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SYNOPSIS OF RECENT DEVELOPMENTS IN VENOMOUS SNAKE SYSTEMATICS, NO. 2

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W. Wüster, P. Golay and D. A. Warrell. Synopsis of recent developments in venomous snake systematics, No. 2. *Toxicon* **36,** 299–307, 1998.—Developments in our understanding of the systematics of venomous snakes since the beginning of 1996 are discussed and reviewed with special emphasis on their relevance and implications for toxinologists and clinicians. Groups of snakes affected by recent developments include the genera *Elapomorphus*, *Rhabdophis*, *Vermicella*, *Atheris*, *Daboia*, *Agkistrodon*/*Gloydius*, *Bothrops*/*Bothriopsis* and *Trimeresurus*. Other important publications on venomous snakes are noted. © 1998 Elsevier Science Ltd. All rights reserved

INTRODUCTION

In recent years, there has been a growing awareness among many researchers that a sound taxonomic framework is essential for toxinological research and can be of critical importance for the formulation of antivenom treatment strategies for envenomed patients (Warrell, 1986, 1997; Wüster and Thorpe, 1991; Golay *et al.*, 1993; Wüster and McCarthy, 1996). However, much of the literature on the systematics of venomous snakes is widely scattered in often rather obscure references and there is frequent disagreement between different herpetologists on the affinities of some taxa. As a result, there is obvious confusion among many biomedical workers about the nomenclature of the snakes they are working with. One consequence is that, in many cases, experimental venoms or snakes involved in accidents are mislabelled or misidentified in publications. This is often irrecoverable due to lack of relevant information (Wüster and McCarthy, 1996).

In order to aid the penetration of new systematic information into the biomedical literature, it was decided (Wüster and Harvey, 1996) to publish regular synopses of recent changes in the systematic literature in *Toxicon*, where the information will be readily accessible to researchers interested in venomous snakes and their venoms. The first of

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these synopses was published recently (Wüster *et al.*, 1997) and we hope that both it and the present, second instalment of the series will be of assistance to biomedical researchers.

We wish to re-emphasize the point that variation in venom composition is ubiquitous and that many species groups of venomous snakes remain taxonomically unresolved. It therefore remains essential that the locality of origin of snakes involved in accidents or used to produce experimental venoms be published and that the specimens involved be deposited in natural history collections where their identity can later be verified if necessary.

FAMILY COLUBRIDAE

Elapomorphus/phalotris

The genus *Elapomorphus*, as understood until recently (e.g. Golay *et al.*, 1993) comprises a group of brightly coloured, small to medium-sized South American snakes (maximum approximately 100 cm in some species). At least some species have a highly potent venom and a very serious case was described by de Lema (1978). The prolonged bite by a 20 cm specimen of what was referred to as *Elapomorphus bilineatus trilineatus* in the account resulted in severe, burning pain, swelling, hemorrhaging from the gums and the gastrointestinal tract, probable hematuria, oliguria and acute renal failure. No other cases have been reported and these snakes only bite if greatly provoked. However, the species involved, and others in the genus, as well as the closely related genus *Apostolepis*, must be regarded as potentially capable of causing fatal bites.

The genus *Elapomorphus* has recently been extensively revised by Ferrarezzi (1993) and Puorto and Ferrarezzi (1993). Ferrarezzi (1993) revalidated the genus *Phalotris* and assigned the species formerly known as *Elapomorphus bilineatus*, *E. cuyanus*, *E. lemniscatus*, *E. mertensi*, *E. punctatus* and *E. tricolor* to *Phalotris*. In addition, he described three new species in the *P. nasutus* group, *P. concolor* (northwestern Minas Gerais, Brazil), *P. lativittatus* (interior of São Paulo state, Brazil) and *P. nigrilatus* (eastern Paraguay).

Puorto and Ferrarezzi (1993) describe a further species of the *bilineatus* group of this genus, *P. multipunctatus*, from the states of São Paulo and Mato Grosso do Sul, Brazil. The taxon involved in the bite related by de Lema (1978) is now regarded as a subspecies of *Phalotris lemniscatus* (de Lema, 1984). The nomenclature of the *P. bilineatus* group requires clarification: de Lema (1984) used the name *E. spegazzinii* for what was hitherto known as *E. bilineatus*. This was followed by Golay *et al.* (1993), but not by Ferrarezzi (1993) and Puorto and Ferrarezzi (1993).

Rhabdophis

Zhao (1997a) described a new species of *Rhabdophis* from the island of Hainan. *Rhabdophis adleri* is most similar to *R. chrysargos* and references to the occurrence of the latter on Hainan in fact concern the new species. No human accidents involving this species have been documented but the species *R. subminiatus* and *R. tigrinus* have caused serious and, in the case of the latter, fatal envenoming in man (Mittleman and Goris, 1974, 1978; Minton and Mebs, 1978; Ogawa and Sawai, 1986; Minton, 1990; Zotz *et al.*, 1991; Hoffmann *et al.*, 1992; Warrell, 1995).

FAMILY ELAPIDAE

Micropechis

Recent clinical work in Papua New Guinea (Warrell *et al.*, 1996) has resulted in an appreciation of the medical importance of the New Guinea small-eyed snake (*Micropechis ikaheka*). The taxonomy of this species is largely uncontroversial, although the subspecies *M.i. fasciatus* was recognised from the Aru Islands in the older literature. This species is found in New Guinea and surrounding islands, including Aru, Batanat, Jobi, Kar Kar, Mansinam, Mefoor, Mios Num, Misool and Walis (Golay *et al.*, 1993; O'Shea, 1996). The 'shark of the jungle', or Solomons small-eyed snake (*Loveridgelaps elapoides*), from the Solomon Islands, was formerly regarded as belonging to the genus *Micropechis*. Further information on both species can be found in O'Shea (1996).

Vermicella

Keogh and Smith (1996) analysed the systematics of the genus *Vermicella*, a group of small Australian elapids. Prior to their study, two species were widely recognised: *V. annulata* and *V. multifasciata* (e.g., Cogger, 1992). Keogh and Smith show that the form previously known as *V. annulata* actually comprises 4 separate species, *V. annulata* (eastern third of Australia), *V. snelli* (northern Western Australia), the new species *V. intermedia* (northwestern Northern Territory, northeastern Western Australia), and another new species, *V. vermiformis* (southern Northern Territory). These snakes are inoffensive and of no clinical importance, but their venoms remain largely unstudied.

FAMILY VIPERIDAE

Atheris

Broadley (1996), following the conclusions of Groombridge (1987) and Herrmann (1995), described two new genera to accommodate two species previously classified as part of *Atheris*: the species previously known as *Atheris superciliaris* becomes *Proatheris superciliaris* and the species previously known as *Atheris hindii* becomes *Montatheris hindii*. Neither species is of great medical importance.

Trape and Roux-Estève (1995) revived *Atheris laeviceps*. This taxon is a junior synonym of *Atheris squamigera anisolepis*; therefore *anisolepis* is elevated to the rank of full species. The species currently included in the genus *Atheris* are thus the following: *A. anisolepis*, *A. ceratophora*, *A. chloroechis*, *A. desaixi*, *A. hispida*, *A. katangensis*, *A. nitschei* and *A. squamigera*.

Daboia russelii

Belt *et al.* (1997) review the distribution of Russell's viper in Indonesia and provide evidence of the great importance of this species as a cause of snakebite morbidity and mortality in Indonesia. The species appears to be more widespread than previously thought in East Java and on Flores and also occurs on the islands of Solor and Adonara, where it had not been previously recorded.

Agkistrodon/Gloydius

Kraus *et al.* (1996), Cullings *et al.* (1997), Parkinson *et al.* (1997) and Vidal *et al.* (1997) independently used DNA sequence information from three different parts of the mitochondrial genome to analyse the phylogeny of the pitvipers, with particular empha-

sis on the snakes referred to as the '*Agkistrodon* complex', i.e. those rattleless pitvipers with large head shields which were formerly united in the genus *Agkistrodon*.

Previous studies had split several forms off *Agkistrodon* into the genera *Calloselasma*, *Deinagkistrodon* and *Hypnale* and these changes have been widely accepted; however, the status of several Asiatic species, including medically important forms such as *Agkistrodon blomhoffii* and *A. halys* had remained uncertain: some authors continued to regard them as belonging to the genus *Agkistrodon* (e.g. Gloyd and Conant, 1990), whereas others assigned them to the genus *Gloydius* (e.g. Hoge and Romano-Hoge, 1978/1979).

The results of Kraus *et al.* (1996), Parkinson *et al.* (1997) and Vidal *et al.* (1997) confirm the distinctness of *Calloselasma*, *Deinagkistrodon* and *Hypnale*. All four studies show clearly that the remaining Old World *Agkistrodon* are not closely related to the New World *Agkistrodon*; consequently, the genus *Gloydius* should be recognised for the Old World species. *Gloydius* thus contains the species *blomhoffii*, *halys*, *himalayanus*, *intermedius*, *monticola* (not to be confused with *Ovophis monticola*, formerly known as *Trimeresurus monticola*, a totally different species), *saxatilis*, *shedaoensis*, *strauchi*, *tsushimaensis* and *ussuriensis*. For a discussion of the species-level systematics of this genus, see Wüster *et al.* (1997a).

Bothrops and Bothriopsis

Salomão *et al.* (1997) used mitochondrial DNA sequence information to infer the phylogeny of a number of neotropical pitvipers. In their analysis, it was shown that the genus *Bothrops* (*sensu* Campbell and Lamar, 1989) is paraphyletic with respect to *Bothriopsis taeniata*. *Bothriopsis taeniata* was found to be more closely related to some species of *Bothrops* (e.g. *B. atrox*, *B. jararacussu*) than these were to other species of *Bothrops* (e.g. *B. alternatus*).

These results confirm previous studies by Werman (1992) and Cadle (1992), based on morphological data, isozyme analysis and immunological distances. In addition, Werman (1997) analysed lactate dehydrogenase isozyme variation in a number of species of pitviper and also found no consistent differences between *Bothriopsis taeniata* and various species of *Bothrops*. However, he did find consistent differences between *B. taeniata* and three species of the genus *Bothriechis*, providing further evidence to contradict Schätti *et al.* (1990), who synonymised *Bothriopsis* with *Bothriechis*: these two arboreal lineages are almost certainly unrelated. This is also confirmed by the mitochondrial DNA analyses of Kraus *et al.* (1996) and Vidal *et al.* (1997).

In view of the consensus of evidence suggesting that *Bothriopsis* is rooted within the genus *Bothrops*, some adjustments of the nomenclature are necessary in order to recognise only monophyletic taxa. This would require either a split of *Bothrops* into several smaller genera, or the synonymization of *Bothriopsis* with *Bothrops*. Since the former option would involve changes to the names of a number of clinically and toxinologically important species, (e.g. *Bothrops alternatus*, *B. jararaca*), the latter option was preferred by Salomão *et al.* (1997): the species previously assigned to *Bothriopsis* are generally rare and of relatively little clinical or toxinological importance, so that name changes would cause little confusion. Consequently, all species previously assigned to *Bothriopsis* were reassigned to *Bothrops*.

Bothrops atrox group

The problems of species definition in the *Bothrops atrox* complex were addressed by Wüster *et al.* (1996, 1997a). These authors investigated patterns of variation in morphology in populations assigned to the nominal species *B. atrox*, *B. isabelae*, *B. leucurus*, *B. marajoensis*, *B. moojeni*, and *B. pradoi* and inferred the population phylogeny of the complex by means of mitochondrial DNA sequence analysis. Morphologically, the populations commonly referred to *B. moojeni* are distinct from all other populations; the remaining species are not clearly distinct. Where the range of *B. moojeni* meets that of *B. atrox*, a number of morphologically intermediate populations occur. The mtDNA phylogeny shows that none of the conventional species represents a discrete evolutionary lineage: the conventional species are either heterogeneous or represent localised populations. However, it is as yet unclear whether this complex can be treated as a single species, or whether several species should be recognised. Further work is in progress.

In most toxinological studies, the conventional species of the *Bothrops atrox* group have been treated as discrete entities; however, it is clear from this study that this is an erroneous assumption. While there is currently no new taxonomic framework in place for these snakes, it is important to emphasise that the conventional species names are not adequate as labels for venoms or snakes. In order to allow current clinical and toxinological work to be related to future developments in the systematics of these snakes, it is essential that precise locality data be obtained and published in all work dealing with these snakes and their venoms. There is currently no evidence of sympatry between different forms of the *B. atrox* complex, so that an indication of locality will unambiguously allow toxinological data to be reconciled with future taxonomic developments.

Trimeresurus

In a very valuable piece of work, David and Tong (1997) prepared a translation of recent descriptions of new taxa of the *Trimeresurus* complex from China and Tibet. A number of taxa have been described in the Chinese literature in recent years, but, for linguistic reasons, had remained largely inaccessible to non-Chinese researchers. Some had previously been illustrated in Zhao and Adler (1993), but no description in a language using the Latin alphabet had been published. The papers covered include Djao and Jiang (1977) (description of *T. monticola zayuensis* [now part of genus *Ovophis*] and *Trimeresurus medoensis*, both from Tibet), Zhao *et al.* (1978) and Zhao (1979) (description of *T. xiangchengensis*, from Sichuan Province, China), Huang (1982) (description of *T. tibetanus*, from Tibet), Zhao and Chen (1990) and Chen (1990) (description of *T. mangshanensis*, from Hunan Province, China), Zhao (1995a) (description of the subspecies *T. stejnegeri chenbihuii* [from Hainan, of doubtful validity according to David and Tong, 1997] and *Ovophis monticola zhaokentangi* from Yunnan). A second translation of Zhao (1995a) appeared in Zhao (1997b). In addition, Zhao (1995b) raised the subspecies *Ovophis monticola zayuensis* and *Trimeresurus stejnegeri yunnanensis* to the status of full species. *Trimeresurus mangshanensis* was transferred to its own monotypic genus, *Ermia*, by Zhang (1992, 1993), but this was not followed by Zhao and Adler (1993) and Golay *et al.* (1993).

Most of these new species appear to have highly localised ranges, generally at high altitudes and are thus unlikely to be of any great medical significance. However, *Trimeresurus/Ermia mangshanensis* grows to lengths of over 2 m and must be presumed to be highly dangerous. Nothing is known of the venoms of these forms.

In addition to the translations, David and Tong (1997) also provide annotations to the translations and a key to the species of the *Trimeresurus* group currently known to exist in China (including Taiwan, Hong Kong and Macau) and Tibet, as well as species known to occur in the immediate vicinity of these two countries but not recorded from within their borders.

Malhotra and Thorpe (1997) present a preliminary analysis of the phylogeny of the genus *Trimeresurus*, with particular emphasis on the green species, which have traditionally been a source of much taxonomic confusion (Warrell, 1986; Hutton *et al.*, 1990; Wüster *et al.*, 1997a). A phylogenetic hypothesis based on restriction fragment analysis of a PCR-amplified fragment of the mitochondrial cytochrome *b* gene suggests the existence of several hitherto undescribed species of *Trimeresurus*: *Trimeresurus stejnegeri* may be polyspecific; a red-eyed form from northern Thailand, which is generally similar to *T. albolabris*, may belong to an as yet undescribed species and *T. purpureomaculatus* from the Andaman Islands was found to be unrelated to *T. purpureomaculatus* from Malaysia, again suggesting that they are not conspecific. Clearly, many problems remain with the systematics of the genus *Trimeresurus*, especially the green forms, and their classification may remain labile for some years. Further work on this group is in progress.

The green *Trimeresurus* thus continue to present a number of problems for toxinologists and clinical researchers: most species are extremely similar to each other and are almost impossible to distinguish without detailed anatomical examination; several species coexist in many localities, so that an indication of the locality of origin of a specimen will often be insufficient to ensure identification and several undescribed and unnamed species remain to be found in the genus. It is therefore essential that clinicians and venom suppliers endeavour to preserve any specimens involved in snakebite accidents or used for venom production and deposit them in natural history collections, so that their identity can be verified.

Kraus *et al.* (1996), using mtDNA sequence analysis, found that some of the large, terrestrial species normally assigned to *Trimeresurus* (*T. flavoviridis*, *T. elegans*) do not group with the remaining species of *Trimeresurus* included in their study. This may require these species (and presumably also the species *jerdoni*, *kaulbacki*, *mucrosquamatus*, *strigatus* and *tokarensis* as well as some of the new Chinese taxa mentioned earlier) to be transferred to the genus *Protobothrops*. This genus was described by Hoge and Romano-Hoge (1981), but has not been widely recognised until now.

OTHER PUBLICATIONS

David and Vogel (1996) present the first treatment on the snake fauna of Sumatra. The book includes a key to the species, a synonymy for each species (with taxonomic comments in some cases) and information on distribution. A few venomous species are illustrated.

Lee (1996) presents a monograph on all the amphibians and reptiles of the Yucatán Peninsula, with descriptions, information on distribution and keys to the families, genera and species.

O'Shea (1996) provides the first comprehensive guidebook to the snakes of Papua New Guinea. All medically important species and most of the less dangerous venomous species are illustrated. This is an important reference for anyone contemplating medical studies in Papua New Guinea and adjoining territories.

The first available monograph on the New World coral snakes has appeared in the shape of Roze (1996). It covers most aspects of the biology of the genera *Micrurus*, *Leptomicrurus* and *Micruroides* and in particular their identification and classification. The genus *Leptomicrurus* was regarded as a synonym of *Micrurus* by Slowinski (1995). The 3 species included in *Leptomicrurus* (*collaris*, *narduccii* and *scutiventris*) may thus be found in the literature under either this genus or *Micrurus*.

Schleich *et al.* (1996) provide a guide to the reptiles and amphibians of northern Africa (defined as Morocco, Algeria, Tunisia and Libya, but excluding Egypt). Venomous snakes are included. Points of note include the recognition of *Echis arenicola* for the *Echis* populations of western North Africa. Other recent reviewers have not recognised this form as distinct from *E. pyramidum* (e.g. Golay *et al.*, 1993; Spawls and Branch, 1995).

A symposium volume edited by Thorpe and Malhotra (1997) contains a number of papers dealing with the interrelationships between snake systematics, evolution, venom variation and toxinology, as well as other snake and venom-related papers. Several of the papers have been discussed individually in this review.

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