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STUDIES ON PAKISTAN REPTILES

PT. 1. THE GENUS *ECHIS* (VIPERIDAE)

Walter Auffenberg and Hafeezur Rehman

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STUDIES ON PAKISTAN REPTILES
PT. 1. THE GENUS *ECHIS* (VIPERIDAE)

Walter Auffenberg and Hafeezur Rehman*

ABSTRACT

This is the first of a series of studies intended to analyze the geographic patterns in the meristic characters of Pakistan reptiles. This part concerns the saw-scaled vipers, *Echis carinatus*. The scales analyzed are numbers of ventrals, subcaudals, dorsal rows, rows of oblique dorsals, gulars, suboculars and supraoculars; color patterns include number of dorsal spots, ventral pattern, infralabials, lateral body and head. Maps of geographic variation in the means of each of these characters are provided and the patterns of variation within Pakistan are discussed.

Each of the characters studied tends to have a different geographic distribution of mean values. However, one recurrent pattern is a rapid change in character state between Iranian Plateau populations (Chagai area, Pakistan) and those of the Quetta highland area. Coastal populations are also rather distinctive, but are generally similar to those in the Indus River Plain. Himalayan foothill populations are often similar to those of coastal areas, suggesting that these geographical peripheral populations are also peripheral in regard to genetic adaptation. In the Indus River Delta, populations can be subdivided into several distinct subgroups. The resulting mosaic of character states is attributed to historic factors concerned with changing positions of the deltaic distributaries during geologic time. Finally, the population in the Cholistan-Thar Desert at the Indo-Pakistan border is distinctive in both color and scalation. These differences are probably adaptive responses to local arid conditions. Several character states of this population and that in the Chagai Desert of northwest Pakistan are convergent.

Of those climatic factors believed important within the adaptive mileau of this species, mean daily maximum and minimum temperatures during June and July (when they are most active) are considered most important. Some of the population differences probably reflect adaptations to water and heat loss.

Contrary to recently published opinion, we conclude there is only one species of saw-scaled viper in Pakistan; its scientific name is *Echis carinatus*. Within Pakistan we recognize three distinct geographic races--*E.c. multisquamatus* Cherlin, *E. c. sochureki* Stemmler and *E. c. astolae* Mertens.

The geographic distribution of characters analyzed shows that the major barrier to gene flow between *E. c. sochureki* and *E. c. multisquamatus* is the central north-south massif (Sulaiman Range, et al.). For *E. c. sochureki* and *E. c. astolae* it is the Arabian Sea, and for *E. c. sochureki* and *E. c. carinatus* (Indian Peninsula) it is largely a matter of overall distance. In general, the race *E. c. sochureki* is intermediate between *E. c. multisquamatus* and *E. c. carinatus*.

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RESUMEN

Este es el primero de una serie de estudios que pretenden analizar los patrones geográficos en los caractees merísticos de los reptiles de Pakistán. Esta parte concierne a las víboras de escamas aserradas (saw-scaled) *Echis carinatus*. Se analiza el número de escamas ventrales, subcaudales, filas de escamas dorsales, filas de oblicuas dorsales, gulares, suboculares y supraoculares; los patrones de color incluyen número de manchas dorsales, patrón ventral, infralabiales, lados del cuerpo y cabeza. Mapas de variación geográfica en los promedios de cada uno de estos caracteres son provistos y se discuten los patrones de variación dentro de Pakistán.

Cada uno de los caracteres estudiados tiende a mostrar una distinta distribución geográfica de sus valores promedio. Sin embargo, un patrón recurrente es un cambio rápido en la condición de un caracter entre las poblaciones de la placa iraní (Chagai, Pakistán) y aquellas de la región alta de Quetta. Las poblaciones de la costa son también distintas, pero generalmente similares a las que se encuentran en la planicie del río Indo (Indus River). Las poblaciones que ocupan el pie de montaña de los Himalaya son a menudo similares a las costeras, lo cual sugiere que estas poblaciones geográficas periféricas son también periféricas en cuanto a sus adaptaciones genéticas. En el delta del río Indo, las poblaciones pueden subdividirse en varios subgrupos. El mosaico de condiciones de caracteres resultante es atribuído a factores históricos relacionados al cambio de posción de los distributarios del delta en el tiempo geológico. Finalmente, la población del desierto de Cholistan-Tar en el límite indo-pakistaní es distinta en color y escamación. Estas diferencias son probablemente respuestas adaptativas a condiciones áridas locales. Varias de estas condiciones de caracter de esta población y la del desierto Chagai en el Noroeste de Pakistán son convergentes.

Entre los factores climáticos que se creen importantes dentro el medio ambiente de esta especie, la temperaturas medias máxima y mínima durante Junio y Julio (cuando la especie es más activa) se consideran los más importantes. Algunas de las diferencias entre poblaciones probablemente reflejen adaptaciones a la pérdida de agua y calor.

En contraste con opiniones recientemente publicadas, nosotros concluimos que sólo hay una especie de víbora de escamas aserradas en Pakistán; su nombre científico es *Echis carinatus*. Dentro Pakistán reconocemos tres razas geográficas--*E. c. multisquamatus* Cherlin, *E. c. sochureki* Stemmler y *E. c. astolae* Mertens.

La distribución geográfica de los caracteres analizados muestra que la mayor barrera para el flujo genético entre *E. c. sochureki* y *E. c. multisquamatus* es el macizo central Norte-Sur (Sulaiman Range, et al.). Para *E. c. sochureki* y *E. c. astolae* es el Mar Arábigo, y para *E. c. sochureki* and *E. c. carinatus* (Península de la India) es por demás una cuestión de distancia. En general, la raza *E. c. sochureki* es intermedia entre *E. c. multisquamatus* y *E. c. carinatus*.

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INTRODUCTION

For many years all Pakistan *Echis* populations were considered a single species (i.e., *E. carinatus* (Schneider) 1801; type loc. nr. Madras, India). Constable (1949) suggested that the Pakistan (and other) populations should be referred to *E. carinatus pyramidium* (Geoffroy 1827; type loc. Egypt). Stemmler (1969) modified this arrangement by placing all Pakistan (and some other) populations in *E. carinatus sochureki* (Stemmler 1969, type loc. Ban Kushdil Khan, nr. Pishin, Baluchistan, Pakistan). He also demonstrated that within the geographic confines of his new race, the populations from southern Russia were larger and possessed a distinctive scalation when compared to those from more southern parts of the range, but he did not describe them as a separate subspecies. In 1969, Mertens described *E. carinatus astolae* from the Mekkran Coast of Pakistan (type loc. Astola Island, Baluchistan). In 1981, Cherlin described *E. multisquamatus* from Russian Turkistan (type loc. Bayram Ali, Turkmen SSR). He referred some of his material from Chagai District, northern Baluchistan to his new species, and stated that in this same area it was sympatric with populations of *E. carinatus*. Following additional analysis, Cherlin (1983a) raised Stemmler's *sochureki* to a full species and restricted *E. carinatus* to peninsular India. All mainland Pakistan populations (except those in northwestern Chagai) were to be called *E. sochureki sochureki* Stemmler; the insular form was now *E. sochureki astolae* Mertens. *Echis carinatus* was divided into two races, *E. c. carinatus* on the Indian peninsular mainland, and *E. c. sinhalensis* Deraniyagala (1951) on Sri Lanka.

Being committed to produce a book-length compendium of the reptiles and amphibians of Pakistan, we were anxious to determine the range and character limits of these two species in Pakistan. To do this we examined all available *Echis* material from Pakistan and neighboring areas. This was particularly important because no geographic sympatry of the two species believed to exist in Pakistan (Cherlin 1981) had actually been clearly demonstrated. We initially presumed that the available material (in museums and the several hundred specimens we had collected during field work for the larger project on the herpetology of Pakistan) would establish such areas of overlap. As shown below, we soon learned that such sympatry could not be demonstrated and that the current taxonomic arrangement as it applies to Pakistan is probably incorrect. The results of our studies are presented below. Mr. Colin McCarthy, British Museum of Natural History, is presently completing his broader analysis of all *Echis* "*carinatus*" material from southern Asia and northern Africa. This important study will allow our own geographically restricted one to be placed in proper perspective.

We believe our data demonstrate a pattern of variation in scalation and color character states that is significant in zoogeographic interpretations regarding Pakistan. This study is the first of several we have planned, each covering one or more reptile taxa, through which we hope to develop a zoogeographical overview of Pakistan reptiles based on analyses of more specimens than has been available to earlier workers.

MATERIAL

Sources

This study is based on 658 specimens from the twenty one institutions listed below. The museum source of those specimens specifically referred to are identified by the abbreviations given. The numbers in parentheses indicate the number of individuals examined in each institution.

American Museum of Natural History, New York (AMNH 9). Natural History Museum, London (BMNH 11). Bombay Natural History Society (BNHS 51). California Academy of Sciences, San Fransisco (CAS 5). Field Museum of Natural History, Chicago (FMNH 21). University of Humboldt Museum, Berlin (ZMB 1). Naturhistoriches Museum, Basel (NMBA 8). Museum of Comparative Zoology, Harvard University, Cambridge (MCZ 9). Natural History Museum of Vienna (NMW 2). Pakistan Museum of Natural History, Islamabad (PMNH 2). Royal Scottish Museum, Edinburgh (RSM 17). Senckenberg Museum, Frankfurt (SMF 88). University of Florida/Florida Museum of Natural History, Gainesville (UF 28). University of Michigan Museum of Zoology, Ann Arbor (UMMZ 4). National Museum of Natural History, Washington, D.C. (USNM 11). Zoological Survey Department of Pakistan, Karachi (ZSD 328). Zoological Survey of India, Calcutta (ZSI 55). National Institute of Zoology, Academy of Sciences, Leningrad (ZIN 18), and Alexander Koenig Museum, Bonn (ZFMK 5).

All drawings were done by the senior author.

Localities

Figure 1 shows the localities from which specimens were examined. Appendix 1 provides data on museum holdings of specimens examined from different geographic locations. No specimens with general, questionable, or erroneous locality data have been included; nor have we included any literature records.

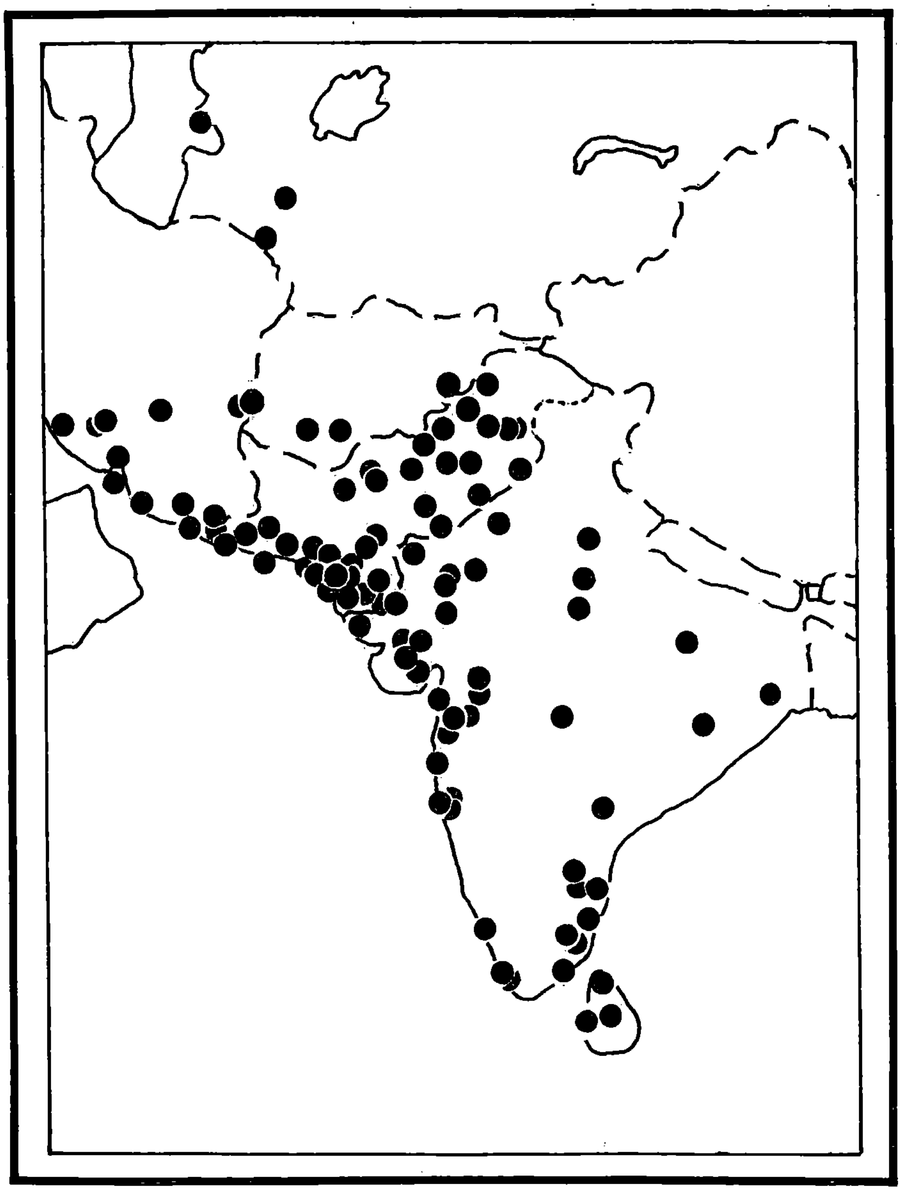

Figure 1. Map showing the localities from which specimens of *Echis* were examined during this study.

ACKNOWLEDGEMENTS

We particularly thank the United States Fish and Wildlife Service (Washington), the Deutscher Akademischer Austauschdienst (Bonn, Germany), and the Office of Sponsored Research (University of Florida) for making funds available for us to conduct this study. To all the curators and collection managers of the institutions listed above, we extend our sincere thanks for helping us locate material, putting specimens at our disposal for study, and for the many other ways in which they have contributed to the success of this project. Finally we wish to acknowledge the support offered by our respective institutions.

CHARACTERS

Characters Used Previously

Cherlin (1981) separated *Echis multisquamatus* from *Echis carinatus sochureki* on the basis that the former possesses a higher number of ventral scales (mean 188.1, vs. 173.4), a greater number of dorsal scale rows (mean 37.1, vs. 32.7), lateral serrated scales (both sides added together, mean 10.3, vs. 8.8), supraocular absent (vs. present), the light-colored lateral crescent markings are connected to form a zigzag (vs. separated crescents), and a light-colored, narrow, cross-like dorsal head marking (vs. a spear or broad "cross," see Cherlin 1983a, fig. 2).

In his studies of Indo-Pakistan *Echis* populations, Stemmler (1969) separated his *Echis carinatus sochureki* from congeners on the bases of being viviparous (vs. oviparous), dorsal color pattern (white spots, vs. other colors), wide head with a short snout, relatively small eyes, short tail, higher dorsal scale rows, enlarged supraoculars, head color pattern and lower number of ventral and subcaudal scales. Of these, the most important characters from the standpoint of the Pakistan material have also been studied by Cherlin.

Characters Used in This Study

The following characters were tabulated for all the specimens listed above: (1) number of ventral scales, (2) number of subcaudals, (3) number of dorsal scale rows, (4) number of serrated oblique dorsal scale rows, (5) number of gular scale rows, (6) number of subocular scales, (7) presence of supraoculars, (8) number of dorsal spots, (9) ventral color pattern, (10), color of infralabials and chin, (11) lateral color pattern, (12) dorsal color pattern, (13) head and nape pattern. Several of these have been used in previous studies of *Echis*, others are used here for the first time. When

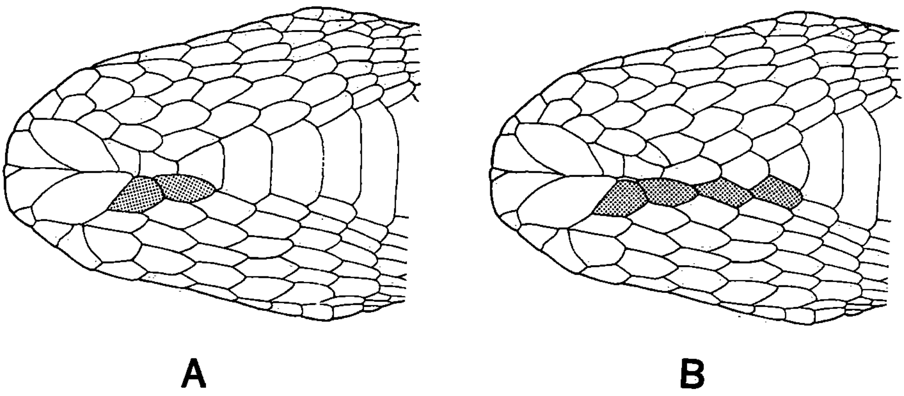

Figure 2. Variation in number of gular rows. (A) two rows between the enlarged chin shields and the first ventral shield; (B) four rows.

pertinent, sex was determined by dissection. Definitions for characters analyzed follow.

Number of ventrals.-- The first scale immediately posterior to the last chin shield to (but not including) the anal scute. Partial scutes were counted if they were larger than one third the width of a normal scute.

Number of subcaudals.-- Counts were made from the first normal-sized subcaudal behind the cloaca to, but not including the terminal spine. Specimens with a truncated tail were not included in the analyses.

Number of dorsal and oblique scale rows.-- In all specimens of *Echis* examined, a number of lateral rows were reduced in size, inclined in orientation (oblique), and distinctly serrated. This reduction in size and the attendant close packing of these scales sometimes makes counting dorsal scale rows difficult. If the change in orientation is not followed and the person making the count continues the standard manner along the diagonal set by the first pair of dorsals bordering the ventrals, the counts may regularly be two to four scales too low.

In this paper all scale row counts were made at midbody. An acceptable degree of reproducibility is attained by starting the counts caudad and reversing in the standard manner at the vertebral ridge. The number of oblique scale rows were counted on only one side and always at midbody. The oblique, smaller, serrated scales begin on scale rows three or four and continue caudo-dorsally for from two to six scale rows. The remaining dorsal scales are normal in both size and position. Neonates from the same geographic area have the same number of oblique scales as adults and they seem to be serrated to the same degree.

Number of gulars.-- The gular rows are those scales extending from immediately between the posterior pair of enlarged chin shields and the most anterior ventral scale (Fig. 2). They are more or less arranged in pairs, one following the other, each pair straddling the midline.

Subocular development.-- In the populations examined, a series of scales always surrounds the orbit (circumorbital ring); those in the lower part of the ring are termed suboculars. The subocular count was tabulated as the least number of scales vertically in the ring below the eye and between it and the supralabials below. This least number was usually above supralabial number five, rarely four (Figs. 3, 4).

Supraocular shield.-- Within the circumorbital ring, the most dorsally located scale above the eye is sometimes larger (longer and often wider) than the remaining adjacent dorsal head scales. This condition was interpreted as one in which the supraocular was well developed ("yes"). In other individuals none of the scales in the dorsal section of the circumorbital series was larger than the remaining dorsal head scales; this condition was interpreted as lacking a supraocular ("no") (Fig. 4).

Dorsal body color pattern.-- Figure 5 is a diagrammatic view of the dorsal scale area of *Echis carinatus* at mid-body. Both mid-dorsal and lateral color pattern elements are indicated. The dorsal portion is comprised of a median longitudinal series of darker dorsal blotches, separated by inter-blotch patches, both of which are located on a ground color of intermediate density. Dorsal blotches vary in the density of melanin, number of blotches, and their size. Melanin density was subjectively noted. Some of the notes taken also indicated whether the scales were completely or partially darkened and whether the blotch was lighter in the center or not. Blotch size was approximated by counting the scales in both the longitudinal and transverse directions. The number of dark dorsal blotches was counted from the first one immediately after the light-colored marking on the head and nape, continuing to the last one over the cloaca (or immediately anterior to it if no spot above it). Due to considerable bilateral asymmetry in the markings, counts were always made on the right side of the vertebral ridge. If the blotches were dim their light interspaces (always evident) were used as a guide.

The lateral color pattern is constructed around two longitudinal rows of smaller spots, each spot usually covering only a few scales. The lower row of smaller, usually dimmer spots is designated as I, the upper row of larger, often

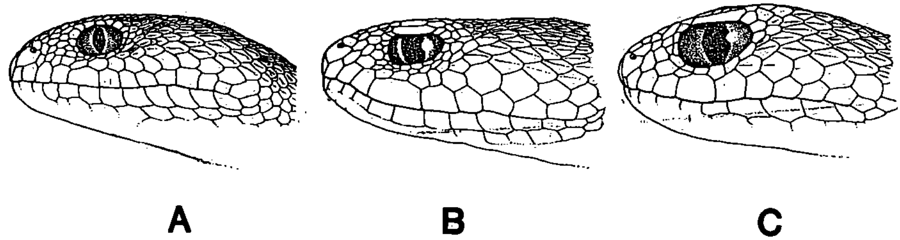

Figure 3. Lateral view of head, showing typical variation in the minimum number of rows beneath the eye. (A) minimum subocular rows two SMF 21054, Duschak, Transcaspia USSR; (B) minimum subocular rows two BNHS 2448, Dhera Ismail Khan, Pakistan; (C) subocular rows one BNHS 2425, Cumbun, Madura, Tamil Nadu, India. Head shape differences due mainly to age and size; C smallest, B largest.

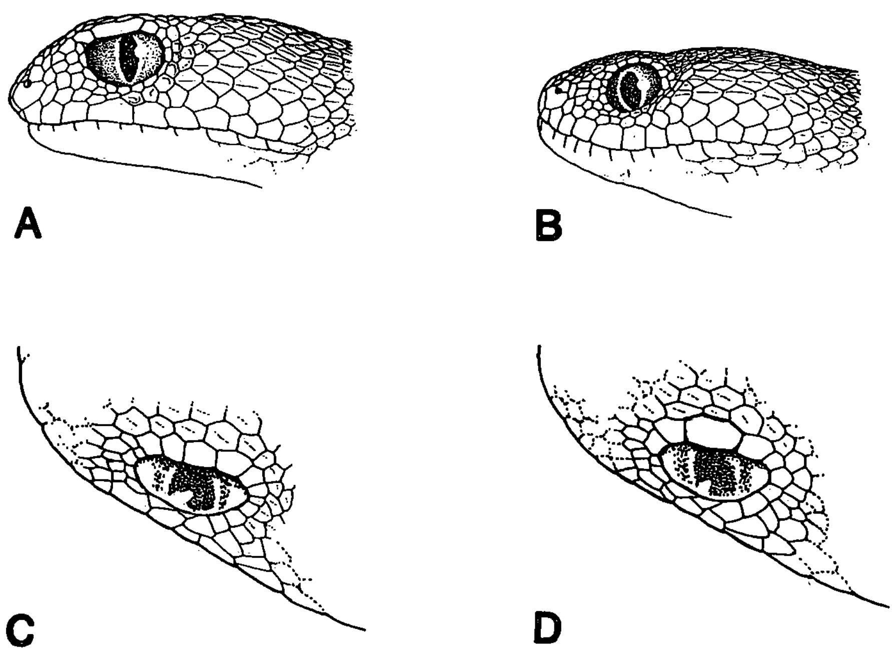

Figure 4. Above, lateral views of head. (A) supraocular shield differentiated from remaining head scales (BNHS 2359, Chabar, Persian Gulf); (B) supraocular not differentiated (SMF 57356, Astola Island, Baluchistan; holotype *E. c. astolae*). Below, top view of left side of head. (C) supraocular not differentiated (SMF 57356, same data as above); (D) supraocular differentiated (BNHS 2441, Mand, Baluchistan, Pakistan). Head shape differences due to age and size.

darker spots is designated as II. I or II may be absent and this fact was noted. Spot size was estimated by counting the total number of scales covered. Finally the relative darkness of the spots in both rows was noted. A longitudinal series of lighter (usually white) marks is associated with row II (Fig. 5, see remarks below).

The dorsal body color pattern was placed into an additional one of two categories: individuals with reduced melanin in the dorsal spots, the spots usually with light centers (Fig. 6A) and those with dark, clearly marked blotches (though these may vary in size) (Fig. 6C).

Ventral color pattern.-- In the populations studied this character ranges from uniformly clear (no markings), to heavily spotted. The markings of each specimen were subjectively placed in one of four categories; 0 = uniform white, cream, etc., without traces of any spots; 1 = very dim spots; 2 = medium intensity spots; 3 = deeply pigmented spots (Fig. 7). Additionally, the color of the ventral markings varied from greyish brown to nearly black, and in size from small to large dots. The last two variables were not tabulated.

Infralabial pattern.-- Many individuals have three dark blotches on the infralabials. Others grade from this condition to uniform white or cream. We use 0 for clear, 1 for dim, 2 for medium, and 3 for dense melanin (Fig. 8).

Lateral body color pattern.-- A series of white crescentic marks usually occur on the lateral body surface in association with pattern cycle II (Fig. 6). In some parts of Pakistan the crescent tips join to form a zig-zag line (= zig-zag "yes"), and in other areas they fail to touch (= zig-zag "no") (Fig. 5). Additionally, the number of rows of small lateral dark spots was tabulated for a random sample of specimens (see above and Fig. 5).

Head color pattern.-- The top of the head and nape is always marked with a distinct pattern. These markings vary from an arrow- to a cross-shaped mark (Fig. 9), in which the figure may be broad or narrow. For analytic purposes, we tabulated the trident mark (Fig. 9A) as 4, and the arrow mark (Fig. 9B) as 3, the broad cross (Fig. 9C) as 2, the narrow cross as 1. Intermediate conditions are indicated by a decimal (i.e., 3.5, 2.5).

SAMPLE AREAS

Figure 10 shows the locations and general size of sample areas chosen for this study. The geographic limits of the samples were selected primarily on the basis of sample size (museum material available), but in some cases partly on

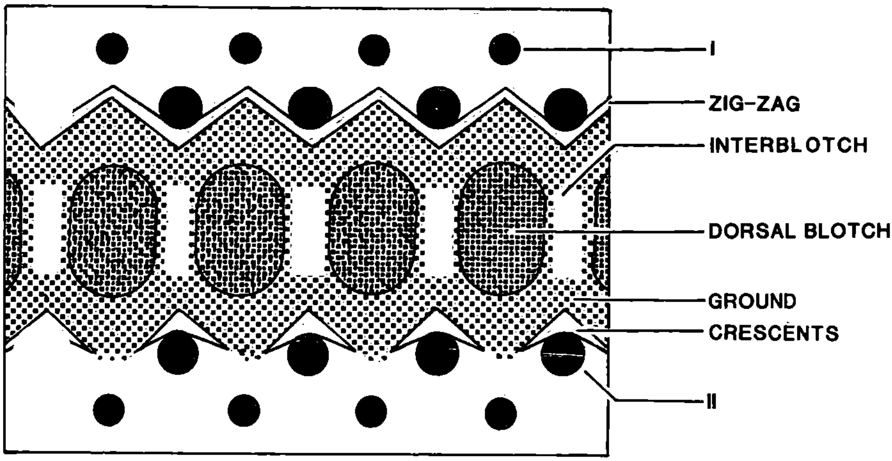

Figure 5. Color pattern elements on dorsal and lateral body surfaces of *Echis*.

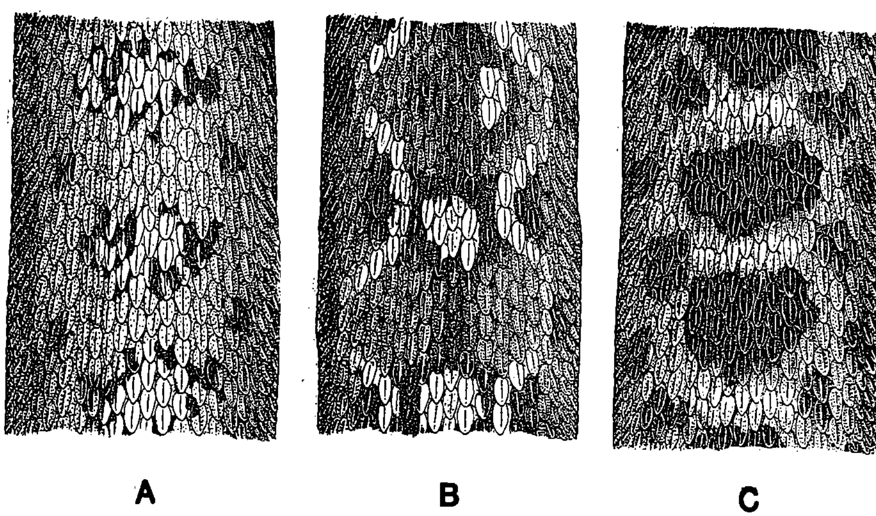

Figure 6. Major variational types of dorsal body color patterns. (A) BMNH 86-9-2-23-42, Chilez (= Chilas), Baluchistan; (B) UF 61232, Makli Hill, Sindh, showing an abnormal vertebral dark zig-zag in an otherwise typical pattern; (C) SMF 57356, Astola Island, Baluchistan, holotype *E. c. astolae*.

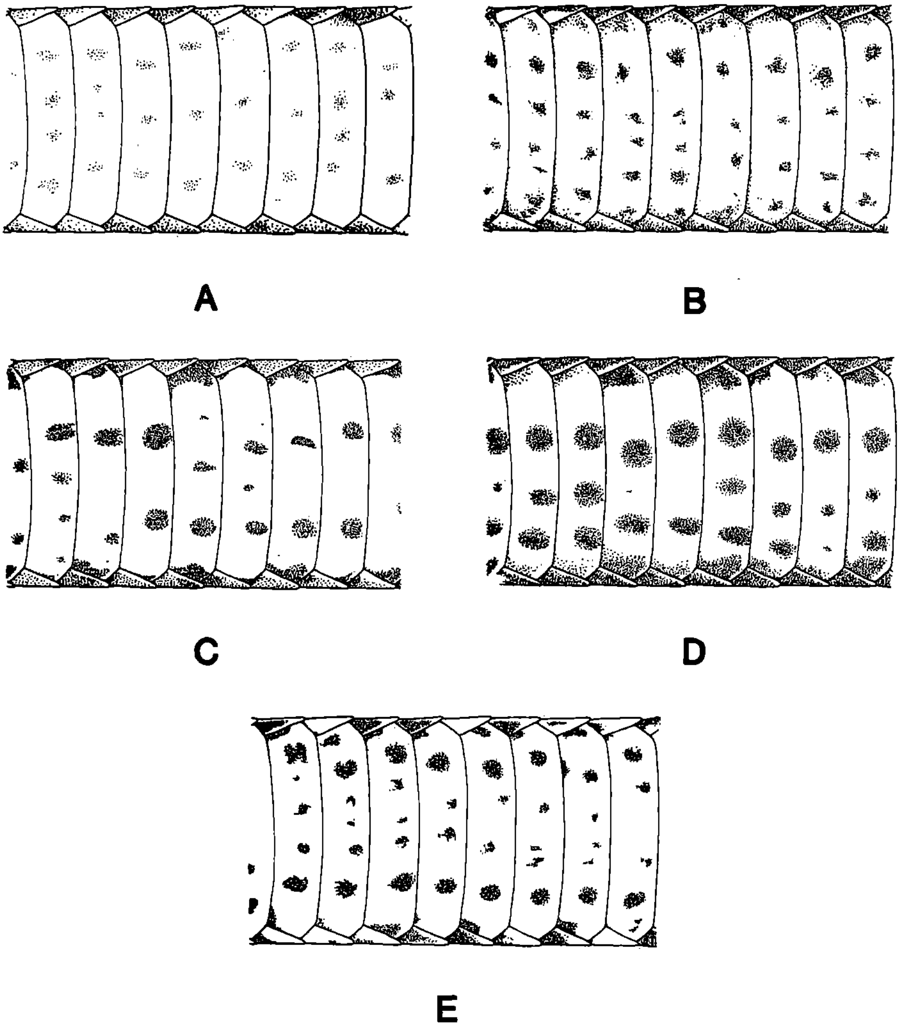

Figure 7. Ventral pattern categories used in this study. (A) uniform, or nearly so, no obvious pattern = 0, MCZ 5405A, 100 mi. S Amballa, U.P., India; (B) markings dim, small, = 1, BNHS 2437, Gosht, Baluchistan, Iran; (C) medium intensity, larger markings, = 2, MCZ 1839, Mednapur, West Bengal, India; (D) darker, larger markings, = 3, MCZ 2247, 100 mi. S Amballa, U. P., India; (E) dark, smaller, = 4, SMF 57356, holotype, *E. c. astolae*, Astola Island, Baluchistan.

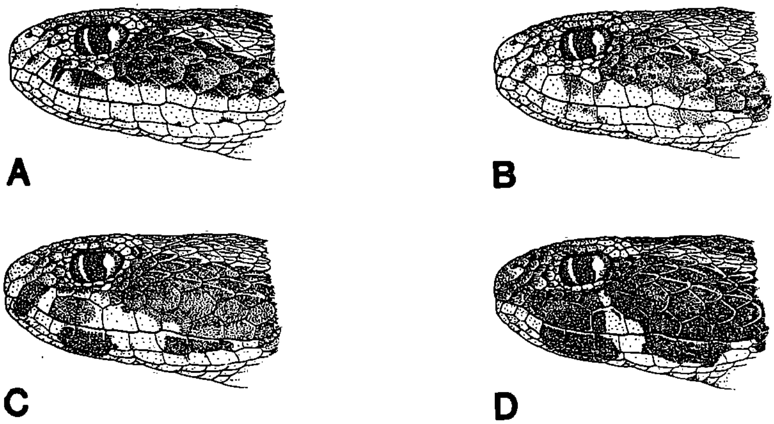

Figure 8. Infralabial pattern categories used in this study. (A) uniform, no pattern = 0, SMF 57356, holotype, Astola Island, Baluchistan; (B) dim markings = 1, SMF 63137, Nushki, Baluchistan; (C) medium intensity = 2, SMF 63136, Hingol, Baluchistan; (D) intensely pigmented = 3, SMF 55015, Turkmen SSR.

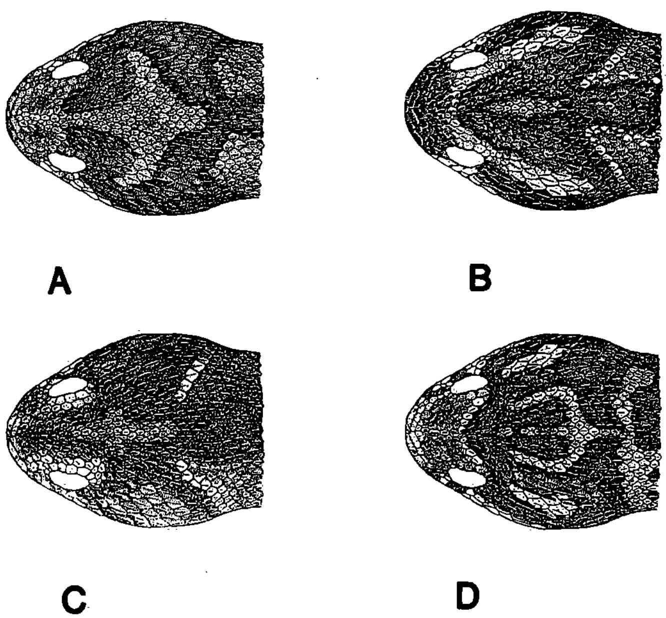

Figure 9. Head pattern categories used in this study. (A) broad cross, = 2, BNHS 2441, Mand, Baluchistan, Pakistan; (B) arrow, = 2, SMF 63136, Killi Mangal (Hingol), Baluchistan; (C) narrow cross, = 1, BMNH 86-9-21-124, Chilez, Baluchistan; (D) a rare trident pattern form (not tabulated separately, but placed with "arrow" category), SMF 57256, holotype, *E. c. astolae*, Astola Island, Baluchistan.

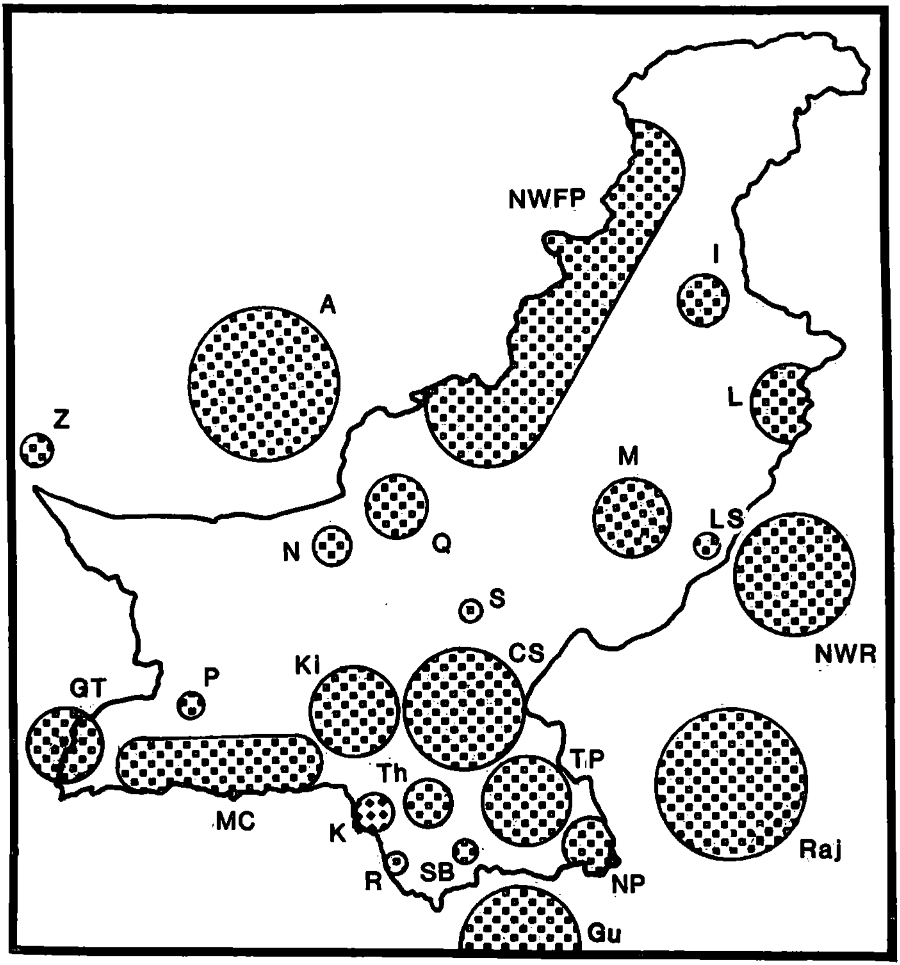

Figure 10. Location (and general size) of sample areas used in this study. Abbreviations used are as follows: A, Afghanistan; CS, Central Sindh; GT, Gosht; Gu, Gujarat; I, Islamabad; K, Karachi; Ki, Kirthar Range; L, Lahore; LS, Lal Suharna National Park; M, Multan; MC, Mekkran Coast; NP, Nagar Parkar;; N, Nushki; NWFP, Northwest Frontier Province; NWR, Northwest Rajasthan. P, Panjgur; Q, Quetta; Raj, Rajasthan; R, Rattankot; S, Shadadkot; SB, Shah Bundar; TP, Thar Parkar; Th, Thatta; Z, Zabol.

environmental differences between closely approximated geographic areas (i.e., elevation, major environment). Each of these sample areas served as the basis for all calculations and evaluations, so that all specimens available from each area were considered as constituting the same sample for computational purposes.

VARIATION

Geographic Variation

Ventrals.-- Within Pakistan the number of ventrals vary from 145 to 189 and sample means from 155 to 189 (Islamabad and Nushki samples). The general geographic pattern produced by the sample means is shown in Figure 11.

The geographic pattern is characterized by an area of high ventral counts in both northwest Baluchistan (mean 181-183) and the northern Thal Desert (mean 181) areas; and areas of low counts in both the northern mountains (154-158) and the southern part of the Thal Desert (158). The means of geographically intermediate sample areas are numerically intermediate. The means of the two areas with high mean values are significantly different from those with low means (*t*-test, at at least the 2 % level, see Table 1). Along the Mekkran Coast the mean number of ventrals decreases steadily from west to east and the trend is continued into adjacent coastal India (172 Gosht, Iran, to 162 in Gujarat, India). Separately, these coastal populations are significantly different in mean ventral counts from inland populations in Baluchistan and Sindh (Table 1), though the zone of high ventral counts in the coastal areas of the latter is quite narrow (Fig. 11). The trend is reversed along the frontal ranges of the Himalayas (154 NWFP to 162 Lahore), but without statistical evidence for any significant differences in the means of mountain and plains populations. There is no significant difference in mean ventrals of northern Pakistan and northern India (Ganges Plain, 157) from that in southern Pakistan and adjacent Gujarat. However, both coastal and mountain samples from India southeast of Gujarat have mean ventral counts significantly lower than those of southern Pakistan (Bombay 146, Poona 146) (Table 1). On the Indian peninsula the trend to decrease ventrals southeastward is continued, with the lowest values of all observed in the Goa sample (143; a significant difference in means occurs between the adjacent Goa-Bombay samples, $p <$ 0.05 % level, though not between any other population pair members in the rest of the peninsula).

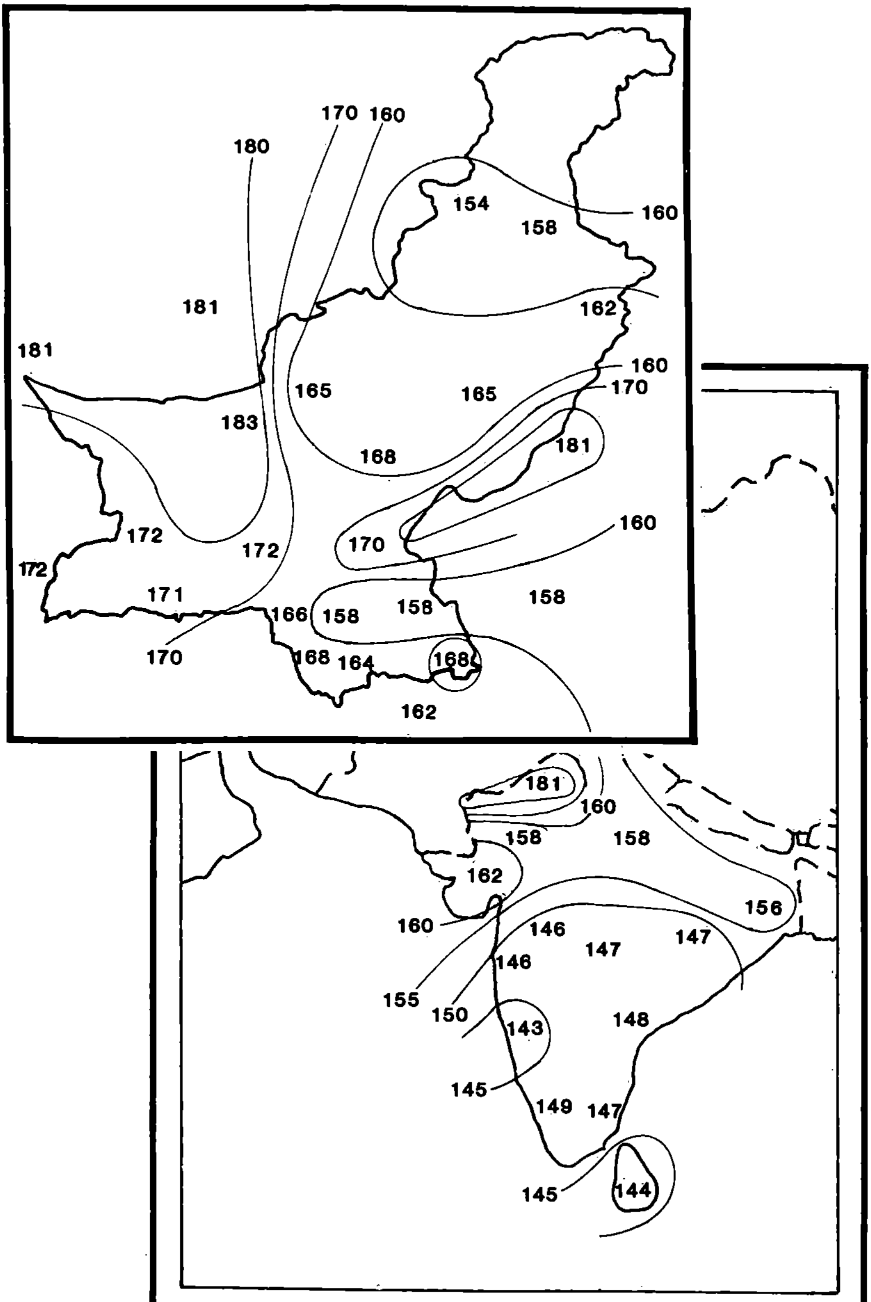

Figure 11. Mean number of ventral scales in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

In the Chagai area (Nushki sample) the high mean value (183) cannot be statistically separated from that of the Zabol, Iran (181), and Afghanistan samples. However, the Nushki mean is very significantly different from the adjacent Quetta one (165, $p < 0.001$). In the same way, the high mean value of the northern NW Rajasthan sample is very significantly separated from all surrounding samples (p's all < 0.05).

Several neonate samples were available for study (UF, SMF, ZSI). These samples demonstrate something of the level of variation occurring in the ventral and subcaudal scales among the siblings of single broods (Table 2). These broods were available from mothers originating in Shadatkot, Karachi, Thar Parkar, Quetta, Goa and Kerala. No significant difference between the mean number of either ventrals or subcaudals of the siblings and the means of these variables in the home area of the female was shown in t-test analyses.

Subcaudals.-- Analysis of the subcaudal counts results in a geographic pattern similar to, but less pronounced than that for the ventrals (Fig. 12). The highest mean values of subcaudals are found in the non-coastal areas of Baluchistan, adjacent Iran and Afghanistan. The most significant difference in means of these populations and adjacent ones occurs between the Nushki-Quetta pair populations (means 34-29, t-test = 7.2, df 22, $p < 0.001$). The seaboard populations demonstrate generally low, but not significantly different values from those of the remainder of Baluchistan. Nor are any of the other values significantly different for adjacent pair members through the remainder of the country. The general trend is for values to be reduced into and through peninsular India, but with the Goa and Kerala coastal populations again showing a significantly different mean value. NW Rajasthan (and Lahore) have high mean values (33-34), but they are not significantly different by t-test analysis.

Dorsal Scale Rows.-- Figure 13 shows the geographic pattern of the mean number of dorsal scale rows in Pakistan. The pattern is simple, with no demonstrable significant differences between the means of any adjacent samples. However, the general aspect is similar to that for the subcaudals. Thus the Nushki sample is statistically indiscriminate from the Afghan sample. The Indus River Valley means tend to be low, continuing into India, where peninsular samples have lower means than northern ones. However, the means of the west coast peninsular samples are not significantly different from those of the remaining ones. The NWFP and Islamabad samples are low when compared to the Indus Plains samples (but not significantly different). There is no demonstrable difference between the mean of the NW Rajasthan sample and those of surrounding areas.

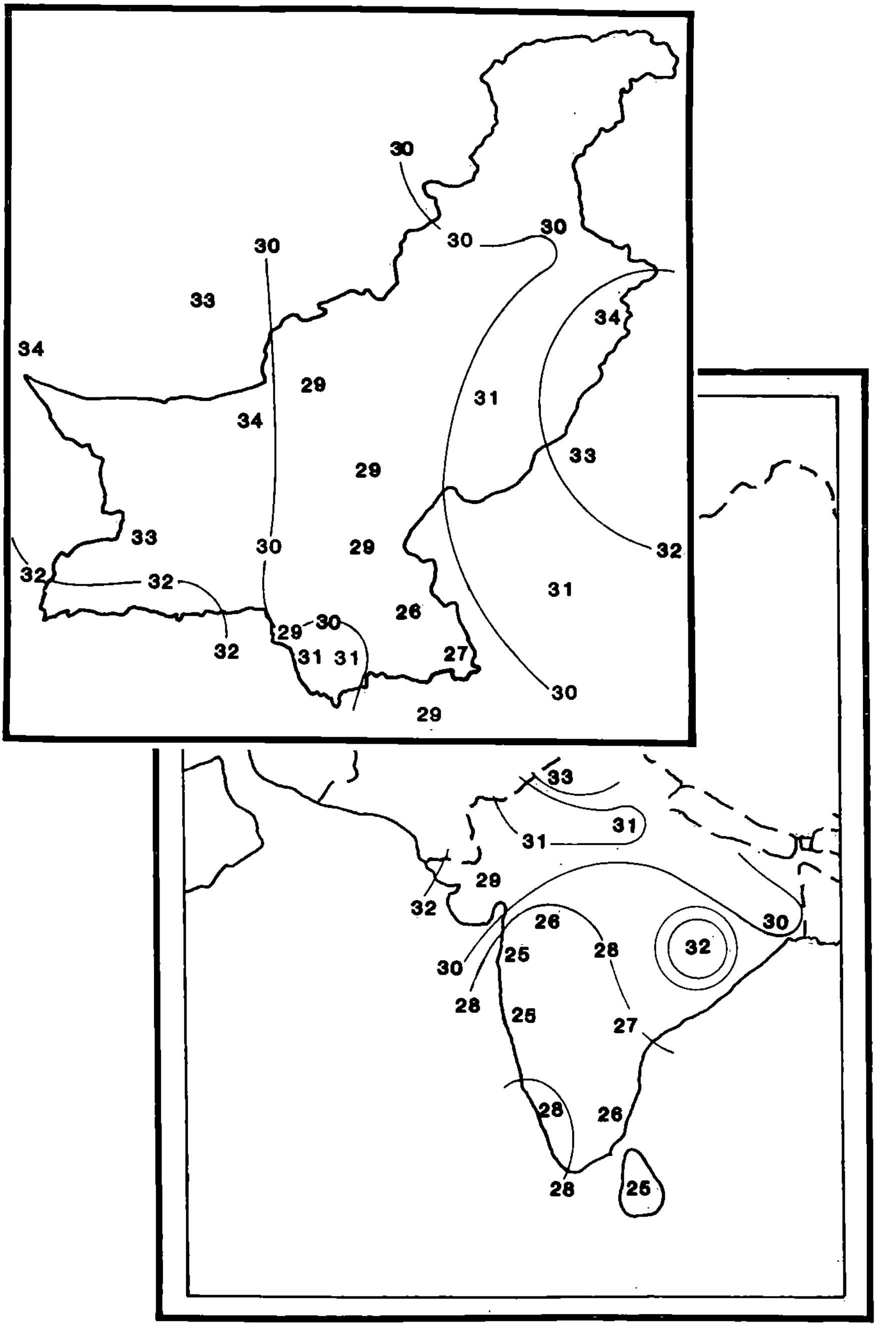

Figure 12. Mean numbers of subcaudal scales in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

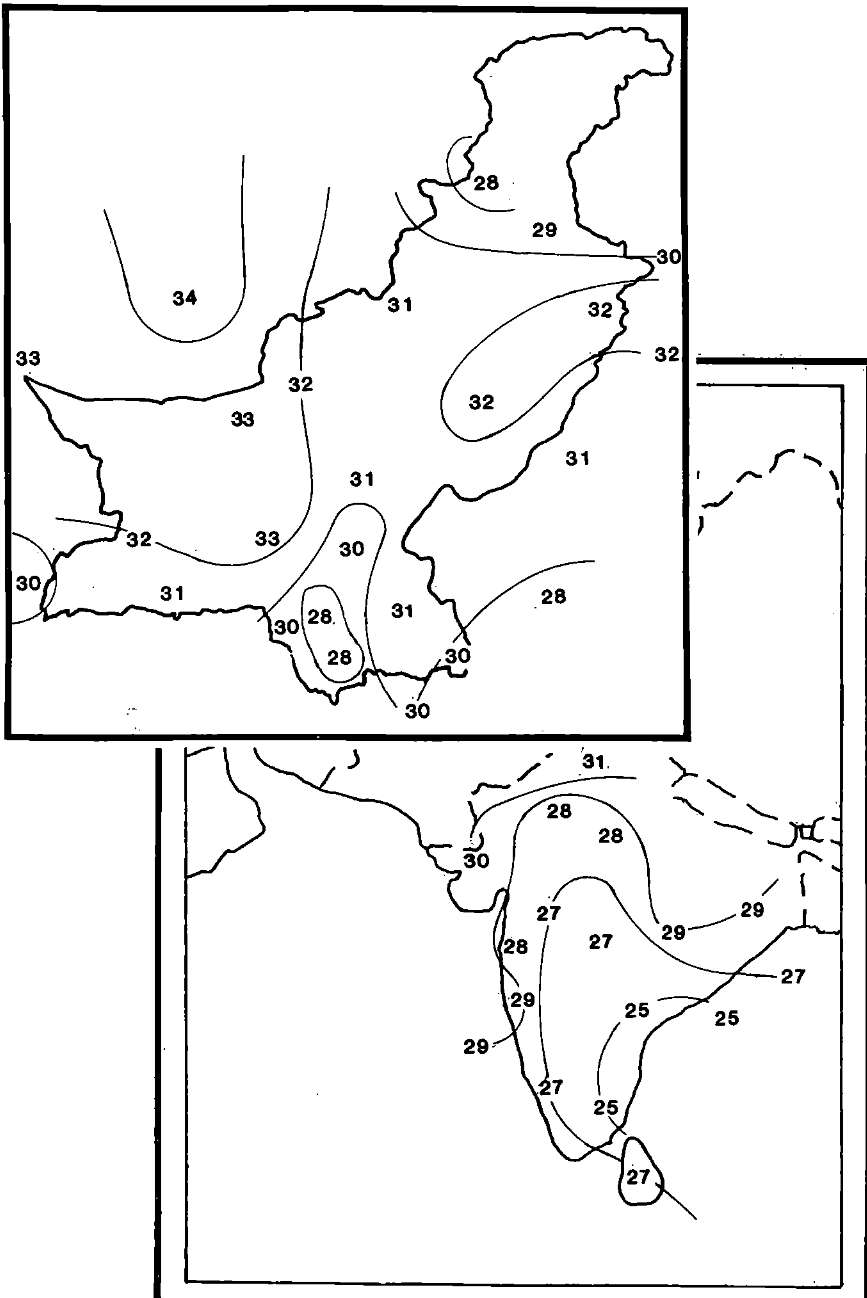

Figure 13. Mean numbers of dorsal scale rows in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

Oblique Scale Rows.-- The general pattern for this character (Fig. 14) is similar to the previous one for dorsal scale rows. The two, are in fact, correlated ($R = 0.88$). There is no demonstrable statistical difference in means between any adjacent Pakistan population. The means of samples from eastern Iran (7), western Baluchistan (7) and Afghanistan (8) are very clearly higher than the means for any other part of the country (3-6), with the exception of NW Rajasthan (7). The lowest value (3) occurs in Nagar Parkar. In general, the Indus Valley has rather low values.

Gular Scale Rows.-- In spite of the fact that the range in gular scale row variation is rather narrow, means of adjacent samples are often significantly different. The geographic pattern is shown in Figure 15. Means range from 5.0 (northwestern Baluchistan and Karachi) to 3.0 (Shah Bundar). The entire Thar Desert and Ganges areas are higher than surrounding samples, but the means are not significantly different. However, the Nushki sample mean (5.0) is significantly different from that of the Quetta sample mean (3.9; $t = 9.4$, df 19, $p < 0.001$). The Shah Bundar and adjacent Gujarat mean values (3.0, 3.3) are significantly different from all the surrounding ones ($p < 0.025$--< 0.001). While none of the peninsular Indian samples differ significantly from one another, that from Gujarat is clearly separable from that from Bombay ($t = 6.7$, df 24, $p < 0.001$). South along the west coast of India there are additional significantly different mean values in adjacent populations, especially that separating the Goa sample from it's neighbors ($t = 5.5$, df 42, $p < 0.001$). The Sri Lanka and Tamil Nadu mean values are also significantly different ($t = 8.6$, df 11, $p < 0.001$).

Number of Suboculars.-- The lowest mean values for subocular scale rows are found in southern peninsular India and Shri Lanka and the highest ones in the northwestern parts of the range, such as Afghanistan and the border area surrounding it. Typical examples of geographic variation in subocular scalation is shown in Figure 3; the pattern of geographic variation is shown in Figure 16.

Supraocular development.-- In some individuals, an enlarged supraocular scale may be present on one side and not on the other (to 25% of those with developed supraoculars). However, the majority are symmetrical. The geographic variation in the presence of enlarged supraocular scales is shown in Figure 17. Here, the pattern is one in which there are significant changes between the southern Afghanistan population (identical to Transcaspian material) and all border samples in adjacent Iran and Pakistan. The Cholistan-Thar Desert and Nagar Parkar samples are also distinctive in all individuals having a well-developed supraocular. However, the Shah Bundar sample,

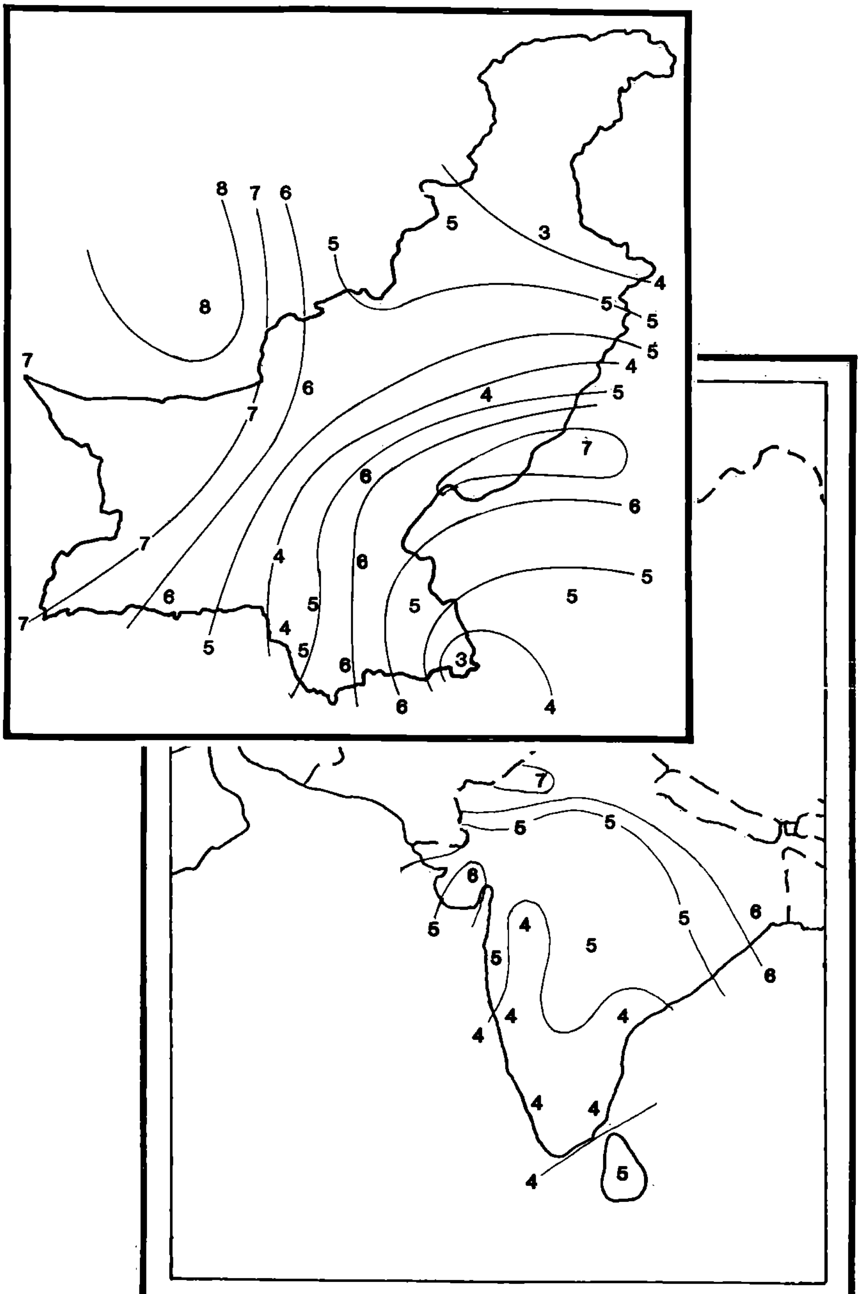

Figure 14. Mean numbers of oblique scale rows in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

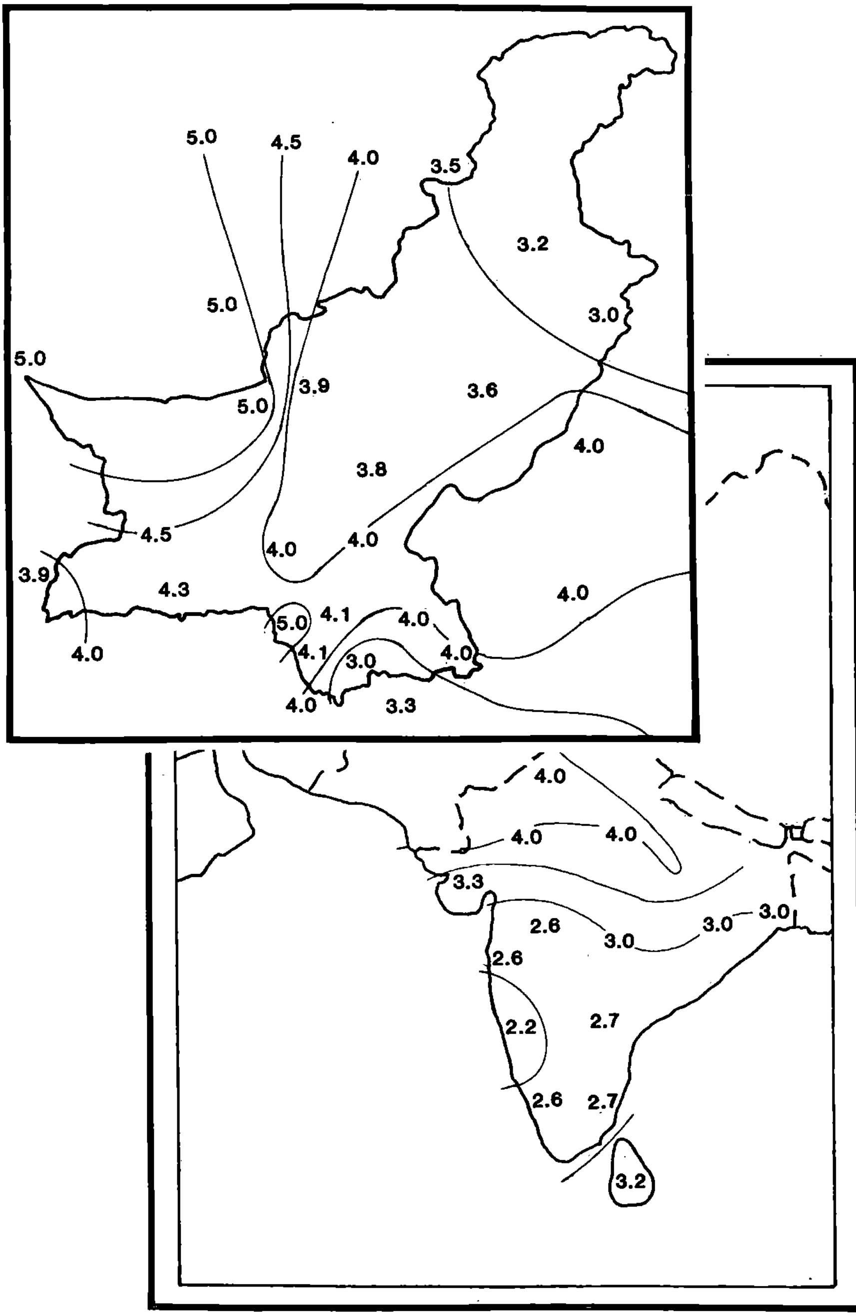

Figure 15. Mean numbers of gular scale rows in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

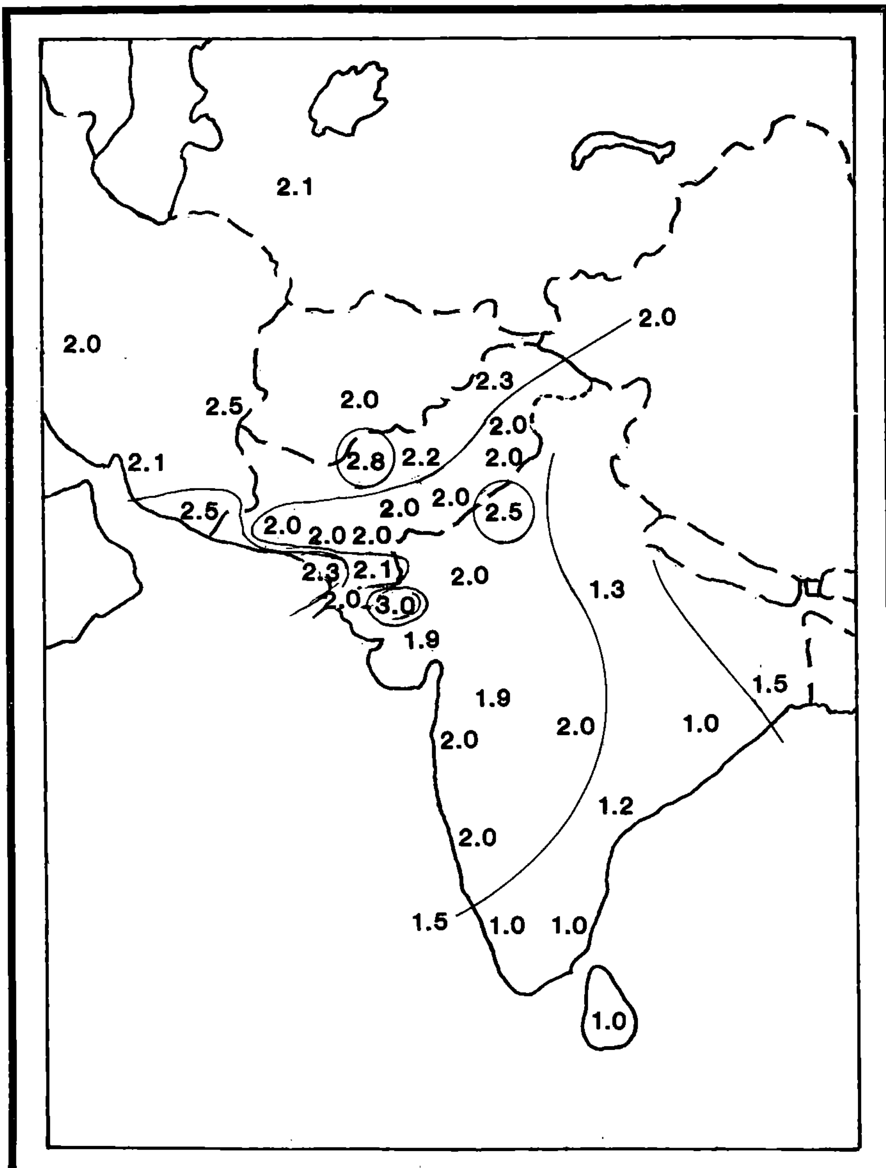

Figure 16. Mean minimum numbers of subocular scale rows in *Echis carinatus* populations studied in Pakistan (left) and in India (right), with estimated positions of isophenes of identical values.

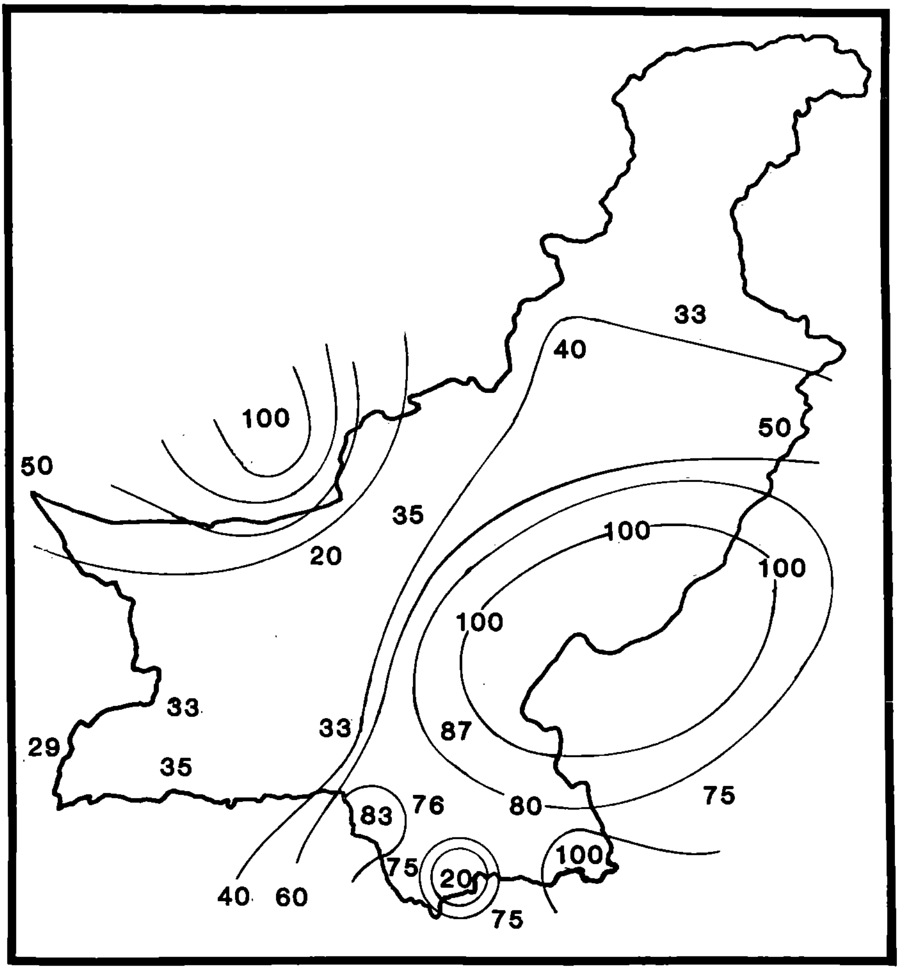

Figure 17. Mean percent of sample areas with developed supraoculars in *Echis carinatus* populations studied in Pakistan and India, with estimated positions of isophenes of identical values.

having a low proportion of individuals with well developed supraoculars, is surrounded by samples in which significantly few individuals have supraoculars.

Dorsal body color pattern.-- Figure 6 shows the extremes of dorsal color pattern found in Pakistan samples. The dorsal color pattern of Pakistan saw-scaled vipers is characterized by having a series of short, light, transverse ovals across the the paravertebral area (Figs. 5, 6) from just behind the head to at least above the cloaca, often onto the tail. These ovals are often broken into two paravertebral spots that are sometimes connected with a diagonal dark zone that in some individuals produces a dark vertebral zig-zag, part or all the way down the back (Fig. 6); in the Astola Island population (*E. c. astolae*) these markings become distinct narrow transverse bars (Fig. 6). Specimens from the adjacent Mekkran Coast population are sometimes similar, but less distinctly barred. Table 4 summarizes the most common color pattern types in each sample area. A single individual out of over 350 examined by the junior author from Makli, Sindh, was provided with three vivid longitudinal stripes, without any evidence of spot rows I and II.

In Pakistan, the mean number of dorsal body spots varies from 31 (Lahore and Rattankot) to 40-41 (Cholistan-Thar Desert area). Baluchistan populations have more dorsal spots than those in the Indus Valley (Fig. 18). In spite of the low level of variation over the entire area studied, there are many statistically significant differences between adjacent population means, suggesting that this is a sensitive character, useful in differentiating *Echis carinatus* populations. These differences are shown in Table 3.

In general, the Pakistan pattern is part of the general trend within the Indian Subcontinent, i.e., higher values northwestward and lower values southeastward. The trend into peninsular India is an extension of the Pakistan pattern, except that Goa and Kerala have a significantly lower mean number of spots of all of the remaining Indian samples. It differs most from the Tamil Nadu sample ($p < 0.001$). The Sri Lanka and Tamil Nadu samples are not significantly different from one another.

The density and distribution of melanin in the dorsal blotches varies geographically in Pakistan, though exhibits a fair degree of variation within single populations. Character state A (Fig. 6A), in which the melanin distribution may be dense, though found on only parts of the scales making up the blotch (mean number of scales involved 13, only a few of which are completely covered), is more or less restricted to arid environments (soil types camborthids and torri- and ustipsamments, fide Atlas of Pakistan, Govt. Pakistan: Islamabad, 1986). It is most common in individuals from extreme western Punjab and the Irano-Pakistan borderlands.

The most common and widespread category in Pakistan is represented as B in Figure 6. It is one in which the melanin is dense and tends to cover most scales entirely. However, the spots tend to be rather small (total 18 scales in

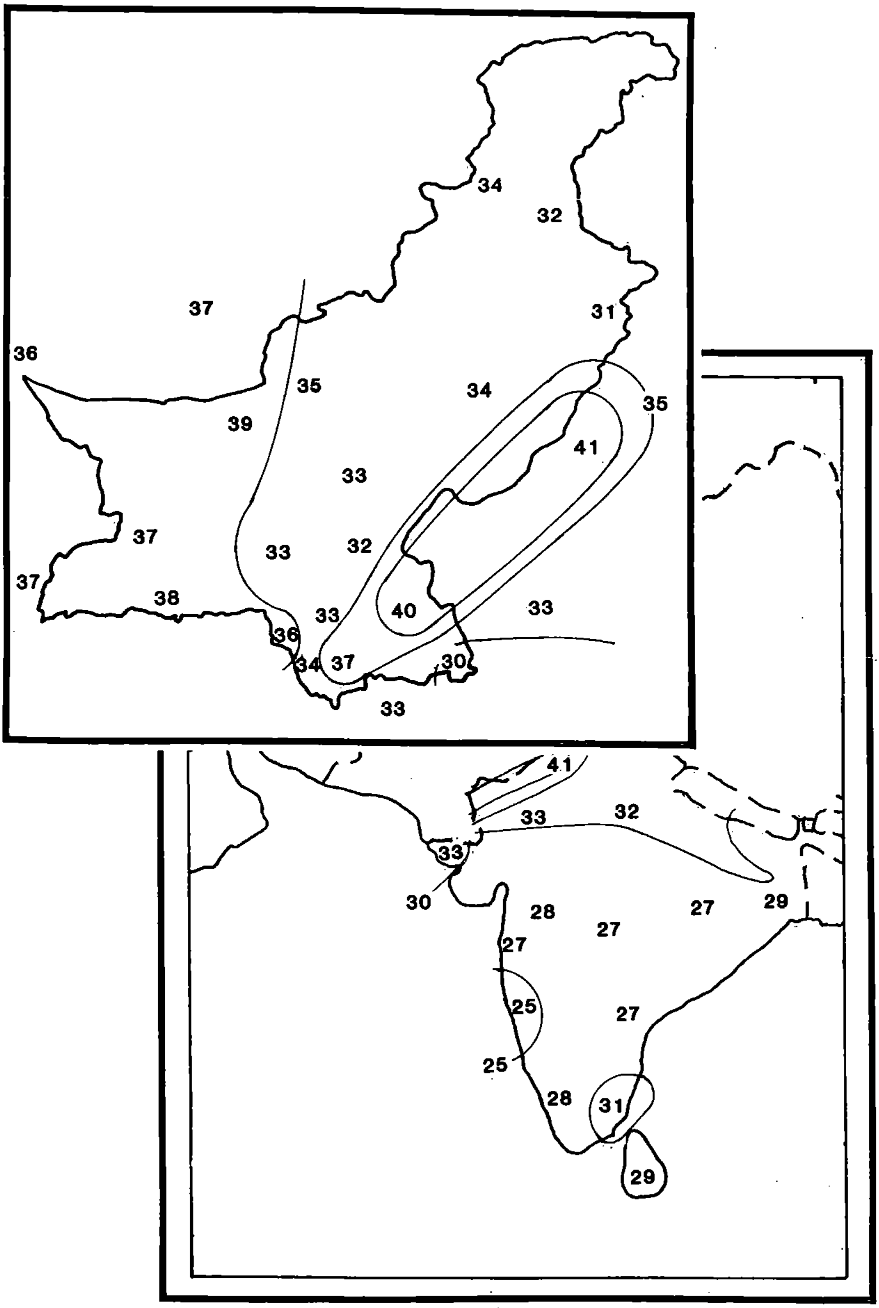

Figure 18. Mean numbers of dorsal body spots in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

mid-body blotches). It is found throughout most of the country, occurring on a variety of soil types (ustorthents to ustipsamments).

The largest blotches are found in the population of Astola Island, Baluchistan (Fig. 6C; blotches include a mean of 22 scales at mid-body). In this population the center of the blotches are usually dark brown and the outer scales black.

As expected, there is significant variation in ground color. In general, it is lightest in populations living on light-colored soils, though not necessarily darkest on the darkest soils. Within Pakistan the darkest individuals are apparently found at Parachinar, NWFP, in which the ground color is grayish brown. In most other localities it is a shade of grey, sometimes locally with tinges of greyish-yellow or pinkish-yellow in life (locally).

Ventral Color Pattern.-- In general, the geographic variation in this character is the same as that exhibited by other variables described above, except that the values tend to be reversed (high means in the other patterns tend to be low means in this one). The highest mean values (darkest spots) are found in inland localities of eastern Iran (Zabol, Gosht, etc.), extreme northern Pakistan (NWFP) and western coastal India (Goa, Kerala). The lowest means (lightest ventral color) are found in central Sindh, NW Rajasthan, and the Dekkan Plateau of peninsular India. Figure 19 shows the geographic pattern of variation in this character. Table 4 gives the values and significance levels for sample pair comparisons.

The density of the color of the ventral markings, or whether they even occur at all, is often rather variable within a single sample. Thus, along the Persian Gulf and Mekkran Coast ($N = 38$) individuals with class 0 belly pattern (clear) occur in 8 percent, class 1 in 50 percent, class 2 in 21 percent, and class 3 in 21 percent. The same level of variation can be demonstrated in the Gujarat and Rajasthan samples. On the other hand, some populations are very homogeneous in this regard, particularly those in desert areas (Nushki, Cholistan-Thar Desert, etc.), where the spots are consistently light in intensity.

Of all the variables examined, the most significant interpopulational differences occur in this character. Table 4 provides pertinent data for those population pairs in which the means of the degree of ventral spotting are significantly different. Figure 19 shows that the trends established through Pakistan are continued into the adjacent parts of India. Prominent features are the slightly darker venters of those populations from both the northern Gangetic and Indus Plain in both countries, extending east to the delta of the Ganges River in West Bengal. The lightest venters are found in a somewhat diagonal strip running from the northwest to the southeast. The Goa area stands out as having significantly darker bellies than surrounding populations (Goa-Bombay, *t*-test, df 32, $p < 0.001$; Goa-Kerala, df 16, $p < 0.005$).

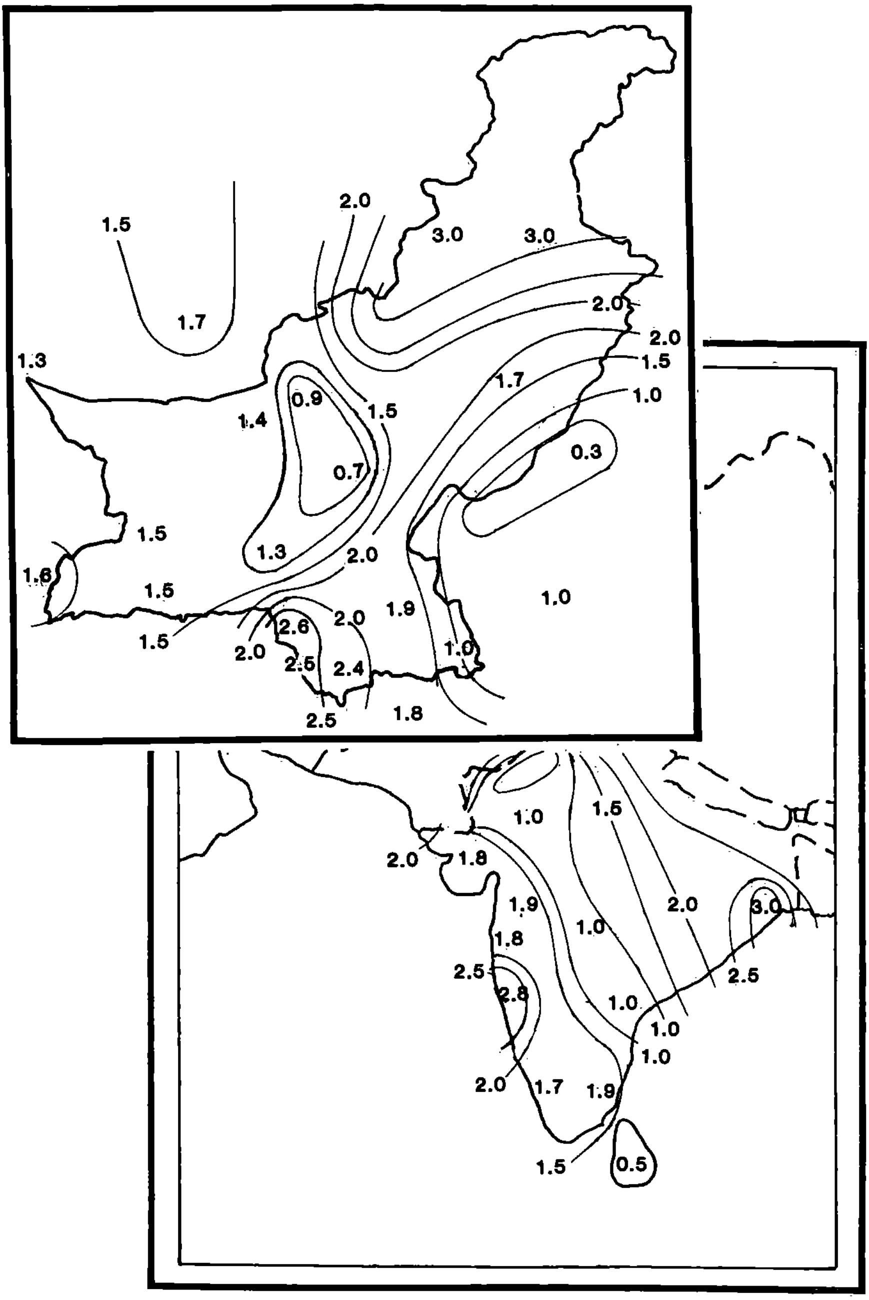

Figure 19. Mean intensities of belly spotting in *Echis carinatus* populations studied in Pakistan (left) and in Indian peninsula (right), with estimated positions of isophenes of identical values.

The size of the ventral spots also varies geographically. In general the spots are largest in those Pakistan populations from both coastal and northern mountain areas, and smallest in individuals from interior desertic environments. The character was not easily divisible into clearly recognizable categories and so was not treated statistically.

Infralabial and genial scale color.-- While the infralabials of some Pakistan populations are more or less uniform white to light grey, others possess up to three (usually two) dark spots on the infralabial scale series. Figure 8 shows the extent of variation in the distribution and density of melanophores on the infralabials and genial scales. In general, those populations with the least melanin are found from northwest India west through most of central Pakistan, thence into adjoining Iran and Afghanistan. Regions in which dark infralabial spots are found are the west coast of India, coastal Pakistan, and the front ranges of the Himalayas in both these countries.

Most Pakistan *Echis* have no melanin on the genial series on the throat; some do. When present, a dusky mark is seen on each of the scales. This character is statistically correlated with the presence of dark infralabial marks (R = 0.72) and has the same general distributional pattern, but less easy to categorize. We have not analyzed this character in detail. Darkness of the infralabials and chin is positively correlated with darkness of ventral spotting (R = 0.78).

Lateral Body Color Pattern.-- The Pakistan populations can be separated into two major groups on the basis of lateral body patterns, those with light lateral zig-zag markings and those with light-colored lateral crescents (Figs. 7, 20A, C). In the material we examined, the zig-zag condition occurs in all individuals in Chagai and adjacent Afghanistan (Fig. 21). It remains common through all of western Pakistan, being present in from 50 to 64 percent of the population. Samples from the entire Indus Valley eastward, except Lahore and Shah Bundar, lack the zig-zags entirely. Instead, the marks are represented by light inverted crescents. In the Himalayan foothills from NWFP east and into the Ganges Plain in India, the zig-zag lateral pattern is found in from 25 to 50 percent of each of the samples. The populations are thus intermediate between the two extreme character states, if not in geographic location. The coastal populations of both Iran and Pakistan are similar. Those from NWFP south along the foothills of the Sulaiman Range are intermediate in both condition and location. Along coastal Iran lateral light markings of any kind are often entirely absent, as they nearly are in insular populations in western Pakistan (i.e., Astola Island). In the eastern half of Pakistan the crescent type pattern predominates (Fig. 21). Between the two extremes (zig-zag and crescent) every gradation of intermediate condition, including bright, evident crescents connected by faint zig-zags. In some populations both zig-zag,

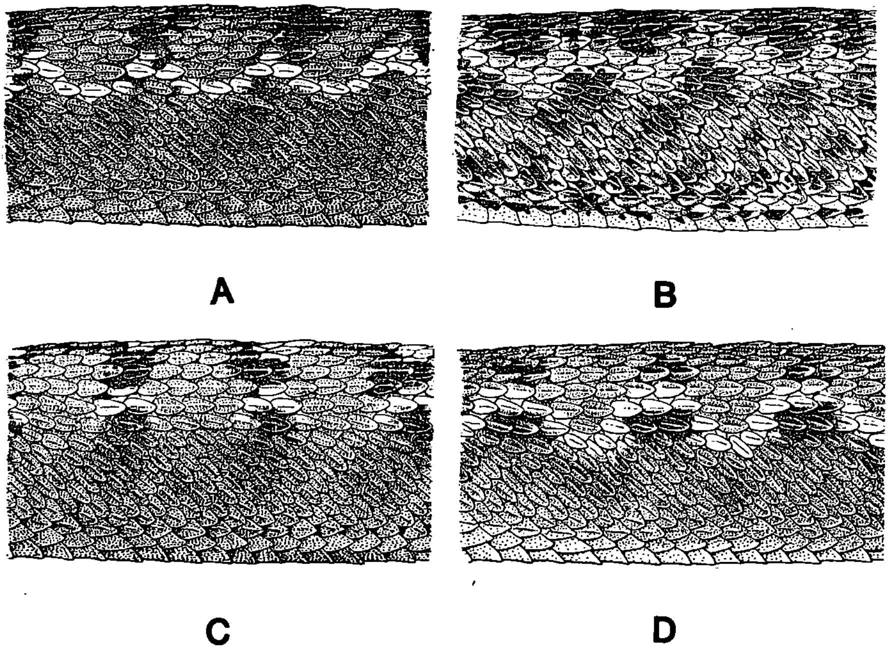

Figure 20. Typical lateral body patterns. (A) dark ground color, bright narrow zig-zag, no evidence of spot row I, faint traces of spots on II, no light crescents, BNHS 2448, Dera Ishmael Khan, Punjab, Pakistan; (B) medium ground color, very dim, wide zig-zag, spot rows I and II both evident, SMF 57356, holotype *E. c. astolae*, Astola Island, Baluchistan; (C) light ground color, crescents present, spot row I absent, II evident, AMNH 81980, Las Bela, Baluchistan; (D) light ground color, zig-zag present, no evidence of spot rows I and II, SMF 63136, Killi Mangal (Hingol), Baluchistan.

crescent and intermediates are equally common; a few individuals have both pattern cycles on their body, the zig-zag usually being found anteriorly and the crescents posteriorly.

Lateral spot rows I and II also vary geographically. Over much of Pakistan, row I is completely missing or very faint, while the spots of row II may be very dark (Fig. 20D). In western Punjab row II may also be absent or only faintly indicated (Fig. 20A). On Astola Island, both rows, with spots of medium density, are present (Fig. 20B).

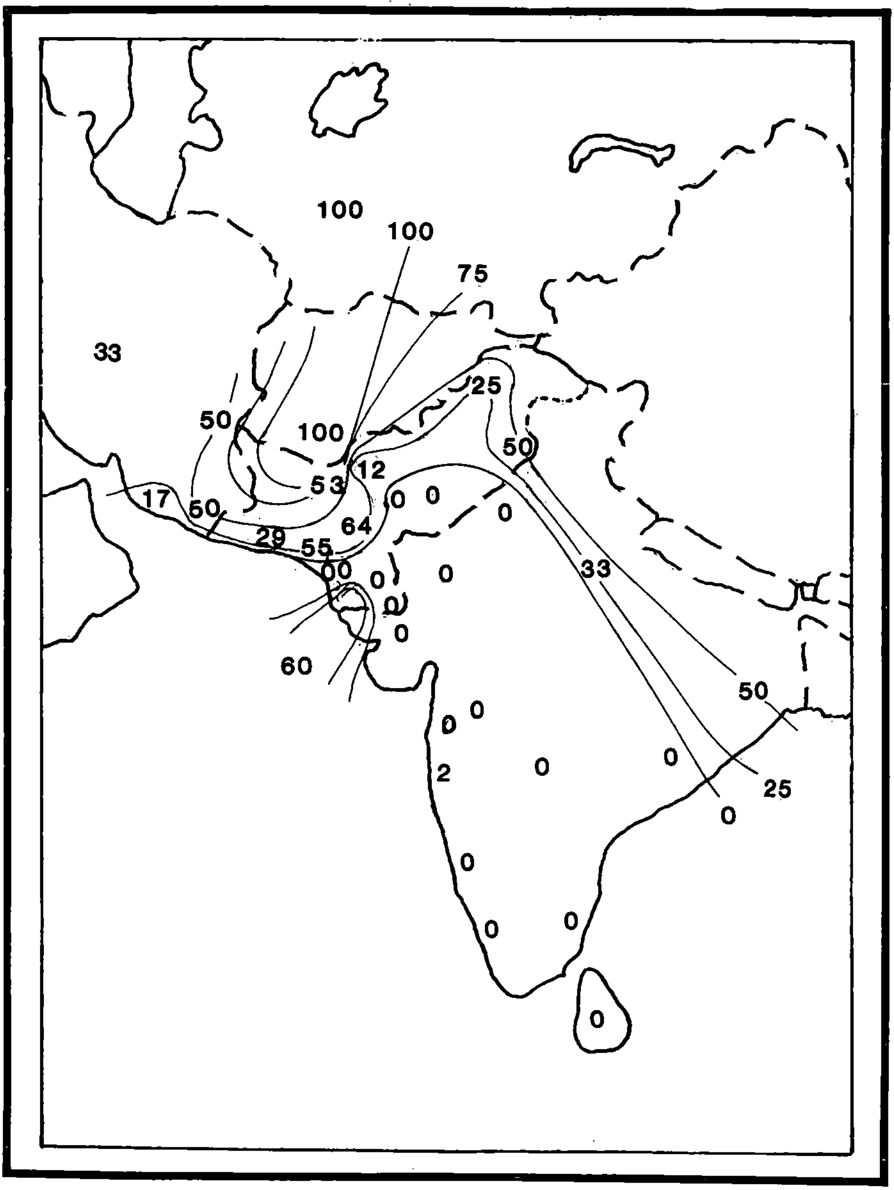

Figure 21. Percent of sample populations with evident light lateral zig-zag.

Head and Nape Color Pattern.-- Figure 9 illustrates major pattern categories seen on the head and neck of Pakistan *Echis*. The trident pattern (Fig. 9D) has only been seen in the Astola Island population. It is undoubtedly a modification of the wide arrow type. The most common types in Pakistan are "arrow" (Fig. 9B) and"cross" (Fig. 9A, C). In general, the narrow cross pattern is mainly found in Baluchistan and adjacent parts of Iran and Afghanistan to as far north as Turkmen SSR. In Chagai District, Baluchistan, it is found in almost all individuals. It occurs in a few individuals of all samples as far east as Andra Pradesh, India. The arrow type is most common in Sri Lanka and southern peninsular India. The wide cross type is most common in the geographically intermediate areas. It is rarely dominant in any of the Pakistan samples studied, the narrow cross type being the most prevalent.

Sexual Variation

An analysis of the entire sample demonstrates that there is no significant difference in the number of males and females, the sex ratio being essentially 1:1. However, Rehman (MS) shows that this sample ratio varies seasonally, depending primarily on the activity level of the males and females during different months of the year. He shows that such differences as exist are correlated primarily with different phases of the reproductive cycle in both the males and the females.

A sample of 64 adult males and an equal number of adult females was randomly drawn from the largest sample available (Thatta, N = 387). On these specimens, the ventrals, subcaudals, dorsal scale rows and the number of dorsal spots were counted, keeping individuals of the two sexes separated. In addition, 66 neonates from several Pakistan and Indian localities (see Table 2 for sample sizes and localities) were similarly examined. No statistically significant differences could be demonstrated between sex and the mean of any of the variables analyzed, except the mean number of ventral scales. For this variable, the mean number in females was significantly higher at a level of about one percent (t = 2.84, df 62 , $p < 0.01$), though the differences between them are slight (males 164.9 ± 6.6, mean deviation 4.6 ventrals; females 169.6 ± 7.7, mean deviation 8.2 ventrals. The females not only have a slightly higher mean number of ventral scales, but they are more variable (CV = 4.5 percent, as opposed to 4.0 in the males).

SUMMARY AND DISCUSSION

Systematics

There is no evidence to suggest that more than one species of *Echis* occurs within the boundaries of Pakistan. We base this on three major points.

First, all the characters studied showed complete blending between them. All gradations of intermediacy were observed, although many of the intermediate conditions were restricted geographically (see below). If two species are represented in the Pakistan populations, one would expect evidence of bimodality in at least some of the characters studied. There is no such evidence in any of the characters. As an example, one of the most geographically sensitive characters we analyzed is the mean number of ventral scales in different populations. Figure 22 compares the frequency curves for ventral scales in individuals taken from Pakistan, where two species of *Echis* were believed to occur, and the same for central to southern Indian peninsula populations, where all workers agree that only one species is found. Neither curve shows any visual evidence of bimodality; nor is there any statistical evidence of bimodality; (moment coefficients of skewness 4.06 for the Pakistan populations and 3.92 for those from the Indian peninsula). However, both are highly kurtotic (moment coefficient of kurtosis 21.52 for the Pakistan sample and 20.90 for the extra-Pakistan samples). This flattening of the frequency distribution is caused by the demonstrated geographic variation in ventral scales in both geographic areas.

Second, at least two forms previously called species (*Echis carinatus* and *E. sochureki*) have bred in captivity and produced young with completely intermediate characters (preserved hybrid HUB 18565).

Third, there is no hiatus in the saw-scaled viper populations of the Indian Subcontinent from at southern Afghanistan and eastern Iran through Pakistan to the furthest reaches of Peninsular India and Sri Lanka. Nor is there any morphological evidence to support the contention that two or more species exist throughout this area. All of the characters we have studied blend completely from west to east through a series of variously intermediate steps. We see no evidence of sympatry in northern Pakistan and/or southern Afghanistan populations of *Echis c. multisquamatus* and *E. c. sochureki* (as presumed by Cherlin 1981).

The name available for this species is *Echis carinatus*. However, within the Indo-Pakistan area we recognize four distinct geographic races. On the basis of priority rule, the nominate form is *Echis carinatus carinatus* (Schneider), found in southern peninsular India and Sri Lanka. It's northern limit is not clear to us because the geographic variation in all the characters examined in peninsular India represent broad morphoclines in which narrow zones of intergradation are not easily defined. An exception is the coastal plain

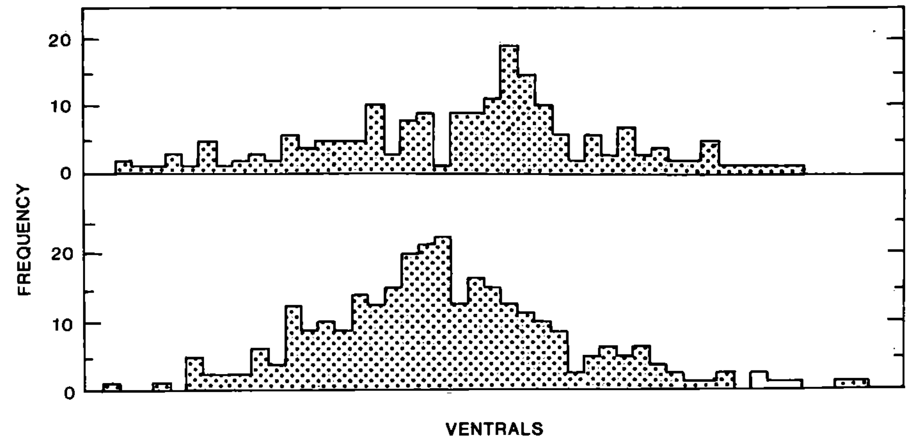

Figure 22. Frequency distribution of ventral scales. Above, Pakistan specimens only; below, peninsular India specimens only.

of Goa and Kerala (India). Here each of a suite of several important characters can be shown to be distinctly different from all surrounding populations. Since the taxonomy of Indian populations is beyond the scope of this paper, we leave clarification of the nomenclatorial status of these populations to others in the future.

Within Pakistan three races of *Echis carinatus* are easily distinguished. These are to carry the names already given them by other workers in the past. One of these is to be called *Echis carinatus multisquamatus* (Cherlin). In Pakistan it occurs in relatively "pure" form in the Chagai area of northwestern Baluchistan (Fig. 23). From here its range extends generally northwest to the type locality in Turkistan, USSR. Southward in western Baluchistan it is replaced by variously intermediate populations. It extends to the Mekkran Coast. The second race is *Echis carinatus sochureki* Stemmler. It is found primarily in the Indo-Gangetic Plain, including most of eastern Pakistan and a large part of northern India (Fig. 23). Intermediates between it and *E. c. multisquamatus* occur in sometimes apparently isolated populations in mountainous areas of eastern Baluchistan and western Sindh. Unfortunately, the type locality (Pishen, Baluchistan) borders on a zone of intergradation with *E. c. multisquamatus*. Relatively pure forms of both races occur closest to one another in the Nushki-Quetta transect, between which there is a narrow band of intergradation. Variously intermediate populations occur in a large part of coastal Baluchistan. As pointed out above, intermediate populations between *E. c. sochureki* and *E. c. carinatus* occur over a large part of central India. A

Figure 23. Taxonomic allocation of Pakistan *Echis carinatus* populations as applied in the current study. The clear area represents the major zone of intergradation.

third subspecies, *Echis c. astolae* Mertens occurs only on Astola Island, Baluchistan. Presumed intermediates between it and *Echis c. sochureki* X *E. c. multisquamatus* are known from several localities along the Mekkran Coast. In many ways this is the most distinct *Echis* population in Pakistan, probably because of its isolated, insular distribution.

Diagnoses of the races occurring in Pakistan are as follows:

Echis carinatus multisquamatus.-- A race characterized by generally more scales in almost all parts of the body and head when compared to conspecifics; i.e., more gulars (means of local populations usually > 4.5), ventrals (means of local populations > 180), subcaudals (means 30-34), serrated oblique lateral scales (means > 7), dorsal scale rows (means > 32), and suboculars (means 2.0-2.8). The supraoculars are almost always discernable. Mean number of dorsal body spots 36-39, distinct white blotch interspaces, and a lateral color pattern, while similar to that of the other races, is provided with a rather wide, vivid light zig-zag stripe. The belly is marked with scattered dark dots; there are usually three dark spots on the infralabials.

Echis carinatus astolae.-- A race characterized by fewer scales of the types mentioned under *Echis c. multisquamatus* (population mean of ventral scales 170 subcaudals 31, dorsal scale rows 31 oblique scales 5.5 gulars 4.3; supraoculars variably distinct or not). It has a body pattern that is considerably darker than that of the other races, with larger dorsal blotches (mean number 38), almost no white blotch interspaces, and in which there are two distinct rows of alternating, rather large dark spots laterally. The belly is marked with scattered small but dark dots. Only about 25 percent of the individuals have a light lateral zig-zag.

Echis carinatus sochureki.-- A much more variable race in regard to almost all of the characters studied. In local populations the mean scalation is as follows: ventrals 154-181, subcaudals 27-34, dorsal scale rows 28-32, oblique serrated scale rows 3-7, gulars 3.2-5.0, subocular scale rows 2, discernable supraoculars in from 33 to 100 percent of local populations. The mean number of dorsal spots varies from 31 to 41; white blotched interspaces are always present; belly spotting varies from none to very intense and lateral zig-zag ranges from none to about half of the individuals in some local populations.

Within the range of *Echis c. sochureki* there are several smaller areas that are important because they contain populations unlike those typical of the subspecies. One of these areas is NWFP and northwestern Punjab. Here a series of characters are statistically different from typical *E. c. sochureki*. With additional material, some future workers may prefer to segregate them as a separate race. We feel that the nomenclature used here defines the biological situation with sufficient accuracy.

A second area of interest lies in the Cholistan-Thar Desert, straddling the Indo-Pakistan border. Here populations of *E. c. sochureki* are distinctly different from surrounding populations in both color and scalation. We believe this population represents an incipient geographic subspecies of *Echis carinatus* that is adapted for life in sandy deserts. However, we do not think it warrants nomenclatorial status.

Zoogeographical Implications

Pakistan (24-37° N lat., 61-77° E long.) is a rather large country (ca. 2000 km east-west and 2200 km north-south, or ca. 805,000 km^2). It serves as a northwest to southeast link between the highly distinct biotas of the steppe, deciduous forests and deserts of temperate Central Asia and the deciduous forests and deserts of Tropical South Asia on the one hand, and as an east to west, arid to mesic link along the northern mountain ranges.

Climatic conditions of Pakistan are characterized by great areas of aridity in almost all parts of the country, including some of the high northern mountain ranges. Except for the Indus River and its tributaries, large rivers and hydric or even mesic riverine forests are few and then only of small extent. Mean annual precipitation varies from less than 100 mm/year in some regions (Chagai and Cholistan-Thar Deserts) to nearly 2000 mm in others (parts of Azad Kashmir); within the range of *Echis carinatus*, it ranges only to about 500 mm. For the most part, abundant rainfall is only experienced in the southern ranges of the northern mountain areas. Within the distribution of the saw-scaled viper, mean warm season temperatures vary from 25-38°C. This viper inhabits southern temperate, subtropical and tropical climatic regions and the following major physiographic provinces: Northern Mountains, Iranian Plateau (much of western Baluchistan), Indus Valley, the Central Mountain Borderland (separating the last two provinces), and the Coastal Plain along the Arabian Sea.

The only previous study of the zoogeography of the entire Pakistan reptile fauna is by Khan (1980), which is more a compilation than an analysis and provides little new information. Other than the current study on *Echis carinatus*, there is no single-species analysis of reptiles for Pakistan that provides details on the probable boundaries of geographically distinct population gene pools. We would have liked to be able to analyze such boundary effects in greater detail, especially from a statistical standpoint. Unfortunately, there are no satisfactory statistical tests of ordination for zoogeographical studies (Gauch 1982). As a result, our conclusions regarding such factors rest on a series of Student *t*-tests between adjacent sample populations. Concordance of statistically significant differences in the mean values between the same adjacent populations suggests significant differences between them in several characteristics. We take this level of concordance as a primary factor in determining the location of zones of least gene flow. We hope to analyze other species in the future and to examine the degree of concordance in gene barriers between species to obtain a more accurate picture of the factors important in the zoogeography of Pakistan reptiles.

Analysis of geographic variation in 13 morphological characters of *Echis carinatus* makes obvious a small number of underlying geographic patterns in this species within Pakistan. Most of the statistically significant differences in mean character values can be shown to exist in a limited number of sample pairs. These sample pairs and the number of characters that are significantly different between them are shown in Figure 24. It illustrates that of all the potentially interacting sample pairs, the greatest number of differences is between the Nushki-Quetta pair (7). It also shows that there is a north-south line representing many differences between adjacent east-west sample pairs from Shadatkot through Central Sindh to Rattankot, separating the Indus Valley populations from those of central and western Baluchistan. There are few significant differences between the various mainland Mekkran Coast samples. Nor are there many significant differences between samples in the remainder of central and northern Pakistan. However, NW Rajasthan is significantly different in a number of characters from all surrounding samples. Lastly, the Indus delta area is represented by a character complex in which almost all samples are significantly different from neighboring ones in one or more characteristics. A similar mozaic pattern of deltaic populations has been described from the mouth of the Mississippi River (U. S. A.) (Wilson 1970). In Pakistan the Indus Delta is the site of some species endemism among both the lizards and the turtles (Minton 1966). We presume that this mozaic of character state distributions in the Indus Delta was produced through repeated isolation of populations caused by dramatic changes in deltaic water distribution channels. The appearance, disappearance, and changing courses of distributaries in the Indus Delta during the past several hundred years are well documented (De Terra and Hutchinson 1936, see Flam 1986 for a recent review) and much older changes during the Quaternary are known for several sites in eastern Pakistan and adjacent India (Oldham 1886, Marshall 1931, De Terra and Patterson 1939, Erikkson 1959). We believe the isolation and reconnection of populations of *Echis carinatus* in this area by changing distributary patterns are directly responsible for the mosaic pattern of character states seen in the delta area. Thus the major part of the between-sample differentiation in this area is believed to have a historic basis.

The north-south line of differentiated populations paralleling the Sulaiman Range and its outliers also seems to have a largely historic basis, for environmental conditions are largely identical on both sides of the dividing zone (Fig. 25). We conclude that the populations on either side of the

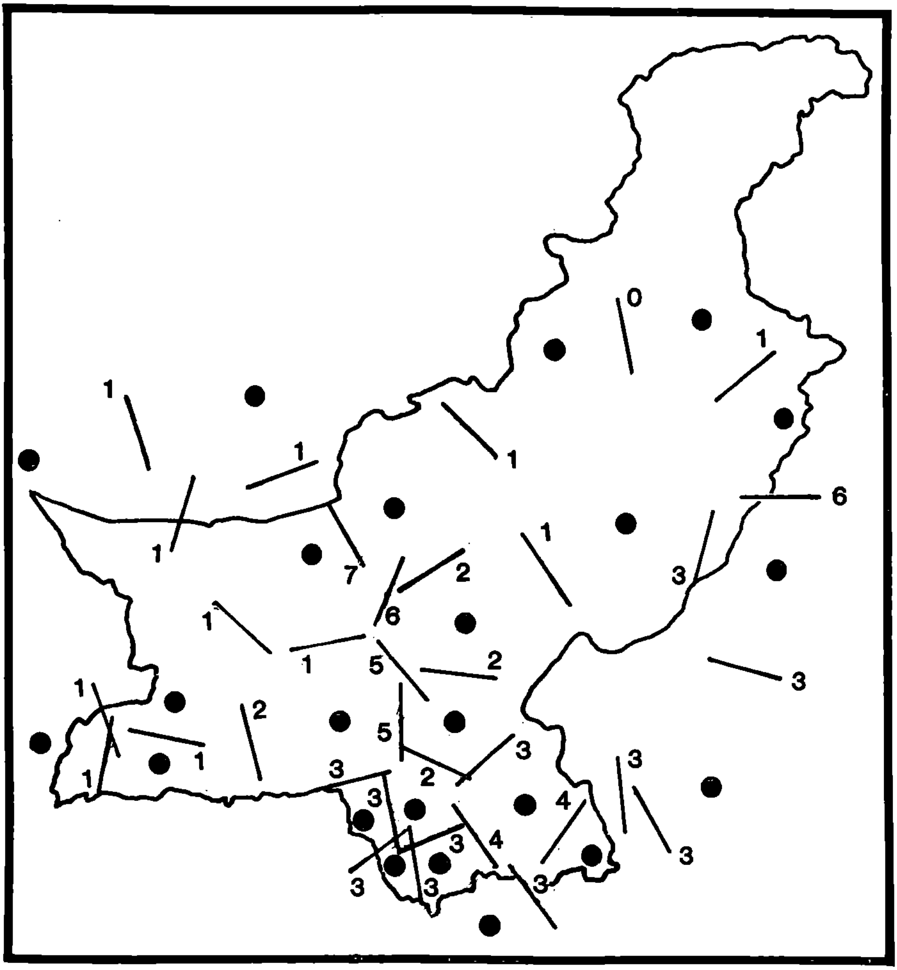

Figure 24. Numbers of statistically different character states between adjacent populations in Pakistan.

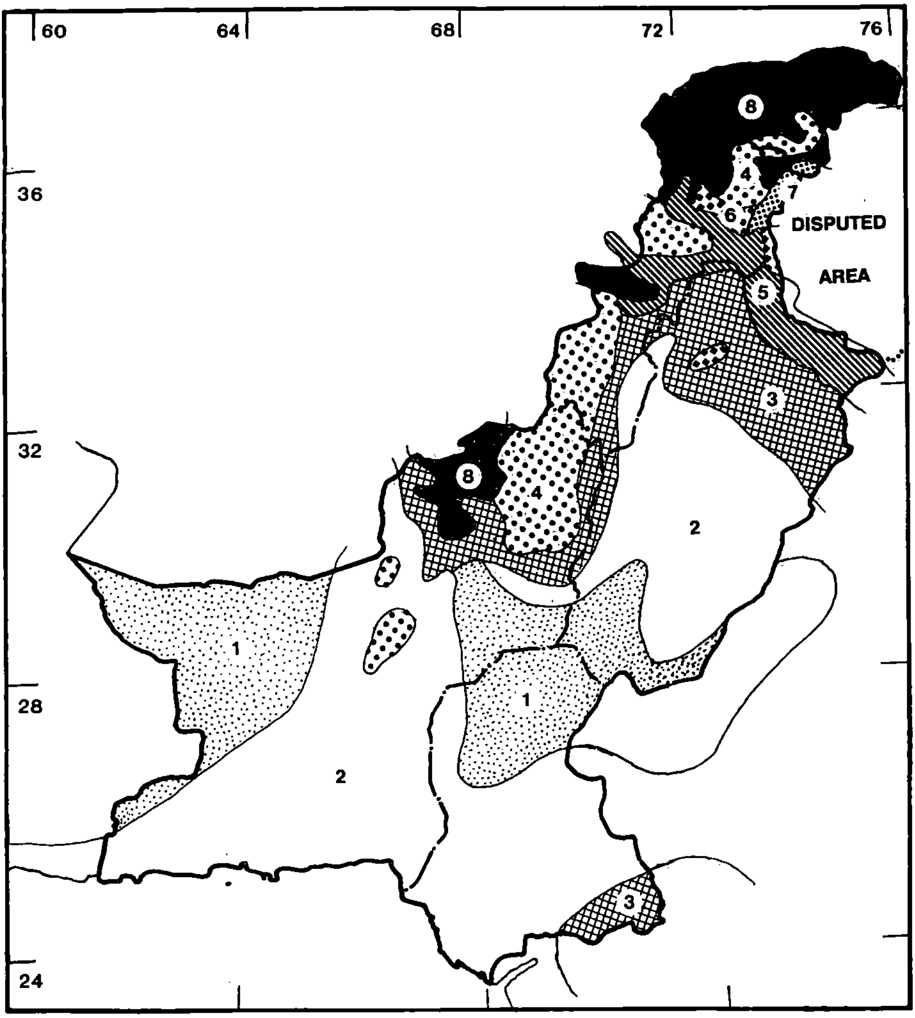

Figure 25. General distribution of natural vegetation types in Pakistan (simplified, but based on Map 52, The Atlas of Pakistan, 1985, Rawalpindi, Pakistan). (1) Desertic; (2), Tropical thorn forests; (3) Tropical deciduous forests; (4) Temperate pine-juniper forests; (5) Subtropical dry pine forests; (6) Temperate dry pine forests; (7) Temperate broad-leafed forests; (8) Temperate pine/steppe (usually interspersed between mountain ranges in north, variously mixed with juniper in south).

mountains arrived there from different directions. Those west of the mountains are clearly closely related to Transcaspian and Iranian Plateau populations and must have arrived from the west and/or northwest. Those east of the mountains have been associated with the Indus Plain for thousands of years. The two populations are more or less genetically isolated by the high Sulaiman Range, the mountains having few passes at low elevations. However, a natural avenue leading from lowland arid lands in the Indus Plain to the arid lands of the Iranian Plateau occurs from near Jacobabad (and the Shadadkot sample) to Quetta across the Bolan Pass (1650 m). This pass is unquestionably a major path for genetic interchange between the Trans-Sulaiman population in northwestern Baluchistan and those of the central Indus Plains. Through appropriate similar habitat (Fig. 25) and climate, the Quetta population is also genetically closely related to those of the NWFP. Thus the fact that the Quetta sample is more closely related to those from Shadadkot (Indus Plain) and from NWFP than to the geographically much closer Nushki sample (Iranian Plateau) seems to be largely a matter of more rapid gene flow through similar habitats than across the borders of dissimilar ones. Apparently a more southern lowland gene pool and/or an eastern subtropical one of *Echis* (*sochureki*) was brought into close juxtaposition with a temperate plateau pool (*multisquamatus*). There is no evidence that the two populations are genetically incompatible, or that they are sympatric, i.e., forming the northern ends of a *Rassenkreis* around the Sulaiman Mountains and through the Bolan Pass. Rather, the two forms seem to blend evenly and completely into one another over a narrow zone of intergradation.

The fact that the *E. c. multisquamatus* character complex is approached by populations in similar desert environments along the eastern borderland of Pakistan (Thar-Cholistan Desert) suggests substantial similarity in certain selective pressures, in spite of the fact that the northwestern deserts are temperate, and the eastern ones are tropical. While populations from this area are distinct from surrounding ones in several characters, the number and kind of differences suggest they are most closely related to those of the Indo-Gangetic Plain. The differentiation witnessed is probably based on factors associated with the Pleistocene local desertification of the area (Karpov and Nebolsine 1964, and others).

The character differences exhibited between the Nushki-Quetta and NW Rajasthan-Multan populations reflect points along two ecoclines (sensu Auffenberg 1955), rather than geoclines, for environmental conditions on either side of the intermediate zones are significantly different (desert versus non-desert). Other ecoclines may include the change in characters between the population of northern and southern India, and from Nushki to the Mekkran Coast. Probably most significant are the series of clines between the Himalayan foothills (more mesic) to the central Indus Plain (more arid). The differences in the latter are along a north to south, cooler to warmer environmental gradient. Among others, Edgren (1961), Smith (1956), and Christman (1980) have demonstrated the common existence of important north-south clines in the mean scale values of snakes, so that this particular series of clines in *Echis* is perhaps expected. However, other important clines in Pakistan *Echis carinatus* are clearly east-west. The several character clines along the Mekkran Coast Coast are examples. While the Himalaya-Indus Plain changes are clearly ecoclines of some sort, those of the Mekkran Coast are not, for environmental conditions from the Iran border to at least the Hab River are very similar, yet changes in mean character states occur in a regular pattern. Fox et al. (1961) have shown a positive correlation between developmental temperature and meristic counts in snakes. Thus the developmental temperatures of embryonic snakes may be the mechanism maintaining the clines witnessed, but if so, the adaptive significance remains to be discovered.

Possible Selective Forces

In *Echis carinatus* some of the most important characters showing significant geographic variation are scales. Some of the clines demonstrated in *Echis* meristic characters are clearly ecoclines (sensu Auffenberg 1955), maintained by adaptation to environmental conditions that also vary clinally. A true geocline occurs in northern peninsular India. Within Pakistan, the patterns of variation in such characters as ventral scales are ecoclines on the basis of the fact that they are repeated at the ecotones between desert and non-desert environments at opposite ends of the country.

Cherlin (1983b) suggested there is an important positive relationship between the mean number of body scales (longitudinal ventral rows and transverse dorsal rows) of *Echis* species and climate (mean relative humidity X average annual temperature/average annual daily range of air temperature). However, his formula has never been tested by analysis of meristic characters within a single species.

Scrutiny of the isophenic maps of geographic variation in the scalation of *Echis* in Pakistan suggest that these patterns may indeed be correlated with climatic condition. Thus, higher scale counts and lighter colors are often associated with arid environments (particularly the Cholistan-Thar Desert [=NW Rajasthan sample, in part] and Chagai Desert [=Nushki sample, in part]; see Fig. 25 for major vegetation zones in Pakistan; Table 5 relates our sample areas to these vegetative zones). We thus turn our attention to an analysis of these characters in reference to climatic factors.

Spearman Rank Correlation values (= R_S) and corrected *z* values were calculated for the relationship between a number of the more distinctive geographic patterns of meristic characters and certain climatic factors. The meristic characters selected were the mean number of dorsal spots, ventrals, and gulars; the climatic factors were mean annual temperature, and the mean daily maximum and mean daily minimum temperatures for April, May, June and July (separately). These are the months when saw-scaled vipers are most active in Pakistan (Rehman, MS). We also obtained correlation for these important meristic characters and the Cherlin climatic "equitability" formula.

Our results show there is no significant correlation between the mean number of ventral scales and Cherlins climatic value for the same geographic points (R_S 0.10, z 0.36). However, we found a significant negative correlation (p 0.02) between mean ventrals and mean annual rainfall at each sample site (R_S 0.35, z 1.22, p 0.02). Samples with low rainfall areas are not only arid, but hot in summer, and we believe that temperature is, in this instance, more important than precipitation (many desert areas in Pakistan fail to get rain for several successive years). The correlation between ventrals and mean annual daily maximum temperature is not significant (R_S 0.06, z 0.21, $p < 5\%$). Nor is there a significant correlation between mean daily maximum temperatures and mean ventral number in April (0.22, z 0.45 respectively). However, the same correlations for June (0.33, 1.15) and July (0.32, 1.12) are both barely significant at the five percent level. For May, the correlation shows a higher significant value (0.53, 1.84, $p < 4\%$). In general, the mean daily minimum temperatures shows a similar range of from poor to fair correlations with mean ventral number (May R_S 0.43, z 1.46, June R_S 0.18, z 0.64). July daily minimum temperatures shows the best correlation of all (R_S 0.63, z 2.18, $p < 0.05$). These minimum temperatures occur during the night, when most individuals forage (Rehman, MS).

The number of dorsal blotches also show a geographic pattern significantly correlated with the mean number of ventral scales (R_S 0.79, z 3.96, $p < 0.02$), but a consistently low correlation with mean daily maxima or minima. Nor is there a good correlation between any climatic factor and the mean number of gulars. Thus of all the significant geographic patterns in meristic characters, ventral scales appear to show the best correlation with climatic factors.

Figure 26 provides data on the distributional pattern of mean summer high temperatures. It shows that within the Pakistan area the highest mean summer highs are achieved in western Baluchistan and NW Rajasthan--exactly those areas in which most of the mean scale counts are highest. Within the range of *Echis carinatus* in Pakistan, the mean daily minimum summer temperatures occur in areas of deciduous and mixed, rather than thorn brush habitats (Table 5, Fig. 26). These areas also tend to have proportionately lower scale counts. The same pattern can be demonstrated in dorsal and ventral color density, for the colors are least intense in desert areas and most intense in forested areas (a typical, world-wide pattern). In the Indian peninsula, *Echis carinatus* from the relatively cooler (Fig. 26), more moist and

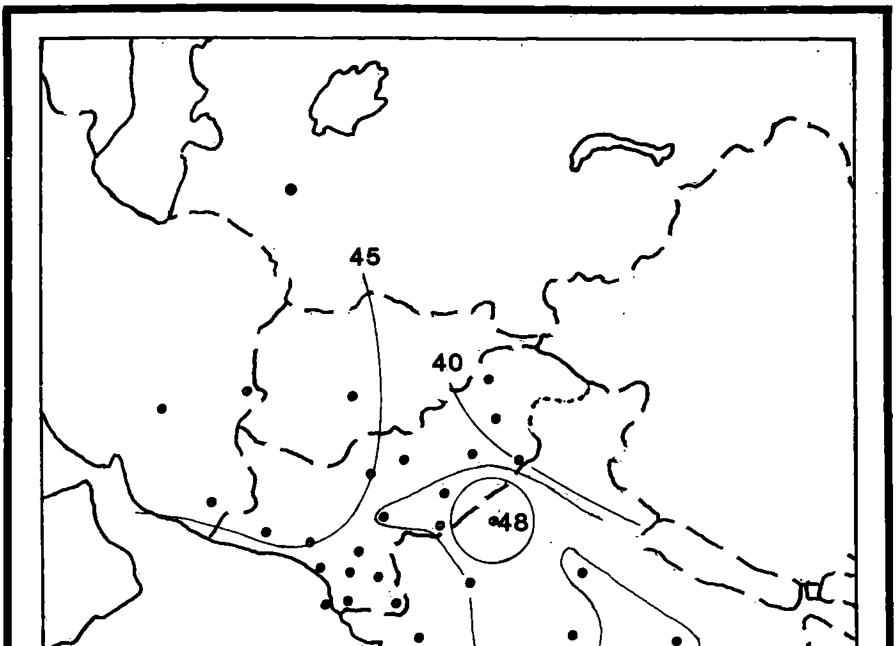

Figure 26. Mean high summer temperatures in the Indian Subcontinent (modified from Atlas of Pakistan 1986 and Koteswarum 1974).

more heavily forested Goa-Kerala area are significantly darker and with fewer scales than those populations in the remainder of the peninsula.

In his study of the effects of temperature on the scalation of *Echis* species, Cherlin (1983b) developed what he termed a "dorsal scale index." It is determined by multiplying the number of ventrals by the number of middorsal scale rows. This is a very useful statistic, for it provides a comparative statement of the relative number of scales covering the back. From a physiological standpoint it is useful in providing an index of the amount of skin between the scales, for this is where water loss occurs, and thus evaporation takes place. Snakes with more scales have proportionately more skin exposed per body surface. The more evaporation the greater potential for lowering high body temperatures during near-lethal limits at the high end. The physiological basis of the importance of Cherlin's index has not yet been unquestionably demonstrated. However, when we plot the values geographically we find that the geographic pattern of mean values follows the common one shown previously for ventral and dorsal scales; i.e., highest values in northwestern Baluchistan (Chagai Desert) and northwestern Rajasthan and adjacent Pakistan (Cholistan-Thar Desert), the lowest in NWFP and along the foothills of the Himalayas. Statistically significant differences in the means of adjacent populations occur between Nushki-Quetta, Karachi-Kirthar, Multan-NW Rajasthan, Lahore-NW Rajasthan, and Rajasthan-NW Rajasthan samples. There is no statistical correlation between Cherlin's scale index and mean daily maximum summer temperatures (R_2 0.01), or the scale index and mean minimum summer temperatures (R_2 0.03).

While critical thermal maximum value has not yet been determined for *Echis carinatus*, we presume it is close to 40°C, as such values are for most snakes (Lillywhite 1987), regardless of their environmental preferences (Spellerberg 1972). Thus, during the hottest seasons of the year it is only at night when temperatures are sufficiently reduced to allow active foraging on the surface (30-37°C Rehman, MS). It follows that the daytime highs are probably the most critical during the hot seasons, and though the snakes are then usually in abandoned rodent burrows (Rehman MS), daytime burrow temperatures sometime exceed 35°C in arid parts of Pakistan (Auffenberg MS).

Brown (1957) defines centrifugal speciation as that process by which populations central to the point of speciation for that subspecies evolve much faster than peripheral populations. Thus the most distant populations receive adaptive genes more slowly, determined by the rate of gene flow in that direction. The more distant a population, the more time it will take for an evolutionary change to reach it. Populations completely isolated (such as *Echis carinatus astolae*, on an island) may never acquire newer adaptations, and thus remain "primitive" with respect to those adaptations. We believe this hypothesis best explains most of the kind and degree of geographic variation witnessed in this study.

Our studies on *Echis* populations in the Indo-Pakistani area suggest there are five recognizable major adaptive centers. These are Transcaspia, Iranian (out of our main area of study), Astola Island (minor), Indo-Gangetic Plain, Himalayan foothills, and Cholistan-Thar Desert. We believe that the gene flow from these four adaptive areas account for most of the geographic patterns seen in the characters we studied. The only other factor considered important is the pattern mosaic in the Indus Delta, which is believed due to distributory shifts during the Pleistocene and possibly Post-Pleistocene.

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TABLES

Table 1. Geographic variation in number of mean ventral scales in those adjacent populations (Pakistan and border sites) showing significant differences in their means.

Sample Pairs	Ventrals	df*	*p**
Afghanistan-Quetta	181-165	22	< 0.001
Quetta-Nushki	165-183	22	< 0.001
Thar Parkar-Gujarat	158-162	27	< 0.01
Thar Parkar-Nagar Parkar	158-168	25	< 0.01
Multan-NW Rajasthan	165-181	10	< 0.03
Lahore-NW Rajasthan	162-181	8	< 0.05
NW Rajasthan-Rajasthan	181-158	14	< 0.01

* df, degrees of freedom; *p*, probability on basis of Student's *t*-test.

Table 2. Variation in ventral and subcaudal scales among siblings in single broods of Pakistan and Indian *Echis*.

Locality	Ventrals			Subcaudals		
(N)	OR*	Mean	SD*	OR*	Mean	SD*
Goa, India (4)	140-143	142.2	1.7	24-26	25.3	1.0
Kerala, India (3)	149-152	150.3	1.3	29-30	29.7	0.6
Thar Parkar, Pakistan (7)	154-160	157.0	1.9	25-27	26.3	1.0
Thar Parkar, Pakistan (12)	154-162	158.6	2.6	23-30	26.4	2.5
Karachi, Pakistan (12)	159-173	164.8	4.7	27-35	29.1	2.1
Shadadkot, Pakistan (20)	162-177	169.6	5.0	26-36	29.4	2.4
Quetta, Pakistan (8))	162-171	165.7	3.1	24-34	28.4	3.7

* OR, Overall range; SD, standard deviation.

Table 3. Geographic variation in number of dorsal spots in those adjacent populations (Pakistan and border sites) showing significant differences in their means ($p < 0.5$) (abbreviations as in Table 1).

Sample	Means	df	p
Nushki-Quetta	39-35	22	< 0.001
Quetta-Shadadkot	35-31	19	< 0.1
Karachi-Ratan kot	36-31	31	< 0.001
Karachi-Mekkran Coast	36-38	29	< 0.25
Shah Bundar-Thatta	37-33	302	< 0.01
Shah Bundar-Thar Parkar	37-40	33	< 0.1
Shah Bundar-Gujarat	37-33	27	< 0.1
Thar Parkar-Thatta	40-33	310	< 0.1
Thar Parkar-Gujarat	40-32	27	< 0.01
Thar Parkar-Central Sindh	40-32	22	< 0.1
Thar Parkar-Rajasthan	40-33	15	< 0.5
NW Rajasthan-Lahore	41-31	8	< 0.1
NW Rajasthan-Multan	41-34	11	< 0.1
NW Rajasthan-Central Sindh	41-32	12	< 0.1

Table 4. Geographic variation in degree of darkness of ventral spots in those adjacent populations (Pakistan and border sites) showing significant differences in their means ($p < 0.5$) (abbreviations as in Table 1).

Sample	Means	df	*p*
Nushki-Quetta	1.4-0.9	22	< 0.001
Karachi-Mekkran Coast	2.6-1.5	28	< 0.001
Shadatkot-Cent. Sindh	0.7-2.0	15	< 0.010
Lahore-NW Rajasthan	2.0-0.3	8	< 0.050
NW Rajasthan-Cent. Sindh	0.3-2.0	11	< 0.050
Rajasthan-Thar Parkar	1.0-1.9	27	< 0.025
Thar Parkar-Nagar Parkar	1.9-1.0	23	< 0.025
Gujarat-Nagar Parkar	1.8-1.0	22	< 0.010
Karachi-Kirthar	2.6-1.3	32	< 0.010

Table 5. *Echis* sample areas and the general vegetative zones in which each is located.

Sample Area	Zone	Sample Area	Zone
Multan	Thorn Brush	Islamabad	Subtrop. Pine
Cent. Sindh	Thorn Brush	Lahore	Trop. Decid.
Thar Parkar	Thorn Brush	NWFP	Trop./Subtr. Pine
Thatta	Thorn Brush	Quetta	Temp. Jun./Pine
Karachi	Thorn Brush	Nagar Pakar	Trop. Decid.
Ghost	Thorn Brush	Zabol	Temp. Desert
Mekkran Coast	Thorn Brush*	Afghanistan	Temp. Desert
Panjgur	Thorn Brush	Nushki	Temp. Desert
Rattankot	Thorn Brush	NW Rajasthan	Trop. Desert
Shah Bundar	Thorn Brush	Shadadkot	Trop. Desert
Rajasthan	Thorn Brush	Gujarat	Thorn Brush
Parachinar**	Temp. Pine		

* Mekkran Coast thorn brush is rather different from that of the remaining Indus Valley types (see Beg 1983 for review).

** Included in NWFP throughout this publication, but separated here because *Echis carinatus* from Parachinar are very dark.

APPENDIX I

Locality data and present museum location for specimens examined during this study.

Locality	Museum
nr. Abadan, Iran	SMF
Ajmere, Rajasthan, India	ZSI
Allahabad, Gujarat, Iran	ZSI
Amballa (100 mi. S), India	ZFMK, MCZ
Aram, Fars, Iran	FMNH
Aschabad, Turkmen SSR	SMF
Astola Isl., Baluchistan, Pakistan	SMF
Badin, Sindh, Pakistan	ZSD
Balchany, Transcaspia SSR	ZIN
Bampur, Iran	SMF
Bamrud, Iran	ZIN?
Bangalore, Karnataka, India	ZSI
Bhavnagar, Gujarat, India	BNHS
Bhit Poochari, (Punjab ?), Pakistan	RSM
Bombay, Maharashtra, India	BNHS
Bushire, Iran	ZSI
nr. Cancona, Goa, India	ZSI
Cape Monze, Sindh, Pakistan	RSM
Chabar, Persian Gulf, Iran	BNHS
Chumbum, Tamil Nadu, India	BNHS
Colombo, Sri Lanka	SMF
Deesa, Gujarat. India	BNHS
Dera Ismail Khan, NWFP, Pakistan	BNHS
Dhabiji, Sindh, Pakistan	ZSD
Dir, NWFP, Pakistan	PMNH
Dureji, Baluchistan, Pakistan	RSM
Durun, Transcaspia SSR	ZIN?
Duschak, Transcaspia SSR	SMF
Fars, Iran	CAS
Fatehjang, Punjab, Pakistan	PMNH
Ft. Sandeman, Zhob, NWFP, Pakistan	BNHS
Goa, India	UF
Gondal. Gujarat, India	BNHS
Gosht, 42 mi. N Dizak, Seistan, Iran	ZSI, BNHS
Gumtur Dist., A. P., India	ZSI
Gurshir, Iran	ZIN?
Hab Chouki, Baluchistan, Pakistan	AMNH, RSM
Henjam Isl., Persian Gulf, Iran	BNHS
Hinadan crossing, Baluchistan, Pakistan	AMNH
Hingol Natl. Park, Baluchistan, Pakistan	UF
Hingolgadh, Gujarat, India	BNHS
Hungo, Kohat, NWFP, Pakistan	UF, ZSD
Hyderabad, Sindh, Pakistan	AMNH
Islamabad	UMMZ, PMNH
Jabalpur, Madha Pradesh, India	ZSI

Locality	Museum
Jaisalmere, Rajasthan, India	ZSI
Jamsanda (nr. Bombay) Maharashtra, India	USNM
Jask, Persian Gulf. Iran	BNHS
Jati, Sindh, Pakistan	RSM
Jiwani, Baluchistan, Pakistan	SMF
Jhang, Punjab, Pakistan	UMMZ
Jungshai, Sindh, Pakistan	RSM
Kacha, Baluchistan, Pakistan	BNHS
Kalagan, Baluchistan, Pakistan	ZSI
Kalicut, Kerala, India	BNHS
Kanpur, U. P., India	FMNH, USNM
Karachi Dist., Sindh, Pakistan	SMF, ZSD, NMW, UF
between Karman amd Shiraz, Iran	ZSI
Kaur, Baluchistan, Pakistan	BNHS, BMNH
Kaweit, Iran	BNHS
Kerman, Iran	ZIN?
Kerula, Punjab, India	FMNH, MCZ
Khandahar, Afghanistan	ZFMK
100 mi SW Khandahar, Afghanistan	CAS
Khandala, Afghanistan	FMNH
Khar Centre, Sindh, Pakistan	UF
Khokhrapur, Baluchistan, Pakistan	SMF
Khudsil Khan (nr. Quetta), Baluchistan, Pakistan	ZSD
Khuzistan, Iran	NMBA
Killi Mangal, Baluchistan, Pakistan	SMF
Killi Jamaldini, Baluchistan, Pakistan	SMF
Kirthar Natl. Park, Sindh, Pakistan	ZSD
Kojdar, Mekkran Coast, Iran	BNHS
Krasnowodki, Transcaspia SSR	USNM
Lal Suharna Natl. Park, Punjab, Pakistan	UF
Larkana, Sindh, Pakistan	BNHS, UF
Madras, Tamil Nadu, India	BNHS, MCZ
Makli, Sindh, Pakistan	ZSD, UF
Mand, Baluchistan, Pakistan	BNHS
nr. Manjhand, Sindh, Pakistan	AMNH
Mango Pir, Sindh, Pakistan	ZSD
Matiari (nr. Hyderabad), Sindh, Pakistan	ZSD
Mednapur, West Bengal, India	FMNH, MCZ
Megas, E. Iran	ZIN
Mekkran Dist., Baluchistan, Pakistan	BNHS
Miranshah, NWFP, Pakistan	BNHS
Mithi, Sindh, Pakistan	SMF
Mohen-jo-daro, Sindh, Pakistan	SMF
Multan, Punjab, Pakistan	ZSD, UF
Munbhum Dist., Bihar, India	ZSI
Nabisar Nota, Sindh, Pakistan	RSM
Nagaur Dist., Rajasthan, Pakistan	ZSI
Nasrie, Iran	ZIN
Nazirabad, Iran	BNHS
Nellore Dist., Andra Pradesh, India	BNHS
Nushki, Baluchistan, Pakistan	SMF, RSM
Panjgur, Baluchistan, Pakistan	SMF, ZSM
Patho Pass (Pab Hills), Baluchistan, Pakistan	RSM

Locality	Museum
Persepolis, Iran	FMNH
Peshawar, NWFP, Pakistan	UF, ZSD
Point Calimere, Tamil Nadu, India	BNHS
Pol-Absinch, Fars, Iran	FMNH
Poona, Maharashtra, India	ZSI
Pugal, Rajasthan, India	ZSI
Puttur (Chittor) Andra Pradesh, India	USNM
Quetta, Baluchistan, Pakistan	SMF, ZSD, RSM
Quilon, Kerala, India	AMNH, UF
Ratan Kot, Sindh, Pakistan	SMF
Saman (Dasht Dist.), Baluchistan, Pakistan	ZSI
Sehirabad, (nr. Buchara, Afghanistan ?)	ZIN
Schechradj, Baluchistan, Pakistan	ZMFK
Shah Bundar. Sindh, Pakistan	CAS
Shadadkot, Sindh, Pakistan	SMF
Soman Dist., Baluchistan, Pakistan	ZSI
Spinkaras, Baluchistan, Pakistan	SMF
Sirohi, Rajasthan, India	ZSI
nr. Stalinabad, Uzbekistan SSR	NMBA
Thar Parkar, Sindh, Pakistan	SMF
Thatta, Sindh, Pakistan	UF, ZSD, AMNH, SMF, RSM
Trivandrum, Kerala, India	UF, UMMZ
Turkmen SSR	SMF, ZMFK
nr. Urak, Baluchistan, Pakistan	SMF
Valpoi, Goa, India	ZSI
nr. Zabol, Iran	SMF, FMNH
Zhor, Sindh, Pakistan	ZSD
nr. Zirkuch, E. Iran	ZIN?

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