

DENTITIONAL PHENOMENA IN COBRAS REVISITED:  
SPITTING AND FANG STRUCTURE IN THE ASIATIC  
SPECIES OF *NAJA* (SERPENTES: ELAPIDAE)

WOLFGANG WÜSTER AND ROGER S. THORPE

*Department of Zoology, University of Aberdeen, Tillydrone Avenue,  
Aberdeen AB9 2TN, Scotland, U.K.*

**ABSTRACT:** We compare the fang morphology of the Asiatic cobra species, with particular reference to the occurrence of spitting behavior. The two nonspitting species, *Naja naja* and *N. oxiana*, have unmodified fangs with large venom discharge orifices; the other seven species, which have all been reported to spit, show varying degrees of reduction in discharge orifice size. There is considerable variation in the degree of fang modification among the species of spitting cobras, and only a small reduction in discharge orifice size seems to enable spitting. Some species show geographic variation in fang structure, and *N. philippinensis* shows sexual dimorphism in discharge orifice size.

**Key words:** *Naja*; Serpentes; Elapidae; Asia; Spitting cobra; Fang structure; Geographic variation; Sexual dimorphism; Antipredator mechanisms

AMONG snakes, the ability to spit venom at an aggressor is a feature unique to some species of the elapid genus *Naja* and the closely related South African genus *Hemachatus*. The phenomenon has been

known for a long time, prompting, for instance, Boie (1827) to describe the Javan cobra as *Naja sputatrix*. However, the mechanism of this defensive behavior was only elucidated in Bogert's (1943) classic

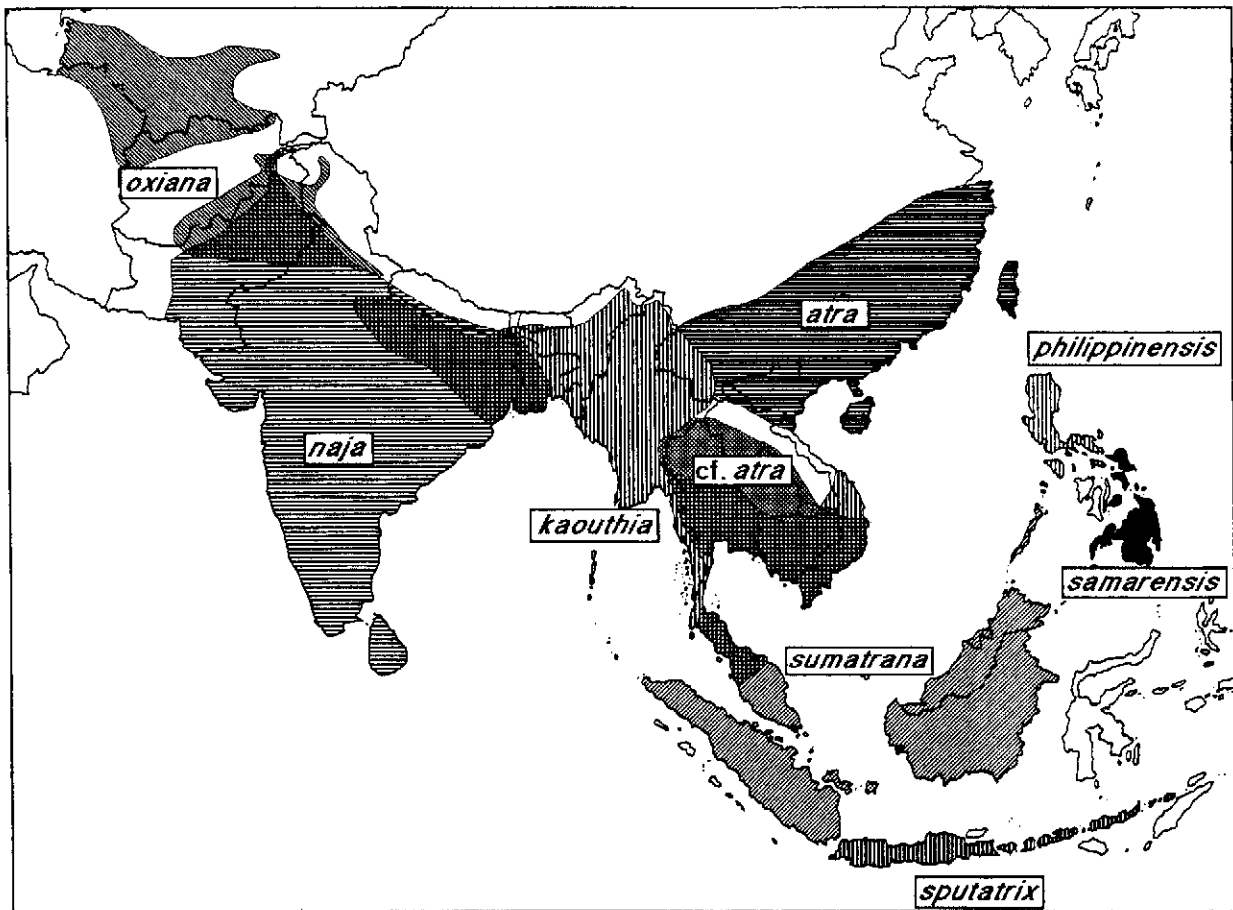


FIG. 1.—Distribution of the nine species of Asiatic cobras. The distribution limits of *Naja kaouthia*, *Naja atra* and *Naja cf. atra* in Laos, parts of Burma, southwestern China, and central Vietnam are poorly known, and the unshaded area in that region is a reflection of this lack of knowledge. At least one of these species is very likely to occur in any part of that region.

study on dentitional phenomena in cobras and related genera. He was the first to demonstrate that the spitting cobras have smaller, more rounded venom discharge orifices than nonspitting cobras.

In Asiatic cobras, Bogert noted geographic variation in the structure of the fangs: populations from Central Asia and the Indian subcontinent were rated as non-spitting cobras, those from Indochina and China as partially adapted to spitting, and those from the Malayan Peninsula, Indonesia, the Philippines, and Sri Lanka as fully adapted spitting cobras. Like most workers, Bogert regarded all populations of Asiatic cobras, with the exception of *Naja oxiana*, as part of a single species, *N. naja*. Recent studies (Wüster and Thorpe, 1987, 1989, 1990, 1991, 1992) have shown that the Asiatic cobra complex comprises a total of at least eight separate species,

with numerous areas of sympatry between species pairs. Comparative sequencing of parts of the mitochondrial genome (Wüster and Thorpe, unpublished data) has since shown that the populations grouped provisionally as *Naja atra* by Wüster and Thorpe (1991) in fact comprise two species, *Naja atra sensu stricto*, from China and northern Vietnam, and a species of as yet unclear affinities, from Thailand, Cambodia, and southern Vietnam. The status of the latter is still under investigation, and this taxon will be referred to in this paper as *Naja cf. atra*, bringing the total number of Asiatic species of *Naja* to nine (Fig. 1).

Because of the hitherto misunderstood taxonomy of these snakes, there has been considerable controversy as to which populations actually spit venom. By relating reports of spitting behavior in Asiatic cobras to the revised taxonomy of these

snakes, we have been able to determine, with a reasonable degree of certainty, which species exhibit spitting behavior.

The two most westerly species, *Naja naja* and *N. oxiana*, have never reliably been reported to spit. Bogert (1943), basing himself on Wall (1921), but without examining any specimens himself, regarded the Sri Lankan populations of *N. naja* as spitting cobras. However, Wall (1921) was writing from personal experience of cobras in many parts of Asia, and he did not state specifically that Sri Lankan cobras spit. More recent authors, with experience of hundreds of specimens in the wild and in captivity, have not noted spitting in Sri Lankan *N. naja* (de Silva, 1990), and we did not observe it either in our captive specimens. Consequently, we regard Bogert's classification of Sri Lankan cobras as spitters as erroneous (Wüster and Thorpe, 1992).

Cobras from the Malayan Peninsula and Sumatra, assignable to *Naja sumatrana*, are well-known to be spitters (Lim and Bakar, 1970; Lim and Lee, 1989; Ngim, 1989; Shattock, 1968; Tumwipat and Nutphand, 1982; Tweedie, 1983). The southern Indonesian *N. sputatrix* is also well known as a spitting cobra (Kopstein, 1930, 1932), although at least the population from Komodo seems reluctant to use this defensive strategy (Auffenberg, 1980). In the Philippines, *N. philippinensis* is known to spit (Taylor, 1922; G. Watt, personal communication). Taylor (1922) stated that this behavior was absent in *N. samarensis*, but later (Taylor, 1975) reported having been spat at in the field by this species. In Indochina, *Naja* cf. *atra* has been reported by numerous authors to spit (Cox, 1991; Lingenhölle and Trutnau, 1989; Saint Girons, 1972; Taylor, 1965; Tumwipat and Nutphand, 1982). The snakes in question were sometimes erroneously assigned to "*N. n. kaouthia*", but, from the description of the specimens (low ventral scale counts, spectacled rather than monocellate hood mark), they were clearly *Naja* cf. *atra*.

Bogert (1943) stated that cobras from China (*Naja atra*) had not been observed to spit. However, Herklots (1938) reported

spitting in cobras from Hong Kong (and pictured a *N. atra* in a cage with glass panes covered in venom), Reitingger and Lee (1978) mentioned spitting "over a distance of several feet" in two specimens of cobra from Hong Kong, and Karsen et al. (1986) stated that some specimens were capable of spitting, but "without the accuracy of true spitting cobras." The literature thus indicates that this species is capable of spitting, but apparently does so infrequently, and in a less accomplished manner than other spitting cobras.

Problems in the verification of records of spitting behavior concern especially *Naja kaouthia*. In Thailand, *N. kaouthia* is always regarded as a nonspitting cobra. Neither we nor anyone with experience with the species in that country (local snake collectors and workers at snake farms) with whom we have spoken have noted spitting in *N. kaouthia*. However, Duckett (1964) reported that cobras with a monocellate hood mark caught in Wellesley Province, northwestern Malaysia, "spread their hood and spit and hiss as with *sputatrix* [= *N. sumatrana*]" and figured a specimen which is unquestionably *N. kaouthia*. Unfortunately, the behavioral description is too vague to assess whether the snakes were really ejecting venom like highly specialized spitting cobras, or just "spitting" like cats: i.e., hissing explosively; however, Duckett likened the behavior of these *N. kaouthia* to the spitting *N. sumatrana*, suggesting that he observed real spitting behavior. Spitting cobras have also been reported from Mandalay, Burma (Goring Jones, 1900), and from northeastern India and Sikkim (Shaw and Shebbeare, 1930; Whitaker, 1978). *Naja kaouthia* is the common species of cobra in those areas, but other species may also occur there, so that incidents of spitting cannot be definitely attributed to *N. kaouthia*. In the absence of more reliable records of spitting in this species, the evidence must be regarded as equivocal.

In this paper, we compare fang size and structure of the nine species of Asiatic cobras. The results are related to the literature on spitting in Asiatic cobras, in order to identify morphological correlates of

TABLE 1.—Sample sizes of the species of *Naja* used in this study.

	Males	Females
<i>N. naja</i>	76	39
<i>N. kaouthia</i>	70	59
<i>N. oxiana</i>	26	19
<i>N. atra</i>	31	26
<i>N. cf. atra</i>	23	11
<i>N. sumatrana</i>	80	67
<i>N. sputatrix</i>	38	21
<i>N. samarensis</i>	21	18
<i>N. philippinensis</i>	10	7
Total	375	267

spitting behavior and to arrive at a synthesis of the information available on this interesting defensive behavior pattern in the Asiatic species of *Naja*.

#### MATERIALS AND METHODS

##### *Characters Examined*

This study is based on the measurement of the fangs of 642 preserved museum specimens. A complete list is available from the first author. The sample sizes for each sex and species are shown in Table 1.

Inasmuch as the ability to spit venom is dependent on the modification of the fangs, which involves a shortening of the discharge orifice (Bogert, 1943), it follows that

the degree of adaptation to spitting venom can be expressed as the relative length of the discharge orifice: the smaller the discharge orifice relative to the length of the fang, the higher the degree of adaptation to spitting venom. We therefore measured the fang length and the discharge orifice length of each specimen in order to gauge the degree of fang modification.

In each specimen, the mucosal tissue surrounding one of the two fangs was pushed back, in order to reveal the basal orifice. The length of the fang was measured, as by Bogert (1943), as the straight-line distance between the distal end of the basal orifice and the tip of the fang. The length of the venom discharge orifice was measured as the straight-line distance between the basal and the distal ends of the discharge orifice (Fig. 2). The length of the head was measured as the straight-line distance between the tip of the snout and the posterior end of the compound bone of the lower jaw. This measurement was taken on both sides of the head, and the mean was used in all analyses. All measurements were taken to the nearest 0.01 mm with the aid of digital callipers, the fang measurements under a binocular dissecting microscope.

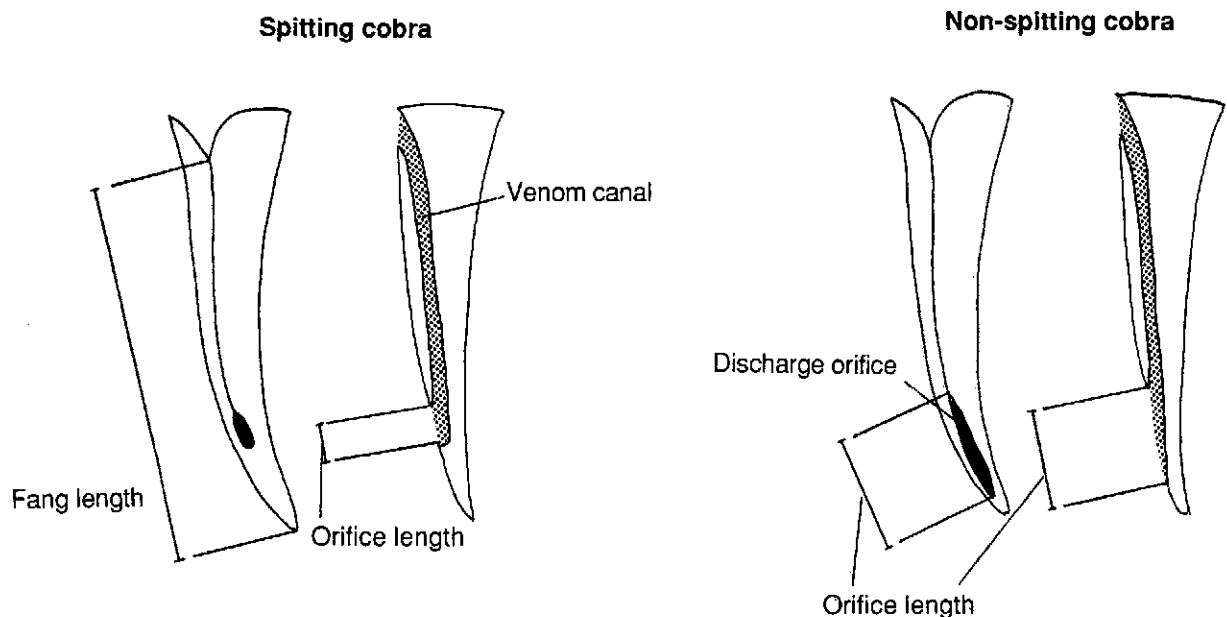


FIG. 2.—Fang structure in Asiatic spitting and nonspitting cobras: frontolateral view and longitudinal section. Fang measurements used in this study are indicated.

TABLE 2.—OTUs and sample sizes of *Naja kaouthia* used in ANCOVA 3. OTU numbers correspond to those used in Wüster and Thorpe (1992), where the specimens involved are listed.

OTU	Locality	Sample size	
		Males	Females
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.	Hué area, Vietnam	3	0
29.	Assam, India	0	3
30.	Yongde, Yunnan, China	0	1
31.	Central Cambodia	0	1
Total		70	59

### Construction of Operational Taxonomic Units

Because it was considered desirable to investigate in some detail the pattern of geographic variation in the fang structure of *Naja kaouthia*, we grouped specimens into a total of 13 operational taxonomic units (OTU's). Details on the pooling of localities are given in Wüster and Thorpe (1992), and the OTU's of *N. kaouthia* used here are the same as in that study. The OTU's and their sample sizes are listed in Table 2.

### Data Analysis

Bogert (1943) expressed the length of the fangs of his specimens as a proportion of the body length of the animals. However, in view of the spatial requirements of the fangs, the size of the head is more likely to determine the size of the fang, and not the length of the body. Consequently, we used head size, rather than body length, as an independent variable against which size of the fang was regressed. Similarly, because the degree of spitting adaptation depends on the relationship between discharge orifice size and length of the fang, the latter was taken as

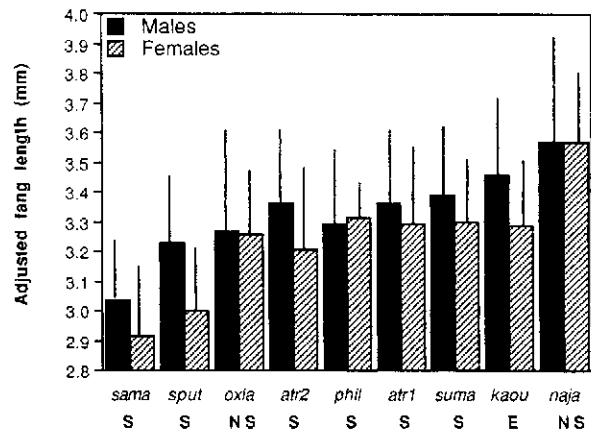


FIG. 3.—Mean adjusted fang size of the Asiatic species of cobra. Error bars indicate 1 SD. Species abbreviations: sama = *N. samarensis*, sput = *N. sputatrix*, oxla = *N. oxiana*, atr2 = *N. cf. atra*, phil = *N. philippinensis*, atr1 = *N. atra*; suma = *N. sumatrana*, kaou = *N. kaouthia*; naja = *N. naja*. Abbreviations for evidence of spitting behavior: S = spitting cobra, NS = nonspitting cobra, E = equivocal.

the independent variable against which discharge orifice length was regressed.

For all analyses, the specimens were grouped according to species and sex. In order to compare the structure of the fangs of the different species, it is necessary to remove the effect of growth from the analysis. This was done by regressing the length of the fang against the length of the head, and the length of the discharge orifice against the length of the fang, using in each case the pooled within-group regression coefficient, which was computed by means of analysis of covariance (ANCOVA), using the BMDP 1V program (Dixon, 1985).

The relationships between fang length, fang orifice length and head length are nonlinear, and therefore violate the assumptions of the ANCOVA. The characters were therefore log-transformed as required to achieve a linear relationship. In regressions of the fang orifice length against fang length, the fang orifice length was log-transformed, and in regressions of fang length against head length, both characters were log-transformed.

In order to illustrate fang length differences between the various species, we regressed the fang length of all specimens to a standard head length of 30.45 mm (mean

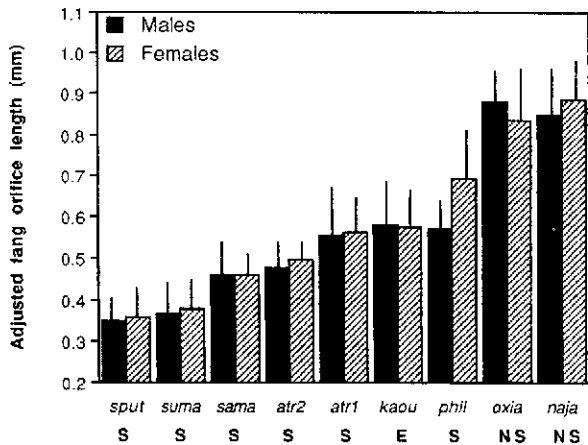


FIG. 4.—Mean adjusted fang discharge orifice length of the Asiatic species of cobra. Error bars indicate 1 SD. Species abbreviations as in Fig. 3. Note the sexual dimorphism in fang orifice size in *Naja philippinensis*.

head length of all specimens examined) (Fig. 3). Similarly, we regressed the length of the fang discharge orifice to a standard fang length of 3.621 mm (mean fang length of all specimens examined) to visualize differences in fang orifice length (Fig. 4).

To determine the relative contribution of sexual dimorphism and interspecific variation to the observed variance in relative fang discharge orifice length, a two-way analysis of covariance (ANCOVA 1) was run on all specimens of all species, using the BMDP 2V program (Dixon, 1985). In this, the discharge orifice length was regressed against the fang length. Because *Naja philippinensis* appeared to exhibit a conspicuously greater degree of sexual dimorphism in discharge orifice length than the other species, a further two-way ANCOVA was run, excluding this species (ANCOVA 1a). A similar two-way ANCOVA (ANCOVA 2) was run on fang length regressed against head length, in order to determine whether there are significant interspecific or intersexual differences in length of the fang.

Because *Naja kaouthia* has been reported to exhibit geographic variation in the incidence of spitting behavior, we ran a two-way ANCOVA (ANCOVA 3) of discharge orifice length regressed against fang length on all OTU's (both sexes) of this species. For each OTU, the fang orifice

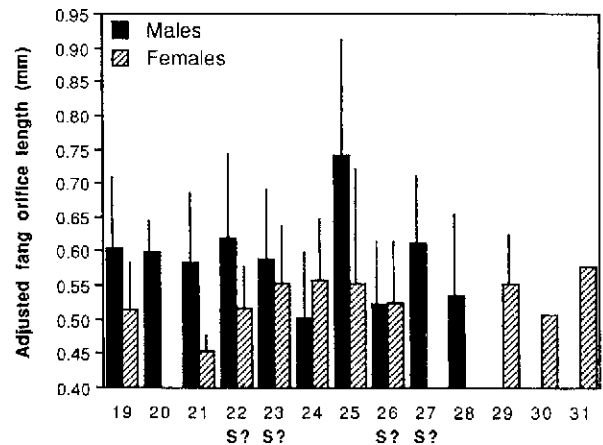


FIG. 5.—Comparison of the adjusted fang discharge orifice length of the various populations of *Naja kaouthia*. Error bars indicate 1 SD; the numbers on the x-axis indicate the OTU's of this species (Table 2). Populations reported to spit are indicated by S?; note that these do not generally have smaller discharge orifices than populations not reported to spit.

length was regressed to the standard fang length of 3.621 mm, in order to illustrate differences between OTU's (Fig. 5). In addition, we ran a one-way analysis of covariance (ANCOVA 4) on the specimens of *Naja philippinensis*, in order to determine whether the apparent sexual dimorphism in discharge orifice length in that species is statistically significant.

## RESULTS

The results of this study indicate considerable differences in both fang length (regressed against head length) and fang discharge orifice length (regressed against fang length) between the nine Asiatic cobra species. The adjusted fang lengths of the nine species are shown in Fig. 3. *Naja naja* has the longest fangs of any Asiatic cobra species, whereas *N. samarensis* and females of *N. sputatrix* have very short fangs. The remaining species are all rather similar to each other in length of the fang.

The relative lengths of the fang discharge orifices are shown in Fig. 4. *Naja naja* and *N. oxiana* both have very long discharge orifices, suggesting a relative lack of adaptation to spitting. In the case of the male specimens, there is a clear, categorical difference between these two species and all the others, whereas in the females, *N. philippinensis* takes up an intermediate

TABLE 3.—Sources of variance in ANCOVAs, and statistical significance. Asterisks denote statistically significant differences. ANCOVA 1 tests for interspecific and sex differences in fang discharge orifice length across all species. ANCOVA 1a does the same but excludes *Naja philippinensis*. ANCOVA 2 tests for interspecific and sex differences in fang length, ANCOVA 3 tests for geographic variation in discharge orifice size in *Naja kaouthia*, and ANCOVA 4 for sexual dimorphism in discharge orifice size in *Naja philippinensis*.

	Source of variance	F	df	P
ANCOVA 1 (discharge orifice length, all species)	Species	303.14	8	<0.0001*
	Sex	4.18	1	0.0412*
ANCOVA 1a (discharge orifice length, all species except <i>N. philippinensis</i> )	Species	341.52	7	<0.0001*
	Sex	0.99	1	0.3190
ANCOVA 2 (fang length, all species)	Species	28.15	8	<0.0001*
	Sex	13.77	1	0.0002*
ANCOVA 3 (discharge orifice length, geographic variation in <i>N. kaouthia</i> )	OTU	2.78	6	0.0152*
	Sex	0.37	1	0.5435
ANCOVA 4 (sexual dimorphism in <i>N. philippinensis</i> )	Sex	5.08	1	0.0410*

position. The latter species shows considerable sexual dimorphism in fang orifice length: for a standard fang length of 3.621 mm, males have a mean discharge orifice length of 0.57 mm (1 SD = 0.068 mm), whereas females have a mean orifice length of 0.69 mm (1 SD = 0.125 mm).

The results of all ANCOVAs are shown in Table 3. The interspecific differences in fang orifice length, regressed against fang length, are significant, as is sexual dimorphism over all species (ANCOVA 1). However, if *Naja philippinensis* is excluded from the analysis, there is no significant sexual dimorphism among the remaining species, whereas the interspecific differences remain highly significant (ANCOVA 1a). This shows that *N. philippinensis* is the only species with pronounced sexual dimorphism in discharge orifice size.

Interspecific differences in length of the fang are statistically highly significant, and there is highly significant sexual dimorphism in this character (ANCOVA 2).

There is significant between-locality variation in the size of the discharge orifice in *N. kaouthia* (ANCOVA 3). The differences in structure of the fang between the OTU's of this species are shown in Fig. 5. In *Naja philippinensis*, there is significant sexual dimorphism in fang orifice length (ANCOVA 4). This confirms the results of ANCOVAs 1 and 1a, in which it was found that the inclusion of *N. philippinensis* affects the overall significance of sexual dimorphism.

#### DISCUSSION

This study reveals considerable variation in size and structure of the fang and in the degree of spitting modification in Asiatic cobras. Regarding adaptation to spitting, one can establish two categories of fang structure within the genus. One is exhibited by the two most westerly species, *Naja naja* and *N. oxiana* (Fig. 1); these have never reliably been reported to spit and have very long venom discharge orifices. The remaining species, which have all been reported, albeit with varying degrees of reliability, to spit, have much shorter orifices. In the males, the difference between spitters and nonspitters is very clear, whereas in the females, *N. philippinensis* is intermediate between the two nonspitters and the other species. Contrary to Bogert (1943), the results presented here do not indicate the existence of a clear category of species with fangs "partially adapted for spitting." The fangs of the populations included by Bogert in this category (i.e., *N. kaouthia* and *N. atra*) are not categorically distinct from the fangs of more highly modified species.

The results presented here do not indicate any relationship between adaptation for spitting and length of the fang. Bogert (1943) stated that, in the case of his specimens, the spitting cobras had shorter fangs than the nonspitting cobras. However, he did not have the opportunity to examine specimens of *Naja oxiana*, which has

shorter fangs than several of the spitting cobras. The nonspitting *N. naja* has by far the longest fangs of the Asiatic cobras, and the spitters *N. samarensis* and *N. sputatrix* have conspicuously short fangs, but the remaining species are very similar to each other with regard to size of the fang. According to Bogert (1943), the African spitting cobras have longer fangs than African nonspitting cobras, so there seems to be no fixed relationship between fang size and spitting ability. Because even very small spitting cobras (e.g., 40 cm Thai *Naja* cf. *atra*, personal observation) are capable of spitting effectively, it seems that size of the fang does not affect the ability to spit, at least within the limits of fang dimensions encountered in the genus *Naja*.

The most important point to emerge from this study is the broad range of degrees of fang modification found among known spitting cobra species. In females, the difference in mean discharge orifice length between *Naja sputatrix* and *N. philippinensis*, both known spitting cobras, is considerably greater than the difference between *N. philippinensis* and the two nonspitting species, *N. naja* and *N. oxiana*. Clearly, only a slight degree of modification of fang structure is required to enable these species to spit venom, as is evidenced by *N. atra* and *N. philippinensis*.

Furthermore, it can be seen, from a comparison of literature-data with the analysis of fang structure presented here, that the frequency of display of spitting behavior is only partly related to the structure of the fang. Thus, *Naja samarensis* and *N. atra* apparently rarely spit, whereas *N. philippinensis*, which has larger fang discharge orifices, spits readily (Taylor, 1922; G. Watt, personal communication). Similarly, *N. cf. atra*, which has fangs similar to those of *N. samarensis*, spits readily (Cox, 1991; Lingenhölle and Trutnau, 1989). Individual specimens of at least some species differ greatly in their propensity to spit, which accounts for some of the conflicting data in the literature.

Bogert (1943) pointed out that, in the absence of any obvious selective disadvantages of a reduction in discharge orifice size, such a modification could persist in populations that lack the behavioral ad-

aptations necessary for spitting. This is clearly the case in species such as *Naja atra* and especially *N. kaouthia*, which show the same degree of fang adaptation as *N. philippinensis*, but rarely or never spit.

More data are needed on other behavioral correlates of spitting, especially regarding defensive behavior. Because spitting allows effective defense from a safe distance, it represents a low-risk defensive strategy, whereas biting requires physical contact with the predator, involving higher risk to the snake. One would therefore expect spitting cobras to be much more likely to face an adversary than nonspitting cobras, for which flight might be a safer alternative. This is at least partially borne out by our observations. In Thailand, the nonspitting *Naja kaouthia* is generally timid, placid, and reluctant to confront an adversary, whereas the spitting *N. cf. atra* and *N. sumatrana* generally defend themselves vigorously. However, quantitative data are needed on the defensive behavior of other Asiatic species of cobra, as well as the African forms, to test whether this is a significant and general trend.

In *Naja kaouthia*, there may be geographic variation in the occurrence of spitting behavior. Whereas specimens from Thailand apparently never spit (Cox, 1991), what appears to be spitting by this species was reported by Duckett (1964) from northwestern Malaysia, by Goring Jones (1900) from Mandalay, Burma, and by Shaw and Shebbeare (1930) and Whitaker (1978) from northeastern India. In all cases, however, the identity of the species concerned, or the nature of the phenomenon reported, cannot be reliably determined. Although there is significant geographic variation in the size of the venom discharge orifice of *N. kaouthia*, this does not correlate with the reports of spitting behavior. The specimens of OTU 22, representing the northwest Malaysian populations reported to spit by Duckett (1964), do not have smaller venom discharge orifices than specimens from central Thailand, which do not spit. The same is true of the specimens from northeastern India (OTU 23), Sikkim (OTU 27), and northern



Burma (OTU 26), areas from which spitting in cobras has been reported, without being confidently assignable to *N. kaouthia*.

Because *Naja kaouthia* occurs sympatrically with one of several other species in most of its range, reports in the literature regarding the behavior of this species are subject to the possibility of mistaken identity. Thus, Saint Girons (1972) and Taylor (1965) ascribed spitting behavior to "*N. n. kaouthia*"; the specimens concerned were in fact *N. cf. atra*. Goring Jones (1900) reported an incident of spitting in a specimen from Mandalay, Burma. *Naja kaouthia* is the only species of cobra with reliable records from Burma, where it is widespread throughout. However, we have seen six specimens of a species with highly modified spitting fangs from "Rangoon or Mandalay", Burma (Stockholm Museum, NHRM MAL. 1935.809.3321 A-F). On the basis of multivariate analysis of a range of morphological characters, these are not clearly assignable to any of the nine species that we currently recognize. The affinities of these specimens, and their provenance, are thus unclear, but it appears that a species of cobra with spitting fangs occurs sympatrically with *N. kaouthia* in parts of Burma. Consequently, Goring Jones' report cannot be ascribed with certainty to *N. kaouthia*. Similar specimens have also been found in northeastern India (Bombay Natural History Society, BNHS 2249 and 2250—Wüster and Thorpe, 1992), so there is a possibility that the same hitherto unidentified species is responsible for incidents of spitting in northeastern India.

The fangs of *Naja kaouthia* are as adapted to spitting as those of such spitting cobras as *N. philippinensis* and *N. atra*, so that there is no clear mechanical reason why this species should not be able to spit. However, if this behavior occurs at all in *N. kaouthia*, it is clearly exceptional, and apparently restricted to localized populations. The placid temperament of most specimens further reduces the probability of this behavior being observed by persons aware of its significance.

The biological function, if there is one, of the pronounced sexual dimorphism in

discharge orifice size in *N. philippinensis* is unknown, especially as this species is the only one with such a marked degree of sexual dimorphism in this character. The males have significantly smaller discharge orifices than the females, but it is hard to see any functional reason why the males should be better adapted for spitting than the females. We do not know whether there is any difference in the incidence or the accuracy of spitting between the two sexes of *N. philippinensis*, or any other species of spitting cobra. The use of spitting in combat between males appears unlikely; because the eyes of all snakes are covered by a transparent scale, these animals are unlikely to be affected by venom sprayed into their eyes. We have, on a number of occasions, seen *N. cf. atra* spit at each other in their cages when aroused, and we never noted any resulting ill-effects. Alternatively, the sexual dimorphism may be due to differences in the rate of development of the fang (heterochrony), and unrelated to the function of the fang.

The phylogeny of cobras is as yet incompletely understood, so that the evolution of fang modifications and spitting behavior cannot be fully traced. On the basis of skull osteology and maxillary dentition, Szyndlar and Rage (1990) consider the Asiatic cobras to be monophyletic, *Naja naja* and *N. oxiana*, the two nonspitting species, constituting a clade within the Asiatic group. However, Szyndlar and Rage presented no evidence that the Asiatic spitting cobras form a monophyletic group. We are currently investigating the phylogeny of the Asiatic cobra complex. Among African cobras, the spitting species (*N. nigricollis*, *N. mossambica*, *N. katiensis*, and *N. pallida*) probably form a monophyletic group, because they share the possession of two preoculars (Broadley, 1968), a condition not found in other cobra-like elapids, and therefore probably a synapomorphy.

In view of the obvious selective advantage of a spitting ability, and the lack of an obvious selective disadvantage, it seems unlikely that a reduction in discharge orifice size, once evolved, would reverse to the nonspitting condition. If this assumption is correct, spitting modifications have

evolved at least three times in the Elapidae: once in *Hemachatus*, once in the African spitting *Naja*, and at least once among the Asiatic *Naja*.

No detailed study of the medical effects of spitting in Asiatic cobras has been published. The few available case reports mention pain and conjunctivitis (Kopstein, 1930, 1932—*Naja sputatrix*; personal observation—Thai *N.* cf. *atra*), swelling of eyelids and surrounding parts (Goring Jones, 1990—species unknown, Burma; Lim and Lee, 1988—*N. sumatrana*) and temporary blindness in humans (Kopstein, 1930, 1932—*N. sputatrix*) and dogs (Tweedie, 1983—*N. sumatrana*). Shattock (1968) reported that *N. sumatrana* frequently causes blindness in dogs in northern Sumatra, but there are no reliable reports of very severe symptoms, or permanent blindness, in humans. Such sequelae have been reported to be fairly common in cases of venom ophthalmia from *Naja nigricollis* in Nigeria (Warrell and Ormerod, 1976).

*Acknowledgments.*—We thank the curators and staff of the numerous American, European, and Indian museums (listed in Wüster and Thorpe, 1989, 1992) for the loan of the specimens used in this study. M. J. Cox (Bangkok) and D. A. Warrell (Oxford) provided much useful information about Thai cobras, and the former provided invaluable cooperation and support during the authors' research visits to Thailand. S. A. Minton (Indianapolis) and G. Watt (San Francisco) provided much useful information on Philippine cobras. This study was funded by the Science and Engineering Research Council, the Natural Environment Research Council, and the Leverhulme Trust.

#### LITERATURE CITED

- AUFFENBERG, W. 1980. The herpetofauna of Komodo, with notes on adjacent areas. *Bull. Florida State Mus., Biol. Sci.* 25:39-156.
- BOGERT, C. M. 1943. Dentitional phenomena in cobras and other elapids, with notes on adaptive modification of fangs. *Bull. Am. Mus. Nat. Hist.* 81:285-360.
- BOIE, H. 1827. Bemerkungen über Merrem's Versuch eines Systems der Amphibien. *Isis* 20:508-566.
- BROADLEY, D. G. 1968. A review of the African cobras of the genus *Naja* (Serpentes: Elapinae). *Arnoldia*, 3:1-14.
- COX, M. J. 1991. The Snakes of Thailand and Their Husbandry. Krieger, Malabar, Florida.
- DIXON, W. J. (Ed.) 1985. BMDP Statistical Software. University of California Press, Berkeley, California.
- DUCKETT, J. E. 1964. The cobras of Batu Kawan, Province Wellesley. *Malayan Nature J.* 18:210-211.
- GORING JONES, M. D. 1900. Can a cobra eject its venom? *J. Bombay Nat. Hist. Soc.* 13:376.
- HERKLOTS, G. A. C. 1938. Land snakes of Hong Kong. Part IV. *Naja* (the cobras). *Hong Kong Nat.* 8:189-200.
- KARSEN, S. J., M. W. LAU, AND A. BOGADEK. 1986. *Hong Kong Amphibians and Reptiles*. Urban Council Publications, Hong Kong.
- KOPSTEIN, F. 1930. Die Giftschlangen Javas und ihre Bedeutung für den Menschen. *Z. Morphol. Ökol. Tiere* 19:339-363.
- . 1932. Die Gifttiere Javas und ihre Bedeutung für den Menschen. *Meded. Dienst Volksgezondheid Ned. Indie* 4:222-256.
- LIM, B.-L., AND ABU BAKAR BIN IBRAHIM. 1970. Bites and stings by venomous animals with special reference to snake bites in West Malaysia. *Med. J. Malaya* 25:128-141.
- LIM, F. L. K., AND M. T.-M. LEE. 1989. Fascinating Snakes of Southeast Asia—An Introduction. Tropical Press Sdn. Bhd., Kuala Lumpur.
- LINGENHÖLE, S., AND L. TRUTNAU. 1989. Über die Kobras der Gattung *Naja* Laurenti, 1758 in Thailand. *Herpetofauna* 11:6-13.
- NGIM, R. 1989. A close encounter of the cobra kind. *Malayan Nat.* 42:12-14.
- REITINGER, F. F., AND J. K. S. LEE. 1978. Common Snakes of South-east Asia and Hong Kong. Heinemann, Hong Kong, Singapore, Kuala Lumpur.
- SAINT GIRONS, H. 1972. Les serpents du Cambodge. *Mém. Mus. National d'Hist. Nat., Ser. A.* 74:1-165.
- SHATTOCK, F. M. 1968. Injuries caused by wild animals. *Lancet* 1968:412-415.
- SHAW, G. E., AND SHEBBEARE, E. O. 1930. The snakes of northern Bengal and Sikkim. *J. Darjeeling Nat. Hist. Soc.* 5:23-29.
- SILVA, A. DE. 1990. Colour Guide to the Snakes of Sri Lanka. R & A Publishing, Portishead, U.K.
- SZYNDLAR, Z., AND J.-C. RAGE. 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): Interrelationships among extinct and extant species. *Amphibia-Reptilia* 11:385-400.
- TAYLOR, E. H. 1922. The snakes of the Philippine Islands. *Monogr. Bur. Sci., Manila* 16:1-312.
- . 1965. The serpents of Thailand and adjacent waters. *Univ. Kansas Sci. Bull.* 45:609-1096.
- . 1975. Philippine adventures: An autobiographical memoir. Pp. 1-108. In R. F. Johnston (Ed.), Edward H. Taylor: Recollections of an Herpetologist. *Monogr. Mus. Nat. Hist. Univ. Kansas* 4:1-159.
- TUMWIPAT, B., AND W. NUTPHAND. 1982. [The Treatment of Poisonous Snakebite Victims and the Poisonous Snakes of Thailand]. (in Thai) Peekhanet Print Shop, Bangkok.
- TWEEDIE, M. W. F. 1983. The Snakes of Malaya, 3rd ed. Singapore National Printers, Singapore.
- WALL, F. 1921. Ophidia Taprobanica or the Snakes of Ceylon. H. R. Cottle, Government Printer, Colombo.
- WARRELL, D. A., AND L. D. ORMEROD. 1976. Snake venom ophthalmia and blindness caused by the

- spitting cobra (*Naja nigricollis*) in Nigeria. *Am. J. Trop. Med. Hyg.* 25:525-529.
- WHITAKER, R. 1978. Common Indian Snakes. A Field Guide. Macmillan, New Delhi.
- WÜSTER, W., AND R. S. THORPE. 1987. Geographic variation in the cobras of the genus *Naja* in southeast Asia: A multivariate analysis. Pp. 449-452. *In* J. J. van Gelder, H. Strijbosch, and P. J. M. Bergers (Eds.), Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica. Faculty of Science, Nijmegen, Netherlands.
- . 1989. Population affinities of the Asiatic cobra (*Naja naja*) species complex in Southeast Asia: Reliability and random resampling. *Biol. J. Linn. Soc.* 36:391-409.
- . 1990. Systematics and biogeography of the Asiatic cobra (*Naja naja*) species complex in the Philippine Islands. Pp. 333-344. *In* G. Peters and R. Hutterer (Eds.), *Vertebrates in the Tropics*. Museum A. Koenig, Bonn.
- . 1991. Asiatic cobras: Systematics and snakebite. *Experientia*, 47:205-209.
- . 1992. Asiatic cobras: Population systematics of the *Naja naja* species complex (Serpentes: Elaphidae) in India and Central Asia. *Herpetologica* 48:69-85.

Accepted: 13 February 1992

Associate Editor: David Cannatella