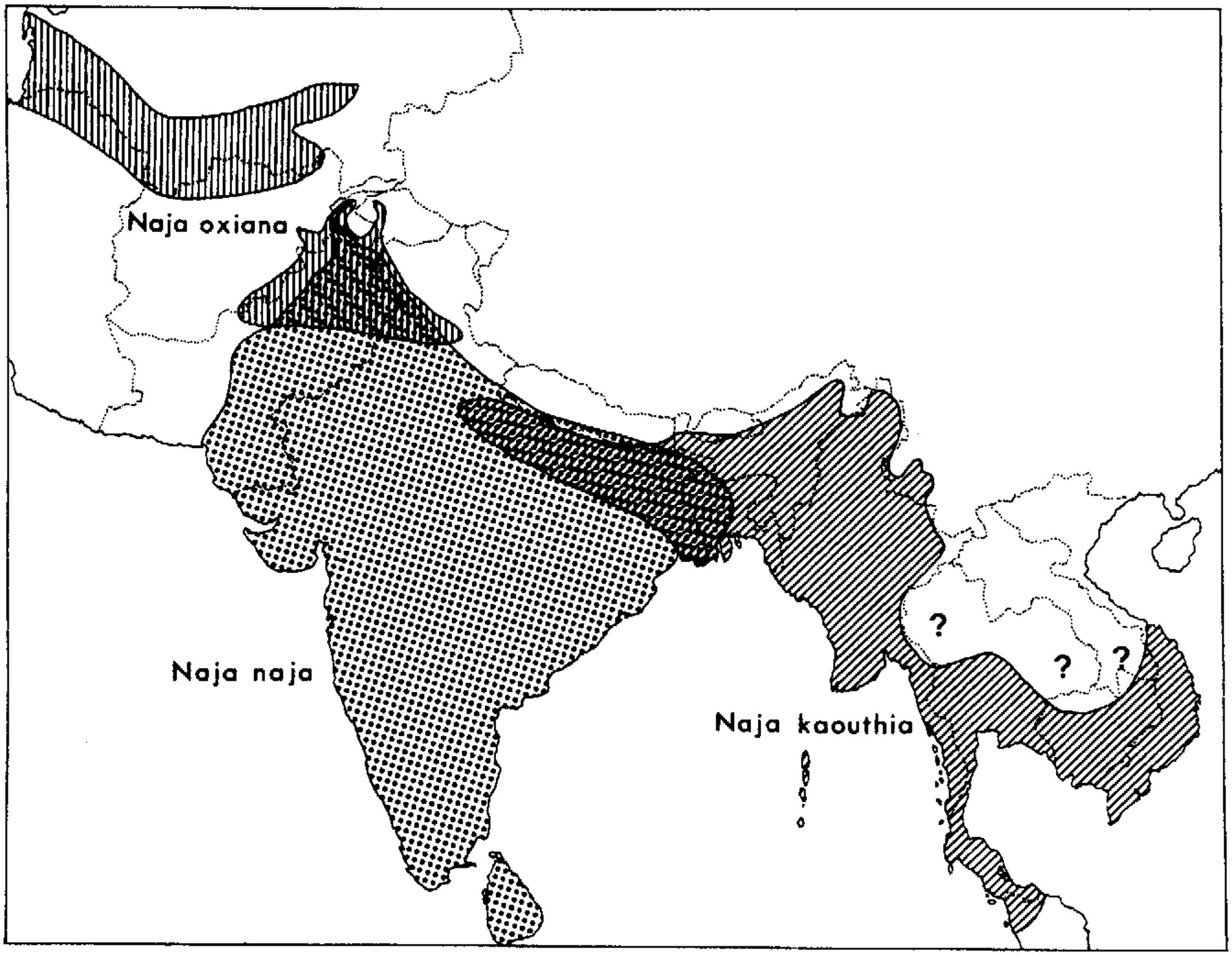

FIG. 7.—Distribution of the central Asian cobra (*Naja oxiana*), the Indian spectacled cobra (*N. naja*) and the monocellate cobra (*N. kaouthia*). Other species not discussed here occur sympatrically with *N. kaouthia* in Indochina.

northern India; (2) the Indian spectacled cobra, *N. naja* (Linnaeus), 1758 from Pakistan, India, Nepal, and Bangladesh; (3) the monocellate cobra, *N. kaouthia* Lesson 1831, from northeastern India, Burma, Thailand, northern Malaysia, and Indochina.

In addition to these three well-defined taxa, we examined two specimens (BNHM 2249 and 2250, from the Indian state of Bihar) that could not easily be classified as specimens of any of the three species recognized here. They could be aberrant specimens of *N. naja* or *N. kaouthia*, a divergent population of other taxa from Indochina, hybrids between *N. naja* and *N. kaouthia*, or an undescribed taxon. Finally, the possibility of false locality data must be taken into account. In view of the paucity of material, nothing more will be said here, but the population affinities of the cobras of northeastern India are in need of further investigation.

Intraspecific Geographic Variation in the Spectacled Cobra, Naja naja

In this paper, we shall discuss only the pattern of intraspecific geographic variation within the Indian spectacled cobra, *Naja naja*. Too little material of *N. oxiana* is available for a useful investigation of geographic variation in that species, and the pattern of geographic variation in *N. kaouthia* will be discussed elsewhere (Wüster and Thorpe, unpublished data).

An investigation of the pattern of geographic variation in *N. naja* is interesting for several reasons. First, it occurs in a wide range of habitats and climatic zones, from semi-arid regions in the northwest to rainforest areas in southwestern India and Sri Lanka; if a distinct pattern of geographic variation does exist in this species, then it will be interesting to relate this to climatic and vegetational factors.

Second, a number of subspecies of *N. naja* (sensu stricto) has been recognized by Deraniyagala (1945, 1960, 1961). In determining whether any populations should be recognized as subspecies, the following criteria, set out by Thorpe (1987*a*), will be adopted. (1) The pattern of geographic variation should be very clear, and categorical in nature. (2) Subspecies should be predictive; i.e., the pattern of variation in one character system should predict that found in other character systems (see Thorpe, 1987*b*, for an example of character congruence across a hybrid zone between the two mainland subspecies of the European grass snake, *Natrix natrix*). (3) The proposed subspecies should constitute categories just below the species level.

CVA 3, run on all available characters, revealed a weakly defined pattern of geographic variation, the populations from the northwest of the range of the species being somewhat distinct from the other populations (Fig. 3).

There is a very clear pattern of geographic variation in scalation, as was demonstrated in CVA 4 (Fig. 4), the northwestern OTUs being clearly separated from the other populations, and the OTUs from Maharashtra state and Madhya Pradesh (OTUs 12 and 13) appearing somewhat intermediate between the northwestern and the other populations. The three-dimensional surface map (Fig. 5), based on the scores of individual specimens along the first canonical variate, shows the essentially clinal nature of the pattern of geographic variation in scalation. There is no evidence of a categorical pattern of variation in this character system. Furthermore, there is no clear pattern of geographic variation in the internal anatomy, body proportions, and dentition (CVAs 5, 6, and 7: Fig. 4). In view of the lack of congruence between different character suites, and of a categorical pattern of variation, it would be inappropriate to recognize subspecies of *N. naja*, at least on the basis of the material examined here.

However, we consider it necessary to discuss the subspecies of *N. naja* described by Deraniyagala (1945, 1960, 1961), because they are based on a number of misconceptions or erroneous assumptions which require correction. Deraniyagala (1945) restricted the type locality of *N. naja* to Sri Lanka, calling the populations of that island *N. n. naja*. He considered the populations from southern India to be different from the Sri Lankan populations, stating that the latter have more dark ventral bands (up to 15 or more) than Indian specimens (usually 1–3), and that they have fangs adapted for spitting venom. He described the southern Indian populations as a new subspecies, *N. n. madrasiensis*. In fact, the Sri Lankan cobras, like all populations of *N. naja*, have non-spitting fangs (Wüster, unpublished data). Sri Lankan specimens do tend to have a higher number of dark ventral bands than Indian specimens, but the CVAs presented here do not reveal any major differentiation in the overall phenotype. We therefore do not consider the minimal differences between southern Indian and Sri Lankan cobras to warrant the recognition of the former as a subspecies.

The cobras of northwestern India and Pakistan, which Deraniyagala (1960) described as *N. n. indusi*, were considered distinct from the southern and eastern populations primarily on the basis of the absence of a solid maxillary tooth. In fact, the number of maxillary teeth is not constant within populations of *N. naja*; there are occasional specimens from Pakistan with solid maxillary teeth, and in other parts of India, some specimens occasionally lack solid maxillary teeth. There is no other indication of phenotypic differentiation between specimens with and without solid maxillary teeth, so that this character cannot be regarded as being of taxonomic importance.

The main differences between northwestern populations of this species and those from the remainder of the range concern the scalation: the northwestern populations have fewer dorsal scale rows around the hood (25–29) and at mid-body (19–21) than those from other regions (29–37 and 23–25, respectively). The pattern of differentiation in the scalation between the northwestern and the other populations appears to be clinal, as CVA 4 shows populations from Maharashtra and Madhya Pradesh (OTUs 12 and 13) to be intermediate between the northwestern populations and the others (Figs. 4A, 5). Because the differentiation between these populations and those from adjoining areas does not appear to be categorical, and does not extend to other character systems, we do not believe that the northwestern populations should be recognized as a separate subspecies under the criteria adopted here.

Deraniyagala (1945) also recognized the populations from the Gangetic Plain as a separate subspecies, *N. n. gangetica*. This "subspecies" was never properly diagnosed from other Indian populations. The preceding CVAs do not indicate that the populations from the Gangetic Plain (OTUs 6, 10, and 11) are strongly differentiated from other populations of this species. Consequently, we do not recognize the subspecies *N. n. gangetica*.

Naja n. karachiensis Deraniyagala, 1961 was described on the basis of most adult specimens being black dorsally, without any sign of a hood mark. The young specimens that we have examined often had a spectacled hood mark. The black color of the adult specimens is an ontogenetic change, superimposed upon the basic color pattern. It may be an ecogenetic adaptation, for instance a thermoregulatory adaptation to cool desert mornings in the winter season. These populations are not consistently distinct from other Pakistani/northwest Indian spectacled populations, either in their overall phenotype (CVA 3) or in individual character suites (CVAs 4–7). We therefore do not consider them to warrant subspecific recognition.

Finally, Deraniyagala (1961) described the Maharashtra populations as *N. n. bombaya*, primarily on the basis of the combination of a lack of maxillary teeth and cuneate scales. Only a single specimen was examined by that author. Deraniyagala's reasons for conferring subspecific status on these populations are misleading: all the specimens from Maharashtra that we have examined have at least one cuneate on each side, and six out of 10 had a solid maxillary tooth. Cuneate scales can occasionally be absent in any of the Asiatic species of *Naja*, so that their absence in one specimen cannot be used to infer a separate taxonomic status. In any case, the description of a new subspecies on the basis of a single specimen is ill-considered, as it ignores the extent of variation within the proposed subspecies. The CVAs described above do not suggest that the Maharashtra populations are distinct from the other populations of this species. We therefore do not recognize the subspecies *N. n. bombaya*.

We conclude that all the subspecies of *N. naja* erected by Deraniyagala are invalid, either because the character differences used to define them are insignificant when related to the pattern of variation in the overall phenotype, or because the data on which the description was based were incorrect or insufficient. The observed pattern of geographic variation in this species fails to meet the criteria for the recognition of subspecies set out by Thorpe (1987*a*), and we therefore regard the species *N. naja* as monotypic.

Further studies of the pattern of geographic variation within this species, using additional material, and other techniques, such as mitochondrial DNA analysis, are needed. Studies of the pattern of variation in the composition and action of the venoms of different populations of *N. naja* would be especially worthwhile, as this species is of considerable medical importance in parts of its range (Sawai et al., 1984; de Silva, 1981; de Silva and Ranasinghe, 1983). There is some evidence that antivenin produced in Maharashtra (western India) is largely ineffective in treating bites by Sri Lankan cobras (Theakston et al., 1989).

Other venomous species of snakes have been shown to exhibit pronounced venom variation within the Indian subcontinent; in Russell's viper, considerable differences between the venoms of populations from various parts of India and Sri Lanka have been documented (Jayanthi and Gowda, 1988), and antivenin against western Indian populations was found to be ineffective in the treatment of bite victims in Sri

Lanka (Phillips et al., 1988). Detailed studies of the pattern of geographic variation in the venoms of snakes widespread on the Indian subcontinent, such as *N. naja*, *Vipera russelli*, and *Bungarus caeruleus*, are urgently required.

Acknowledgments.—We thank the curators and staff of the numerous museums who loaned us the specimens in their care, and especially the staff members of the British Museum (Natural History) for their help and cooperation. S. A. Minton generously made several specimens of his private collection available for this study. Two anonymous reviewers provided constructive criticism on an earlier version of the manuscript. This study was funded by the Science and Engineering Research Council of Great Britain (quota studentship to the senior author), the Natural Environment Research Council (research fellowship to the senior author), and the Leverhulme Trust (fellowship to the junior author).

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Accepted: 11 January 1991
Associate Editor: David Cannatella

APPENDIX I

Specimens Examined

Naja naja: **BANGLADESH**—Madhupur Jungle, Tangail District (SMF 70323). **INDIA**—ANDHRA PRADESH; Hyderabad (AMNH 87485). GUJARAT; Bhuj (BNHM 2230). HARYANA; Ambala (MCZ 5268). HIMACHAL PRADESH; Kulu Valley (MCZ 3229), Sabathu (BNHM 2144), Sutlej Valley (AMNH 2851). KERALA; Calicut (MHNB 2231), Malabar Coast (CAS 17261; MHNB 2230), Punakanaad (BMNH 1924.10.1323). MADHYA PRADESH; Ambikapur (CAS 12292), Mungeli (CAS 12294–5). MAHARASHTRA; Ahmadnagar (NMW 27790:1, 27801: 7), Bombay (MHNB 2234–5; MHNG 2032.30A, 2032.30B; ZMH R 03110–1; ZMUC R 6522, 6530), Khanadala (BNHM 2260), Poona (BNHM 2257, 2259). TAMIL NADU; Madras (CAS 12419; MHNG 1406.30; MNHN 5439; NMW 27801:3; RMNH 4129; SMF 20617, 20619–20), Ennur (CAS12416), Pondicherry (MNHN 7689), Periyakulam (MCZ R 1331), Madurai (NHRM HSG.1934.492.3030). UTTAR PRADESH; Kanpur (FMNH 171332, 171744, 171767, 191886–7; USNM 193293), Lucknow (MCZ 75611), Mussoorie (FMNH 25498). WEST BENGAL; "Bengal" (ANSP 6886–7; RMNH 1314A, 1314B, 1320; ZMH R 03108; ZMUC R 65486), Calcutta (USNM 129743; ZMH R 03313–6; ZMUC R 65319, 65321), Gayshpur Colony, Nadia District (FMNH 165086), Howrah (FMNH 161466–7), Serampore (ZMUC R 65313). **NEPAL**—Devanandpur (MHNG 1328.14–16). **PAKISTAN**—BALUCHISTAN; Duke (SMF 63060, 63063, 63065), Hajargani (BNHM 2226). NORTHWEST FRONTIER PROVINCE; Drosh, Chitral (BNHM 2224). PUNJAB; "Punjab" (UMZC R 9.177/1–2), Chakwal District (AMNH 39396–7), Dera Ismail Khan (BNHM 2225), Multan (BNHM 2228), Rawalpindi (SAM 716). SIND; Sind Prov. (NMW 27790:4), Gharo (SMF 50443), Guyo (SMF 50445), Hab River (UF 65730), Hingora (AMNH 85448), Karachi (BMNH 1900.5.9.14; SMF 63064; ZMUC R 65455), Pir Patto (SMF 50441), Sujawal (UF 65731–5), Tatta (UF 48474–5; NMW 27758:1; SMF 50440, 50444). **SRI LANKA**—"Sri Lanka" (BMNH 58.10.19.24, 1931.5.13.93, 1972.2197, 1987.706–8; CAS 16913; MHNB 2236–7, 10642, 15221, 15581; NHRM 1895.989.4603; NMW 27789:3), Colombo (SMF 41193;

ZMH R 03112), Diyatalawa (BMNH 1910.3.16.27), Kandy (CM 67526), Peradeniya (BMNH 1913.2.7.3–4; CM 67707–8, 67644; USNM 120333), Polonnaruwa (CM 67643), Ratnapura (NMW 27789), Trincomalee (FMNH 122578–9).

Naja kaouthia: **BURMA**—CHIN; Falam (BNHM 2262). IRRAWADDY; Bassein (ZMH R 03117). KACHIN; Bhamo (ZMH R 3105), Myitkyina (AMNH 58524), Sumprabum (BMNH 1974.905), Triangle (BMNH 1940.6.5.64–6). MANDALAY; Pyawbwe (BNHM 2263). PEGU; Rangoon (CAS 12418; NHRM 1935.3.19.3293, NHRM NNN 1975.999.3056A, 1975.999.3056B, 1975.999.3056C, 1975.999.3057B), Taikkyi (UF 48842), Tharawaddy (BMNH 1987.710). SARGAING; Mogok (BMNH 1900.9.20.17–8). **CAMBODIA**—Kampot (FMNH 11545), Snoc Trou (MNHN 1963.735). **CHINA**—YUNNAN; Yongde (UF 63902). **INDIA**—ASSAM; "Assam" (ZMUC 65318, 65344), Dibrugarh (USNM 118974). BIHAR; Bettiah (BMNH 1940.3.7.33). HARYANA; Sonipat (UF 20521), SIKKIM; Sikkim (FMNH 15822–3). UTTAR PRADESH; Rampur (BNHM 2251), Sonaripur (BMNH 1940.3.7.34). WEST BENGAL; "Bengal" (RMNH 1319; SMF 20618; UMZC R 9.177/11, 9.177/14, 9.177/16; ZMUC R 65316–7, 65487, 65495), Burigoalni (MCZ 58407), Calcutta (BMNH 60.3.19.1339, CM 91864; MHNG 1328.17–8, 1328.21–2; NHRM 1828.168.4602; NMW 27755:1; ZMUC R 6513, 6536–7, 65315, 65320, 65323), Canning Thana (FMNH 165076, 165080–3, 165085), Darjeeling (BNHM 2247), Dum-Dum (LACM 104329–30), Howrah (BNHM 2244, 2296), Jalpaiguri (BNHM 2245), Tarda Thana (FMNH 165075, 165077, 165079). **MALAYSIA**—KEDAH; Alor Setar (BMNH 99.9.22.56), Kulim (BMNH 95.10.7.22). KELANTAN; "Kelantan" (BMNH 1905.2.7.9), Kota Baharu (BMNH 1913.7.24.6). PENANG; Georgetown (FMNH 118998), Kapala Batas (ZFMK 16544). **THAILAND**—AYUTTHAYA; Ayutthaya (BMNH 1974.5499). CHACHOENGSAO; Chachoengsao (BMNH 1987.647). CHON BURI: Siracha (BMNH 1968.834–5). KANCHANABURI; Kanchanaburi (BMNH 1987.640), Sai Yok (BMNH 1987.638–9), Tong Pha Phum (BMNH 1987.641). KRABI; Krabi (BMNH 1987.652–3; ZFMK 16678). NAKHON PATHOM; Nakhon Pathom (BMNH 1987.655). NAKHON RATCHASIMA; Sakaerat, Amphoe Pak Thong Chai (FMNH 180603). NAKHON SAWAN; Bung Borapet (USNM 81843), Nakhon Sawan (FMNH 60960). NAKHON SI THAMMARAT; Nakhon Si Thammarat (BMNH 1987.654); PHANGNGA; Phangnga (BMNH 1987.642). PATHUM THANI; Pathum Thani (BMNH 1987.686). PATTANI; Na Pradoo (FMNH 179120). PHATTALUNG; Phattalung (BMNH 1987.645; FMNH 191096), Tha La (NHRM 1912.169.5394). PHITSANULOK; Phitsanulok (BMNH 1987.643). PHRA NAKHON; Bangkok (BMNH 97.10.8.33, 98.11.8.34, 1921.4.1.25; MCZ 8386; MHNG 1328.19–20; NMBE 351A, 351B, 351C, 351D; NHRM 1914.989.3538–9, 1914.989.4550, 1914.989.5531, 1914.989.5550; MNW 22800:2, 27780:2, 27794; UMMZ 65343; USNM 94762; ZMH R 02885, 02896; ZMUC R 65354). PHUKET; Phuket (BMNH 1902.12.12.5, 1977.2027–2031). SAMUT PRAKAN; Bang Phli (BMNH 1987.646, 1987.656). SATUN; (BMNH 1987.637). SONGKHLA; Songkhla (FMNH 179124). SUPHAN BURI; Suphan Buri (BMNH 1987.694). TRANG; Trang (BMNH 1987.628–9). YALA; Biserat (UMZC R 9.177/5). **VIETNAM**—"Cochinchina" (FMNH 11546–7, MNHN 1892.93), Da Lat (BMNH 1921.4.1.43), Ho Chi Minh City/Saigon (MTKD D 24167), Quang Tri (USNM 165072), Thua Luu, Hue (NHRM BJÖ 1939.989.3096A, 1939.989.3096B).

Naja oxiana: **AFGHANISTAN**—Jalalabad (FMNH 161138), Kabul (ZMUC R 6529). **IRAN**—Mashad (FMNH 166975–6; SMF 62599), 100 km E. Mashad (SMF 71083), Shahrabad (FMNH 141614, 141616). **KASHMIR** (DISPUTED TERRITORY)—Gilgit (BMNH 80.3.15.1–3). **PAKISTAN**—BALUCHISTAN; Kach (SAM 709), 6 km W. Kach (AMNH 88469). NORTHWEST FRONTIER PROVINCE; Baffa (SMF 57352), Chitral (BMNH 1910.1.4.7–9), Kampuram (BMHM 2223), Peshawar (AMNH 88443). PUNJAB; Multan (BNHM 2229). **U.S.S.R.**—TADZHIKISTAN; Boba-Tag Mountains (MHNB 21047; MTKD D 16691), Dushanbe (MTKD D 11667, 11676, 21891), 40 km S. Dushanbe (MTKD D 20731), 80 km S. Dushanbe (MTKD D 11659, 11671), 80 km W. Dushanbe (MTKD D 11668), 110 km W. Dushanbe (MTKD D 7660), 80 km SW Dushanbe (MTKD D 13156, 13472), Pyandzh River (MTKD D 17272). TURKMENIA; Badkhiz (ZIK 1218), Danata (ZIK 2771), Kopet Dagh (SMF 20625; ZIK 2192, 2288; ZIL N 19714), Mt. Kugitang (ZIK 2165), Kushka (ZIK 2561; ZIL N 12871), Lake Jashkhan (ZIK 2259), Murgab (NMW 14888), Sharlouk (ZIK 2260), Tedzhen (ZIL N 8481). UZBEKISTAN; Bukhara (ZIL N 8578, 12147), Charast District (ZIL N 16583), Gussar (ZIL N 16602).

Uncertain affinities: **INDIA**—BIHAR; Jogderi, Hazaribagh (BNHM 2250), Pusa (BNHM 2249).

Appendix II

Characters Used

1. Number of ventral scales.
2. Number of subcaudal scale pairs.
3. Percentage of undivided subcaudals.
4. Number of cuneates.
5. Number of posterior temporal scales.
6. Number of temporal and nuchal scales in contact with the parietal scales.
7. Number of dorsal scale rows at the level of the tenth ventral scale.
8. Number of dorsal scale rows at 20% VS length.
9. Number of dorsal scale rows at 40% VS length.
10. Number of dorsal scale rows at 60% VS length.
11. Number of dorsal scale rows at 80% VS length.
12. Number of dorsal scale rows at the level of the last ventral.
13. % CS tail segments with two scale rows.
14. % CS position of the reduction from 6 to 4 scale rows on tail.
15. % CS position of the reduction from 8 to 6 scale rows on tail.
16. % CS position of the reduction from 10 to 8 scale rows on tail.
17. % VS position of the anterior edge of the thyroid
18. % VS position of the posterior tip of the heart.
19. % VS position of the systemic junction.

20. % VS position of the anterior tip of the liver.
21. % VS position of the posterior tip of the liver.
22. % VS position of the anterior tip of the pancreas.
23. % VS position of the anterior tip of the right testis.
24. % VS position of the posterior tip of the right testis.
25. % VS position of the anterior tip of the left testis.
26. % VS position of the posterior tip of the left testis.
27. % VS position of the anterior tip of the right kidney.
28. % VS position of the posterior tip of the right kidney.
29. % VS position of the anterior tip of the left kidney.
30. Number of palatine teeth.
31. Number of pterygoid teeth.
32. % VS position of last ventral involved in the formation of the light throat area.
33. Number of lateral throat spots.
34. % VS position of the anterior edge of the largest pair of lateral throat spots.
35. % VS length of the largest pair of lateral throat spots.
36. % DS encroachment of the largest pair of throat spots onto the sides of the neck.
37. % VS width of first dark ventral band.
38. Length of frontal scale.
39. Width of frontal scale.
40. Distance between anterior edge of frontal scale and posterior tip of rostral scale.
41. Length of the supraocular scales (mean of both).
42. Length of the suture between the prefrontal scales.
43. Length of the suture between the parietal scales.
44. Length of the parietal scales (mean of both).
45. Tail length.
46. Maximum width of head across supraoculars.
47. Distance from snout tip to the posterior end of the interparietal suture.
48. Distance from snout tip to the posterior end of the lower jaw bone (mean of both sides).
49. Head depth across the middle of the supraoculars.
50. Head depth from lower edge of supralabials to the top surface of the supraoculars.
51. Fang length.
52. Fang discharge orifice length.
53. Distance from upper edge of discharge orifice to tip of fang.