Population systematics of Russell's viper: a multivariate study

WOLFGANG WÜSTER, SATOKO OTSUKA*, ANITA MALHOTRA AND ROGER S. THORPE

Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TN, Scotland

A multivariate analysis of the population systematics of Russell's viper, based on scalation and colour pattern characters, reveals that the populations of this viper constitute two well-defined taxa: a western form, comprising all populations from the Indian subcontinent, and an eastern form, comprising all populations from east of the Bay of Bengal. The two forms could be considered either as subspecies of one species, or as two separate species, depending on the species concept used. Within the western form, there is no clear pattern of geographic variation. Within the eastern form, the populations from the Lesser Sunda Islands are clearly divergent from the populations of mainland Asia and Java. The conventionally recognized subspecies of *Vipera russelli* fail to portray this pattern of geographic variation. There is no clear relationship between the pattern of geographic variation in morphology and the pattern of geographic variation in the clinical effects of the venom in human bite victims: some populations with considerable differences in venom effects are equally distinct morphologically, whereas other populations with equally strong venom differences are morphologically very similar. The distribution of Russell's viper can be attributed to Pleistocene changes in climate and sea level, coupled with the viper's ecological requirements, which appear to include a seasonally dry climate.

KEY WORDS:—Serpentes – *Vipera russelli* – population systematics – geographic variation – snakebite – venom – Asia – multivariate analysis – biogeography – subspecies.

CONTENTS

INTRODUCTION

Russell's viper, *Vipera russelli* (Shaw), is one of the most widely known and most widespread Asiatic venomous snakes. Its range extends from Pakistan to Sri

*Present address: 4-9-7 Asahigaoka, Yotsukaido City, Chiba 284, Japan.

97

Lanka, Taiwan and southern Indonesia, including India, Bangladesh, Burma, Thailand, western Cambodia and parts of mainland China (Fig. 1A). Its distribution is remarkably discontinuous: while it occurs more or less throughout India, its range is discontinuous in China and Indo-China, and it is completely absent from the Malayan Peninsula, Sumatra, Borneo and most of Java; it reappears in eastern Java, and on Komodo, Flores and Lomblen.
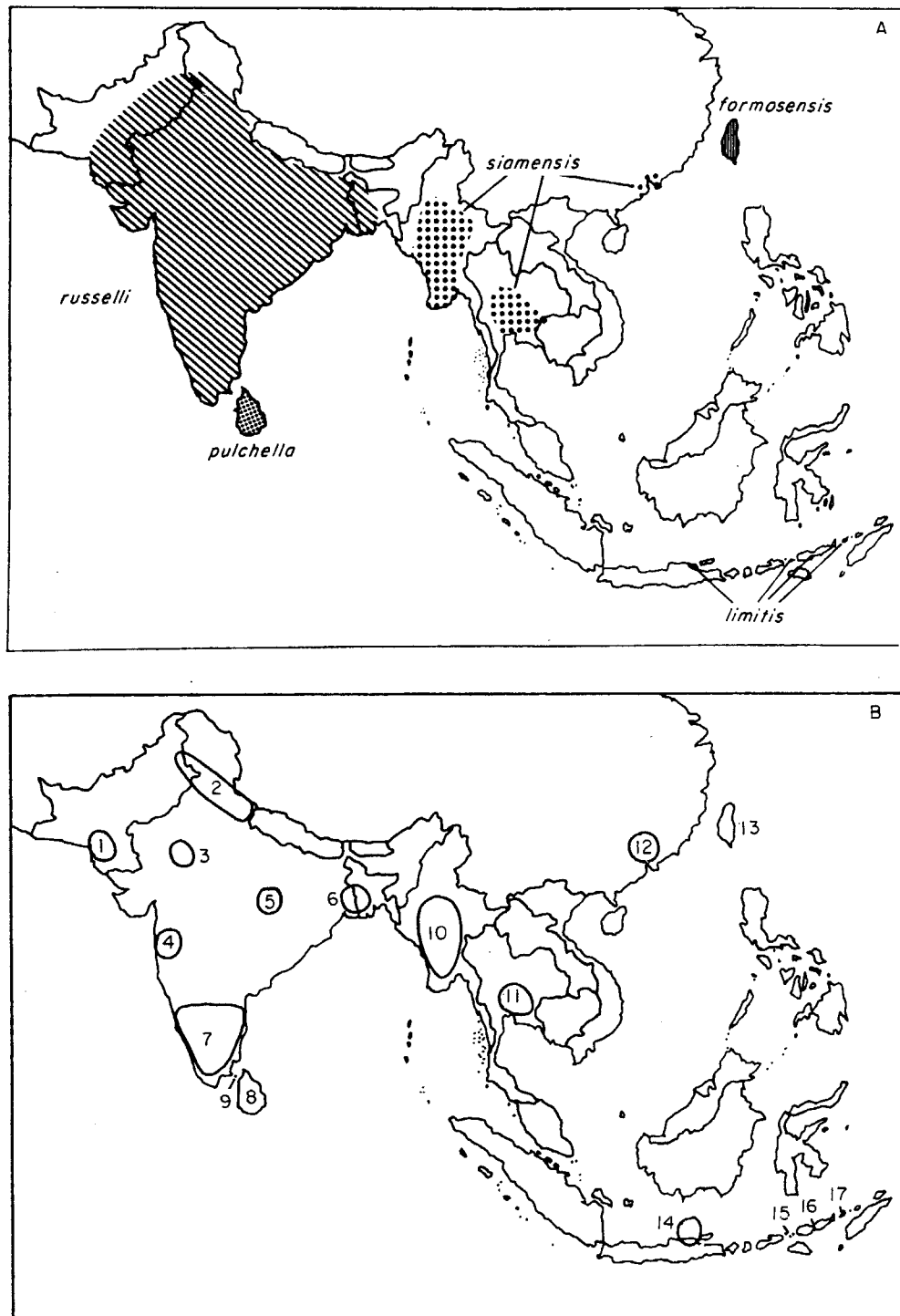

Figure 1. A, Distribution of the conventional subspecies of *Vipera russelli*. Note the extreme discontinuity between the various populations. B, Localities of the operational taxonomic units used in this study.

Most authors (e.g. Harding & Welch, 1980; Leviton, 1968) recognize five subspecies of Russell's viper: *V. r. russelli* (Shaw, 1797) from India, Pakistan and Bangladesh; *V. r. pulchella* (Gray, 1842) from Sri Lanka; *V. r. siamensis* Smith, 1917, from Burma, Thailand, Cambodia and southern China; *V. r. formosensis* Maki, 1931, from Taiwan; and *V. r. limitis* Mertens, 1927, from Java, Komodo, Flores and Lomblen (Fig. 1A). In addition, Kopstein (1936) described the Javan populations as *V. r. sublimitis*, and Deraniyagala (1945) the northern Indian populations as *V. r. nordicus*. The subspecies *V. r. sublimitis* was recognized by van Hoesel (1954, 1958), but *V. r. nordicus* has been ignored by subsequent workers. These subspecies were defined primarily on the basis of the number of rows of dorsal spots, and a few other colour pattern characters; in some cases purported differences, especially in the number of rows of dorsal spots, were artefacts, caused by a misinterpretation of previous published descriptions (Brongersma, 1958). The pronounced similarity between some populations assigned to different subspecies has been noted (Brongersma, 1958; Warrell, 1989).

Thorpe (1980, 1984, 1987) has discussed the shortcomings of conventional subspecies defined on the basis of single characters: different characters may display different patterns of geographic variation, so that subspecies defined on the basis of variation in one character will not predict the pattern of variation exhibited by other characters. Consequently, such conventional subspecies are likely not to represent coherent evolutionary groups, thereby obscuring the actual pattern of geographic variation. Thus, their usage impedes the understanding of the population evolution of the group concerned.

It has been proposed that Russell's viper, and other large species generally assigned to the genus *Vipera* (e.g. *V. lebetina, V. palaestinae, V. xanthina*), should be reassigned to the genus *Daboia* Gray (Obst, 1983). We do not regard this matter as finally settled. Since the question of the relationships between Russell's viper and other viperids is irrelevant in the context of this study, we prefer a conservative approach, and will therefore refer to the species as *Vipera russelli*.

Owing to its occurrence in agricultural areas (especially rice fields), its excellent camouflage, uncertain temper and potent venom, Russell's viper is a major cause of snakebite morbidity and mortality in many areas, such as India (Matthai & Date, 1981), Sri Lanka (Phillips *et al.*, 1988; de Silva, 1981, 1990; de Silva & Ranasinghe, 1983), Burma (Aung-Khin, 1980; Myint-Lwin *et al.*, 1985), Thailand (Looareesuwan, Viravan & Warrell, 1988; Sawai *et al.*, 1972) and parts of Indonesia (Auffenberg, 1980). However, it does not appear to be an important cause of snakebite in Taiwan (Kuo & Wu, 1972; Sawai *et al.*, 1972). The clinical manifestations of Russell's viper bite vary enormously, depending on geographical area (Warrell, 1989). As a result, antivenoms produced on the basis of venom from specimens from one area may be ineffective against the venoms of specimens from other areas, even within the generally accepted subspecies.

In several groups of venomous snakes, it has been found that venom differences correspond to taxonomic differences. Well-known examples include the carpet viper (*Echis carinatus*) complex (Mebs & Kornalik, 1981; Warrell & Arnett, 1976), and the Asiatic cobras of the *Naja naja* species complex (Warrell, 1986; Wüster & Thorpe, 1989, 1991). These examples show how variation in venom composition and effects can parallel variation in morphology, and how an understanding of the population systematics of a group of venomous snakes is essential for the efficient use and production of antivenoms. In Russell's viper,

the link between venom variation and morphological variation has been stated to be very weak (Anonymous, 1985; Warrell, 1989). However, we have recently shown that morphological differences between the Thai and Burmese populations, which exhibit major differences in venom effects, were much more important than had been previously realized (Wüster et al., 1992).

The aim of this study is to elucidate the pattern of geographic variation in *Vipera russelli* across its entire range, using multivariate morphometrics; to test the validity of the conventional subspecies against the pattern of geographic variation; and to relate the geographic variation in bite symptoms reported in the literature to the pattern of geographic variation in the morphology of the species.

MATERIALS AND METHODS

Materials and characters

This study is based on the analysis of morphological characters recorded from preserved museum material. A total of 225 specimens was borrowed from a number of museums in Europe and North America. After the elimination of badly damaged specimens, and specimens with dubious locality records, 208 specimens were left for use in the analyses.

The characters used for analysis were taken from the scalation and colour pattern of the animals, and are listed in Table 1. In order to record the position of characters along the body of the snakes, the ventral scales were numbered from the head to the vent, according to the method of Dowling (1951). The position of a character along the body is recorded as the position of the ventral scale at the level of which it is situated. This is then converted to %ventral scale (%VS) position in order to compensate for variation in the number of ventral scales. Similarly, the relative length of a character is recorded as the number of

TABLE 1. Characters used

1.	Number of ventral scales.
2.	Number of subcaudal scales.
3.	Number of dorsal scale rows at 25% VS length.
4.	Number of dorsal scale rows at 50% VS length.
5.	Number of dorsal scale rows at 75% VS length.
6.	Number of dorsal scale rows at 100% VS length.
7.	Number of upper labials.
8.	Number of lower labials.
9.	Number of scales contacting orbit.
10.	Number of scales between the supraoculars.
11.	Number of scales between the anterior chin shields and the first ventral scale.
12.	Number of scales contacting the rostral scale.
13.	Number of lateral spots between the head and the anus.
14.	Number of rows of spots on dorsum at 50% VS length.
15.	Number of dark spots on the five ventral scales following 50% VS length.
16.	% Lower labials with a dark spot.
17.	% DS width of median dorsal spot at 50% VS length.
18.	% DS width of lateral spot at 50% VS length.
19.	% VS length of lateral spot at 50% VS length.
20.	% DS height of upper edge of lateral spot at 50% VS length.
21.	Width in scale rows of lateral spots on head.
22.	Number of scales between lateral head spots at their closest point.

ventral scales along which it extends, and this is then converted to %ventral scale (%VS) length. The width or height of colour pattern characters on the dorsum of the specimens is recorded as the number of dorsal scale rows on which they encroach. This is then expressed as a percentage of the number of dorsal scale rows at the level of the character (%DS width). See Thorpe (1975) for more details on the recording of morphometric characters from snakes.

Selection of operational taxonomic units

When analysing patterns of geographic variation, it is essential to discriminate between taxonomically relevant variation due to geographic differences, and taxonomically irrelevent within-locality variation. This requires the specimens to be grouped into geographic samples, generally referred to as operational taxonomic units (OTUs).

In studies relying on museum material, which often originates from widely scattered localities, it is necessary to pool specimens from more than one locality in order to maximize OTU size. In this study, such OTUs were initially defined on the basis of collecting gaps, and hypothesized physiographic distribution barriers. When pooling specimens from more than one locality, it is essential to avoid the formation of OTUs which contain geographic variation within them, as this would obscure the pattern of geographic variation to be elucidated. Similarly, it is important to avoid pooling specimens of different, sympatric species in one OTU. The presence of sympatric species may not always be obvious without multivariate analysis (see Thorpe & McCarthy, 1978, for an example).

Single-linkage cluster analysis of cases was used to test for geographic heterogeneity within the putative OTUs. If a proposed OTU appeared to contain geographic variation, it was split into separate OTUs, one for each apparent phenotype. The sexes were analysed separately. The final OTUs are mapped in Fig. 1B, and listed, with sample sizes, in Table 2.

TABLE 2. OTUs and sample sizes

		Sample size	
		Males	Females
1.	Sind Province, Pakistan	15	13
2.	Northern India and northern Pakistan	7	2
3.	Ajmer, Rajasthan, India	1	0
4.	Maharashtra State, India	1	1
5.	Mungeli, Madhya Pradesh, India	1	0
6.	West Bengal (India) and Bangladesh	1	2
7.	Southern India	8	5
8.	Sri Lanka	10	8
9.	Rameswaram, Pamban Island, Palk Strait, India	1	0
10.	Southern Burma	17	15
11.	Central Thailand	10	9
12.	Guangdong Province, China	1	0
13.	Taiwan	9	8
14.	Java, Indonesia	3	2
15.	Komodo Island, Indonesia	35	18
16.	Flores Island, Indonesia	0	3
17.	Lomblen Island, Indonesia	0	2

Multivariate techniques

Two main multivariate methods were used to investigate the population systematics of Russell's viper: principal components analysis (PCA) and canonical variate analysis (CVA). Canonical variate analysis, run on substantial numbers of OTUs, was used in order to elucidate general patterns of geographic variation, whereas PCA, run on individual specimens in situations where only the specimens of very few OTUs were involved, was used to investigate the relationships between pairs of adjoining populations (see Wüster *et al.*, 1992). In addition, PCAs of the OTU means of each character were run in order to test the results of the CVAs.

The following CVAs were run:

CVA 1a: all male OTUs, using characters 1–13, 15–22.

CVA 1b: all female OTUs, using characters 1–7, 9–12, 15–22.

CVA 2a: male OTUs from west of the Bay of Bengal (1–9), using characters 1–13, 15–22.

CVA 2b: female OTUs from west of the Bay of Bengal (1, 2, 4, 6, 7 and 8), using characters 1–7, 9–12, 15–22.

CVA 3a: male OTUs from east of the Bay of Bengal (10–15), using characters 1–13, 15–22.

CVA 3b: female OTUs from east of the Bay of Bengal (10, 11, 13–17), using characters 1–7, 9–12, 15–22.

The following PCAs were run, in order to test the validity of the Sri Lankan subspecies *V. r. pulchella*:

PCA 1a: male specimens from southern India, Sri Lanka and Pamban Island (OTUs 7–9), using characters 1–13, 15–22.

PCA 1b: female specimens from southern India and Sri Lanka (OTUs 7 and 8), using characters 1–13, 15–22.

Character 14 (the number of rows of dorsal spot rows) was not included in any of the analyses listed here. This character is unsuitable for use in CVAs, because it exhibits no variation within the OTUs used, and characters with zero within-group variation cannot be used in this technique. This character was used in PCAs of sample means (not described here in detail), which were employed to test the results of the CVAs.

RESULTS

The canonical analyses run on all OTUs (CVA 1a and 1b, Fig. 2) reveal that the populations of *Vipera russelli* constitute two distinct, geographically coherent forms: a western form, with a range extending from Pakistan to Bangladesh and south to Sri Lanka, and an eastern form, with a highly discontinuous range, which includes Burma, parts of Thailand, parts of southern China, Taiwan, and the Indonesian islands of Java, Komodo, Flores, Ende and Lomblen (Fig. 3).

The CVAs run on the OTUs from west of the Bay of Bengal (CVA 2a and 2b, Fig. 4) do not reveal a very clear pattern of geographic variation within the western form; CVA 2a suggests some subtle differentiation between northern and southern populations, the northern populations having generally higher
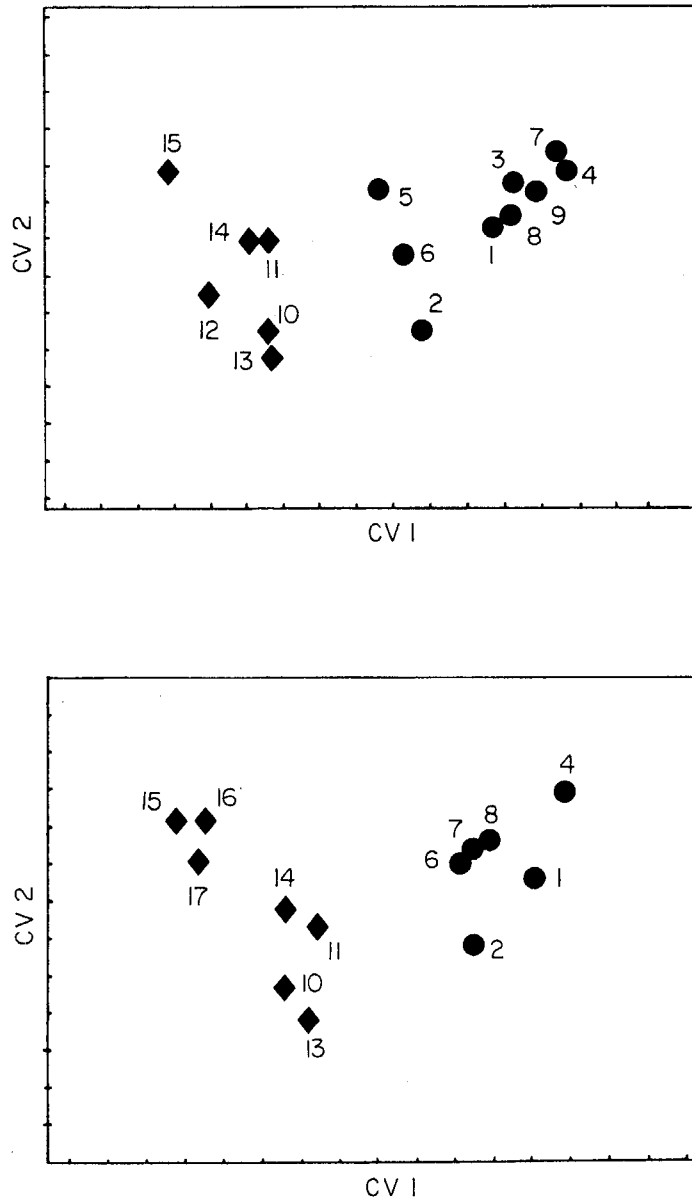
Figure 2. Canonical variate analysis of all populations: ordination of the male (CVA 1a, top) and female (CVA 1b, bottom) OTUs along the first two canonical variates. Circles indicate populations from west of the Bay of Bengal, diamonds populations from east of the Bay of Bengal. OTU numbers correspond to those in Fig. 1B. The axes are graded in units of within-group standard deviation.

scores along the first and second canonical variates than the southern populations. In female specimens (CVA 2b), the trend is less clear, although southern specimens tend to have, on average, lower scores along either the first or the second canonical variates.

The CVAs run on the OTUs from east of the Bay of Bengal (CVA 3a and 3b, Fig. 5) divide the eastern form into two distinct subgroups, one consisting of the populations from the Asian mainland, Taiwan and Java, the other of the populations from the Lesser Sunda Islands of Komodo, Flores and Lomblen.

The principal components analyses, PCA 1a and 1b, do not reveal any differentiation between the populations from southern India and Sri Lanka (Fig. 6).
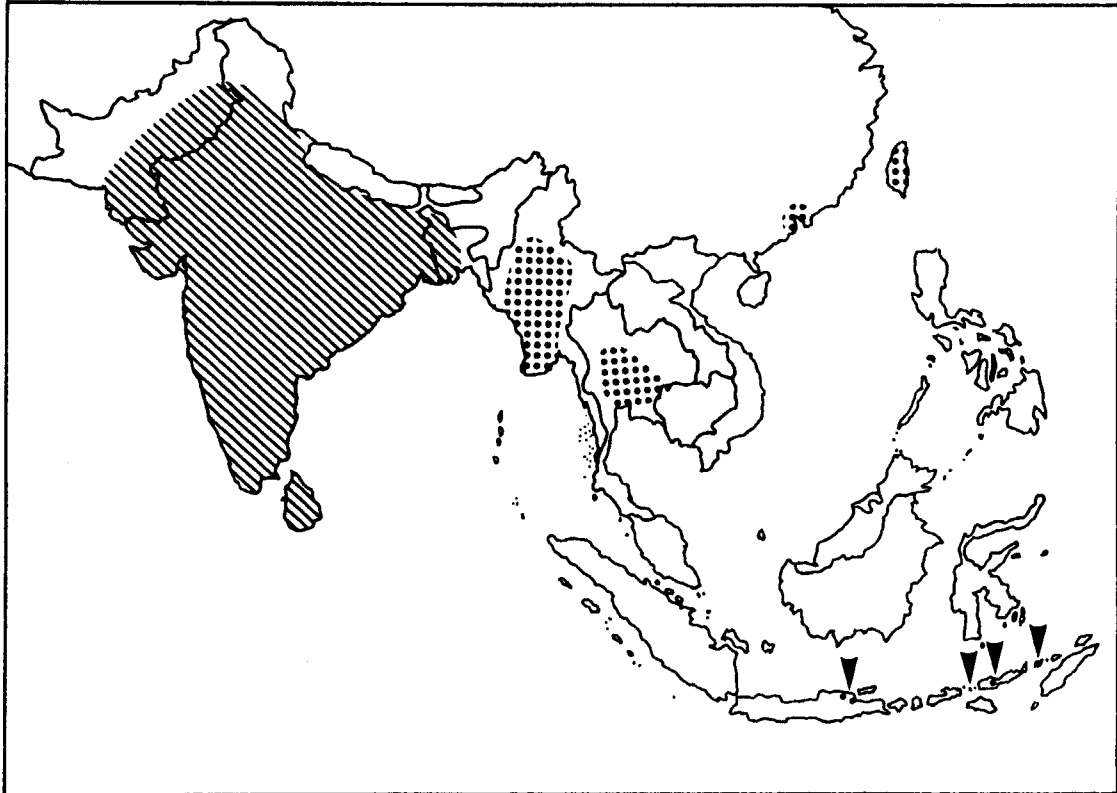
Figure 3. Distribution of the western and eastern forms of Russell's viper. Diagonal hatching indicates the distribution of the western taxon, speckling the distribution of the eastern taxon. Arrows point to the small relict distribution of the eastern form in southern Indonesia.

DISCUSSION

Population systematics and nomenclature

The dominant feature of the pattern of geographic variation in Russell's viper is the differentiation between the western and eastern populations; populations from west of the Bay of Bengal constitute the western form, those from east of the Bay of Bengal the eastern form (Figs 2, 3).

In order to visualize the relationship between the eastern and western forms, a longitudinal transect was plotted across the range of Russell's viper, and the mean score of each OTU along the first canonical variate was plotted against the longitude of the OTU (Fig. 7). The result shows a clear step between the western form, and the western populations of the eastern form. There is some indication of clinical variation in the western form, but the magnitude of the step is such that the two forms must be regarded as clearly distinct. There can be no question of an interrupted gradual cline.

The taxonomic rank of these forms, i.e. whether they should be regarded as subspecies or as separate species, depends on the species concept used. Since the two forms are allopatric, there can be no conclusive evidence of reproductive isolation, or lack thereof. Consequently, the biological species concept, which relies on this criterion, is inoperative in this situation. Adherents of the phylogenetic species concept would split Russell's viper into two species (Cracraft, 1989) on the basis of the evidence presented here. In our opinion, an understanding of the pattern of geographic variation in this group is more
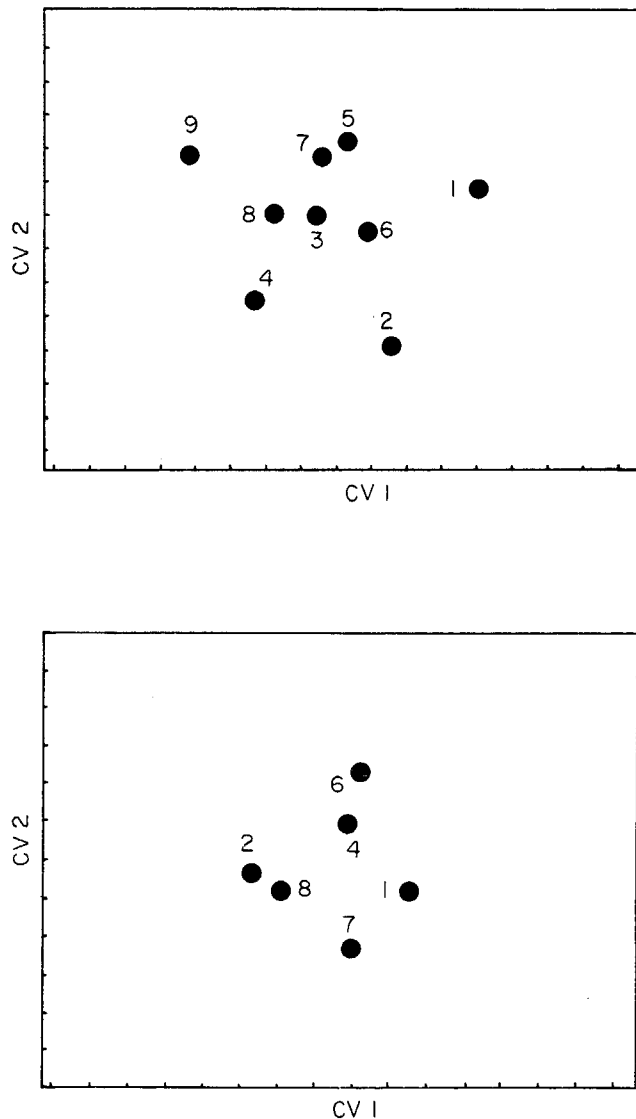
Figure 4. Canonical variate analysis of the western populations: ordination of the male (CVA 2a, top) and female (CVA 2b, bottom) OTUs along the first two canonical variates. OTU numbers correspond to those in Fig. 1B. The axes are graded in units of within-group standard deviation.

important than a decision on taxonomic rank, which is dictated by a subjective decision on the species concept to be used. Further studies on the population systematics of the *V. russelli* group are currently in progress and we therefore feel that it would be premature to definitively alter the nomenclature at this time. The confusion that would result in the biomedical literature from a formal split of Russell's viper into two species makes a conservative approach particularly important in this case. Consequently, we prefer to avoid a definitive alteration of the taxonomy of this species, for the time being, and propose a conservative approach, in which the Russell's viper group is regarded as a single species with two subspecies, *V. r. russelli* being the western form and *V. r. siamensis* the eastern form.

As in other groups of snakes, such as *Natrix natrix* (Thorpe, 1979) or the Asiatic cobra complex (Wüster & Thorpe, 1989, 1991) the conventional subspecies of *V. russelli* have failed to portray the pattern of geographic variation in this species. The Sri Lankan population, conventionally classified as a separate
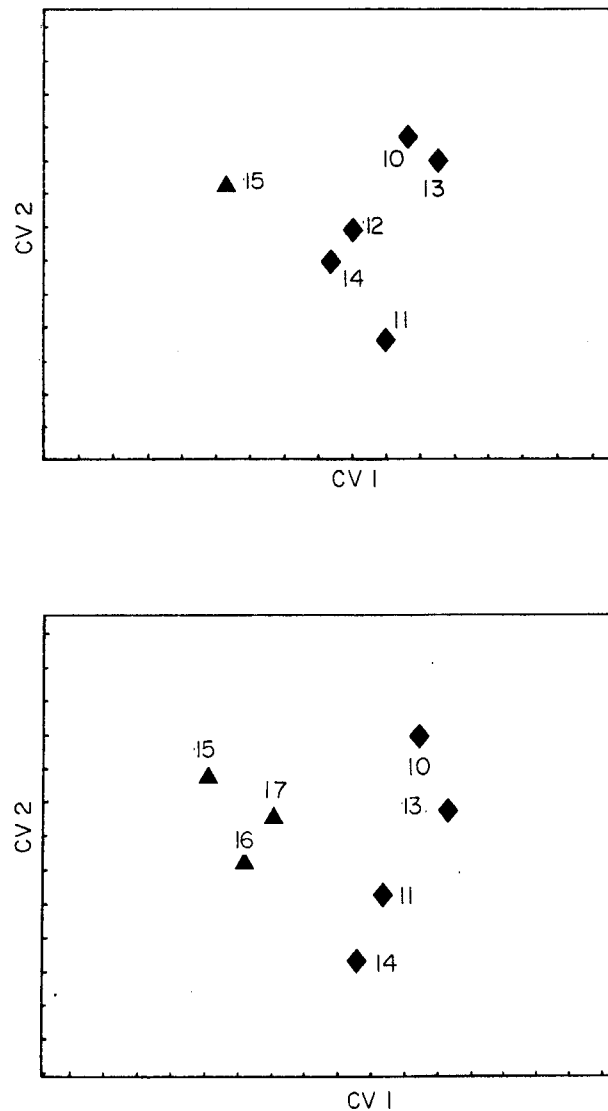
Figure 5. Canonical variate analysis of the eastern populations: ordination of the male (CVA 3a, top) and female (CVA 3b, bottom) OTUs along the first two canonical variates. Diamonds correspond to populations from the Asian mainland, Taiwan and Java, triangles to populations from the Lesser Sunda Islands. OTU numbers correspond to those in Fig. 1B. The axes are graded in units of within-group standard deviation.

subspecies, *V. r. pulchella*, is shown by PCAs 1a and 1b to be virtually indistinguishable from the southern Indian populations, which include those from the type locality of *V. russelli*, the Coromandel Coast of south-eastern India. While there appears to be some north-south differential in the western form, this is weak, and does not justify the recognition of *V. r. nordicus* Deraniyagala. Consequently, both the subspecies *nordicus* and *pulchella* are here regarded as synonyms of *V. r. russelli*.

In the eastern form, the subspecies *V. r. formosensis* Maki is clearly no more distinct from the Thai, southern Chinese and Burmese populations, which are conventionally classified as *V. r. siamensis* Smith, than these are from each other. The fact that the populations from Burma and Thailand, which are conventionally grouped together as *V. r. siamensis*, are quite distinct (Wüster
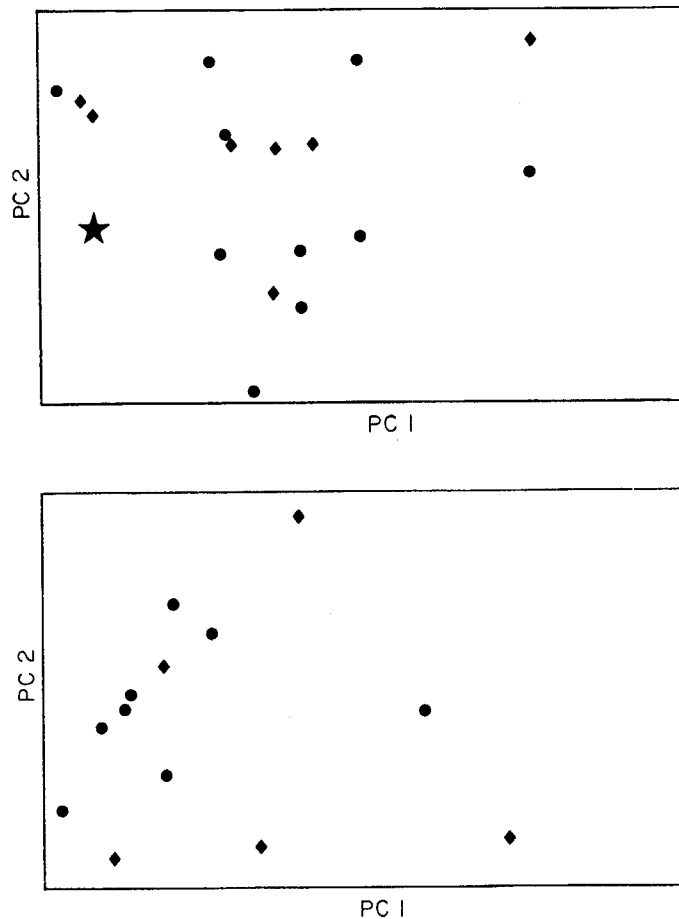
Figure 6. Principal components analysis of individual specimens from southern India and Sri Lanka: ordination of male (PCA 1a, top) and female (PCA 1b, bottom) specimens along the first two principal components. Circles indicate specimens from Sri Lanka, diamonds specimens from southern India, and the star a specimen from Pamban Island, situated in the Palk Strait, between India and Sri Lanka.

et al., 1992), whereas the populations from southern India and Sri Lanka, conventionally assigned to separate subspecies, are virtually indistinguishable, provides a particularly telling illustration of the inadequacy of conventional subspecies, based on perceived differences in single characters.

The Lesser Sunda Island populations, conventionally classified as *V. r. limitis*, are distinct from the remaining eastern populations, but interestingly, the Javan populations, assigned to *V. r. limitis* by Leviton (1968), Auffenberg (1989), Harding & Welch (1980) and others, group with the mainland eastern populations. There is no morphological differentiation between the Javan populations and the populations of the eastern form from the Asian mainland; the subspecies *V. r. sublimitis* Kopstein should therefore be considered as a synonym of *siamensis*. The Lesser Sunda populations are morphologically distinct from the remaining eastern populations, including those from Java; this distinctiveness could be due either to phylogenesis, i.e. separate ancestry or to ecogenesis, i.e. different current selection pressures leading to adaptive modifications of morphological characters. Until this is resolved, we prefer not to take a firm decision on the status of the taxon *limitis*.
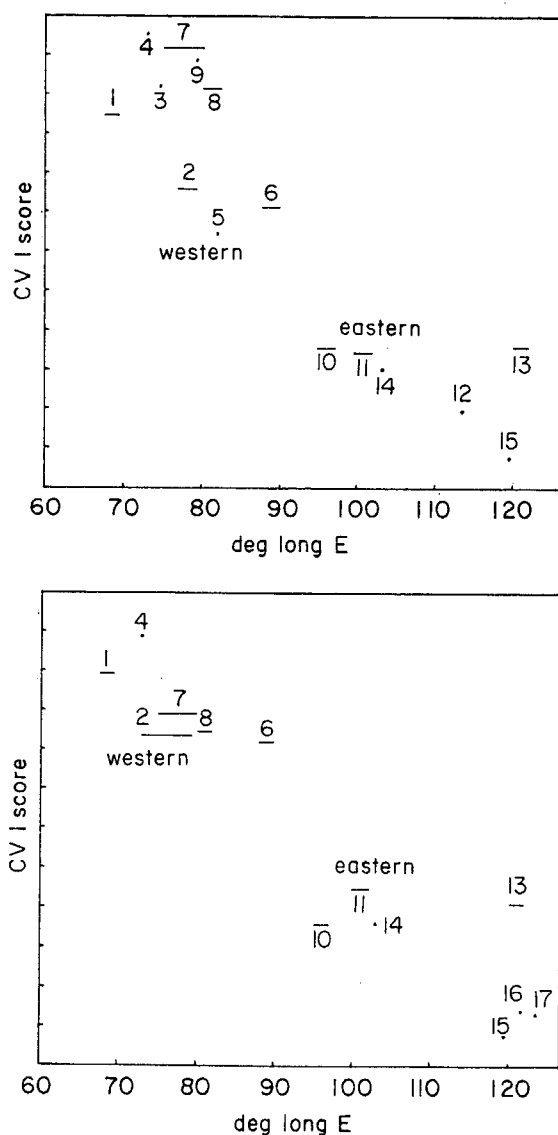
Figure 7. Plot of mean OTU scores along the first canonical variate of CVAs 1a (top) and 1b (bottom) against longitude. Note the clear break between the western and eastern populations. OTU numbers correspond to those in Fig. 1B, the length of the horizontal lines indicates the longitudinal scatter of the specimens of the OTU concerned.

TABLE 3. Geographic variation in Russell's viper venom effects in relation to east-west morphological differentiation (modified from Warrell, 1989)

Taxon	Western		Eastern	
Area	Sri Lanka	India	Burma	Thailand
Coagulability	+	+ +	+ +	+ +
Renal failure	+ +	+	+ +	+
Pituitary infarction	—	+	+ +	—
Intravascular haemolysis	+ +	+	—	+
Neuro-myotoxicity	+ +	+	—	—
Generalized capillary permeability	—	—	+ +	—
Primary shock/hypotension	—	+	+ +	—

Venom variation and its relationship to morphological variation

Recent work on the clinical effects of the venom of Russell's viper, carried out in many parts of its range, has revealed an enormous degree of geographic variation in the effects of its venom on human bite victims (Jeyarajah, 1964; Myint-Lwin et al., 1985; Phillips et al., 1988; Warrell, 1986, 1989) (Table 3). This is related to profound differences in venom composition and enzymatic activity (Jayanthi & Gowda, 1988; Woodhams et al., 1990).

In many venomous snake taxa, venom differences are related to taxonomic differentiation of the populations involved. In the case of Russell's viper, it has been stated that there is practically no relationship between morphological differentiation and venom variation (Anonymous, 1985; Warrell, 1989). This study has revealed considerable morphological differences between some populations with very different venoms (Wüster et al., 1992), which had hitherto been thought to be morphologically very similar. However, as can be seen from Table 3, there is as much variation in venom effects within the eastern and western taxa as there is between them, so that the link between morphological variation and venom variation in Russell's viper must be considered weak.

Antivenom effectiveness in Russell's viper is apparently not related to the principal division into eastern and western taxa, and also not necessarily to differences in the effects of the venom. Despite profound differences in clinical venom effects, antivenom against Burmese Russell's viper (eastern form) was found to be effective against the venom of Thai Russell's vipers (also the eastern form), and even against the venom of Russell's vipers from India (western form) (Phillips et al., 1988). The geographic origin of the Indian venom was not indicated, which is unfortunate. However, since the Indian venom was stated to have been obtained from the Haffkine Institute in Bombay, it is likely to have originated from snakes from the western part of India. The venom of Russell's vipers from western India has been shown by Jayanthi & Gowda (1988) to have a different mode of action than that of the southern Indian populations, which are morphologically indistinguishable from Sri Lankan vipers. The Burmese antivenom was found to be ineffective in protecting mice against the lethal effects of Sri Lankan Russell's viper venom (Phillips et al., 1988), as was Indian (Haffkine) antivenom, presumably produced from the venom of western Indian populations. The latter was found by the same authors to be similarly ineffective in treating human patients envenomated by Russell's vipers in Sri Lanka.

Systematic confusion has pervaded the study of Russell's viper venoms. Woodhams et al. (1990) erroneously assigned the northern Indian populations to Vipera russelli siamensis, and the southern Indian populations to V. r. puchella. In fact, the northern Indian populations belong to the western form (V. r. russelli), just as the southern Indian and Sri Lankan populations, whereas siamensis is the subspecific epithet applicable to the populations east of the Bay of Bengal only. As was already discussed, the Sri Lankan and southern Indian populations are very similar; since the type of locality of the entire species is in southern India, both should be referred to as V. r. russelli.

The relationship between venom variation and morphological variation in Russell's viper thus appears to be unclear. Considerable venom differences, with

problems of antivenom effectiveness, exist between populations with little morphological differentiation (e.g. between northern Indian and southern Indian and Sri Lankan populations), whereas antivenom against Burmese vipers neutralizes the venoms of morphologically distinct Thai vipers, and of highly distinct (?western) Indian populations, which belong to the western form.

Very little information is available on the venoms of Russell's vipers from China, Taiwan, Indonesia and Pakistan, and their clinical effects. Much more information is needed on geographic variation in clinical effects in the western form, and on venom variation, on a finer scale than that provided by Jayanthi & Gowda (1988).

Biogeography

The highly discontinuous range of Russell's viper has elicited comment for many years (Brongersma, 1958; van Hoesel, 1954, 1958; Pope, 1935; Smith, 1943). The isolated populations from Indonesia have posed a particular problem for biogeographers. Russell's viper had been reported from Sumatra and Java in the 19th century, but the material on which this was based was later shown to have originated from India (Brongersma, 1958). Its occurrence in the Lesser Sunda Islands was only discovered in 1927, even though it is common on some (Auffenberg, 1980), and it was only recorded from Java by Neuhaus (1935). There is no evidence that it occurs on Sumatra, the Malayan Peninsula or Borneo, so that the southern Indonesian populations are isolated by over 2000 km from the nearest populations in Thailand.

The distribution of the remaining populations of the eastern form is equally discontinuous, the Burmese, Thai, Chinese and Taiwanese populations being completely isolated from each other. It has not been reported from Laos or Vietnam, and there is only one record from Cambodia, very near the Thai border (Saint Girons, 1972). The western form has a more continuous distribution on a macroscale, but on a finer scale, its distribution on the Indian subcontinent is also discontinuous and irregular (Smith, 1943).

Some of the discontinuity in the distribution of Russell's viper is likely to be due to a combination of habitat preferences and Pleistocene changes in sea levels and climate. In most of its range, Russell's viper prefers at least partially open habitats with dry areas, and avoids rainforests (Auffenberg, 1980; Pope, 1935; Smith, 1943, Warrell, 1989; Whitaker, 1978). This explains its present-day absence from the Malayan Peninsula, Sumatra, Borneo and western Java, and also from Assam and the mountains of western Burma, the area which separates the eastern and western forms. Another venomous snake species which exhibits an equatorial gap in its distribution is the Malayan pit viper, *Calloselasma rhodostoma*, which occurs widely in Indo-China and the northern two-thirds of the Malayan Peninsula, is absent from most of Malaysia, and from Sumatra and Borneo, but occurs on Java and neighbouring islands (Gloyd & Conant, 1990).

The presence of Russell's viper in southern Indonesia can be related to changes in climate and sea level during the Pleistocene. During Pleistocene cold phases, sea levels fell by between 120 m and 200 m below current levels (Heaney, 1985, 1986; Ollier, 1985). As a result, the entire Sunda Shelf was above sea level, and the large islands of Indonesia (Sumatra, Borneo, Java) were part of the Asian mainland. The increase in land area, and the cooling of climates, led

to a drier and more seasonal climate in parts of the Sunda Shelf that are currently covered by evergreen rainforest. Palynological evidence suggests the existence of a corridor of drier, seasonal climate, extending south from Thailand along what is now the Malayan Peninsula to eastern Sumatra and Java (Morley & Flenley, 1987). It is likely that this seasonal corridor provided suitable habitats for Russell's viper, and there may have been a continuous population extending from Thailand to Java. Rising sea levels and more humid climates then acted as vicariance events, eradicating all populations between Thailand and eastern Java.

The Lesser Sunda Islands of Komodo, Flores, Ende and Lomblen were almost certainly not connected to the Asian mainland during periods of low sea levels, since they are separated from the Asian mainland by trenches more than 200 m deep. However, these islands, and several others on which Russell's viper has not yet been found, were connected to each other during the Pleistocene, forming one larger island. In view of the lack of a Pleistocene land connection between these islands and the Sunda Shelf, Russell's viper must have dispersed there overwater from Java or another part of the Sunda Shelf. It is interesting to note that, to date, Russell's viper has not been found on Bali, which was connected to Java during the Pleistocene cold phases, nor on Lombok or Sumbawa, which are situated between the Sunda Shelf and the Greater Flores group.

The canonical variate analyses run on the eastern populations (CVAs 3a and 3b) show that the Russell's viper populations from the Lesser Sunda Islands form a phenetically cohesive group, which is consistently different from the remaining populations, whereas the Javan population grouped with the Asiatic mainland populations. The relative similarity of the Javan and Asiatic mainland populations is not surprising: sea levels were still 120 m below their present level 18 000 years B.P., so that the Javan and mainland populations were only finally separated by rising sea-levels in geologically very recent times. Furthermore, if the size of the Javan population only slowly declined to its present relict status, a founder effect is unlikely.

There are several possible interpretations for the distinctiveness of the Lesser Sunda Island populations. The first is that they are distinct due to a founder effect. This is likely, since the species arrived there by overwater dispersal, which implies a small founder population. The second interpretation is that the colonization of the Lesser Sunda Islands by Russell's viper happened a much longer time ago than the separation of the Javan populations from the Asian mainland populations, and that the phenotypic distinctiveness of the Lesser Sunda populations is an example of divergence due to long separation (phylogenesis). Finally, it is possible that different selection regimes operate on the morphology of the animals in the Lesser Sunda Islands, leading to ecologically induced phenotypic change (ecogenesis).

ACKNOWLEDGEMENTS

their help and cooperation. H.-W. Herrmann (University of Marburg), R. D. G. Theakston (Liverpool School of Tropical Medicine) and D. A. Warrell (Oxford) provided much useful advice. This study was partly funded by NERC and the Leverhulme Trust.

REFERENCES

ANONYMOUS, 1985. The flying death of Rajputana—systematics of dangerously venomous snakes. *Report of the British Musuem (Natural History), 1984–1985:* 34–35.

AUFFENBERG, W., 1980. The herpetofauna of Komodo, with notes on adjacent areas. *Bulletin of the Florida State Museum, Biological Sciences, 25:* 39–156.

AUNG-KHIN, M., 1980. The problem of snakebites in Burma. *The Snake, 12:* 125–127.

BRONGERSMA, L. D., 1958. Note on *Vipera russelli* (Shaw). *Zoologische Medelelingen Leiden, 36:* 55–76.

CRACRAFT, J., 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In D. Otte & J. A. Endler (Eds), *Speciation and Its Consequences:* 28–59. Sunderland, Mass.: Sinauer Associates.

DERANIYAGALA, P. E. P., 1945. Some new races of the python, *Chrysopelea*, binocellate cobra and Tith-Polonga inhabiting Ceylon and India. *Spolia Zeylanica, 24:* 103–113.

DOWLING, H. G., 1951. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology, 1:* 97–99.

GLOYD, H. K. & CONANT, R., 1990. *Snakes of the Agkistrodon complex. A monographic review.* Oxford, Ohio: Society for the Study of Amphibians and Reptiles.

HARDING, K. A., & WELCH, K. R. G., 1980. *Venomous Snakes of the World. A Checklist.* Oxford: Pergamon.

HEANEY, L. R., 1985. Zoogeographic evidence for Middle and Late Pleistocene landbridges to the Philippine Islands. *Modern Quaternary Research in South-East Asia, 9:* 127–143.

HEANEY, L. R., 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society, 28:* 127–165.

HOESEL, J. K. P. VAN, 1954. *Vipera russellii*—its zoogeographical range and local distribution in Indonesia. *De Tropische Natuur, 33:* 133–139.

HOESEL, J. K. P. VAN, 1958. Notities over *Vipera russellii* en enkele andere slangen van Flores. *Lacerta, 16:* 32–36.

JAYANTHI, G. P. & GOWDA, T. V., 1988. Geographical variation in India in the composition and lethal potency of Russell's viper (*Vipera russelli*) venom. *Toxicon, 26:* 257–264.

JEYARAJAH, R., 1984. Russell's viper bite in Sri Lanka—A study of 22 cases. *American Journal of Tropical Medicine and Hygiene, 33:* 506–510.

KOPSTEIN, F., 1936. Über *Vipera russellii* von Java. *Treubia, 15:* 259–264.

KUO, T.-S. & WU, C.-S., 1972. Clinico-pathological studies on snakebites in Taiwan. *Journal of the Formosan Medical Association, 71:* 447–463.

LEVITON, A. E., 1968. The venomous terrestrial snakes of East Asia, India, Malaya and Indonesia. In W. Bücherl, E. E. Buckley & V. Deulofeu (Eds), *Venomous Animals and their Venoms:* 529–576. New York: Academic Press.

LEVITON, A. E., GIBBS, R. H., HEAL, E. & DAWSON, C. E., 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia, 1985:* 802–832.

LOOAREESUWAN, S., VIRAVAN, C. & WARRELL, D. A., 1988. Factors contributing to fatal snake bite in the tropics: analysis of 46 cases in Thailand. *Transactions of the Royal Society of Tropical Medicine and Hygiene, 82:* 930–934.

MATTHAI, T. P. & DATE, A., 1981. Acute renal failure in children following snake bite. *Annals of Tropical Paediatrics, 1:* 73–76.

MEBS, D. & KORNALIK, F., 1981. Schlangengiftseren–Probleme ihrer Wirksamkeit, untersucht am Beispiel von *Echis carinatus*. *Salamandra, 17:* 89–98.

MORLEY, R. J. & FLENLEY, J. R., 1987. Late Cainozoic vegetational and environmental changes in the Malay Archipelago. In T. C. Whitmore (Ed.), *Biogeographical Evolution of the Malay Archipelago:* 50–59. Oxford: Clarendon Press.

MYINT-LWIN, PHILLIPS, R. E., TUN-PE, WARRELL, D. A., TIN-NU-SWE & MAUNG-MAUNG-LAY, 1985. Bites by Russell's viper (*Vipera russelli siamensis*) in Burma: Haemostatic, vascular, and renal disturbances and responses to treatment. *The Lancet, 2:* 1259–1264.

NEUHAUS, H., 1935. Neunachweis von *Vipera russellii* auf Java. *Treubia, 15:* 49–50.

OBST, F. J., 1983. Zur Kenntnis der Schlangengattung *Vipera* (Reptilia, Serpentes, Viperidae). *Zoologische Abhandlungen, 38:* 229–235.

OLLIER, C. D., 1985. The geological background to prehistory in island Southeast Asia. *Modern Quaternary Research in SE Asia, 9:* 25–42.

PHILLIPS, R. E., THEAKSTON, R. D. G., WARRELL, D. A., GALIGEDARA, Y., ABEYSEKERA,

D. T. D. J., DISSANAYAKA, P., HUTTON, R. A. & ALOYSIUS, D. J., 1988. Paralysis, rhabdomyolysis and haemolysis caused by bites of Russell's viper (*Vipera russelli pulchella*) in Sri Lanka—failure of Indian (Haffkine) antivenom. *Quarterly Journal of Medicine, 68:* 691–717.

POPE, C. H., 1935. *The Reptiles of China. Turtles, Crocodilians, Snakes, Lizards.* New York: American Museum of Natural History.

SAINT GIRONS, H., 1972. Les serpents du Cambodge. *Mémoires du Muséum National d'Histoire Naturelle, Série A, 74:* 1–165.

SAWAI, Y., KOBA, K., OKONOGI, T., MISHIMA, S., KAWAMURA, Y., CHINZEI, H., ABU-BAKAR, I., DEVARAJ, T., PHONG-AKSARA, S., PURANANANDA, C., SALAFRANCA, E. S., SUMPAICO, J. S., TSENG, C., TAYLOR, J. F., WU, C. & KUO, T., 1972. An epidemiological study of snakebites in southeastern Asia. *Japanese Journal of Experimental Medicine, 42:* 283–307.

SILVA, A. DE, 1981. Snakebites in Anuradhapura District. *The Snake, 13:* 117–130.

SILVA, A. DE, 1990. *Colour Guide to the Snakes of Sri Lanka.* Portishead: R & A Publishing.

SILVA, A. DE & RANASINGHE, L., 1983. Epidemiology of snake-bite in Sri Lanka: a review. *Ceylon Medical Journal, 28:* 144–154.

SMITH, M. A., 1943. *Fauna of British India: Reptilia and Amphibia, Vol. III, Serpentes.* London: Taylor and Francis.

THORPE, R. S., 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake, *Natrix natrix* (L.) *Biological Journal of the Linnean Society, 7:* 27–43.

THORPE, R. S., 1979. Multivariate analysis of the population systematics of the ringed snake, *Natrix natrix* L.). *Proceedings of the Royal Society of Edinburgh, 78*(B): 1–62.

THORPE, R. S., 1980. Microevolution and taxonomy of European reptiles with particular reference to the grass snake *Natrix natrix* and the wall lizards *Podarcis sicula* and *P. melisellensis. Biological Journal of the Linnean Society, 14:* 215–233.

THORPE, R. S., 1984. Geographic variation in the western grass snake (*Natrix natris helvetica*) in relation to hypothesized phylogeny and conventional subspecies. *Journal of Zoology, London, 203:* 345–355.

THORPE, R. S., 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Bolletino di Zoologia, 54:* 3–11.

THORPE, R. S. & McCARTHY, C. J., 1978. A preliminary study, using multivariate analysis, of a species complex of African house snakes (*Boaedon fuliginosus*). *Journal of Zoology, London, 184:* 489–506.

WARRELL, D. A., 1986. Tropical snake bite: clinical studies in south-east Asia. In J. B. Harris (Ed.), *Natural Toxins: Animal, Plant and Microbial:* 25–45. Oxford: Clarendon Press.

WARRELL, D. A., 1989. Snake venoms in science and clinical medicine 1. Russell's viper: biology, venom and treatment of bites. *Transactions of the Royal Society of Tropical Medicine and Hygiene, 83:* 732–740.

WARRELL, D. A. & ARNETT, C., 1976. The importance of bites by the saw-scaled or carpet viper (*Echis carinatus*): epidemiological studies in Nigeria and a review of the world literature. *Acta Tropica, 33:* 307–341.

WHITAKER, R., 1978. *Common Indian Snakes. A Field Guide.* New Delhi: Macmillan.

WOODHAMS, B. J., WILSON, S. E., XIN, B. C. & HUTTON, R. A., 1990. Differences between the venoms of two sub-species of Russell's Viper: *Vipera russelli pulchella* and *Vipera russelli siamensis. Toxicon, 28:* 427–433.

WÜSTER, W., OTSUKA, S., THORPE, R. S., & MALHOTRA, A., 1992. Morphological variation in Russell's viper in Burma and Thailand. *Herpetological Journal,* in press.

WÜSTER, W. & THORPE, R. S., 1989. Population affinities of the Asiatic cobra (*Naja naja*) species complex in Southeast Asia: Reliability and random resampling. *Biological Journal of the Linnean Society, 36:* 391–409.

WÜSTER, W. & THORPE, R. S., 1991. Asiatic cobras: systematics and snakebite. *Experientia, 47:* 205–209.