Pergamon

0041-0101(95)00139-5

Toxicon, Vol. 34, No. 4, pp. 399–406, 1996

Printed in Great Britain
0041–0101/96 $15.00 + 0.00

REVIEW ARTICLE

TAXONOMIC CHANGES AND TOXINOLOGY: SYSTEMATIC REVISIONS OF THE ASIATIC COBRAS (*NAJA NAJA* SPECIES COMPLEX)

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(*Received* 6 *June* 1995; *accepted* 8 *October* 1995)

W. Wüster. Taxonomic changes and toxinology: systematic revisions of the Asiatic cobras (*Naja naja* species complex). *Toxicon* **34**, 399–406, 1996.—Until recently, all Asiatic cobra populations were regarded as belonging to one single species, *Naja naja*. Recent revisions have shown that there are in fact at least 10 full species of Asiatic *Naja*. In order to allow the existing literature to be reconciled with these recent discoveries, an interpretation of the older nomenclature is provided. Problematic areas, especially concerning the species *N. sumatrana* and *N. siamensis*, are highlighted. Copyright © 1996 Elsevier Science Ltd.

INTRODUCTION

Many of the medically and toxinologically most important snakes are part of complex groups of often very similar and ill-defined species. Well known examples of this include the Asiatic cobras (*Naja naja* species complex), the *Echis carinatus* complex, the *Bothrops atrox* group, the green *Trimeresurus*, *Pseudonaja* spp., *Acanthophis* spp., and the subspecies of *Crotalus durissus*.

The frequently very incomplete understanding of the systematics of such species groups can cause serious problems in toxinology and clinical medicine, as very closely related and very similar species may have very different venoms. Inadequate understanding of the systematics of the *Echis carinatus* complex, for instance, has led to greatly increased numbers of human fatalities when antivenom raised against the venom of Iranian *Echis* (classified as *E. multisquamatus* or *E. carinatus multisquamatus*—see Cherlin (1990) and Auffenberg and Rehman (1991), respectively) was used to treat bites by *Echis ocellatus* in Nigeria (Warrell and Arnett, 1976). Understanding the systematics of species groups of venomous snakes is therefore of paramount importance for the formulation of treatment strategies.

The systematics of many of these complexes are now being investigated by a number of research teams worldwide. In many cases, the revision of such groups reveals that the taxa recognized under the old classification did not represent the species or subspecies actually present. This can cause serious confusion, as it may not be possible to determine

the affinities of a venom or snake simply from the nomenclature used in older publications. In cases where there are venom differences between the species involved, problems of unreplicable experimental results or ineffective antivenoms can result. A prominent example of such a situation is the Asiatic cobra (*Naja naja*) species complex. Venom composition in Asiatic cobras is highly variable among populations, resulting in radically different symptoms after envenomations [compare Reid (1964) and Watt *et al.* (1988)] and ineffectivity of antivenoms raised against venom from geographically distant specimens (Warrell, 1986). However, until now, research into the venoms of these snakes has been seriously hampered by an insufficient understanding of the systematics of this complex.

TAXONOMIC PROBLEMS POSED BY THE ASIATIC COBRAS *NAJA NAJA* SPECIES COMPLEX

Most workers this century have tended to consider all Asiatic cobras to belong to the single species *Naja naja*. In recent years, most authors have recognized 10 subspecies of Asiatic cobra (Klemmer, 1963; Leviton, 1968; Harding and Welch, 1980; Golay, 1985); however, many of these authors expressed misgivings about the extent to which the subspecies represent the evolutionary entities within the *Naja naja* complex, and Golay (1985) felt unable to devise a key to the subspecies due to this state of taxonomic uncertainty.

Several attempts have been made to resolve the problems posed by the Asiatic *Naja* populations, and several recent authors have regarded some populations as specifically distinct from *Naja naja*. Deraniyagala (1960, 1961) proposed a revision of the Asiatic *Naja* which split the complex into four species and described several further subspecies from India and neighbouring areas. However, his revisions have had little impact on later workers, although Viravan *et al.* (1986) and Warrell (1986) followed him in regarding *Naja kaouthia* as a separate species. Tumwipat and Nutaphand (1982) and Nutaphand (1986) described several new taxa from Thailand, and also regarded the *N. naja* complex as consisting of several species. Lingenhöle and Trutnau (1989) adopted parts of Nutaphand's revisions, and again regarded certain Thai populations as specifically distinct from *N. naja*. However, none of these revisions had any impact on the scientific literature, although some new subspecific epithets have been adopted by herpetoculturists. Apart from Deraniyagala's studies, no other project has attempted to address the problems of the systematics of the entire Asiatic *Naja* complex until now.

RECENT REVISIONS OF ASIATIC *NAJA* SYSTEMATICS

Many of the problems of Asiatic cobra systematics were due to the fact that these snakes are often extremely variable even within populations, especially in their coloration and pattern. This variation has often made the identification of individual specimens extremely difficult, as specimens of one population may look more different from each other than from a representative of a population located thousands of miles away.

In order to overcome these problems, the present study used a combination of multivariate analysis of morphological characters and mitochondrial DNA sequence analysis to define evolutionary lineages within the Asiatic cobra complex. Multivariate analysis of morphological variation can reveal patterns of variation in the generalized phenotype which are often obscured at first sight by superficially conspicuous variation in colour pattern or other conventional taxonomic characters. Mitochondrial DNA sequence analysis can reveal cryptic species which may be morphologically similar as a result of convergent evolution.

The revision using these techniques revealed the existence of wide areas of sympatry between different species of cobra in India, Pakistan, Indochina and the Malayan Peninsula (Wüster and Thorpe, 1989, 1991, 1992). In other cases, for instance in the Philippines and on the Andaman Islands, groups of allopatric populations were found to comprise highly distinctive lineages, for which no evidence of conspecificity exist (Wüster and Thorpe, 1990, 1991; Wüster *et al.*, 1995). In all, this revision resulted in the splitting of the formerly single species *N. naja* into no less than 10 full species (Wüster and Thorpe, 1987, 1989, 1990, 1991, 1992, 1994; Wüster *et al.*, 1995) (Fig. 1).

INTERPRETING ASIATIC COBRA NOMENCLATURE

In many cases, the old subspecies of *N. naja* did not correspond to the actual species revealed by these revisions. Some of the conventional subspecies, especially *N. n. sputatrix*, were heterogeneous and included populations of more than one species. This clearly causes some problems in the interpretation of the literature, as in many cases, the subspecific name is the only identification given for snakes involved in experiments or observations, for experimental venoms, or for snakes involved in clinical accidents.

Because of the documented venom variation in the Asiatic cobra complex, which can be related to the actual species of the group, the correct identification of snakes involved

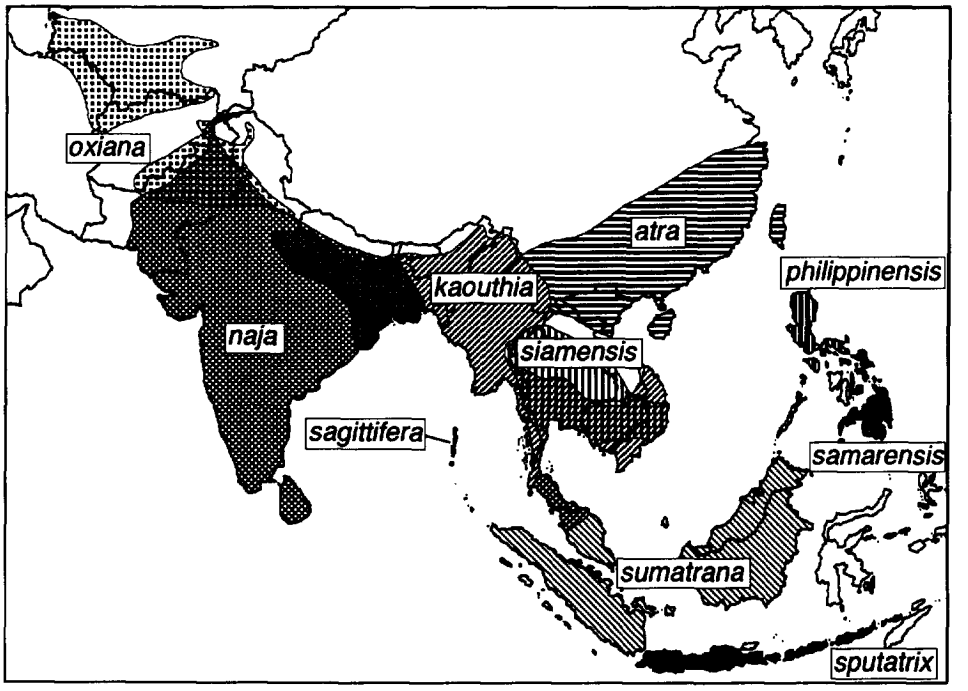

Fig. 1. Distribution of the 10 species of Asiatic cobra.
Note in particular the existence of several areas of widespread sympatry between different species pairs, such as *Naja kaouthia* and *N. siamensis* in Thailand, Cambodia and Vietnam, *N. kaouthia* and *N. sumatrana* in northern Malaysia and southern Thailand, *N. kaouthia* and *N. naja* in northeastern India and *N. naja* and *N. oxiana* in northwestern India and Pakistan.

in accidents or used for the production of venoms and antivenoms is of crucial importance. It is therefore also important that biomedical researchers avail themselves of new systematic results.

Interpreting new results and relating them to an older nomenclature can be a complex matter. As a result, the results of systematic revisions of venomous snakes have often been very slow in finding their way into the biomedical literature. Thus, although the African populations of *Echis* were split off from *Echis carinatus* as early as the middle 1970s (Hughes, 1976; Roman, 1975), it is still common in the toxinological literature to see the African populations referred to simply as *Echis carinatus* (Wüster and McCarthy, in press).

There are several reasons for this. One is the often widely scattered herpetological literature, and the tendency of many herpetologists to publish even major revisions in obscure, unindexed, unabstracted journals. Another problem is that some later herpetological authors, in particular the authors of species checklists, are not always sufficiently familiar with the systematic literature which they are attempting to summarize (see Joger, 1983, for a critique). Such checklists are often used as a convenient source of information by toxinologists, and are sometimes erroneously thought to have some kind of 'official' status. Consequently, it is particularly important that such checklists reflect the current state of knowledge as accurately as possible. Similarly, sources of information specifically designed for the toxinological community, such as the Common Names Index of Rosenberg (1980), should be updated regularly to reflect new insights into the systematics of important groups. Clearly, it is important that systematic revisions of medically important groups of venomous snakes be published so as to maximize the availability of these results to those working outside systematics, i.e. in internationally indexed, refereed journals. However, it is also important that toxinologists and clinicians appreciate the importance of a sound systematic framework and of the correct identification of specimens or venoms for their work, and maximize their efforts to follow new insights into venomous snake systematics (Wüster and McCarthy, in press).

The aim of this paper is to relate the current state of knowledge of the systematics of the Asiatic cobras to the nomenclature which has historically been used in the literature, so that the old literature and the new systematics can be connected as far as possible. Table 1 shows previously used names for the currently accepted species of Asiatic *Naja*, and Table 2 shows the best available interpretation for the old subspecific names as used in the literature. For the sake of simplicity, I have only included names which have been used in the literature since 1970, and have omitted simple misidentifications, with a few exceptions in the case of particularly important papers. I have also ignored entirely contrived or invented names which have on occasion appeared in the literature. For a full synonymy of the Asiatic *Naja* species, see Golay *et al.* (1993).

Several points emerge from these tables. The first is that the continued use of the old, outdated nomenclature is likely to severely impede the taxonomic interpretation of other work relating to these species. Some of the old subspecific epithets have been used to refer to a number of different species of *Naja*, and without further information, it is often impossible to identify the species involved.

The two tables also identify the main problems of Asiatic cobra systematics, as they affect the biomedical literature. These problems center on the species *N. kaouthia*, *N. siamensis*, *N. sputatrix* and *N. sumatrana*.

Naja sumatrana was first recognized as an entity by Wüster and Thorpe (1989). Prior to that paper, different populations of this species had been assigned to three different conventional subspecies of *N. naja*, namely *N. n. sumatrana* (populations from Sumatra),

Table 1. Older names used in the literature for the currently accepted species of Asiatic cobra

Real species (scientific and suggested common names)	Names used in the literature and populations for which used
N. atra (Chinese cobra)	*N. n. atra* (common), *N. sputatrix atra* (China, northern Vietnam—Lingenhöle and Trutnau, 1989)
N. kaouthia (Monocellate cobra)	*N. n. kaouthia* (common), *N. n. siamensis* (common in the toxinological literature), *N. n. sputatrix* (Vietnam, rare), *N. n. leucodira* (Reid, 1964), *N. kaouthia suphanensis* (yellow form from central Thailand, rare)
N. naja (Indian spectacled cobra)	*N. n. naja* (common), *N. n. oxiana* (patternless specimens from northern India), *N. n. indusi* (NW India, northern Pakistan, rare), *N. n. karachiensis* (black form from southern Pakistan), *N. n. polyocellata* (Sri Lanka, rare), *N. n. caeca* (patternless specimens from northern India-rare)
N. oxiana (Central Asian cobra)	*N. n. oxiana*, *N. n. caeca* (rare)
N. philippinensis (Philippine cobra, northern Philippine cobra)	*N. n. philippinensis*
N. sagittifera (Andaman cobra)	*N.* (*n.*) *kaouthia*, *N. n. sagittifera*
N. samarensis (Visayan cobra, southeastern Philippine cobra)	*N. n. samarensis*
N. siamensis (Indochinese spitting cobra)	*N. n. kaouthia* (Thailand, Cambodia, Vietnam, through confusion), *N. n. sputatrix* (Thailand), *N. n. isanensis*, *N. n. atra* (Thailand), *N.* atra (Thailand), *N. sputatrix atra* (rare, Thailand), *N. sputatrix isanensis*, *N. isanensis*
N. sputatrix (southern Indonesian spitting cobra)	*N. n. sputatrix*
N. sumatrana (Equatorial spitting cobra)	*N. n. sumatrana* (Sumatra), *N. n. sputatrix* (common, Malayan Peninsula, Bangka, Belitung), *N. n. miolepis* (Borneo), *N. n. leucodira* (Malayan Peninsula, Sumatra), *N. n. kaouthia* (yellow form from northern Malaysia- Reid, 1964; Tweedie, 1954), *N. sputatrix sputatrix* (Malayan Peninsula, Java- Lingenhöle and Trutnau, 1989)

Table 2. Interpretation of older names used in the literature for the populations of Asiatic cobra

Old name	Current name of species, and populations for which (mis)used
N. atra	*N. atra* (China, Taiwan, northern Vietnam), *N. siamensis* (Thailand)
N. isanensis	*N. siamensis*
N. naja	All Asiatic cobras
N. kaouthia	*N. kaouthia*, *N. sagittifera* (Andamans)
N. kaouthia suphanensis	*N. kaouthia* (Thailand, rare)
N. n. atra	*N. atra* (China, Taiwan, northern Vietnam), *N. siamensis* (Thailand)
N. n. caeca	*N. oxiana*, *N. naja* (patternless specimens from northern India)
N. n. indusi	*N. naja* (NW India, Pakistan)
N. n. isanensis	*N. siamensis*
N. n. kaouthia	*N. kaouthia*, *N. siamensis* (through confusion), *N. sagittifera* (Andaman Islands), *N. sumatrana* (northern Malaysia- Reid, 1964; Tweedie, 1954)
N. n. karachiensis	*N. naja* (southern Pakistan black form)
N. n. leucodira	*N. sumatrana* (Malayan Peninsula, Sumatra), *N. kaouthia* (Reid, 1964).
N. n. miolepis	*N. sumatrana* (Borneo)
N. n. naja	*N. naja*
N. n. oxiana	*N. oxiana*, *N. naja* (patternless specimens from northern India)
N. n. philippinensis	*N. philippinensis*
N. n. polyocellata	*N. naja* (Sri Lanka, rare)
N. n. sagittifera	*N. sagittifera*
N. n. samarensis	*N. samarensis*
N. n. siamensis	Probably *N. kaouthia* (in the toxinological literature),
N. n. sputatrix	*N. sputatrix* (Java, Lesser Sunda Islands), *N. sumatrana* (Malayan Peninsula, Bangka, Belitung), *N. siamensis* (Thailand), *N. kaouthia* (Vietnam, rare)
N. n. sumatrana	*N. sumatrana* (Sumatra)
N. sputatrix atra	*N. siamensis* (Thailand), *N. atra* [China, Taiwan, northern Vietnam (Lingenhöle and Trutnau, 1989)]
N. sputatrix isanensis	*N. siamensis* (Thailand)
N. sputatrix sputatrix	*N. sumatrana* [Malayan Peninsula, Java (Lingenhöle and Trutnau, 1989)]

N. n. miolepis (populations from Borneo and Palawan) and *N. n. sputatrix* (populations from the Malayan Peninsula, Bangka and Belitung). The latter is especially likely to lead to confusion, as the name *N. sputatrix* is applicable to a different species found on Java and the Lesser Sunda islands. It is particularly important to emphasize that the populations formerly referred to as '*N. n. sputatrix*' from the Malayan Peninsula belong to a different species (*N. sumatrana*) than those from Java (*N. sputatrix*).

In the case of *N. siamensis*, the problem is compounded by the fact that in the toxinological literature, the designation '*N. n. siamensis*' has often been used to denote the venom of any cobra from Thailand. In fact, it is likely that these '*N. n. siamensis*' venoms usually originated from specimens of the species *N. kaouthia*, and not from *N. siamensis*. The latter species was only diagnosed as distinct and defined by Wüster and Thorpe (1994) and Wüster *et al.* (1995). Before that, it had been either confused with *N. kaouthia*, or labelled with various inappropriate names such as *N. n. sputatrix*, *N. n. atra* or *N. n. isanensis*.

The crucial importance of locality information for the identification of the species involved is clear from these tables. For instance, a venom from a cobra from Malaysia labelled as *N. n. sputatrix* can be confidently assumed to originate from *N. sumatrana*. The same venom without the locality information could come from any of up to four species, and identification would be impossible. In any case, locality information is important as venom composition can vary considerably even within species and subspecies, as has been demonstrated in a number of cases, including among others the Malayan pit viper

(*Calloselasma rhodostoma*) (Daltry *et al.*, in press), several species of rattlesnake (Glenn *et al.*, 1983; Schenberg, 1959) and Russell's viper (Warrell, 1986, 1989; Wüster *et al.*, 1992). Establishing the locality from which snakes involved in toxinological research or clinical cases originate is therefore of critical importance, even when the taxonomic affinities of the snakes are not in doubt (Warrell and Harvey, 1995; Wüster and McCarthy, in press).

Finally, it is clear that the results of this study call for a major revision of the toxinological nomenclature for *Naja* venom toxins, in order to establish which toxin occurs in which species of the complex. This is clearly a major task which will require a considerable amount of coordination.

It is hoped that this paper will help to clear up some of the confusion which has hitherto pervaded the literature on Asiatic *Naja* because of the problems of the complex systematics of the group. It is also hoped that this paper will encourage biomedical researchers to familiarize themselves with the systematics of those venomous snakes of direct interest to their research.

Acknowledgements—I wish to thank R. S. Thorpe, R. D. G. Theakston and D. A. Warrell for their support, and D. A. Warrell, R. D. G. Theakston and J. C. Daltry for many thought-provoking comments on an earlier draft of this manuscript. The author's research programme on venomous snakes has been funded by SERC (studentship to the author), NERC (postdoctoral fellowship to the author), the Science and Technology for Development programme of the European Community (contract no. TS3-CT91-0024), the Wellcome Trust (Research Career Development Fellowship to the author) and the Leverhulme Trust (fellowship to R. S. Thorpe).

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