



REVIEW ARTICLE

SYNOPSIS OF RECENT DEVELOPMENTS IN
VENOMOUS SNAKE SYSTEMATICSWOLFGANG WÜSTER,¹ PHILIPPE GOLAY²
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W. Wüster, P. Golay and D. A. Warrell. Synopsis of recent developments in venomous snake systematics. *Toxicon* **35**, 319–340, 1997.—Changes to our understanding of venomous snake systematics, and the consequent changes in the nomenclature of these animals, have traditionally been a great source of confusion among biomedical researchers. This paper aims to facilitate access to the taxonomic literature by presenting a synopsis of the changes in venomous snake systematics that have taken place recently (primarily since 1992), together with some comments on the implications of these changes for toxinologists and clinicians. Some long-standing problems in venomous snake taxonomy receive special attention. This includes Asiatic *Naja*, Asiatic *Agkistrodon/Gloydius*, *Bothrops* and related genera, *Trimeresurus*, *Echis*, *Daboia* (including *Daboia russellii*) and *Vipera*. It is hoped that this synopsis will result in the use of a more up-to-date and interpretable nomenclature for venomous snakes in the toxinological literature. © 1997 Elsevier Science Ltd. All rights reserved

INTRODUCTION

The relationship between the systematics of venomous snakes and toxinology has not always been a happy one. The complex nature of many groups of medically important venomous snakes has meant that new discoveries frequently led to radical changes in the classification of some groups. Unfortunately, for a variety of reasons, such advances in our understanding of the systematics of many groups of species were often slow to find their way into the toxinological literature (Wüster and McCarthy, 1996). Part of the reason lies in the often scattered and rather obscure nature of some of the taxonomic literature, as well as existing disagreements between snake systematists on the status of certain forms. The result of this has been that, in the case of some complex groups, up to 75% of experimental venoms or animals involved in accidents cannot be confidently assigned to any one currently recognised species (Wüster and McCarthy, 1996). In view of the importance of interspecific and intersubspecific variation in venom composition, this is clearly a highly unsatisfactory situation.

The present paper is the first of an annual series designed to provide a digest of developments in venomous snake systematics for the use of toxinologists, whose work is affected by these changes, but who for obvious reasons may lack the time and opportunity for wrestling with the complexities of a widely scattered taxonomic literature. We hope that through this digest of systematic developments in venomous snakes, we can facilitate the penetration of systematic information into the toxinological literature.

Given the uncertain status of many groups of venomous snakes, we also wish to reiterate the importance of obtaining precise locality information for experimental venoms and snakes, and of depositing those specimens used for providing experimental venoms, or those which were responsible for published cases of snakebite, in major natural history collections (Warrell and Harvey, 1995; Wüster and McCarthy, 1996). This will allow their identity to be verified and reinterpreted in the light of new systematic discoveries. Furthermore, collections accumulated during medical studies can be invaluable for systematic studies of complex groups. Thus, a collection gathered during an epidemiological study in Thailand (Viravan *et al.*, 1992) has allowed considerable progress to be made in understanding the systematics of complex genera such as *Trimeresurus* (Warrell *et al.*, 1992) and *Naja* (Wüster *et al.*, 1995). In the case of the latter, the collection made during clinical work contributed 65% of the specimens of *Naja siamensis* deposited in European and North American museums, where this species was previously very poorly represented, in spite of being the commonest cobra in Thailand. The identification and definition of this species would have been much more difficult without the existence of this collection gathered during medical research work.

Since our understanding of the systematics of some groups is still in a state of flux, and several interpretations exist regarding the classification of many groups, it is also essential that toxinologists and clinicians should put the identification of their specimens and venoms into an explicit taxonomic framework, with full reference to the interpretation being followed.

Although the present review is concerned entirely with systematics at or above the species and subspecies level, we emphasise that venom variation in snakes happens at all systematic levels, including between individuals and populations of a single subspecies (Warrell, 1997). Obtaining a correct identification to species or subspecies level will not necessarily predict the qualities of the venom to be found. Variation in venom composition within subspecies has been documented in a number of species (e.g. *Daboia russellii*: Warrell, 1989; Belt *et al.*, 1997), and, at least in *Calloselasma rhodostoma*, this appears to be associated with differences in the diet of different populations, but independent of evolutionary descent, and thus intraspecific taxonomy (Daltry *et al.*, 1996). The use of a correct, updated taxonomy does not negate the need to secure precise locality information for the origin of experimental venoms, and geographical variation in venom composition must be taken into account by antivenom manufacturers. A sound systematic framework for toxinology can serve principally as a basic framework, against which other hypotheses on the pattern and cause of venom variation can be tested. A classification alone cannot predict all aspects of patterns of venom variation.

This synopsis will list changes in the taxonomy of various groups of venomous snakes under the heading of the genus concerned, with the exception of the neotropical pitvipers, which are treated as a group owing to the confusion over the generic affinities of several forms. We have generally concentrated on changes which have occurred after 1991, but in some cases, developments before that period are also discussed in order to put more recent changes into context. We also identify some snake names which have been widely

misused, in some cases for many years, misidentifications of snakes responsible for bites and misnaming of toxins. We have made every effort to convey a maximum of information on the various changes within the framework of this synopsis. Nevertheless, we wish to emphasise that this synopsis alone cannot replace a careful study of the original taxonomic literature, and we would urge toxinologists and clinicians working with complex groups of venomous snakes to acquaint themselves with the primary literature cited here.

FAMILY ATRACTASPIDIDAE

Genus Atractaspis

The genus *Atractaspis* has recently become the focus of much toxinological research because of the discovery of a unique group of cardiotoxins named sarafotoxins. So far, these toxins have only been found in *Atractaspis engaddensis* from Israel and *A. bibronii* from southern and eastern Africa. These toxins appear to be homologous with mammalian endothelins.

Unfortunately, the status of *A. engaddensis* as a species distinct from *A. microlepidota* is currently subject to debate. *Atractaspis microlepidota*, as conventionally understood, is a widespread species occurring in dry parts of western, central and eastern Africa south of the Sahara; populations of *Atractaspis* from the southern and western parts of the Arabian Peninsula have been classified as the subspecies *A. microlepidota andersoni*. The species *A. engaddensis* was described from Ein Gedi, on the western shore of the Dead Sea, Israel, in 1950, and generally treated as a localised species restricted to Israel and Sinai. However, Gasperetti (1988) regarded *A. engaddensis* as conspecific with *A. microlepidota*, and treated it as a subspecies thereof. Golay *et al.* (1993) regarded *A. engaddensis* as a synonym of *A. microlepidota andersoni*, whereas Underwood and Kochva (1993) chose to recognise *A. engaddensis* as a full species "for the present". Clearly, a more thorough review of the *A. microlepidota* group is required, but this will have to await the availability of larger samples of these snakes.

In view of the interest generated by the sarafotoxins, and their medical importance in bites by these snakes, it would be of great importance to test the venoms of a greater number of species and/or populations of the genus for the presence of sarafotoxins. This would be of particular importance in the case of *A. microlepidota andersoni* from the southern and south-western Arabian Peninsula. If this form is conspecific with *A. engaddensis*, then there may be some expectation in finding this component in *A. m. andersoni*.

FAMILY ELAPIDAE

Genus Austrelaps

The genus *Austrelaps* (Australian copperheads) was generally regarded as consisting of a single species, *A. superbus* (formerly known as *Denisonia superba*). Most recent workers have followed Shine (1987) and Rawlinson (1991) in treating this complex as three species, *A. superbus* (lowlands of Victoria and Tasmania), *A. labialis* (Adelaide area and Kangaroo Island, South Australia) and *A. ramsayi* (highlands of eastern New South Wales and northern and eastern Victoria) (e.g. Ehmann, 1992; White, 1995b, 1996).

Genus *Bungarus*

Slowinski (1994) studied the phylogeny of the genus *Bungarus*. He found *Bungarus javanicus* to be identical with *B. candidus*. The name *B. javanicus* had been attributed to melanistic specimens of *B. candidus*, but this melanism appears to an incidence of polymorphism without taxonomic implications. *Bungarus javanicus* therefore becomes a synonym of *B. candidus*, and only the latter name should be used.

Genus *Disteira*

The sea snake genus *Disteira* was recognised by McDowell (1972), and used to encompass the species previously known as *Astrotia stokesii*, *Enhydrina schistosa*, *Hydrophis kingii*, *H. major* and *H. nigrocinctus*. Subsequent workers have either ignored this change altogether (e.g. Voris, 1977; Ehmann, 1992) or restricted the use of *Disteira* to the species *kingii*, *major*, *nigrocinctus* and the recently described *walli* (Cogger, 1992; Golay *et al.*, 1993; White, 1995a). The genera *Astrotia* and *Enhydrina* have been widely recognised by practically all subsequent researchers, and these generic names should be used for the species *stokesii* and *schistosa*, respectively. The classification of sea snakes in general requires further revisions, as do species definitions within the speciose genus *Hydrophis*.

Genera *Micrurus* and *Leptomicrurus*

Slowinski (1995) analysed the phylogeny of the New World coral snakes (*Micrurus*, *Micruroides*, *Leptomicrurus*). His analysis showed that *Leptomicrurus* is rooted within the genus *Micrurus*, and should therefore be synonymised with *Micrurus*. The species formerly allocated to *Leptomicrurus* should therefore be referred to as *Micrurus collaris*, *M. narduccii* and *M. scutiventris* (formerly *M. schmidti*). The species of *Leptomicrurus* are rarely encountered and do not constitute a public health hazard.

Roze (1994) re-examined the systematics of several species-groups of South American coral snakes (*Micrurus*). He reclassified the subspecies of *Micrurus psyches* as full species, i.e. *M. psyches* (eastern Venezuela, adjacent Brazil and the Guyanas), *M. medemi* (Villavicencio region, Meta, Colombia), *M. paraensis* (southern Suriname, Pará and Maranhão south-west to Rondônia, Brazil), *M. remotus* (southern Venezuela, adjacent Brazil and south-eastern Colombia) and *M. circinalis* (north-eastern Venezuela and Trinidad).

In the case of the *M. frontalis* group, he split *M. frontalis* (*sensu* Campbell and Lamar, 1989) into three species, *M. frontalis* (with the subspecies *frontalis*, *altirostris*, *baliocoryphus*, *brasiliensis* and *multicinctus*), *M. pyrrhocryptus* (with the subspecies *pyrrhocryptus* and *tricolor*) and *M. diana*. *Micrurus frontalis* is thus found in central-southern and southern Brazil, Uruguay and eastern Argentina (provinces of Misiones, Corrientes and Entre Ríos), *M. diana* in Departamento de Santa Cruz, Bolivia, and *M. pyrrhocryptus* in south-western Mato Grosso do Sul (Brazil), Paraguay, western and south-western Bolivia and Argentina. The *M. frontalis* group is thought to comprise some of the most medically important species of coral snake in South America.

Roze (1994) also proposes species status for *Micrurus meridensis* (formerly *M. dissoleucus meridensis*) on the basis of hemipenis differences, whereas *Micrurus rondonianus*, described as a new species by Roze and da Silva (1990), is regarded as a subspecies of *M. hemprichii*.

Genus *Naja*

Asiatic Naja. The Asiatic species of *Naja* have been extensively revised in recent years (Wüster and Thorpe, 1989, 1990, 1991, 1992a, b, 1994; Wüster *et al.*, 1995). The nomenclatural and biomedical implications of these changes have been discussed in Wüster (1996) and Wüster and McCarthy (1996). The results of the greatest importance for toxinologists are as follows.

- The species *Naja naja* is restricted to India, Pakistan, Sri Lanka, Nepal and Bangladesh. The various other populations are all separate species. Researchers working with the venom of this species should specify that they are working with *Naja naja* in this new taxonomic context, and indicate the geographic origin of the snakes or venoms. Referring to a venom of this species simply as '*Naja naja*', without other details, could lead to confusion with the old concept of *Naja naja*, which included all Asiatic cobra species.

- *Naja kaouthia* and *Naja atra* are full species.

- The Indochinese spitting cobra, the commonest cobra of Thailand, is a distinct species, *Naja siamensis*. However, commercially available venoms sold under the designation '*Naja naja siamensis*' are more likely to be *N. kaouthia* venom, or may even represent a mixture of *N. kaouthia* and *N. siamensis* venoms. The various colour morphs of *Naja siamensis* have been variously confused with *Naja kaouthia* or referred to as '*N. naja isanensis*', '*N. n. sputatrix*' or '*N. n. atra*'.

- *Naja sputatrix* is restricted to Java and the Lesser Sunda Islands. Other populations of cobra formerly referred to as '*Naja naja sputatrix*' belong to *Naja sumatrana* (Malaysia) or *Naja siamensis* (Thailand).

- *Naja oxiana* is a full species.

For more details of these changes, see Wüster (1996), Wüster and McCarthy (1996), Wüster and Thorpe (1989, 1990, 1991, 1992a, b, 1994) and Wüster *et al.* (1995).

African Naja. The classification of the African species of *Naja* has been more stable than that of the Asiatic species. However, it is worth emphasising that the spitting cobras *Naja mossambica*, *N. katiensis* and *N. pallida* are now generally accepted as full species, separate from *N. nigricollis* and *N. mossambica* (Golay *et al.*, 1993; Spawls and Branch, 1995; Warrell, 1995a). It is likely that some venom commercially sold with the label '*Naja nigricollis*' may in fact originate from *N. mossambica*.

Broadley (1995) split *Naja haje* into two species. *Naja haje* (*sensu stricto*) is found in Africa north of the Equator, and south into Kenya and northern Tanzania, as well as in the southern part of the Arabian Peninsula, and includes the subspecies *Naja haje arabica*. The populations from southern Africa (Angola, Botswana, Malawi, Moçambique, Namibia, South Africa, Swaziland, southern Zaire, Zambia and Zimbabwe), formerly regarded as conspecific with *N. haje*, should now be referred to as *Naja annulifera*, which includes the subspecies *N. a. anchietae*.

Genus *Pseudonaja*

The genus *Pseudonaja* has a long and confused taxonomic history. In recent years, the classification of the various forms has been relatively stable, and seven species are now

recognised by most workers (e.g. Ehmann, 1992; Golay *et al.*, 1993). However, it is clear that there is still considerable hidden diversity within some of the currently recognised species, and the populations currently referred to as *P. nuchalis* in particular are likely to comprise several as yet unnamed species (Mengden, 1985). In view of the medical importance of the Australian brown snakes, it is important that current toxinological and clinical work should be interpretable in the light of future improvements of our understanding of the systematics of these snakes. Toxinologists and clinicians working with *Pseudonaja*, and in particular the widespread species *P. nuchalis* and *P. textilis*, should therefore ensure that the geographic origin of their specimens and/or venoms is published, and specimens involved in clinical accidents or used for venom production should be preserved and deposited in a museum collection as vouchers.

FAMILY VIPERIDAE: SUBFAMILY CROTALINAE

Genus Agkistrodon or Gloydus

The generic name of some of the Asiatic pitvipers with large shields on their heads remains unsettled. The classification of *Calloselasma rhodostoma*, *Deinagkistrodon acutus* and the three species of *Hypnale* in their respective genera has been generally accepted by herpetologists, but it remains common to see these species assigned to the genus *Agkistrodon* in the toxinological literature.

The generic status of the remaining Asiatic species remains controversial. They were assigned to *Agkistrodon*, together with the North American species of this genus, in the monograph of Gloyd and Conant (1990), but recent molecular studies (Knight *et al.*, 1992) suggest that the Asiatic species are not closely related to the North American *Agkistrodon*. It is likely that the Asiatic species should be classified as a separate genus, *Gloydus*, as has already been proposed by some previous authors (Hoge and Romano-Hoge, 1978/79), who first proposed this genus.

The nomenclature of many of the species of the Asiatic *Agkistrodon/Gloydus* has a history of great confusion. Until recently, most of the smaller northern and central Asian populations (with the exception of *A. himalayanus*, *A. monticola* and *A. strauchi*) were generally regarded as belonging to one single species, *A. halys* (e.g. Minton *et al.*, 1968). However, recent research has indicated that this putative species in fact consists of a number of separate species. Despite a large monograph on the snakes of the 'Agkistrodon complex' (Gloyd and Conant, 1990), controversy persists, and several recent workers have expressed different ideas about which names should apply to which populations. As a result, some aspects of the systematics of this group have become confused. The relationships between the names commonly used are given in Table 1.

In the light of all recent studies, it is essential to emphasise that the name *A. halys* is only applicable to a species found in Central Asia (Kazakhstan, Uzbekistan, Tadzhikistan, Kirgiziya, Afghanistan, Russia, Mongolia and northern China), whereas populations from the Far East (eastern China, Korea, Japan, south-eastern Siberia) are referable to different species. In particular, the snake referred to as the 'Mamushi' in Japan, eastern China and Korea now bears the scientific name *Agkistrodon blomhoffii*, the Japanese specimens being *A. b. blomhoffii* and the mainland populations *A. blomhoffii brevicaudus*. These snakes have been of considerable importance in toxinological research, but their nomenclature has been confused. It is important to emphasise that the Chinese species known in English as 'Chinese mamushi' or 'short-tailed pit viper', and in Chinese as 'Fu She', which features

frequently in the literature on snakebite and toxinology, is correctly designated as *A. b. brevicaudus* (Zhao and Adler, 1993). Readers should be aware that this species is not infrequently referred to in the literature as 'Agkistrodon halys Pallas'

Paik *et al.* (1993) carried out an isozyme study of Far Eastern *Agkistrodon*, and their results had a number of implications on the systematics of this complex. It appears that the Japanese *A. blomhoffii blomhoffii* is more distantly related to the supposedly conspecific *A. b. brevicaudus* from Korea and China, than to the supposedly non-conspecific *A. ussuriensis* from the Russian and Korean mainland. Furthermore, the results of Paik *et al.* suggest that *A. blomhoffii*, as currently defined, appears to be a composite of several taxa. In particular, specimens from the Japanese island of Tsushima appear to be strongly differentiated from specimens from other islands. On this basis, Isogawa *et al.* (1994) described the Tsushima population as a new species, *A. tsushimaensis*.

Clearly, the Asiatic *Agkistrodon* complex will continue to give rise to taxonomic changes and confusion for some years to come. Since this group is of considerable interest to toxinologists, it is important that venom samples or clinical reports be based on specimens preserved and deposited in major natural history collections. Without such specimens, it will be practically impossible to unravel the taxonomic identities of venoms used in experiments. Furthermore, locality data for specimens and venoms are of extreme importance, as these can in many cases help to establish the identity of the snake involved.

Bour (1993) analysed the available information on the type locality of the species *Agkistrodon halys*, which was not very clear from the writings of its discoverer, Pallas. For a long time, the type locality had been thought to be situated in the region of Krasnoyarsk, central Siberia. However, Bour's analysis of Pallas' writings suggests that the specimen was in fact collected much further west, in the Naryn or Ryn Peski Desert, Kazakhstan, at the northern end of the Caspian Sea.

This has some taxonomic implications, as *Agkistrodon halys* has been subdivided into several subspecies. Until Bour's work, the generally recognised subspecies were *A. halys halys* from Mongolia and southern Siberia, *A. h. caraganus* from the area to the north and east of the Caspian Sea, *A. h. boehmei* from Afghanistan, and *A. h. cognatus* from central China. However, Bour's work shows that the type locality of *A. halys* lies within the range of what was until then called *A. h. caraganus*. This means that the subspecies found near the Caspian Sea now has to be referred to as *A. halys halys*, and *A. h. caraganus* becomes a synonym of this. Since no other name was available for the *A. halys* subspecies from Mongolia and southern Siberia, Bour described these under the new name *Agkistrodon halys mogoi*.

In summary, the effect of Bour's paper is that the populations formerly referred to as *A. h. caraganus* now become *A. h. halys*, and those formerly referred to as *A. h. halys* become *A. h. mogoi*. The other subspecies of *A. halys* are not affected by this change, except that Zhao and Adler (1993) regard *A. h. cognatus* as a subspecies of *A. intermedius*, not *A. halys*. Bour's study demonstrates further the complexity of the systematics of the *A. halys* complex.

Bothrops and related genera

The South American pitvipers of the genus *Bothrops*, as well as the related genera *Bothriechis*, *Bothriopsis*, *Porthidium*, *Cerrophidion*, *Ophryacus* and *Atropoides*, have become a major focus of research by several groups in Europe and the Americas. Unfortunately, considerable conflict has emerged between the interpretations of different

Table 1. Equivalence of scientific names used for various taxa of the *Agkistrodon halys* and *A. blomhoffii* complex in the recent taxonomic literature

Golay <i>et al.</i> (1993)	Bour (1993)	Zhao and Adler (1993)	Gloyd and Conant (1990)	Harding and Welch (1980)
<i>A. blomhoffii blomhoffii</i>			<i>A. blomhoffii blomhoffii</i> , <i>A. affinis</i>	<i>A. blomhoffii blomhoffii</i>
<i>A. blomhoffii brevicaudus</i>		<i>A. blomhoffii brevicaudus</i>	<i>A. blomhoffii brevicaudus</i>	<i>A. blomhoffii brevicaudus</i>
<i>A. blomhoffii dubitatus</i>		<i>A. blomhoffii brevicaudus</i>	<i>A. blomhoffii dubitatus</i>	
<i>A. blomhoffii siniticus</i>		<i>A. blomhoffii brevicaudus</i>	<i>A. blomhoffii siniticus</i>	<i>A. blomhoffii brevicaudus</i>
<i>A. halys halys</i>	<i>A. halys mogoi</i>	<i>A. halys halys</i>	<i>A. halys halys</i>	<i>A. halys halys</i>
<i>A. halys caraganus</i>	<i>A. halys halys</i>		<i>A. halys caraganus</i>	<i>A. halys caraganus</i>
<i>A. halys cognatus</i>	<i>A. halys cognatus</i>		<i>A. halys cognatus</i>	
<i>A. intermedius intermedius</i>		<i>A. intermedius</i>	<i>A. intermedius intermedius</i>	<i>A. halys intermedius</i>
<i>A. intermedius caucasicus</i>		<i>A. intermedius</i>	<i>A. intermedius caucasicus</i>	<i>A. halys caucasicus</i>
<i>A. intermedius stejnegeri</i>		<i>A. intermedius</i>	<i>A. intermedius stejnegeri</i>	
<i>A. saxatilis</i>		<i>A. saxatilis</i>	<i>A. intermedius saxatilis</i>	<i>A. saxatilis</i>
<i>A. ussuriensis</i>		<i>A. ussuriensis</i>	<i>A. caliginosus</i> , <i>A. blomhoffii ussuriensis</i>	<i>A. caliginosus</i> , <i>A. halys ussuriensis</i>

Table 2. Equivalence of scientific names used for various Central and South American pitvipers in the recent taxonomic literature

Freire (1991)	Campbell and Lamar (1989, 1992)*	Schätti and Kramer (1993), Golay <i>et al.</i> (1993)	Werman (1992)
<i>Bothrops asper</i> , <i>B. xanthogrammus</i>	<i>Bothrops asper</i> (Central America) <i>Bothrops asper</i> (western South America)	<i>Bothrops atrox atrox</i> <i>Bothrops atrox xanthogrammus</i>	
<i>Bothrops campbelli</i>	<i>Bothrops pulcher</i> <i>Bothrops microphthalmus</i> <i>Bothrops microphthalmus colombianus</i> # <i>Bothrops colombianus</i>	<i>Porthidium almawebi</i> <i>Porthidium mircrophthalmum</i> <i>Porthidium colombianum</i>	
<i>Bothrops</i> (part)	<i>Porthidium nummifer</i> , <i>P. olmec</i> , <i>P. picadoi</i> <i>Bothriopsis</i> <i>Bothriopsis albocarinata</i> <i>Bothriopsis oligolepis</i> <i>Bothriopsis peruviana</i>	<i>Porthidium nummifer</i> , <i>P. olmec</i> , <i>P. picadoi</i> <i>Bothriechis</i> (part) <i>Bothriechis oligolepis albocarinatus</i> <i>Bothriechis oligolepis oligolepis</i> <i>Bothriechis oligolepis oligolepis</i>	<i>Atropoides nummifer</i> , <i>A. olmec</i> , <i>A. picadoi</i> <i>Bothriopsis</i>
<i>Bothrops osbornei</i>	<i>Bothriopsis punctata</i> (part)	<i>Bothriechis punctatus mahnerti</i>	

*Where the names used for a given taxon differ between the 1989 and 1992 publications, the designations used in the 1992 paper are flagged with #.

researchers. As this group includes a number of medically important species, this confusion is particularly regrettable. Much of the confusion concerns not just the biological realities of the situation, but also procedural arguments about the validity of certain decisions affecting the nomenclature of some forms. The relationships between names used by different authors are shown in Table 2.

Research on the South American pitvipers is still in progress in several laboratories, and it would therefore be premature to write a complete review of the group at this stage. Nevertheless, in view of the medical importance of some of the species involved, it is imperative to clarify some of the outstanding issues. Unfortunately, given the irreconcilable differences between different researchers' views, and the senior author's own research into the systematics of these snakes, it is impossible to write such a review without commenting on the relative merits of some of the views espoused.

Bothrops jonathani

Bothrops jonathani is a new species described by Harvey (1994) from the highlands of Bolivia. In external appearance, it most resembles *B. alternatus*. In view of its restricted distribution in a sparsely populated area, it is unlikely to be of great medical significance.

Bothrops asper, *B. xanthogrammus*, *B. isabelae* and *B. atrox*

The status of *B. asper*, *B. xanthogrammus* and *B. isabelae* vis-à-vis each other and *Bothrops atrox* has been contentious for many years.

Campbell and Lamar (1992) regarded *B. asper* as a distinct species. They further suggested that the western Ecuadorian populations often assigned to *B. xanthogrammus* are conspecific with the western Colombian and Central America populations normally assigned to *B. asper*, so that *B. xanthogrammus* and *B. asper* represent the same species.

However, Schätti and Kramer (1993) argued that all these populations should be classified as the single species, *Bothrops atrox*. Furthermore, they also argued that the Central American populations conventionally assigned to *B. asper* are identical with the Amazonian populations always known as *B. atrox*, whereas the populations from the Pacific lowlands of Ecuador and south-western Colombia should be regarded as a separate subspecies, *B. atrox xanthogrammus*. Unfortunately, it remains unclear how their data support this classification. Preliminary multivariate analyses of morphological characters of Amazonian, Pacific Colombian and Ecuadorian and Central American *Bothrops* do not support Schätti and Kramer's (1993) interpretation. The results, summarised in Theakston *et al.* (1995), show a pattern of morphological variation in which the populations from Central America and the Pacific lowlands of Ecuador and Colombia are morphologically identical, but highly distinct from Amazonian populations normally assigned to *B. atrox*. These results strongly contradict the interpretation of Schätti and Kramer (1993), and support that of Campbell and Lamar (1992). The systematics of these animals are currently under investigation.

The nomenclature of these populations is complicated by the fact that the name *Bothrops xanthogrammus* Cope, 1868 has priority over *Bothrops asper* Garman, 1883. The name *B. xanthogrammus* has only rarely been used, and only for the populations of western Ecuador, whereas the name *B. asper* has been used in a large body of literature. If ongoing studies further support the conclusions of Campbell and Lamar (1992), then a petition to the International Commission on Zoological Nomenclature, with the aim of retaining the

name *B. asper* for this species, would be highly desirable. In the meantime, it would be preferable to continue using the name *B. asper* for all populations of this complex from western Colombia and Ecuador as well as Central America, and *B. atrox* for populations from the Amazonian lowlands on the eastern side of the Andes as well as Venezuela and the Guyanas.

Markezich and Taphorn (1993) examined morphological variation between rainforest and savannah populations of the *B. atrox* complex in Portuguesa State, western Venezuela. The locality had been suggested as a possible zone where the distributions of *B. asper* and *B. atrox* overlap or meet. They found no evidence of the presence of more than one species in the area. The pattern of variation of Venezuelan *Bothrops* is extremely complex, and it is far from certain that the area of Portuguesa State does in fact represent a transition zone.

One of the populations involved in Markezich and Taphorn's study had been described as a distinct species, *B. isabellae*, by Sandner Montilla (1979). Markezich and Taphorn found no reason to believe that the western Venezuelan populations concerned represent a distinct species. This agrees with recent results from multivariate morphometrics and mtDNA sequence analysis, which suggests that these populations should be assigned to *B. atrox* (Wüster *et al.*, 1997).

It should also be emphasised that the assignment of the populations here referred to as *B. asper* to *B. lanceolatus*, as advocated by Sandner Montilla (1990), is erroneous and unsupported by any evidence. *Bothrops lanceolatus* is an endemic species restricted to the island of Martinique, French West Indies.

In view of the confusion surrounding the systematics of this group, it is essential that any study concerning these animals or their venoms should provide precise localities of origin for their specimens. Similarly, venom suppliers must specify the geographical origin of their venoms, so that results can later be correlated with nomenclatural changes. Venom composition differences between some populations of this group have been documented (e.g. Assakura *et al.*, 1992), so that the question of geographical origin is of crucial importance.

Bothrops pulcher, *Bothrops campbelli* or *Porthidium almawebi*

The name *Bothrops pulcher* has long been applied to a stout terrestrial pitviper inhabiting rainforests of the western slopes of the Andes of Ecuador and south-western Colombia. However, Schätti and Kramer (1993) found that the holotype of *B. pulcher* does not belong to this stout species, but is in fact conspecific with a species of arboreal pitviper generally known as *Bothriopsis albocarinata*. This means that the name *B. pulcher* is not available for the stout terrestrial form. They therefore described the species under a new name as *almawebi*. Schätti and Kramer (1993), on the basis of certain superficial morphological and behavioural similarities, assigned this species to the genus *Porthidium*, so that it becomes *Porthidium almawebi*. The species was stated to be most similar to several species of *Porthidium*, including those assigned to the genus *Atropoides* by Werman (1992). In the absence of a thorough phylogenetic analysis of this species and the genera *Bothrops*, *Atropoides* and *Porthidium*, these changes are difficult to evaluate.

To increase further the confusion surrounding this form, the same species had previously been described as *Bothrops campbelli* by Freire (1991). According to Campbell and Lamar (1992) and Schätti and Kramer (1993), Freire's (1991) description of *B. campbelli* (and *Bothrops osbornei*; see below) probably does not fulfil the requirements of the International

Code of Zoological Nomenclature. However, this requires further investigation. If Freire's publication does fulfil the criteria of the Code, then the specific name *campbelli* would have priority over the name *almawebi*. Clearly, the status of this species needs to be reviewed. The problems of nomenclature may require the intervention of the International Commission on Zoological Nomenclature.

Bothrops *or* Porthidium microphthalmus/um, B. *or* P. colombianus/um, Porthidium hyoprora

Campbell and Lamar (1992) raised the subspecies *Bothrops microphthalmus colombianus* Rendahl and Vestergren (1940) to the status of a full species, *B. colombianus*. This very rare species is found in a few localities on the western slopes of the Andes of Colombia. Because of its name, *B. colombianus* could be confused with *B. colombiensis* (Hallowell, 1845). The name *B. colombiensis* has been used for the populations of the *B. atrox* group from northern Venezuela, but was synonymised with *B. atrox* by Johnson and Dixon (1984). The status of these Venezuelan populations is currently under study. Because of the relative rarity of *B. colombianus* and *B. microphthalmus*, they are not likely to be of great medical importance, although *B. microphthalmus* is suspected of causing severe bites in Zamora-Chinchipec Province, Ecuador (Kuch and Freire, 1995), and *B. colombianus* must be regarded as potentially highly dangerous owing to its size.

Schätti and Kramer (1993) drew attention to the superficial similarities between *Bothrops microphthalmus* and *Porthidium hyoprora*, and on that basis assigned *B. microphthalmus* to the genus *Porthidium*. While *P. hyoprora* and *B. microphthalmus* are indeed superficially similar, it remains open to question whether either of them forms part of the genus *Porthidium*. Only a thorough phylogenetic analysis including all taxa of *Bothrops* and related genera of neotropical pitvipers can resolve this problem, as well as many other problems in this group. Regrettably, many of the name changes and assignments of species to new genera have been based on a relatively superficial examination of a limited number of species and specimens. Such changes can only contribute to the confusion surrounding many of these taxa, and should be discouraged (Dixon, in Golay *et al.*, 1993).

Genus *Atropoides*

Werman (1992) described the new genus *Atropoides* to include three stout pitvipers formerly assigned to *Porthidium*: they are *Atropoides nummifer*, *A. olmec* and *A. picadoi*. Together with the assignment of *godmani*, *barbouri* and *tzotzilorum* to *Cerrophidion*, this leaves only the hog-nosed pitvipers within the genus *Porthidium*. This includes the species *lansbergi*, *melanurum*, *nasutum*, *ophryomegas*, *dunni*, *volcanicum*, *yucatanicum*, *hespere* and *hyoprora*. The status of the taxa *microphthalmus* and *almawebi*, assigned to *Porthidium* by Schätti and Kramer (1993), is discussed above.

Genera *Bothriopsis* and *Bothriechis*

Schätti *et al.* (1990) examined the systematics of the neotropical arboreal pitvipers, and came to the conclusion that the species assigned to *Bothriopsis* by Burger (1971) and Campbell and Lamar (1989) should in fact be assigned to *Bothriechis*. Unfortunately, these conclusions were not based on a phylogenetic analysis. A phylogenetic analysis of allozyme, isozyme and morphological characters of all major groups of neotropical pitvipers (Werman, 1992) showed that *Bothriechis* appears to form an outgroup to a clade

which includes *Porthidium* and *Bothrops*. In contrast, *Bothriopsis taeniata*, the type species of the genus *Bothriopsis*, was shown to be rooted within *Bothrops sensu* Campbell and Lamar (1989). Consequently, it is clear that *Bothriopsis* cannot be regarded as a synonym of *Bothriechis*. The analysis of mitochondrial DNA sequence information also supports the placement of *B. taeniata* within *Bothrops* (Salomão *et al.*, 1997), which would imply that all species previously assigned to *Bothriopsis* should be assigned to *Bothrops*.

Bothrops/Bothriopsis/Bothriechis albocarinatus/a, oligolepis and peruvianus/a

Schätti and Kramer (1993) examined the species classified as *Bothriopsis albocarinata*, *B. oligolepis* and *B. peruviana* (while assigning them to the genus *Bothriechis*; see above), and came to the conclusion that they comprise only a single species with two subspecies, *B. oligolepis oligolepis* (including *peruvianus/a*), and *B. o. albocarinatus/a*.

Bothrops/Bothriopsis punctatus/mahnerti/osbornei

Schätti and Kramer (1991) described a new species of arboreal pitviper from Ecuador as *Bothriechis mahnerti*. At approximately the same time, Freire (1991) described the same form as *Bothrops osbornei*. The validity of Freire's description under the International Code of Zoological Nomenclature has been questioned (Campbell and Lamar, 1992), and Schätti and Kramer (1993) suggested that Freire's description appeared after theirs, despite an earlier stated date of publication of Freire's description. The status of this form has remained controversial: Campbell and Lamar (1992) regard it as a population of *Bothriopsis punctata* without separate taxonomic status, whereas Schätti and Kramer (1993) later chose to regard it as a subspecies of *punctata* (as *Bothriechis punctatus mahnerti*). A resolution of this problem will require the use of more advanced techniques of analysis of morphological variation than those employed so far. These snakes are relatively rare and probably not of any public health significance, although *B. punctatus* must be regarded as potentially dangerous on account of its size.

Genus Cerrophidion

The genus *Cerrophidion* was erected by Campbell and Lamar (1992) to include three small species of montane pitvipers from Central America, which were previously classified as *Porthidium*. The species are now *Cerrophidion godmani*, *C. barbouri* and *C. tzotzilorum*.

Genus Porthidium

Schätti and Kramer (1993) described a new subspecies of *Porthidium lansbergi* from Manabí Province, on the western coast of Ecuador: *Porthidium lansbergi arcosae*. It appears to represent an isolated population of the wide-ranging *P. lansbergi*, which is also known from the lowlands of northern Colombia, coastal Venezuela and southern Panama.

Solórzano (1994) described a new species of the genus, *Porthidium volcanicum*, from the Valle del General of Costa Rica. The species appears to be restricted to this valley. On account of their restricted distributions and relatively small sizes, neither of these two species is likely to represent a significant public health problem.

Genus Crotalus: Crotalus durissus

McCranie (1993) published a useful summary of the literature, systematics and distribution of this complex and medically important species. Included are descriptions and detailed distribution maps of the various subspecies, a diagnosis to differentiate this species from other species of *Crotalus*, a discussion of the systematic problems surrounding this species and its subspecies, and a summary of important literature on this species. The medical and toxinological aspects of this species are not discussed.

Crotalus exsul/ruber

Murphy *et al.* (1995) compared mitochondrial DNA sequences, allozyme allele frequencies and morphological characters of the rattlesnakes *Crotalus ruber* (Baja California and southern California) and *C. exsul* (Isla Cedros, Baja California del Norte, Mexico). The absence of consistent differences led them to conclude that these two forms are conspecific. The oldest name available for this species is *C. exsul*. Under the rules of the International Code on Zoological Nomenclature, this would normally be the correct scientific name for this species, with the name *C. ruber* as a synonym. However, owing to heavy use of the name *C. ruber* in the literature, and the relative obscurity of the name *C. exsul*, a petition to conserve the name *C. ruber* has been filed with the International Commission on Zoological Nomenclature. Until the decision of the Commission is published, the name *C. ruber* should continue to be used for the red diamond rattlesnake, in accordance with Article 80 of the International Code of Zoological Nomenclature.

Crotalus lepidus/Crotalus triseriatus/Crotalus aquilus

Dorcas (1992) reviewed the status of the rattlesnake formerly known as *Crotalus triseriatus aquilus*. Phylogenetic analysis of a variety of characters showed that *aquilus* is in fact more closely related to *C. lepidus* than to *C. triseriatus*, and that it should be regarded as a full, separate species, *C. aquilus*. All the species involved in this study are small snakes which occur principally at high altitudes; they are therefore of very little public health significance, although some herpetoculturists keep these snakes and occasionally suffer bites.

Genus Ovophis

The genus *Ovophis* was first described by Burger (1971) in an unpublished dissertation. Since such dissertations do not make a name available under the criteria of the International Code of Zoological Nomenclature, Burger's diagnosis was reproduced verbatim by Hoge and Romano-Hoge (1978/79, published in 1981), which constitutes a valid publication and makes the name available for taxonomic purposes. Smith and Chiszar's (1988) publication had the same intentions, but was redundant because of Hoge and Romano-Hoge's prior publication of Burger's description. The genus includes a group of species previously assigned to *Trimeresurus*: *Ovophis monticola* (including the taxa *convictus* and *tonkinensis*, which have been regarded as separate species by some authors), *O. chaseni* (a localised species from northern Borneo) and *O. okinavensis* (Okinawa and neighbouring islands). These species are rarely encountered and do not represent a significant health hazard, although a few serious or fatal bites have been recorded (Warrell, 1995b).

Genus Trimeresurus: Trimeresurus puniceus/wiroti/brongersmai/borneensis

The taxonomy of the pug-nosed viper group has recently generated some discussion. *Trimeresurus wiroti* was described from southern Thailand by Trutnau (1981), but was synonymised with *T. puniceus* by Nutphand *et al.* (1991). Toriba (1992) compared a specimen of these populations with a specimen from Borneo, and on the basis of this assigned the Malaysian and Thai populations of this complex to *T. borneensis*. However, a revision of this complex requires at the very least an examination of the available type material and/or specimens from the type localities of the various taxa. The matter must therefore be regarded as not settled. These snakes are of no significant public health importance.

Trimeresurus kanburiensis/T. venustus

Vogel (1991) described *Trimeresurus venustus* as a new species from southern Thailand. Warrell *et al.* (1992) compared specimens of this form with new material of *T. kanburiensis*, and came to the conclusion that *T. venustus* is a synonym of *T. kanburiensis*. These snakes are fairly rare and of little public health importance, although a severe bite was described by Warrell *et al.* (1992).

General confusion involving species of Trimeresurus

The green species of *Trimeresurus* have given rise to considerable confusion, primarily because of the great similarity between different forms. In the earlier literature (e.g. Boulenger, 1896), most populations of green *Trimeresurus* were assigned to the species *T. gramineus*. Today, only populations from the south-western hills of India are assigned to this species. However, the name has persisted in the toxinological literature, and it is not uncommon to find the name used for a number of species, such as *T. stejnegeri* from Taiwan. This has even led to the misnaming of toxins, such as 'grambin' (Chang and Huang, 1995), which is almost certainly not from *T. gramineus*, and will probably remain of unidentifiable origin.

The confusion regarding the green species of *Trimeresurus* is particularly acute in Thailand and neighbouring parts of south-east Asia. Owing to the mislabelling of live specimens exported from Thailand, this confusion has permeated not just the Thai literature, but also the toxinological, medical and herpetocultural literature (Hutton *et al.*, 1990; Warrell *et al.*, 1992). Common errors include:

- *T. kanburiensis* misnamed *T. purpureomaculatus* and vice versa;
- *T. macrops* misnamed *T. popeorum*;
- *T. popeorum* misnamed *T. erythrurus*;
- *T. hageni* misnamed *T. sumatranus* and vice versa;
- *T. albolabris* (southern Thailand) misnamed *T. stejnegeri*;
- *T. stejnegeri* (north-eastern Thailand) misnamed *T. popeorum*.

The situation is complicated by the fact that some of the currently recognised species probably comprise more than one species. Because some species are so similar that they cannot be distinguished on the basis of external morphology, information on distribution is also lacking in many cases. Although work on this complex is currently progressing in several research groups, the most recent revision remains that of Kramer (1977) and Regenass and Kramer (1981). Once again, it is imperative that clinical and toxinological researchers and venom providers obtain, provide and publish full information on the

locality of origin of the snakes, and that specimens used for venom production or brought by snakebitten patients be deposited in major natural history collections. The latter aspect is particularly important in this complex, as several virtually indistinguishable species of this complex can occur in the same locality, and identification will be impossible without a preserved specimen (even a photograph is unlikely to permit reliable identification).

Genus *Tropidolaemus*

The genus *Tropidolaemus* is now generally recognised, and includes the single species *T. wagleri* (known in English as Wagler's pitviper or temple viper), which was formerly assigned to the genus *Trimeresurus*). At least some populations of this species secrete lethal peptides known as waglerins. This species shows considerable geographic variation in colour pattern and morphology, and may show similar variation in venom composition. Toxinologists and venom suppliers should ensure that the geographic origin of the snakes producing experimental venoms is known.

FAMILY VIPERIDAE: SUBFAMILY VIPERINAE

Genera *Daboia*, *Macrovipera* and *Vipera*

The status of some of the larger species until recently assigned to the genus *Vipera* has recently started to become the subject of much discussion. Obst (1983) proposed the revalidation of the genus *Daboia* to accommodate the species hitherto known as *Vipera russellii*, *V. lebetina*, *V. mauritanica*, *V. palaestinae* and *V. xanthina* and allied species. However, this proposal had only limited influence on other workers. Herrmann *et al.* (1992) re-examined the phylogeny of the genus *Vipera* (*sensu lato*) by means of albumin immunology. Their findings strongly support the revalidation of *Daboia* as a monotypic genus, including only Russell's viper, now *Daboia russellii*. At the same time, the results of Herrmann *et al.* also necessitate the revalidation of another genus, *Macrovipera*, to include the large vipers of the *lebetina* group, as well as the raising of the Greek island populations of *M. lebetina* and the south-eastern subspecies of *M. mauritanica* and *M. deserti*, to the status of a full species. The genus *Macrovipera* thus includes the species *M. lebetina* (North Africa, Near and Middle East), *M. mauritanica* (north-west Africa), *M. deserti* (North Africa) and *M. schweizeri* (Cyclades Islands).

Daboia russellii

Wüster *et al.* (1992) examined morphological variation within *Daboia russellii* (referred to as *Vipera russelli*) by means of multivariate morphometrics. They found that Russell's viper consists of two highly distinct groups of populations, one from the western part of the distribution (India, Pakistan, Sri Lanka, Bangladesh) and the other from the eastern part (China, Taiwan, Thailand, Burma, Indonesia). Within the eastern form, the populations from the Lesser Sunda Islands (Komodo, Flores, Lombok) are distinct from the Javan and Asian mainland populations. These authors recognised two subspecies of Russell's viper, a western subspecies (*Daboia russellii russellii*), which includes populations formerly known as *D. r. russellii*, *D. r. nordicus* and *D. r. pulchella*, and an eastern subspecies (*D. r. siamensis*), which includes the populations formerly assigned to *D. r. siamensis*, *D. r. formosensis*, *D. r. limitis* and *D. r. sublimitis*.

It is important to emphasise that the enormous venom variation present within Russell's viper (Warrell, 1989) does not fully correspond to either the subspecies recognised by

Wüster *et al.* (1992) or the conventional subspecies previously recognised: there is just as much variation in venom composition and clinical effects within the eastern and western forms as there is between them. Toxinologists using the venom of this species must ensure that their experimental venoms come from specimens of well-documented, precise geographical origin.

Genus *Echis*

The saw-scaled or carpet vipers of the genus *Echis* remain one of the most taxonomically problematic groups of venomous snakes. Although considerable progress has been made, the identification and definition of species remains problematic, particularly in Africa. Until the 1980s, only two species of *Echis* were recognised: *Echis coloratus*, from Egypt, Israel and the Arabian Peninsula, and *Echis carinatus*, encompassing the populations from West Africa to India and Sri Lanka. Whereas *E. coloratus* is a reasonably well-defined species, *E. carinatus* has since been split into a number of species in reviews by a number of workers. However, the various classifications proposed have often been contradictory. In particular, Cherlin (1990) recognised 12 full species, but his analyses have not been widely accepted by subsequent herpetologists.

There is, however, relatively widespread agreement on some issues. In particular, it has become clear that *Echis carinatus (sensu stricto)* is confined to Asia and the eastern and south-eastern coastal areas of the Arabian Peninsula (Arnold, 1980; Joger, 1984). All populations from the western Arabian Peninsula and Africa belong to different species. Within Asia, there is still considerable debate on whether the taxa *sochureki* and *multisquamatus* represent full species or subspecies of *Echis carinatus*. In particular, *multisquamatus* has been regarded as a full species by most workers until the study of Auffenberg and Rehman (1991).

In Africa, the situation is even more complex. Three species (other than *E. coloratus*) have been widely recognised by many researchers (e.g. Spawls and Branch, 1995): *E. pyramidum*, from the western and southern coastal areas of the Arabian Peninsula and Egypt south to Kenya and across the northern edge of the Sahara to Algeria; *E. ocellatus*, from the West African savannahs south of the Sahara, from Senegal east to at least western Chad, and possibly further east to the Central African Republic and possibly Sudan; and *E. leucogaster*, from arid or semi-arid savannahs and semi-deserts in West Africa, as well as isolated areas of the western Sahara, north to southern Algeria. In reality, the status of northern and central African populations in particular remains desperately uncertain, especially as very little material is available from the localities.

Several other African species were described or recognised by Cherlin (1990). Some of these appear to be from isolated localities (*E. hughesi*, northern Somalia; *E. jegeri*, western and central Mali; *E. khosatskii*, southern Arabian Peninsula; *E. megalcephalus*, Nokra Island, Eritrea), whereas others are supposedly widespread (*E. varia*, eastern Africa and south-western Arabian Peninsula—included in most workers' concept of *E. pyramidum*; *E. arenicola*, western parts of the Sahara and the subdesert areas to the south thereof—included in most workers' concept of *E. pyramidum* and/or *E. leucogaster*). Cherlin's *E. froenatus* is an invalid name for the species generally known as *E. coloratus*. The resolution of the problems of this genus will require a considerable effort to obtain more samples from the range of the species, as well as the use of advanced methods of morphological and molecular analysis.

The systematic problems of the genus *Echis* are of enormous importance for toxinologists and clinicians. It has been shown that antivenoms raised against the venoms of one species may be ineffective in treating bites by another species (Warrell and Arnett, 1976; Gillissen *et al.*, 1994). Furthermore, the symptoms of *Echis* bites may differ considerably between populations, and this can lead to unexpected clinical problems (Gillissen *et al.*, 1994). Unfortunately, even the limited progress that has been made in the analysis of *Echis* systematics has not always been reflected in the toxinological and clinical literature. In a recent survey, it was found that less than 50% of experimental venoms or animals involved in accidents could confidently be classified within the currently widely accepted species (Wüster and McCarthy, 1996). It is still common to see venoms of African *Echis* labelled simply as '*Echis carinatus*' in the toxinological literature, and many commercially available venoms lack information on the geographical origin of the relevant specimens.

In the absence of a full, comprehensive resolution to the problems of *Echis* systematics, it is essential that clinicians, toxinologists and venom suppliers make all conceivable efforts to obtain, provide and publish the maximum possible amount of information which will allow a later identification of their venoms or animals. This should include a tentative identification according to a current classification, and a clear and precise statement of the geographical origin of the specimen (several countries may have more than one species of *Echis* present, so the name of the country is not sufficient). Most importantly, any specimens used for venom production or brought by snakebitten patients must be deposited in major natural history collections.

Genus *Vipera*

The species of the Middle Eastern mountain vipers (*Vipera xanthina* group) have been extensively revised over the last 12 years (Nilson and Andrén, 1984, 1985a, b, 1986, 1992; Nilson *et al.*, 1990). This has led to the description of a number of new species (*V. wagneri*, north-eastern Turkey, possibly north-western Iran; *V. albicornuta*, northern Iran; *Vipera bulgardaghica*, southern Turkey; *V. albizona*, central Turkey), and several other taxa were recognised as full species (*V. bornmuelleri*, mountains of the Lebanon; *V. latifi*, Lar Valley, Iran; *V. raddei*, Armenia, eastern Turkey, north-western Iran). According to these studies, *Vipera xanthina* only occurs in the western third of Asiatic Turkey, as well as in European Turkey, extreme north-eastern Greece and a number of Greek islands off the coast of Anatolia. These taxonomic changes were severely criticised by Schätti *et al.* (1991), who only recognised two species as distinct, *V. xanthina* (including *V. albizona*, *V. bulgardaghica* and *V. bornmuelleri*) and *V. raddei* (including *V. latifi* and *V. albicornuta*). Until a full analysis of the population phylogeny of these forms is carried out, using large samples and preferably a wide range of characters, and in particular molecular markers, the situation is likely to remain confused. Fortunately, the most medically important populations are those least affected by these name changes: they include those populations found over wide, populated areas, namely *V. xanthina* in western Anatolia and European Turkey, and *V. raddei* in Armenia and neighbouring areas. The populations from the Iranian Zanzan valley, termed *V. albicornuta* by Nilson and Andrén (1985a), may also be responsible for a large number of bites.

Gumprecht (1994) provides a summary of the morphology and natural history of *Vipera nikolskii*, a small viper resembling *V. berus* found in the region of Kharkov (Ukraine).

The small eastern European/western Asian vipers of the *berus/kaznakovi/ursinii* groups have received a considerable amount of attention in recent years. This has led to the description of several new species, as well as the revalidation of various synonyms and the elevation of several formerly recognised subspecies to the status of full species. The process of revision of these taxa is by no means finished, so that further changes in the nomenclature must be expected. The species involved are small, relatively inoffensive snakes, and bites are probably only rarely life-threatening. It is possible that bites may be relatively common among mountain farmers in the region, but no statistics appear to exist.

Joger *et al.* (1992) suggested that some of the groups of populations within the *Vipera ursinii* group should be regarded as separate species, but without formally altering the nomenclature. Höggren *et al.* (1993) elevated the subspecies *Vipera ursinii eriwanensis* to the status of a full species, *V. eriwanensis*. This form is found at high altitudes in Armenia and neighbouring areas. Nilson *et al.* (1995) describe a population of vipers from the northern foothills of the Caucasus, formerly assigned to *V. ursinii renardi*, as the new species *V. lotievi*. This form is found in semi-arid valleys along the northern slopes of the Caucasus mountains in Russia.

A total of nine species of small vipers formerly associated with *V. ursinii*, *V. berus* and *V. kaznakovi* is now known from the general area of the Caucasus, south-eastern Europe and south-western Asia:

- *V. barani*: near Adapazari, north-western Anatolia, Turkey;
- *V. darevskii*: restricted to Dzhavakhetsky mountains, Armenian–Georgian border;
- *V. dinniki*: northern slopes of the Caucasus, from Georgia to Azarbaijan;
- *V. eriwanensis* (formerly *V. ursinii eriwanensis*): high plateaux of Armenia;
- *V. kaznakovi*: north-eastern shores of the Black Sea, at low to moderate altitudes;
- *V. lotievi*: valleys of the northern slopes of the Caucasus;
- *V. nikolskii*: region of Kharkhov, Ukraine;
- *V. pontica*: known from Coruh Valley, Artvin Province, northern Turkey;
- *V. renardi* (formerly *V. ursinii renardi*): steppes north of the Caucasus.

OTHER IMPORTANT PUBLICATIONS

A number of books providing updated information on the venomous snakes of various parts of the world has been published in recent years. In the following paragraphs, we wish to draw attention to those which we feel to be of particular value to toxinologists and physicians. These should be consulted to check the identification and distribution of venomous species.

Spawls and Branch (1995) provide the first fully illustrated guide to the venomous snakes of the entire African continent, and thus an extremely important reference for anyone carrying out research on African venomous snakes, their venoms or their bites.

Zhao and Adler (1993) produced a complete listing of the reptiles and amphibians of China and Taiwan, including information on the distribution of all species.

Warrell (1995a, 1995b) discusses the medically important species of snakes of Africa, the Middle East and Asia, and provides details on the clinical consequences of their bites and suggested treatment.

Culotta and Pickwell (1993) published a comprehensive bibliography of the venomous sea snakes, an important source of references for anyone interested in these animals.

An important checklist of the venomous snakes of the world was published by Golay *et al.* (1993). Unlike previous checklists (e.g. Harding and Welch, 1980), this checklist was produced collaboratively by a team of specialists in the venomous snake faunas of different continents, and it also includes a full synonymy of all species.

The venomous snakes of Australia are presented and illustrated in the authoritative works of Cogger (1992) (a new, fully illustrated edition of his well-known compendium), Ehmann (1992) and Mirtschin *et al.* (1990). The dangerous snakes of neighbouring Papua New Guinea are presented and described by O'Shea (1990).

Ernst (1992) provides a thorough bibliographical review of the biology of all venomous reptiles occurring in the United States and Canada. There have been few recent systematic changes concerning these animals.

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