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The venomous coral snakes (genus Micrurus) of Costa Rica

by

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ABSTRACT: Four species of venomous coral snakes (*Micrurus*) occur in Costa Rica. The single bicolor species, *M. mipartitus* has previously been defined as two subspecies; however, variations in diagnostic characters demonstrate a clinal shift that precludes recognition of geographic races.

Presence of the tricolor *M. clarki* is concluded from but a single Costa Rican specimen, although the species is otherwise definitely known from adjacent areas in Panamá.

Variation among tricolor coral snakes allied to *M. nigrocinctus* suggests the presence of three populations that occupy southwestern Pacific Costa Rica, northwestern Pacific Costa Rica and western Nicaragua, and Atlantic lowland Costa Rica. Gradual intergradation in the Pacific lowlands, as well as more complex intergrading patterns in the Meseta Central and Arenal regions and over a broad area of Nicaragua, eliminate the value of subspecific designations. Where *M. nigrocinctus* occurs sympatrically with populations of the closely related *M. alleni*, they can be consistently distinguished by differences in head cap patterns and segmental counts.

Micrurus alleni is composed of three allopatric populations in the Atlantic lowlands of Costa Rica and Nicaragua, the southwestern Pacific lowlands of Costa Rica and adjacent southwestern Panama, and Pacific lowland Darién in eastern Panama. Because of limited information on variation among these populations we prefer not to apply the trinomials.

To the *campesinos* and *peones* of Latin America and to most better educated people as well, any snake with a considerable amount of red or pink in its coloration is a *coral* (pl. *corales*). Although scientific English usage is probably based on the Spanish colloquialism, the name coral snake has

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become generally restricted to venomous proteroglyphodont snakes of the New World genera *Leptomicrurus, Micruroides,* and *Micrurus,* usually placed in the family Elapidae. Several venomous opisthoglyphodont snakes belonging to the large family Colubridae as well as a number of non-venomous colubrid genera, show a striking resemblance in coloration to the coral snake genera. Although these forms are also called *corales* throughout Latin America, the term coral snake applies only to the venomous proteroglyphodonts in the present account.

Coral snakes are secretive snake-eating forms that tend to be most active at night. Most species have the body completely encircled by bright red and black rings and usually yellow or white rings as well. Because these snakes are venomous and because of the close resemblance of many other species to them, a considerable discussion of possible coral snake mimicry has developed (DUNN, 7; HECHT and MARIEN, 12; MERTENS, 19; WICKLER, 35).

Of the three recognized coral snake genera, only *Micrurus* occurs in Costa Rica. The obvious extensive color variation and rather meager samples from the country have made identification for taxonomic and medical purposes difficult and sometimes misleading. It therefore was with more than the usual interest that we undertook this study at the suggestion of the authorities at the Medical School of the Universidad de Costa Rica as a preliminary step towards the completion of a popular illustrated book on the venomous reptiles of Costa Rica to be written by the junior author.

In the latest review of Costa Rican snakes, TAYLOR (33) recognized eight forms of venomous coral snakes from the republic: *Micrurus clarki* K. Schmidt, 1936; *M. mipartitus multifasciatus* (Jan, 1858); *M. nigrocinctus alleni* K. Schmidt, 1936; *M. nigrocinctus mosquitensis* K. Schmidt, 1933; *M. nigrocinctus nigrocinctus* (Girard, 1854); *M. nigrocinctus yatesi* Dunn, 1942; *M. pachecoi* Taylor, 1951; and *M. richardi* Taylor, 1951.

ROZE (22) in a preliminary summary of his revisionary studies on New World coral snakes recognized *M. alleni alleni* (including Taylor's *richardi*) and *M. alleni yatesi* as forming a species distinct from *M. nigrocinctus*, and placed *M. pachecoi* in the synonymy of *M. nigrocinctus melanocephalus* (Hallowell, 1861). Neither of these conclusions are substantiated in Roze's checklist but they are based in part upon the materials and ideas developed in the present paper and made available to him by us in earlier stages of manuscript preparation in 1963-65. ROZE (23) amplified his conclusions in the form of keys separating the species and subspecies without further discussion.

MATERIALS AND ACKNOWLEDGEMENTS

The majority of the specimens examined for this paper were collected by the University of Southern California field teams in Costa Rica from 1959 to the present. Additional material, to bring the total to 180 *Micrurus,* was made available through the kindness of the curators at the following institutions. The abbreviation in parentheses is used in the text to identify catalogued specimens. The abbreviation CRE is used for Costa Rican series at the University of Southern California.

Academy of Natural Sciences, Philadelphia (AP); American Museum of Natural History (AM); Field Museum of Natural History (FM); University of Kansas (KU); Los Angeles County Museum of Natural History (LA); Museum of Comparative Zoology, Harvard College (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley; Texas A and M University (TAM); University of Florida; University of Michigan, Museum of Zoology (UM); and the United States National Museum (US). We greatly appreciate the courtesies extended to us by these institutions and their personnel.

Jesús Ma. Jiménez P., Norman J. Scott, and Jaime Villa R. obtained or loaned from their own collections, valuable examples to provide crucial data from poorly collected areas. We have discussed our tentative findings on several occasions with Janis Roze, the pre-eminent authority on *Micrurus*. Ronald T. Harris executed all figures for this report in his usual fine style. Our thanks are extended for the special aid provided by these scientists.

SYSTEMATIC CHARACTERISTICS

The following characteristics have been used by previous workers or have been found of taxonomic significance in the present study. Discussion is restricted to variations found in Costa Rican populations or closely allied forms that throw light on the local situation.

SCUTELLATION. *Segmental counts*: The numbers of ventral and caudal scutes exhibit considerable intraspecific variation but are diagnostic for several populations. There is marked sexual dimorphism in the counts with females having around 10 more ventrals than males from the same sample and males having about 10 more caudals than females from the same area. For this reason our analysis of variation is based upon the total segmental count (ventrals plus caudals) which can be treated geographically without reference to sex. The variation in ventrals plus caudals is from 20-25 scutes in large samples.

Supra-anal Keels: In adult males of most populations keels are present on the scales above the anal plate, but do not occur in *Micrurus clarki* and are rather weak in *M. mipartitus*. In all other Costa Rican members of the genus the supra-anal keels are strongly developed in adult males. Keels also occur on the supra-anal scales in adult females as well in several populations.

COLORATION: *Head pattern*: The upper surfaces of the anterior portions of the head are covered by a black cap in all Costa Rican species. The posterior extent and outline of the posterior margin of the black head cap is characteristic of each population. Four basic patterns occur in Costa Rican materials (Fig. 1):

A. black head cap extending posteriorly no further than anterior portions of supraocular and frontal plates; posterior margin of cap concave, straight or slightly wavy in outline;

B. black head cap including interorbital region, extending posteriorly no further than suture between supraoculars and parietals; most of frontal plate black, but posterior tip light, not included in head cap; posterior margin of cap straight or wavy in outline often with a slight posteriorly directed projection on frontal;

C. black head cap extending posteriorly onto anterior portion of parietals, but posterior tip of frontal usually not included in head cap; posterior margin of cap straight or weakly concave in outline;

D. black head cap extending far onto parietals as an ovate to lanceolate extension centered on the interparietal suture; frontal completely included in head cap; cap sometimes interrupted to form a shorter lanceolate extension and a posterior black blotch on parietals;

E. black head cap extending to posterior tips of parietals.

Nuchal black ring: The location and longitudinal extent onto the body of the first black ring or nuchal ring is diagnostic for most Costa Rican populations (Fig. 1). The anterior margin of the ring crosses and includes the posterior tips of the parietals (P) or lies posterior to them (O). The relation between the black head cap and nuchal ring determines the extent of light color (yellow in most cases) on the posterior portions of the head. In addition to location, the longitudinal extent onto the body of the nuchal ring is important and varies in Costa Rican material from 4 to 13 scale rows. The type of nuchal ring pattern and the extent of the ring onto the body are represented by a formula such as: O 6. The letter represents the pattern and the number, the number of scale rows that the ring extends onto the body.

Basic pattern on body: Three basic patterns of alternating light and black rings that completely encircle the body occur in *Micrurus*: 1) bicolor pattern of alternating black and light (usually red) rings; 2) tricolor pattern of black rings, bordered on either margin by light (yellow or white) rings that separate the black rings from the red rings that alternate with them; 3) tricolor-triad pattern of black rings arranged in groups of three, alternating with red rings between each triad; the black rings in each triad are separated from one another by yellow or white rings.

In Costa Rica *Micrurus mipartitus* is consistently bicolor in pattern. No examples are known from the country that represent species having the tricolor-triad pattern. All other forms of the genus currently known from Costa Rica have a tricolor pattern. In one population of the latter a striking modification in dorsal pattern occurs ontogenetically. The juveniles and young adults of this population are tricolor, red, black and yellow, but the red becomes suffused and gradually obliterated by black pigment with age, so that mature adults are black and yellow above. On the ventral surface, the basic pattern of red-yellow-black-yellow-red rings is retained, although the red areas are heavily mottled with black pigment. This modification is discussed more fully under the account of the *alleni-nigrocinctus* problem in the systematic section below.

Basic pattern on tail: Although other patterns are known elsewhere in *Micrurus,* the tail pattern in all Costa Rican forms consists of alternating black and light (red, yellow or white) rings. In most examples the tail is bicolored with alternating black and yellow rings. Several juvenile specimens have two or three of the light rings red and the remainder yellow. The red rings on the tail have each of the scales tipped with black in three specimens. The black pigment apparently expands with age and obliterates the red areas to form additional black rings in the adults.

Body and tail rings, number and size: The number of rings around the body and tail is characteristic for each population. The numbers of rings of each color are correlated closely with one another depending upon the basic color pattern. In counting rings the nuchal black ring is considered the first body ring. The last body ring is usually black and lies just anterior to or covers part of the anal scute. In bicolor coral snakes the number of black and light rings on the body are equal or there is one less light ring than black rings. In tricolor *Micrurus* the number of yellow rings is usually two less than twice the number of black rings and the number of red rings is almost always one less than the number of black rings. The number of tail rings of the several colors is somewhat more variable. In the bicolor pattern, the number of black tail rings equals the number of light rings or exceeds the latter by one. In juveniles from some populations with tricolor body patterns, two or three red tail rings are present, but the red seems to disappear with age and the adults have a bicolor tail pattern. Because of these several factors, we selected the numbers of black rings as a basis for variational study. Further work indicated no significant interpopulational variation in the numbers of black tail rings so that detailed analysis of geographic and populational variation is based upon the numbers of black body rings. In material from Costa Rica, the number of black body rings ranges from 10-63.

The longitudinal extent of the variously colored rings at or near mid-body shows some variation but tends to be typical for each population. In the bicolor species *Micrurus mipartitus* the black rings are 4-6 mid-dorsal scale rows in extent and light rings 2-3 scale rows. In the tricolor forms in Costa Rica, the black rings vary between 2½-9 mid-dorsal scale rows in longitudinal extent near mid-body, the red rings range between 5-12 scale rows and the yellow rings between ½-2½ scale rows. We have not undertaken a similar comparison for the size of the tail rings, since a preliminary survey showed very little populational variation and suggested no trends not already indicated by the geographic pattern of body ring size.

COLOR: The color of the light areas on the head, body and tail may be white, cream, pink, scarlet or yellow. In *Micrurus mipartitus,* the light parietal area is usually bright scarlet, but the light body rings are red, pink, or cream or white in different specimens. A few dark flecks may be present on the scale tips in the light rings. The light tail areas are almost always bright scarlet above and below in Costa Rican examples of the species. In the remaining Costa Rican coral snakes of this genus the parietal region is yellow as are the light rings bordering the black body rings and the red rings are bright scarlet. In most specimens each scale in the red rings is tipped by a regular black spot, that may be restricted to the tip or occupy up to a third or more of the scale. A few examples lack dark-tipped scales in the red rings. The tail is yellow and black, except in juveniles, with bright red tail rings as well.

MEASUREMENTS: Standard (head and body) and tail length measurements have been included for representative series of all species by sex, although differences in size are not striking nor particularly useful for species recognition in the Costa Rican forms. The standard lengths are recorded in millimeters and the tail lengths as a percentage of standard length.

THE COSTA RICAN BICOLOR SPECIES

A single species of bicolor venomous coral snake, *Micrurus mipartitus* Duméril, Bibron and Duméril, 1854; type locality: Colombia: Río Sucio or Senis) is known from Costa Rica. ROZE (22, 23) in the latest review of the group recognized six subspecies in the species, one of which, *M. mipartitus hertwigi* (Werner, 1897; type locality: Central America) occurs in Costa Rica. Earlier workers (TAYLOR, 32; SCHMIDT, 31; ROZE 21) referred examples from this country to *M. m. multifasciatus* (JAN, 16; type locality: Central America). The races were differentiated primarily on the basis of segmental counts and coloration. According to ROZE's key (23: 213) there is a gradual cline toward increased numbers of ventrals running from Nicaragua and Costa Rica (males 237-244, females 256-269) through central Panama (males 247-265, females 278-311) into western Colombia and Ecuador (males 246-275, females 251-355) and a similar cline from northern Colombia (males 224-247, females 244-287) into Panama (males 247-265, females 278-311). We suspect that detailed analysis of segmental counts in this species will indicate a gradual continuum of change along these clines. Ten examples available to us from Costa Rica (3 males and 7 females) have ranges of 233-241 and 260-276, respectively for male and female ventral counts. The latter figures suggest that ventrals alone will not distinguish between Costa Rican and central Panamanian material. Because the tails are short in this species the number of caudals is low for both sexes (males 31-33, females 23-29) and the total segmental counts (males 264-274, females 288-305) are sexually dimorphic as a reflection of the marked differences between males and females in ventral counts.

Life colors also show more variation than recognized by ROZE (23). According to his key, the eastern Panamanian and South American populations of the species have alternating black and yellow body rings, while those of central Panama to Nicaragua are black and red. The yellow body rings of most specimens as well as the red rings may lose their color after sometime in preservative and fade to white. In live examples from Costa Rica, the light rings may be scarlet, pink or white. The light ring between the black head cap and nuchal ring may be yellow or white and is usually suffused with red. The light rings on the tail are usually red. Generally the juveniles are the most brightly colored (red and black). Most adults are pale pink and black with the posterior portion of the head and light tail rings a brighter shade of red. We have seen one large live adult that was completely black and white, except for bright red under the tail. Occasional examples are black with cream-yellow rings that are faintly suffused with red and the snake appears to be black and yellow. Since the Costa Rican sample encompasses and exceeds the color variation described elsewhere for this species, the use of body coloration for the recognition of subspecific populations does not seem warranted.

All known records for *Micrurus mipartitus* in Nicaragua and Costa Rica are from the Atlantic versant, except for two examples from the latter country: CRE 7246, from just west of the continental divide at Puntarenas: Monteverde, and UM 72015 from Guanacaste: Hacienda Santa María, also just west of the continental divide. Several collections have snakes of this species labeled simply "Costa Rica: Guanacaste", and these may be from Pacific slope areas under conditions similar to those at Monteverde or Hacienda Santa María. The species has also been listed from San José: San José, based upon AP 6808 and Alajuela, based on AM 17312. We have seen no others from the Meseta Central Occidental and suspect errors in locality. *M. mipartitus* has not been taken at or near San José nor Alajuela during the extensive fieldwork by University of Southern California teams during the past decade nor have we seen any brought into the snake venom laboratory at the Universidad de Costa Rica where several hundred venomous snakes are purchased each year. The Alajuela record may be for the province of that name, which includes a substantial area of the Atlantic lowlands. We know of no authentic records of the species from western Nicaragua and presume that a specimen labeled "Chontales" is from the eastern portion of that department. In Panama *M. mipartitus* occurs over the Atlantic and Pacific lowlands in the Canal Zone and eastern provinces. To the west of the zone, records are restricted to the Atlantic versant.

MICRURUS CLARKI

Micrurus clarki Schmidt, 1936 (type locality: Panama: Darién, Yavisa) has been recorded from Costa Rica on the basis of a single male specimen (US 14062) without specific data. This form is a tricolor coral snake well distinguished from other species in the region in having the parietal plates completely included in the black head cap, most of the infracephalic scales light, although some are peppered with black, the scales in the area between the nuchal ring and head cap tipped or outlined in black and the males lacking supra-anal keels. The locality data of SCHMIDT (30) and DUNN (5, 6) indicate a documented distribution from western Chiriquí to Darién and ROZE (22, 23) included western Colombia in its range. Since all known records for the species from western Panama are from the Pacific lowlands and DUNN (5) reported three examples from Farm Two, near Puerto Armuelles, only 10 km from the Costa Rican frontier, it appears certain that the range of the species in Costa Rica is centered on the Golfo Dulce forests. This area includes adjacent parts of Panama where *M. clarki* has been taken.

ROZE (23: 198) implied that the light areas on the head and neck of this species are white and stated that none of the infracephalic plates are black. Although we have not seen a live specimen, available preserved material suggests that the light head areas may be yellow in life. In at least one specimen (US 14062) the posterior chin shields are solid black. The more anterior infracephalic plates (mental, infralabials and anterior chin shields) are never completely black in this species although outlined by black.

DIFFERENTIAL CHARACTERISTICS OF TRICOLOR *MICRURUS* FROM THE ATLANTIC LOWLANDS OF COSTA RICA AND NICARAGUA

SCHMIDT (29) was the first worker to attempt allocation of the specimens of tricolor coral snakes from the Atlantic lowlands of Central America. Previous students of the genus had followed BOULENGER (1), who regarded these snakes as representatives of *Micrurus fulvius*. Among the most important contributions of Schmidt to coral snake systematics was his gradual breaking up of the composite *M. fulvius* in the sense of Boulenger into a number of recognizable and distinctive species and races (27, 28, 29, 30). He (29) referred all available tricolor coral snake material from the Atlantic slope of western Panama, Costa Rica and Nicaragua to a new form, *Micrurus nigrocinctus mosquitensis* (type locality: Panama: Panama: Bahía de Panama: Isla Taboga) that ranges from Chiapas, Mexico south along both Atlantic and Pacific slopes to northwestern Colombia. *Mosquitensis* was characterized as having 182-194 ventrals in males, 203-209 in females; 10-19 black body rings; yellow rings well developed and scales in red rings uniformily tipped with black.

In 1936, SCHMIDT (30) described a second race from Atlantic lowland Nicaragua as *Micrurus nigrocinctus alleni* (type locality: Nicaragua: Zelaya: on Río Mico, 11 km above Rama) that differed from *mosquitensis* in having higher ventral counts (males 205-227, females 230-240 versus males 188-192, females 203-208 in the latter) and in having a backward projecting black marking on the head (head cap with an even posterior margin in *mosquitensis*). The distribution pattern suggested by Schmidt has the two subspecies sympatric at Nicaragua: Matagalpa: Matagalpa, and hybridizing at two localities, one on the

Río Pis Pis (AM 12701 from Big Falls) in northern Nicaragua, another (AM 12700 from Kanawa) from south of Bluefields. He stated that intergradation does not seem to occur between *alleni* and other *nigrocinctus* populations.

TAYLOR (32) recognized the biological peculiarities of Schmidt's arrangement since he collected *mosquitensis* and *alleni* sympatrically in Costa Rica: Limón: Los Diamantes. Although not fully discussing the basis for his conclusion, Taylor regarded the two forms as representatives of distinct species and described his example of *alleni* as a new form *Micrurus richardi.* The single type specimen was separated from Nicaraguan *alleni* primarily on the basis of differences in details of body coloration. In 1954, TAYLOR (33) presented another arrangement after collecting a specimen of typical *alleni* at Los Diamantes. He regarded *alleni* and *mosquitensis* as races of *nigrocinctus* and retained *richardi* as a distinct species.

The extensive material now at hand provides a basis for clarifying the relations of the Atlantic lowland populations of tricolor coral snakes. Preliminary study of these animals showed that they could be placed into two groups primarily on the basis of head patterns. In one series, including the holotype of *mosquitensis,* the black head cap usually reaches no further posteriorly than to the suture between the supraocular (Fig. 1, B1) and parietals or occasionally includes the anteriormost portions of the parietals (Fig. 1, C). The posterior margin of the head cap is straight or slightly uneven. In the second group the black head cap extends posteriorly onto the parietals as an ovate to lanceolate extension centered on the interparietal suture (Fig. 1, D). The holotypes of the nominal forms *alleni* and *richardi* have this pattern of head cap. A comparison was made for other characteristics between the sample of coral snakes with a D pattern black head cap and the series with a B or C pattern (Table 1). The series with a D pattern head cap is very homogeneous in its features but the other series shows substantial geographic variation. For this reason we have broken the series into geographic subunits so as not to obscure the differences between samples. In the table, attributal characters separated by a colon (:), for example B:C, indicate almost equal frequencies of the conditions; in those separated by a dash (-) the first letter indicates the usual (> 80%) condition, the second the rare condition. As may be seen from this table, coral snakes with the D head cap pattern may be consistently separated from the other form on the basis of segmental counts and usually by the number of black body rings. The distribution and discontinuous variation in the black head cap pattern and segmental counts leaves no question but that two sympatric biological species are involved (Fig. 2). The earliest name for the form with high segmental counts and D black head cap pattern is *Micrurus alleni* K Schmidt, 1936. The only available name for the population with low segmental counts and with a B or C head cap pattern is *Micrurus nigrocinctus mosquitensis* K. Schmidt, 1933.

TABLE 1

Comparisons of Atlantic slope tricolor Micrurus

	N	Ventrals plus caudals	Black body rings	Head cap	Nuchal ring	Extent of nuchal ring
D Head Cap	20	259-286	14-23	D	O	7-11
Non-D Head Cap						
COSTA RICA:						
Limón-La Lola	7	233-242	12-14	B	O	8-11
Turrialba	20	222-251	10-15	B:C	O-P	8-12
Los Diamantes-La Tigra	9	236-245	10-12	B	O	10-13
Arenal	5	236-243	11-15	B	O	9-13
NW	3	236-245	10-12	B	O	10-12
NICARAGUA:						
SE	4	237-256	12-16	B-C	P-O	4-11
NE	6	240-256	12-15	B	O:P	6-8

Part of the past confusion regarding the status of specimens from the Atlantic lowlands of Nicaragua and Costa Rica derives from the fact that Schmidt's type series for *alleni* contained representatives of both Atlantic species and a third form allied to *mosquitensis* from Pacific Nicaragua. Schmidt recorded 13 types from throughout Nicaragua. The holotype (UM 79794 a female) has a count of 277 for ventrals plus caudals, 17 black body rings, a D pattern black head cap, the nuchal ring not involving the parietals and extending 11 scale rows onto the body. Seven of the paratypes (US 15306, 20688; UM 79795-97; AM 12703-04) are unquestionably conspecific with the holotype. Five of the paratypes belong to other forms. One example (AP 6844) from Departamento Río San Juan: Machuca, has the following features: ventrals plus caudals 252, black body rings 14, head cap pattern C, nuchal ring extending onto parietals and reaching posteriorly onto body for 4 scale rows. In most regards this example agrees with *nigrocinctus* from more western portions of Nicaragua. Another specimen (MCZ 9569) from Matagalpa: Matagalpa, has 262 ventrals plus caudals, 22 black body rings, head cap pattern C, nuchal ring on parietals and extending onto body 5 scale rows. Although the segmental count agrees with *alleni*, the head pattern and nuchal ring features indicate that the snake is not conspecific with this species. Actually this individual resembles a western population of *nigrocinctus* found in Nicaragua and Pacific Costa Rica. The three paratypes (MCZ 3802, 5486, 5486a) from Departamento León: El Polvón, on the Pacific lowlands of northern Nicaragua also belong to the western population and have ventral plus caudal counts of 255, 260, and 268 and black body rings 19, 20, and 22, respectively; the head cap of pattern C, and the nuchal ring involving the parietals and five dorsal scale rows. The relations of the western form to *mosquitensis* will be discussed in detail in a subsequent section below.

We have also examined the two Nicaraguan specimens thought by Schmidt to be hybrids between *mosquitensis* and *alleni*. The data for the two is as follows: AM 12700, Zelaya: Kanawa; 256 ventrals plus caudals; 16 black body rings; head cap pattern B; nuchal ring P, extending 5 scale rows onto body; AM 12701, Zelaya: Río Pis-Pis: Big Falls; 256 ventrals plus caudals; 14 black body rings, head cap pattern B; nuchal ring O, extending 8 scale rows onto body. These snakes in no way approach *M. alleni,* except for their high segmental counts. In all respects they are typical of southwest (Kanawa) and northwest (Big Falls) Nicaraguan populations called *mosquitensis* by SCHMIDT (30) and ROZE (22, 23).

Examination of the unique specimen (KU 25189) of TAYLOR'S (32) *richardi* leaves no question as to its conspecificity with *M. alleni.* The type has 273 ventrals plus caudals, 18 black body rings, the head cap pattern D, and the nuchal ring not reaching parietals. The relatively narrow yellow rings on this example, with the yellow scales tipped with black, as emphasized by Taylor occurs as an occasional variant throughout the range of *alleni.*

GEOGRAPHIC VARIATION IN *MICRURUS NIGROCINCTUS* IN NICARAGUA AND COSTA RICA

The evidence presented in the preceding section confirms the occurrence of two sympatric species of venomous coral snakes on the Atlantic lowlands of Nicaragua and Costa Rica, *M. alleni* and a series of populations usually referred to *M. nigrocinctus* (22, 23, 30, 32, 33). The long confusion of the two Atlantic versant species derives from a lack of data on variation in *nigrocinctus* and the absence of an evaluation of the relation of Atlantic populations to those of western Nicaragua and adjacent northwestern Costa Rica. Particularly confusing is the similarity in segmental counts between *alleni* and presumed *nigrocinctus* from western Nicaragua and Costa Rica that led SCHMIDT (30) to include examples of the latter in his type series of the former and to believe that intergradation occurred between the two species. Schmidt's misunderstanding of the situation in the region stemmed mostly from the limited sample, not more than eight snakes, then available from the area.

The term western Nicaragua as used in the present paper requires amplification since considerably more than the area west of the very low continental divide is included. The Pacific slope of Nicaragua is very narrow and exceeds 35 km in width only north of the great freshwater lakes in the Departamentos de León, Chinandega, and extreme western Estelí. The lakes themselves lie east of the divide in a depression that drains southeastward through Lago de Nicaragua via the Río San Juan into the Caribbean. Physiographically, climatologically and biotically, the Pacific slope and drainage areas of the lakes form a geographic unit dominated by dry tropical vegetation formations that develop under conditions of markedly seasonal rainfall (5-7 dry months) as constrasted with the evergreen forests of the Atlantic lowlands to the east. The eastern margins of this area are demarcated by the Cordillera Horno Grande (altitudes up to 1300 m), north and east of the lakes, a series of irregular hills and low peaks (up to 1400 m), Departamento de Matagalpa and the Cordillera de Amerrique (greatest elevations near 1100 m) east of the lakes. For these reasons, we use western Nicaragua to encompass the Pacific lowlands, the areas to the east surrounding the lakes and the western slopes of the hills and mountains that drain westward into the lakes. This usage includes all of the Departamentos de Chinandega, León, Managua, Masaya, Carazo, Granada and Rivas, the extreme western portions of Estelí and Matagalpa, the western regions of Boaco and Chontales and the northwestern part of Río San Juan. This terminology makes western Nicaragua essentially equivalent to the Nicaraguan lowland of geographers (JAMES, 15) comprised of the Pacific Coastal Plain and the Nicaraguan Depression (MCBIRNEY and WILLIAMS, 17).

In the present section, the geographic variation in segmental counts, black body rings, nuchal ring pattern and extent onto the body for all tricolor coral snakes with a black head cap of B or C pattern is analyzed. Our objective is to establish the status of Pacific slope populations and their relations to the several Atlantic versant populations called *mosquitensis* by SCHMIDT (29, 30) and subsequent authors. The analysis includes all coral snakes from Nicaragua and Costa Rica previously referred to *mosquitensis, melanocephalus, pachecoi* and *nigrocinctus*. The nominal form *Micrurus nigrocinctus yatesi* Dunn, 1942, from the Pacific slope is excluded from discussion at this point, since it has a black head cap of pattern D, like Atlantic *M. alleni*. A consideration of its status will be undertaken later in this paper.

SEGMENTAL COUNTS. VARIATION IN CHARACTERISTICS: The segmental counts (ventrals plus caudals) are plotted for all specimens examined by locality (Fig. 3). The pattern for segmental counts for Atlantic slope samples have been discussed above in the section on *Micrurus alleni* (Fig. 2, Table 1). The counts for these samples range from 222-256, with the southernmost populations (Costa Rica) having somewhat lower counts than those to the north in Atlantic lowland Nicaragua (237-256). On the Pacific the samples from the region west of the eastern margins of the great Nicaraguan lakes, northwest Costa Rica and the Meseta Central Occidental of Costa Rica resemble one another closely in segmental counts:

Western Nicaragua	248-268
Northwestern Costa Rica	251-267
Meseta Central, Costa Rica	247-267

The population from southwestern Pacific Costa Rica differs markedly from the more northern series in having a much lower count, 237-244.

Populations from areas intermediate between the Atlantic lowlands and the localities for the westernmost samples suggest intermediacy between eastern and western populations (Table 2). The specimens from Nicaragua: Departamento de Matagalpa, exhibit almost as much variation as in the entire sample. The counts for most coral snakes from this area are intermediate between those from Atlantic lowland Nicaragua and western populations, although they tend toward the latter in the frequency of higher counts. The two examples from near Boaco to the south of Matagalpa are typical of the western population with counts (236-264) substantially higher than in the Atlantic lowland Nicaraguan series (237-256). The single snake from Acoyapa with a count of 245, agrees with the latter population in contrast to the western series which has higher counts (248-268).

TABLE 2

Characteristics of populations geographically intermediate between eastern and western lowland Micrurus nigrocinctus

	N	Ventrals plus caudals	Black body rings	Head cap	Nuchal ring	nuchal Extent of ring
NICARAGUA:						
NW Matagalpa	4	250-255	14-15	B:C	O-P	6-7
Vic. Matagalpa	7	229-262	11-22	B:C	O-P	5-12
SE Matagalpa	1	263	19	C	P	6
Vic. Boaco	2	263-264	16-18	C	P	5-6
Acoyapa	1	245	20	B	O	5
COSTA RICA:						
Arenal	5	236-243	11-15	B	O	9-13
Monteverde	1	256	16	B	P	7
Meseta Central	16	248-267	12-24	C-B	P-O	4-6
Cachi	1	250	20	—	—	—
Turrialba	20	230-251	10-15	B:C	O-P	8-11

In Costa Rica, the series from the Atlantic slope area around Laguna de Arenal is typical of Atlantic lowland samples. A single snake from the Pacific slope near the continental divide at Provincia de Puntarenas: Monteverde, has a count (256) typical of the lowland sample to the west. The Meseta Central series already has been discussed, but a few snakes with low counts, 247-248, from the immediate vicinity of Provincia de San José: San José, show some resemblance to the Pacific lowland and Meseta Central Occidental samples. One snake from Provincia de Cartago: Cachi (BM 1912. 9. 14. 2), 30 km southeast of San José has a ventral plus caudal count of 250. The count is well within the limits of variation for the western populations of this coral snake, but is substantially higher than for any Costa Rican Atlantic lowland example (233-245). Further evidence suggesting an influence of the Pacific slope population on Atlantic examples is provided by the series from Turrialba, about 18 km northeast of Cachi, further down the gorge of the Río Reventazón. The average count for this series is 240 and most individuals fall well within the variational limits for Atlantic lowland samples in Costa Rica. Five examples have more than 245 ventrals plus caudals, with one having 251.

BLACK BODY RINGS: The Atlantic and western lowland populations overlap only slightly in the counts of black body rings (Fig. 3). Comparisons of these counts, exclusive of samples from east of the lakes in Nicaragua and/or the Costa Rican montane slopes are:

ATLANTIC

	Range	Mean
Costa Rica	10-14	11.1
SE Nicaragua	12-16	14
NE Nicaragua	11-15	13.3

WESTERN

	Range	Mean
Nicaragua	12-22	18.7
NW Costa Rica	15-19	16.1
SW Costa Rica	15-19	16.8

The low values for Atlantic Costa Rican populations are strikingly consistent, since only three examples have more than 12 black rings (2 with 13, 1 with 14, all from Limón: La Lola) out of a sample of 20. The high values in western Nicaragua (west of the eastern margins of the great lakes) are also very consistent as only three examples from southwestern Nicaragua near the Costa Rican frontier have less than 16 black body rings. The series from eastern Nicaragua is closest to the Costa Rican Atlantic lowland population in body ring counts, although with somewhat higher numbers. The Pacific Costa Rican examples have slightly lower values than the western Nicaraguan population.

Coral snakes of this series from geographically intermediate localities tend to be intermediate between Atlantic and western samples. In Nicaragua specimens from near Matagalpa have 11-22 black body rings, mean 15.7, to encompass counts for both lowland populations. Examples from the eastern margin of western Nicaragua to the southeast of Matagalpa are intermediate in values, although closer to western rather than Atlantic lowland populations.

In Costa Rica, the Laguna de Arenal sample is close to Atlantic lowland snakes with counts of 11-12 black body rings in all but one specimen with 15. The single snake from Monteverde is similar in the number of black body rings to Pacific lowland samples just to the west. On the Meseta Central Occidental the range is 12-24, mean 17.1. Most examples have values typical of western lowland samples, but one example has 12, one 14, and four 15 black body rings. At Turrialba, 40 km east of San José, on the Atlantic slope, the converse pattern is seen: most examples agree with eastern lowland samples, range 10-15, mean 12.1; two examples have 14 black rings and two have 15.

HEAD PATTERN: The black head cap patterns are plotted by locality for all specimens examined (Fig. 2). On the Atlantic lowlands all examples except one have a head cap of pattern B, with the black extending onto the supraoculars and frontal for about two-thirds of their length, to leave the posterior thirds yellow. A single snake (AP 6844) from Nicaragua: Río San Juan: Machuca, on the Río San Juan has a head pattern like those found in members of the complex in western Nicaragua and adjacent northwestern Costa Rica. On the Pacific versant all samples from west of the eastern margins of the great lakes in Nicaragua and in northwestern Costa Rica have black head caps of pattern C. Coral snakes from extreme southwestern Costa Rica have black head caps of pattern B. The figure suggests a rather rapid shift from north to south in head cap pattern along the Pacific coast of Costa Rica, over the distance of 55 km between the vicinity of Parrita and the low coastal range southwest of San Isidro de El General, both in Provincia de Puntarenas. The examples at Parrita have C head patterns and agree with the samples from the northwest. Examples from near San Isidro de El General have a black head cap of the B pattern with the supraoculars completely included in the cap and only the posterior one-fourth of the frontal is yellow. Examples from southwest of San Isidro de El General toward the coast have B head cap patterns but with the posterior third of both supraoculars and frontal yellow. In this regard, the specimens resemble Atlantic lowland examples and specimens from further south on the Pacific versant toward the Panama boundary.

Samples from areas intermediate between the Atlantic lowlands and the westernmost localities show indications of intermediate conditions between eastern and western populations (Table 2). In the examples from Nicaragua: Departamento de Matagalpa, the head cap condition varies from the pattern typical of Atlantic lowland populations (B with posterior third of supraoculars and frontals yellow, Fig. 1,B1), through examples with B head patterns in which the black covers the supraoculars and all but the posterior tip of the frontal (Fig. 1,B2) to snakes with head patterns identical to Pacific lowland samples (Fig. 1,C). At Boaco the caps are of the C pattern and at Acoyapa of the B pattern.

In Costa Rica in the region around Laguna de Arenal on the Atlantic versant near a low divide (700 m) between the Atlantic and Pacific slopes most examples have a head pattern typical of Atlantic lowland populations (B with posterior parts of supraoculars and frontal yellow). One example (CRE 6279) from near the divide has the black extending as three posterior projections, two to the supraocular-temporal sutures and one about two-thirds of the length of the frontal from the main area of the head cap. Another (CRE 6229) from El Silencio de Tilarán (780 m) just over the divide on the Atlantic slope, contrary to HEYER (13), who erroneously regarded it as on the Pacific drainage, has the black cap including all of the supraoculars and frontal as in Pacific lowland samples. Further to the south at Monteverde, the black head cap on the single available specimen covers the supraoculars and frontal completely. The sample from the Meseta Central region strongly indicates a trend linking western and eastern lowland populations. Most examples from the area have head caps of pattern C. Specimens from Santa Ana and La Uruca just southwest and northwest of San José, respectively, agree with those from several other intermediate localities in having the head cap of the B pattern that includes the supraoculars and frontal completely in the black. At San José, most examples have a C head cap pattern, but one snake (CRE 1956) with a B pattern has only the intermost posterior corner of each supraocular and the posterior one-fourth of the frontal yellow. An example (CRE 1963) from Desamparados, just south of San José, also has a typical C head pattern. In the series from the vicinity of Turrialba (600 m) on the Atlantic versant, 40 km east of San José, six examples have B head patterns with a substantial portion of the supraoculars and frontal yellow, as in Atlantic lowland samples; six examples have the supraoculars completely black but at least the posterior eighth of the frontal yellow; and five have C patterns typical of Pacific populations.

These data demonstrate that the relative distinctness of the Pacific lowland population (head cap C) and Atlantic lowland sample (head cap B, with substantial yellow on supraoculars and frontal) is bridged in intermediate geographic areas where high frequencies of head caps of pattern B with the supraoculars and frontals completely black occur. Various intermediate conditions between the two extremes in B head patterns also occur in the uplands of Costa Rica on the Meseta Central and at Turrialba.

Nuchal Ring: The location of the nuchal black ring, whether it involves the parietals (P) or not (O), and its extent onto the body shows some populational consistency (Fig. 4) as follows for lowland samples:

ATLANTIC

	Range	Mode
Costa Rica	O 8-13	O 11
SE Nicaragua	O 11; P 4-5	P 5
NE Nicaragua	O 6-8; P 6	P 6

WESTERN

	Range	Mode
Nicaragua	P 4-7	P 5
NW Costa Rica	P 3-7	P 5
SW Costa Rica	O 6-7; P 6-8	P 7

The Atlantic Costa Rican population and the western Nicaraguan and similar northwestern Costa Rican samples are absolutely distinguishable from one another on this basis. Lowland samples from southeastern Nicaragua are intermediate between the two, although closest to the western Nicaraguan population. The northeast Nicaraguan lowland sample is intermediate in nuchal ring location, but has a less extensive development of the ring (6-8 scale rows onto the body) in snakes with the ring not intersecting the parietals, than in Costa Rican lowland examples. The Pacific lowland population in southwestern Costa Rica agrees with the northeastern Nicaraguan samples in this regard. In addition, the former has a tendency for development of a more extensive nuchal ring (6-8 scale rows onto the body) in snakes with the ring intersecting the parietal than in more northern Pacific lowland samples.

Series from geographically intermediate localities in Nicaragua show extensive variation that encompasses most of the variants included in other populations: O 5-12, P 4-6. Specimens from Costa Rica near Laguna de Arenal and at Monteverde are typical of Atlantic Costa Rican lowland samples. On the Meseta Central Occidental of Costa Rica, most examples P 4-6 agree with Pacific lowland samples with one snake (MCZ 55118) from La Uruca resembling Atlantic lowland examples (O) but with a very narrow ring extending only 4 scale rows onto body. At Turrialba, to the east of San José in the Atlantic drainage, most individuals agree with the lowland Atlantic population (O 8-12). One example from this locality, CRE 1961, has the nuchal ring pattern (P) as in Pacific lowland snakes with the ring extending 11 scale rows onto the body as in Atlantic lowland samples.

POPULATIONAL PATTERNS

As may be seen from the discussion of character variation above, the populations of venomous coral snakes allied to *Micrurus nigrocinctus* in Nicaragua and Costa Rica exhibit a complex variation pattern. Three populational samples are clearly separable from one another on the basis of this analysis:

I. Southwestern Pacific Costa Rica: ventrals plus caudals 237-244; black body rings 15-19; black head cap of pattern B; nuchal ring P 6-8 or O 6-7.

II. Northwestern Costa Rica and Nicaragua west of the eastern margins of the great lakes: ventrals plus caudals 248-269; black body rings 12-22; black head cap of pattern C; nuchal ring P 4-7.

III. Atlantic Lowland Costa Rica: ventrals plus caudals 233-245; black body rings 10-14; black head cap of pattern B; nuchal ring O 8-13.

The individual snakes from each of these populations are always completely distinguishable from one another and each population has been recognized by TAYLOR (32, 33) and ROZE (22, 23) as a distinct form. Population I appears to be closely allied to the typical form *M. nigrocinctus* from Panama and has been regarded as being from the same population by SCHMIDT (29, 30), DUNN (4) and the two previously cited authors. SCHMIDT (29) proposed the name *Micrurus nigrocinctus mosquitensis* for examples from population III and was followed in this usage by subsequent workers. Population II has been formally named on two occasions: first as *Elaps melanocephalus* by HALLOWELL (11) and then as *Micrurus pachecoi* by TAYLOR (32). The former name is based upon a male Nicaraguan example (US 7331) from Ometepec (=Isla Ometepe), in Lago de Nicaragua, with 250 ventrals plus caudals, 17 black body rings, the frontal cap of pattern C and the nuchal ring crossing the parietals. The female holotype (KU 25188) of *M. pachecoi* is from Costa Rica: Provincia de Guanacaste, and has 256 ventrals plus caudals, 22 black body rings, the frontal cap of pattern C and the nuchal ring crossing the parietals. There can be no question but that these snakes agree in every respect with other examples from population II.

There is no evidence of possible genetic interchange between populations I (Pacific) and III (Atlantic) in Costa Rica or Panama, although previous workers have always regarded the two as conspecific. The two populations are similar in segmental counts and head cap pattern, although consistently separable on the basis of the number of black body rings and nuchal ring differences. Coral snakes resembling population III occur in Panama only in the extreme northwest around Bahía Almirante and possibly the Laguna de Chiriquí. Population I appears to be continuous with similar samples along Pacific slope western Panama and both Atlantic and Pacific versants of central and eastern Panama into northwestern Colombia. The major mountain axis of Costa Rica and western Panama effectively isolates populations I and III from any direct contact. Determination of whether or not this isolation is complete awaits the collection of coral snakes from the Caribbean slopes of western Panama between Laguna de Chiriquí and the Canal Zone, where intermediate populations are to be expected solely on geographic grounds.

Intergradation between populations I and II is suggested by examples from Costa Rican localities at the adjacent peripheries of their respective ranges. The closest approach between lowland Pacific samples is between the northern population at Finca San Miguel de Barranca (CRE 709, FM 34488) and specimens (CRE 8257, 8263) agreeing with the southern population in segmental counts from Finca La Ligia, near Parrita. Both localities are in Provincia de Puntarenas and are separated by a distance of 70 km. Parrita is 55 km northwestward of the nearest localities to the south for population I in the area around San Isidro de El General, Provincia de San José. The salient features for these samples are compared below:

	San Miguel	Parrita	San Isidro
Ventrals plus caudals	251-264	237-242	237-244
Black body rings	14-17	15-15	15-19
Head cap	C-C	C-C	B
Nuchal ring	P 5	P 7-P 7	P 6-8; O 6-7

The Parrita examples resemble population I in segmental counts and population II in head cap pattern. In other features, the two snakes are equally similar to either population. They strongly suggest a continuum of gradual change from population I into population II along the Pacific lowlands of Costa Rica.

All of the remaining population samples from Nicaragua and Costa Rica show various sorts of intermediacy in characteristics between populations II and III, although most samples resemble one more closely than the other. Although placed by SCHMIDT (29, 30) and ROZE (22, 23) together with Costa Rican population III within their concepts of *Micrurus nigrocinctus mosquitensis*, Atlantic lowland Nicaraguan material (Table 1) differs markedly away from the characteristics of population III in the direction of population II. The snakes from southeastern Nicaragua have much higher ventral plus caudal counts, a higher number of black body rings (mean 14 as opposed to 11.1 in Costa Rica) and a high frequency of nuchal rings intersecting the parietals (75%, as opposed to 0% in Costa Rica). Partially influenced by all of these features, but primarily because of the high ventral counts, SCHMIDT (30) included an example from the southeast Nicaraguan population (AP 6844 from Machuca) as a paratype of *Micrurus alleni*. Schmidt was convinced that *nigrocinctus* in Atlantic Nicaragua resembled the Costa Rican lowland sample and his material from western Nicaragua and northwestern Costa Rica was insufficient to allow recognition of the similarities between the latter population and his Atlantic

Nicaraguan specimens. Certainly the situation is rather complex in Atlantic lowland Nicaragua. Three of the four available examples from southeastern Nicaragua agree closely with specimens to the west in most features. The fourth example (AM 69716) is typical in every regard of specimens from Atlantic Costa Rica:

	V + C	BBR	HC	NR
ZELAYA:				
Kanawa (AM 12700)	256	16	B	P 5
Corozo (AM 70248	251	14	B	P 5
Corozo (AM 69716)	237	12	B	O 11
RÍO SAN JUAN:				
Machuca (AP 6844)	252	14	C	P 4

The Machuca specimen agrees in head cap pattern with western Nicaraguan examples while the others are identical in this regard to snakes from population III. Were it not for the concordance in head cap patterns between low and high ventral specimens, we would be tempted to suggest that three species, *alleni*, *nigrocinctus*, and *mosquitensis* (conspecific with population III) occur in eastern Nicaragua.

Another aspect of the situation involves variation in the extent of the black head cap within the series grouped under pattern B. In the Costa Rican lowland series, the head cap never includes more than three-fourths of the supraocular and frontal plates, so that their tips are yellow. In many examples from eastern Nicaragua, the black completely covers the supraoculars and often the frontal and in this regard approaches the C pattern uniformly found along the Pacific coast from Nicaragua into Costa Rica.

The samples from further north in Nicaragua clarify the situation to some extent:

	V + C	BBR	HC	NR
ZELAYA:				
Cum (LA, formerly UCLA 14717)	252	15	B	O 6
Bonanza (AM 75464)	253	11	B	P 6
(KU 86262)	245	13	B	O 7
(KU 86263)	240	14	B	P 6
Musawas (75220)	250	12	B	P 6
Big Falls (12701)	256	14	B	O 8

As can be noted, each of these examples shares characteristics with both populations II and III in a variety of combinations, although all have B head cap patterns. The specimen (KU 86262) most like population III in segmental counts and nuchal pattern agrees with western Nicaraguan series in the extent of the nuchal ring; the specimen (AM 75220) with the highest segmental counts like population II has the nuchal pattern like population III. The samples from Atlantic Nicaragua, thus, indicate a mixture of characteristics found in the western Nicaraguan and Atlantic Costa Rican populations. An occasional individual (AM 69716) shares all of its characteristics in common with the Costa Rican populations, while another (AP 6844) is typical of the western series. All other examples, while having a B head cap pattern (as in population III) and a nuchal pattern approaching that in population II, show a series of combinations of intermediacy between the two. Some of the variation may also indicate the influence of the Atlantic lowland Honduras population that has been called *M. nigrocinctus divaricatus* (22, 23, 29, 30), with segmental counts of 248-260, 11-26 black body rings and the nuchal ring variable, involving the parietals or not.

SCHMIDT (30) thought that two of the specimens (AM 12700-01) from eastern Nicaragua included above indicated intergradation between *alleni* and *nigrocinctus*. As previously discussed in the section on the status of *alleni*, both examples are unquestionably *nigrocinctus*, but with higher ventral counts than in the Costa Rican population that Schmidt thought also occurred on the Atlantic lowlands of Nicaragua. In fact these snakes are typical of the Atlantic lowland population of *nigrocinctus* in Nicaragua that is intermediate in most features between populations II (western Nicaragua and northwestern Costa Rica) and III (Atlantic lowland Costa Rica).

The material of coral snakes of this population series from the area between the eastern margins of the great Nicaraguan lakes and the Atlantic lowlands supports the concept of intergradation between the eastern and western populations. The features for the 14 available examples from this area are given in tabular form (Table 3). The sample from Provincia de Matagalpa shows a wide range of variation with some examples (MCZ 9570, 17087; UM 56498) almost identical in every respect with Costa Rican members of population III. Others (MCZ 9569; UM 1165-09; TAM 4926, 19250), are typical of specimens from population II from western Nicaragua. The remaining specimens have various combinations of characteristics that make them intermediate between the two populations and in agreement with Atlantic lowland Nicaraguan samples. These Matagalpa snakes agree with the Atlantic Costa Rican population (III) in having a head cap of B pattern, and the nuchal ring not involving the parietals. They resemble the western form (population III) in high segmental counts and the extent of the nuchal ring (6-7 scale rows). The number of black body rings (14-15) overlaps the upper limits of population III and the lower values for population II. The Matagalpa series exhibits the same pattern of variation found in the smaller sample from southeastern Nicaragua and further confirms the extensive zone of intermediate populations connecting populations II and III. The examples (Table 3) from Boaco are typical of population II. The single example from near Acoyapa is intermediate in characteristics.

TABLE 3

Characteristics of coral snakes from intermediate geographic samples of Micrurus nigrocinctus *in Nicaragua*

	Ventrals plus caudals	Black body rings	Head cap	Nuchal ring	Extent of nuchal ring	
MATAGALPA:						
26 km N Matagalpa						
UM 116535	252	14	B	O	7	
UM 116536	250	14	B	O	7	
19 km N Matagalpa						
UM 116508	245+	15	B	O	6	
UM 116509	255	15	C	P	5	♀
Matagalpa						
MCZ 9569	262	22	C	P	5	♀
MCZ 9570	---	12	B	O	9	♂
MCZ 17087	238	13	B	O	11	♂
KU 86264	243	15	B	O	..	
UM 56498	229	11	B	O	12	♂
TAM 4926	257	22	C	P	5	♂
145 km SE Matagalpa						
TAM 19250	263	19	C	P	6	
BOACO:						
Nr. Boaco						
JV 1243	264	16	C	P	6	♂
JV 1244	263	18	C	P	5	♂
CHONTALES:						
1.5 km WNW Acoyapa						
KU 63911	245	20	B	O	5	♂

All of these data strongly suggest intergradation between the nominal forms *mosquitensis* (population III) and *melanocephalus* (population II) over a broad portion of Atlantic versant Nicaragua east of the great lakes region.

Population samples from throughout the area have variation in characteristics intermediate between the Atlantic Costa Rican form and the western Nicaraguan population. Analysis of the intermediate samples, exclusive of the series from northeastern Nicaragua, shows that many individuals within the intermediate populations agree in all features with one or the other of the named forms, with about a third of the examples combining features of both. Of the 18 specimens known from the intermediate zone, four snakes are typical of population III, with low segmental counts (229-238), low numbers of black body rings (11-13), a B head cap pattern with the posterior third to fourth of the supraoculars not included in the cap, and the nuchal ring extensive on the body (9-12 scale rows), but not involving the parietals. Three of these specimens are from Matagalpa and one is from Corozco. In the total sample, seven examples are typical of population II. They have high segmental counts (251-264), high numbers of black body rings (14-22), a C head cap pattern and the nuchal ring involving 4-6 scale rows on the anteriormost part of the body, and crossing the parietals. Examples of this morphology occur at Machuca, Matagalpa and vicinity, and Boaco. The other seven examples combine the characteristics of both forms but regularly agree more closely with one or the other in a particular feature as follows (number in parentheses indicates number of examples):

	resembles population II		resembles population III	
ventrals plus caudals	245-256	(6)	243	(1)
black body rings	15-20	(4)	14	(3)
head cap pattern	C	(1)	B	(6)
nuchal ring pattern	P	(2)	O	(5)
extent of nuchal ring	4-7	(7)	—	—

Most of these examples have the black head cap of pattern B, with the black covering all of the supraoculars and often all of the frontal as well. In this feature they are intermediate between population II (head cap pattern C) and population III (head cap pattern B, but with the posterior part of the supraocular and frontal plates yellow).

Throughout much of Nicaragua, east of the eastern margin of the great lakes, exclusive of the northeastern lowlands, coral snakes of the *nigrocinctus* group occur together. For purposes of further discussion, the morphs may be designated as follows: a morph agreeing in all features with snakes from population III from the Atlantic lowlands of Costa Rica—*mosquitensis* morph; a morph agreeing with individuals from population II of western Nicaragua and adjacent northwestern Costa Rica—*melanocephalus* morph; and a morph sharing characteristics with both of the others, but distinct from both as indicated above—intermediate morph. In the sample available, the morphs have the following ratios (in the order given in the last sentence) 4:7:7. Since the population (III) to the south is composed exclusively of snakes of the *mosquitensis* morph and that to the west (II) of individuals of the *melanocephalus* morph, the situation in Nicaragua suggests a zone of secondary intergradation (MAYR, 18: 369) between formerly geographically isolated populations. This possibility is further supported by the sporadic occurrence of the *mosquitensis* morph over the entire area at great distances from the next closest records (Costa Rican lowlands; 160 km to Corozo; 150 km to Matagalpa) and a similar pattern for *melanocephalus* morphs involving shorter distances (nearest records in western Nicaragua to Matagalpa, 150 km; to Boaco, 75 km; and to Acoyapa 75 km). The intermediate morph occurs at most of these localities and apparently extends further east and north than either of the others.

While the hypothesis of secondary intergradation has some appeal as an explanation of the situation in eastern Nicaragua at least one other possible alternate also fits the available evidence. Under circumstances of primary intergradation, the most frequent pattern involves a gradual clinal shift in variables from one population to another. In terms of segmental counts and the correlated features of numbers of black body rings, the eastern Nicaraguan samples are intermediate between populations II and III and suggest primary intergradation (Figs. 2, 3). Nevertheless, individual snakes of the *mosquitensis* morph from the critical zone always have low segmental and body ring counts and those of the *melanocephalus* morph high counts. The close correlation between these counts, the head cap patterns and the nuchal ring features, suggest that control of morph characteristics involves a relatively few gene loci that are probably linked. In the Costa Rican lowland population and in the *mosquitensis* morph in Nicaragua, the black head cap is of a B pattern, with the posterior portions of the supraoculars and frontal yellow and the nuchal ring never crossing the parietal but extending posteriorly for 8-13 scale rows. In the western Nicaraguan sample and the *melanocephalus* morph, the black head cap is of the C pattern and the nuchal ring always crosses the parietals and extends posteriorly only 4-7 scale rows. Its seems possible that the absolute correlation of these features may derive from a single pair of alleles, or a closely linked series of genes forming a supergene in the sense of FORD (8: 146). If this is the case, the situation involves incomplete or partial dominance and the several presumed genotypes may be recognized most easily on the basis of the head cap pattern and nuchal ring pattern and extent (Figs. 2, 4) as the other features correlate with them. According to this hypothesis, the *mosquitensis* morph is homozygous for one allele and the *melanocephalus* morph is homozygous for the other. The intermediate morph, with a B head cap that covers the supraoculars and a nuchal ring that crosses the parietal and extends no more than 7 scale rows onto the body is probably heterozygous. Population II is homozygous for one allele, population III is homozygous for the other and in an extensive area of mixing all three morphs appear through random segregation. If this hypothesis can be confirmed, the intermediate area shows primray intergradation even though the variants show discontinuous variation.

Although this view cannot be proven on the basis of available specimens, it can be further tested through reference to the situation in areas further to the south lying between the ranges of populations II and III.

In Costa Rica, just east of the continental divide near Laguna de Arenal, all examples agree with Atlantic lowland population III except that one example has 15 black body rings and another has the black head cap completely enclosing the supraoculars and frontal. At Monteverde, on the Pacific slope near the divide, the single available specimen is the intermediate morph (Table 2). A specimen from near La Tigra on the Atlantic foothills, just north of Volcán Poás is typical of the Atlantic lowland populations, except that the black head cap includes all of the supraocular and most of the frontal plates. The Arenal and La Tigra examples suggest that the B head cap patterns are not indicative of the typical *mosquitensis* morph (supraoculars and frontal with posterior portion yellow) or the intermediate morph (all of supraoculars and most or all of frontal black), since both head cap patterns occur in association with nuchal rings that do not cross the parietals (O) that have substantial extent (9-13 scale rows onto the body).

On the Meseta Central Occidental of Costa Rica, almost all examples are typical of population II in every character. Several scattered specimens have one or the other of the features of population III. Only one example from La Uruca, just northwest of San José has the nuchal ring not crossing the parietals, but even in this example the ring extends only four scale rows onto the body (8-13 in population III). One example from Desamparados has the typical Atlantic lowland head cap but in all other regards is like population II and we include it as an intermediate. The intermediate morph occurs at three localities near Santa Ana, La Uruca, and San José. The ratios of *mosquitensis*, intermediate, and *melanocephalus* morphs in the sample are: 0:4:11. These data suggest some intergradation between Atlantic and Pacific Costa Rican populations via the Meseta Central, but on the Pacific slope at least, the effect of *mosquitensis* genes is slight.

On the Atlantic slope an example from Juan Viñas is a typical *mosquitensis*. At Turrialba and the nearby localities of Pavones and La Suiza, a complex mixture of characters is represented (Table 4). All examples but one have the nuchal ring pattern typical of population III. Even this example from Pavones has all other features similar to population III, including the nuchal ring extent of 11 scale rows. These specimens may be grouped as follows: 11 *mosquitensis* morphs and 9 intermediates. The sample shows the converse of the material from the Meseta Central Occidental, where *melanocephalus*-like examples predominate. The evidence is conclusive that gene exchange takes place across the divide between Atlantic and Pacific slope Costa Rica in the Central region between San José and Turrialba. On the Pacific side, subtle but definite Atlantic influences affect the population of the Meseta Central and on the Atlantic side a comparable western influence is seen.

These data do not provide insight into the possible nature of intergradation between Atlantic lowland Costa Rican and western Nicaraguan samples. The head cap pattern (B) in which the cap includes all of the supraoculars and usually the frontal may occur with either a *mosquitensis* nuchal ring (O 8-13) or the *melanocephalus* type (P 4-7). In Costa Rica it is usually associated with the former, in Nicaragua with the latter. Although our hypothesis regarding the genetics of *mosquitensis* and *melanocephalus* morphs does not seem to be borne out in Costa Rica, it is clear that a rather continuous intergrading series connects populations II and III in Nicaragua and across the continental divide in northern and central Costa Rica. Populations I and II are also connected in southern Pacific Costa Rica by intermediate examples.

In view of the geographic extent, degree of differentiation and complexity of variation in the intermediate populations, we do not believe that the use of trinomials contributes to understanding the evolutionary patterns in *Micrurus nigrocinctus* and follow SAVAGE and HEYER (26) in describing the situation rather than arbitrarily naming population segments within the pattern. As a case in point, ROZE (22) recently described as a distinct subspecies, three examples of *nigrocinctus* from Isla de Maíz Grande off southern Caribbean Nicaragua. They are recognized as *M. nigrocinctus babaspul* solely because they combine the black body ring counts (18-23), head cap pattern (C), nuchal ring pattern (P) and extent (4 scale rows in holotype, not given for the paratypes) of *melanocephalus* morphs with segmental counts (240-241) of Atlantic lowland samples. Although this particular combination is not exactly duplicated elsewhere in Nicaragua, examples occur in western portions of that country and the Meseta Central Occidental of Costa Rica with 247 ventrals plus caudals and all other characters in common with *babaspul*. In view of the extensive variation in mainland *nigrocinctus* it seems inappropriate to regard the Isla del Maíz sample as distinctive when several unnamed mainland populations of equal distinctiveness have been shown to be part of a series of intergrading populations. We remain convinced that the variational patterns in most organisms are more complicated than usually recognized and that neither biology or evolutionary theory are served by arbitrarily breaking-up the patterns through concentration on, or manipulation of a few characters so that parts of the variational continuum may be named.

MICRURUS ALLENI: STATUS, DISTRIBUTION AND VARIATION

As pointed out in an earlier section, *Micrurus alleni* is a valid species of tricolor coral snake that occurs sympatrically with populations of *Micrurus nigrocinctus* in the Atlantic lowlands of Nicaragua and Costa Rica. The two species are completely separable in the area of geographic overlap on the basis of head cap patterns and segmental counts. Further to the west in Nicaragua, the populations of *nigrocinctus* have much higher segmental counts (248-267)

TABLE 4

Variation in Micrurus nigrocinctus *from near Turrialba, Costa Rica*

	Ventrals plus caudals		Black body rings						Head cap			Nuchal ring		Extent of nuchal ring				
	>247	<248	10	11	12	13	14	15	B1	B2	C	O	P	8	9	10	11	12
N	1	19	2	7	4	3	2	2	13	2	5	19	1	2	3	6	5	1
%	5	95	10	35	20	15	10	10	65	10	25	95	5	12	18	35	29	6

than on the Atlantic lowlands and overlap the variation for *alleni.* The head cap pattern typical of the western populations (C) also approaches the pattern in *alleni* to the extent that it involves the parietals (O). In all *alleni* there is a distinct posterior linear or ovate to lanceolate projection of the black head cap onto the parietals while the posterior margin of the head cap in western Nicaraguan *nigrocinctus* is even or wavy in outline, but is always essentially parallel to the anterior edge of the nuchal ring (Fig. 1, B2, C). In addition to the head cap distinction, *alleni* may always be separated from the western Nicaraguan population by having the nuchal ring posterior to the parietals (involving the parietals in western *nigrocinctus*). Most *alleni* may be further distinguished from the western population by having the nuchal ring extending 7-11 scale rows onto the body (4-7 in *nigrocinctus* with high segmental counts). *M. alleni* does not occur in western Nicaragua or northwestern Costa Rica. Part of the past confusion regarding the status of *alleni* derived from SCHMIDT (30) who did not discriminate between Nicaraguan *nigrocinctus* with high segmental counts and *alleni,* leading him to include some examples of the former in his type series of the latter. *Micrurus alleni* and the western Nicaraguan and northwestern Costa Rican snakes called population II in the section on *M. nigrocinctus* variation above seem to be completely allopatric. *M. alleni* occurs sympatrically with the Costa Rican Atlantic lowland population (III) and with several of the Nicaraguan samples that link populations II and III. The intergradation among populations II and III of *M. nigrocinctus* and the intermediate samples from eastern Nicaragua confirms the conspecificity of these populations as demonstrated earlier in this paper and eliminates from consideration any concept that *M. alleni* and population II might be allopatric races of one species because of their overlapping segmental counts.

M. alleni samples from Atlantic Nicaragua and Costa Rica occur only in the humid lowlands. Several examples are known from along the Río San Juan and the upper Río Escondido drainage on the Río Mico in Nicaragua, where the nearest approach to population II localities are between Zelaya: 16 km W of El Recreo on the Río Mico (*alleni*) and the area around Managua: Managua (population II) a distance of about 160 km, and Río San Juan: near

San Carlos (*alleni*) and Rivas: near Peñas Blancas (population II) a distance of 90 km. Examples from the Atlantic drainage of Nicaragua forming part of the complex intergradation between *nigrocinctus* populations II and III, resembling individuals from population II occur to the east and west of *alleni*. Records of such examples are from Río San Juan: Machuca, 60 km east of San Carlos in the region of Matagalpa: Matagalpa and Boaco: Boaco, places between El Recreo on the east and Managua to the west. These specimens further support the distinctness of *M. alleni* from any other tricolor coral snake in Nicaragua or Atlantic and northwestern Costa Rica.

A single snake (UM 71370, a male) presumably from Nicaragua: Granada: Granada: is perfectly typical *alleni* with a segmental count of 276, 19 black body rings, a D head cap pattern and the nuchal ring not involving the parietals and extending 9 scale rows onto the body. Granada lies between Lagos de Managua and Nicaragua and *nigrocinctus* have been taken at many sites near Granada or to the north and west of the city. If the record is not an error, it provides evidence for predicting sympatry between *M. alleni* and the western Nicaraguan form of *nigrocinctus* around the margins of the great lakes. Until further samples test this possibility, we remain skeptical of the occurrence of *alleni* this far to the west. The nearest authentic record for this species is from 125 km to the east on the Río Mico of Atlantic lowland Nicaragua.

The above discussion clearly establishes *Micrurus alleni* as a distinct species of Atlantic versant Nicaragua and Costa Rica. Examination of Pacific slope tricolor *Micrurus* indicates that a population very closely allied to *alleni* occurs sympatrically with *Micrurus nigrocinctus* populations in southwestern Costa Rica and adjacent Panama. The *alleni*-like coral snakes of the latter area agree with Atlantic examples of the species in consistently having a D black head cap, high segmental counts (256-272), a moderate number of black body rings (13-26) and the nuchal ring not involving the parietals and extending 6-8 scale rows onto the body. Typical *Micrurus nigrocinctus* occur sympatrically with the D black head cap form in Pacific Costa Rica and Panama, but have many fewer ventrals plus caudals (237-244) and a head cap of pattern B.

The first available name for coral snakes with a D pattern black head cap on the Pacific is *Micrurus nigrocinctus yatesi* Dunn, 1942 (type locality: Panama: Chiriquí: near Puerto Armuelles, Farm Two, Chiriquí Land Company). Although Dunn had only severed heads for study, he correctly pointed out the remarkable ontogenetic change in this population. Immature examples are typical tricolor red, yellow and black, with black tips on the scales in the red rings. With age, the black expands over the red to completely obscure it except as faint red outlines on some scales. Dorsally, the adults are black and yellow, ventrally, the red persists so that they are black, yellow and red below. Black pigment eventually invades the ventral red areas to a substantial degree, almost obscuring them completely in the largest available specimen (CRE 2662, a female, 1035 mm in total length). TAYLOR (33) correctly pointed out the occurrence of this form in Costa Rica and its sympatry with *Micrurus nigrocinctus*.

ROZE (23: 201) separated the Atlantic from the Pacific population, which he recognized as a subspecies of *M. alleni*, on the basis of a clever manipulation of several features closely correlated with the number of body and tail vertebrae as follows:

	Atlantic *alleni*	Pacific *yatesi*
ventrals		
males	214-224	209-215
females	229-237	221-230
black body rings		
females	17-23	20-26
caudals		
males	50-55	48-50

We presume that the number of black body rings in males and caudals in females were similar in both samples available to Roze.

Our material shows that these differences do not hold up for a larger series. Pacific males have as many as 223 ventrals, although the female ventral counts are not changed. Atlantic females have 17-23 black body rings, Pacific females 18-28. Atlantic males have 48-59 caudals, Pacific males 47-52. We suspect that the difference in ventral counts in females (Atlantic 229-244, Pacific 221-230) will show further overlapping in a larger series since only 8 Atlantic and 6 Pacific examples are currently available.

Aside from the remarkable differences in adult coloration, contrary to ROZE (23), no feature distinguishes the Pacific population from typical *alleni*. The range of variation in the two overlaps extensively, although the averages or modes for some features suggest slight populational differences. The segmental counts for all available examples of the two samples are indicated by locality (Fig. 2). Generally the highest counts occur in Atlantic Costa Rica (263-281, mean 276) but they are extensively overlapped by the Nicaraguan (259-286, mean 273) and Pacific (256-272, mean 261) samples. The number of black body rings shows a similar pattern: 14-21, mean 17.4 in Nicaragua; 16-23, mean 18.8, in Atlantic Costa Rica and 16-26, mean 18.6 in Pacific Costa Rica and Panama. The black head cap (Fig. 1) is consistently of the D pattern in all examples, but there is a considerable range of variation in the details of the pattern (Fig. 5). The basic head cap pattern D (Fig. 1, D) predominates in all samples and there is no clear geographic pattern of variation except that in Pacific examples, the parietals tend to have considerable dark pigment lateral to the main black figure in adults. This correlates with the increased expansion of black over lighter areas with age in this population.

The nuchal ring does not cross the parietals in any member of this group, but the extent to which it extends onto the body is higher in the Pacific sample although the ranges of all series overlap (Nicaragua 8-11, mode 9; Atlantic Costa Rica 7-11, mode 9; Pacific 6-8, mode 6).

Available locality records indicate that the two populations, Atlantic Nicaragua and Costa Rica and Pacific Costa Rica and Panama are completely allopatric. *Micrurus alleni* is to be expected from extreme northwestern Panama since it has been collected a few kilometers from the border in Costa Rica in the same type of habitat found inland from Almirante and the Laguna de Chiriquí in the former country. It seems unlikely that the Atlantic and Pacific populations are connected by intergradation. Atlantic *M. alleni* are restricted to the very humid lowland forests of Nicaragua, Costa Rica and probably extreme northwestern Panama. The nominal taxon *yatesi* is restricted to similar areas of heavy rainfall and associated vegetation in southern Pacific Costa Rica and adjacent extreme southwestern Panama. This latter population is confined to a very small area centered on the Golfo Dulce by the dry forest environments of Costa Rica to the north and the dry forest and western savanna areas of Panama to the east. It is isolated from its Atlantic congener by the towering Talamanca-Chiriquí axis to the north. This pattern of distribution, as has been pointed out by one of us (SAVAGE, 24), with allopatric Caribbean lowland and Golfo Dulce populations is common for many lowland evergreen forest forms.

The systematic problem of how best to interpret the relationships of distinct but closely allied allopatric forms has always been and remains a difficult task for the practicing taxonomist (see GRANT, 10: 344 and MAYR, 18: 181 for two distinctive views). The present case parallels many others where moderately to well-differentiated populations occur around the Golfo Dulce completely isolated from their closest relatives across the continental divide on the Atlantic versant. Details of this pattern have been documented for *Agalychnis helenae-callidryas* (SAVAGE and HEYER, 26) and *Dendrobates pumilio* and *granuliferus* and *Phyllobates lugubris-vittatus* (SAVAGE, 25) while a number of cases of little or no differentiation in the isolated Golfo Dulce population are discussed for the tree-frog family Hylidae by SAVAGE and HEYER (26) and DUELLMAN (2).

Previous students of the problem always have regarded *yatesi* to be a subspecies of either *nigrocinctus* (5, 23) or *alleni* (22, 23), although a case might be made for considering *alleni* and *yatesi* allopatric semispecies. We do not believe that the differences in adult coloration in themselves justify an assumption of genetic incompatibility between the two populations. In the sense employed by GRANT (10), the two appear to represent allopatric disjunct geographic races. While we concur with WILSON and BROWN (36) and SAVAGE and HEYER (26) in their delineation of the many objectionable features of trinomial nomenclature, we also empathize with those who would use subspecies designations for distinctive disjunct allopatric populations of the kind treated here. Nevertheless, we believe that the interest of an evolutionary taxonomy is best served by regarding both Atlantic and Pacific populations as representative of a single species, with the recognition that the two isolates differ in details of adult coloration. It seems preferable to us to speak of Atlantic *alleni* or Pacific *alleni,* where reference is made to either population, rather than by formal Latin names.

A single male specimen (US 140673) from the Pacific versant of eastern Panama: Darién: El Real de Santa María, some 550 km east of the nearest record for *M. alleni* in western Panama seems to belong to this species. The snake has a segmental count of 264 (209 ventrals and 55 caudals), 13 black body rings, a D head cap pattern and the nuchal ring not reaching the parietals but extending for 5 scale rows onto the body. In the total segmental counts, the El Real snake is similar to the Pacific population of *alleni* in Costa Rica and western Panama (256-272, mean 261) rather than the other most proximate geographic sample from Atlantic lowland Costa Rica (263-281, mean 276). The number of black body rings is lower in this snake than for any other known *alleni,* but suggests a closer affinity to the Atlantic population (black body rings 14-23) than to the Pacific sample (16-24). The number of scale rows included by the nuchal ring (5) is also lower than in any other known *alleni,* but approaches the lower limit of variation in the Pacific sample (6-8) more closely than the Atlantic (7-11). The Darién snake appears to represent a third allopatric population of the species from another region of high rainfall and associated lowland evergreen forest. An essentially similar pattern is known for the poisonous *Phyllobates* frogs of the *lugubris-vittatus-aurotaenia* series, with allopatric populations in 1) Atlantic lowland Costa Rica and adjacent western Panama, 2) the Golfo Dulce region of Pacific Costa Rica and 3) the Chocó of northwestern Colombia (SAVAGE, 25) and may be expected for other species of amphibians and reptiles restricted to humid lowland forests and apparently unable to penetrate the drier habitats of central Panama.

SPECIES DIAGNOSES

The following section presents parallel comparisons of diagnostic characteristics for the four Costa Rican species of venomous coral snakes. These diagnoses will also apply to members of the genus from Nicaragua and western Panama. Features that unequivocally separate a species from the others are italicized.

Micrurus alleni: 1) *black head cap extending as a linear, oblong or lanceolate figure along interparietal suture* (head cap pattern D. Figs. 1, 5); 2) scales in light area between black head cap and nuchal black ring, including lateral head plates, yellow in life, none or a few outlined by black; 3) 13-26 black body rings; 4) tricolored black-yellow-red in life, but with red rings completely obscured by black above in some large Pacific versant adults, although still indicated ventrally; in these examples the snake is black and yellow above;

5) 256-281 ventrals plus caudals; 6) several infracephalic plates, usually the mental and several infralabials, black; 7) nuchal ring not involving parietals, extending 5-11 scale rows onto body; 8) supra-anal scales strongly keeled in adult males and large adult females; 9) males to 800 mm in standard length, females to 951; tail length as percentage of standard length 14-19 in males, 8-12 in females.

Micrurus clarki: 1) *black head cap completely involving the parietal plates* (head cap pattern E, Fig. 1); 2) *scales in light area between black head cap and nuchal ring, including lateral head plates, all outlined by black;* 3) 13-20 black body rings; 4) tricolored black-yellow-red, in life; 5) 241-257 ventrals plus caudals; 6) most infracephalic plates, light, the mental and infralabials never black, although some scattered black peppering present; 7) nuchal ring not involving parietals, extending 6 scale rows onto body; 8) *no keels on supra-anal scales in either sex;* 9) standard length to 550 mm in males, tail length as a percentage of standard length 17-20 in males.

Micrurus mipartitus: 1) *black head cap involving the rostral, nasal and prefrontal plates, rarely extending onto anterior margin of the supraoculars and frontal* (head cap pattern A, Fig. 1); 2) scales in light area between black head cap and nuchal ring, including lateral head plates, white, cream, pink or red, immaculate; 3) 25-33 black body rings; 4) *bicolored black and white, cream, pink, or red in life;* 5) 264-305 ventrals plus caudals: 6) most infracephalic plates light; 7) nuchal ring not involving parietals, extending 5-8 scale rows onto body; 8) supra-anal scales weakly keeled in adult males; 9) unlike other species in the area, this form shows sexual dimorphism in total segmental counts, (264-274 in males, 288-305 in females) probably correlated with the very short tails.

Micrurus nigrocinctus: 1) *black head cap including a substantial portion or all of supraocular and frontal plates, sometimes extending onto anterior margin of parietals* (head cap patterns B1, B2 and C, Fig. 1); 2) scales in light area between black head cap and nuchal ring, including lateral head plates, yellow, not outlined by black; 3) 10-22 black body rings; 4) tricolored black-yellow-red, in life; 5) 222-268 ventrals plus caudals; 6) several infracephalic plates, usually the mental and several infralabials, black; 7) nuchal ring involving posterior tips of parietals or not, extending posteriorly onto body 4-13 scale rows; 8) supra-anal scales strongly keeled in males; 9) standard length to 575 mm in males, to 760 mm in females; tail length as a percentage of standard length 16-26 in males, 9-13 in females.

The latter species is the most variable and widely distributed venomous coral snake in Central America. Its range overlaps the ranges of the three other Costa Rican species. Because of geographic variation in *nigrocinctus* additional features may serve to distinguish it from the others where sympatry occurs. *M.*

nigrocinctus differs from *M. alleni* where the two co-exist on the Atlantic lowlands of Nicaragua and Costa Rica in segmental counts (less than 257 in the former versus 259 or more in *alleni*) and usually in numbers of black body rings (never more than 16 in the former versus usually 15 or more in *alleni*). In the second area of sympatry in Pacific southwestern Costa Rica and adjacent southwestern Panama, *alleni* has a segmental count of 256-272 versus 237-244 in *nigrocinctus*.

M. nigrocinctus and *M. mipartitus* occur together in Atlantic lowland Costa Rica and Nicaragua. The latter has a much higher number of black body rings (25-33) than is found in *M. nigrocinctus* in the same area (12-20).

Aside from the features already discussed, *M. clarki* and *M. nigrocinctus* are difficult to distinguish because they resemble one another very closely in the area of geographic overlap in western Panama and adjacent Pacific lowland Costa Rica in segmental counts (241-257 in the former versus 237-244 in *nigrocinctus*) and numbers of black body rings (13-20 in the former versus 15-19 in the latter).

The most distinctive population of *M. nigrocinctus* in the region ranges from central Costa Rica along the Pacific lowlands into western Nicaragua and is apparently not sympatric with any other venomous coral snake.

DISTRIBUTIONAL PATTERNS

GEOGRAPHIC OCCURRENCE: The following lists contain records of unquestionable identity based upon examination of specimens or the literature. We have presented all available records for *Micrurus alleni* and *clarki*. ROZE (22, 23) included western Colombia in the range of the latter species without further data, but we have seen no specimens from that country. Only Central American records for *Micrurus mipartitus* are listed, although the species has an extensive range in northern South America. Although *Micrurus nigrocinctus* occurs from southern Mexico to Colombia, we have concentrated our study on the species in Nicaragua, Costa Rica and Panama and have made no attempt to fully document distribution to the north or south of these countries. The records for Nicaragua, Costa Rica and western Panama for *nigrocinctus* are exhaustive, but we have not attempted to be as complete for the remainder of Panama, since it lies outside our area of extensive analysis and many specimens known to be in collections from Panama have not been studied by us.

Micrurus alleni — NICARAGUA: GRACIAS A DIOS: Cabo Gracias a Dios; RÍO SAN JUAN: nr. El Castillo; Camp Machado; Río San Juan; nr. San Carlos; San Juan del Norte; ZELAYA: Bluefields; Bonanza; La Hunter; Río Mico, 11.2 km E Rama; Río Siquia; Río Siquia, 16 km N Rama: COSTA RICA. ALAJUELA: nr. Ciudad Quesada; HEREDIA: La Selva; LIMÓN: Los Diamantes; La Lola, Pandora; Talamanca; Tortuguero; PUNTARENAS: Golfito; nr. km 33; 8 km S Palmar Sur; 3 km WSW Rincón de Osa; SAN JOSÉ: Boquete

Camp; 15 km SW San Isidro de El General; PANAMA: CHIRIQUÍ: Boquete; Farm 2 nr. Puerto Armuelles; El Hato del Volcán; Potrerillos; DARIÉN: El Real de Santa María.

Micrurus clarki — COSTA RICA: no definite locality; PANAMA: CHIRIQUÍ: Farm 2, nr. Puerto Armuelles; PANAMÁ: Chagres areas; Sabanas areas; DARIÉN: Cana; Jaqué; Tuira areas; Yavisa; SAN BLAS: Puerto Armila.

Micrurus mipartitus — NICARAGUA: CHONTALES: no definite locality; ZELAYA: San Juan del Norte; COSTA RICA: ALAJUELA: nr. Ciudad Quesada; Muelle San Carlos; drainage of Río San Carlos; CARTAGO: Peralta; Turrialba; GUANACASTE: Santa María; HEREDIA: Cariblanco; LIMÓN: Barra Colorado; Los Diamantes; 4 km W Guápiles; Jiménez; La Lola; Pandora; Suretka; PUNTARENAS: Monteverde; SAN JOSÉ: Carrillo; PANAMA: BOCAS DEL TORO: Punta de Pena; CANAL ZONE: Barro Colorado; Corozal; Island; France Field Fort Sherman. DARIÉN: Cana; PANAMA: Cerro Bruja; Chagres areas; Punta Bruja; Sabanas areas; San Pablo, Tuira areas; VERAGUAS: Río Concepción.

Micrurus nigrocinctus — NICARAGUA: BOACO: nr. Boaco; CHINANDEGA: San Antonio; CHONTALES: 1.5 km WNW Acoyapa; Corozo; GRANADA: nr. Granada; LEÓN: El Polvón; MANAGUA: 1.2 km E Casa Colorada; Finca El Encanto; Laguna Xiloa; nr. 9.6 km WSW Managua; Las Nubes; Los Robles; 1 km N Sabana Grande; MATAGALPA: 26, 19 km N, nr. 14.5 km SE, Matagalpa; NUEVA SEGOVIA: Ocotal; RÍO SAN JUAN: Camp Machado; Machuca; Río San Juan; 1.6 km W mouth Río San Juan; San Juan del Norte; ZELAYA: Big Falls on Río Pis Pis; Bonanza; Cum, 72 km WSW Suina; Río Escondido; La France on Río Grande de Matagalpa; Kanawa; Isla de Maíz Grande; Isla de Maíz Pequeña; Musawas on Río Pis Pis; Topaz Mine; Wounta Haulover. COSTA RICA: ALAJUELA: Alajuela; La Tigra nr. Peñas Blancas; CARTAGO: Cachí; Instituto Interamericano de Ciencias Agrícolas; nr. Juan Viñas; Pavones; La Suiza; 5 km SE and Turrialba; GUANACASTE: 3.2 km N Bagaces; Bebedero; Finca Río Chiquito: nr. Guadalupe; 1 km N, 4 km S Irigaray; 2, 4 km NW Hacienda Los Angeles; nr. Nicoya; Bahía de Salinas; Finca El Silencio de Tilarán; Finca Taboga; Río Tempisquito at Interamerican Highway; Hacienda Tenorio; 4 km ENE Tilarán; HEREDIA: Barreal; Puerto Viejo; Finca La Selva; LIMÓN: La Argentina; Barra Colorado; La Castilla; Coen; Los Diamantes; Guápiles; Puerto Limón; La Lola; Parismina; Siquirres; Alta Talamanca; Tortuguero; Zent; PUNTARENAS: 2 km E and Barranca; Boruca; Buenos Aires; Esparta; 1.5 km NW Río Guacimal, nr. Interamerican Highway; 24 km WSW San Isidro de El General on road to Dominical; La Ligia; Monteverde; San Miguel de Barranca; SAN JOSÉ: Cerros del Aguacate; Carrillo; vic. Desamparados; Escazú; Hatillo; Orotina; Patarrá; nr. Repunta; Salitral de Desamparados; 11.2 km SW San Isidro de El General; San José, San Juan de Acosta; San Pedro de Montes de Oca; nr. Santa Ana; Santiago de Puriscal; La Uruca; Zapote. PANAMA: BOCAS DEL TORO: Bocas del Toro; Coco Plum Estate; Farm 6; Boca de Río Teribe; CHIRIQUÍ: Boquete; COCLÉ: Agua Dulce; El Valle de Antón; Penonomé; DARIEN: Boca de Cupe; Jaqué; Río Pihuila; Río Tucuiti; Tuira areas; CANAL ZONE: Alajuela; La Boca; Ancón; Balboa; Barro Colorado Island; Cárdenas; Corozal; Cristóbal; Culebra; Empire; Fort Clayton; Fort Davis; Fort Gulick; Fort Sherman, Frijoles; Gamboa; Gatun; Isla Gigante; Juan Diaz; Juan Mina; Madden Road; Monte Lirio; Obispo; Quarry Heights; Pedro Miguel; Punta Toro; Tabernilla; PANAMA: Punta Bruja; Cerro Campana; Chagres areas; La Chorrera; New San Juan; Panama; Panama Viejo; Pequeni; Islas del Rey; Isla San Miguel; Santa Cruz de Chagres; Sabanas areas; Isla Taboga; VERAGUAS: Isla de Coiba; Cerro Manglillo; San Francisco.

The distribution for *alleni, mipartitus* and *nigrocinctus* in Costa Rica is shown in the accompanying maps (Figs. 6, 7).

ECOLOGIC OCCURRENCE: The venomous coral snakes are essentially tropical in latitudinal distribution although several species occur in subtropical regions in Mexico, the United States and in South America. In the area under study temperature as correlated with increasing altitude and extremely dry situations appear to limit the distribution of *Micrurus.* Members of the genus range from near sea level on both coasts of Nicaragua, Costa Rica, and Panama to an altitude of 700-750 m in Nicaragua, 1200 m in Atlantic slope Costa Rica, at least 1400 m in Pacific slope Costa Rica and western Panama and up to 500-600 m in central and eastern Panama. With the exception of one specimen of *Micrurus alleni* discussed below, all records for the genus lie in the Tropical Lowland and Premontane altitudinal zones according to the system of HOLDRIDGE (14).

Micrurus alleni ranges from near sea level to an altitude of 656 m on the Atlantic versant, with all Nicaraguan records from below 200 m in altitude. The species is generally restricted to humid evergreen forest habitats (Lowland Moist and Wet Forests and Premontane Wet Forests, after HOLDRIDGE, 14) on the Atlantic lowlands and adjacent foothills. A record (San Carlos) in Nicaragua is from within the limits of the Lowland Dry Forest bioclimate, but the snake was probably taken from a moist situation in a lacustrine or riparian habitat included in the dry forest.

On the Pacific versant, this species ranges from near sea level to over 1400 m in altitude. The species in Pacific Costa Rica and adjacent southwestern Panama is generally found in humid evergreen forest bioclimates (Lowland Wet and Premontane Wet) but localities in Panama are from within Lowland Dry (Potrerillos) and Premontane Moist Forest (Boquete) regimens.

One example (KU 25190) collected by E. H. Taylor from the Pacific population is recorded as from Boquete Camp, a place located on the Pacific slope of the Cordillera de Talamanca of Costa Rica north of San Isidro de El General at an elevation of 2000 m. The specimen represents the highest point at which a venomous coral snake has been taken in the region under study, at an elevation 500-600 m higher than any other locality. Boquete Camp was used for construction and maintenance of the Interamerican Highway during the 1940's and early 1950's, but has been abandoned for sometime. The area supports Lower Montane Rainforest and stands as the only location in Nicaragua, Costa Rica or Panama, where a *Micrurus* occurs in this altitudinal zone. Perhaps the example was inadvertently transported from a lower elevation since there seems no question but that it was collected at this locality. The single snake referred to this species from eastern Panama (US 140,673) El Real is from a point below 50 m in elevation in Lowland Moist Forest.

Micrurus clarki ranges from near sea level to around 500 m in the vicinity of Cana, eastern Panama. Most records are from Lowland Wet Forest situations but the species has also been taken at several Lowland Dry Forest localities in western Panama. It seems likely that it is restricted to moist riparian situations in the latter vegetational formation.

Micrurus mipartitus is known from localities near sea level to a maximum altitude of 1200 m near Monteverde de Puntarenas, Costa Rica. Most records for Central America are from Lowland Moist and Wet and Premontane Wet and Rainforest formations.

Micrurus nigrocinctus occurs from near sea level to as high as 1400 m in central Costa Rica. The species has the widest geographic and ecologic range of the genus in the area under study and is common in the lowlands throughout the region. Only in Costa Rica and western Panama does it occur in the Premontane altitudinal zone above 1000 m. In eastern Nicaragua, Costa Rica and much of Panama, the species is found in association with Lowland Moist and Wet Forest conditions. The range extends upward well into the Premontane zone in Nicaragua, Costa Rica and western Panama in association with Premontane Moist and Wet Forest formations. It also has an extensive distribution in the Lowland Dry Forest of western Nicaragua and northwestern Costa Rica and similar habitats in lowland Pacific Panama.

SYMPATRY AND THE CORAL SNAKE MIMICRY PROBLEM

The occurrence of two or more species of *Micrurus* at the same locality in lowland Nicaragua, Costa Rica and Panama is the rule rather than an exception. Only in the dry lowlands of western Nicaragua and northwestern Costa Rica and on the moist uplands of the Meseta Central of the latter country is a single species, *M. nigrocinctus,* present.

Micrurus alleni has been taken at the same locality with each of the other three species. It was taken with *M. clarki* in the lowlands of western Panama (Chiriquí: nr. Puerto Armuelles). The two probably have an extensive sympatry in the humid evergreen forests of the lowlands around the Golfo Dulce in extreme western Chiriquí, Panama and adjacent southwestern Costa

Rica. *M. alleni* and *M. mipartitus* are known to occur together at several localities in the eastern (Atlantic) lowlands of Nicaragua and Costa Rica from San Juan del Norte on the north to Pandora on the south. Extensive sympatry between the two species at elevations below 700 m is indicated by available records from the area. *M. alleni* and *M. nigrocinctus* have many records of known sympatry from Atlantic lowland Nicaragua and Costa Rica at elevations below 200 m. The two also occur together at Boquete in Panama. Although no actual records of sympatry are known for adjacent southwestern Pacific Costa Rica, the distribution of the two species in that region makes sympatric occurrences almost certain (Fig. 2). The range of *M. nigrocinctus* includes all known records for *alleni* and extensive sympatry between the two is to be expected anywhere within the range of *alleni.*

In addition to sympatry with *M. alleni* as discussed above, the range of *M. clarki* overlaps the ranges of *mipartitus* and *nigrocinctus*. *M. clarki* and *mipartitus* have been taken at Panama: Darién: Cana. The species are also known through the Clark snake collections (DUNN 6) from the same general region (Chagres and Sabanas) of Provincia de Panamá, mostly east of the Canal Zone. *M. nigrocinctus* is also very well represented in the three heterogenous Clark samples so that *M. clarki* and *nigrocinctus* may be expected together in central Panama. The two forms apparently overlap in the Darién since both have been reported from Jaqué and together from the Tuira areas by DUNN (6).

In addition to the instances of sympatry mentioned above, *M. mipartitus* and *M. nigrocinctus* have been taken at the same locality from southeastern Nicaragua (San Juan del Norte) and at a number of Atlantic lowland sites below 700 m in elevation in Costa Rica. The two also occur together on the Pacific slope of Costa Rica, just west of the continental divide at Monteverde de Puntarenas. Areas of known sympatric occurrence for these two species in Panama include the Canal Zone and probably most of central Panama. Records by DUNN (6) for Tuira areas in Provincia de Darién indicate a probable extensive overlap in range in eastern Panama.

Definite sympatry (taken at the same locality) for three venomous coral snake species is known for *M. alleni, mipartitus* and *nigrocinctus* along the Caribbean lowlands of southern Nicaragua (San Juan del Norte) and Costa Rica (Los Diamantes and La Lola). *M. clarki, mipartitus* and *nigrocinctus,* probably occur together over much of their ranges in central and eastern Panama, while *M. alleni, clarki,* and *nigrocinctus* may occasionally occur together in the lowlands of southwestern Panama and adjacent Costa Rica.

The following list summarizes the sympatric distribution of venomous coral snakes in Nicaragua, Costa Rica and Panama. The letters: A, C, M, and N are abbreviations for *alleni, clarki, mipartitus,* and *nigrocinctus,* respectively. For the sake of completeness, we have included the Panamanian species *M. ancoralis* (AN), *dissoleucus* (D) and *stewarti* (S) in the summary so that the distributional relationships of all known forms from the three republics may be discussed. Adult coral snakes of the seven species in this region are bicolor

(B): Pacific versant *alleni, mipartitus* and *stewarti;* tricolor (T): Atlantic versant *alleni, clarki,* and *nigrocinctus;* or tricolor-triad (TT): *ancoralis* and *stewarti.* The sympatric occurrence of the various basic color patterns is also indicated in summary form:

area	number of species by pattern		species
NE Nicaragua	2T	=2	A-N
SE Nicaragua	1B+2T	=3	A-M-N
Atlantic Costa Rica	1B+2T	=3	A-M-N
E Panama	1B+2T+2TT	=5	AN-C-D-M-N
Central Panama	2B+2T+2TT	=6	AN-C-D-M-N-(S)
SW Panama	1B+2T	=3	A-C-N
SW Costa Rica	IB+2T	=3	A-C-N
Meseta Central	1T	=1	N
NW Costa Rica	1T	=1	N
W Nicaragua	1T	=1	N

The situation in the lowland evergreen forests and adjacent premontane zone of southwestern Panama and southwest Costa Rica is not clear-cut because of the remarkable ontogenetic change from tricolor in juveniles to bicolor in adults that occurs in the Pacific population of *Micrurus alleni.* Bicolor *alleni* are sympatric with tricolor *M. nigrocinctus* over most of the region and with tricolor *M. clarki* in humid lowland sites. Although *alleni, clarki* and *nigrocinctus* have not been taken in this area in sympatry, it is probable that all three occur at the same locality throughout the range of *clarki* in western Panama and adjacent Costa Rica. When juvenile *alleni* are considered, three tricolor venomous coral snakes are sympatric only in this area within the three republics. As adults, one bicolor (*alleni*) and two tricolor forms are present. Significantly, *M. alleni* appears to be an ecogeographic replacement for the other bicolor species *M. mipartitus* in the region. The latter form seems well-adapted to humid evergreen forest situations elsewhere in its range but is unknown from the area of overlap between bicolor adult *alleni, clarki* and *nigrocinctus* on the Pacific versant of southwestern Panama and adjacent Costa Rica.

It is questionable that six species of venomous coral snakes occur at a single locality in central Panama. Records for the bicolor (red and black) species *M. stewarti* are few and mostly from upland areas east and west of the Canal Zone at higher elevations than localities for the other five essentially lowland species. Most likely there is no locality in this area where the two bicolor forms, *M. mipartitus* and *M. stewarti* are sympatric.

These distributional patterns suggest a number of interesting relations that seem to apply throughout the study area:

1) no more than two tricolor species are sympatric in any area
2) where tricolor-triad species occur, no area has only one tricolor-triad species
3) no two bicolor species are sympatric in any area.

TABLE 5

Color patterns in Costa Rican coral snakes exclusive of micrurus

	NON-VENOMOUS		REAR-FANGED
		Bicolor	
	Dipsas articulata		*Scolecophis atrocinctus*
	Dipsas tenuissima		
RINGED	*Lampropeltis triangulum*		
	Pliocercus euryzonus		
	Sibon annulata		
	Sibon anthracops		
		Tricolor	
	Dipsas bicolor		*Erythrolamprus bizona*
			Erythrolamprus mimus
	Lampropeltis triangulum		*Rhinobothryum bovalli*
		Bicolor	
	Leimadophis epinephalus		*Oxyrhopus petola*
BANDED		Tricolor	
	Scaphiodontophis venustissimus		*Tantilla annulata*

These relationships suggest that in the region covered, the maximum number of venomous coral snake ecologic niches is five (1 B + 2 T + 2 TT) and that fewer numbers of species occur in areas of unfavorable habitat. We accept the view that *Micrurus* and its allies are aposematically colored (see DUNN, 7; HECHT and MARIEN, 12; and MERTENS, 19 for a full discussion) and serve as models for both Batesian and Mullerian mimics among a number of diverse and distantly related genera of colubrid snakes. For a distinctly different and original view, see WICKLER (35), who believes that *Micrurus* and its allies are mimics of rear-fanged colubrid models. At the same time it seems that the sharing of the same basic color pattern by sympatric venomous coral snakes has strong adaptive value since avoidance of the pattern by a predator will benefit both venomous forms as any misadventure with an example of one species will lead to reduced predation for both. The presence of several venomous species in sympatry thus reinforces the efficacy of the warning pattern. Why then do not all coral snakes, venomous and non-venomous, have the same color pattern in a given region? And if the patterns are various, why is there a distinct limit on the number of forms with a particular pattern? Perhaps a detailed study of the distribution of similarly colored models (à la WICKLER, 35) or mimics (à la DUNN, 7) could aid in solving these problems.

Reference to the pattern and distribution of other Costa Rican snakes that resemble *Micrurus* in coloration does not seem to provide ready answers (Table 5). The data reveal additional information that, taken with DUNN'S (7) work on Panama, may lead to a more appropriate field analysis of the problem. Within the Costa Rica snake fauna of 119 species, 19 have a coral snake pattern of alternating black and red (or yellow or white) dorsally. Only 15 of these taxa, including the representatives of *Micrurus,* have a "true" coral snake pattern in which the alternating colors form complete rings around the body and across the venter. Of the 19 coral snake species, 10 have a bicolor pattern throughout life, and 9 are tricolor at least when young. These snakes belong to three categories: *Micrurus* (M); rear-fanged venomous (R) and nonvenomous (N). The proportions of the three adaptive types by color pattern are: bicolor 1 M: 1 R: 6 N; tricolor 3 M: 4 R: 4 N. These figures are slightly changed when the ontogenetic shift from tricolor in young Pacific slope *M. alleni* and *Lampropeltis triangulum* to bicolor black and yellow in the former and through bicolor black and red to uniform black in the latter. If the juveniles and adults for these forms are counted as two taxa, the figures are: bicolor: 2 M: 1 R: 7 N: tricolor: 3 M: 4 R: 4 N

Close concordance in color pattern among several sympatric species adds support to the concept that the coral snake patterns are aposematic. In this regard, although their bicolor patterns suggest that they are involved in the coral snake mimicry problem, the strictly arboreal species of *Dipsas* and *Sibon* probably do not need to be considered further.

Of the remaining 10 species outside the genus *Micrurus*, the following similarities in patterns are significant:

1) *Pliocercus euryzonus* (including the nominal forms *annellatus, arubicus* and *dimidatus*) closely resembles *Micrurus mipartitus* in Costa Rica; the various names in *Pliocercus* seem to be based on individuals spanning the coloration variation (light rings white, yellow, pink or red) of *M. mipartitus;* the ranges of the two species overlap extensively on the Atlantic versant of Costa Rica; neither is known from the evergreen lowland forests around the Golfo Dulce on the Pacific.

2) *Erythrolamprus bizona* approaches closely the pattern of the Pacific northwest Costa Rican sample of *M. nigrocinctus* (population II) with which it has extensive sympatry; they differ in the sequence of colors, B-Y-R-Y-B-Y

in *Micrurus,* B-Y-B-R-B in *Erythrolamprus,* but the extent of red and black rings is very similar; *E. bizona* barely overlaps the range of Atlantic (population III) *M. nigrocinctus.*

3) *Erythrolamprus mimus* approaches very closely the pattern of Atlantic lowland *M. nigrocinctus* (population III) with which it occurs sympatrically; the species does not occur with Pacific populations (I-II) of *M. nigrocinctus* except at one locality near the Panamanian border.

4) over much of its range in Costa Rica, *Lampropeltis triangulum* closely resembles sympatric samples of *M. nigrocinctus* (populations II and III).

5) *Rhinobothryum bovalli* is known only from the Atlantic lowlands in Costa Rica and has exactly the same dorsal color pattern as Atlantic lowland *M. alleni,* with which it is sympatric and does not resemble the other Atlantic versant coral snake *M. nigrocinctus.*

6) *Lampropeltis triangulum* from the Pacific slope of the Cordillera de Talamanca-Chiriquí of Costa Rica and western Panama are tricolor as juveniles and resemble *M. nigrocinctus* (population I) and juvenile *M. alleni* in the area; the kingsnakes become bicolor red and black with increasing age as the black pigment expands to obliterate the yellow rings and finally nearly uniform black as the red is replaced as well; a similar process occurs in *M. alleni*; but the bicolor adults are black and yellow and no uniformly black examples are known; *L. triangulum* and *M. alleni* from these populations apparently occur together at moderate elevations 1400-1500 m, on the slope of Volcán Chiriquí in Panama northward to above San Isidro de El General in Costa Rica.

7) *Scaphiodontophis venustissimus* resembles Atlantic *M. nigrocinctus* (population II) in dorsal coloration and has extensive sympatry with it; the range of the species on the Pacific versant overlaps slightly with the southern population (I) of *nigrocinctus.*

8) *Tantilla annulata* has a pattern closely resembling *Erythrolamprus bizona* when viewed from above, but is banded B-Y-B-R-B, with a uniform bright red venter, while the latter is ringed; the pattern of *annulata* thus approaches that of the ringed venomous tricolor coral snakes *Micrurus alleni* and *Micrurus nigrocinctus* (populations I and III), with which it is sympatric in eastern and southwestern Costa Rica.

The Costa Rican species of *Leimadophis, Oxyrhopus,* and *Scolecophis* are bicolor and have a dorsal pattern of alternating black and red areas. They are often mistaken for coral snakes by the local people, but do not closely resemble any *Micrurus* known from Costa Rica.

Micrurus clarki, a tricolor species, closely resembles *Erythrolamprus mimus* in color pattern. It seems likely that the two occur sympatrically near the Panama frontier on the Pacific versant of Costa Rica, since both are known from adjacent western Panama and the former from "Costa Rica" and the latter from Costa Rica: Puntarenas: near San Vito de Java.

The numerous cases recorded above of close concordance in coral snake patterns between sympatric species pairs strongly supports the concept of aposematic mimicry for this clique (7, 12). They do not allow discrimination between the hypothesis of these authors that the *Micrurus* are the model and the others are mimics or that of WICKLER (35) that the rear-fanged snakes are the models and both the non-venomous species and the *Micrurus* are mimics.

KEY TO THE CORAL SNAKES OF COSTA RICA

The following key is designed to identify as readily as possible any Costa Rican snake having the coral snake pattern of alternating dorsal bands or rings encircling the body, without dissection of the jaw to determine the nature of the venom apparatus. Some snakes called *corales* by Costa Ricans are omitted, since they have the entire body, red (especially juvenile *Clelia clelia,* a rear-fanged snake); a considerable portion of the venter orange, pink, or red; a number of red spots on the body; or a nuchal red area and cannot be confused with *Micrurus* or the possibly toxic rear-fanged forms with coral snake patterns. It is hoped that even a novice will be able to make a quick and accurate identification with this key, in order to insure immediate and appropriate treatment of a toxic bite. Life colors are emphasized for this reason, since living or recently dead snakes will be available for study. An illustrated translation of this key in Spanish is being made available to all Costa Rican public health officials.

1a. Dorsal pattern bicolor, of alternating black and light (white, yellow, orange, rust, pink or red) bands or rings 2

1b. Dorsal pattern tricolor, of alternating black and light bands or rings of two different colors (white, yellow, reddish brown or red) 12

2a. (1a) Pattern of alternating black and light rings that completely encircle body 3

2b. (1a) Pattern of alternating red and black bands 11

3a. (2a) Anal plate single 4

3b. (2a) Anal plate divided 7

4a. (3a) One or two pairs of elongate chin shields and a distinct mental groove 5

4b. (2a) No elongate chin shields nor mental groove 6

5a. (4a) Dorsal scale rows at mid-body 13 .... *Sibon anthracops*

5b. (4a) Dorsal scale rows at mid-body 15 .... *Sibon annulata*

6a. (4b) Posterior light rings heavily streaked and spotted with dark pigment on dorsum; 1 preocular, usually 3 postoculars .... *Dipsas tenuissima*

6b. (4b) Posterior light rings not or only lightly spotted with dark pigment on dorsum; no preoculars, usually 2 postoculars .... *Dipsas articulata*

7a. (3b) 17 or more dorsal scale rows at mid-body 10

7b. (3b) 15 dorsal scale rows at mid-body 9

8a. (7a) Scale rows at mid-body 19 or more; undivided anal plate; 2 apical pits .... *Lampropeltis triangulum*

8b. (7a) Scale rows at mid-body 17; divided anal plate; no apical pits .... *Pliocercus euryzonus*

9a. (7b) Two scales (a loreal and postnasal) on side of head between eye and nostril 10

9b. (7b) Three scales (a preocular, loreal and postnasal) on side of head between eye and nostril .... *Scolecophis atrocinctus*

10a. (9a) Black head cap restricted to an area well forward of the middle of the orbit (Fig. 1A) .... *Micrurus mipartitus*

10b. (9a) Black head cap extending posteriorly to cover interorbital area and reaching posteriorly onto parietal scales as a linear oblong or lanceolate figure (Figs. 1D, 5) .... *Micrurus alleni*

11a. (2b) Venter light, almost immaculate; 19 dorsal scale rows at mid-body; dorsal dark and red bands about equal in longitudinal extent .... *Oxyrhopus petola*

11b. (2b) Venter with numerous dark bands and blotches; 17 dorsal scale rows at mid-body; dark dorsal bands with a much greater longitudinal extent than red bands .... *Leimadophis epinephalus*

12a. (1b) Elongate chin shields and a mental groove present; anal plate divided 13

12b. (1b) No elongate chin shields or mental groove; anal plate entire .... *Dipsas bicolor*

13a. (12a) Dorsal scales in less than 21 rows at mid-body, smooth, except for a few above the anal region in some forms 14

13b. (12a) Dorsal scales keeled .... *Rhinobothryum bovalli*

14a. (13a) Dorsal scale rows 15 at mid-body 15

14b. (13a) Dorsal scale rows 17-19 at mid-body 19

15a. (14a) Black rings bordered on either margin by yellow or white rings to completely separate black rings from red rings 16

15b. (14a) Black rings or bands in broad contact with red areas 18

16a. (15a) Parietal shields not completely covered by black head cap 17

16b. (15a) Parietal shields completely covered by black head cap (Fig. 1E) .... *Micrurus clarki*

17a. (16a) Black head cap not or barely involving parietal shields (Figs. 1B1, 1B2, 1C) .... *Micrurus nigrocinctus*

17b. (16a) Black head cap extending as a linear oblong or lanceolate figure on both parietals along interparietal suture (Figs. 1D, 5) .... *Micrurus alleni*

18a. (15b) Black rings in pattern completely encircling body; ventrals 180 or more 20

18b. (15b) Pattern includes black bands that do not encircle body; ventrals less than 170 .... *Tantilla annulata*

19a. (14b) Black rings in broad contact with red rings; yellow rings separated from red rings by black rings; dorsal scale rows at mid-body 19 or more .... *Lampropeltis triangulum*

19b. (14b) Black bands separated from red areas by yellow or white bands; dorsal scale rows at mid-body 17 .... *Scaphiodontophis venustissimus*

20a. (18a) Most black rings weakly split dorsally by white or yellow areas .... *Erythrolamprus mimus*

20b. (18a) Paired black rings clearly separated by an intervening yellow ring .... *Erythrolamprus bizona*

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Fig. 1. Head patterns and nuchal ring development in lower Central American coral snakes. Black areas stippled so that plates, scales and sutures are not obscured. Symbols represent patterns described in the text. A. *M. mipartitus;* B1. *M. nigrocinctus* from Atlantic lowland Costa Rica; B2. *M. nigrocinctus* from some areas geographically intermediate between Atlantic and Pacific lowland sites; C. *M. nigrocinctus* from Pacific northwestern Costa Rica and western Nicaragua; D. *M. alleni;* E. *M. clarki.*

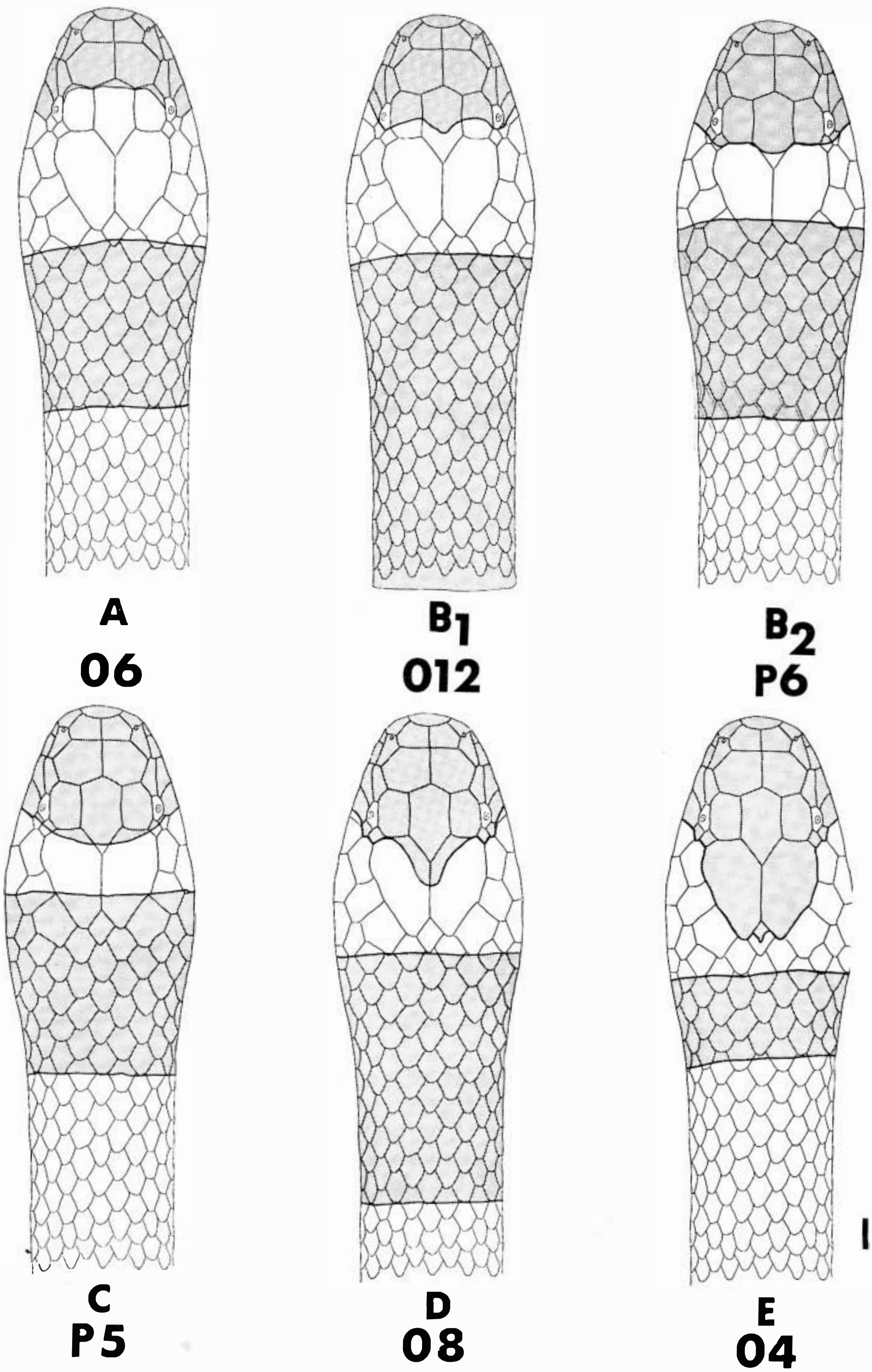
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Fig. 2. Geographic variation in head patterns and segmental count totals for tricolor coral snakes of the *alleni-nigrocinctus* stock in Nicaragua, Costa Rica and western Panama. Open circles represent localities for snakes with head cap pattern B; half circles represent localities for snakes with head cap pattern C; solid circles represent localities for snakes with head cap pattern D. The stippled area represents the Meseta Central Occidental of Costa Rica, where records are too numerous to plot individually. The dotted line indicates the 1500 m contour.

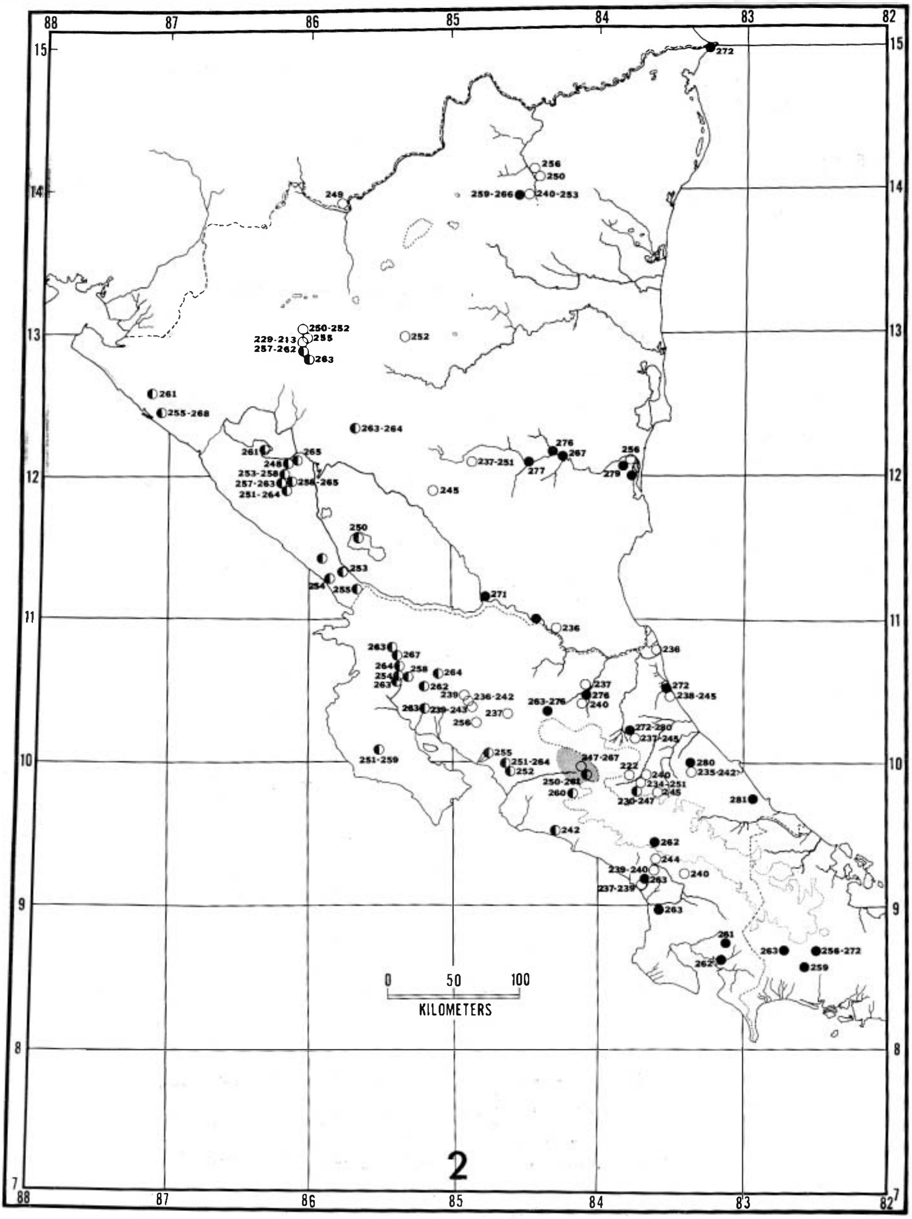

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Fig. 3. Geographic variation in number of black body rings for tricolor coral snakes of the *Micrurus nigrocinctus* stock in Nicaragua, Costa Rica and western Panama. The stippled area represents the Meseta Central Occidental of Costa Rica, where records are too numerous to plot individually. The dotted line indicates the 1500 m contour.

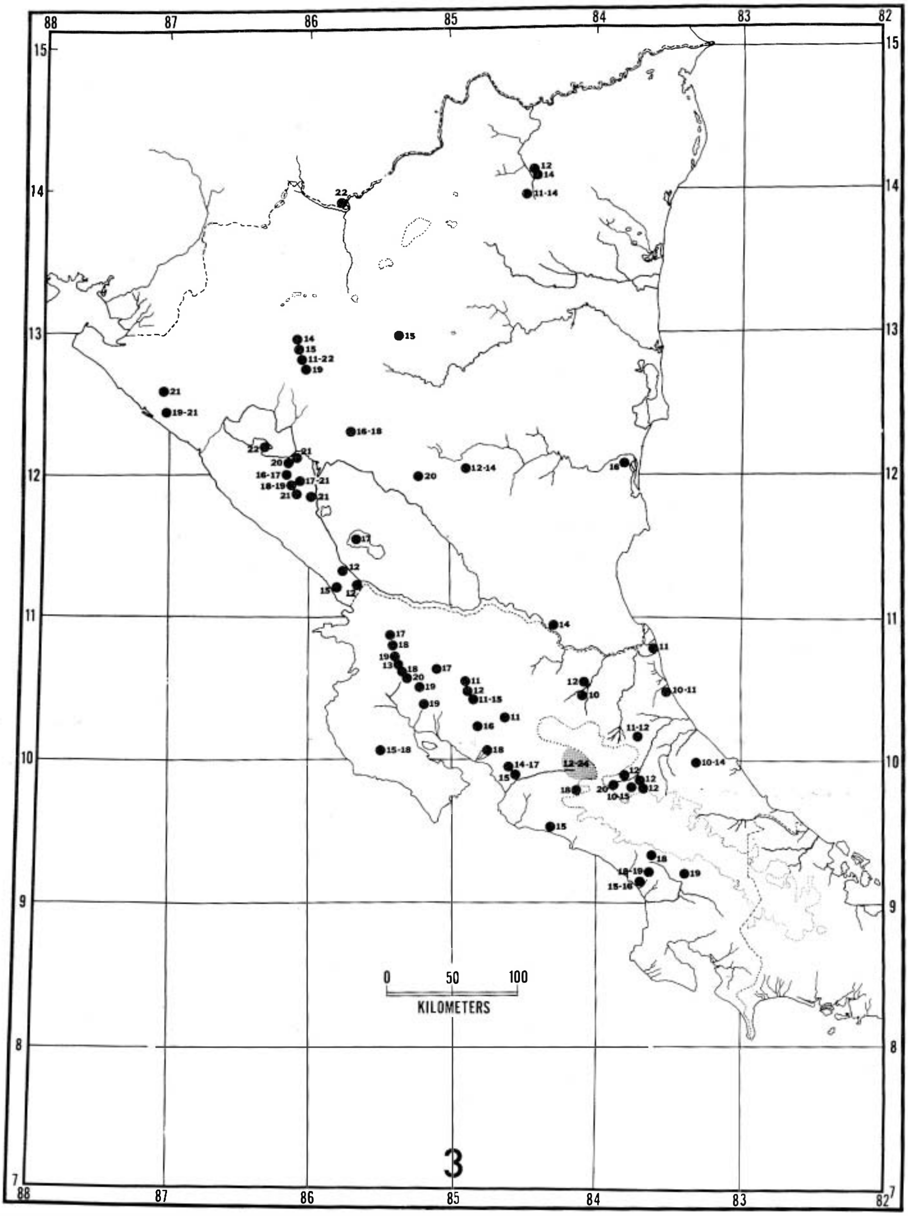

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Fig. 4. Geographic variation in nuchal black ring location and longitudinal extent onto body in coral snakes of the *Micrurus nigrocinctus* stock in Nicaragua, Costa Rica and western Panama. See text for explanation of formulae. The stippled area represents the Meseta Central Occidental of Costa Rica, where records are too numerous to plot individually. The dotted line indicates the 1500 m contour.

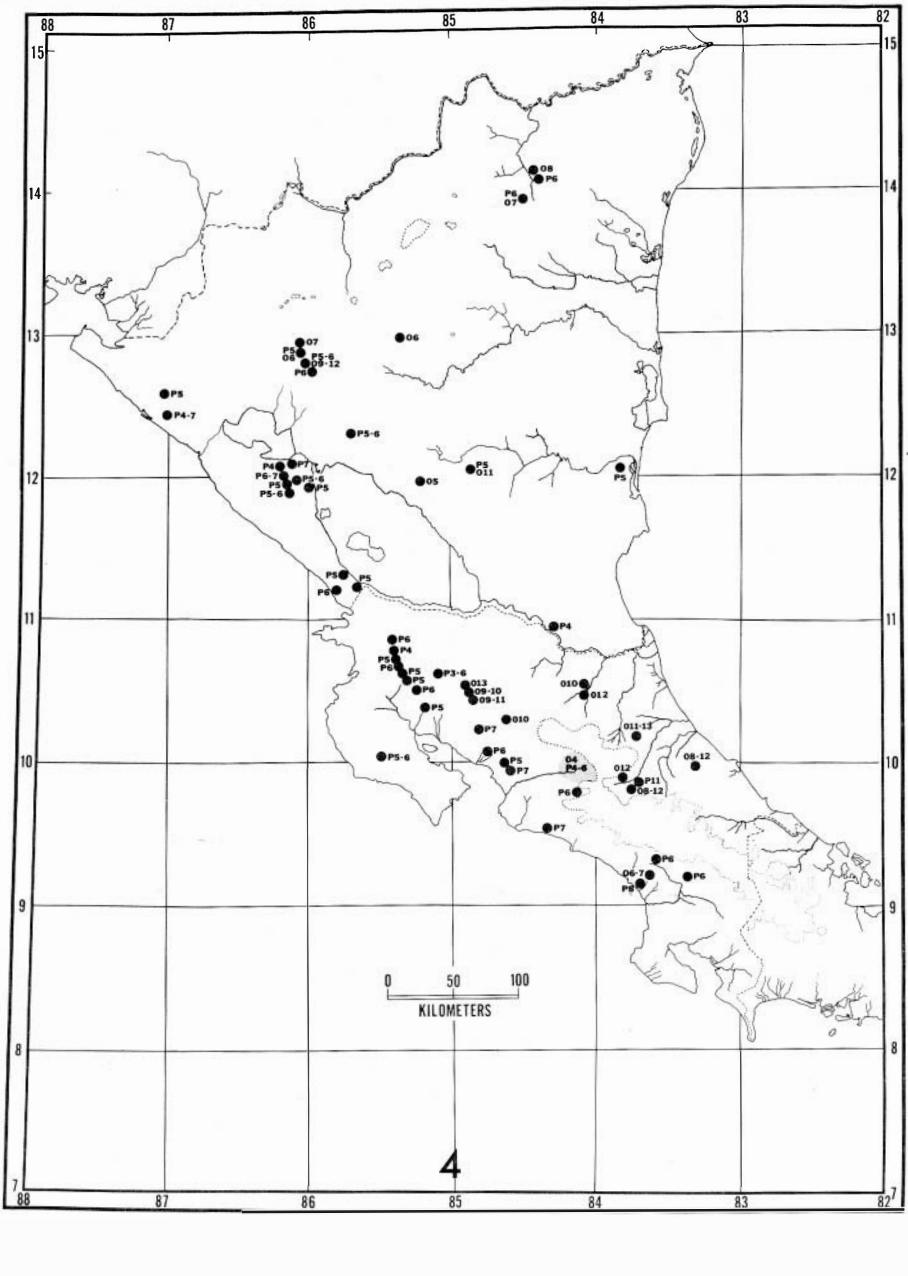

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Fig. 5. Variation in black head caps of individual *M. alleni*, all included in pattern D; only posterior head plate area shown; black areas stippled so that plates and sutures are not obscured. Left to right, CAS 79029, Panama: Chiriqui, Boquete; holotype *Micrurus alleni richardi*; KU 25189, Costa Rica: Limón: Los Diamantes; CRE 655, Costa Rica: Limón: La Lola; CAS 79023, Panama: Chiriquí: Boquete; UM 79797, Nicaragua: Zelaya: Río Siquia; AM 62987, Panama: Chiriquí: El Volcán; CRE 2662, Costa Rica: Puntarenas: Kilometer 33; CRE 2863, Costa Rica: Puntarenas: Golfito; CRE 7188, Costa Rica: Limón: Pandora.

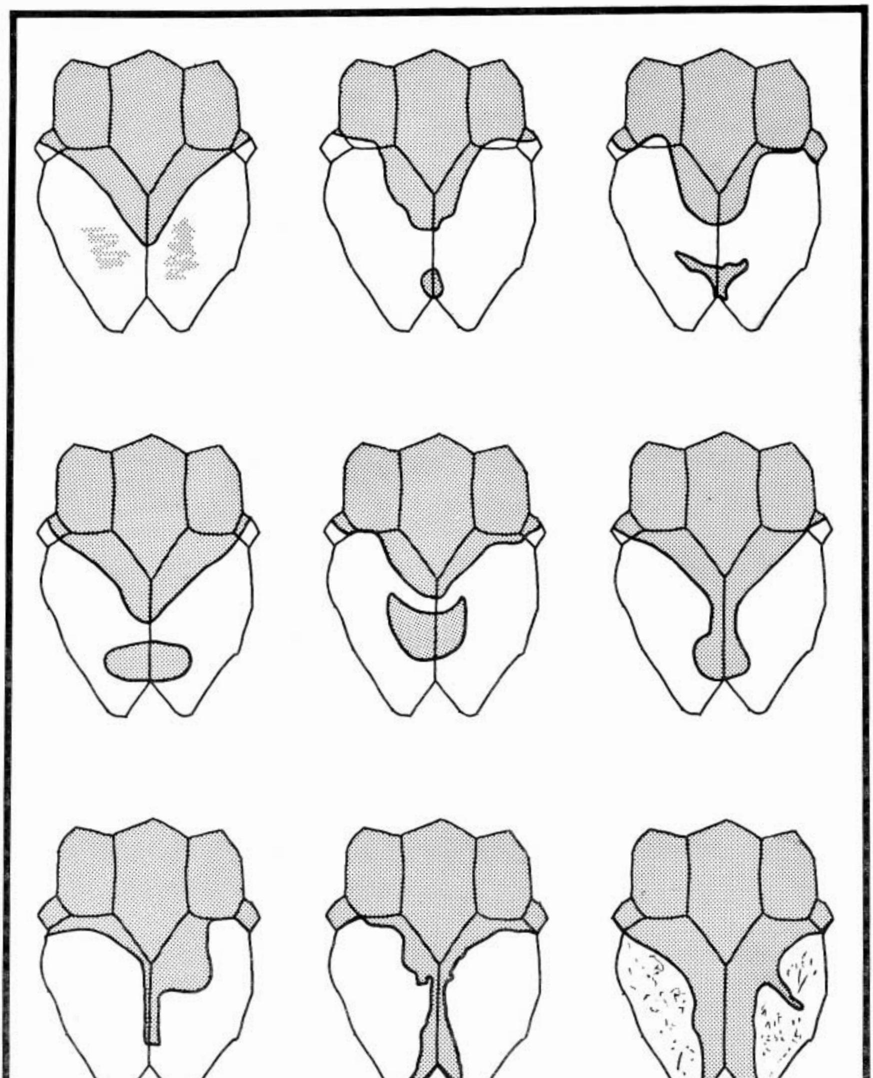

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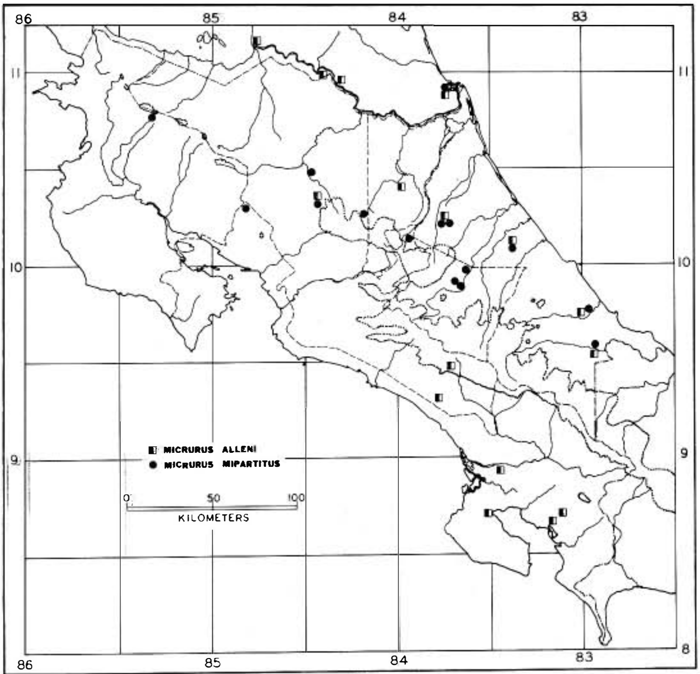
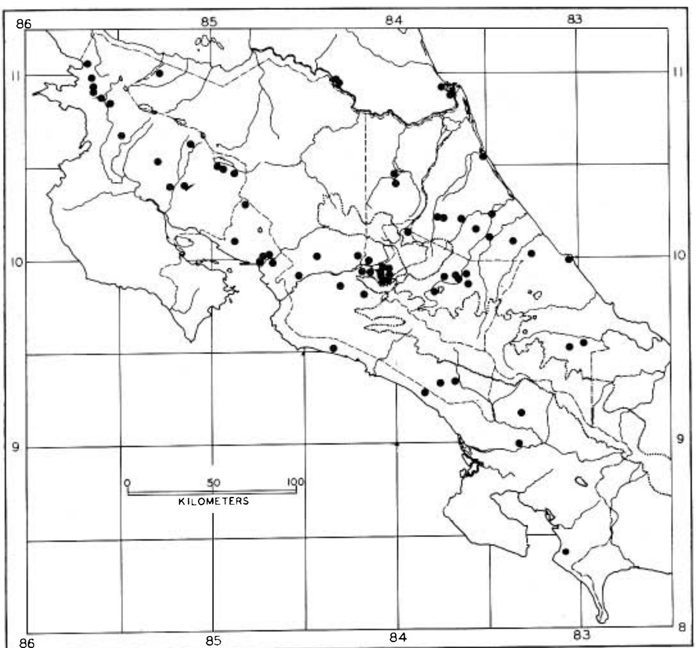
Fig. 6. Distribution of *Micrurus alleni* and *Micrurus mipartitus* in Costa Rica. The dotted line indicates the 1500 m contour.

Fig. 7. Distribution of *Micrurus nigrocinctus* in Costa Rica. The dotted line indicates the 1500 m contour.


86
85
84
83
11
10
9
8
MICRURUS ALLENI
MICRURUS MIPARTITUS
0
50
100
KILOMETERS

6


86
85
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83
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8
0
50
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KILOMETERS

7