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The Biogeography of the Cloud Forest Herpetofauna of Middle America, with Special Reference to the Sierra de las Minas of Guatemala

by Jonathan A. Campbell

B. A., University of Mississippi, 1969

M. A., University of Texas at Arlington, 1977

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THE BIOGEOGRAPHY OF THE CLOUD FOREST HERPETOFAUNA OF MIDDLE AMERICA, WITH SPECIAL REFERENCE TO THE SIERRA DE LAS MINAS OF GUATEMALA

JONATHAN A. CAMPBELL

1982

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Dissertation Committee

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CONTENTS

INTRODUCTION

This study deals with the historical biogeography of species of amphibians and reptiles inhabiting the cloud forests of Middle America, with a particular focus on the herpetofauna of the Sierra de las Minas of Guatemala. I have striven to integrate data relevant to extant distributional patterns, comparisons of herpetofaunal assemblages, systematic relationships, and the geological record in order to formulate a theory of the development of the cloud forest herpetofauna of the region as a whole.

Because my special interest is in the herpetofauna of the Sierra de las Minas of Guatemala, perhaps a brief overview of this country is in order. Guatemala is a relatively small country, encompassing some 109,000 square kilometers of northern Central America. It is bounded by the Pacific and Atlantic Oceans, and shares borders with Mexico to the west and north, and with Honduras and El Salvador to the east. Notwithstanding its modest size, most of the Nuclear Central American highlands lie within the boundaries of Guatemala, producing a diversity of climate and vegetation scarcely rivaled elsewhere in the New World Tropics.

Beginning with French and English naturalists during the mid-1800's, Guatemala has been the focus of considerable biological investigation. Since the 1930's Americans, especially the indefatigable L. C. Stuart, have dominated Guatemalan herpetology and have undertaken studies of particular subregions that collectively take in most of the country: the Peten lowlands (Stuart, 1934, 1935, and 1937; Duellman, 1963); the southern volcanic highlands (Schmidt, 1936); the Guatemalan

Plateau (Stuart, 1951); the Sierra de los Cuchumatanes (Stuart, 1943); the southeastern highlands (Stuart, 1954); and Alta Verapaz (Stuart, 1948 and 1950). The Pacific Coast as yet has not been formally addressed, but a number of collections have been assembled; the herpetofauna of this area is known to be composed primarily of generalized lowland species and is similar to that of adjacent El Salvador and Chiapas, Mexico.

In spite of intensive herpetological explorations in Guatemala, several mountainous regions in the country have been inadequately sampled if not neglected altogether, namely the Sierra de Chuacus, Sierra de las Minas, and Montanas del Mico. These ranges are connected by low ridges and form an axis that extends in a roughly east-west direction from central Guatemala to the Gulf of Honduras (Fig. 2). The dearth of material available in collections from these mountains is particularly evident from a quick perusal of the map provided by Stuart (1963) of herpetological collecting localities in Guatemala. Within the entire highland region formed by the Chuacus-Minas-Mico uplifts only one minor collection is indicated--Finca Buccaral, located on the south slope of the Sierra de las Minas above the xeric middle Motagua Valley.

The Sierra de Chuacus and Sierra de las Minas are connected by a narrow ridge scarcely exceeding 1500 m elevation that separates the Rio Negro drainage of the Salama Basin from the Rio Motagua. At its lowest elevation along the crest lying between points south of Salama and San Geronimo, Baja Verapaz, this ridge is covered with xeric vegetation to about the 800 m contour, above which a dry pine-oak forest extends to its summit. Thus the wet montane forests of the western portion of the

Sierra de Chuacus are isolated from other such forests to the east in the Sierra de las Minas. The Montanas del Mico is a small, isolated range to the northeast of the Sierra de las Minas. This range is covered primarily with lush tropical vegetation although cloud forest-like conditions exist at higher elevations on its two highest peaks--Cerro Las Escobas and Cerro San Gil--which reach about 1000 m. The Montanas del Mico are separated from the Sierra de las Minas by several low passes less than 200 m in elevation to the southeast of Lago de Izabal.

Because of its geographical position and geological history, the isolated cloud forest of the Sierra de las Minas possesses an assemblage of amphibians and reptiles that is of great zoogeographic interest. Prior to the 1970's, collections from the Sierra de las Minas were virtually limited to the lower elevations of the Motagua and Polochic Valleys. Field parties from the University of Texas at Arlington and the University of California at Berkeley have recently assembled collections from the higher elevations of the Sierra de las Minas. Unfortunately both institutions have been somewhat limited in their efforts, the former making generalized collections in only a small area of the western portion of the range, and the latter putting emphasis on the acquisition of salamanders.

The Sierra de las Minas extends for approximately 135 km in east-central Guatemala across portions of five departments: Alta and Baja Verapaz, El Progeso, Izabal, and Zacapa. This mountain range is part of ancient Nuclear Central America (Sapper, 1894; Schuchert, 1935; McBirney, 1963) and physiographically is among the most complex in

Middle America (West, 1964). The main crest of the Sierra de las Minas is oriented in roughly an east-west direction with the northern and southern faces of the range drained by tributaries of the Rio Polochic and Rio Motagua, respectively. This massif extends unbroken above the 2100 m contour for 65 km. Two peaks, Cerro Pinalon and Cerro Raxon, attain elevations greater than 3000 m. The Sierra de las Minas is bounded abruptly to the west by the Salama Basin, while in the east it gradually loses elevation, and southeast of Lago de Izabal it decreases to less than 200 m in elevation.

Northeast tradewinds create extremely moist conditions along the northern escarpment of the Sierra de las Minas; from low elevations up to about 1300 m a tropical forest prevails; above this elevation precipitation exceeds 5000 mm annually in some areas, and cool, damp cloud forest is the dominant vegetation. The Sierra de las Minas is a barrier to moisture, and rain-shadow conditions exist on the southern side of the range. In the Middle Motagua Valley pine forest descends to about 800 m; below this level less than 500 mm of precipitation is received annually (Vivo, 1964; Stuart, 1966), and a distinctly subhumid vegetation extends to the valley floor.

The upper reaches of the Sierra de las Minas differ from all other major highland regions of Guatemala in being virtually unsettled. The aboriginal population was historically centered in the western highlands and to a lesser extent in the central and Alta Verapaz highlands, a trend followed through recent times (Marino Flores, 1967). A few roads of poor character snake their way up precipitous ridges from the Motagua Valley on the south side; no roads extend above the 300 m contour on the north face, which has remained practically inaccessible because of extremely steep slopes, slick lateritic soils, heavy precipitation, and dense vegetation. Lumbering operations initiated recently are beginning to modify drastically this splendid forest in the vicinities of La Union Barrios, Baja Verapaz; San Lorenzo, Zacapa; and Aldea Vista Hermosa, Izabal.

I had my first glimpse of the Sierra de las Minas in the mid-1960's when I had occasion to travel on what has now become known as the "old road" from Guatemala City to Coban. The road at that time extended over 100 unpaved tortuous kilometers from El Rancho in the Motagua Valley through Salama to Coban. This road did not cut across any portion of the Sierra de las Minas, but at several locations a vantage point was attained making it possible to look across to this range and see what seemed like endless tracts of virgin forest covering its slopes. A major highway to Coban was completed in 1972 allowing me easy access into the range in the summer of 1975. In July and August of this year I spent several weeks making general collections in the western portion of the Sierra de las Minas between the two small villages of Nino Perdido and La Union Barrios. The collection resulting from this initial trip indicated the herpetofauna of the Sierra de las Minas shared many species with the Alta Verapaz highlands, but nevertheless had a distinctive quality of its own. I returned to the Sierra de las Minas each subsequent year from 1975 to 1980 for varying periods of several weeks to several months. Most of these visits were during the early rainy season (May--August), but I also collected in the region around La Union Barrios during the drier part of the year

(January--April). Most of my collecting efforts were concentrated on two mountains which at that time were mostly covered with virgin cloud forest. The first, Cerro Quisis, extends southward from Purulha to past La Union Barrios which lies at about 1520 m to the west of the main crest. The second, Cerro Verde, is located to the east and southeast of La Union Barrios.

In December 1980 I arrived at the Biotopo "Mario Dary" located on the eastern slopes of Cerro Quisis on the headwaters of the Rio Polochic and set up my base camp for an extended stay of eight months. During this time I was able to explore the eastern portion of the Sierra de las Minas, including the magnificent forest covering the higher elevations near the crest of Cerro Raxon, the highest point in the range. Additionally I gained access to the totally unexplored north face of the range to the south of Lago de Izabal, as well as the higher elevations of the Montanas del Mico. I was joined on some of these forays by L. S. Ford, W. W. Lamar, and R. F. Savage who made valuable contributions through their collecting skills.

During the course of my investigations I secured over 5000 specimens exclusive of tadpoles from the Sierra de las Minas. This collection represents the effort of about 60 weeks of cumulative time in the field. Although all major habitats were sampled, the major collecting emphasis was concentrated in the wet montane forest on the windward slopes from about 400 to 2300 m. As a result of these collections, the herpetofauna inhabiting the cloud forest on the Sierra de las Minas, especially the western portion, is probably as completely known as that of any cloud forest in Middle America. Nevertheless, it would be presumptuous to assume that the herpetofauna of this region is fully known. Surprises, although progressively less frequent, still seem to be an integral part of every trip and novelties undoubtedly remain to be discovered.

Besides permitting a fuller understanding of the distributions of many montane species, these field investigations have led to the discovery of many novel species and/or provided material allowing for reassessment of relationships. The descriptions of some of these have been prepared or are underway (Campbell and Ford, 1982; Campbell and Savage, in prep; Duellman and Campbell, 1982; Ford and Savage, 1983; Savage and Campbell, in prep; Wake and Campbell, in press). My ultimate goal in undertaking field work in east-central Guatemala has been a biogeographic study of the entire region. However, because of time constraints I have limited the scope of this study to the mesic forest herpetofauna of the northeastern Guatemalan highlands, with an emphasis on the Sierra de las Minas. Therefore this should not be considered a final summation, but rather a preliminary effort. For example, I ignore data relating to the xeric interior valleys of the Salama Basin and the upper and middle Motagua Valley, and to a large extent data derived from the widespread lowland herpetofaunal assemblage.

The total herpetofauna of the Sierra de las Minas including the lowlands is composed of about 200 species. My collections have revealed the presence of 56 species of amphibians and reptiles from a single locality in a cloud forest near Purulha, verifying the great diversity within this forest. When the total herpetofaunal assemblage of the mesic upland forest is considered, the number of cloud forest species increases to over 100.

The objectives of the present study are, to describe briefly the physiography, climate, and vegetation of the Sierra de las Minas and assay the composition and ecological distributions of the wet forest herpetofauna; second, to describe the extent, distribution, and salient features of Middle American cloud forests in general; third, to compare the herpetofaunal assemblage inhabiting the wet montane forest of the Sierra de las Minas with other such forests that are isolated on windward slopes throughout Middle America; fourth, to perform cladistic analyses of selected mesic upland groups; and fifth, to present a hypothesis for origins and recent distributions of these selected groups and relate this to the Middle American cloud forest herpetofauna as a whole.

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MATERIALS AND METHODS

Field work was carried out in the Sierra de las Minas for a total of approximately 14 months over a period beginning in 1975 and ending in 1981. Collections of amphibians and reptiles were made during the wet and dry seasons. In excess of 5000 specimens were secured, exclusive of tadpoles, with particular note made of habitat and elevation.

For comparison of the herpetofauna of the Sierra de las Minas with other highland areas in Middle America, I have placed special emphasis on material collected by me in the Sierra Juarez and the Cerro Baul region, Oaxaca; the Sierra Madre del Sur, Guerrero; the Mesa Central, Chiapas; the various mountain ranges of Alta Verapaz; and the Pacific highlands of Guatemala. Specimens I collected from 1972 to 1978 were deposited in the University of Texas at Arlington Collection of Vertebrates (UTACV), whereas those taken from 1979 to 1981 are housed in the Museum of Natural History at the University of Kansas (KU).

The nomenclature I follow is from a variety of sources and therefore is sure to offend just about everyone. In dealing with salamanders I follow the most recent work by D. B. Wake and his associates at the University of California at Berkeley. I have adhered to the various studies of J. D. Lynch and J. M. Savage in dealing with the leptodactylid frogs, especially those of the genus <u>Eleutherodactylus</u>. Nevertheless I have encountered numerous problems with this dismaying genus--many species in Middle America are yet undescribed and little is known about their relationships at any level. This situation is especially unfortunate with the <u>gollmeri</u> group inasmuch as members of this group are widely distributed in the mesic upland forests of Middle America. The difficult task of unraveling the systematic mysteries of this group is currently being undertaken by J. M. Savage. During the course of my investigations I have examined what purportedly are, on geographical grounds, *Bufo coccifer* and *B. ibarrai*; as I cannot distinguish between them, I consider the later a junior synonym of the former. The Middle American hylid frogs are relatively well understood thanks to the monumental efforts of W. E. Duellman (1970); I generally have followed his taxonomy and distributions, except where my own collections or recently published material augment his data. The only exception is the genus *Ptychohyla* in which I propose specific status for several populations previously recognized as subspecies. Until the evolutionary history of the iguanids is better understood, I see nothing to be gained by recognizing the genus *Norops* and have retained *Anolis*. I have retained the name *Dryadophis* Stuart, 1939, in favor of *Mastigodryas* Amaral, 1934, for reasons given by Smith (1963). I follow in part the unpublished proposals of Burger (1971) in dealing with the pitvipers by recognizing the genus *Bothriechis* for the Middle American tree vipers. However, I do not concur with him in recognizing the genus *Porthidium* for many of the Middle American terrestrial pitvipers; this group appears to include several distinctive and not particularly closely related lineages, and I therefore prefer to retain the genus *Bothrops* for all other Middle American pitvipers exclusive of those species placed herein in *Bothriechis*.

It seems advantageous to define a few terms at the outset. For determining particular scales, I have followed the definitions proposed by Dowling (1951a, 1951b); other definitions may be found in Peters (1964). Duellman (1965a) distinguished the terms "herpetofauna," "faunal assemblage," and "faunal element," all of which have continued to be used ambiguously. I have made an effort not to be guilty of using them synonymously.

The methods of biogeographic analysis are described in the appropriate sections; the methods of cladistic analysis are those of Hennig (1966) so clearly put forth by Wiley (1981) (See "Relationships within mesic upland groups"). I have profited from the use of the Wagner 78 program and the BMDP, Minitab, and Clustan statistical packages implemented on the Honeywell 66/60 at the University of Kansas.

It was with much hesitancy that I first approached this task of trying to synthesize data pertinent to the historical biogeography of the cloud forest herpetofauna, and I continue to be impressed by how much there is yet to be learned. The problems in undertaking a study of this nature are plentiful. First, by their very nature, the concepts "species" and "cloud forest" are evasive things that defy any rigid definitions likely to enjoy a widespread consensus. In dealing with allopatric populations isolated in wet patches of forest on mountain slopes and tops, it is perhaps more practical to adhere to the evolutionary species concept (Simpson, 1961; Wiley, 1981) rather than the biological species concept (Mayr, 1963). There are problems with both concepts. It seems inappropriate to embrace the biological species concept while concurrently recognizing various allopatric populations as species without any evidence of intrinsic reproductive isolation. Even if the basic tenet of reproductive isolation were accepted as a criterion for species recognition, it is not possible in most instances to secure empirical data demonstrating any such segregation. Contrarily, strict interpretation of the evolutionary species concept will ultimately lead to recognition of every isolated population as a distinct species--a position that is neither desirous for pragmatic reasons or accurate if one believes that species are more than man-made artifacts.

Different kinds of vegetation grade into each other over short to long distances; therefore, arguing about where precisely to draw a line between kinds is futile. Thus, in attempting to decide whether or not the range of a particular species enters cloud forest, a decision may be hampered not only by imprecise knowledge about the range of the species, but also of where exactly cloud forest begins or ends. Cloud forest characteristics and distributions are discussed in detail in the appropriate sections ("The cloud forest environment" and "Extent and distribution").

Although many events of the geological history of Middle America are well documented (Dengo, 1968; Schuchert, 1935), conflicts of opinion concerning the geographical history of the region and its bearing on the distributions of the cloud forest (see Savage, 1966; Stuart, 1966) are discussed in a later section.

The species richness of the Middle American mesic highlands is fairly large, involving some 450 species. Because any accurate assessment of the historical biogeography for a group is dependent on a knowledge of the systematics of that group, it is unfortunate that the relationships within and among most of the Middle American species groups is only now beginning to be investigated.

Lastly, many of the Middle American cloud forests remain inaccessible. As a result, studies on the fauna or flora of cloud forests are often hampered by a dearth of material.

My objective in essaying some of the problems associated with this type of study is to address what I think are relevant shortcomings. Nevertheless trying to combine species' relationships and ecology with historical geology is intriguing and attracted me to pursue this study.

THE CLOUD FOREST ENVIRONMENT IN MIDDLE AMERICA

Classification.-- The wet, cool forest that characterizes the windward slopes of tropical mountains has been variously called "cloud forest" (Beebe and Crane, 1947; Carr, 1950; Myers, 1969; Leopold, 1950), "montane or temperate rainforest" (Beard, 1944), "lower montane wet forest" (Holdridge, 1964), "mist forest" (Walter, 1971), and a host of other names that all stress some aspect of the dampness and/or montane distribution (and therefore resulting lower temperatures) of this type of forest.

Cloud forests sometimes have been classed as a subtype of the lowland rainforest because it was thought that the amount and distribution of precipitation in all cloud forests were similar to that of lowland rainforests (Pittier, 1926). However, there is good evidence that in some cloud forest the moisture supply comes more from fogs or mists than from rain (Barbour, 1942; Carr, 1950; Grubb and Whitmore, 1966). Because cloud forests differ greatly from rainforests in their floristics, distribution, climate, and physiognomy (Barbour, 1942; Grubb and Whitmore, 1966), there is an increasing tendency to accord them primary status in classification of tropical forests.

According to Koeppen's classification of climate, based on annual and monthly averages of temperature and precipitation, most Middle American cloud forests occur in regions of the Cfa climatic type--humid temperate climates with rain in every month (but with most rain in summer and fall) and warm summers (mean of warmest month >22°C) (Vivo Escoto, 1964).

A series of formations have been recognized within the cloud forest: "lower montane rainforest, montane rainforest, and elfin woodland" (Beard, 1944); "high ocotal, pinabetal, and hardwood cloud forest" (Carr, 1950); and "lowland, lower montane, and upper montane rainforest" (Richards, 1952). These subdivisions of cloud forest are no doubt influenced by the particular regions of the world worked in by these authors, but nonetheless are indicative of the heterogeneity of different elevational belts within what is called cloud forest.

Formation.-- Probably the two most important prerequisites for the formation of a cloud forest are sufficient elevation to have a cooling effect on ascending air and exposure to moisture-laden winds coming off the oceans. Undoubtedly other factors such as latitude and extent of land mass are important in determining the distribution of cloud forests. The northeast trades are the most important source of moisture for the slopes along the Gulf of Mexico and Caribbean. Both of these receive water from a branch of the Atlantic North Equatorial Current and thus are relatively warm. A branch of the Pacific Equatorial Countercurrent brings warm water along the western coast of Central America and southern Mexico. Winds passing across these warm waters pick up abundant moisture and as they come ashore and make contact with land, the great inequalities of surface configuration give rise to an extremely complicated pattern of wet and dry areas. The air that is forced up mountain slopes cools at 6--10^{o}C/Km depending on humidity (MacAurthur, 1972). At elevations between 1000--2000 m average yearly temperatures are between 15--20^{o}C. Because cool air holds less moisture than warm air, this causes heavy condensation or rain at certain elevations on the slopes. By the time this air reaches the lee side of a mountain range, it often has lost most of its moisture. Consequently not only is precipitation less frequent on the leeward side, but the descending dry wind increases aridity in the area. Numerous interior valleys of Middle America are of subhumid aspect including parts of the Balsas-Tepalcatepec, Negro, Motagua, and Aguan Valleys. These dry valleys are of considerable importance in limiting distributions of mesophilic fauna and flora. The distribution of some of these rather dramatic rainshadows and their biogeographic implications have been amply described by Stuart (1954b). Surface temperatures in these valleys frequently reach as high as 30°C owing to the warming affect of the "dry adiabatic" lapse rate of the air descending into these valleys from adjacent mountain ranges. These valleys form an almost continuous corridor of xerophytic vegetation from the Pacific Coast of northern Mexico southward across the interior valleys of Nuclear Central America and then along the south coasts of Nicaragua and Costa Rica (Stuart, 1954b, map 2). Rainfall in much of these valleys is less than 1000 mm per year and in the middle Motagua is only about 500 mm annually (Stuart, 1966; Vivo Escoto, 1964).

Seasonality.-- The amount and distribution of precipitation in cloud forests in general is closely associated with general climatic patterns for the entire region. In southern Mexico and Central America the rainy season extends from about May through October during which time areas receive over 80% of their annual precipitation. It is during this period that cloud forests likewise receive the largest amounts of rainfall. These rains are brought on by the northward migration of the thermal equator causing the tradewinds to become unstable. Air flow has a tendency to move upward as it approaches the thermal equator, thus cooling and producing rainfall. Conversely, from October to April the thermal equator has migrated southward and Middle America experiences masses of descending air, or subtropical calms, that bring on the dry season (Vivo Escoto, 1964).

The extremely wet, humid conditions that frequently prevail in cloud forests have been stressed by numerous authors (Duellman, 1966; Savage, 1966b; Stuart, 1966; Wagner, 1964). A little appreciated fact is that all Middle American cloud forests are seasonal and subject to considerable fluctuations in climate. The extent and effects of these fluctuations have been nicely summarized by Grubbs and Whitmore (1966) for an Ecuadorian cloud forest. Because diversity of temperature and precipitation is fundamental in the distribution of natural vegetation and animal life, and because extremes of these factors, even if for only brief periods, may be the limiting factors in the distributions of particular species, recognition of seasonality in a region takes on special importance.

For eight months of the year cloud forests along the Caribbean slopes tend to be enveloped in clouds for at least part of every day and daily extremes in temperature and humidity vary little; whereas during January, February, March, and April there may be periods of several days to several weeks which are cloud free, producing relatively great fluctuations in climatic conditions and having an overall drying affect on the cloud forest. The cold fronts or "nortes" that pass through the region during the winter months augment these extremes. Species of cloud forest amphibians and reptiles are notorious for their inability to withstand even moderate amounts of desiccation. Because humidity is one of the significant factors that regulates the amount and rate of moisture loss, fluctuations in humidity no doubt greatly affect the distribution and behavior of many of these species.

Precipitation.-- Carr (1950) presented meterological data on several localities in Honduras that suggest that some cloud forests, particularly those situated on high peaks far from oceans, may receive about the same amount of rainfall as the surrounding subhumid lowlands, and that these forests develop more as a result of the heavy fogs and resulting low evapotranspiration rates characteristic of these forests. Although this seems to be true for some cloud forests, it does not seem to be the case for all of them and certainly does not describe the situation of the piedmonts along either ocean that characteristically receive more rainfall than adjacent areas.

Total annual rainfall in cloud forests may vary from less than 2000 mm to over 5000 mm (Leopold, 1950; Portig, 1965; Stuart, 1964, 1966; Vivo Escoto, 1964). In general the Atlantic versant of Middle America is wetter than that of the Pacific (Vivo Escoto, 1964). Localities in the highlands of Alta Verapaz (Stuart, 1966) and the Sierra de las Minas may receive as much as 5000 mm of precipitation annually. Nevertheless localized areas along the Pacific escarpment such as that along the Guatemalan-Chiapan border may receive up to 4000 mm of annual precipitation (Stuart, 1964), most of this coming during the summer months. The Pacific cloud forests from Guerrero through El Salvador tend to be more seasonal than those on the Atlantic and experience heavy rains during the summer months followed by a relatively harsh dry season.

Altitudinal limits.-- Depending on variables such as latitude, direction and intensity of prevailing winds, and distance from the oceans, the lower limit of cloud forest may vary from about 1000 to 1800 m. Carr (1950) noted that cloud forests in Honduras develop at lower elevations on the Caribbean slopes than in the interior owing to their strategic location with respect to the prevailing northeasterly tradewinds. Most of the major tracts of Atlantic-facing cloud forest in Mexico and Central America have their lower limits at about 1300 m. Exceptions to this are the more northern cloud forests of the Sierra Madre Oriental of Mexico which may descend to about 1000 m or lower (Martin, 1958), and the Montanas del Mico in Guatemala and the Sierra de Omoa in Honduras which owing to their proximity to the Gulf of Honduras, possess cloud forest-like vegetation as low as 800 m. In the Sierra Madre del Sur, cloud forest may be encountered as low as 1300 m to the north of Atoyac; however, a little to the east in the vicinity of Omilteme I have not found it below about 2000 m, possibly because of the effect of the drying winds that blow through the relatively low passes in the Chilpancingo region. The cloud forest of the Pacific versant of the southern volcanic highlands of Guatemala and Chiapas descends to about 1300 m over most of the region with the exception of an area in the Guatemalan-Chiapan border region which receives greater precipitation and in which cloud forest descends to at least 1000 m.

The upper limits of cloud forest may vary even more than the lower limits. At higher elevations, much of the moisture may have been extracted from the air and the forest becomes drier, species of pines or fir prevail, and the trees become spaced farther apart. This situation is characteristic of the Guerreran highlands, the Sierra Juarez, and Cerro Baul. The upper slopes and crests of some mountains are exposed to high winds on an almost daily basis. Trees become stunted and gnarled; this type of forest has been termed "elfin woodland" (Beard, 1944) and is characteristic of the upper reaches of the Cerro Baul region and some of the higher mountains in Costa Rica. Rarely, conditions prevail that allow a dense primary cloud forest of tall trees to extend to high crests. Such is the situation in the Sierra de las Minas where hardwood cloud forest extends to over 3000 m on Cerro Raxon (Fig. 3), giving refuge to a considerable population of howler monkeys and one of their chief predators, the harpy eagle.

Characteristic plants.-- The diversity of plants growing in cloud forests is overwhelming. On the forest floor are numerous selaginellas, ferns, small palms, liverworts, mosses, terrestrial bromeliads and orchids, begonias, and myriad other herbaceous plants. Along the cascading streams grow giant equisetums and dense stands of lilies. The limbs and trunks of trees support a luxuriant epiphytic growth that includes algaes, mosses, ferns, lichens, bromeliads, and orchids.

Along rather specific contours in Middle American cloud forests brakes of bamboos and small palms sometimes occur. To my knowledge these have never been described in detail, and I made no detailed study of their distribution in my field work. However, I have seen brakes of bamboo between 140--2000 m in the Sierra Madre del Sur in Guerrero, Cerro Baul in Oaxaca, Sierra de las Minas, and two distinctive bamboo belts on the Volcan de Agua in Guatemala. Small palms may be distributed in a more random fashion, but also seem to be more abundant between certain elevations, especially in ravines.

Perhaps the most characteristic cloud forest plants are the giant tree ferns that may reach heights of over 10 m. These are represented in Middle America by the family Cyatheaceae. Although tree ferns occur at less than 300 m in the Montanas del Mico and the northern escarpment of the Sierra de las Minas and other areas where local conditions are relatively wet the year round, tree ferns seem to reach their greatest abundance between 1500 and 2200 m and have been referred to as cloud forest "indicator" species (Leopold, 1950).

In Mexico and Central America a complex admixture of elements come together to form the flora of cloud forests. Leopold (1950) noted that whereas the biota as a whole is of tropical origin, many of the often immense and strongly buttressed dominant trees are of temperate origin.

The drier portions of the cloud forest often possess pines (*Pinus*) and sweetgum (*Liquidambar*). These trees may occur in almost pure stands or be intermingled with numerous species of oaks (*Quercus*) that also occur in the hardwood cloud forest. Along the upper limits, cypress (*Cupressus*) and fir (*Abies religiosa*) may mix with hardwoods. A few of the more common trees of temperate origin making up cloud forests include beeches (*Fagus*), dogwoods (*Cornus*), laurels (*Persea*, *Nectandra*), basswoods (*Tilia*), tupelos (*Nyssa*), mahoganies (*Cedrela*), myrtles (*Eugenia*), hollies (*Ilex*), sweetleaves (*Symplocos*), maples (*Acer*), birch (*Carpinus*), buckthorns (*Rhamnus*), snowbells (*Styrax*), marlberries (*Ardisia*), osmanthes (*Osmanthus*), rapaneas (*Rapanea*), and roses

(Prunus). Other trees of tropical origin are Chaetoptelea, Clethra, Billia, Inga, Engelhardtia, and Podocarpus. A number of epiphytic trees seem to replace the lowland Ficus, including Oreopanax and Topobea (Miranda, 1952).

Forest floor.-- Most cloud forests have a moderate amount of humus covering the forest floor. A few forests have small amounts of humus production (Carr, 1950) and others such as that on Cerro Raxon and a nearby ridge known locally as "Volcan del Mono" in the Sierra de las Minas possess a spongy layer of humus almost a meter deep. The mat formed by this humus gives it an almost trampoline quality as one proceeds through the forest.

Owing to steep slopes, soils that often are relatively poor, cool temperatures, and heavy precipitation, Middle American cloud forests have been one of the last forest types to be seriously threatened by man's encroachment. However, the major tracts of cloud forest are presently in danger of almost complete destruction except perhaps for small remnants left in ravines and on crests. The lower portion of cloud forest has long been known to be well-suited for coffee growing and as that industry continues to expand the cloud forest inevitably diminishes. With the burgeoning population of Middle America even "milpa" agriculture employing traditional slash and burn techniques is slowly creeping up mountain slopes previously either inaccessible or considered unsuitable for agriculture. As these areas are deforested, the fragile soils soon wash away exposing the underlying bedrock such as part of the Mesa Central de Chiapas or the ocherous lateritic clays of the Sierra de las Minas. In spite of the back-breaking effort required to clear the land, I was told that in Guatemala only two or three years of crops may be produced from a field before exhaustion of the soil required moving on and deforesting the next plot up the mountainside.

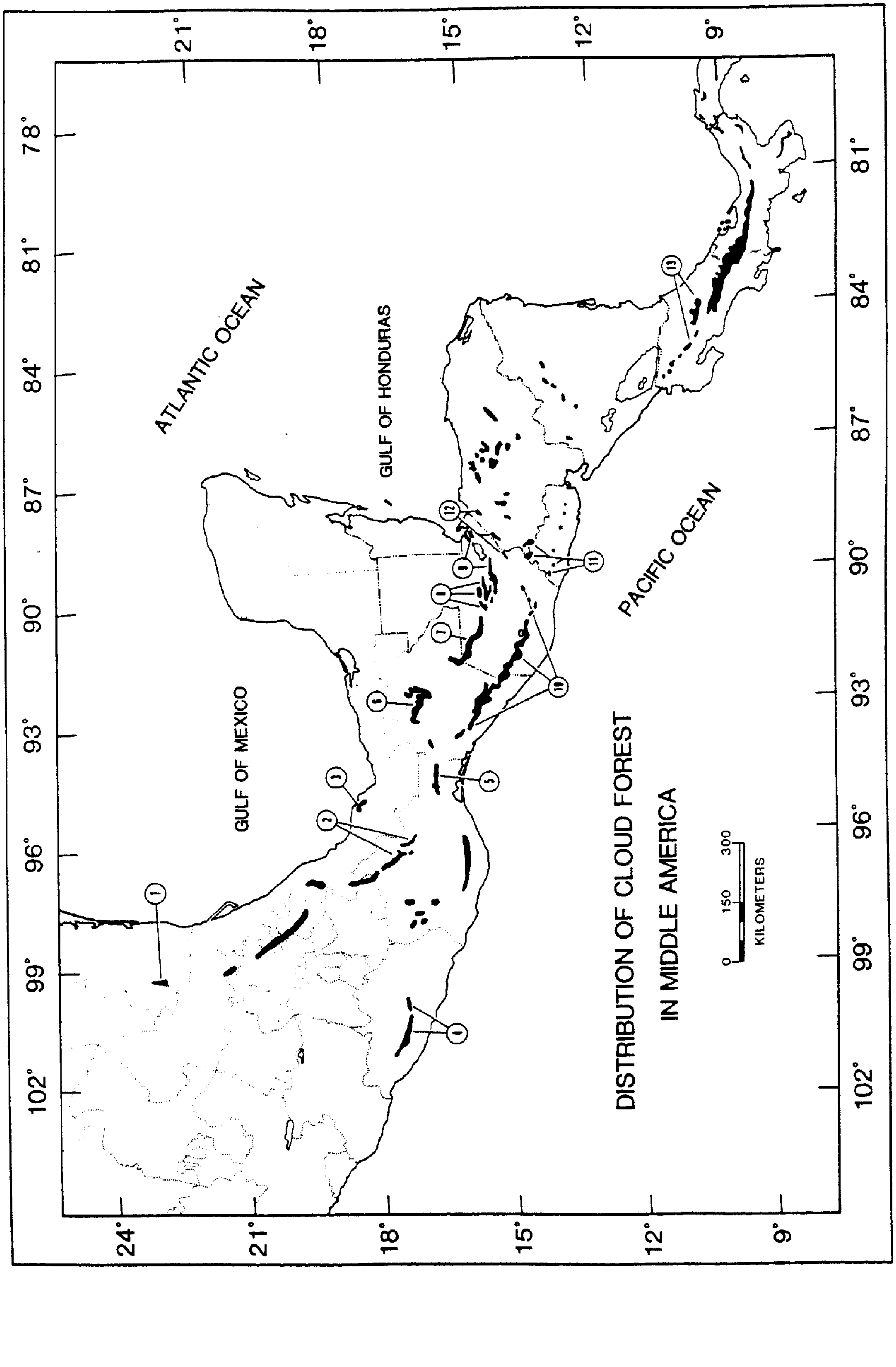
Many of the mountainous regions of Middle America were previously unapproachable by vehicle. However, owing to the economics of lumbering valuable hardwoods as well as pine, it now has become feasible to construct temporary roads into a region, extract the desired timber, usually by felling the entire forest, and allow the roads to wash down the mountainside the first rainy season after operations are completed. The Sierra Juarez, Cerro Baul, Mesa Central of Chiapas, and Sierra de las Minas, to mention a few, all have intensive lumbering operations in progress at present.

EXTENT AND DISTRIBUTION OF MIDDLE AMERICAN CLOUD FORESTS

Cloud forest is distributed on windward escarpments of Middle America from moderate to high elevations. Of the various montane vegetation zones generally recognized, cloud forest occupies a smaller percentage of total land area than any other except a few specialized types such as boreal forest (Leopold, 1950) or paramo, limited to a few high Costa Rican peaks (Wagner, 1964). Leopold (1950) estimated that in Mexico cloud forest covers about 3,800 square miles comprising about 0.5% of the total land area. Such estimates are not published for Central America, but certainly cloud forest is more predominant in the region than in Mexico.

In chorographing the cloud forest of Middle America (Fig. 1) I have utilized the information contained in a great number of sources including Goldman (1951) and Leopold (1950) for Mexico in general; Hernandez X. (1951) and Martin (1958) for Tamaulipas; Caldwell (1974) for Oaxaca; Davis and Dixon (1959) for Guerrero; Breedlove (1973) and Miranda (1952) for Chiapas; and Andrle (1964) for southern Veracruz. In Central America I have benefited from information provided by Stanley (1941), Stanley and Steyermark (1945), and Stuart (1950) for Guatemala; Carr (1950) for Honduras; Lauer (1954) for El Salvador; Myers (1969) for Panama; Stuart (1966) and Wagner (1964) for the region in general; and especially the series of ecological maps of the various Central American countries prepared by L. R. Holdridge and published by the Instituto Interamerican de Ciencias Agricolas de la Organizacion de Estados Unidos in San Jose, Costa Rica.

FIGURE 1. The distribution of Middle American cloud forests. Numbers refer to regions analyzed: 1, southwestern Tamaulipas, Mexico; 2, northern Oaxaca, Mexico; 3, southern Veracruz, Mexico; 4, Sierra Madre del Sur of Guerrero, Mexico; 5, southeastern Oaxaca, Mexico; 6, northern Chiapas, Mexico; 7, Sierra de los Cuchumatanes, Guatemala; 8, highlands of Alta Verapaz, Guatemala; 9, Sierra de las Minas, Guatemala; 10, Pacific highlands of Guatemala and Chiapas; 11, El Salvador highlands; 12, northwestern Honduras; 13, eastern Costa Rica.



DISTRIBUTION OF CLOUD FOREST IN MIDDLE AMERICA

On the Carribean versant cloud forest extends northward to about the Tropic of Cancer in southwestern Tamaulipas, Mexico (Martin, 1958). Southward along the Atlantic escarpment disjunct cloud forests occur on the higher crests of the Sierra Madre Oriental in the Xilitla region in San Luis Potosi and Queretaro; this highland region appears as the Sierra de Jalpan on some maps. Floristically this forest closely resembles that of the Gomez Farias region with the dominant trees being oak, pine, madrono, cedar, sweetgum, and walnut (Dixon et al., 1972). This cloud forest is isolated from the next cloud forest to the south by the deep entrenchment of several tributaries of the Rio Moctezuma.

An extensive tract of cloud forest extends along the eastern slopes of the Sierra Madre Oriental from northeastern Hidalgo to the Teziutlan area of Puebla. The crest of the Sierra Madre Oriental swings eastward to the east of Teziutlan and forms a spur known locally as the Sierra de Teziutlan. Because of the orientation of this portion of the massif to prevailing winds, as well as the effects of a rain-shadow caused by the highlands of the Volcan Cofre de Perote, a disjunction of cloud forest occurs between the Teziutlan area and the next cloud forest to the south in the Jalapa region of Veracruz, where the main crest of the Sierra Madre Oriental is once again oriented more or less perpendicularly to the prevailing moisture-laden winds from the Gulf of Mexico.

The Atlantic versant from Volcan Pico de Orizaba to the Sierra Mixe to the west of the Isthmus of Tehuantepec supports several isolated cloud forests that are fragmented by a low pass in the Cordoba-Orizaba area and the deep entrenchment of the Rio Santo Domingo, the major tributary of the Rio Papaloapan.

I consider the northernmost extent of cloud forest on the Pacific escarpment to be in the Sierra Madre del Sur in Guerrero, although cloud forest-like conditions have been reported for the southern slopes of Cerro Barolosa and Cerro Tancitaro (Duellman, 1965; Leavenworth, 1946). As pointed out by Duellman (1965), these Michoacan forests have little in common with the cloud forests in eastern Mexico, either physiognomically or floristically.

To the southeast of the Isthmus of Tehuantepec, cloud forest occurs on the Atlantic slopes of the southeastern Oaxacan highlands, sometimes referred to as the Sierra de Niltepec, Zanatepec, or Atravesada. This cloud forest spills over to the Pacific versant on the higher crests. Several peaks in the region, most notably Cerro Azul and Cerro Baul, attain elevations of about 2408 and 2018 m, respectively. This cloud forest is isolated from cloud forests to the southeast and northeast by several low passes between Tapanatepec and Arriaga, and the xeric Rio Grijalva Valley, respectively.

Two major blocks of cloud forest occur in the northern Chiapan highlands. The first covers the northwestern portion of the Mesa Central and is known locally as the "selva negra." The second occurs to the east of Comitan in the region of the Lagos de Montebello and continues into Guatemala on the northern escarpment of the Sierra de los Cuchumatanes. The Rio Negro gorge effectively isolates the cloud forest biota of the northwestern Guatemalan highlands from that of Alta Verapaz where cloud forests occur on several mountain ranges including the Sierra de Pocolha, Sierra de Xucaneb, Sierra de Pansal, and the highlands between Coban and the Rio Negro. The interior highland valleys of Alta Verapaz tend to support seasonally dry pine-oak forests that intervene between these cloud forests. One such seasonally dry forest extends up the upper course of the Rio Matanzas in the vicinity of Purulha, Baja Verapaz, thus separating the Alta Verapaz cloud forests from that of the Sierra de las Minas which extends across the northern escarpment from Cerro Quisis and Cerro Verde in the west to almost a level due north of Gualan, Zacapa. Along the higher crests of the Sierra de las Minas luxuriant cloud forest spills over and covers the southern escarpment down to 1700--1900 m. A small isolated cloud forest occurs on the higher portions of the Montanas del Mico in eastern Guatemala.

Along the Pacific versant of Chiapas and Guatemala a band of cloud forest, continuous except for minor breaks caused by deep valleys, occurs from Cerro Tres Picos across the southern volcanic highlands onto the Las Nubes block of southeastern Guatemala. There is a major lowland depression, supporting subhumid types of vegetation, in southeastern Guatemala that extends through the departamentos of Santa Rosa, Jutiapa, Jalapa, and Chiquimula. On the eastern side of these lowlands several isolated highland areas in El Salvador support cloud forest including Cerro Montecristo, Cerro El Pital, Volcanes Santa Ana, San Vicente, and San Miguel, and the highlands in the Ahuachapan region.

The highlands of Honduras are not as extensive as those to the north. Nevertheless, several high crests of the northern cordilleras receive abundant moisture and support small tracts of cloud forest. The largest of these are on the Sierra de Omoa, Sierra de Espiritu Santo, Cerro Santa Barbara, Sierra de Sulaco, Sierra de Nombre de Dios, and Sierra de Agalta.

The only areas I am aware of in Nicaragua that support cloud forest are several of the mountains in the northern portion of the country including the higher crests of the Cordillera Isabella.

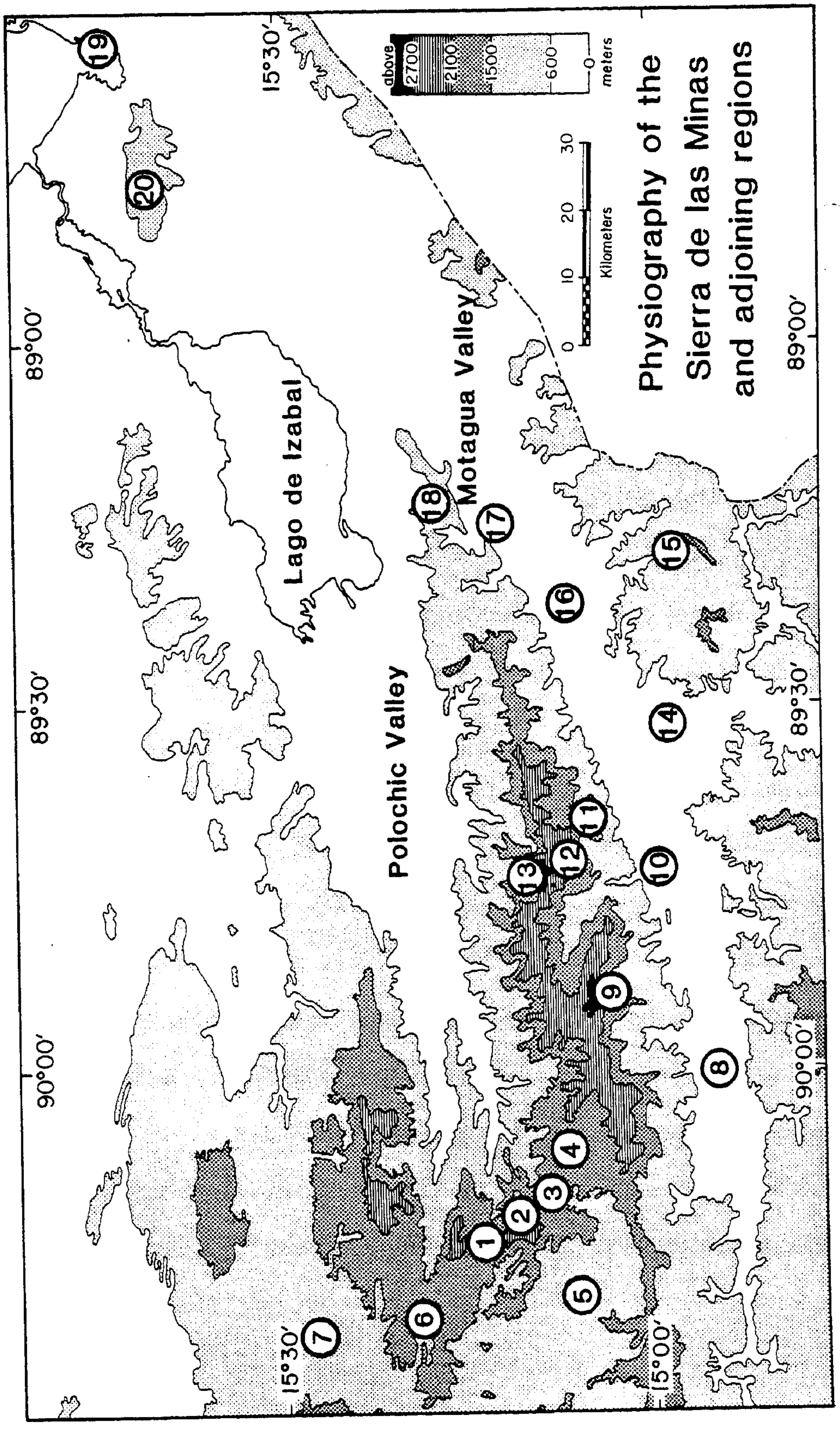
A hiatus of over 250 km occurs between the cloud forest in northern Nicaragua and the most proximate cloud forest to the south in Costa Rica on the northern end of the Cordillera de Guanacaste in the vicinity of Volcan Orosi. Cloud forest occurs on the higher crests of the Cordillera de Guanacaste and Cordillera Central through the Cordillera de Talamanca to western Panama.

THE NATURAL LANDSCAPE OF THE SIERRA DE LAS MINAS

Physiography and geology.-- Most of the Guatemalan highlands exceeding 2000 m are west of the Pacific drainage of the Rio Michatoya and of the Rio Negro, which ultimately discharges into the Gulf of Mexico. This corresponds roughly with a line drawn north--south through Guatemala City. In the southeastern portion of the country the terrain is broken and areas exceeding 2000 m are small. Isolated crests and peaks rise above this contour on the Volcan de Pacaya, the Las Nubes block, and Cerro Montecristo. Several ranges in Alta Verapaz also exceed 2000 m, but the most extensive highland region is that of the Sierra de las Minas (Fig. 2) stretching across five departments in east-central Guatemala.

Approximately 350 km^2 lie above the 2100 m contour in the Sierra de las Minas which is one of the northernmost of the WSW--ENE trending mountain ranges that run parallel to each other through eastern Guatemala, Honduras, and northern Nicaragua. Termer (1936) pointed out that a striking physiographic feature of the Sierra de las Minas was the existence of an ancient erosion surface at elevations of 1700--2200 m. He was also the first to point out that the crest of the Sierra de las Minas and adjoining parts of the Sierra de Chuacus were of reasonably uniform elevation. Several high mountains in the western portion of the range, Cerro Quisis and Cerro Verde, attain elevations of over 2300 m and are connected by elevations exceeding 1600 m. Just to the southwest of Cerro Verde and to the west of the village of Chilasco a high ridge, known locally as Cerro Miranda, rises to elevations of over 2300 m and forms a portion of the high crest of the Sierra de las Minas that

FIGURE 2. Relief map of the Sierra de las Minas, the highlands of Alta Verapaz, and adjacent territory. Numbers refer to the following: 1, Purulha; 2, La Union Barrios; 3, Nino Perdido; 4, Chilasco; 5, Salama; 6, Tactic; 7, Coban; 8, El Rancho; 9, Cerro Pinalon; 10, Teculutan; 11, San Lorenzo; 12, Finca Sitio Nuevo; 13, Cerro Raxan; 14, Zacapa; 15, La Union; 16, Gualan; 17, Dona Maria; 18, Aldea Vista Hermosa; 19, Puerto Barrios; 20, Montanas del Mico. Cerros Raxon and Pinalon slightly offset to show relief.



Physiography of the Sierra de las Minas and adjoining regions extends unbroken below the 2100 m contour for 65 km. A narrow ridge connects Cerro Miranda with Cerro Pinalon, the second highest mountain in the Sierra de las Minas cresting at about 2960 m, and forms one of the three radiating highland crests; to the west of Cerro Pinalon a ridge connects Cerro Bandera Perdida (2390 m) which subsequently drops off into the Motagua Valley, while the main crest of the Sierra de las Minas continues to the north of Cerro Pinalon to the vicinity of peaks called Cerro Guaxabaia (2650 m) and Cerro Mululja (2690 m), and then west to the Cerro La Cucaracha (2950 m), Cerro Raxon (2990 m), Montana El Imposible (2610 m), and Monatana del Licenciado (2350 m), respectively (Fig. 2).

Two highland areas of high relief connect the Sierra de las Minas with highlands to the north and west. The eastern extension of the Sierra de Chuacus separates tributaries of the Rio Negro and Rio Motagua and forms a narrow highland bridge that connects the Sierra de las Minas with the western Guatemalan highlands. A number of extensive, rugged ranges connected by high valleys extend northward from the northwestern spur of the Sierra de las Minas in the vicinity of the village of Purulha and join this range with those of Alta Verapaz. The Sierra de las Minas gradually loses elevation at its eastern terminus and to the south of Lago de Izabal only a low ridge of less than 300 m separates the Rio Motagua drainage from Lago de Izabal. The Montanas del Mico to the east-northeast of the main axis of the Sierra de las Minas reach elevations of about 1000 m.

The Sierra de las Minas is bordered to the north and south by two large structural depressions that correspond to two major faults-- the

Motagua and the Polochic. The range is bounded to the west by the pumice-filled Salama-San Jeronimo Basin. The exceedingly steep northern face of the Sierra de las Minas is drained by tributaries of the Rio Polochic which are torrential streams. The Polochic empties into Lago de Izabal which occupies the eastern portion of the Polochic depression. Tributaries of the south face flow into the Rio Motagua, the largest river system in Guatemala. The Rio Motagua flows through arid country along its upper course and has a relatively small discharge, but along its lower course it flows through a region of abundant rainfall and widens to about 200 m with an average depth of 5 m. A major tectonic depession can be traced from the Cayman trench up the Motagua Valley and continues through the Grijalva Valley of central Chiapas. One of the largest tributaries of the Motagua flowing out of the Sierra de las Minas is the Rio Teculutan, known locally as the Rio Blanco (as are many other Guatemalan rivers) along its upper course. This river intervenes between two of the arms of the crest of the Sierra de las Minas with Cerros Pinalon and Bandera Perdida to the south and the Cerros Raxon and La Cucaracha to the north. The middle Motagua Valley is widest in the Zacapa region where an extensive semi-arid plain extends from the base of the Sierra de las Minas far up the Rio Grande de Zacapa Valley, a southern tributary of the Rio Motagua.

An excellent study of the geology of central Guatemala including the Sierra de las Minas was presented by McBirney (1963) and I have summarized much of the geological information for the Sierra de las Minas from his work. The Sierra de las Minas and Montanas del Mico are composed largely of Paleozoic rocks that are among some of the oldest in Central America; they include pre-Pennsylvanian schists and gneisses, and possess a crystalline, highly deformed basement complex. This mountain range is built on upthrust basement rocks including a thick sequence of these rocks as well as amphibolites and marbles. A wide belt of serpentized rock extends along the northwestern margin of the Sierra de las Minas, although the eastern extent of this belt has not been determined. A narrower belt, consisting of more highly sheared and more completely serpentized rocks, runs along the south side of the range and extends to the Gulf of Honduras. The northern margin of the southern belt is a well defined fault zone of considerable displacement. The rocks were subjected to intense metamorphism during the pre-Permian, prior to the influx of the sea during the end of the Carboniferous that covered much of the lands north of the Sierra de las Minas. Shallow marine conditions prevailed through most of Permian time depositing a thick layer of sediment. The interval between the end of the Paleozoic and end of the Triassic is thought to have been an important orogenic period, although probably only mild metamorphism and little plutonism occurred during this time. The re-emergence at the end of the Paleozoic caused a depositional hiatus that lasted until the end of the Triassic.

With a renewed orogenic disturbance during the Late Cretaceous and Eocene time, the basement rocks of the Sierra de las Minas were remetamorphosed along with the lower part of the overlying sedimentary rocks. The Sierra de las Minas were subsequently reduced to low relief during the early Tertiary, but the region was again elevated and deeply incised starting in the early Pliocene.

Although the highlands above 1500 m are broadly continuous from the northwestern portion of the Sierra de las Minas through the highlands of Alta Verapaz, the geological histories of the regions are stikingly different. The arc formed by the Chuacus-Minas-Mico ranges arose before the Carboniferous period and thus are considerably older than the highlands to the north that gained their present elevations during the Pliocene orogeny. The Alta Verapaz highlands are folded and faulted ranges of marine clastics and limestones (West, 1964). These highlands are a continuation of the plateau-like surfaces of the highlands of Chiapas and northwestern Guatemala that similarly are upfaulted blocks capped by nearly horizontal strata of Cretaceous and Tertiary limestone. These highlands are highly karstic with numerous sinkholes or "siguans" dotting the countryside. Between the northwestern terminus of the Sierra de las Minas and the Alta Verapaz lowlands to the north, severe faulting has transformed the limestone surface into three major east--west ranges: the Sierra de Pansal, the Sierra de Xucaneb, and the Sierra de Pocolha (Chama), respectively. The configuration of these and other minor ranges has been compared with "a stormy sea breaking into parallel billows" (Walper, 1960).

Stream capture of the Rio Salama and its tributaries by the Rio Chixoy was first suggested by Sapper (1937). It seems likely that the streams that presently comprise the headwaters of the Rio Chixoy encompass a region that originally was drained by the Rio Polochic. The extremely narrow and steep Rio Negro gorge is evidence of the differential erosion of relatively weak sedimentary rocks, but whether or not this stream capture was the result of a more rapid erosion of one stream system than another or caused by a relatively greater uplift in the eastern Baja Verapaz region is unknown.

I am uncertain from where the Sierra de las Minas derives its name. Serpentine deposits within the Sierra de las Minas have been documented as a source of artifacts found throughout Central America and Mexico (Foshag, 1955; Sapper, 1937). Also, marble has been quarried from the south side of the range since the early part of this century. Possibly the range receives its name from human activities relating to one of these two rocks.

The Polochic and Motagua Valleys are covered with alluvial soils; soils at higher elevations tend to be intensely weathered and subject to leaching and belong to the reddish lateritic group of soils.

Climate.-- In the Sierra de las Minas, as elsewhere in the tropics, temperature is determined largely by elevation, and the orientation of elevated areas to the prevailing tradewinds is an important factor determining the amount of precipitation in the region. Nightly low temperatures of 5--15°C are the rule regardless of season at the Biotopo "Mario Dary" located at 1520 m on the northwestern slopes of the Sierra de las Minas, although slightly lower temperatures occur during the winter months. Elevations as low as 1300--1500 m in the Sierra de las Minas may experience occasional frosts.

The amount of precipitation in the Sierra de las Minas is subject to vast differences over short distances. Areas in the Alta Verapaz highlands and upper Rio Polochic drainage receive in excess of 4000 mm of precipitation annually and preliminary data from the few isolated recording stations on the north face of the Sierra de las Minas indicates this area receives at least as much. The cloud forest of the Sierra de las Minas receives less rain during the months of January through May when between 50 and 150 mm of precipitation falls monthly. A dramatic increase occurs in June, the wettest month, when over 500 mm may be received, and continues from July through September when generally upwards of 400 mm of rain is received monthly. October through December are subject to considerable fluctuations in rainfall with a monthly average of about 250 mm. During a nine month period extending from 12 December 1979 to 31 August 1980 when detailed meterological data were recorded at a station on the Biotopo "Mario Dary," a total of 177 days experienced rain. Only 9 rainy days occurred in March when dry periods marked by bright, blue skys persisted from one to six days. The amount and duration of precipitation generally increases the last week of May and the months of June, July, and August are especially dreary with rain almost every day. Whereas the region around the Biotopo Mario Dary is extremely humid (Fig. 3), a little to the north along the upper headwaters of the Rio Panima it is considerably drier owing to the rainshadow effects created by the Sierra de Pansal.

A rather consistent pattern of fluctuation of relative humidity characterizes the cloud forest. The monthly mean at early morning (7:00 AM) is between 93--95% during all months of the year, decreasing to 53--73% by about mid-day (1:00 PM), but then gradually rising to 91--95% just before dark (6:00 PM) owing to the fogs that generally pervade the valleys in the afternoon. Thus, the relative humidity at dawn and dusk (and presumably throughout the dark hours) is high and comparable all

FIGURE 3. Cloud forest on the eastern slopes of Cerro Quisis, 3.8 km SE Purulha, Baja Verapaz, Guatemala; taken at 1520 m, 16 March 1981, on the Biotopo Mario Dary.

months of the year, but as might be expected, a more precipitous drop occurs at mid-day in the dry season (March--May) than during the rainy period.

The west to east dip in elevation of the crest of the Sierra de las Minas plays an important role in the precipitational pattern of the lower Motagua Valley. The higher crests of the Sierra de las Minas creat rainshadow conditions in the middle Motagua Valley where less than 500 mm of precipitation is received annually. There is a rather abrupt increase in rainfall to the east of Gualan owing to the low crest of the Sierra de las Minas to the north of that region.

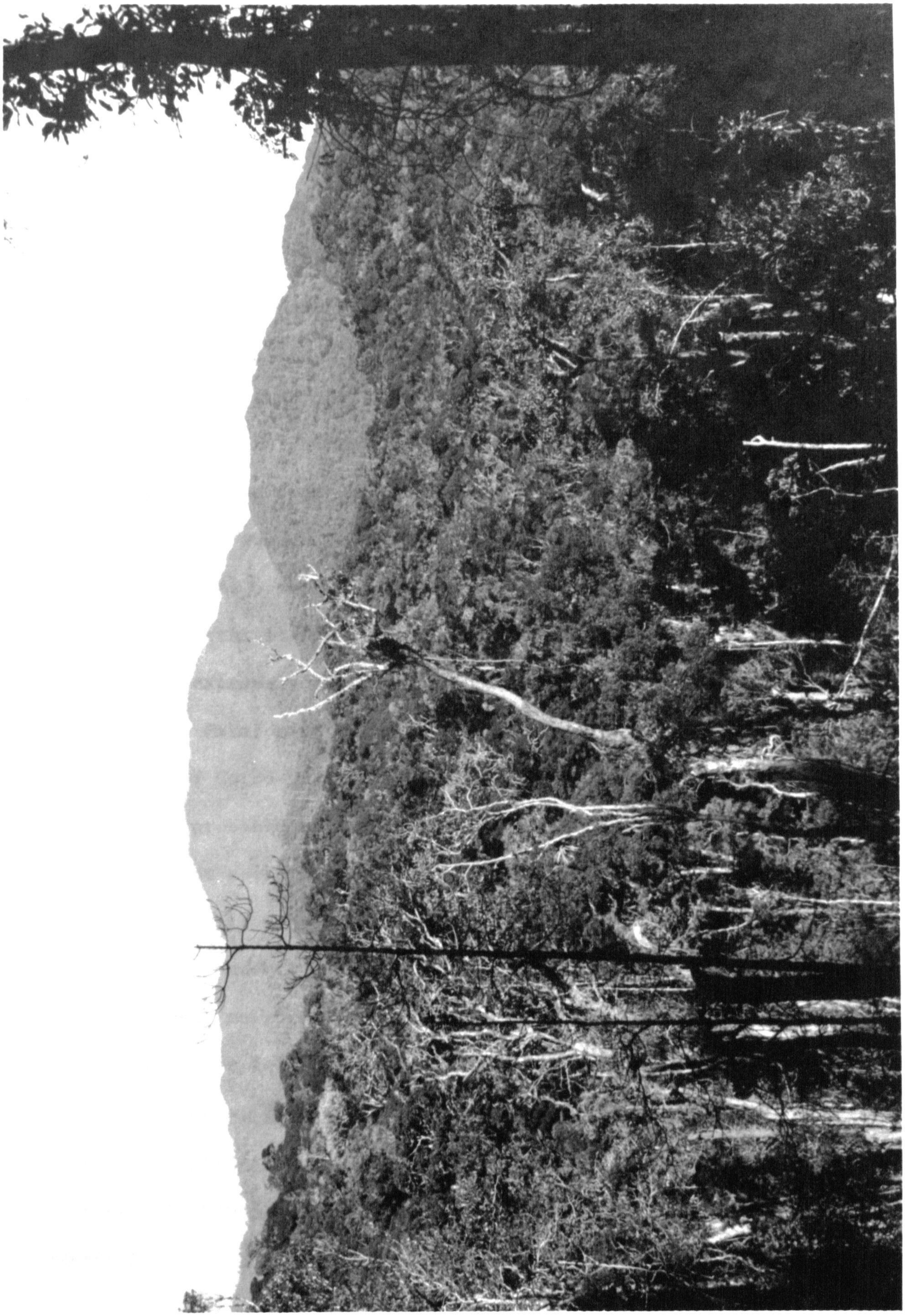
Vegetation.-- The kind of vegetation that occurs in any particular region of the Sierra de las Minas is highly dependant on elevation (temperature) and precipitation of that region. No doubt other factors such as soils also play an important role in plant distributions. For purposes of this discussion I will employ the classification and terminology of Holdridge (1964) with the exception of term "cloud forest," which I use interchangeably with his Lower Montane and Montane Rainforest.

A fairly accurate picture of the vegetational complexity of the Sierra de las Minas may be visualized by imagining a trek over Cerro Raxon, the highest point in the range, starting from Teculutan in the middle Motagua Valley and ending in the Polochic Valley. After leaving the narrow strip of gallery forest that consists predominantly of *Salix*, a xeric vegetation type consisting of columnar cactus, *Melocactus*, and trees of the genera *Acacia*, *Prosopis*, *Bauhinia*, *Casearia*, *Crecentia*, *Croton*, *Diphysa*, *Jacquinia*, *Piptadenia*, *Pithecellobium*, and *Randia*.

From about 300 m upwards, a dry low forest consisting of many of these genera and other deciduous trees including Bursura, Calycophyllum, Cedrela, Cochlospermum, Cordia, Eysenhardtia, Godmania, Pseudobombax, Spondia, Tabebuia, and Triplanis begins to dominate the landscape. At about 1200 m some tree species, especially small oaks, are covered with "Spanish moss" and other species of Tillandsia. As still higher elevations are attained, Liquidambar larger species of Quercus, and several species of pines become dominant. A thin humus layer may be present in some areas, epiphytes are more common, and distinctly cloud forest-like conditions prevail along streams, especially in the deeper ravines. At about the 2200 m level the forest is composed almost entirely of hardwoods (Fig. 4); Liquidambar athough still present, is not nearly as common as it was just a few hundred meters below and pine has become rare. Although we are still on the south face of the Sierra de las Minas, we are now in cloud forest.

The boundaries of the cloud forest are at times well defined, with transition from dense stands of pine to hardwoods occurring over several hundred meters. However, more frequently the change is more gradual. Three types of forest may border (and be inseparable from) the hardwood cloud forest: upper Subtropical Wet Forest that occurs along the lower limits of cloud forest, and Liquidambar forest and humid pine-oak forest which occur at comparable elevations at which cloud forest is found but on drier slopes. Of these different forests, distinguishing between hardwood cloud forest and upper Subtropical Wet Forest is perhaps the most difficult. The distinction between the two is based primarily on elevation (and therefore temperature) and the absence, presence, or

FIGURE 4. Cerro Raxon (elevation about 2960 m) in the Sierra de las Minas, Guatemala, as seen looking NW from a distance of 6--7 km on a peak known locally as Volcan del Mono, 2290 m; taken 2 March 1981. Although this view is of the south side of the crest of the Sierra de las Minas, note the dense cloud forest in the foreground.



relative abundance of indicator species. The dominant indicator trees are (Monterroso Salinas, 1976): Podocarpus oleifolius, Alforaoa costaricensis, Engelhartia sp., Billiae hipocastanum, Magnolia guatemalensis, and Brunellia sp. Other relatively common species are: Clethra johnstonii, Alchornea latifolia, Quercus purulhana, Chaetoptelia mexicana, Roupola borealis, Exothae paniculata, Zanthoxylum procerum, Chlorophora tintictoria, Perimenium stringuillosum, Nectrandra sanguinea, and Ediosmun mexicana. The humus layer may be thin in some areas but tends to be continuous and there is a profusion of epiphytes, mosses, lichens, and other small moisture-loving plants. Tree ferns of the genus Cyathea abound along streams and on the sides of ravines, as do stands of giant bamboo. Above the 2700 m contour the forest becomes of slightly shorter stature, the trees are windblown, and the humus layer becomes extremely thick. This type of cold, wet forest has been called Montane Rainforest by Holdridge (1964). The cloud forest extends to the crest of Cerro Raxon and down the north face of the Sierra de las Minas. It is probable that this area receives more precipitation than the cloud forest covering the crest or upper portion of the Motagua (=south) facing slopes, but data are lacking. On the north face, the cloud forest extends roughly to about the 1300 m level, below which occur relatively narrow bands of subtropical wet and moist forests, respectively. The following trees are found between 300 and 750 m: Bernoullia flammea, Blepharidium guatemalensis, Brosium alicastram, Calophyllum brasiliense, Cecropia sp., Dialum guianense, Ficus sp., Guarea sp., Karwinskia humboltiana, Lonchocarpus sp., Pimienta dioca, Podocarpus sp., Pouteria mammosa, Pseudobombax ellipticum, Schizolobium *parahybum*, *Simarouba glauca*, *Simphonia globulifera*, *Spondias mombia*, *Sterculia mexicana*, *Tabebaia guayacan*, *Vatairea lundelli*, *Virola* sp., *Vitex cooperi*, and *Vochysia hondurensis*. Below the 300 m level the forest is mostly destroyed, but small remnant of what must have been tropical rainforest still persist locally.

In contrast to the Sierra de las Minas, the Montanas del Mico do not possess well defined vegetation belts, although above 600 m a lush Subtropical Wet Forest prevails. Wet forest, and on the crests of Cerros San Gil and Las Escobas cloud forest-like conditions exist. The vicinity of Puerto Barrios in the lower Motagua River Valley was covered by Tropical Rainforest (now reduced almost entirely to secondary growth). A gradient from wet to distinctly subhumid vegetation is encountered proceeding up the Motagua Valley from Puerto Barrios owing to the direction of the prevailing moisture-laden tradewinds and the rainshadow effects of the Sierra de las Minas. A distinct break in vegetation type occurs over relatively few kilometers between Los Amates and Dona Maria, and progressively more xeric conditions are encountered proceeding up the Motagua, with the driest conditions being found from the region around Zacapa to the western border of the Departamento de El Progreso, thus corresponding to the highest elevations to the north.

COMPOSITION AND DISTRIBUTION OF THE CLOUD FOREST HERPETOFAUNA

A total of 110 species of amphibians and reptiles is known to occur in the upper subtropical wet and cloud forest of the Sierra de las Minas. All but two species are represented in my collections, an undescribed salamander and *Pliocercus euryzonus* of questionable occurrence. Not surprisingly, many of these specimens represent the first records of the region. The composition of the herpetofauna is shown in Table 1.

Table 1. Composition of the mesic upland herpetofauna of the Sierra de las Minas.

	Families	Genera	Species
Caecilians	1	1	1
Salamanders	1	4	10
Anurans	6	10	26
Lizards	5	10	21
Snakes	5	33	52
TOTAL	18	58	110

In addition, a dozen other species, mostly wide-ranging and generally distributed in the lowlands, may reach cloud forest, namely:

Gymnopis multiplicata
Bolitoglossa dofleini
Phrynohyas venulosa
Bufo marinus
Anolis capito
Anolis laeviventris
Eumeces sumichrasti
Xenosaurus grandis
Boa constrictor
Drymarchon corais
Rhadinaea decorata
Sibon nebulata

Most of these species have been taken in the foothills of the Sierra de las Minas in wet forest; and in the case of *Boa constrictor*, I have taken it slightly above 1000 m in the Sierra de las Minas and Montanas del Mico. Certainly, if *Bufo marinus* has not already invaded portions of the cloud forest that have been recently cleared, it probably will in the not too distant future.

The numerous descriptions I received at several localities of a "pink two-headed snake" about a meter in length that is discovered when excavating tree ferns makes me believe in the existence of an undescribed caecilian in the western portion of the Sierra de las Minas. Unfortunately, attempts to locate specimens were unsuccessful.

Four major animal habitats are recognizable on the upper portion of the Sierra de las Minas: upper subtropical wet forest, hardwood cloud forest, *Liquidambar* forest, and humid pine-oak forest (see above). Although these forests are sometimes sharply delimited, most frequently they so tightly interdigitate or almost imperceptibly grade into each other that it is impossible to decide where one ends and another begins; I consider all, in a loose sense, as subsets of cloud forest.

Despite the intensive collecting carried out in this cloud forest during all seasons, much remains to be learned concerning habitat and altitudinal distributions of the herpetofauna. The most critical area in need of further investigation is the elevational belt comprising the transitional zone between upper subtropical wet and cloud forests that lies between about 800 and 1200 m. The number of species recorded from these elevations was relatively low (Table 2). However, considering the short time spent between the 800--1200 m contours, I find it remarkable that so many species were collected.

TABLE 2. Species recorded from different elevational belts in the wet forests of the Sierra de las Minas.

Elevation	No. species
400--800	56
800--1200	39
1200--1600	57
1600--2000	52
>2000	14

I have included those species taken from the upper portion of subtropical wet forest and indicated probable occurrence in hardwood cloud forest (Table 3). The greatest proportion of the hardwood cloud forest herpetofauna also occur at lower elevations in the subtropical wet forest. Relatively few species are recorded from only one habitat. In actuality, probably more species occur in this transition zone than in any altitudinally comparable zone. Data derived from my limited collections at these elevations suggest that species adapted to the cool, wet uplands descend to lower elevations in especially wet regions. For example, *Agalychnis moreleti*, *Ptychohyla spinipollex*, and *Centrolenella fleischmanni* occur at 600 m or less in the Sierra de las Minas, but only in wet forests along steams. Alternatively, species generally considered to be lowland rainforest inhabitants tend to extend their altitudinal distributions upward in regions where there is a continuum of wet forest types progressing up mountainous slopes. Species whose altitudinal distributions reach or exceed 1100 m include *Sphenomorphus cherriei*, *Dryadophis melanolomus*, *Leptodeira annulata*, *Leptophis mexicanus*, *Spilotes pullatus*, *Tropidodipsas sartori*, and *Bothrops asper*. Several species that are widely distributed in the lowlands occur at elevations exceeding 1500 m: *Ameiva undulata*, *Drymobius margaritiferus*, *Imantodes cenchoa*, and *Pliocercus elapoides*. *Leptodeira septentrionalis* possesses the greatest vertical range of any species of amphibian or reptile in the Sierra de las Minas, occurring in wet forests from about sea level in rainforest to well above 2000 m in *Liquidambar* forest.

The altitudinal distributions of amphibians and reptiles of the cloud forest of the Sierra de las Minas and the forest types they inhabit are summarized in Table 3. I have followed the subjective classification of Duellman (1965) and Stuart (1950) in designating the relative abundance of a species as abundant (A), moderately abundant (M), rare (R), of questionable occurrence (?), or apparently absent (-). For species that occur in at least two types of forest this

TABLE 3. Forest type and altitudinal distributions of cloud forest amphibians and reptiles in the Sierra de las Minas.

SPECIES	Subtropical Wet Forest	Hardwood Cloud Forest	Liquidambar Forest	Humid Pine-oak Forest	Altitudinal Range in meters
Minascaecilia sartoria	R	?	-	-	650
Bolitoglossa helmrichi	-	A	M	-	1300--2290
Bolitoglossa meliana	-	M	-	-	1550--2730
Bolitoglossa mexicana	A	?	-	-	100--460
Bolitoglossa odonelli	R	?	-	-	150
Bolitoglossa rufescens	A	?	-	-	100--770
Bolitoglossa sp. A	R	?	-	-	>550
Bolitoglossa sp. B	-	R	-	-	1900
Chiropterotriton veraepacis	-	M	-	-	1610--2290
Nyctanolis pernix	-	R	-	-	1610
Oedipina elongata	R	?	-	-	770
Eleutherodactylus bocourti	-	M	-	-	1580--1710
Eleutherodactylus brocchi	-	A	M	M	1460--2130
Eleutherodactylus daryi	-	M	-	-	1520--1710
Eleutherodactylus lineatus	-	A	M	R	1520--1980
Eleutherodactylus milesi	M	?	-	-	400--800
Eleutherodactylus rostralis	A	?	-	-	100--800
Eleutherodactylus rugulosus	A	?	-	-	10--1200
Eleutherodactylus xucanebi	-	M	-	-	1520--1610
Eleutherodactylus sp. F	-	R	M	-	1900--2290

TABLE 3. Forest type and altitudinal distributions of cloud forest amphibians and reptiles in the Sierra de las Minas. --continued

Eleutherodactylus sp. G	A	?	-	-	100--650
Bufo coccifer	-	R	R	A	1030--1610
Bufo valliceps	A	R	-	-	10--1000
Agalychnis moreleti	M	R	R	A	550--2130
Hyla bromeliacea	-	M	-	-	1610--1650
Hyla valancifer	?	R	-	-	1490--1830
Plectrohyla guatemalensis	-	M	R	M	1580--1900
Plectrohyla hartwegi	-	M	R	-	1460--1890
Plectrohyla quecchi	-	A	M	M	1490--1710
Ptychohyla panchoi	A	?	-	-	550--770
Ptychohyla spinipollex	A	A	A	A	600--1890
Smilisca baudini	A	R	R	M	10--1000
Smilisca cyanosticta	R	?	-	-	770
Centrolenella fleischmanni	A	A	M	?	100--1610
Hypopachus barberi	-	R	A	A	1500--1680
Rana maculata	M	M	A	A	500--1900
Rana sp. D (pipiens-group)	M	R	A	M	100--1650
Anolis biporcatus	M	?	-	-	500--770
Anolis cobanensis	-	A	M	-	1500--1830
Anolis haguei	-	M	M	A	1480--2290
Anolis humilus	A	?	-	-	100--900
Anolis limifrons	M	?	-	-	140--770
Anolis petersi	-	M	R	-	1520--2130

TABLE 3. Forest type and altitudinal distributions of cloud forest amphibians and reptiles in the Sierra de las Minas. --continued

Corytophanes cristatus	A	?	-	-	100--700
Corytophanes percarinatus	-	R	R	M	1610--1830
Sceloporus acanthinus	-	-	M	M	900--1900
Sceloporus smaragdinus	-	-	M	M	1700--1900
Sceloporus taeniocnemis	-	M	M	A	1500--2290
Lepidophyma flavimaculata	A	?	-	-	150--870
Ameiva festiva	A	?	-	-	100--900
Ameiva undulata	A	?	R	R	250--1650
Mabuya mabouya	M	?	-	-	10--910
Sphenomorphus cherriei	A	-	-	M	10--1300
Sphenomorphus incertum	-	A	M	R	1520--1980
Abronia aurita	-	R	-	-	1610--1830
Abronia fimbriata	-	R	-	-	1680
Barisia moreleti	-	A	M	M	1580--1980
Celestus rozellae	R	?	-	-	150--650
Leptotyphlops goudoti	R	R	?	R	900--1610
Typhlops tenuis	-	R	R	?	1370--1520
Adelphicos quadrivirgatus	M	-	?	?	600--650
Adelphicos veraepacis	-	M	M	?	1500--1710
Amastridium veliferum	R	?	-	-	500--550
Coluber constrictor	R	?	-	-	500--800
Coniophanes fissidens	A	?	-	-	150--770
Dendrophidion vinitor	M	R	-	-	450--1100

TABLE 3. Forest type and altitudinal distributions of cloud forest amphibians and reptiles in the Sierra de las Minas. --continued

Dryadophis dorsalis	-	M	A	A	1350--2290
Dryadophis melanolomus	A	M	-	-	70--1100
Drymobius chloroticus	-	A	A	M	1500--1980
Drymobius margaritiferus	A	R	M	M	10--1710
Hydromorphus concolor	R	?	-	-	100--650
Imantodes cenchoa	A	M	?	?	10--1600
Lampropeltis triangulum	M	M	M	M	100--1610
Leptodeira annulata	A	R	-	-	90--1100
Leptodeira septentrionalis	A	-	R	M	100--2290
Leptodrymus pulcherrimus	M	?	-	-	140--650
Leptophis ahaetulla	A	?	-	-	100--700
Leptophis mexicanus	A	?	-	R	20--1360
Leptophis modestus	-	M	M	R	1510--1900
Ninia diademata	?	?	M	M	1470--1500
Ninia maculata	?	R	-	-	1500
Ninia sebae	A	?	A	A	10--1590
Oxybelis aeneus	A	?	-	-	100--850
Oxybelis fulgidus	M	?	-	-	100--750
Oxyrhopus petola	R	?	-	-	600--650
Pliocercus elapoides	R	M	-	-	770--1600
Pliocercus euryzonus?	-	R?	-	R?	?
Pseustes poecilonotus	R	?	-	-	650
Rhadinaea godmani	-	M	M	M	1830--1900

TABLE 3. Forest type and altitudinal distributions of cloud forest amphibians and reptiles in the Sierra de las Minas.--continued

Rhadinaea hempsteadae	-	M	R	-	1680--2300
Rhadinaea kinkelini	?	R	-	-	1300--1830
Scaphiodontophis annulatus	R	?	-	-	150--850
Sibon dimidiata	R	?	-	-	650
Spilotes pullatus	A	R	-	-	100--1200
Stenorrhina degenhardti	A	A	?	-	100--1740
Storeria dekayi	?	A	-	-	1520--1710
Tantilla bairdi	-	?	R	-	1520
Tantilla schistosa	R	?	-	-	400--650
Tantilla taeniata	R	?	-	-	580--650
Thamnophis fulvus	-	M	A	A	1460--2290
Tropidodipsas kidderi	-	A	M	-	1520--1900
Tropidodipsas sartori	A	M	-	-	10--1350
Xenodon rhabdocephalus	M	?	-	-	10--400
Micrurus diastema	A	R	-	-	150--1200
Micrurus elegans	-	M	R	-	1300--1620
Bothriechis aurifer	-	A	R	R	1520--2290
Bothriechis schlegeli	M	?	-	-	400--770
Bothrops asper	A	R	-	-	10--1100
Bothrops godmani	-	A	M	A	1520--2290
Bothrops nummifer	M	R	-	-	450--1520

classification has the advantage of indicating relative abundance (Duellman, 1965). I have included a few species that, although unknown from the higher elevations of the Sierra de las Minas, are known from elevations supporting cloud forest in the adjacent range of the Montanas del Mico.

It is difficult to work in a region for extended periods without becoming aware of certain features that restrict or affect the distributions of animals within a particular habitat. For example, species that are characteristic of, and apparently limited to throughout most of their ranges, areas of relatively deep leaf litter and/or humus are:

Oedipina elongata
Eleutherodactylus lineatus
Eleutherodactylus rostralis
Anolis cobanensis
Anolis humilis
Lepidophyma flavimaculata
Sphenomorphus cherriei
Sphenomorphus incertum
Barisia moreleti
Adelphicos veraepacis
Amastridium veliferum
Coniophanes fissidens
Ninia maculata
Pliocercus elapoides
Rhadinaea hempsteadae
Rhadinaea kinkelini
Storeria dekayi
Tantilla taeniata
Xenodon rhabdocephalus
Micrurus elegans

A riparian habitat is characteristic for many stream-breeding frogs and a few species of snakes that feed on these frogs or are aquatic. Species that occur along streams are:

Minascaecilia sartoria
Plectrohyla hartwegi

Bolitoglossa mexicana
Bolitoglossa odonelli
Eleutherodactylus brocchi
Eleutherodactylus daryi
Eleutherodactylus milesi
Eleutherodactylus sp. F
Eleutherodactylus sp. G
Plectrohyla guatemalensis
Plectrohyla quecchi
Ptychohyla panchoi
Ptychohyla spinipollex
Centrolenella fleischmanni
Rana maculata
Drymobius margaritiferus
Hydromorphus concolor
Leptodeira septentrionalis
Thamnophis fulvus

Bromeliads, both epiphytic and terrestrial, are one of the most conspicuous features of the cloud forest; the relative abundance of many species is correlated to of bromeliads and the life histories of a few seem inextricably linked to these plants. Bromeliads may give refuge, protect against dessication, and serve as breeding sites. Species commonly found in bromeliads include:

Bolitoglossa helmrichi
Bolitoglossa meliana
Chiropterotriton veraepacis
Hyla bromeliacia
Plectrohyla guatemalensis
Ptychohyla spinipollex
Abronia aurita
Abronia fimbriata
Tropidodipsas kidderi

Eleutherodactylus bocourti and *E. xucanebi* are most frequently found at night sitting on the leaves of terrestrial bromeliads or low vegetation near slumps of terrestrial bromeliads. Nevertheless, in spite of the search of hundreds of bromeliads during the day, I have never taken these species from these plants, and their sanctuary during the day remains a mystery. Stuart (1948) reported taking a *Bothriechis aurifer* from a bromeliad in Alta Varapaz. Although I have not taken one from within a bromeliad, I often found this species by day stretched out in clumps of large terrestrial bromeliads. These snakes gave every indication of actively foraging, slowly crawling through the bromeliads and inspecting leaf axils by inserting their heads and frequently flicking their tongues. A typical resident of bromeliads, *Hyla bromeliacia*, is known to be included in their diet (Stuart, 1948).

The evasive habits of arboreal species may preclude them from being readily encountered and consequently species presumed to be rare might be in fact be common. *Hyla valancifer* was taken on wet nights one to five meters above the ground while sitting on limbs or large bromeliads. The larva of this species has never been taken from streams despite intensive collecting of streams that has resulted in the capture of the tadpoles of all the species of anurans known to be stream-breeders in the region. It seems highly unlikely that any member of the group to which *H. valancifer* belongs utilizes streams as breeding sites as suggested by Savage (1981). The only other adults of this species obtained in the region were collected in large bromeliads (Duellman, 1978). It seems reasonable to assume that *H. valancifer* generally remains sequestered in bromeliads by day and probably utilizes the reservoirs of these plants as breeding sites.

The two largest species of anoles in the Sierra de las Minas, *Anolis biporcatus* and *A. petersi*, are canopy dwellers and venture to the ground infrequently. *Anolis petersi* where most often taken in areas where trees where being felled and an *A. biporcatus* was dislodged at night from the top of a tree over 30 m high by a foraging micoleon or kinkajou (*Potos flavus*). *Sceloporus taeniocnemis* tends to be abundant on logs and rocks in disturbed areas, but also occurs in virgin cloud forest. Its presence in this habitat might have gone undetected if it were not for the sharp eyes of several bird watchers who first spotted these lizards basking on high branches of dead trees and pointed them out to me. Other arboreal lizards include *Abronia aurita* and *A. fimbriata* that were generally taken on or near the ground, but whose arboreality can scarcely be doubted and which generally tried to escape by ascending large vertical tree trunks. Among the snakes, *Splilotes pullatus* and *Pseustes poecilonotus*, known bird predators (Beebe, 1946; Scott, 1969), are notable for frequenting the upper canopy. These snakes were seen occasionally (and collected infrequently) coiled 20--35 m above the ground.

Mention should be made of two arboreal species of pitvipers. *Bothriechis aurifer* and *B. schlegeli* are not uncommon and generally found coiled on low vegetation. I presume from field observations and preliminary analysis of stomach contents that these species forage not only in low vegetation but also move freely on the ground. Nevertheless I was advised by natives that both species are encountered in the crowns of recently felled trees.

Some frogs seem to be incapable of breeding in the cascading, often torrential streams that descend through the cloud forest. Therefore, a fairly subtle albeit important prerequisite for a few cloud forest inhabitants is the presence of relatively level ground allowing for either the formation of small pools or relatively calm stretches of a stream. Pools of water are a rarity in most portions of the cloud forest and this probably accounts for the limited distribution and/or rarity of some species within the cloud forest. All of the species listed below are present in cloud forest, but require quiet water in which to breed and are more widely distributed in other habitats.

Bufo coccifer
Bufo valliceps
Agalychnis moreleti
Smilisca baudini
Smilisca cyanosticta

Rana maculata and Rana sp. (pipiens-group) breed in either woodland pools or the less turbulent sections of streams.

Some species are drastically affected by even a limited amount of clearing in the cloud forest. Species that tend to be eliminated or whose abundance is drastically reduced by man's alteration of virgin cloud forest are:

Eleutherodactylus bocourti
Eleutherodactylus daryi
Eleutherodactylus xucanebi
Hyla valancifer
Anolis humilis
Abronia aurita
Abronia fimbriata
Pliocercus elapoides
Rhadinaea hempsteadae
Rhadinaea kinkelini
Tantilla bairdi
Tropidodipsas kidderi
Micrurus elegans
Bothriechis aurifer

Conversely, a larger number of species, especially reptiles, tend to be more abundant in, and in some cases restricted to natural or artificial breaks. Species that are essentially lowlanders, but that penetrate the upland cloud forest in the more open areas of secondary growth include:

Bufo valliceps
Smilisca baudinii
Anolis lemurinus
Ameiva undulata
Mabuya mabouya
Drymobius margaritiferus
Lampropeltis triangulum
Leptodeira annulata
Leptodeira septentrionalis
Leptophis ahaetulla
Leptophis mexicanus
Ninia sebae
Oxybelis aeneus
Oxybelis fulgidus
Bothrops asper

Species that possess essentially upland distributions that tend to be more abundant in disturbed portions of cloud forest are:

Bufo coccifer
Agalychnis moreleti
Hypopachus barberi
Rana maculata
Rana sp. (*pipiens-group*)
Anolis haguei
Corytophanes percarinatus
Sceloporus acanthinus
Sceloporus smaragdinus
Sceloporus taeniocnemis
Dryadophis dorsalis
Ninia diademata
Thamnophis fulvus

The species that tend to be more common in areas of light clearing or along the edges of cloud forest are:

Bolitoglossa helmrichi
Eleutherodactylus lineatus
Ameiva festiva
Barisia moreleti

Anolis cobanensis

Lepidophyma flavimaculata

Leptophis modestus

Stenorrhina degenhardti

Bothrops godmani

COMPARISION OF CLOUD FOREST HERPETOLOGICAL ASSEMBLAGES

Material used in analyses.-- Now that the herpetofauna inhabiting the cloud forest of the Sierra de las Minas has been described, an obvious question is how this assemblage compares with other cloud forests in Middle America. Comparisions of total number of species, number of shared species, and number of endemic species can provide insight into other problems such as relative times that regions may have been isolated from one another, relative effectiveness of ecological and/or physical barriers, and possible origins of faunas.

Although the cloud forests of Middle America in general have not been completely explored, I have selected 12 cloud forests that have been sampled sufficiently well to allow meaningful comparisions to be made with the Sierra de las Minas. I have indicated the distributions of 464 species of amphibians and reptiles that occur in these forests in Table 4. I have omitted from my analysis the following species:

Bufo marinus
Bufo valliceps
Smilisca baudinii
Sceloporus variabilis
Ameiva undulata
Mabuya mabouya
Sphenomorphus cherriei
Lepidophyma flavimaculata
Dryadophis melanolomus
Lampropeltis triangulum
Leptodeira annulata
Leptodeira septentrionalis
Leptophis ahaetulla
Leptophis mexicanus
Oxybelis aeneus
Oxyrhopus petola
Spilotes pullatus
Tropidodipsas sartorii
Xenodon rhabdocephalus
Bothrops asper

Even though I have taken all of these species along the lower fringes of one or more cloud forests, they range widely in the lowlands and tend not to have extensive upland distributions. Therefore, I do not consider them to be primary components of the cloud forest herpetofauna and, in any event, their inclusion or exclusion does not significantly alter my analysis owing to their wide distributions.

Analyses of the herpetofauna of the Sierra Juarez in northern Oaxaca, the Cerro Baul region in southeastern Oaxaca, and the Sierra Madre del Sur of Guerrero are based largely on my own collections, and that of the Sierra de las Minas are based almost entirely on my material. Additionally, I have examined pertinent material in the University of Kansas (KU) and the University of Texas at Arlington (UTACV) collections. I have drawn freely from published records and, although it has not been possible to check all material, I have made an attempt to verify questionable records whenever possible, and have omitted species that I consider to be of highly questionable occurrence for a particular region. In instances where a species has not been documented for a particular cloud forest, but is known from adjacent cloud forests on either side, its possible occurrence is indicated in Table 4 by a "?," and it is treated as though present in the subsequent comparative analysis.

The tracts of cloud forest and primary sources of information are (for more complete information, see Appendix II): (1) southwestern Tamaulipas (Martin, 1955a, 1955b, 1958); (2) northern Oaxaca (KU; UTACV); (3) southern Veracruz (Darling and Smith, 1954; Perez Higareda, 1978, 1980, 1981; Shannon and Werler, 1955; Werler and Smith, 1952; KU);

TABLE 4. Distribution and altitudinal ranges for the herpetofauna in selected Middle American cloud forests. 1 = southwestern Tamaulipas, México; 2 = northern Oaxaca, México; 3 = southern Veracruz, México; 4 = Sierra Madre del Sur of Guerrero, México; 5 = southeastern Oaxaca, México; 6 = northern Chiapas, México; 7 = Sierra de los Cuchumatanes, Guatemala; 8 = Alta Verapaz, Guatemala; 9 = Sierra de las Minas, Guatemala; 10 = Pacific highlands of Chiapas and Guatemala; 11 = El Salvador highlands; 12 = northwestern Honduras; 13 = eastern Costa Rica. Altitudinal limits are those described by Stuart (1963): A = low (sea level to about 600 m), B = moderate (600 m to about 1500 m), C = intermediate (1500 to about 2700 m), and D = high (>2700 m). See Appendix II for information sources.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Dermophis mexicanus	—	—	—	—	—	—	—	—	—	ABC	AB	—	B
Dermophis oaxacae	—	—	—	AB	AB	—	—	—	—	AB	—	—	—
Dermophis parviceps	—	—	—	—	—	—	—	—	—	—	—	—	AB
Gymnopis multiplicata	—	—	—	—	—	—	—	B	?	—	—	?	AB
Minascaecilia sartoria	—	—	—	—	—	—	—	—	B	—	—	—	—
Bolitoglossa alvaradoi	—	—	—	—	—	—	—	—	—	—	—	—	B
Bolitoglossa arborescandens	—	—	—	—	—	—	—	—	—	—	—	—	B
Bolitoglossa brevipes	—	—	—	—	—	—	—	—	—	C	—	—	—
Bolitoglossa cuchumatana	—	—	—	—	—	—	C	—	—	—	—	—	—
Bolitoglossa dofleini	—	—	—	—	—	—	A	AB	?	—	—	B	—
Bolitoglossa dunni	—	—	—	—	—	—	—	—	—	—	C	BC	—
Bolitoglossa engelhardti	—	—	—	—	—	—	—	—	—	C	—	—	—
Bolitoglossa epimela	—	—	—	—	—	—	—	—	—	—	—	—	BC
Bolitoglossa flavimembris	—	—	—	—	—	—	—	—	—	C	—	—	—
Bolitoglossa flaviventris	—	—	—	—	—	—	—	—	—	A	—	—	—
Bolitoglossa franklini	—	—	—	—	—	—	—	—	—	C	—	—	—
Bolitoglossa hartwegi	—	—	—	—	—	CD	—	—	—	—	—	—	—
Bolitoglossa helmrichi	—	—	—	—	—	—	—	BC	BC	—	—	—	—
Bolitoglossa lincolni	—	—	—	—	—	—	C	—	—	—	—	—	—
Bolitoglossa meliana	—	—	—	—	—	—	—	—	C	—	—	—	—
Bolitoglossa mexicana	—	—	AB	—	?	AB	A	AB	A	—	—	AB	—
Bolitoglossa morio	—	—	—	—	—	—	—	—	—	CD	—	—	—
Bolitoglossa mulleri	—	—	—	—	—	—	—	AB	—	—	—	—	—
Bolitoglossa nigroflavescens	—	—	—	—	—	—	—	—	—	C	—	—	—
Bolitoglossa occidentalis	—	BC	AB	—	B	ABC	—	—	—	BC	—	B	—
Bolitoglossa odonnelli	—	—	—	—	—	—	—	AB	A	—	—	—	—
Bolitoglossa omniumsanctorum	—	—	—	—	—	—	C	—	—	—	—	—	—
Bolitoglossa platydactyla	—	AB	AB	—	—	—	—	—	—	—	—	—	—
Bolitoglossa resplendens	—	—	—	—	—	C	—	—	—	CD	—	—	—
Bolitoglossa robusta	—	—	—	—	—	—	—	—	—	—	—	—	BC
Bolitoglossa rostrata	—	—	—	—	—	D	D	—	—	D	—	—	—
Bolitoglossa rufescens	—	AB	—	—	?	AB	AB	AB	AB	—	—	AB	—
Bolitoglossa salvini	—	—	—	—	—	—	—	—	—	B	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Bolitoglossa schmidti	—	—	—	—	—	—	—	—	—	—	—	B	—
Bolitoglossa stuarti	—	—	—	—	—	C	—	—	—	—	—	—	—
Bolitoglossa subpalmata	—	—	—	—	—	—	—	—	—	—	—	—	CD
Bolitoglossa veracrucis	—	—	—	—	A	—	—	—	—	—	—	—	—
Bolitoglossa sp. A	—	—	—	—	—	—	—	—	B	—	—	—	—
Bolitoglossa sp. B	—	—	—	—	—	—	—	—	C	—	—	—	—
Bolitoglossa sp. C	—	—	—	—	—	—	—	—	—	C	—	—	—
Chiropterotriton bromeliacia	—	—	—	—	—	—	—	—	—	C	—	—	—
C. chiropterus	—	BC	—	—	—	—	—	—	—	—	—	—	—
C. chondrostega	BC	—	—	—	—	—	—	—	—	—	—	—	—
Chiropterotriton cuchumatanus	—	—	—	—	—	—	D	—	—	—	—	—	—
Chiropterotriton diminuta	—	—	—	—	—	—	—	—	—	—	—	—	C
C. multidentatus	ABC	—	—	—	—	—	—	—	—	—	—	—	—
Chiropterotriton nasalis	—	—	—	—	—	—	—	—	—	—	—	C	—
Chiropterotriton picadoi	—	—	—	—	—	—	—	—	—	—	—	—	BC
Chiropterotriton richardi	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Chiropterotriton veraepacis	—	—	—	—	—	—	—	—	C	—	—	—	—
Chiropterotriton xolocalcae	—	—	—	—	—	—	—	—	—	C	—	—	—
Lineatriton lineola	—	B	AB	—	—	—	—	—	—	—	—	—	—
Nyctanolis pernix	—	—	—	—	—	B	B	—	C	—	—	—	—
Oedipina elongata	—	—	—	—	—	B	?	B	B	—	—	—	—
Oedipina ignea	—	—	—	—	—	—	—	—	—	B	—	—	—
Oedipina poelzi	—	—	—	—	—	—	—	—	—	—	—	—	BC
Oedipina uniformis	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Pseudoeurycea belli	BC	C	—	C	—	—	—	—	—	—	—	—	—
Pseudoeurycea brunnata	—	—	—	—	—	—	—	—	—	CD	—	—	—
Pseudoeurycea cephalica	BC	—	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea expectata	—	—	—	—	—	—	—	—	—	C	—	—	—
Pseudoeurycea goebeli	—	—	—	—	—	—	—	—	—	CD	—	—	—
Pseudoeurycea juarezi	—	CD	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea nigromaculata	—	—	C	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea rex	—	—	—	—	—	—	CD	—	—	D	—	—	—
Pseudoeurycea scandens	BC	—	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea smithi	—	D	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea werleri	—	—	B	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. A	—	CD	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. B	—	C	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. C	—	C	—	—	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. D	—	—	—	C	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. E	—	—	—	D	—	—	—	—	—	—	—	—	—
Pseudoeurycea sp. F	—	—	—	—	C	—	—	—	—	—	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Pseudoeurycea sp. G	—	—	—	—	—	BC	—	—	—	—	—	—	—
Pseudoeurycea sp. H	—	—	—	—	—	—	—	—	—	CD	—	—	—
Thorius macdougalli	—	D	—	—	—	—	—	—	—	—	—	—	—
Thorius narisovalis	—	C	—	—	—	—	—	—	—	—	—	—	—
Thorius pennatus	—	—	B	—	—	—	—	—	—	—	—	—	—
Thorius pulmonaris	—	CD	—	—	—	—	—	—	—	—	—	—	—
Thorius sp. A	—	CD	—	—	—	—	—	—	—	—	—	—	—
Thorius sp. B	—	—	—	CD	—	—	—	—	—	—	—	—	—
Eleutherodactylus altae	—	—	—	—	—	—	—	—	—	—	—	—	B
Eleutherodactylus andi	—	—	—	—	—	—	—	—	—	—	—	—	B
Eleutherodactylus angelicus	—	—	—	—	—	—	—	—	—	—	—	—	BC
E. berkenbuschii	—	ABC	AB	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus bocourti	—	—	—	—	—	—	—	B	C	—	—	—	—
Eleutherodactylus bransfordi	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Eleutherodactylus brocchi	—	—	—	—	—	—	—	B	BC	—	—	—	—
E. caryophyllaceus	—	—	—	—	—	—	—	—	—	—	—	—	B
E. crassidigitus	—	—	—	—	—	—	—	—	—	—	—	—	BC
Eleutherodactylus cruentus	—	—	—	—	—	—	—	—	—	—	—	—	BC
Eleutherodactylus cuaquero	—	—	—	—	—	—	—	—	—	—	—	—	C
Eleutherodactylus daryi	—	—	—	—	—	—	—	BC	C	—	—	—	—
Eleutherodactylus decoratus	ABC	—	—	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus diastema	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Eleutherodactylus escoces	—	—	—	—	—	—	—	—	—	—	—	—	BC
E. fitzingeri	—	—	—	—	—	—	—	—	—	—	—	—	ABC
E. fleischmanni	—	—	—	—	—	—	—	—	—	—	—	—	BC
Eleutherodactylus glaucus	—	—	—	—	—	C	—	—	—	—	—	—	—
Eleutherodactylus gollmeri	—	—	—	—	—	—	—	—	—	—	—	ABC	ABC
Eleutherodactylus greggi	—	—	—	—	—	—	—	—	—	C	—	—	—
E. guerreroensis	—	—	—	B	—	—	—	—	—	—	—	—	—
Eleutherodactylus hylaeformis	—	—	—	—	—	—	—	—	—	—	—	—	C
Eleutherodactylus lineatus	—	—	—	—	—	C	C	BC	BC	C	—	—	—
Eleutherodactylus loki	—	—	AB	—	—	—	—	—	—	—	—	—	—
E. macdougalli	—	—	—	—	AB	—	—	—	—	—	—	—	—
Eleutherodactylus matudai	—	—	—	—	—	—	—	—	—	C	—	—	—
E. megalotympanum	—	—	B	—	—	—	—	—	—	—	—	—	—
E. melanostictus	—	—	—	—	—	—	—	—	—	—	—	—	BC
Eleutherodactylus mexicanus	—	BC	—	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus milesi	—	—	—	—	—	—	—	—	AB	—	—	BC	—
Eleutherodactylus moro	—	—	—	—	—	—	—	—	—	—	—	—	B
E. omiltemanus	—	—	—	C	—	—	—	—	—	—	—	—	—
Eleutherodactylus podiciferus	—	—	—	—	—	—	—	—	—	—	—	—	BC

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Eleutherodactylus pygmaeus	—	—	B	BC	B	—	—	—	—	C	—	—	—
Eleutherodactylus rhodopis	—	—	BC	—	AB	—	—	—	—	BC	B	—	—
Eleutherodactylus ridens	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Eleutherodactylus rostralis	—	—	—	—	—	AB	AB	AB	AB	—	—	—	—
Eleutherodactylus rugulosus	—	—	—	BC	AB	ABC	AB	AB	AB	ABC	ABC	ABC	AB
Eleutherodactylus saltator	—	—	—	C	—	—	—	—	—	—	—	—	—
Eleutherodactylus sartori	—	—	—	—	—	—	—	—	—	C	—	—	—
Eleutherodactylus silvicola	—	—	—	—	B	—	—	—	—	—	—	—	—
Eleutherodactylus spatulatus	—	BC	—	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus stuarti	—	—	—	—	—	BC	—	—	—	—	—	—	—
Eleutherodactylus talamancae	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Eleutherodactylus taylori	—	—	—	—	—	C	—	—	—	—	—	—	—
Eleutherodactylus werleri	—	BC	B	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus xucanebi	—	—	—	—	—	—	—	B	C	—	—	—	—
Eleutherodactylus sp. A	—	—	—	C	—	—	—	—	—	—	—	—	—
Eleutherodactylus sp. B	—	—	—	—	—	B	—	—	—	—	—	—	—
Eleutherodactylus sp. C	—	—	—	—	—	B	—	—	—	—	—	—	—
Eleutherodactylus sp. D	—	—	—	—	—	—	BC	—	—	—	—	—	—
Eleutherodactylus sp. E	—	—	—	—	—	—	—	B	—	—	—	—	—
Eleutherodactylus sp. F	—	—	—	—	—	—	—	—	C	—	—	—	—
Eleutherodactylus sp. G	—	—	—	—	—	—	—	—	AB	—	—	—	—
Syrrhophus cystignathoides	AB	—	—	—	—	—	—	—	—	—	—	—	—
Syrrhopus leprus	—	AB	AB	—	AB	?	?	A	—	—	—	—	—
Syrrhophus longipes	ABC	—	—	—	—	—	—	—	—	—	—	—	—
Syrrhopus pipilans	—	—	—	ABC	—	ABC	—	—	—	—	—	—	—
Syrrhopus rubrimaculatus	—	—	—	—	—	—	—	—	—	AB	—	—	—
Tomodactylus dilatus	—	—	—	C	—	—	—	—	—	—	—	—	—
Atelopus senex	—	—	—	—	—	—	—	—	—	—	—	—	C
Atelopus varius	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Bufo bocourti	—	—	—	—	—	CD	CD	—	—	CD	—	—	—
Bufo coccifer	—	—	—	—	—	—	—	—	BC	C	ABC	—	AB
Bufo cavifrons	—	BC	B	—	ABC	C	—	—	—	—	—	—	—
Bufo holdridgei	—	—	—	—	—	—	—	—	—	—	—	—	C
Bufo occidentalis	—	BC	—	BC	—	—	—	—	—	—	—	—	—
Bufo periglenes	—	—	—	—	—	—	—	—	—	—	—	—	BC
Bufo tacanensis	—	—	—	—	—	—	—	—	—	BC	—	—	—
Agalychnis annae	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Agalychnis moreleti	—	BC	B	B	?	B	B	B	ABC	BC	BC	B	—
Anotheca spinosa	—	BC	B	—	?	B	—	—	—	—	—	—	AB
Hyla angustilineata	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla arborescandens	—	C	—	—	—	—	—	—	—	—	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Hyla bromeliacea	—	—	—	—	—	—	B	B	C	—	—	BC	—
Hyla chaneque	—	BC	BC	—	C	C	—	—	—	—	—	—	—
Hyla chryses	—	—	—	C	—	—	—	—	—	—	—	—	—
Hyla colymba	—	—	—	—	—	—	—	—	—	—	—	—	B
Hyla crassa	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla cyanomma	—	CD	—	—	—	—	—	—	—	—	—	—	—
Hyla debelis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla dendroscarta	—	C	BC	—	—	—	—	—	—	—	—	—	—
Hyla echinata	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla erythromma	—	B	—	B	—	—	—	—	—	—	—	—	—
Hyla fimbrimembra	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla hazelae	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla juanitae	—	—	—	B	—	—	—	—	—	—	—	—	—
Hyla lancasteri	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Hyla melanomma	—	—	—	BC	—	C	—	—	—	—	—	—	—
Hyla miliaria	—	—	—	—	—	—	—	—	—	—	—	—	B
Hyla miotympanum	ABC	—	ABC	—	—	B	—	—	—	—	—	—	—
Hyla mixe	—	BC	—	—	—	—	—	—	—	—	—	—	—
Hyla mykter	—	—	—	CD	—	—	—	—	—	—	—	—	—
Hyla pentheter	—	C	—	C	—	—	—	—	—	—	—	—	—
Hyla picadoi	—	—	—	—	—	—	—	—	—	—	—	—	CD
Hyla pictipes	—	—	—	—	—	—	—	—	—	—	—	—	CD
Hyla pinorum	—	—	—	B	—	—	—	—	—	—	—	—	—
Hyla pseudopuma	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla rivularis	—	—	—	—	—	—	—	—	—	—	—	—	BCD
Hyla rufioculis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla sabrina	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla salvadorensis	—	—	—	—	—	—	—	—	—	—	BC	—	—
Hyla siopela	—	CD	—	—	—	—	—	—	—	—	—	—	—
Hyla thorectes	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla tica	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla trux	—	—	—	C	—	—	—	—	—	—	—	—	—
Hyla uranochroa	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla valancifer	—	—	AB	—	?	?	?	?	BC	—	—	—	—
Hyla xanthosticta	—	—	—	—	—	—	—	—	—	—	—	—	C
Hyla zeteki	—	—	—	—	—	—	—	—	—	—	—	—	BC
Hyla sp. A	—	C	—	—	—	—	—	—	—	—	—	—	—
Hyla sp. B	—	—	—	C	—	—	—	—	—	—	—	—	—
Phyllomedusa lemur	—	—	—	—	—	—	—	—	—	—	—	—	BC
Plectrohyla avia	—	—	—	—	—	—	—	—	—	C	—	—	—
Plectrohyla dasypus	—	—	—	—	—	—	—	—	—	—	—	C	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Plectrohyla glandulosa	—	—	—	—	—	—	D	—	—	CD	C	—	—
Plectrohyla guatemalensis	—	—	—	—	—	C	C	B	C	C	CD	C	—
Plectrohyla hartwegi	—	—	—	—	BC	—	BC	B	BC	BC	—	C	—
Plectrohyla ixil	—	—	—	—	—	C	B	—	—	—	—	—	—
Plectrohyla lacertosa	—	—	—	—	—	—	—	—	—	C?	—	—	—
Plectrohyla matudai	—	—	—	—	C	—	—	—	—	BC	—	B	—
Plectrohyla pycnochila	—	—	—	—	—	C	—	—	—	—	—	—	—
Plectrohyla quecchi	—	—	—	—	—	—	BC	B	BC	—	—	—	—
Plectrohyla sagorum	—	—	—	—	—	—	—	—	—	C	C	—	—
Plectrohyla sp.	—	—	—	—	—	—	D	—	—	—	—	—	—
Ptychohyla chamulae	—	—	—	—	B	C	—	—	—	—	—	—	—
Ptychohyla euthysanota	—	—	—	—	ABC	C	—	—	—	B	BC	—	—
Ptychohyla ignicolor	—	BC	—	—	—	—	—	—	—	—	—	—	—
Ptychohyla leonhardschultzei	—	BC	—	B	—	—	—	—	—	—	—	—	—
Ptychohyla panchoi	—	—	—	—	—	—	—	—	B	—	—	—	—
Ptychohyla schmidtorum	—	—	—	—	—	—	—	—	—	BC	—	—	—
Ptychohyla spinipollex	—	—	—	—	—	—	C	B	BC	BC	—	BC	—
Smilisca cyanosticta	—	B	AB	—	?	B	AB	A	B	—	—	—	—
Smilisca phaeota	—	—	—	—	—	—	—	—	—	—	—	—	AB
Centrolenella colymbiphyllum	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Centrolenella euknemos	—	—	—	—	—	—	—	—	—	—	—	—	BC
Centrolenella fleischmanni	—	AB	A	B	B	A	B	AB	ABC	B	C	AB	ABC
Centrolenella prosoblepon	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Centrolenella valerioi	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Glossostoma aterrimum	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Hypopachus barberi	—	—	—	—	—	CD	C	B	BC	BC	C	—	—
Rana berlandieri	ABC	—	AB	—	—	—	—	—	—	—	—	—	—
Rana maculata	—	—	—	—	C	C	BC	B	ABC	B	BC	ABC	—
Rana omiltemana	—	—	—	C	—	—	—	—	—	—	—	—	—
Rana vibicaria	—	—	—	—	—	—	—	—	—	—	—	—	C
Rana warschewitschi	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Rana sp. A	—	BC	—	—	—	—	—	—	—	—	—	—	—
Rana sp. B	—	—	—	—	—	C	—	—	—	—	—	—	—
Rana sp. C	—	—	—	—	—	—	BC	—	—	—	—	—	—
Rana sp. D	—	—	—	—	—	—	—	AB	ABC	—	—	—	—
Rana sp. E	—	—	—	—	—	—	—	—	—	BC	BC	ABC	—
Rana sp. F	—	—	—	—	—	—	—	—	—	—	—	—	C
Anolis altae	—	—	—	—	—	—	—	—	—	—	—	—	C
Anolis anisolepis	—	—	—	—	—	C	—	—	—	—	—	—	—
Anolis barkeri	—	—	A	—	AB	AB	—	—	—	—	—	—	—
Anolis biporcatus	—	B	?	—	AB	AB	AB	A	AB	—	—	AB	AB

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Anolis bradlovei	—	—	—	—	B	C	—	—	—	—	—	—	—
Anolis cobanensis	—	—	—	—	—	BC	?	B	BC	—	—	—	—
Anolis compressicaudus	—	—	—	—	AB	AB	—	—	—	—	—	—	—
Anolis crassulus	—	—	—	—	—	C	C	—	—	C	C	—	—
Anolis cupreus	—	—	—	—	—	—	—	—	—	AB	AB	—	AB
Anolis cuprinus	—	—	—	—	AB	—	—	—	—	—	—	—	—
Anolis damulus	—	BC	—	—	—	—	—	—	—	—	—	—	—
Anolis dollfusianus	—	—	—	—	—	—	—	—	—	AB	—	—	—
Anolis duellmani	—	—	B	—	—	—	—	—	—	—	—	—	—
Anolis dunni	—	—	—	B	—	—	—	—	—	—	—	—	—
Anolis godmani	—	—	—	—	—	—	—	—	—	—	—	—	BC
Anolis haguei	—	—	—	—	—	—	—	B	BC	—	—	—	—
Anolis heteropholidotus	—	—	—	—	—	—	—	—	—	—	C	—	—
Anolis humilis	—	—	—	—	—	AB	AB	A	AB	—	—	B	ABC
Anolis insignis	—	—	—	—	—	—	—	—	—	—	—	—	AB
Anolis intermedius	—	—	—	—	—	—	—	—	—	—	—	—	BC
Anolis laeviventris	—	—	AB	—	—	C	C	B	—	BC	—	—	—
Anolis limifrons	—	—	—	—	AB	AB	AB	AB	AB	—	—	AB	AB
Anolis liogaster	—	—	—	C	—	—	—	—	—	—	—	—	—
Anolis lionotus	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Anolis macudai	—	—	—	—	—	—	—	—	—	B?	—	—	—
Anolis megapholidotus	—	—	—	B	—	—	—	—	—	—	—	—	—
Anolis microtus	—	—	—	—	—	—	—	—	—	—	—	—	B
Anolis milleri	—	B	—	—	—	—	—	—	—	—	—	—	—
Anolis omiltemanus	—	—	—	C	—	—	—	—	—	—	—	—	—
Anolis pachypus	—	—	—	—	—	—	—	—	—	—	—	—	C
Anolisparvicirculatus	—	—	—	—	—	B	—	—	—	—	—	—	—
Anolis petersi	—	BC	BC	—	C	B	B	B	C	B	—	—	—
Anolis polyrhachis	—	C	—	—	—	—	—	—	—	—	—	—	—
Anolis pygmaeus	—	—	—	—	AB	AB	—	—	—	—	—	—	—
Anolis subocularis	—	—	—	AB	—	—	—	—	—	—	—	—	—
Anolis tropidolepis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Anolis tropidonotus	—	—	AB	—	B	B	—	—	—	—	—	ABC	—
Anolis woodi	—	—	—	—	—	—	—	—	—	—	—	—	BC
Corytophanes cristatus	—	—	—	—	—	AB	AB	AB	AB	—	—	AB	AB
Corytophanes hernandezi	—	B	AB	—	—	AB	—	—	—	—	—	B	—
Corytophanes percarinatus	—	—	—	—	BC	—	BC	B	C	BC	C	—	—
Polychrus gutterosus	—	—	—	—	—	—	—	—	—	—	—	—	AB
Sceloporus acanthinus	—	—	—	—	B	—	—	—	BC	BC	B	—	—
Sceloporus adleri	—	—	—	CD	—	—	—	—	—	—	—	—	—
Sceloporus cyanogenys	B	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Sceloporus formosus	—	BC	AB?	CD	—	—	—	—	—	—	—	—	—
Sceloporus grammicus	—	CD	—	CD	—	—	—	—	—	—	—	—	—
Sceloporus hartwegi	—	—	—	—	—	CD	—	—	—	—	—	—	—
Sceloporus internasalis	—	—	—	—	AB	AB	—	—	—	BCD	—	—	—
Sceloporus malachiticus	—	—	—	—	—	—	—	—	—	—	BC	BC	BCD
Sceloporus mucronatus	—	C	—	C	—	—	—	—	—	—	—	—	—
Sceloporus prezygus	—	—	—	—	—	BC	—	—	—	—	—	—	—
Sceloporus smaragdinus	—	—	—	—	—	—	CD	—	C	BCD	—	—	—
Sceloporus taeniocnemis	—	—	—	—	—	—	BC	BC	BC	—	—	—	—
Ameiva festiva	—	—	—	—	—	A	AB	AB	AB	—	—	AB	AB
Anadia ocellata	—	—	—	—	—	—	—	—	—	—	—	—	B
Ptychoglossus plicatus	—	—	—	—	—	—	—	—	—	—	—	—	BC
Lepidophyma pajapanensis	—	—	B	—	—	—	—	—	—	—	—	—	—
Lepidophyma sawini	—	BC	—	—	—	—	—	—	—	—	—	—	—
Lepidophyma tuxtlae	—	C	AB	—	—	—	—	—	—	—	—	—	—
Eumeces dicei	ABC	—	—	—	—	—	—	—	—	—	—	—	—
Eumeces ochoterenae	—	—	—	BCD	—	—	—	—	—	—	—	—	—
Scincella gemmingeri	—	BC	BC	—	BC	—	—	—	—	—	—	—	—
Scincella silvicola	—	—	B	—	—	—	—	—	—	—	—	—	—
Sphenomorphus assatum	—	—	—	—	B	C	—	—	—	AB	B	—	—
Sphenomorphus incertum	—	—	—	—	—	C	?	B	C	BC	—	—	—
Abronia aurita	—	—	—	—	—	—	—	C?	C	—	—	—	—
Abronia bogerti	—	—	—	—	B	—	—	—	—	—	—	—	—
Abronia chiszari	—	—	A?	—	—	—	—	—	—	—	—	—	—
Abronia deppei	—	—	—	CD	—	—	—	—	—	—	—	—	—
Abronia fimbriata	—	—	—	—	—	—	—	C?	C	—	—	—	—
Abronia fuscolabialis	—	C	—	—	—	—	—	—	—	—	—	—	—
Abronia lythrochila	—	—	—	—	—	C	—	—	—	—	—	—	—
Abronia matudai	—	—	—	—	—	—	—	—	—	C	—	—	—
Abronia mitchelli	—	D	—	—	—	—	—	—	—	—	—	—	—
Abronia ochoterenai	—	—	—	—	—	—	C	—	—	—	—	—	—
Abronia reidi	—	—	C	—	—	—	—	—	—	—	—	—	—
Abronia taeniata	BC	—	—	—	—	—	—	—	—	—	—	—	—
Abronia vasconcelosi	—	—	—	—	—	—	—	—	—	C	—	—	—
Abronia sp. A	—	—	—	—	C	—	—	—	—	—	—	—	—
Abronia sp. B	—	—	—	—	—	—	—	—	—	—	C	—	—
Abronia sp. C	—	—	—	—	—	—	—	—	—	—	C	—	—
Abronia sp. D	—	—	—	—	—	—	—	—	—	—	—	C	—
Barisia gadovi	—	C	—	CD	—	—	—	—	—	—	—	—	—
Barisia monticola	—	—	—	—	—	—	—	—	—	—	—	—	CD
Barisia moreleti	—	—	—	—	—	CD	C	B	C	CD	C	?	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Barisia viridiflava	—	CD	—	—	—	—	—	—	—	—	—	—	—
Barisia sp.	—	C	—	—	—	—	—	—	—	—	—	—	—
Celestus atitlanensis	—	—	—	—	—	—	—	—	—	BC	B	—	—
Celestus cyanochloris	—	—	—	—	—	—	—	—	—	—	—	—	BC
Celestus enneagrammus	—	C	C	—	—	—	—	—	—	—	—	—	—
Celestus montanus	—	—	—	—	—	—	—	—	—	—	—	B	—
Celestus rozellae	—	—	—	—	AB	AB	AB	A	AB	—	—	—	—
Diploglossus bilobatus	—	—	—	—	—	—	—	—	—	—	—	—	BC
Diploglossus monotropis	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Gerrhonotus liocephalus	ABC	C	BC	BC	C	BC	—	—	—	D	—	—	—
Xenosaurus grandis	—	BC	BC	—	BC	BC	?	B	—	—	—	—	—
Leptotyphlops goudoti	—	?	A	—	B	?	AB	B	BC	B	?	AB	—
Typhlops costaricensis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Typhlops tenuis	—	BC	A	—	?	?	?	B	BC	—	—	—	—
Exiliboa placata	—	C	—	—	—	—	—	—	—	—	—	—	—
Adelphicos daryi	—	—	—	—	—	—	—	—	—	C	—	—	—
Adelphicos latifasciatus	—	—	—	—	C	—	—	—	—	—	—	—	—
Adelphicos nigrilatus	—	—	—	—	—	C	—	—	—	—	—	—	—
Adelphicos quadrivirgatus	—	B	AB	—	AB	AB	AB	B	AB	B	—	AB	—
Adelphicos veraepacis	—	—	—	—	—	—	BC	BC	BC	—	—	—	—
Adelphicos sp.	—	—	—	—	—	—	—	—	—	C	—	—	—
Amastridium veliferum	B	?	AB	—	?	?	?	A	AB	B	—	?	AB
Chironius carinatus	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Chironius grandisquamus	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Clelia scytalina	—	—	—	—	—	—	—	—	—	AB	—	—	ABC
Coluber constrictor	—	—	—	—	—	—	—	—	AB	—	—	—	—
Coniophanes fissidens	—	?	AB	—	AB	ABC	AB	A	AB	ABC	AB	AB	AB
Cryophis hallbergi	—	BC	—	—	—	—	—	—	—	—	—	—	—
Dendrophidion paucicarinatum	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Dendrophidion percarinatum	—	—	—	—	—	—	—	—	—	—	—	AB	AB
Dendrophidion vinitor	—	—	AB	—	?	AB	AB	AB	AB	—	—	—	—
Dryadophis dorsalis	—	—	—	—	B	—	B	—	BC	BC	B	—	—
Drymobius chloroticus	—	C	B	—	BC	—	—	BC	BC	BC	C	BC	—
Drymobius melanotropis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Enulius flavitorques	—	—	—	—	—	—	—	—	—	AB	B	B	—
Erythrolamprus bizonus	—	—	—	—	—	—	—	—	—	—	—	—	AB
Geophis anocularis	—	C	—	—	—	—	—	—	—	—	—	—	—
Geophis brachycephalus	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Geophis cancellatus	—	—	—	—	—	—	—	—	—	B	—	—	—
Geophis carinosus	—	—	B	—	?	BC	B	—	—	—	—	—	—
Geophis duellmani	—	C	—	—	—	—	—	—	—	—	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Geophis fulvoguttatus	—	—	—	—	—	—	—	—	—	—	C	—	—
Geophis godmani	—	—	—	—	—	—	—	—	—	—	—	—	BC
Geophis hoffmani	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Geophis immaculatus	—	—	—	—	—	—	—	—	—	C	—	—	—
Geophis laticinctus	—	B	?	—	B	BC	—	—	—	—	—	—	—
Geophis nasalis	—	—	—	—	—	—	—	—	—	BC	—	—	—
Geophis omiltemanus	—	—	—	C	—	—	—	—	—	—	—	—	—
Geophis rhodogaster	—	—	—	—	—	—	—	—	—	C	C	—	—
Geophis ruthveni	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Geophis semiannulatus	BC	—	—	—	—	—	—	—	—	—	—	—	—
Geophis sieboldi	—	—	—	C	—	—	—	—	—	—	—	—	—
Geophis zaldoni	—	—	—	—	—	—	—	—	—	—	—	—	C
Geophis sp.	—	—	—	—	C	—	—	—	—	—	—	—	—
Hydromorphus concolor	—	—	—	—	—	—	—	—	AB	—	—	AB	AB
Imantodes cenchoa	—	AB	AB	—	AB	AB	AB	AB	ABC	BC	—	AB	ABC
Imantodes inornatus	—	—	—	—	—	—	—	—	—	—	—	—	AB
Leimadophis epinephalus	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Leptodrymus pulcherrimus	—	—	—	—	—	—	—	—	AB	—	B	AB	AB
Leptophis modestus	—	—	—	—	—	B	C	?	C	?	C	—	—
Ninia atrata	—	—	—	—	—	—	—	—	—	—	C	—	BC
Ninia diademata	—	BC	AB	—	B	BC	B	B	BC	BC	—	AB	—
Ninia maculata	—	—	—	—	—	—	—	B	BC	—	—	?	ABC
Ninia psephota	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Ninia sebae	—	AB	AB	—	AB	ABC	BC	AB	ABC	ABC	AB	ABC	AB
Oxybelis fulgidus	—	—	—	—	?	AB	AB	AB	AB	AB	—	AB	AB
Pituophis lineaticollis	—	?	—	BC	BC	C	C	—	—	BC	—	—	—
Pliocercus elapoides	B	B	AB	—	BC	C	B	AB	BC	BC	B	AB	—
Pliocercus euryzonus	—	—	—	—	—	—	—	B	B?	—	—	?	ABC
Pseustes poecilonotus	—	B	A	—	?	AB	B	A	AB	—	—	?	ABC
Rhadinaea bogertorum	—	CD	—	—	—	—	—	—	—	—	—	—	—
Rhadinaea calligaster	—	—	—	—	—	—	—	—	—	—	—	—	BC
Rhadinaea decipiens	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Rhadinaea gaigeae	BC	—	—	—	—	—	—	—	—	—	—	—	—
Rhadinaea godmani	—	—	—	—	C	C	BC	—	C	C	C	?	BC
Rhadinaea guentheri	—	—	—	—	—	—	—	—	—	—	—	—	AB
Rhadinaea hannsteini	—	—	—	—	—	—	—	—	—	B	—	—	—
Rhadinaea hempsteadae	—	—	—	—	—	C	C	BC	C	—	—	—	—
Rhadinaea hesperia	—	—	—	BC	—	—	—	—	—	—	—	—	—
Rhadinaea kinkelini	—	—	—	—	—	—	—	C	BC	—	C	?	—
Rhadinaea lachrymans	—	—	—	—	—	—	—	—	—	BC	—	—	—
Rhadinaea macdougalli	—	—	—	—	B	—	—	—	—	—	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Rhadinaea montecristi	—	—	—	—	—	—	—	—	—	—	C	—	—
Rhadinaea omiltemana	—	—	—	C	—	—	—	—	—	—	—	—	—
Rhadinaea pacyura	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Rhadinaea pinicola	—	—	—	—	—	—	—	—	—	—	BC	—	—
Rhadinaea posadasi	—	—	—	—	—	—	—	—	—	B	B	—	—
Rhadinaea pulveriventris	—	—	—	—	—	—	—	—	—	—	—	—	BC
Rhadinaea serperaster	—	—	—	—	—	—	—	—	—	—	—	—	BC
Rhadinaea taeniata	—	—	—	C	—	—	—	—	—	—	—	—	—
Rhadinophanes monticola	—	—	—	D	—	—	—	—	—	—	—	—	—
Scaphiodontophis annulatus	—	—	—	—	—	—	AB	B	AB	—	—	AB	—
Scaphiodontophis zeteki	—	—	—	—	—	—	—	—	—	B	—	—	—
Sibon annulata	—	—	—	—	—	—	—	—	—	—	—	—	AB
Sibon dimidiata	—	BC	?	—	?	AB	?	A	B	AB	—	BC	B
Stenorrhina degenhardti	—	B	AB	—	BC	BC	AB	B	ABC	—	—	AB	AB
Storeria dekayi	—	—	—	—	—	—	—	B	BC	—	—	?	—
Storeria occitomaculata	BC	—	—	—	—	—	—	—	—	—	—	—	—
Tantalophis discolor	—	CD	—	—	—	—	—	—	—	—	—	—	—
Tantilla armillata	—	—	—	—	—	—	—	—	—	—	—	—	AB
Tantilla bairdi	—	—	—	—	—	—	—	C	C	—	—	—	—
Tantilla brevicauda	—	—	—	—	—	—	—	—	—	C	BC	—	—
Tantilla jani	—	—	—	—	AB	—	—	—	—	AB	—	—	—
Tantilla mexicana	—	—	—	—	—	—	—	—	—	B	—	—	—
Tantilla reticulata	—	—	—	—	—	—	—	—	—	—	—	—	AB
Tantilla rubra	AB	—	—	—	—	—	—	—	—	—	—	—	—
Tantilla schistosa	—	B	A	—	?	?	B	AB	AB	—	—	?	ABC
Tantilla taeniata	—	AB	?	—	AB	?	?	?	AB	—	—	AB	—
Thamnophis chrysocephalus	—	BC	—	C	—	—	—	—	—	—	—	—	—
Thamnophis cyrtopsis	C	?	—	BC	—	—	—	—	—	—	—	—	—
Thamnophis fulvus	—	—	—	—	?	CD	CD	B	BC	BC	C	—	—
Thamnophis mendax	BC	—	—	—	—	—	—	—	—	—	—	—	—
Thamnophis scalaris	—	CD	—	CD	—	—	—	—	—	—	—	—	—
Toluca conica	—	CD	—	C	—	—	—	—	—	—	—	—	—
Trimetopon gracile	—	—	—	—	—	—	—	—	—	—	—	—	BC
Trimetopon pliolepis	—	—	—	—	—	—	—	—	—	—	—	—	ABC
Trimetopon slevini	—	—	—	—	—	—	—	—	—	—	—	—	C
Tropidodipsas fischeri	—	—	—	—	C	—	CD	—	—	C	C	—	—
Tropidodipsas kidderi	—	—	—	—	—	—	—	BC	C	—	—	—	—
Micrurus browni	—	—	—	BC	BC	ABC	—	—	—	BC	—	—	—
Micrurus diastema	—	AB	AB	—	AB	AB	B	AB	AB	—	—	AB	—
Micrurus elegans	—	BC	AB	—	BC	AB	B	B	BC	—	—	—	—
Micrurus latifasciatus	—	—	—	—	—	—	—	—	—	BC	—	—	—

TABLE 4 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
Micrurus limbatus	—	—	AB	—	—	—	—	—	—	—	—	—	—
Micrurus mipartitus	—	—	—	—	—	—	—	—	—	—	—	—	AB
Micrurus nigrocinctus	—	—	—	—	BC	—	—	—	—	ABC	AB	AB	AB
Micrurus nuchalis	—	—	—	—	AB	—	—	—	—	—	—	—	—
Micrurus stuarti	—	—	—	—	—	—	—	—	—	B	—	—	—
Bothriechis aurifer	—	—	—	—	—	—	BC	B	BC	—	—	—	—
Bothriechis bicolor	—	—	—	—	—	—	—	—	—	ABC	C	—	—
Bothriechis lateralis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Bothriechis marchi	—	—	—	—	—	—	—	—	—	—	—	ABC	—
Bothriechis nigroviridis	—	—	—	—	—	—	—	—	—	—	—	—	BC
Bothriechis rowleyi	—	—	—	—	BC	BC	—	—	—	—	—	—	—
Bothriechis schlegeli	—	—	—	—	—	B	B	AB	AB	—	—	AB	ABC
Bothrops barbouri	—	—	—	CD	—	—	—	—	—	—	—	—	—
Bothrops godmani	—	—	—	—	C	C	CD	B	C	CD	C	BC	BC
Bothrops nummifer	—	B	AB	—	BC	ABC	AB	AB	ABC	B	BC	AB	AB
Bothrops picadoi	—	—	—	—	—	—	—	—	—	—	—	—	AB
Bothrops undulatus	—	C	—	C	—	—	—	—	—	—	—	—	—
Crotalus durissus	BC	—	—	—	—	—	—	—	—	—	—	—	—
Crotalus intermedius	—	D	—	CD	—	—	—	—	—	—	—	—	—
Crotalus lepidus	BC	—	—	—	—	—	—	—	—	—	—	—	—
Sistrurus ravus	—	C	—	C	—	—	—	—	—	—	—	—	—
Caecilians	-	-	-	1	1	-	-	1	2	2	1	1	3
Salamanders	5	15	7	4	5	10	11	7	11	20	1	7	10
Anurans	5	28	17	22	18	28	21	21	24	26	13	13	53
Lizards	4	20	17	13	20	27	17	17	17	17	11	10	23
Snakes	10	33	22	16	36	31	32	34	39	39	24	32	50
TOTAL	24	96	63	56	80	96	81	80	93	104	50	63	139

(4) Sierra Madre del Sur of Guerrero (Davis and Dixon, 1959, 1961, 1965; KU; UTACV); (5) southeastern Oaxaca (Lynch and Smith, 1965a, 1966; UTACV); (6) northern Chiapas (Alvarez del Toro, 1972; Johnson et al., 1976; KU); (7) Sierra de los Cuchumatanes (Stuart, 1943, 1963; KU); (8) Alta Verapaz (Stuart, 1948, 1950; KU; UTACV); (9) Sierra de las Minas (KU; UTACV); (10) Pacific highlands of Chiapas and Guatemala (Stuart, 1963; KU; USAC; UTACV); (11) El Salvador highlands (Mertens, 1952; Rand, 1957; Uzzell and Starrett, 1958; KU); (12) northwestern Honduras (Meyer, 1969; Meyer and Wilson, 1971); (13) eastern Costa Rica (Savage, 1980a; Scott, 1969; Taylor, 1951a, 1952a, 1952b, 1953, 1954; KU).

Comparison of cloud forest similarity coefficients.-- A number of similarity coefficients have been proposed. Simpson (1960) and Cheetham and Hazel (1969) summarized most of the similarity coefficients available for binary data that may be used for the calculation of various measures of faunal resemblance. Biogeographers traditionally have employed the similarity coefficients between two samples as the primary elements in more detailed analyses. Baroni-Urbani and Buser (1976) pointed out that similarity for binary data may be affected by five possible parameters: A, the number of attributes in common between two samples; B, the number of attributes present in the first but not the second; C, those present in the second but not the first; D, the number of attributes absent in both samples compared but present in others; and N, the total number of attributes. Since N represents the sum of all the attributes (A+B+C+D), any function taking this parameter into account while ignoring some of the others will incompletely express similarity. I have used the Baroni-Urbani and Buser coefficient as it seems to more properly evaluate the four basic parameters affecting similarity than other available coefficients. A new similarity coefficient suggested by Baroni-Urbani and Buser (1976) is:

$$S = \frac{\sqrt{AD} + A}{\sqrt{AD} + B + C}$$

I have calculated the Baroni-Urbani and Buser coefficient for all possible pairs of the 13 major cloud forests in Middle America (Table 5), and used these coefficients for construction of a phenogram and prim network of the various regions (for program used to obtain these coefficients, consult Appendix III). Further, I have ranked them in the method suggested by Peters (1971) for biogeographic analysis.

Examination of the similarity coefficients in Table 5 reveals that the values of the two regions located at either extreme of the area under consideration, southwestern Tamaulipas and eastern Costa Rica, are significantly different ($P<0.001$). This is not especially astonishing because of the considerable hiates between these regions and the most proximate cloud forests. Similarly, the cloud forest herpetofauna of the Sierra Madre del Sur in Guerrero, the northernmost terminus of cloud forest on the Pacific, differs significantly ($P<0.001$) from all other cloud forests compared except for northern Oaxaca. Other trends obvious from Table 5 are that the cloud forests fringing the northern highlands of Nuclear Central America and, to a lesser degree, the Sierra de los Tuxtlas share a large number of species and therefore have correspondingly high similarity coefficients, and that the assemblages along the Pacific versant of Chiapas, Guatemala, and El Salvador have little in common with any of the cloud forests west of the Isthmus

TABLE 5. Comparison of herpetofaunal assemblages of 13 Middle American cloud forests. The diagonal from upper left to lower right shows the number of species occurring in each The number of species shared between any two regions are indicated above the diagonal; the similarity coefficient of Baroni-Urbani and Buser (1976) is given below. Shaded values are highly significant (P<0.001).

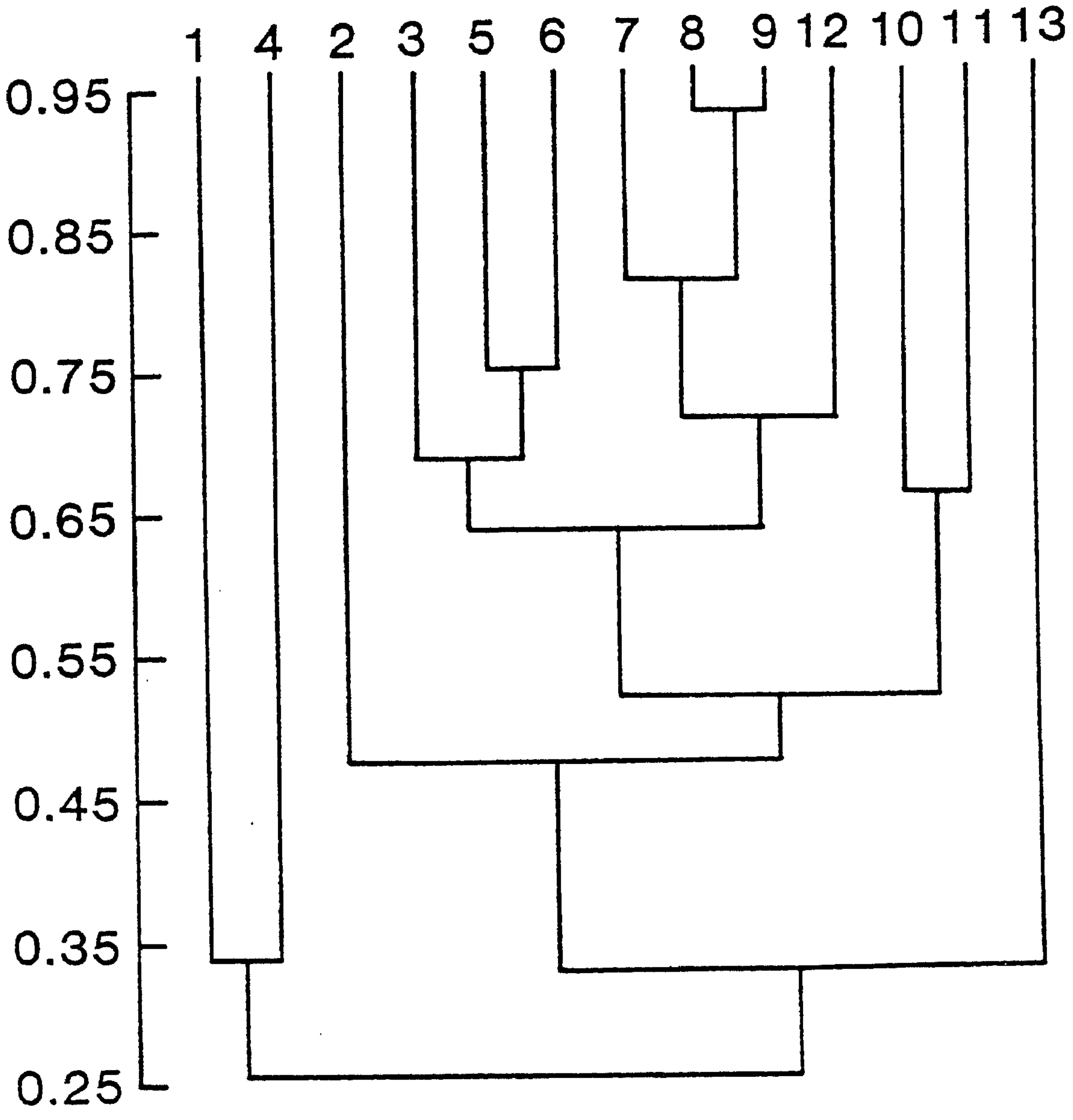
		Southwestern Tamaulipas (1)	Northern Oaxaca (2)	Southern Veracruz (3)	Sierra Madre del Sur of Guerrero (4)	Southeastern Oaxaca (5)	Northern Chiapas (6)	Sierra de los Cuchumatanes (7)	Alta Verapaz (8)	Sierra de las Minas (9)	Pacific highlands of Chiapas and Guatemala (10)	El Salvador highlands (11)	Northwestern Honduras (12)	Eastern Costa Rica (13)
Southwestern Tamaulipas	(1)	24	5	5	3	3	4	2	2	2	3	1	2	1
Northern Oaxaca	(2)	0.298	96	41	20	34	33	26	26	24	17	8	22	12
Southern Veracruz	(3)	0.387	0.675	63	5	40	39	29	29	26	19	9	23	12
Sierra Madre del Sur of Guerrero	(4)	0.334	0.475	0.301	56	8	8	4	3	3	8	3	3	2
Southeastern Oaxaca	(5)	0.269	0.562	0.718	0.333	80	56	43	39	40	39	22	33	18
Northern Chiapas	(6)	0.269	0.514	0.657	0.301	0.753	96	58	50	49	37	19	35	21
Sierra de los Cuchumatanes	(7)	0.222	0.482	0.601	0.238	0.687	0.766	81	60	61	38	21	37	20
Alta Verapaz	(8)	0.224	0.484	0.604	0.210	0.654	0.703	0.835	80	75	29	18	42	22
Sierra de las Minas	(9)	0.201	0.435	0.534	0.192	0.625	0.658	0.799	0.913	93	33	23	46	26
Pacific Highlands of Chiapas and Guatemala	(10)	0.222	0.342	0.428	0.287	0.587	0.531	0.575	0.495	0.503	104	38	27	16
El Salvador Highlands	(11)	0.224	0.312	0.410	0.264	0.562	0.478	0.546	0.509	0.536	0.662	50	21	14
Northwestern Honduras	(12)	0.262	0.482	0.588	0.238	0.647	0.618	0.685	0.737	0.731	0.516	0.606	63	29
Eastern Costa Rica	(13)	0.102	0.236	0.279	0.116	0.320	0.325	0.338	0.359	0.373	0.268	0.324	0.454	139

of Tehuantepec.

The resemblances of the various cloud forest herpetofaunas to one another becomes more apparent through cluster analysis using similarity coefficients. Inspection of the phenogram (Fig. 5) reveals several major clusters. Regions 8 and 9 have highly similar herpetofaunas, sharing 75 of a total of 98 (77%) species. These regions in turn cluster with regions 7 then 12. Another major cluster involves regions 5 and 6 that share 56 of a total of 120 (47%) species, and region 3. The pattern that emerges is that the Sierra de los Tuxtlas of southern Veracruz (Region 3) and the cloud forests along the Atlantic escarpment of Nuclear Central America from southeastern Oaxaca across to the northwestern highlands of Honduras (Regions 5, 6, 7, 8, 9, and 12, respectively) constitute a fairly discrete biogeographic unit. The degree of association between these herpetofaunas is high with the most distinctive break occurring between northern Chiapas (6) and the Cuchumatanes (7). The physiography of the intervening region gives no strong indication that a physical barrier exists and this break suggests that the ecological barriers that presently occur between the regions are comparatively old in relation to barriers between the other regions.

In view of the geographical proximity of the cloud forests fringing some of the Pacific versant of Chiapas, Guatemala, and El Salvador (9, 10) to the cloud forests on the Atlantic slopes to the north, a priori it might be predicted that these cloud forest herpetofaunas would bear their strongest resemblance to those of the Sierra de los Cuchumatanes (Region 7) that has an extensive highland connection with the southwestern Pacific highlands of Guatemala. However the Pacific

FIGURE 5. Cluster analysis of 13 Middle American cloud forests on the basis of presence or absence of amphibians and reptiles using the Baroni-Urbani and Buser (1976) similarity coefficient. Numbers refer to the following localities: 1, southwestern Tamaulipas, Mexico; 2, northern Oaxaca, Mexico; 3, southern Veracruz, Mexico; 4, Sierra Madre del Sur of Guerrero, Mexico; 5, southeastern Oaxaca, Mexico; 6, northern Chiapas, Mexico; 7, Sierra de los Cuchumatanes, Guatemala; 8, highlands of Alta Verapaz, Guatemala; 9, Sierra de las Minas, Guatemala; 10, Pacific highlands of Guatemala and Chiapas; 11, El Salvador highlands; 12, northwestern Honduras; 13, eastern Costa Rica.

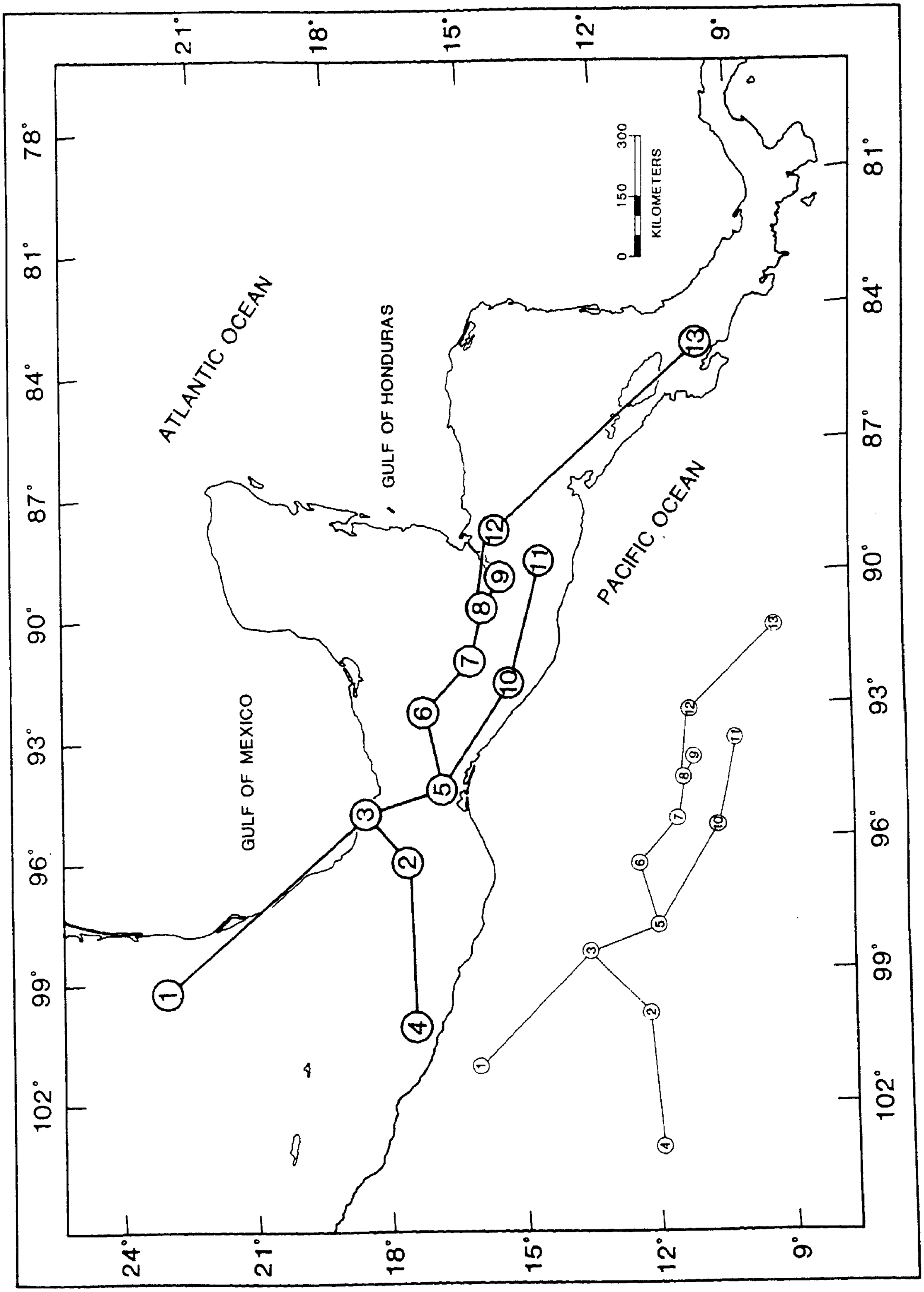

1
4
2
3
5
6
7
8
9
12
10
11
13
0.95
0.85
0.75
0.65
0.55
0.45
0.35
0.25

highlands cluster out at a relatively low level and do not bear any striking resemblance to other cloud forests. The herpetofauna of the highlands of northern Oaxaca (2) most closely resembles that inhabiting the Atlantic escarpments to the south in Nuclear Central America.

Not surprisingly, the assemblage of reptiles and amphibians inhabiting the cloud forests at the northeastern terminus of its distribution (Region 1), northwestern terminus (Region 4), and to the east of the Nicaraguan Depression (Region 13) have little in common with each other or other intermediate cloud forest assemblages. Southwestern Tamaulipas (Region 1) and the Sierra Madre del Sur of Guerrero (Region 4) cluster at a very low level (0.33) and share only 3 of a total of 77 (4%) species. These two assemblages have only weak affinities with other Middle American cloud forest herpetofaunas. Another dramatic faunal break occurs on either side of the Nicaraguan Depression with the herpetofauna of the eastern Costa Rican cloud forests being especially distinctive from that to the northwest.

Another way to represent phenetic information is a Prim network, which connects each cloud forest with its most similar neighbor. Whereas this method does not use all of the information contained in a similarity matrix, it does not distort any of the information it uses. The similarities of Middle American cloud forest herpetofaunas become readily apparent from a Prim network (Fig. 6). Regions 5, 6, 7, 8, and 9 are highly similar with similarity coefficients greater than 0.75 between adjacent regions. Regions 3 and 12 to the north and east of these regions also possess similar herpetofaunas with similarity coefficients only slightly smaller for their nearest neighbors. The

FIGURE 6. Prim network connecting Middle American cloud forests using the Baroni-Urbani and Buser (1976) similarity coefficient. Network below drawn to scale.

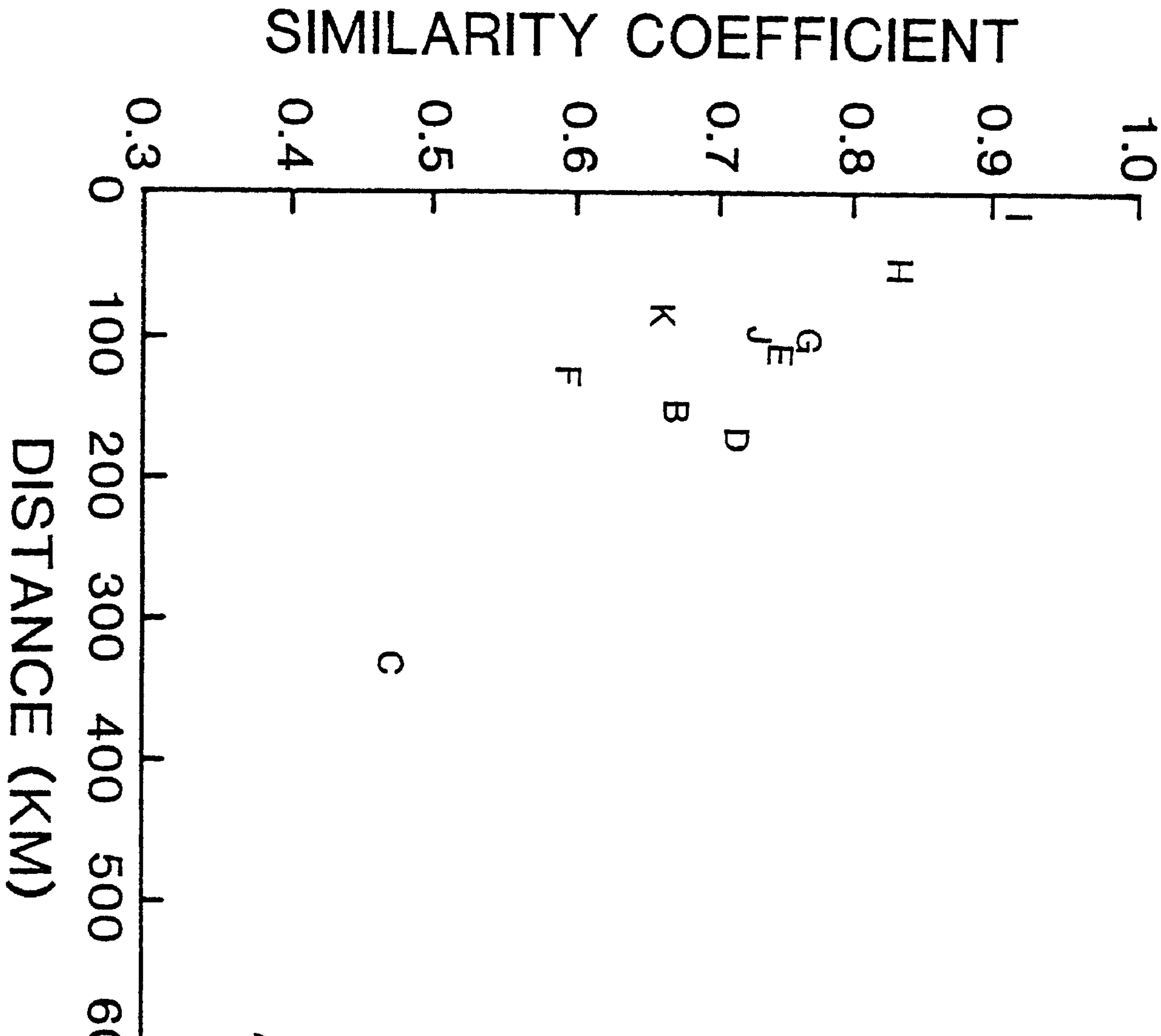

ATLANTIC OCEAN
GULF OF HONDURAS
GULF OF MEXICO
PACIFIC OCEAN
0
150
300
KILOMETERS
78°
81°
84°
87°
90°
93°
96°
99°
102°
24°
21°
18°
15°
12°
9°
1
2
3
4
5
6
7
8
9
10
11
12
13

herpetofauna of the Pacific versant is rather distinctive and possesses only a moderate degree of similarity with other regions. It is most similar to that of southeastern Oaxaca, but the similarity values are almost as large for some of the regions of the northern escarpment of the Nuclear Central American highlands (Regions 6, 7, 8, and 9) and the Pacific versant (Regions 10 and 11). Figure 7 shows the relationships of distance and the similarity coefficients for the pairs of regions interconnected by the Prim network (Fig. 6). The value of the similarity coefficient decreases with distance along a descending curve. It seems that most cloud forest species are relatively poor dispersers, causing a rapid initial drop in similarity coefficients. However, a few euryplastic species cause the curve to become more horizontal as distance increases.

Northern Oaxaca (Region 2) possesses a herpetofauna that is most like that of the Tuxtlas (Region 3), and secondarily most resembles that of southeastern Oaxaca.

The Gomez Farias region of southwestern Tamaulipas (Region 1), the Sierra Madre del Sur of Guerrero (Region 4) and the eastern Costa Rican highlands (Region 13) are geographically remote from other cloud forests in the analysis and possess relatively low values for their similarity coefficients of their most similar counterparts. In the north, Regions 1 and 4 are each most similar to the most proximate cloud forests, Regions 3 and 2 respectively, but the degree of similarity is not great. Region 13 in eastern Costa Rica is more similar to Region 12 in northwestern Honduras than it is with Region 11 which is geographically closer. The extended dry season of the Pacific Coast

FIGURE 7. Scatter plot of similarity coefficients of Prim network pairs versus distance between cloud forests. Letters refer to the following region pairs: A, 1--3; B, 2--3; C, 2--4; D, 3--5; E, 5--6; F, 5--10; G, 6--7; H, 7--8; I, 8--9; J, 8--12; K, 10--11; L, 12--13. See Figure 4 for reference to numbers of cloud forests.


SIMILARITY COEFFICIENT
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
DISTANCE (KM)
0
100
200
300
400
500
600
I
H
K
G
J
E
F
B
D
C
L
A

undoubtedly serves as a more effective barrier than the Atlantic Coast in which a milder dry season occurs and for which there is some faunal evidence that an extremely wet corridor of forest persisted for some time in the past (Wake and Campbell, in prep).

Peter's approach to biogeographic data.-- The resemblance between any two areas is expressed by the similarity coefficient; this is the basis for cluster analysis. However a problem with analyzing data in this way is that some of the information available in the similarity matrix (Table 5) is ignored, namely the relationship of each region with all the other regions in the analysis. Peters (1971) suggested an alternate method for estimating the degree of similarity between any two regions by ranking coefficients for each locality. Peters contended that there was a greater probability that position within the ranking would indicate faunal resemblance more accurately than would single similarity coefficients or averaging a subset of these coefficients. The various levels of bias of information available concerning the fauna of particular regions is more likely to be avoided or lessened by considering its relative position within rankings with other regions. The ranked coefficients for the Middle American cloud forests and their respective regions are given in Table 6. Table 7 contains the number of crossovers for all possible combinations of Middle American cloud forests and their respective correlation coefficients. I have followed Peters (1971) in calculating the coefficients using the following formula:

$$C = 1 - \frac{2D}{N^2}$$

Table 6. Ranked similarity coefficients of Middle American cloud forests. See Figure 4 for explanation of regions. Numbers representing particular regions have been placed in front of their respective coeficients and connected by a dash. Vertical lines represent "ties."

1	2	3	4	5	6	7	8	9	10	11	12	13
3--0.387	3--0.675	5--0.718	2--0.475	6--0.753	7--0.766	8--0.835	9--0.913	8--0.913	11--0.662	10--0.662	8--0.737	12--0.454
4--0.334	5--0.562	2--0.675	1--0.334	3--0.718	5--0.753	9--0.799	7--0.835	7--0.799	5--0.587	12--0.606	9--0.731	9--0.373
2--0.298	6--0.514	6--0.657	5--0.333	7--0.687	8--0.703	6--0.766	12--0.737	12--0.731	7--0.575	5--0.562	7--0.685	8--0.359
5--0.269	8--0.484	8--0.604	3--0.301	8--0.654	9--0.658	5--0.687	6--0.703	6--0.658	6--0.531	7--0.546	5--0.647	7--0.338
6--0.269	7--0.482	7--0.601	6--0.301	12--0.647	3--0.657	12--0.685	5--0.654	5--0.625	12--0.516	9--0.536	6--0.618	6--0.325
12--0.262	12--0.482	12--0.588	10--0.287	9--0.625	12--0.618	3--0.601	3--0.604	11--0.536	9--0.503	8--0.509	11--0.606	11--0.324
8--0.224	4--0.475	9--0.534	11--0.264	10--0.587	10--0.531	10--0.575	11--0.509	3--0.534	8--0.495	6--0.478	3--0.588	5--0.320
11--0.224	9--0.435	10--0.428	7--0.238	11--0.562	2--0.514	11--0.546	10--0.495	10--0.503	3--0.428	3--0.410	10--0.516	3--0.279
7--0.222	10--0.342	11--0.410	12--0.238	2--0.562	11--0.478	2--0.482	2--0.484	2--0.435	2--0.342	13--0.324	2--0.482	10--0.268
10--0.222	11--0.312	1--0.387	8--0.210	4--0.333	13--0.325	13--0.338	13--0.359	13--0.373	4--0.287	2--0.312	13--0.454	2--0.236
9--0.201	1--0.298	4--0.301	9--0.192	13--0.320	4--0.301	4--0.238	1--0.224	1--0.201	13--0.268	4--0.264	1--0.262	4--0.116
13--0.102	13--0.236	13--0.279	13--0.116	1--0.269	1--0.269	1--0.222	4--0.210	4--0.192	1--0.222	1--0.224	4--0.238	1--0.102

TABLE 7. Matrix showing relationships among Middle American cloud forests. The values in the lower left of the matrix are the actual counts of discrepancies between any two localities; the upper half shows the values of Peters′ correlation coefficient. See Figure 4 for explanation of regions.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1		0.95	0.83	0.95	0.79	0.74	0.66	0.66	0.68	0.68	0.63	0.63	0.61
2	4		0.95	0.80	0.94	0.89	0.81	0.76	0.79	0.80	0.85	0.76	0.75
3	14	4		0.80	0.91	0.88	0.82	0.79	0.81	0.81	0.72	0.81	0.75
4	4	17	17		0.72	0.67	0.62	0.59	0.59	0.72	0.64	0.59	0.51
5	18	5	8	24		0.95	0.92	0.87	0.88	0.87	0.80	0.86	0.85
6	22	9	10	28	4		0.95	0.92	0.92	0.86	0.83	0.91	0.85
7	29	16	15	32	7	4		0.96	0.96	0.86	0.83	0.95	0.93
8	29	20	18	35	11	7	3		1.00	0.82	0.85	0.98	0.94
9	27	18	16	35	10	7	3	0		0.82	0.83	0.99	0.96
10	27	17	16	24	11	12	12	15	15		0.92	0.83	0.83
11	31	23	24	30	17	14	14	13	14	7		0.86	0.87
12	31	20	16	35	12	8	4	2	1	14	12		0.99
13	33	21	21	41	13	13	6	5	3	14	11	1	

where D is the number of discrepancies between two regions, and N represents the total number of regions in the analysis. The possible range of values is from zero, indicating no similarity between regions, to one, indicating complete agreement.

After a diminishing ranking of similarity coefficients has been listed for each region, the next step is to compare the ranked coefficients, excluding regions of adjacent columns which are based on their relationships with each other. Because the samples of the herpetofauna for each of the regions are undoubtedly incomplete with respect to the total number of species occurring in these regions, I have arbitrarily considered values with 0.01 of each other as "ties," and allowed such values complete freedom of movement within the span of the tie to minimize the number of crossovers for that region.

For example, in Table 8 in which regions have been selected at random for illustrative purposes, it can be seen that if lines are drawn between adjacent columns connecting coefficients for a single region, regions having relatively similar rankings will be evident by mostly parallel lines such as between columns representing Regions 8 and 9; however, if the rankings represent a considerable amount of rearrangement, such as demonstrated by columns 9 and 13, a large number of crossovers in the connecting lines result and it can be inferred that the faunal units are considerably different. Simply stated, the higher the number of discrepancies of ranking, the more different any two faunal assemblages. A visual presentation of the number of crossovers among adjacent Middle American cloud forests is given in Table 8.

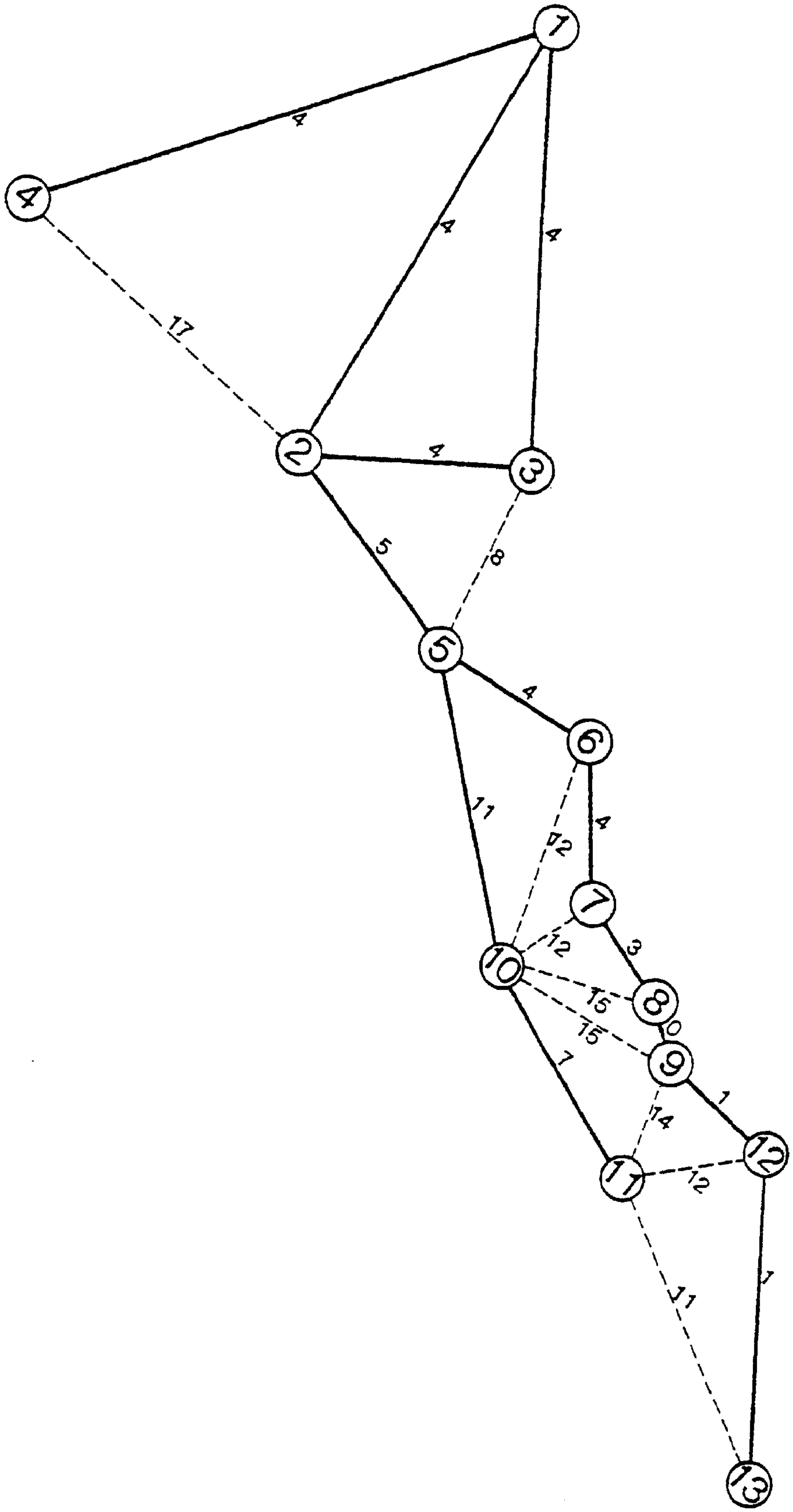
TABLE 8. Selected Middle American cloud forests comparing ranking and showing between column discrepancies. Numbers representing regions associated with the similarity coefficients arranged in descending order are listed below each of the regions. Solid lines connect coefficients for a single locality. Vertical lines represent "ties."

7	8	9	11
8--0.835	9--0.913	8--0.913	10--0.662
9--0.799	7--0.835	7--0.799	12--0.606
6--0.766	12--0.737	12--0.731	5--0.562
5--0.687	6--0.703	6--0.658	7--0.546
12--0.685	5--0.654	5--0.625	9--0.536
3--0.601	3--0.604	11--0.536	8--0.509
10--0.575	11--0.509	3--0.534	6--0.478
11--0.546	10--0.495	10--0.503	3--0.410
2--0.482	2--0.484	2--0.435	13--0.324
13--0.338	13--0.359	13--0.373	2--0.312
4--0.238	1--0.224	1--0.201	4--0.264
1--0.222	4--0.210	4--0.192	1--0.224

Crossovers: 3 0 14

The major significance of the ranking method is the information conveyed in comparing adjacent regions. I believe this method is useful for gaining insight into the relative degree of isolation or barriers between adjacent regions and into the origin of a particular fauna. If two samples in a study were in actuality representative of a single herpetofauna, the relationships of these two samples would be the same to all other samples, and this would be reflected in similar ranking with no crossovers. This is the situation between the herpetofauna of Alta Verapaz (Region 8) and the Sierra de las Minas (Region 9). Conversely, the more distantly related the faunas, the higher the number of discrepancies. If the network of lowest values connecting adjacent areas in Figure 8 is compared with the Prim network (Fig. 6) connecting the similarity coefficients for these regions, a high degree of congruence is noted. Regions from southeastern Oaxaca (5) across the Atlantic versant of Central America to eastern Costa Rica (12) are connected, although the Prim network differs from the crossover network in that Region 12 connects with Region 9 rather than 8. However, in view of the similarity between Regions 8 and 9, I do not find this distressing. Although Region 12 in northwestern Honduras and Region 13 in eastern Costa Rica contain a large number of endemic species and over-all are quite distinctive from one another, comparison of these regions reveals a high correlation coefficient. This is because the influence of endemic species tends to be minimized by this method. The value of the correlation coefficient between these regions is a reflection of their similar relationships to all others, and is not

FIGURE 8. Network of adjacent Middle American cloud forests connected to show number of ranking crossovers. Numbers refer to regions in Figure 4. Heavy lines represent minimum values.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13

especially surprizing their geographic positions.

The major pivotal point linking the Atlantic and Pacific versant herpetofaunas of Nuclear Central America in both networks is southeastern Oaxaca. The relatively low correlation coefficients between Regions 5 and 10, and between 10 and 11, and the slightly lower coefficients between Regions 10 and 11 and regions to the north (Regions 6, 7, and 9) can be inferred to be the result of two compounding factors: intervening barriers and diverse origins of these two herpetofaunas. As stated previously, herpetofaunas with common origins will have high correlation coefficients, but those that may have drawn on several regions will tend to have lower coefficients. Analysis of the herpetofauna of the Pacific versant of Chiapas, Guatemala, and El Salvador gives strong indication that these regions have derived portions of their herpetofaunas from several regions on the Atlantic escarpment.

The situation west of the Isthmus of Tehuantepec becomes less clear. Northern Oaxaca (Region 2) and the Sierra de los Tuxtlas (Region 3) are connected in both networks, but their relationships with the cloud forests in Nuclear Central America as well as outlying cloud forests in Tamaulipas (Region 1) and Guerrero (Region 4) differ. This appears to reflect simply the emphasis of the two methodologies: the Prim network stresses the greatest over-all similarity of a single region with that of another; the ranking method, while taking this into account, stresses the similarity of a region with all others. Thus, although Region 4 shares more species with Region 2 than any other, and this is reflected in the Prim network, the relationships of Region 2 with adjacent regions (1, 3, and 5) is such that similarity of species shared with Region 4 is obscured.

That there is congruence in both networks is reassuring, but discrepancies should not be construed as conflicting data, for these methods attempt to answer slightly different questions. One seeks to answer what is the greatest degree of resemblance between regions based solely on number of shared species; the other indicates the possible relative influence of all adjacent regions on a particular region and compares the order of magnitude of these influences with that of all adjacent regions. Nevertheless, both methods appear to be highly compatible in biogeographic analyses.

Island biogeography.-- An additional method of analysis employing the theory of island biogeography (MacArthur and Wilson, 1967) has been used in various mainland studies (Brown, 1978; Vuilleumier, 1970, 1973). Cloud forests, isolated as they are, may be considered to be ecological islands. Some of the problems associated with such an approach were addressed by Simpson (1975). She pointed out that fundamental to the concept of predictable island species diversity is the assumption that the "islands" under analysis have remained constant in size and distance from one another for a sufficient period of time for an equilibrium of species number to have been reached. Because presently isolated cloud forests have expanded and contracted along mountain corridors according to periodic climatic fluctuations through Recent time, it seems undesirable to apply this fundamental assumption to cloud forests. Furthermore, we cannot assume that the rates of immigration have been uniform; much to the contrary, we might predict that the exchange of species among cloud forests has at times been great and practically negligible at others. Additionally, cloud forests do not have well defined boundaries such as the shores of islands and, therefore, it is difficult to circumscribe the areas of the various cloud forests except in the most general terms. Cloud forests differ in their altitudinal distributions and floristics, and thus not one but several subjective criteria would have to be selected to define cloud forest areas. Another problem is that the ranges of species do not tend to coincide with the distributions of cloud forests. Practically every species either inhabits only a portion of cloud forest or is wide ranging and occurs in several habitats. It seems reasonable to assume that any particular cloud forest could have been a primary source area for other cloud forests. Geographic isolation and divergence has and is occurring in all of them. It seems to me that geographic position with regard to highland corridors and the numbers of other particular cloud forest forests to which a particular cloud forest shares proximity are more important factors in determining cloud forest species diversity than is area. Some of the relatively small cloud forests possess a large number of species and a high degree of endemicity (Table 4). For example, the cloud forest of the Sierra de los Tuxtlas covers a small area relative to that of the Sierra Madre del Sur in Guerrero, but nevertheless harbors more species of amphibians and reptiles, 63 versus 56, respectively.

RELATIONSHIPS WITHIN MESIC UPLAND GROUPS

The present day cloud forests and their faunas are isolated from one another by various physical and ecological barriers. However, as was demonstrated by the biogeograpic analyses in the preceding section, all of these cloud forests share some components of their herpetofauna with adjacent cloud forests. Although it can be scarcely doubted that some species inhabiting cloud forests possess considerable ecological valence and may be capable of dispersing across intervening barriers, many cloud forest species seem to be restricted to cool, damp conditions and explanations of their present distributions solely by dispersal across these barriers requires considerable imagination. It is more reasonable to assume that fluctuations in paleoclimates and the complex geological history of the region have produced the vicariance events leading to the separation of many populations. In some instances isolation of these populations may have been comparatively recent, or else the various populations have failed to differentiate over long periods of time, thus contributing to a large number of shared species between some regions. However many species appear to belong to well defined groups and possess distributions more or less coinciding with that of cloud forest, giving evidence of longer separation. Therefore, the next logical step is to examine the relationships of some of these closely related species.

I have chosen seven species groups on the basis of the following criteria: all have members occurring in the Sierra de las Minas, my primary focus of interest; all are reasonably widespread in Middle America, but have hiates in their distributions that correspond to breaks in mesic forest; all are represented in collections sufficiently well to allow an assessment of variation in various characters and an interpretation of interspecific relationships; and each of these groups contains from 3 to 13 species.

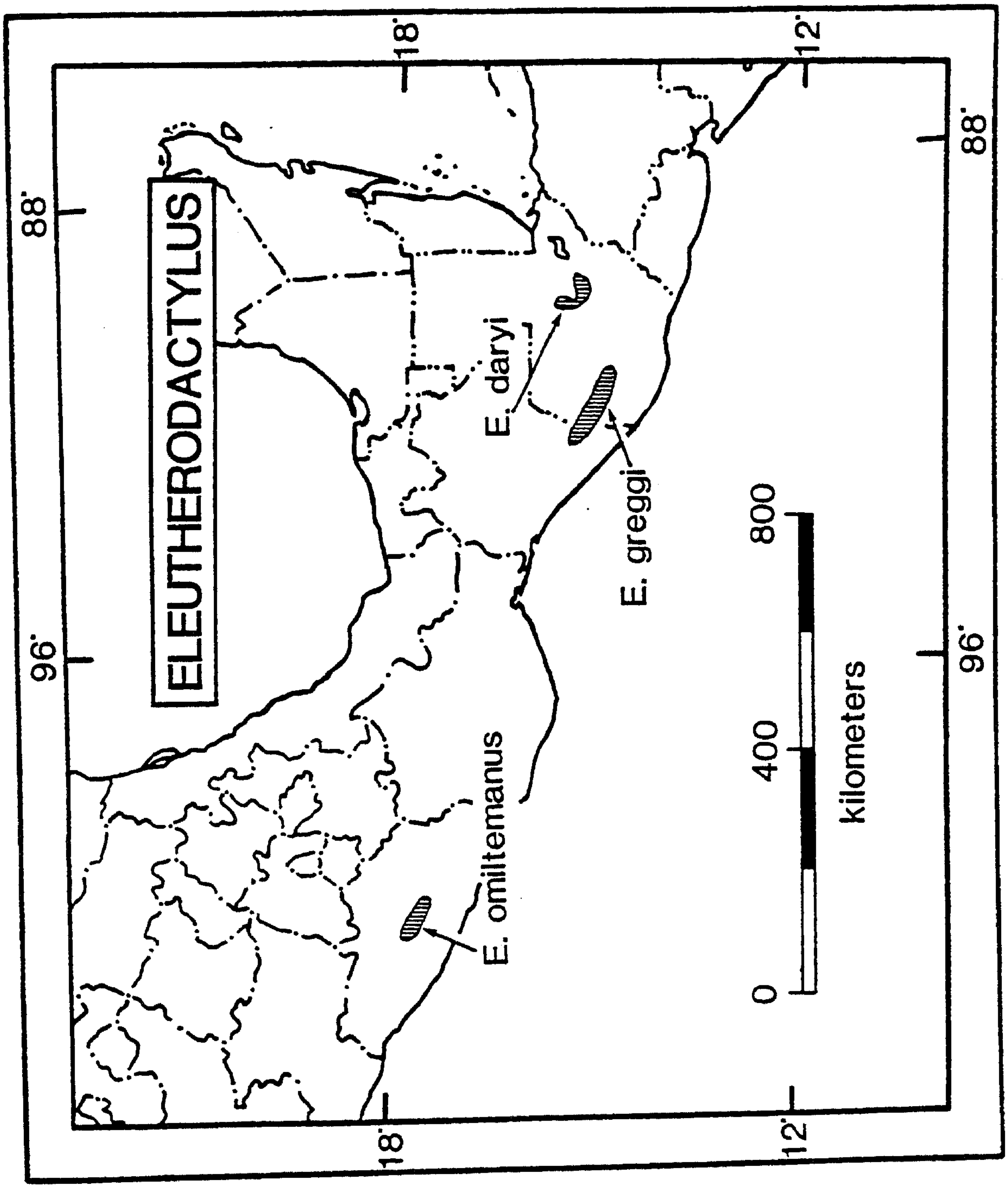
The ELEUTHERODACTYLUS OMILTEMANUS group

Composition.-- The genus *Eleutherodactylus* contains over 400 species distributed throughout the Neotropics. The relationships of most species groups of *Eleutherodactylus* are poorly known and even the delimitation of most of the species groups is unresolved. However, the species group comprised of *E. omiltemanus*, *E. greggi*, and *E. daryi* appears to be morphologically distinctive and represents a monophyletic lineage. I have taken information relating to species in this group from Ford and Savage (1983) who defined the group in their description of *E. daryi*.

Distribution.-- The species of the *E. omiltemanus* group occur allopatrically at moderate and intermediate elevations from central Guerrero to Guatemala (Fig. 9). *Eleutherodactylus omiltemanus* occurs in the cloud forest and humid pine-oak forest of the Guerreran highlands; *E. greggi* occurs in cloud forest of the Pacific versant of Chiapas and Guatemala; and *E. daryi* is distributed in cloud forest of the highlands of Alta Verapaz and the Sierra de las Minas.

Outgroup comparisons.-- In their description of *E. daryi*, Ford and Savage (1983) compared the *E. omiltemanus* group primarily with the *E. unistrigatus* group and commented on *E. mexicanus* and its relatives;

FIGURE 9. Distribution of the members of the *Eleutherodactylus omiltemanus* group.


ELEUTHERODACTYLUS
88'
96'
18'
12'
E. daryi
E. greggi
E. omiltemanus
0
400
800
kilometers

accordingly, I have used these as my outgroups.

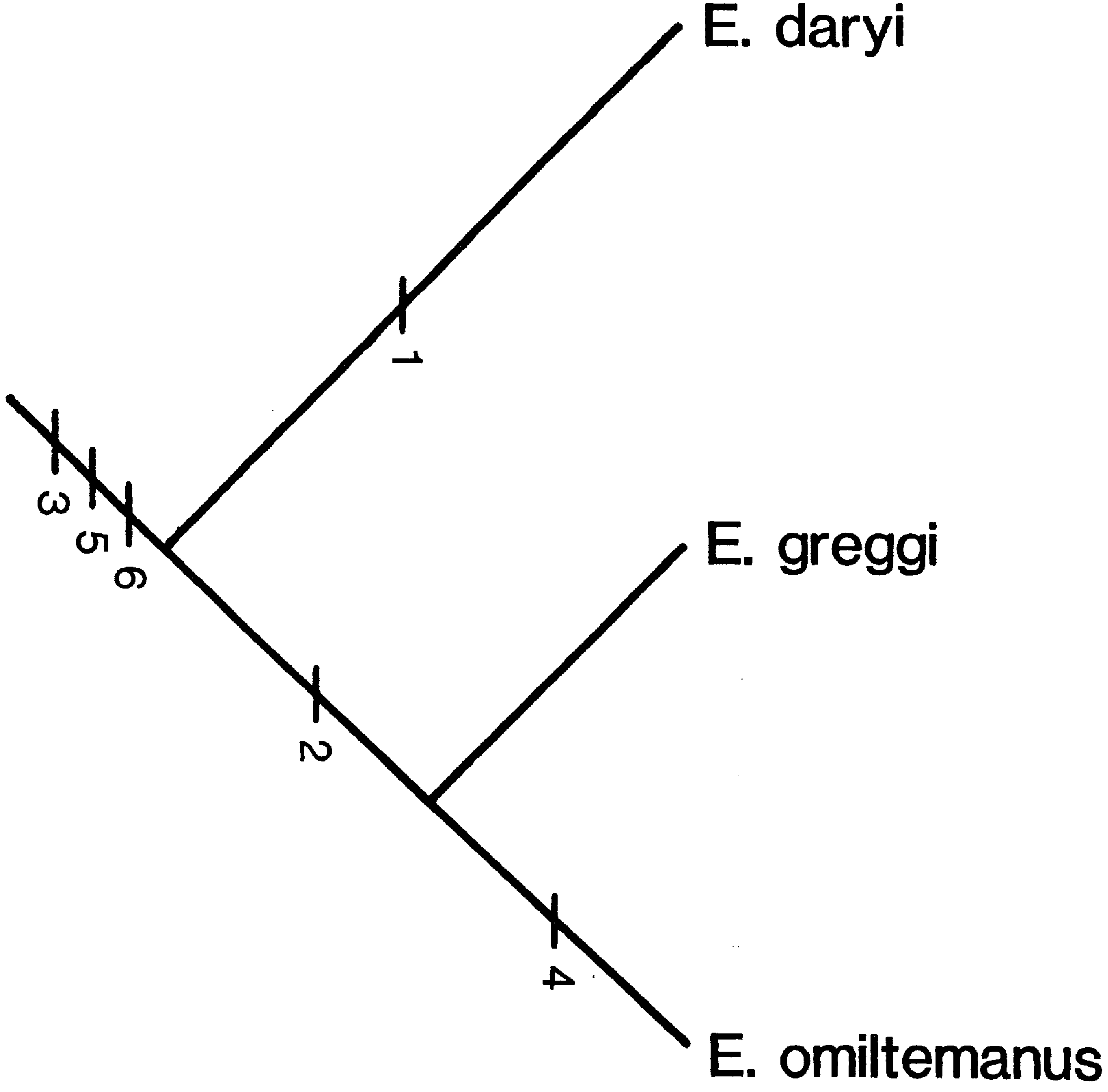
Character analysis and relationships.-- The E. omiltemanus group was defined by narrow, nonemarginate finger and toe discs, no tarsal fold or tubercle, no toe webbing, finger I shorter than II, strongly granulate (areolate) venter, distinct subintegumentary inguinal gland and no vocal slits in adult males. The inner metatarsal tubercle of E. omiltemanus is enlarged and elongate, being almost as long as the first toe. Members of this group possess a distinctive type of jaw musculature. Three discrete slips of the depressor mandibulae originate from the dorsal fascia, the squamosal, and the annulus typanicus. An adductor mandibulae externus superficialis is present. The only member of the group that has been examined karyologically, E. greggi, possesses 2N = 22, whereas members of the E. unistrigatus group have 2N = 26, 32, and 34 (Ford and Savage, 1983).

Characters that might serve to define relationships within the E. omiltemanus group are few (Table 9). However, the condition of the jaw musculature, lack of vocal slits and nuptial pads, and enlarged metatarsal tubercle seem to be derived. I propose a geneology for the species of the E. omiltemanus group in Figure 10, where E. daryi is considered the sister species to the geographically widely separated species E. greggi and E. omiltemanus. Owing to the long hiatus between the ranges of members of the E. omiltemanus group (Fig. 9), additional taxa belonging to this group may lurk in the cloud forests in the Cerro Baul region of southeastern Oaxaca, the Sierra Madre del Sur of southern Oaxaca, and the northern highlands of Chiapas; it is possible that *E. glaucus* from Chiapas, known only from the type, is a member of this group.

TABLE 9. Comparison of certain features in species of the *Eleutherodactylus omiltemanus* group.

Character	*E. greggi*	*E. daryi*	*E. omiltemanus*
1. Dorsal surface	Without pustules	Prominent pustules	Without pustules
2. Nuptial pad	Absent	Present	Absent
3. Vocal slits	Absent	Absent	Absent
4. Metatarsal tubercles	Subequal	Subequal	Inner about twice size of outer
5. Depressor mandibulae	Three slips	Three slips	Three slips
6. Adductor mand. ext. superficialis	Present	Present	Present

FIGURE 10. A theory of relationships within the *Eleutherodactylus omiltemanus* group. Numbers refer to the following characters: 1, prominent pustules; 2, loss of nuptial pad; 3, vocal slits absent; 4, large inner metatarsal tubercle; 5, three slips of depressor mandibulae; 6, adductor mandibulae externus superficialis present.


E. daryi
E. greggi
E. omiltemanus
1
2
3
4
5
6

The genus PLECTROHYLA

Composition.-- The genus *Plectrohyla* includes thirteen monotypic species of stream-breeding highland frogs. Two of these species are undescribed: one was previously referred to as *Plectrohyla sp*. and another was confused with *P. guatemalensis* (Table 4); these will be subsequently referred to as *Plectrohyla* species A and B, respectively.

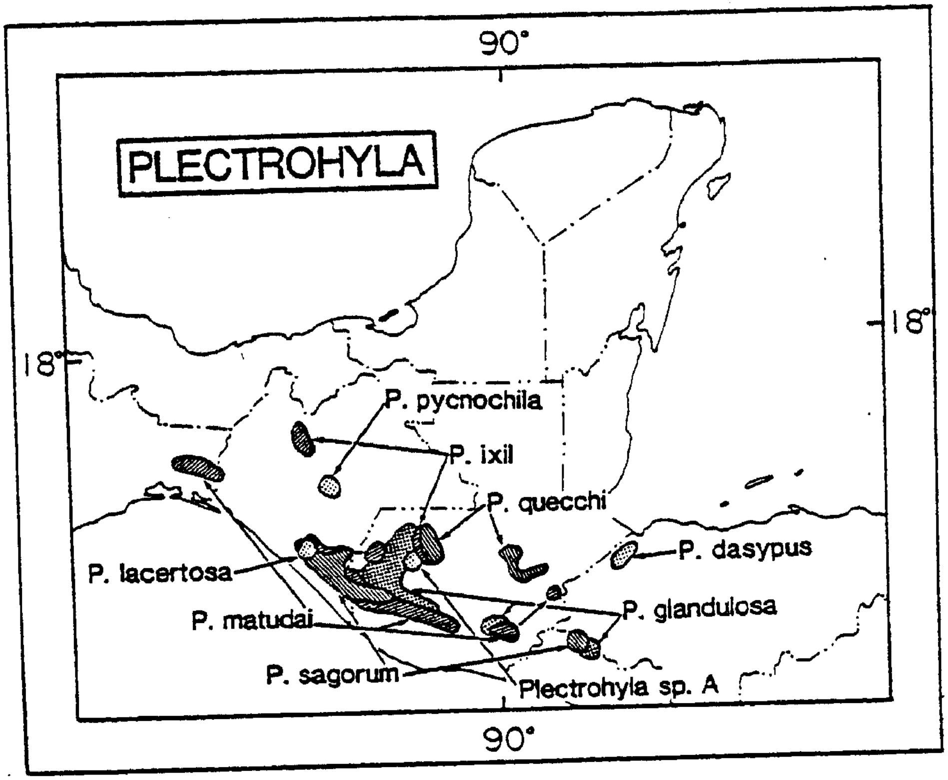
Distribution.-- The genus is endemic to the highlands of Nuclear Central America, ranging from the southeastern Oaxacan highlands to western Honduras and northern El Salvador (Fig. 11). Four species, *P. avia*, *P. lacertosa*, *P. matudai*, and *P. sagorum* have distribtions mainly along Pacific drainages; whereas *P. pycnochila*, *P. ixil*, *P. quecchi*, and *Plectrohyla* species A and B are restricted to Atlantic forests. Several species including *P. guatemalensis*, *P. glandulosa*, and *P. hartwegi* have distributions on both Atlantic and Pacific-facing forests. All species are cloud forest or humid pine-oak forest inhabitants and range from 1000--3500 m (Duellman, 1970).

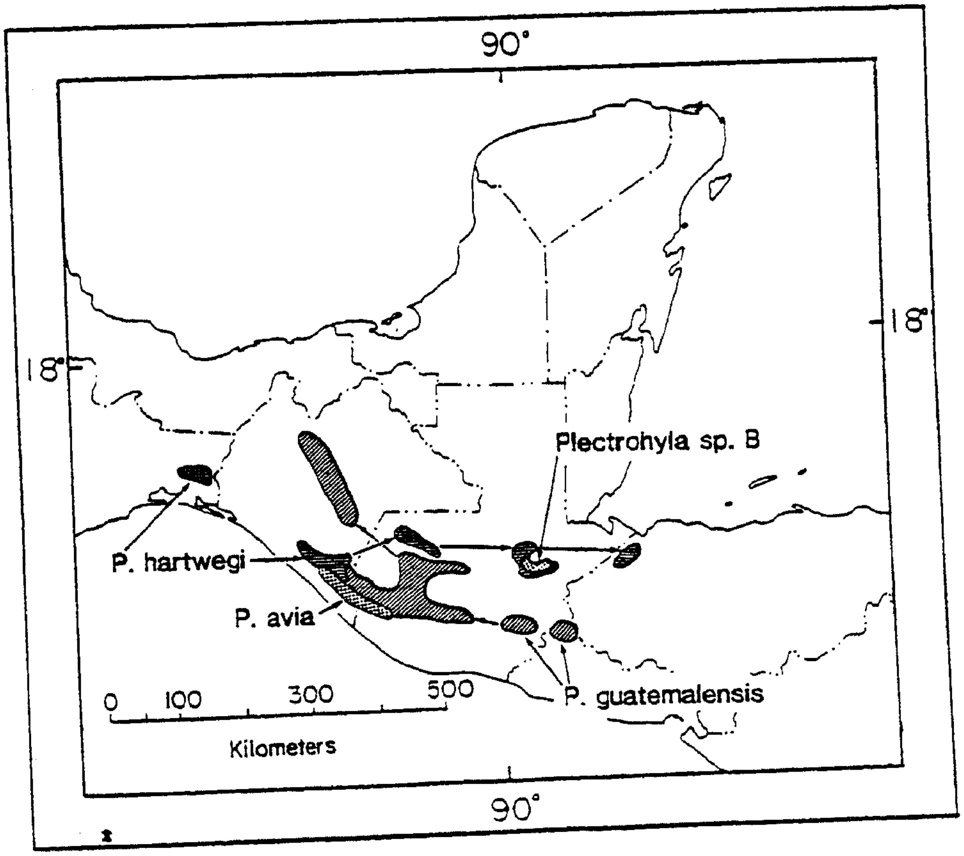
The distributions of eleven species were outlined by Duellman (1970). Since that time additional material has become available allowing the following observations:

1. *Plectrohyla matudai*, previously recorded as far west as the Las Nubes block, occurs at least to the Departamento de Zacapa in the La Union region.

2. *Plectrohyla dasypus* McCranie and Wilson (1981) occurs in the Sierra de Omoa, Honduras.

FIGURE 11. Distribution of the genus Plectrohyla. Upper, distributions for members that possess vocal slits and/or blunt prepollices; lower, large members of the genus that possess bifid prepollices and/or perpendicular transverse processes on eighth presacral vertebra and first and second metacarpals separated by distal carpal 2.


90°
PLECTROHYLA
18°
18°
P. pycnochila
P. ixil
P. quecchi
P. dasypus
P. lacertosa
P. glandulosa
P. matudai
P. sagorum
Plectrohyla sp. A
90°


90°
18°
18°
Plectrohyla sp. B
P. hartwegi
P. avia
P. guatemalensis
0
100
300
500
Kilometers
90°

3. *Plectrohyla* species A, currently being described, is a distinctively spotted species inhabiting high elevations of the Sierra de los Cuchumatanes in the region of Chemal.

4. *Plectrohyla hartwegi*, previously known from only a few specimens from the Pacific versants of southeastern Oaxaca and Chiapas, is now known from various localities on the Atlantic escarpment including the Sierra de los Cuchumatanes, the highlands of Alta Verapaz, the Sierra de las Minas, and the Sierra de Omoa.

5. *Plectrohyla guatemalensis* is the most widely ranging member of the genus and perhaps is a composite of several species. It seems that specimens reported from Alta Verapaz are actually *P. hartwegi* lacking the distinctive pale and dark markings on the flanks and thighs that characterize some specimens. *Plectrohyla guatemalensis* can be most readily distinguished from *P. hartwegi* by its relatively smooth skin bearing large, scattered tubercles, especially between the eyelids, on the posterior of the dorsum, tibia and soles of the feet; and its smaller size. I have not seen females that exceed 55 mm snout-vent length. *Plectrohyla hartwegi* is a larger frog, adult females having a body length of over 60 mm, and the skin is finely granular. The granular nature of the skin is especially noticeable on top of the head between the eyelids. The tibia and soles of the feet tend to be smooth. It seems that *P. hartwegi* occurs primarily in virgin cloud forest, whereas *P. guatemalensis* occurs in humid pine-oak forests. These two species are largely allopatric but their distributions converge in western Guatemala/eastern Chiapas (Fig. 11).

6. On re-examination of Plectrohyla specimens from the Sierra de las Minas that I referred previously to as P. guatemalensis (Table 4), I find that these specimens represented an undescribed species referred to herein as Plectrohyla species B. They resemble P. guatemalensis in some features and P. hartwegi in others, and differ from both by possessing well developed vocal slits.

7. I believe the unidentified tadpole of Stuart (1948a) and Duellman (1970) is the larva of P. hartwegi. This tadpole was known previously only from Arroyo Las Palmas at Finca Los Alpes, Departamento de Alta Verapaz, Guatemala. I have taken it from four sites in the Sierra de Las Minas: Biotopo "Mario Dary," Plantacion Santa Teresa, and near San Jose El Espinero on a tributary of the Rio Sananja, Baja Verapaz; and Finca Sitio Nuevo on the Rio Porton, Zacapa. Considering that all other tadpoles taken at these localities are clearly allocable to known species of frogs and that the adults of P. hartwegi were also taken at all of the above localities, the circumstantial evidence that these tadpoles are the larvae of P. hartwegi becomes convincing. In view of the abundance of this species along streams in the cloud forest in the Sierra de las Minas and the ease with which the tadpoles of other species of Plectrohyla are collected, it is unlikely that P. hartwegi tadpoles have not been found. A re-examination of the adult Plectrohyla from Finca Los Alpes, previously identified as P. guatemalensis, reveals they are P. hartwegi, thus providing a fifth instance in which these larvae have been taken in association with adult P. hartwegi and reinforcing the hypothesis that these tadpoles may be allocated with the proper species. I should note that morphologically, except for the

tremendous development of the mouth, these tadpoles are similar in many respects to other *Plectrohyla* larvae. They possess at least one complete row of labial papillae, 2/3 denticle rows, robust beaks, ovoid bodies, and shallow caudal fins. The tadpoles of *P. hartwegi* seem to occur most frequently in the deeper portions of streams, especially the plunge pools at the bases of waterfalls.

Outgroup comparisons.-- For an outgroup I have compared species of *Plectrohyla* with members of the *Hyla bistincta* group. A thick glandular skin, absence of quadratojugal, rather drab appearance, extremely short snout, and a broad ossified prepollex characterize both groups and support the notion that both share a common ancestor. Their larvae show similar adaptations to swift mountain streams with ventral mouths, a generalized number of 2/3 denticle rows, and strongly muscular tails.

Character analysis.-- A number of osteological characters found in *Plectrohyla* seem to be derived. The upward projecting alary processes of the premaxillaries are bifurcate (Table 10); the anterior bifurcation contacts the anterior portion of the sphenethmoid and the posterior bifurcation contacts the ventral surface of the sphenethmoid and the prevomers. In members of the *H. bistincta* group the alary processes are not bifurcate and they do not contact the sphenethmoid of prevomers.

The sphenethmoid extends anteriorly and widely separates the nasals in *Plectrohyla* which articulate antero-laterally with the sphenethmoid. In members of the *H. bistincta* group the sphenethmoid is not ossified anteriorly and their nasals are usually in broad contact with each other. An exception is *H. cyanomma*, in which the nasals are relatively

TABLE 10. Comparison of certain features in species of *Plectrohyla*. See text for details.

PLECTROHYLA

Characters	*P. ixil*	*P. matudai*	*P. sagorum*	*P. quecchi*	*P. dasypus*	*P. pycnochila*	*P. glandulosa*	*Plectrohyla* sp. A	*P. lacertosa*	*P. avia*	*P. hartwegi*	*P. guatemalensis*	*Plectrohyla* sp. B
1. Premaxillary	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid	Bifid
2. Nasals	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated	Separated
3. Prepollex	Curved spine	Curved spine	Curved spine	Curved spine	Rounded, blunt	Rounded, blunt	Rounded, blunt	Rounded, blunt	Rounded, blunt	Curved spine	Bifid spine	Bifid spine	Bifid spine
4. Teeth	Blunt	Blunt	Blunt	Blunt	Blunt	Blunt	Long, pointed	Long, pointed	Long, pointed	Long, pointed	Blunt	Blunt	Blunt
5. Transverse processes	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Angled ant.	Perpen.	Perpen.	Perpen.	Perpen.
6. Distal carpal 2	Contact	Contact	Contact	Contact	Contact	Contact	Contact	Contact	Contact	Separate	Separate	Separate	Separate
7. Rostral	Normal	Normal	Keeled	Keeled	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal
8. Vocal slits	Present	Present	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present
9. Linea musculina	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
10. Tadpole fangs	Present	Present	Absent	Absent	Absent	Absent (?)	Absent	Absent	Absent (?)	Absent	Absent	Absent	Absent
11. Prehallux	T-shaped	T-shaped	T-shaped	T-shaped	Short spine	T-shaped (?)	T-shaped	T-shaped	T-shaped (?)	Short spine	Long spine	Long spine	Long spine

small and separated, but nevertheless are located anteriorly to the sphenethmoid similarly to other members of the *H. bistincta* group.

The ventral ramus of the squamosal is more strongly recurved posteriorly and is relatively longer in *Plectrohyla* than in the *H. bistincta* group. The pars fascialis is more strongly developed in *Plectrohyla*, broadly contacting the nasals. The palatines, along with the nasals, form a bridge that firmly connects the sphenethmoid with the maxillary. The prevomers in *Plectrohyla* possess anteriorly projecting stuts that anchor them to the pars fascialis.

All members of the *H. bistincta* group and most *Plectrohyla* have ordinary-looking pedicellate teeth divided into distinct crowns and pedicels that are separated by a transverse line resembling a suture between two bones. The crowns are terminally rounded and laterally compressed. However, the teeth in at least four species of *Plectrohyla* are long and pointed and the crown is not separated from the pedicel by a transverse suture. Species having long, pointed teeth are *P. glandulosa*, *P. avia*, *P. lacertosa*, and *Plectrohyla* species A. The condition is unknown in *P. pycnochila*.

Male *Plectrohyla* use their teeth in antagonistic encounters with other males. I have observed numerous specimens, especially of *P. guatemalensis*, *P. hartwegi*, *P. sagorum*, *P. quecchi*, and *Plectrohyla* species B, that have parallel scratches on their limbs and dorsum. Direct comparison of the size and spacing of these scratches with tooth conformation leaves little doubt of their origin. Male *P. quecchi* when held will angle their heads downward and attempt to abrade the skin and fingernails by moving their heads vertically and laterally. They do not open their mouths but press firmly with their upper jaws pushing back the upper lip and exposing the teeth. The hypertrophied forelimbs bearing prepollical spines also seem to enable male *Plectrohyla* to engage effectively in combat. A male *Plectrohyla* sp. B that I grabbed roughly from the wet face of a boulder in a splash zone was able to draw blood from my thumb.

The transverse process on the eighth presacral vertebrae is sharply angled anteriorly in the *H. bistincta* group and all *Plectrohya* except *P. hartwegi*, *P. guatemalensis*, *P. avia*, and *Plectrohyla* species B. In these species the transverse processes are more or less perpendicular to the long axis of the vertebral column, and in *P. avia* the processes are relatively short.

One of the most distinctive characters in *Plectrohyla* is the shape of the prepollex. In members of the *H. bistincta* group the prepollex tends to be short, flat, and inwardly curved. In *Plectrohyla* it may be a short, flat, straight, and terminally blunt bone; an elongate, outwardly curved spine; or bifid with two outwardly curved spines. Another character that seems almost equally distinctive, but that has escaped attention as a taxonomic character, is the shape of the prehallux. The prehallux is composed of two or three poorly ossified or cartilaginous elements with the distalmost two or three elements characteristically differing amoung various species. Members of the *H. bistincta* group, *P. sagorum*, *P. ixil*, *P. matudai*, and *P. quecchi* possess distal elements that are laterally expanded in such a manner as to resemble half of the head of an executioner's ax. The distal element is somewhat poorly developed in *P. glandulosa* and *Plectrohyla* species

A, but nonetheless resembles the plesiomorphic condition. In *P. hartwegi*, *P. guatemalensis*, and *Plectrohyla* species B the distal elements form an elongate spine projecting parallel to the digits. The condition in *P. avia* and *P. dasypus* is somewhat intermediate; a short spine projects from one side of the distal element, and a short blunt process projects from the other.

Despite reports to the contrary, at least some males of all species of *Plectrohyla* that are represented in collections by even small series have nuptial spines on the skin covering the prepollical spine and first finger.

The distal carpal 2 intervenes broadly between the first and second metacarpals thus separating these bones in *P. hartwegi*, *P. guatemalensis*, *P. avia*, and *Plectrohyla* species B. In other species of *Plectrohyla* and the *H. bistincta* group the distal carpal 2 does not figure prominently along the inside margin between the first and second fingers and the metacarpals are narrowly separated on in contact.

The loss of vocal slits seems to have occurred in many different lineages of frogs, but nevertheless the presence of vocal slits seems to be the plesiomorphic condition. Vocal slits occur in some members of the *H. bistincta* group, and in *P. ixil*, *P. matudai*, *P. sagorum*, *P. quecchi*, *P. dasypus*, and *Plectrohyla* species B. The presence of vocal slits in *Plectrohyla* species B is of special interest because it strongly suggests that vocal slits may be derived repeatedly.

Two species of *Plectrohyla* possess a distinctive rostral keel, and two other species possess a linea masculina. Both of these traits show up from time to time in diverse lineages of anurans and I consider them to be derived.

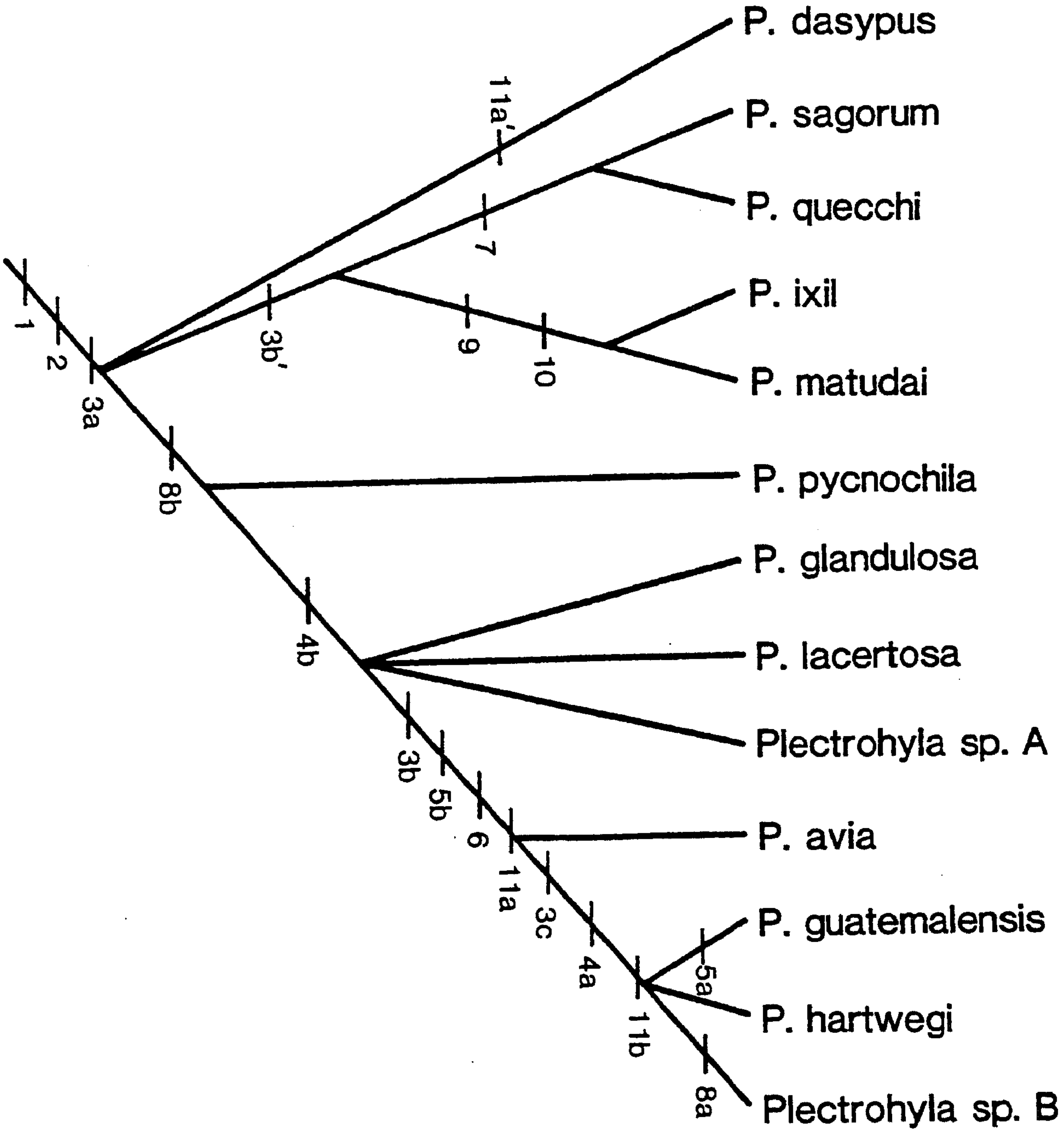
The tadpoles of *P. ixil* and *P. matudai* possess enlarged, fang-like serrations on their beaks. This character is not known in tadpoles of the *H. bistincta* group or in other species of *Plectrohyla*; accordingly, it is considered to be derived.

Relationships.-- A general pattern of the relationships within the genus *Plectrohyla* is beginning to emerge (Fig. 12). The five smaller species that possess vocal slits seem to form the sister unit to all other species. Two pairs of sister species, *P. sagorum*--*quecchi* and *P. ixil*--*matudai* seem to form a distinctive group of small frogs united by the presence of a curved spine-like prepollex, although *P. avia* seems to possess a similar prepollex. The exact relationship of *P. dasypus* to members of this vocal group is unclear, but the nature or the prepollex and prehallux in this species suggests that it is relatively primitive.

Three species of large frogs, *P. hartwegi*, *P. guatemalensis*, and *Plectrohyla* species B, share a distinctive bifid prepollex. These species are united with the large *P. avia* by the presence of a spine-shaped prehallux, relatively perpendicular transverse process on the eighth presacral vertebra, and a distal carpal 2 that separates the first and second metacarpals.

Plectrohyla pycnochila and *P. lacertosa* are known from two and one specimens, respectively, and a clear understanding of their relationships must await the collection of adequate material for dissection. They seem to be intermediate with respect to their position on the cladogram and may have close affinities with *P. glanulosa* and *Plectrohyla* species A.

FIGURE 12. A theory of the relationships of the frogs of the genus *Plectrohyla*. Numbers refer to the characters presented in Table 10. The letters a, b, and c suffixed to numbers refer to the sequence of character transformations; a and a' denote independently derived characters. Characters 3 (prepollex) and 11 (prehallux) are homoplasious. Characters 4a (bifid teeth), 5a (angular transverse processes on eighth presacral vertebra), and 8a (presence of vocal slits) are reversals.


P. dasypus
P. sagorum
P. quecchi
P. ixil
P. matudai
P. pycnochila
P. glandulosa
P. lacertosa
Plectrohyla sp. A
P. avia
P. guatemalensis
P. hartwegi
Plectrohyla sp. B
1
2
3a
8b
4b
3b
5b
6
11a
3c
4a
11b
8a
5a
3b'
11a'
7
9
10

The genus PTYCHOHYLA

Composition.-- The genus *Ptychohyla* was defined (Taylor, 1944) primarily on the basis of thickened, pigmented ventrolateral glands and a reduced number of enlarged nuptial spines in breeding males. The problems of recognizing the genus have been summarized by Duellman (1963). Previously, five species were placed in two distinct lineages, the *euthysanota* and *schmidtorum* groups (Duellman, 1963b). Although each of these groups possesses a suite of unique characters that appear to establish their monophyly, the only character that was proposed to unite the two groups, and that sets the genus apart, was the presence of ventrolateral glands in males. These groups are so distinctive from each other that were it not for the presence of the ventrolateral glands, each group might be considered to have its closest affinities with different species groups of stream-breeding Middle American *Hyla* rather than each other. That various types of glands have been independently derived many times in different families of frogs is troubling in that it suggests the possibility that the genus *Ptychohyla* is paraphyletic. However, Duellman (1963) suggested that it was more reasonable to assume that the development of ventrolateral glands took place only once in the common ancestor of the genus. The recent discovery of a distinctive new species, *Ptychohyla panchoi*, in the Sierra de las Minas of Guatemala that has a unique combination of characters seemed to support the notion of monophyly for the genus and allowed for a theory of the relationships of the two groups and *P. panchoi* (Duellman and Campbell, 1982).

I also consider *P. chamulae* and *P. macrotympanum* to be distinct species. Thus, I recognise the following 8 species as comprising the genus *Ptychohyla*: *euthysanota*, *macrotympanum*, *leonhardschultzei*, *spinipollex*, *panchoi*, *ignicolor*, *schmidtorum*, and *chamulae*.

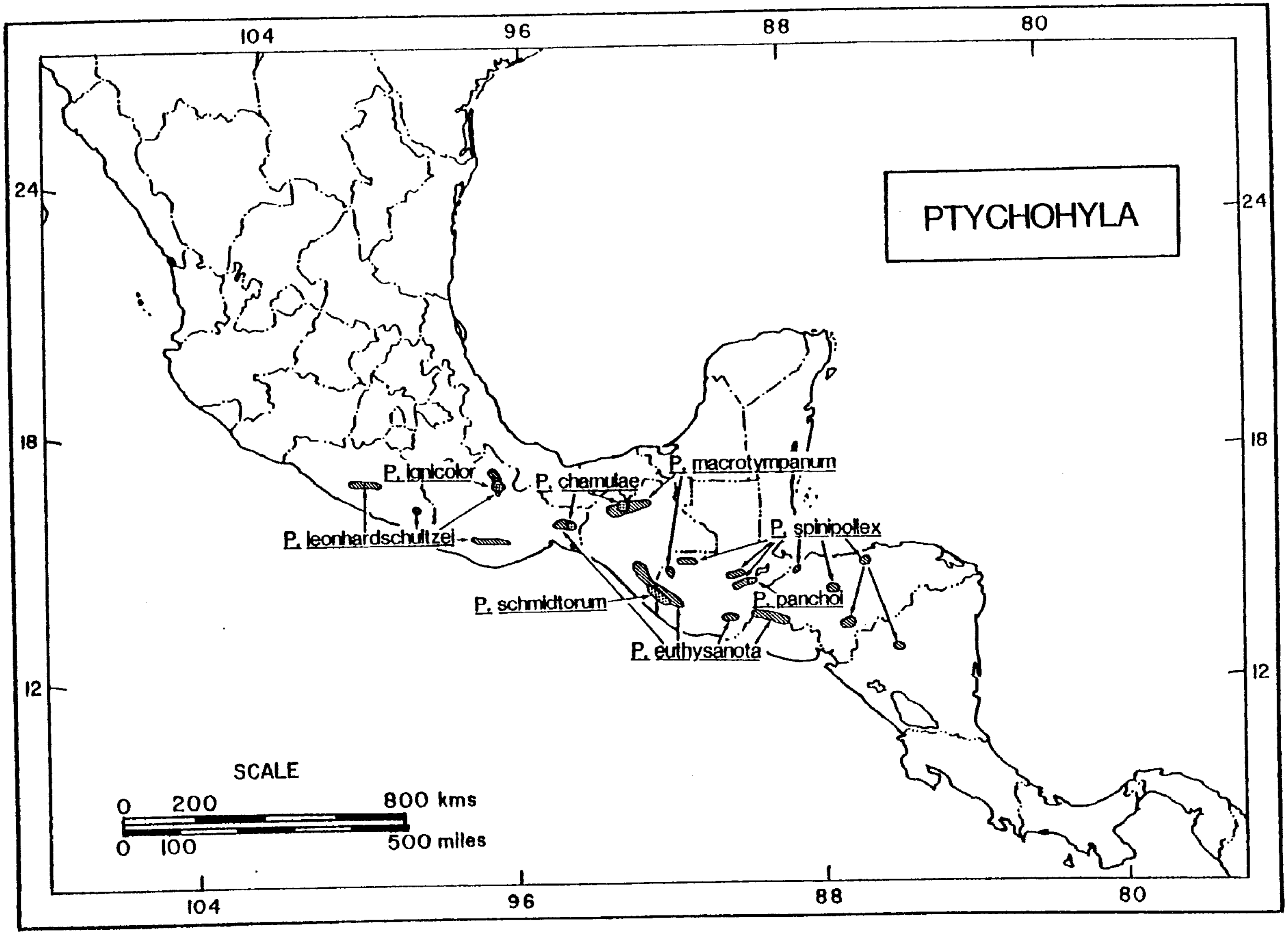
Distribution.-- The combined distributions of the members of this genus includes the mesic forests flanking the highlands of southern Mexico and Nuclear Central America (Fig. 13). The species of *Ptychohyla* primarily inhabit cloud forests, but will invade drier highland forests along the fingers of wet forest that follow streams. Members of the genus may range up to 2200 m and in a few areas of high relief characterized by cascading, cold streams, several species may descend to about 350 m in upper tropical wet forest.

Outgroup comparisons.-- A major problem with a phlogenetic analysis of the genus *Ptychohyla* is the selection of an outgroup. Various lineages of *Hyla* have been suggested to be closely related to *Ptychohyla* including the *H. pinorum*, *H. erythromma*, *H. salvadorensis*, and *H. uranochroa* groups. For determining the polarity of characters, I have used these groups as well as the *H. melanomma*, *H. bogotensis* (information on this group also provided by Duellman, 1972), and *H. rivularis* groups. I have examined preserved and skeletal material of all the species of *Ptychohyla* as well as members of the outgroups.

CHARACTER ANALYSIS

Head shape.-- The snout may be acuminate or truncate in dorsal profile. I consider acuminate to be pleisiomorphic and truncate the derived condition. A rostral keel is a derived feature found in three

FIGURE 13. Distribution of the genus *Ptychohyla*. Distributions for members of the *P. schmidtorum* group and *P. panchoi* are stippled; those of members of the *P. euthysanota* group are indicated by parallel lines.


PTYCHOHYLA
P. ignicolor
P. leonhardschultzei
P. chamulae
P. macrotympanum
P. spinipollex
P. schmidtorum
P. panchoi
P. euthysanota
SCALE
0 200 800 kms
0 100 500 miles
104
96
88
80
24
18
12

species of *Ptychohyla* with acuminate snouts and appears to have been derived at least twice in this genus. The development of a fleshy rostral keel has occurred in several divergent lines of Middle American hylids including *Hyla* (*chryses* and *siopela*) and *Plectrohyla* (*ixil* and *matudai*). The snout may be round or truncate in lateral view. Profiles of the head are more than merely convenient characters as they reflect the distinctive and usually consistent shapes of the underlying premaxillae and nasal bones. I consider round to be the derived condition.

Hands and feet.-- Many different groups of hylids possess nuptial excrescences. Among most of the stream-breeding hylids of Middle America these generally occur as a large patch of tiny spinules and this appears to be the pleisiomorphic condition. In the *P. euthysanota* group and *P. panchoi* the spines are enlarged, whereas in the *P. schmidtorum* group the nuptial excrescences are absent. I consider the enlargement or loss of nuptial excrescences as being derived.

Many stream-breeding hylids have hands that are approximately one-half to one-third webbed. This condition characterizes members of the *P. euthysanota* group. I agree with Duellman (1970) in his use of the term "vestigial" to describe the webbing of the *P. schmidtorum* group as it connotes a secondary loss or the apomorphic condition. The small ridge of skin extending from the inner metatarsal tubercle along the inner edge of the tarsus is not strongly developed in any of the frogs examined, nor is it universally present in the outgroups. Nevertheless I regard the absence of a tarsal fold in three species of *Ptychohyla* as a derived condition.

Glands.-- Previously, the single character that defined the genus *Ptychohyla* was the presence of ventrolateral glands in breeding males; the nature and function of these glands is uncertain but they appear to be composed of large concentrations of mucous glands. The considerable intraspecific variation in the development and extent of the gland, compounded with seasonal variation, makes assessment difficult, but the presence of the gland is no doubt a derived feature. *Hyla erythromma* also possesses a ventrolateral gland, although it is not greatly developed. *Hyla salvadorensis* and *H. legleri* both possess a pale, thin subcutaneous layer of cells that appear to be glandular. Previous consideration of the relationships of the various species of *Ptychohyla* have only considered the derivation of the ventrolateral glands with little regard to the possibility of their secondary loss. The members of the *H. uranochroa* group lack this gland, but possess other distinctive features that might place them as a sister group to the *P. schmidtorum* group within the genus *Ptychohyla*. Some specimens of *H. uranochroa* have numerous small, yellow, mucous glands on the venter, and these extend up onto the flanks in some male specimens. Until evidence to the contrary becomes available, I somewhat reluctantly believe that members of this group should be considered convergent on some members of the genus *Ptychohyla* and that members of the *H. uranochroa* group independently derived the mucous glands that characterize species of *Ptychohyla*. It is perhaps notable that male *H. bogotensis* possess numerous, small, yellow mucous glands scattered over the flanks and dorsum; these glands seem to be totally absent in females. When present in *Ptychohyla*, the mental gland also is composed of many small mucous glands that are concentrated on the throat. *Ptychohyla ignicolor* and *P. chamulae* are the only members of the genus *Ptychohyla* that have this character. The only other hylid in Middle America possessing a mental gland is *H. colymba* that obviously has its affinities with other South American species (Duellman, 1972).

Pattern and coloration.-- Generally there is so much variation in characteristics of color and pattern that it is safest to exclude these features from analysis. Within the genus *Ptychohyla* however there are several relatively distinctive traits worth considering. The dorsal pattern of the *P. euthysanota* group tends to be usually mottled, spotted, or flecked whereas that of the *P. schmidtorum* group is uniformly colored. The pattern of the flanks is one of the most distinctive characters and, for the sake of consistency, I have used the pattern found in large females because they often possess a better defined pattern than males. The pattern may be mottled, spotted, or striped. The upper arm may be pigmented above and unpigmented below or possess a white patch or stripe. In the *P. euthysanota* group the white stripe is generally poorly defined or absent. Some members of the genus possess a distinctive white suborbital spot that may be confluent with a broad white stripe on the upper lip. Iris color may be bronze or copper in the *P. euthysanota* group. *Ptychohyla panchoi* and members of the *P. schmidtorum* group have yellow, orange, or bright red irises, often with a metallic reflectance. Members of the *H. salvadorensis* group are variable with one member (*salvadorensis*) having a deep copper colored iris and the other (*legleri*) having an iris that is metallic red.

Larval morphology.-- Tadpoles reflect different kinds of adaptations to different environments than those of the adults; therefore correlation between the larval features and those of the adults may be lacking (Duellman, 1970). Nevertheless, tadpole morphology is of considerable taxonomic importance and was used extensively in defining Middle American groups of hylids (Duellman, 1970). The larvae of the *P*. *euthysanota* group possess large, ventral mouths, and those of the *P*. *schmidtorum* group have greatly enlarged funnel-shaped mouths. The lips of *H*. *legleri* and *H*. *salvadorensis* are folded laterally and in this respect resemble *H*. *erythromma*, *P*. *panchoi*, and the *P*. *euthysanota* group. The greatest proliferation of denticle rows is found in tadpoles inhabiting the swift waters of mountain streams. The ancestor of *Ptychohyla* probably possessed a generalized number (2/3) of denticle rows. Invasion of mountain streams was accompanied by the selection for a higher number (4/6) of long denticle rows, a conspicuous feature of the *P*. *euthysanota* group. A separate lineage comprised of members of the *P*. *schmidtorum* group adapted to plunge pools and the quieter portions of the streams developing 3/3 short denticle rows. Species with 4/6 denticle rows have a double row of oral papillae and short, blunt serrations on the beak; species with 3/3 denticle rows have a single row of oral papillae and long, pointed beak serrations.

The depth of the dorsal fin relative to the caudal musculature is greater in the *P*. *euthysanota* group and less in *P*. *panchoi* and the *P*. *schmidtorum* group.

Mating call.-- The mating call of species in the genus *Ptychohyla* may consist of a single, low-pitched note that has been described as "wraaack" (*P. euthysanota*, *P. macrotympanum*, *P. leonhardshultzei* and *P. spinipollex*) (Duellman, 1970), or it may consist of a series of notes that are short, raucous, and low-pitched (*P. ignicolor*, *P. schmidtorum* and *P. chamulae*) or short, high-pitched "peeps" (*P. panchoi*). The various habitats occupied by different species of frogs has played an important role in determining the call characteristics. It seems reasonable to assume that the ancestor of *Ptychohyla* possessed a single, low-pitched call note. A high-pitched, piercing, multinote call was derived as an adaptation to the environment along mountain streams.

Osteology.-- The nasal may be in broad contact with the sphenethmoid or may be reduced where no contact occurs. However there is considerable discordancy within and among species in this character. The shape and size of the prevomers varies considerably, but in general they may be characterized as small or large with regard to the amount of contact they have with the sphenethmoid. They are most extensively developed in *P. spinipollex* and relatively small in the *P. schmidtorum* and *H. uranochroa* groups. *Hyla legleri*, *H. rufioculis*, *H. uranochroa*, and probably *H. lythrodes* possess a foramen in the prevomer that is lacking in members of the genus *Ptychohyla*. The extent of the development of the quadratojugal seems to vary among species and generally does not contact the maxillary except in *P. spinipollex* and *P. leonhardschultzei*. The pars facialis contacts the posterior process of the maxillary in only two species of the *P. euthysanota* group. The pars palatina and the lingually projecting flap of skin extending from this ridge is weakly developed in the _P_. _schmidtorum_ and _H_. _uranochroa_ groups. The zygomatic ramus is short and slightly expanded in _P_. _euthysanota_ and _P_. _macrotympanum_.

Table 11 summarizes the characters used to construct a phylogeny (Fig. 14) of the genus _Ptychohyla_.

RELATIONSHIPS

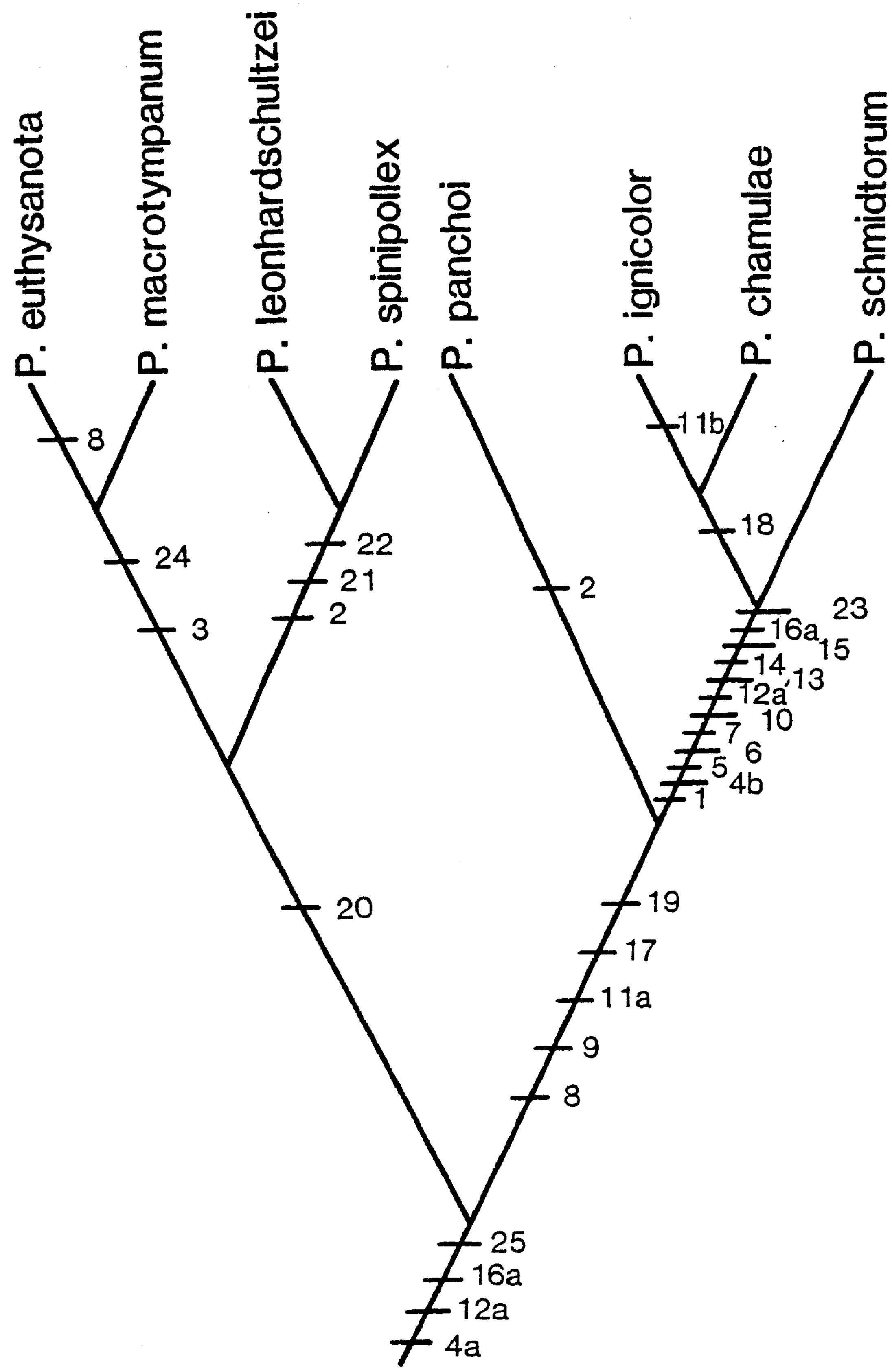
Comparing the proposed phylogeny of _Ptychohyla_ (Fig. 14) with species distributions (Fig. 13), it is apparent that the areas of sympatry are inhabited by only fairly distantly related species, generally with different kinds of tadpoles. Perhaps competition between tadpoles is the limiting factor, or perhaps this is a reflection of the evolutionary history of the group. These hypotheses need not be mutually exclusive.

Two distinctive lineages of _Ptychohyla_ are defined primarily on the basis of larval morphology, call, and presence or absence of nuptial excrescences. The _P_. _schmidtorum_ group in particular is well differentiated by a number of derived characters. _Ptychohyla_ _panchoi_ shares characters with both groups. Two pairs of sister species, _P_. _leonhardschultzei_--_P_. _spinipollex_ and _P_. _ignicolor_--_P_. _chamulae_ are separated by the Isthmus of Tehuantepec, and each of these sister species pairs in turn form the sister unit to a species inhabiting the Pacific cloud forest of Chiapas and Guatemala.

TABLE 11. Comparison of certain features in species of *Ptychohyla*. * refers to larval characteristics. See text for details.

PTYCHOHYLA Character	*P. euthysanota*	*P. macrotympanum*	*P. leonhardschultzei*	*P. spinipollex*	*P. panchoi*	*P. ignicolor*	*P. chamulae*	*P. schmidtorum*
1. Premaxillae	acuminate	acuminate	acuminate	acuminate	acuminate	truncate	truncate	truncate
2. Rostral keel	absent	absent	present	present	present	absent	absent	absent
3. Lateral profile	round	round	truncate	truncate	truncate	truncate	truncate	truncate
4. Nuptial escrescences	large	large	large	large	large	absent	absent	absent
5. Hand webbing	moderate	moderate	moderate	moderate	moderate	vestigial	vestigial	vestigial
6. Tarsal fold	presnet	present	present	present	present	absent	absent	absent
7. Dorsal pattern	mottled	mottled	mottled	mottled	mottled	uniform	uniform	uniform
8. Flanks	striped	mottled	spotted	spotted	striped	striped	striped	striped
9. Upper arm	dark	dark	dark	dark	pale	pale	pale	pale
10. Suborbital coloration	dark	dark	dark	dark	pale	pale	pale	pale
11. Iris color	bronze	bronze	bronze	bronze	red	yellow	red	red
12.* Mouth shape	large, ventral	large, ventral	large, ventral	large, ventral	large, ventral	funnel-shaped	funnel-shaped	funnel-shaped
13.* Lateral fold	present	present	present	present	present	absent	absent	absent
14.* Rows oral papillae	2	2	2	2	2	1	1	1
15.* Beak serrations	short, blunt	short, blunt	short, blunt	short, blunt	short, blunt	long, pointed	long, pointed	long, pointed
16.* Denticle rows	4/6	4/6	4/6	4/6	4/6	3/3	3/3	3/3
17.* Depth of dorsal fin	greater	greater	greater	greater	less	less	less	less
18. Mental gland	absent	absent	absent	absent	absent	present	absent	present
19. Call	single	single	single	single	multinote	multinote	multinote	multinote
20. Prevomers	large	large	large	large	small	small	small	small
21. Quadratojugal-maxillary	separated	separated	contact	contact	separated	separated	separated	separated
22. Pars fascialis-maxillary	separated	separated	contact	contact	separated	separated	separated	separated
23. Pars palatina	strong	strong	strong	strong	strong	weak	weak	weak
24. Zygomatic ramus	broad	broad	narrow	narrow	narrow	narrow	narrow	narrow
25. Ventrolateral glands	present	present	present	present	present	present	present	present

FIGURE 14. A theory of the relationships of the frogs of the genus *Ptychohyla*. Numbers refer to the characters presented in Table 11. The letters a and b suffixed to numbers refer to sequence of character transformations; a and a' denote independently derived characters. Characters 2 (keeled rostral) and 8 (white stripe on flanks) are homoplasies.


P. euthysanota
P. macrotympanum
P. leonhardschultzei
P. spinipollex
P. panchoi
P. ignicolor
P. chamulae
P. schmidtorum
8
24
3
22
21
2
2
11b
18
23
16a
15
14
13
12a
10
7
6
5
4b
1
20
19
17
11a
9
8
25
16a
12a
4a

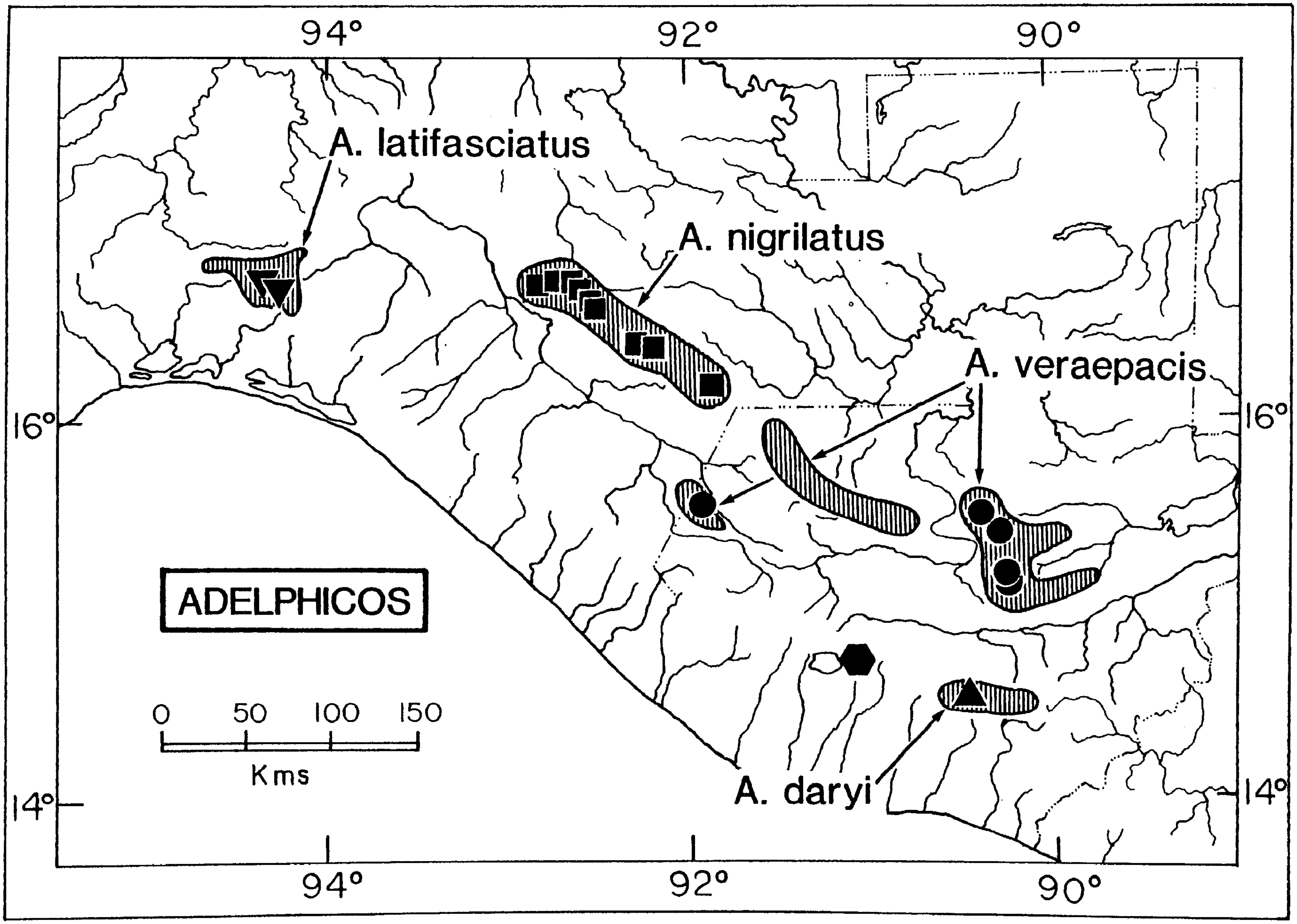
The genus ADELPHICOS

Composition.-- The genus *Adelphicos* is comprised of five or six species of small burrowing colubrids. Only *A. quadrivirgatus* is polytypic with three subspecies. The genus is defined by the posterior part of the body lacking hypapophyses, and undivided sulcus spermaticus, usually seven supralabials with the third and fourth entering the orbit, an elongate loreal that borders the eye, dorsal scales in 15 unreduced rows, a divided anal, and a pattern on the body that some combination of vertebral, paravertebral and/or lateral stripes. The genus was most recently reviewed by Campbell and Ford (1982) and much of the information herein is taken from that source.

Distribution.-- One species, *A. quadrivirgatus*, is distributed in the lowlands and foothills of the Atlantic drainage from central Veracruz, Mexico, through Guatemala; on the Pacific it occurs from central Oaxaca, Mexico, to Guatemala. The remaining species are distributed at moderate and intermediate elevations in the highlands of Nuclear Central America (Fig. 15). The highland species are most frequently encountered in cloud forests, but also range into humid pine-oak forests.

Adelphicos latifasciatus is apparently restricted to the highlands of southeastern Oaxaca; *A. nigrilatus* ranges across the northern portion of the Mesa de Chiapas; *A. veraepacis* is discontinuously distributed in Guatemala with populations in the Montanas de Cuilco, Sierra de los Cuchumatanes, Sierra de las Minas, and the highlands of Alta Verapaz; and *A. daryi* is known from the highlands to the southeast of Guatemala

FIGURE 15. Distribution of snakes of the genus *Adelphicos*. Hexagon represents unallocated specimen. Specimens originating from the Sierra de los Cuchumatanes lack precise locality data and therefore are not plotted.


94°
92°
90°
A. latifasciatus
A. nigrilatus
A. veraepacis
16°
16°
ADELPHICOS
0
50
100
150
Kms
A. daryi
14°
14°
94°
92°
90°

City that are referred to as the Las Nubes block region. The status of an isolated population on the Pacific versant of Guatemala was deferred by Campbell and Ford (1982) until additional material became available.

Outgroup comparisons.-- The relationships of *Adelphicos* with other Middle American colubrids remain obscure. Therefore, for purposes of phylogenetic analysis, a number of other burrowing xenodontine colubrids were examined, with particular emphasis on the genera *Geophis* and *Atractus*. Both of these genera have been suggested to have close affinities with *Adelphicos* (Downs, 1967; Dunn, 1928; Smith, 1942); however, the unforked sulcus spermaticus and divided anal of *Adelphicos* precludes its placement in either genus.

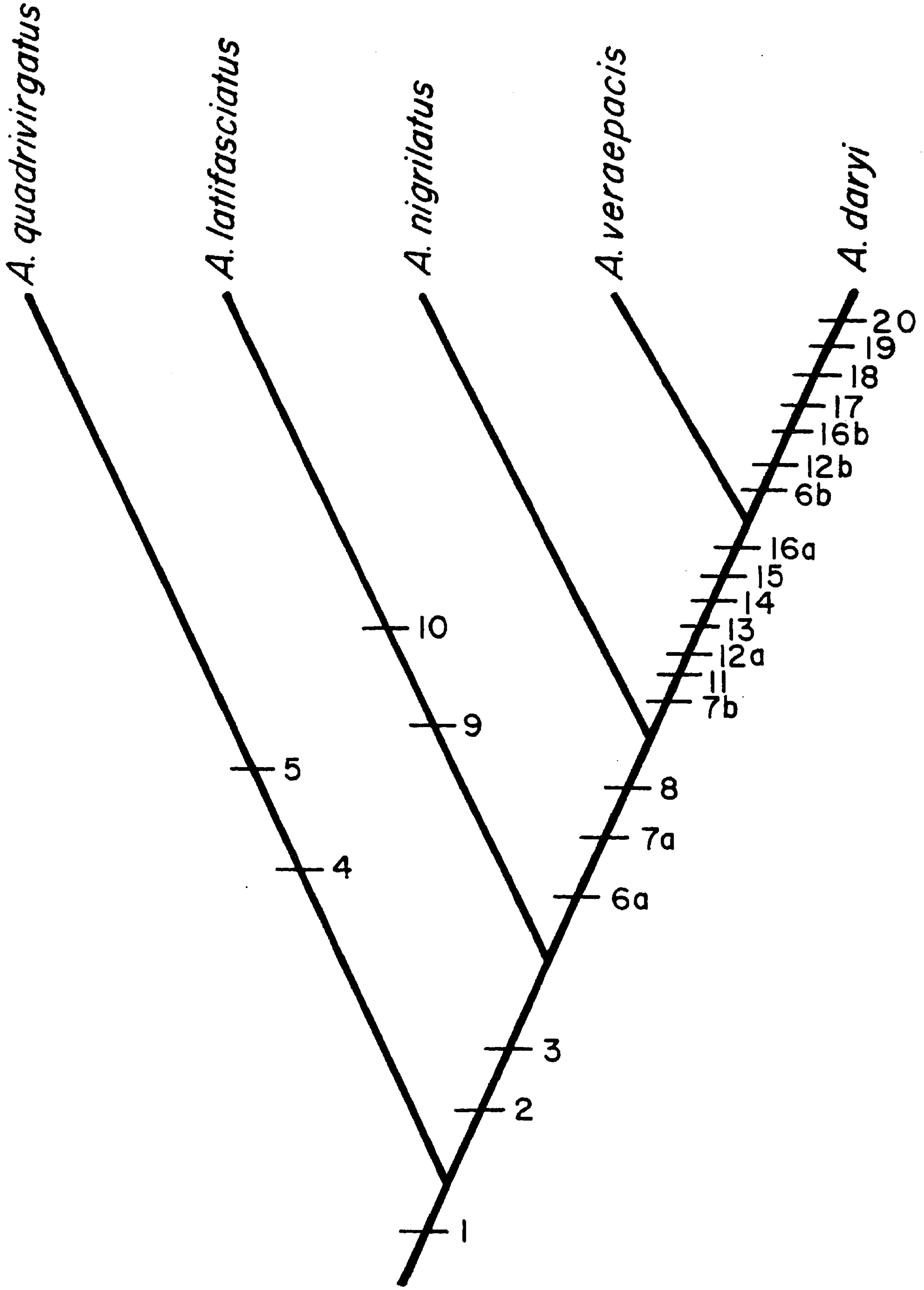
Character analysis.-- A thorough account of characters distinguising species of *Adelphicos* was given by Campbell and Ford (1982); these are summarized in Table 12. Characters such as size and proportion, number of ventrals and subcaudals, cranial and vertebral osteology, and color and pattern clearly differentiate the species.

Relationships.-- The proposed phylogeny of *Adelphicos* (Fig. 16) places the highland members of the genus closer to each other than any is to the lowland *A. quadrivirgatus*. *Adelphicos daryi* is the most derived and possesses a number of characters that seem to firmly establish it as the sister species to *A. veraepacis*. These two species form the sister group to *A. nigrilatus*, which in turn forms the sister group to *A. latifasciatus*. The latter species possesses several plesiomorphic characters not present in other highland species of *Adelphicos* including a high number of subcaudals, an immaculate venter,

TABLE 12. Comparison of certain features in species of *Adelphicos*.

ADELPHICOS Characters	*A. quadrivirgatus*	*A. latifasciatus*	*A. nigrilatus*	*A. veraepacis*	*A. daryi*
1. Sulcus spermaticus	Single	Single	Single	Single	Single
2. Lateral stripes	Narrow	Broad	Broad	Broad	Broad
3. Hemipenial spines	Few	Many	Many	Many	Many
4. Chin shields	Enlarged	Small	Small	Small	Small
5. Position of first ventral	Anterior	Posterior	Posterior	Posterior	Posterior
6. Number of subcaudals (females)	38—45	37—41	26—36	24—31	19—22
7. Ventral pigmentation	Immaculate	Immaculate	Usually some pigmentation	Moderately pigmented	Heavily pigmented
8. Number of dentary teeth (mode)	10—11(11)	11(11)	10—11(10)	10—11(10)	8—9(9)
9. Vertebral stripe	Narrow or absent	Broad	Narrow or absent	Narrow	Narrow
10. Paravertebral stripe	Present	Absent	Present	Present	Present
11. Dorsal coloration	Yellow, tan, red	Reddish to pale brown	Orange, red, or pale brown	Dark brown or grey	Dark brown
12. Anterior processes	Weakly developed	Weakly developed	Weakly developed	Moderately developed	Well developed
13. Median parietal crest	Absent	Absent	Absent	Present	Present
14. Dorsolateral edges of parietal	Poorly defined	Poorly defined	Poorly defined	Well defined	Well defined
15. Maximum size	322 mm	437 mm	451 mm	524 mm	574 mm
16. Profile	Acuminate	Acuminate	Acuminate	Subtruncate	Truncate
17. Hypapophyses of anterior trunk vertebrae	Narrow	Narrow	Narrow	Narrow	Expanded
18. Teeth	Slender	Slender	Slender	Slender	Stout
19. Frontal	Narrow	Narrow	Narrow	Narrow	Broad
20. Premaxilla	Not flared	Not flared	Not flared	Not flared	Flared

FIGURE 16. A theory of the relationships within the genus *Adelphicos*. Numbers refer to the characters presented in Table 12.


A. quadrivirgatus
A. latifasciatus
A. nigrilatus
A. veraepacis
A. daryi
20
19
18
17
16b
12b
6b
16a
15
14
13
12a
11
7b
10
9
8
7a
6a
5
4
3
2
1

and a moderate number of teeth.

If the cladogram is compared with the distribution of members of the genus (Fig. 15), it suggests that fragmentation of the ranges has proceeded in a west to east direction. The single specimen known from the highlands to the west of Lago de Atitlan (UMMZ 127837) most closely resembles *A. nigrilatus* on the Mesa de Chiapas rather than more proximate populations of *A. daryi* or *A. veraepacis*. The implications of this specimen are discussed later.

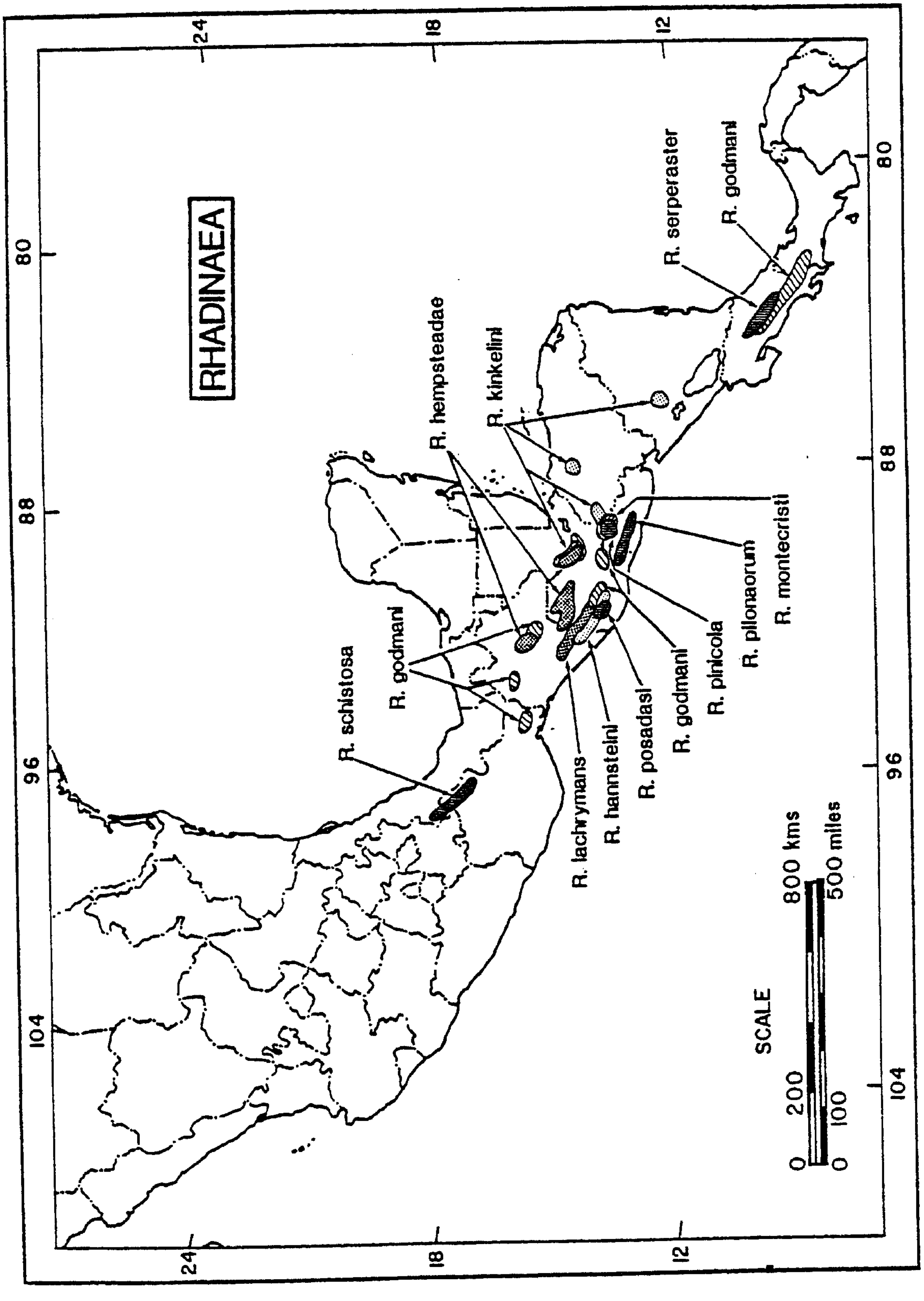
The *RHADINAEA GODMANI* group

Composition.-- The genus *Rhadinaea* is a diverse and widespread assemblage of New World colubrid snakes for which Myers (1974) proposed eight species groups. The *R*. *godmani* group is one of the largest of these, containing eleven monotypic species: *R*. *godmani*, *hannsteini*, *hempsteadae*, *kinkelini*, *lachrymans*, *montecristi*, *pilonaorum*, *pinicola*, *posadasi*, *schistosa*, and *serperaster*. Myers (1974) defined this group as having the last maxillary tooth in line with the others, a diastema that is absent or small and variable, a slightly bilobated hemipenis with a basal naked pocket, a variable number of scale rows (17, 19, or 21), the subpreocular absent, anal ridges often present, an inverted "U"-shaped marking on the rostral, and the anterior supraoculars with dark edges and pale centers.

Distribution.-- This group is essentially montane with most of the members occurring in the Nuclear Central American highlands (Fig. 17). One species (*R*. *schistosa*) is in Veracruz; another (*R*. *serperaster*) occurs in Costa Rica; and the most widespread species of the group (*R*. *godmani*) ranges from Oaxaca to Panama. Two species have most of their ranges on the Atlantic drainage of Nuclear Central America: *R*. *hempsteadae* and *R*. *kinkelini*; and six species are restricted to the Pacific versant: *R*. *lachrymans*, *R*. *montecristi*, *R*. *hannsteini*, *R*. *posadasi*, *R*. *pilonaorum*, and *R*. *pinicola*.

Most species in the *R*. *godmani* group inhabit cloud or pine-oak forests at moderate or intermediate elevations, but *R*. *pilonaorum*, *R*. *posadasi*, and *R*. *schistosa* have been taken at less than 1000 m from

FIGURE 17. Distributions of the snakes of the *Rhadinaea godmani* group.


RHADINAEA
R. schistosa
R. godmani
R. hempsteadae
R. kinkelini
R. serperaster
R. godmani
R. montecristi
R. pilonaorum
R. pinicola
R. godmani
R. posadasi
R. hannsteini
R. lachrymans
SCALE
0 200 800 kms
0 100 500 miles
24
18
12
80
88
96
104

banana and coffee groves.

Outgroup comparisons.-- Although there is growing evidence that the genus *Rhadinaea* is paraphyletic (Cadle, 1982), it seems reasonable to assume that the various groups proposed by Myers (1974) form monophyletic lineages, and that various combinations of these groups may be each others closest relatives. For an outgroup to the *R. godmani* group I have used the *R. taeniata* and *R. decorata* groups because they occur in a geographically adjacent region and I am familiar with most of the species in these groups.

Character analysis.-- The *R. godmani* group contains the only species of *Rhadinaea* with more than 17 dorsal scale rows. *Rhadinaea godmani* (and occasionally *R. hempsteadae*) have 21 dorsal scale rows; *R. hempsteadae*, *R. montecristi*, and *R. serperaster* usually have 19 dorsal scale rows; all other species possess 17 dorsal scale rows. Although 19 or 21 dorsal scale rows is unique to the *R. godmani* group in *Rhadinaea*, Myers (1974) indicated this was probably a primitive rather than derived feature. Most members of the *R. godmani* group have a moderate number of teeth, 15--23, with a modal number of 16--20. However, *R. pilonaorum*, *R. pinicola*, and *R. posadasi* possess a reduced number of teeth, 11--13, that seems clearly to be the derived condition. Six species are diminuitive (<350 mm) and have a low number of ventrals (see Table 13), characters that I consider derived from a larger size (>450 mm) with more numerous ventrals. *Rhadinaea schistosa*, *R. pinicola*, *R. pilonaorum*, and *R. posadasi* have a dark dorsum, usually with a pale streak in the center of each scale, a unique coloration in

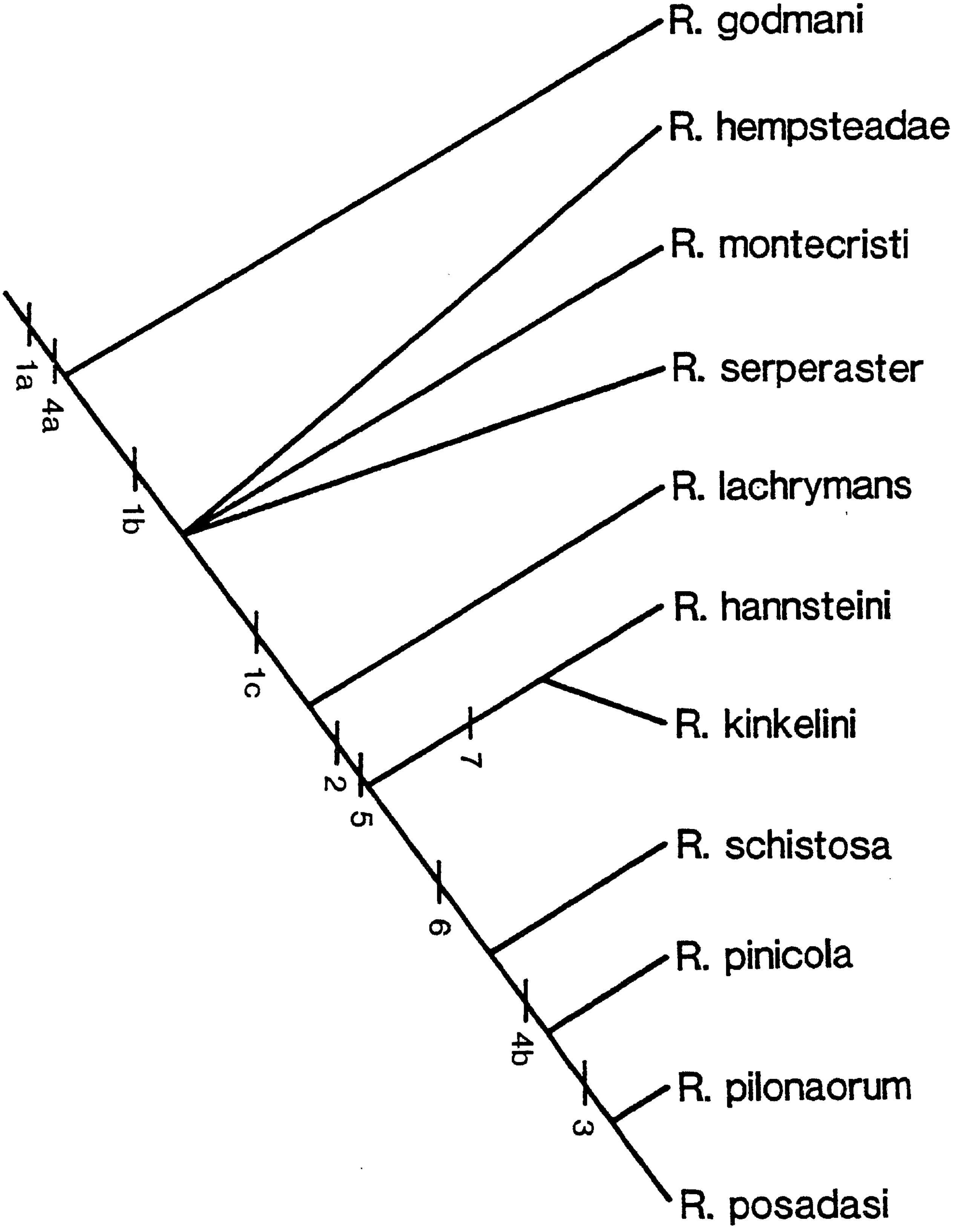
TABLE 13. Comparison of certain features in species of the *Rhadinaea godmani* group. Data taken from Myers (1974) and specimens in KU and UTACV.

RHADINAEA	*R. godmani*	*R. hempstaedae*	*R. montecristi*	*R. seperaster*	*R. hannsteini*	*R. kinkelini*	*R. lachrymans*	*R. pilonaorum*	*R. pinicola*	*R. posadasi*	*R. schistosa*
1. Dorsal scale rows	21	19	19	19	17	17	17	17	17	17	17
2. Ventrals (males)	160--177	162--174	158--165	156--159	140--147	136--148	154--170	151	150	136--139	145--147
	(169.8)	168.4)	161.0)	(157.4)	(143.9)	(142.0)	(163.8)	--	--	(137.5)	(146.3)
(females)	168--186	168--189	164--176	165--172	145--152	148--163	160--183	159--164	--	143--146	153--154
	(176.6)	(178.9)	(167.2)	(167.7)	(150.0)	(157.3)	(168.0)	(161.5)	--	(144.3)	(153.5)
3. Subcaudals (males)	78--95	89--94	79--87	69--79	67--75	81--83	75--89	--	77	92--95	40--42
	(86.8)	(91.6)	(82.9)	(74.2)	(71.3)	(82.0)	(82.8)	--	--	(93.5)	(41.0)
(females)	71--81	74--82	71--79	66--71	62--68	70--73	61--77	98	--	86--93	31--34
	(75.6)	(77.1)	(74.6)	(68.6)	(65.3)	(72.0)	(70.4)	--	--	(88.4)	(32.5)
4. Number of maxillary	16--20	17--19	19--23	16--17	15--17	15--16	18--21	11	13	11	16--17
teeth (mode)	(19)	(18)	(20)	(17)	(16)	(16)	(19)	(11)	(13)	(11)	(16)
5. Size	Large	Large	Large	Large	Small	Small	Large	Large	Large	Large	Large
6. Dorsum	Striped	Stiped	Striped	Striped	Striped	Striped	Striped	Dark	Dark	Dark	Dark

Rhadinaea. Within these species that have a dark dorsum, *R. schistosa* has a uniquely short tail with a low number of subcaudals, whereas *R. pilonaorum* and *R. posadasi* have a greater number of subcaudals than any other member of the group (Table 13). The hemipenes of *R. hannsteini* and *R. kinkelini* are similar in most respects and seem to be derived from the primitive condition as exemplified by *R. godmani*.

Relationships.-- A theory of the relationships among the members of the *R. godmani* group is given in Figure 18. The most widespread member of the group, *R. godmani*, appears to be the sister species of all other members. I am unable to find satisfactory characters that might shed some light on the relationships of *R. hempsteadae*, *R. montecristi*, and *R. serperaster* to each other, but the presence of 19 scale rows suggests that these species are derived with respect to *R. godmani* and plesiomorphic compared to other members of the group. Myers (1974) suggested that peripherally isolated populations of *R. godmani* gave rise to these species; however, that these species have a common ancestor with 19 dorsal scale rows seems to be more parsimonious. Within the group of species that has 17 dorsal scale rows, *R. lachrymans* seems to be the least derived; it is of moderate size and possesses a relatively high number of ventrals. Four species of *Rhadinaea* possess a derived dorsal coloration and appear to comprise a monophyletic lineage. Of these, *R. schistosa* seems to have been split off at a comparatively early time and become subsequently isolated to the west of the Isthmus of Tehuantepec. The other three species occur along the Pacific versant of Nuclear Central America and are similar by having few maxillary teeth.

FIGURE 18. A theory of the relationships of the snakes of the *Rhadinaea godmani* group. Numbers refer to the characters presented in Table 13.


R. godmani
R. hempsteadae
R. montecristi
R. serperaster
R. lachrymans
R. hannsteini
R. kinkelini
R. schistosa
R. pinicola
R. pilonaorum
R. posadasi
1a
4a
1b
1c
2
5
7
6
4b
3

The genus *BOTHRIECHIS*

Composition.-- The approximately 60 species of Neotropical pitvipers comprising the genus *Bothrops* (sensu lato) (Peters and Orejas-Miranda, 1970; Hoge and Romano-Hoge, 1982) are amazingly widespread, occurring in the north from the states of Tamaulipas and Colima in Mexico southward to Chubut Province in Argentina. This group of snakes occupies ecologically diverse habitats, including the deserts of south-central Mexico, the rainforests of Central and South America, the wet montane forests found on the windward slopes of the major ranges in Middle and South America, and subalpine and paramo regions in Mexico and northern South America. They encompass a great number of morphological types. Many species are terrestrial; several groups are arboreal. Most lowland species tend to be nocturnal, whereas highland species may confine their activity to short periods during the day. The limited ecological data available reveals that life history strategies are accordingly varied. Therefore it is not surprising that there has been a great deal of confusion and controversy regarding the nomenclature and relationships of the Neotropical pitvipers. Perhaps the best partitioning of the Neotropical pitvipers to date is that of Burger (1971). I believe his proposed divisions are an attempt to group these snakes in "natural taxa" (for a discussion of the connotations of this concept see Wiley, 1981). Unfortunately, Burger's doctoral dissertation was never published and therefore has no validity under the rules of the International Code of Zoological Nomenclature. Accordingly, the changes proposed by Burger have not been generally followed except by Smith (1976).

I recognize a closely related group of seven arboreal species in the genus *Bothriechis* occurring primarily in Middle America (*B. schlegeli* extends into northern South America). These species are characterized by:

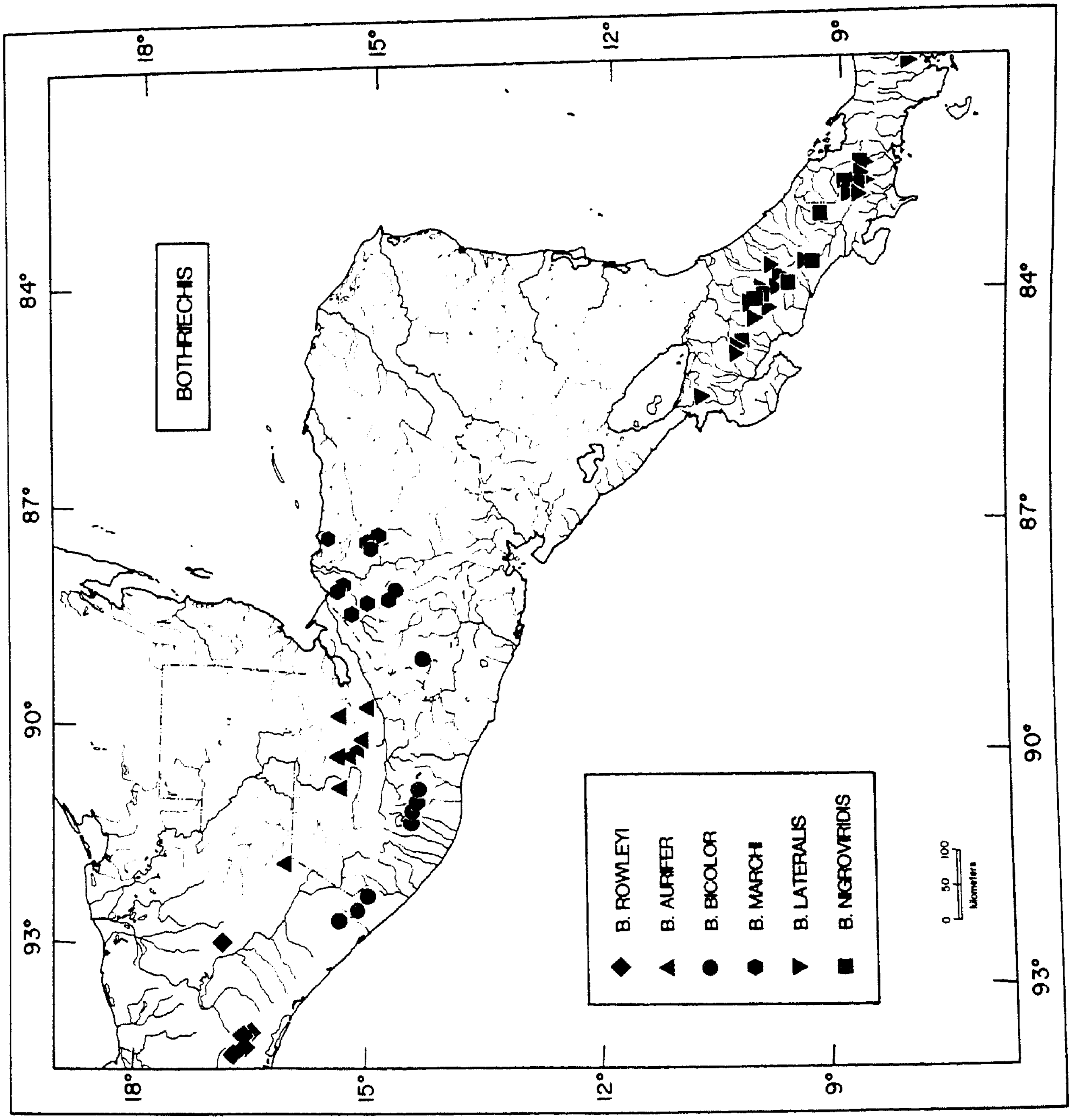
1. A sharp canthus rostralis, but unelevated snout, rostral broader than high.
2. Supralabials 9--12 (except in *B. schlegeli* which generally has 8).
3. A nasal pore that is situated deep in the nostril.
4. A relatively long prehensile tail.
5. Undivided subcaudals.
6. A relatively short, blunt tail spine, generally no longer than the preceeding two subcaudals.
7. Paraventral scale row smooth (weakly keeled in *B. rowleyi*).
8. First and second parasubcaudal scale rows strongly keeled.
9. Ground color of the dorsum usually bright green or yellow.
10. Venter without blotches (except in *B. schlegeli*).
11. A broad and slightly curved ectopterygoid, without truncate dorsolateral projections.
12. A triangular palatine with the apex near or posterior to mid-palatine.
13. Pleurapophyses of caudal vertebrae projecting downward, from about mid-tail not projecting laterally to prezygapophyses in dorsal view.
14. Haemapophyses of caudal vertebrae greatly elongate and narrow, not greatly expanded distally.

The oldest available name for this group is *Bothriechis*, proposed by Peters (1859) in his description of *B. nigroviridis*. I propose that this genus be retained for eight Middle American species that seem to be clearly monophyletic and easily distinguishable from other New World pitvipers. Characters 1, 4, 6, 9--11, and 13--14 distinguish this group from the snakes of the *Bothrops nasutus* group commonly known as the "hog-nosed vipers." Characters 4, 6, 8, 9--10, and 13--14 distinguish the group from the terrestrial Middle American pitvipers: *Bothrops barbouri*, *B. godmani*, and *B. nummifer*. Characters 2, 4--7 and 9--14 distinguish the group from the large, terrestrial lowland pitvipers of Middle and South America (e.g. *Bothrops asper* and its relatives), and characters 2--3 and 5--6 generally distinguish members of this group from the arboreal group that includes *Bothrops bilineatus* and *B. castelnaudi* which occurs from Panama to Bolivia. Several species inhabiting the southern portion of the Mexican Plateau, *Bothrops undulatus* and *B. melanurus*, do not seem to fit into any of the groups outlined above, but differ in many respects from *Bothriechis*.

DISTRIBUTION

The genus *Bothriechis* is composed of seven upland species occurring in Middle America (Fig. 19) and one widespread lowland species ranging from southern Mexico to Ecuador. The upland species may occur as low as 500 m and range above 2200 m. All have fairly restricted distributions in wet montane forests. *Bothriechis aurifer*, *B. marchi*, *B. bicolor* and *B. rowleyi* occur north of the Nicaraguan Depression in the Nuclear Central American highlands, and *B. lateralis* and *B. nigroviridis* occur to the south in the Isthmian Middle American

FIGURE 19. Distribution of the highland members of *Bothriechis*. The range of *B. schlegeli* is not mapped, but the species is almost continuously distributed in wet lowland forests from Chiapas, Mexico, to Ecuador.


BOTHRIECHIS
18°
15°
12°
9°
84°
87°
90°
93°
◆ B. ROWLEYI
▲ B. AURIFER
● B. BICOLOR
⬢ B. MARCHI
▼ B. LATERALIS
■ B. NIGROVIRIDIS
0 50 100
kilometers

highlands of Costa Rica and Panama. Although *B. schlegeli* has occasionally been taken up to 1300 m, it is essentially a lowland species with an extensive distribution. The following is a brief outline of the distribution of these species. I have listed specific localities under "Specimens Examined" and Additional Records" in Appendix IV.

Bothriechis rowleyi seems to be restricted to the Sierra Madre de Chiapas in Oaxaca, Mexico. On some maps the highlands of southeastern Oaxaca are indicated as the Sierra de Niltepec or Atravesado. Mountains of this area extend northwest from Cerro Baul near the Oaxaca-Chiapas border unbroken below the 1500 m contour for about 65 km. They reach their highest elevations in the northwest with several peaks, including one known locally as Cerro Azul, exceeding 2300 m. *Bothriechis rowleyi* has been taken at 1372--2134 m. The major portion of its range appears to be in cloud forest on the Atlantic drainage, but it occurs along streams at elevations exceeding 1500 m on the Pacific drainage in humid pine-oak forest. The mesic upland forest inhabited by *B. rowleyi* is isolated from other cloud forests by relatively dry low regions. The Rio Grijalva Valley which supports tropical deciduous forest provides an effective barrier to the interchange of highland fauna between the cloud forests on the northern escarpment of the Mesa Central of Chiapas and that of southeastern Oaxaca. To the east-southeast, several low passes north of Tapanatepec and Arriaga cut across the Sierra Madre de Chiapas and descend below 1500 m, precluding dispersal of mesophilic species between Cerro Baul and the nearest high peak approximately 50 km to the east-southeast, Cerro Tres Picos. The low ridge between these two mountains is covered by tropical deciduous forest and a dry, sparse pine forest.

Bothriechis bicolor occurs along the Pacific versant of the southern Volcanic Cordillera of Guatemala into Chiapas, where the mountains become known as the Sierra Madre de Chiapas. This area is called the "boca del monte" in Guatemala and, as is characteristic of piedmonts, receives a greater amount of precipitation than either the Pacific coastal plain or the Guatemalan Plateau. The species is recorded from the south slopes of Volcan de Agua, Volcan de Fuego, and Volcan Atitlan to Cerro Ovando in southeastern Chiapas. It has been taken at elevations of 457--2000 m in subtropical wet and montane wet forests.

Bothriechis aurifer is distributed across the northern highlands of Guatemala and northeastern Chiapas in montane wet and upper subtropical wet forests. It is known from the Sierra de las Minas, Sierra de Xucaneb, Meseta de Coban, and eastern portion of the Sierra de los Cuchumatanes in Guatemala; and in Mexico from a single locality in eastern Chiapas to the northeast of Comitan. The species probably occurs in the northern part of the Departamento de Huehuetenango in Guatemala. The distribution of B. aurifer is not continuous and is broken by the Rio Negro gorge in Guatemala and possibly also in the relatively low region between the Sierra de los Cuchumatanes and the Chiapan highlands. The species has been collected at 1585--2286 m.

Bothriechis marchi inhabits the subtropical wet and lower montane wet forests of several disjunct mountain ranges in northwestern Honduras including the Sierra de Omoa, Sierra de Espiritu Santo, Sierra de

Sulaco, and Cerro Santa Barbara. Specimens reported from San Pedro Sula and Tela, both at low elevations in tropical moist forest, probably were collected in the Sierra de Omoa and Montanas El Tiburon, respectively. Accordingly, Meyers' (1969) report that the species occurs from near sea level to 1500 m is probably in error. If this species possesses ecological requirements similar to other montane, green, arboreal pitvipers of Middle America, it probably does not descend much below the 500 m contour, the lower limit for B. bicolor. The Sierra de Espiritu Santo lies on the Guatemalan-Honduran border and it is therefore probable that this species occurs in Guatemala in the virgin, uncollected forests of the mountains that flank the lower Motagua Valley to the south. Bothriechis marchi probably also occurs in the virtually uncollected ranges in eastern Honduras such as the Sierra de Agalta, and if Villa's (1962) assertion that it occurs in Nicaragua is correct, it may occur as far south as the Cordillera de Isabella.

Bothriechis nigroviridis occurs in subtropical wet and montane rainforests, and possibly subalpine moist forests in the Cordillera Central and the Cordillera de Talamanca in Costa Rica and Panama. In the Cordillera Central it occurs from Volcan Poas to Volcan Irazu and Volcan Turrialba. A hiatus in its distribution seems to occur between the Cordillera Central and Cordillera de Talamanca. In the Cordillera de Talamanca the species is recorded from Cerro Dragon west to Boquete, Panama. The species inhabits both the Pacific and Atlantic drainages. Taylor, et al. (1974) reported the species as most abundant at elevations exceeding 1500 m and Scott (1969) gave the altitudinal range as 1150--2410 m, pointing out that records for San Isidro El General lying at approximately 700 m, were probably in error. Specimens from this locality may have come from higher portions of the Pacific slope north of this town where the species is known to occur.

Bothriechis lateralis has a wider distribution than *B. nigroviridis* and inhabits lower montane moist and wet forests, subtropical moist and wet forests, and lower montane rainforest. It occurs from Cerro Orosi in the Cordillera de Tilaran through the Cordillera Central and Cordillera de Talamanca to western Panama. It has been collected at several localities on the slopes of Volcan Chiriqui, and Peters (1862) reported the species from near "Veragua," presumably what is now Santiago, the capital of the state of Veragua in Panama. This represents the easternmost record for the species and the mountains north of this locality appear to support an adequate habitat for the species. *Bothriecis lateralis* occurs at lower elevations than *B. nigroviridis*; Taylor, *et al*. (1974) stated it is most common between 1000--1500 m; and Scott (1969) gave its range as 850--1980 m, thus the two species broadly overlap elevationally. Villa's (1962) report that this species occurs "south of Managua" in Nicaragua has not been verified.

Outgroup comparisons.-- For determination of derived features I have used Neotropical pitvipers of the genus *Bothrops*, with particular consideration of some of the Central American species: *B. godmani*, *B. nummifer*, and several members of the *B. nasutus* and *B. asper* groups. I have also compared species of *Bothriechis* with *Bothrops bilineatus*, *B. castelnaudi*, *B. melanurus*, and *B. undulatus*.

CHARACTER ANALYSIS

For purposes of analysis I examined approximately 250 specimens of Bothriechis, exclusive of B. schlegeli. This number constitutes most of the material available in collections in the United States.

Body dimensions and proportions.-- The maximum size attained by snakes of the genus Bothriechis is generally less than a meter, although a few species may occasionally exceed this length. As pointed out by Fitch (1981), sexual size dimorphism is subject to variation in time and space, and is difficult to express in quantitative terms. Nevertheless, there seems to be general trends in sexual size differences in the samples of species of Bothriechis I have examined, and these trends are reflected in the maximum lengths of preserved specimens. Females of B. schlegeli and B. nigroviridis tend to be larger than males and thus are similar to some species of large, terrestrial Bothrops and the arboreal South American group containing B. bilineatus and B. punctatus (Fitch, 1981), whereas the other species of Bothriechis are similar to Bothrops godmani and B. nummifer in that the males attain greater lengths than females (Campbell, ms.). Within the Neotropical pitvipers, the greater size of males seems to be derived. The greatest lengths I have observed in these species are: B. rowleyi, male, 875 mm; B. aurifer, male, 891 mm; B. bicolor, male, 967 mm; B. marchi, male, 968 mm; B. lateralis, male, 815 mm; B. nigroviridis, female, 825 mm; and B. schlegeli, female, 789 mm.

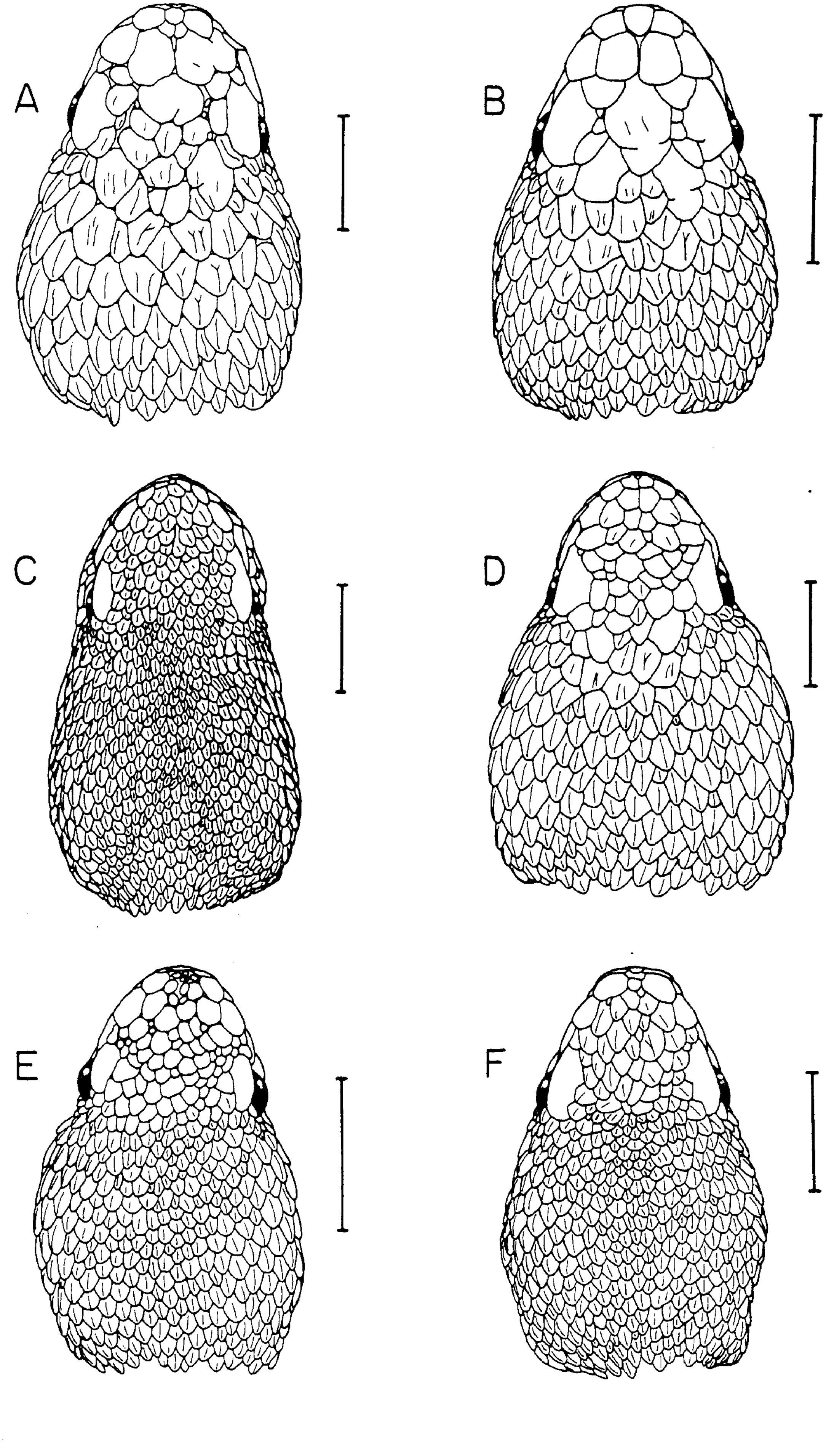
The snout of B. rowleyi and B. aurifer, amd B. nigroviridis tends to be broad and rounded anteriorly in dorsal view, whereas it tends to be more acute in B. bicolor, B. marchi, and B. lateralis. The relative head length (head length/body length) varies little among species and comprises between 5 and 6% of the body length in adults with juveniles having proportionally larger heads. The mean relative tail lengths (tail length/total length) of males is slightly less in *B. schlegeli* (17.1%) and *B. nigroviridis* (17.4%) than in other species (17.8--18.7%), and in females the mean relative length of the tail of *B. schlegeli* is less (15.3%) than the other species (16.6--17.6%). The relatively longer tail lengths seem to be derived and associated with arboreality.

Lepidosis.-- Species of *Bothriechis* are readily distinguishable on the basis of distinctive characters of squamation (Table 14). The scales on the dorsum of the snout and between the supraoculars may be large and either smooth or rugose, but lacking straight, well-formed keels (*B. rowleyi*, *B. aurifer*), intermediate in size and smooth (*B. nigroviridis*), or medium to small with most scales having a sharply raised keel (*B. marchi*, *B. bicolor*, *B. lateralis*, *B. schlegeli*) (Fig. 20). Two pairs of canthals are invariably present; these are larger in *B. rowleyi* and *B. aurifer*, small in *B. bicolor* and *B. schlegeli*, and intermediate in size in the other species. The relative size of dorsal head scales is reflected by the number of scales between the anterior pair of canthals and between the supraoculars which is low in *B. rowleyi* and *B. aurifer*, intermediate in *B. marchi*, *B. lateralis*, *B. nigroviridis*, and *B. schlegeli*, and highest in *B. bicolor*. The number of scales separating the posterior canthal from the supraocular is generally 0 in *B. aurifer*, 0 or 1 in *B. rowleyi*, 1 in *B. marchi*, *B. lateralis*, and *B. nigroviridis*, 2 in *B. bicolor*, and 3 in *B. schlegeli*. Many vipers possess large, flat cephalic plates that are arranged in the

TABLE 14. Aspects of interspecific variation in *Bothriechis*. The following statistics are given: Above, range followed by number of specimens in parentheses; below, mean and standard deviation. See text for details.

	rowleyi	aurifer	bicolor	marchi	lateralis	nigroviridis	schlegeli
Intercanthals	2--4(10) 2.6±0.70	0--2(60) 1.3±0.64	2--7(10) 3.7±1.42	1--4(46) 2.2±0.51	0--3(41) 2.2±0.67	2--4(19) 2.2±0.54	2--6(49) 4.0±0.88
Inter-supraoculars	3--5(10) 4.0±0.82	1--5(61) 3.0±0.82	7--11(11) 9.3±1.27	3--7(46) 5.4±1.07	4--10(41) 7.3±1.51	4--8(19) 5.6±1.43	5--10(50) 7.3±1.31
Inter-rictals	15--19(8) 17.0±1.31	16--21(60) 18.7±1.35	21--31(10) 27.4±3.41	16--24(46) 20.2±1.62	21--28(41) 24.7±1.92	17--25(19) 20.4±2.32	23--34(48) 28.8±2.64
Ventrals(males)	155--163(7) 160.1±3.29	150--162(26) 156.1±2.35	161--175(4) 167.0±6.06	156--174(22) 164.2±4.46	158--171(24) 166.0±3.45	139--156(7) 146.0±6.89	137--169(25) 158.2±5.65
(females)	154--160(5) 157.6±2.19	152--166(36) 156.6±2.91	160--174(7) 165.4±4.83	157--171(24) 163.0±4.13	157--168(17) 162.6±3.22	142--158(12) 150.4±6.35	137--161(24) 152.4±5.45
Subcaudals(males)	58--66(7) 63.1±3.63	57--66(26) 60.6±2.42	61--72(4) 65.8±4.65	59--69(22) 63.0±2.54	56--70(23) 65.6±3.64	49--58(7) 54.0±2.83	53--64(26) 58.6±2.76
(females)	53--57(4) 55.8±1.89	46--61(35) 54.4±3.37	58--65(5) 61.4±2.61	55--65(24) 59.6±2.81	54--66(17) 60.2±3.73	47--58(12) 53.6±3.37	42--56(24) 50.5±3.16
Midbody scale rows	19(12)	18--21(62) 19.1±0.45	21(11)	19--21(46) 19.2±0.64	21--23(41) 22.3±0.93	17--21(19) 19.5±1.07	21--25(50) 22.8±1.02
Supralabials	18--20(12) 19.6±0.67	16--23(58) 19.1±1.07	18--23(10) 20.9±1.66	19--24(46) 20.6±1.16	17--22(41) 20.0±1.03	17--21(19) 19.2±0.96	14--19(50) 16.7±1.10
Infralabials	19--24(12) 21.5±1.57	18--25(58) 21.1±1.27	20--26(10) 23.3±1.83	20--26(46) 22.8±1.41	21--26(41) 23.2±1.43	17--24(19) 20.3±1.59	17--24(50) 21.7±1.22
Relative head length	.049--.056(8) .051±.002	.049--.069(55) .055±.003	.049--.069(9) .057±.006	.046--.071(44) .054±.006	.043--.071(39) .056±.007	.043--.075(17) .056±.007	.049--.075(48) .060±.006
Relative tail length (male)	.167--.198(7) .187±.012	.166--.195(25) .178±.008	.168--.192(3) .178±.012	.171--.197(22) .184±.007	.137--.192(24) .179±.013	.153--.196(7) .174±.013	.154--.189(26) .171±.008
(female)	.162--.185(3) .175±.012	.146--.190(35) .166±.010	.165--.185(5) .176±.007	.153--.197(23) .176±.010	.153--.178(17) .168±.008	.150--.189(12) .168±.012	.132--.171(22) .153±.009

FIGURE 20. Dorsum of the heads of montane species of *Bothriechis* showing arrangement and size of scales. Vertical lines = 10 mm. A) *B. rowleyi*, male, UTACV 6207; B) *B. aurifer*, male, KU 187436; C) *B. bicolor*, female, UMMZ 94644; D) *B. marchi*, male, KU 180263; E) *B. nigroviridis*, female, UTACV 9637; F) *B. lateralis*, male, UTACV 7634.


A
B
C
D
E
F

typical colubrid pattern. This almost certainly represents the plesiomorphic condition whereas more finely divided head scales is derived. Within the genus *Bothriechis* the presence of well defined keels on the anterior portion of the dorsum of the head is probably derived whereas those species that have larger scales without keeling probably possess the primitive condition. Because of the irregularity of the size and shape of the cephalic plates in these snakes (Fig. 20) and the considerable intraspecific variation, it is difficult to assess this character. I suspect that the grossly irregular head plates with multiple keels in *B. aurifer* and *B. rowleyi* are the result of a secondary fusion of small head plates and represents a derived condition. The size and arrangement of cephalic plates no doubt is an important factor influencing cranial kinetics. Generally at least a pair of large scales are present on the parietal region in *B. rowleyi* and *B. aurifer*; these may be smooth or with irregular ridges, but not with straight keels. *Bothriechis marchi* has scales of moderate size in the parietal area that may be either smooth or weakly keeled. Relatively small scales with definite keels cover the parietal region in *B. bicolor*, *B. nigroviridis*, *B. lateralis*, and *B. schlegeli*.

The interrictals are the scales across the back of the head between the ultimate supralabials. *Bothriechis rowleyi* and *B. aurifer* possess the fewest interrictals, 15--21, and *B. bicolor* and *B. schlegeli* have the most, 21--31 and 23--34 respectively. The number of interrictals seems to be correlated with the number of dorsal scale rows. The mean number of ventrals and subcaudals is relatively low in *B. schlegeli* and *B. nigroviridis*, intermediate in *B. rowleyi* and *B. aurifer*, and high in

B. bicolor, *B. marchi*, and *B. lateralis*. The modal number of scale rows at midbody is 19 in *B. rowleyi*, *B. aurifer*, *B. marchi*, and *B. nigroviridis*, 21 in *B. bicolor*, and 23 in *B. lateralis* and *B. schlegeli*. Two trends seem apparent in *Bothriechis* with regard to body scales: first, an increase in the number of ventrals and subcaudals and, second, a decrease in the number of dorsal scale rows; both of these features seem to be derived and associated with arboreality. The numerous examples of arboreal colubrids (*Oxybelis*, *Leptophis*, *Sibon*, *Imantodes*) that possess these traits support this notion.

There are usually 8 pairs of supralabials in *B. schlegeli*, whereas all other species of *Bothriechis* generally possess 10 pairs. The infralabials in three species, *B. bicolor*, *B. marchi*, and *B. lateralis*, tend to be more numerous (generally 11--13) than in other species. A lacunalabial is invariably present in the samples of *B. aurifer* and *B. lateralis*, in all but one specimen of *B. schlegeli*, in about half the specimens of *B. marchi*, on one side of two specimens of *B. bicolor*, and in one specimen of *B. rowleyi*; it is absent in all specimens of *B. nigroviridis*. Most species of *Bothrops* have a lacunalabial and a relatively low number of labials; therefore a high number of supralabials and the loss of the lacunalabial appear derived.

The paraventral scale row is smooth in most species, but is weakly keeled in most specimens of *B. rowleyi*, and a few specimens of *B. aurifer* and *B. lateralis*.

Pattern and coloration.-- The ground color of all the montane species of Bothriechis is green with the undersurfaces of the free edges of the scales black. The young of some species possess coloration and pattern similar to that of the adults. However, the juveniles of several species including, B. lateralis, are brown. Although ecological data are lacking, I suspect that juvenile coloration is an adaptation to the habitat and habits of these snakes. The understory of some mesic upland forests is verdant, covered with terrestrial bromeliads, ferns, mosses, and low leafy plants, whereas the forest floor of other forests is covered with decaying twigs and branches and has a deep, exposed mulch layer.

In 1972 I observed two recently captured female B. lateralis giving birth. The females were maintained in an enclosure 1.5 m high and remained coiled on the branches in the upper portion of the cage for several weeks prior to giving birth, refusing food and showing little activity by day or night. At the time of birth, which in both instances occurred shortly after the lights had been turned off in the evening, the females descended to the floor of the cage. Such behavior would seem advantageous to the alternative of dropping young from heights. Further, the young of some species of Bothriechis, including B. lateralis, are known to feed on Anolis and Eleutherodactylus, typical leaf-litter inhabitants. Therefore, it is logical to speculate that the brownish coloration of the young of some species has a selective advantage for foraging strategies near the ground where young would tend to be more cryptically colored than if they possessed the bright green coloration of the adults. In captivity the young of all species of

Bothriechis are observed more frequently on the floor of their cages and more readily utilize ground cover than do adults. My observations in the field suggest that the young, if not actually less arboreal than the adults, at least tend to be found lower in the vegetation.

The distal portion of the tail of juveniles of montane *Bothriechis* is differently colored from that of the rest of the body and I have observed *B. bicolor* and *B. lateralis* luring in a fashion similar to that described by Greene and Campbell (1972) for *Bothrops bilineatus*. Juveniles colored differently than adults are not unique and several species of greenish arboreal boids are known to have brown or rufous young: *Corallus canina*, *Chondropython viridis*, and *Sanzinia madagascarensis*. Caudal luring has been documented in *Chondropython* (Murphy, *et al.*, 1978).

The green pigment of *Bothriechis* is soluble in alcohol, and preserved specimens rapidly lose their life colors becoming pale green, bluish, or black depending on the strength and kind of preservative. Except where noted, the following color descriptions are taken from life. Aspects of color and pattern for members of the genus *Bothriechis* are presented in Table 15.

The dorsum is essentially a uniform green in *B. rowleyi*. A few scattered light blue markings are usually present on the proximal portion of some dorsal scales and about half of the paraventral scales are pale blue. A postocular stripe is absent, but the temporal region in some specimens is strongly suffused with blue. The labials, gular area, and venter are greenish yellow. Two juveniles had a pale green ground color, 18--23 purple or brown dorsal blotches, and a smokey grey

TABLE 15. Aspects of pattern and color in species of Bothriechis. * refers to juveniles. See text for more complete descriptions.

	rolweyi	aurifer	bicolor	marchi	lateralis	nigroviridis	schlegeli
PATTERN							
Top of head	Uniformly green; *brown or purple dorsal blotches	With black markings, sometimes forming parietal stripes	Uniformly green	Uniformly green; *with dark brown markings	Uniformly green; *with dark brown markings	With black markings, often forming parietal stripes	Highly variable, generally with reddish brown parietal and occipital blotches
Postocular stripe	Absent	Present, black	Usually absent	Absent; *present, dark brown	Present but weakly defined, especially in large adults; *dark brown	Present, black	Present, generally reddish-brown
Dorsum	Generally without pattern, rarely with black and yellow markings	Generally with black and yellow markings, occassionally uniformly green	Generally without pattern, occassionally with black dots and/or irregular bluish mottling	Without pattern; *dark brown or blue paravertebral blotches	With alternating or opposite yellow paravertevral vertical bars; *bars bordered with dark brown	Strongly mottled with black, pale green black-edged dorsal blotches	Generally with reddish-brown blotches, these often fused forming a zig-zag dorsal band
Venter	Uniform yellowish-green	Uniform yellowish-green	Uniform yellowish-green	Uniform yellowish-green	Uniform yellowish-green, bordered by yellow paraventral stripes	Lightly mottled with black	Generally distinctly stippled, mottled, or blotched; yellow blotches or stripes often present
COLOR							
Iris	Yellow	Bronze, yellowish-green	Green	Yellow, greenish-yellow; *bronze	Yellow; *bronze	Black	Highly variable
Ground color of dorsum	Green; *pale yellowish-green	Green; *pale lime green	Green, bluish-green; *yellow-green	Green; *pale brown or yellowish-green	Green, bluish-green; *brown	Dark green, yellowish-green	Olive, yellowish-green, yellow, or reddish-brown
Tip of tail	Black	Yellow	Black	Black	Yellow	Black	Yellow

tail tip. The iris is yellow with black flecks in juveniles and adults. One adult female (AMNH 102895) has about 31 small yellow blotches on the head and dorsum; a few of these have back scales bordering them either anteriorly or posteriorly. The pattern somewhat resembles that of _B_. _aurifer_ except that postocular stripes are absent.

In _B_. _aurifer_ the dorsum is lime to dark green. A well defined postocular stripe extends from the eye to above the rictus. A few specimens are uniformly green; however most specimens possess an irregular undulating black dorsal stripe that sometimes is expanded to form blotches. Twenty to 39 bright yellow spots occur on the body in the center of the blotches or on the inside of the curves of the black dorsal stripe. Irregular black markings, sometimes forming longitudinal parietal stripes, are generally present on the head. The black markings on the body fade on the tail, becoming blue-green. The venter is paler than the dorsum and is usually greenish yellow. The iris may be bronze, copper, or yellowish green. Juveniles are patterned similarly to the adults, but the pattern is more distinct, the ground color is greenish yellow, the tip of the tail is yellow or chartreuse, and the iris is deep bronze.

Bothriechis _bicolor_ possesses a bright green dorsum. The interstitial skin and generally the edges of the dorsal scales are pale blue or turquoise. The postocular stripe is generally absent and the venter is pale green or greenish yellow. In two juveniles the bluish coloration was more evident, the ground color was bright yellow green, and the tip of the tail was smokey grey. The majority of specimens lack a dorsal pattern. However, snakes from the extremes of the range, Chiapas and Honduras, possess a distinctive dorsal pattern. A specimen from Cerro Ovando in Chiapas (UMMZ 94644) possesses numerous small round black spots on the dorsum of the head and body; another snake from the same locality (UMMZ 87707) also has small black dots, but these are smaller and fewer than in the former specimen, and tend to be concentrated in blue-green blotches on the dorsum. Two specimens of _B. bicolor_ are known from Honduras and their colors from life were reported by Meyer and Wilson (1971). A juvenile from 23 km E Nueva Ocotepeque, Departamento de Ocotepeque, had a chartreuse green dorsum, grayish green dorsal blotches, sky blue lateral blotches, a pale green venter, finely peppered with darker flecks; lateral edges of most ventrals chartreuse green; a chartreuse green head with two dark grayish green bands extending posteriorly from the snout to the angle of the jaw, a similar but paler postocular stripe; a chartreuse iris with black reticulations. An adult male (LSU 11638) from the southeastern slope of Cerro Santa Barbara, Departamento de Santa Barbara, was described as having a grass-green dorsum with powder blue chevrons and a yellowish-green venter. The dorsum of this specimen is heavily spotted and mottled with black forming irregular blotches. A postocular stripe and black markings are present on the head.

The smallest juvenile I have examined (UMMZ 131661), 214 mm in total length, is from near Yepocapa, Departamento de Chimaltenango, Guatemala. In preservative this specimen has a light brown dorsum with dark brown dorsal blotches that are usually connected forming a zig-zag pattern. No postocular stripe is present. Whether or not the ground color reflects the actual life color for at least some juveniles of this species or is merely an artifact of preservation I cannot be certain.

In the description of *B. ornatus* Julia and Varela (1977) give no characters that separate this species from *B. bicolor*. Inasmuch as the type locality of *B. ornatus* falls within the range of *B. bicolor*, there is little doubt that the former species is a junior synonym of *B. bicolor*.

The dorsum is green and often has irregular pale blue mottling in adult *B. marchi*. The postocular stripe is absent and the venter and iris are greenish yellow. Several specimens (MCZ 27567 and 27568) are uniformly green with distinctly black-edged scales. This appears to be an artifact of preservation with the coloration of the black undersurfaces of the free edges of the scales showing through. At birth this species may be one of two distinctive color phases. Most frequently the dorsum is pale brown with irregular dark brown paravertebral blotches that are eded posteriorly with yellow, the postocular stripe is dark brown, a yellow or cream-colored paraventral stripe and grey tail tip is present, and the iris is bronze. A green female of uncertain provence gave birth to 6 young that had a yellowish-green ground color, blue paravertebral blotches narrowly edged with black, blue scales scattered on the side of the body, blue postocular stripes and parietal markings, pale yellow paravertebral stripes, and yellowish-green irises.

The adults of *B. lateralis* are green dorsally with yellow vertical paravertebral bars. These yellow markings may be bordered with black and blue. A poorly defined bluish black postocular stripe edged below with yellow is usually present. A distinctive sharply defined paraventral stripe involving the outside edges of the ventrals and first scale row extends along the body and tail. The labials, the portion of head below the postocular stripe, gular area, and venter are pale green. The iris is greenish yellow.

At birth juveniles are brown with blackish-brown paravertebral markings. These markings are often arranged in pairs and yellow edged. A cream-colored or yellow paraventral stipe extends along the body and tail. A dark brown postocular stripe, yellow edged below, extends from behind the eye to the rictus. The tail tip is yellow or chartreuse and the iris is deep bronze. A few dark markings usually are present on the head. The brown coloration of juveniles is retained for about six months. After about 10 months the ground coloration is a dull lime green, and the yellow of the paravertebral markings becomes more prominent with black edging, but the deep bronze color of the iris is retained. At about a year and a half the ground color becomes bluish green, the paravertebral markings become essentially yellow with narrow back and/or blue borders, and the iris yellow. The emerald green coloration characteristic of adults does not seem to be attained until after two years of growth.

Bothriechis *nigroviridis* possesses a dark emerald green dorsum. In a few specimens the ground color is yellowish green. The dorsum is strongly mottled with black forming dorsal blotches with pale green centers. The postocular stripes, parietal stripes, and head markings are black. The venter is pale or bluish green. The iris is bronze or yellow, but so heavily speckled with black that these colors are mostly obscured.

I have not seen juveniles of this species, but color slides available to me and the description given by Picado (1931) verify that they are patterned and colored essentially as are adults.

The black coloration of the undersurface of the free edge of the dorsal scales, the presence of a yellow paraventral stripe, the absence of ventral pattern and postocular stripe, and the black tail tip and rufous or brown coloration of the young seem to be derived features.

Descriptive osteology.-- A small sample of osteological material was available for study. To avoid confusion arising from ontogenetic change, only osteological material from large adult snakes was compared. Even with the small sample at hand it is apparent that there is individual and geographic variation in the shapes of certain bones, their processes, and foramina. Therefore I make no attempt in the following description to mention all of the minor differences noted in various specimens, but rather attempt to point out only the more salient differences. Undoubtedly I have missed or ignored some features that might be of taxonomic importance and perhaps have placed importance on others that will prove trivial when additional material becomes available.

The premaxilla is shaped more or less like an inverted "T" in frontal view with a lingual notch in the ventral crossbar. It is wider than high and the vertical process is posteriorly curved. The most noticeable interspecific variation occurs in the shape of the lateral ventral projections. These are greatly dorsoventrally compressed and expanded with posteriorly projecting processes on the tips in B. schlegeli and B. nigroviridis. In B. lateralis, B. aurifer (Fig. 21), and *B. rowleyi* the ventral projections are almost round in cross section; *B. lateralis* has dorsal bumps on each side of the vertical process that form ridges, *B. rowleyi* has posteriorly projecting processes on the tips. *Bothriechis marchi* has ventral projections that are slightly compressed with bumps or ridges on each side of the vertical processes, and in *B. bicolor* the ventral projections are somewhat laterally compressed proximally with a distinctive dorsal ridge; distally they become dorsoventrally compressed with posteriorly projecting tips.

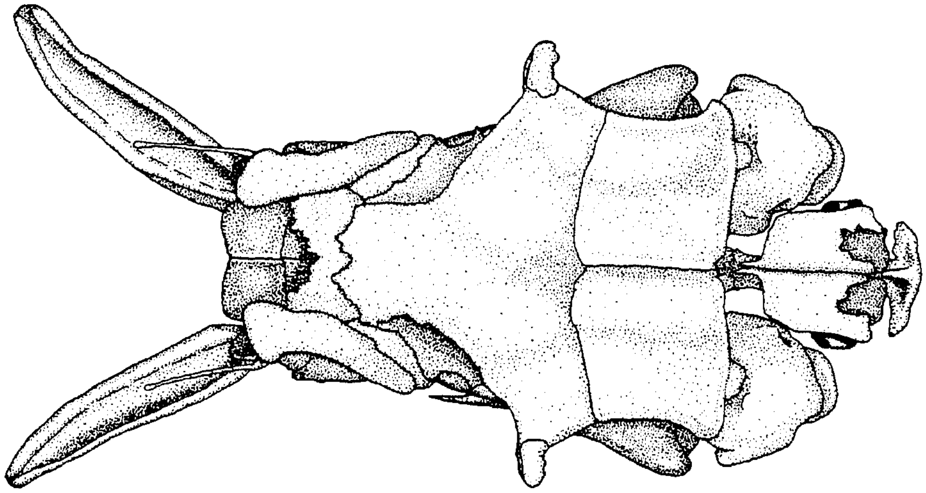
The paired nasals are convex and longer than wide. They are proportionately larger in *B. nigroviridis* than in other species, and in *B. nigroviridis* and *B. schlegeli* the lateral edges form a more obtuse angle. The anterior edges are variable and may be relatively straight or irregular; in *B. nigroviridis* they tend to be more deeply indented than those of other species.

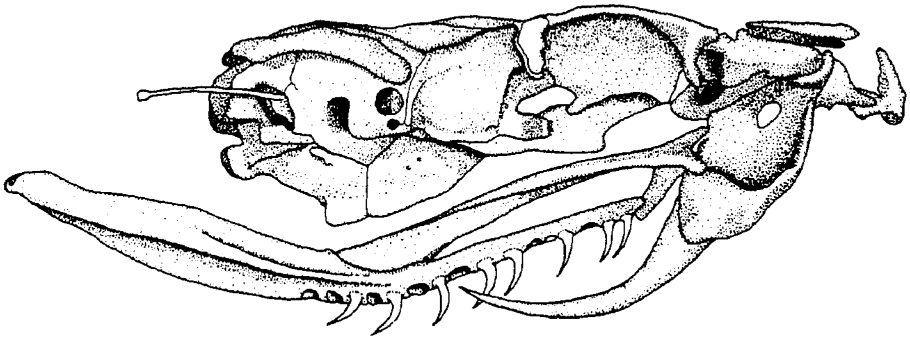
The shape of the prefrontals varies slightly among species; *B. schlegeli* possesses the most prominent lateral processes.

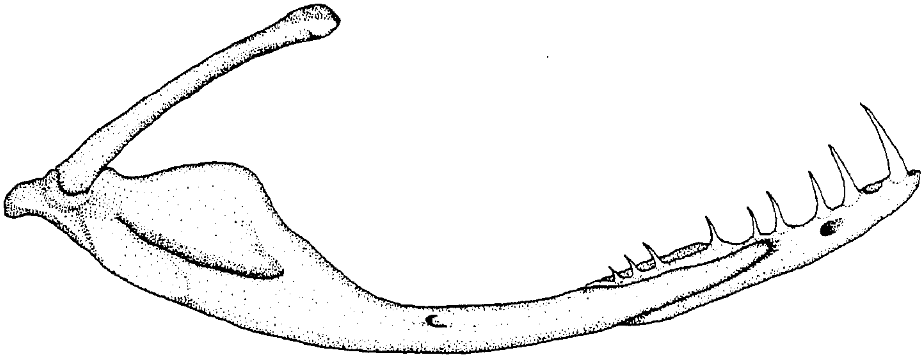
The frontals are roughly quadrangular and relatively broad; in *B. rowleyi*, *B. aurifer*, and *B. schlegeli* they are very nearly as wide as long. They are strongly notched anteriorly along their suture in all species except *B. bicolor* and *B. aurifer* (Fig. 21). A median ridge is present at their juncture; the ridge is most raised in *B. schlegeli*.

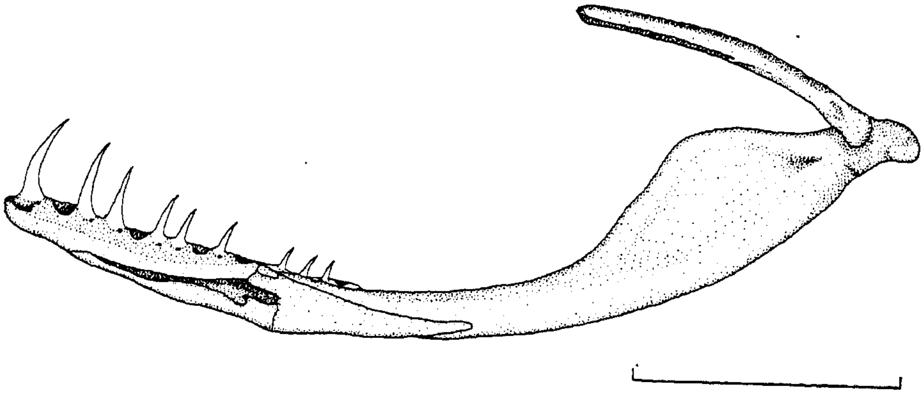
All species have a well defined lateral ridge on the parietal extending posteriorly from the orbital processes almost to the posterior tip of the parietal. In *B. bicolor* and *B. nigroviridis* these ridges project as a shelf of bone behind the postorbital processes, and in

FIGURE 21. From top to bottom: dorsal and lateral aspects of skull and lateral and medial views of right mandible, respectively, of *Bothriechis aurifer* (KU 191201). Vertical line represents 10 mm.









B. schlegeli the shelf-like projections extend even more posteriorly and the parietal is expanded laterally and is contiguous with the anterior portion of the supratemporal, a unique condition. A second parietal ridge is present laterally in all species except *B. schlegeli* and may have a small laterally projecting process about midway along its length.

The postorbital is much reduced in size. It is largest in *B. lateralis* where its greatest length is about equal to its distance to the parietal-frontal suture.

The supratemporal is short and flat in these species and a great amount of intraspecific variation is present. In most specimens this bone does not extend beyond the posterior edge of the exoccipital. The blunt lateral processes of the supratemporal is more posteriorly located in *B. nigroviridis* making the posterior end more truncate.

The bar of bone separating the pro-otic foramina is exceptionally thin in *B. marchi*.

The maxillary foramen is relatively small in *B. aurifer* (Fig. 21) and *B. rowleyi*, while it is large in *B. nigroviridis*. Several species have exceptionally long fangs; in *B. bicolor* the fang tips reach a point equal to the ectopterygoid-pterygoid articulation when the fangs are in the resting position, and in *B. nigroviridis* nearly so. The anterior edge of the pit cavity is irregular possessing anteroventral processes; these are particularly prominent in *B. schlegeli* and barely discernible in *B. rowleyi* and *B. aurifer*.

Palatines are more or less triangular in lateral aspect and curved in ventral view. They bear 3--5 relatively long, slender teeth, the first of which may originate slightly posterior to the anterior tip of the bone. The anterodorsal edge of the bone may be slightly emarginate; however this condition is variable within a species or even in a single specimen as is the relative height compared to width.

The pterygoid-ectopterygoid articulation shows considerable variation among species. The ectopterygoid in *B. nigroviridis* and *B. schlegeli* articulates deeply into the pterygoid and the medial flange of the pterygoid that flanks the ectopterygoid is particuarly well developed. *Bothriechis rowleyi*, *B. aurifer*, and *B. marchi* possess shallow articulations and the medial pterygoid ridge is poorly developed or absent. The pterygoid bears 12--17 teeth in *Bothriechis*.

The ectopterygoid is flat and thin; it is relatively broad thoughout its length in *B. schlegeli* and relatively slender in *B. lateralis*. The anterior portion of the bone is more expanded in *B. aurifer*, *B. bicolor*, *B. rowleyi* and *B. marchi* than in *B. lateralis* or *B. nigroviridis*.

The ventrally projecting shelf of bone on the basisphenoid is poorly developed in most of these species. It is best developed in *B. schlegeli* and *B. bicolor* and extends almost the entire length of the bone. It is moderately well developed in *B. nigroviridis* and weakly developed in *B. lateralis*, *B. marchi*, *B. aurifer*, and *B. rowleyi*, usually not extending onto the posterior hump of the basisphenoid.

The ventral process of the basioccipital is high and strongly bifid in *B. schlegeli*, moderately elevated, weakly bifid, and with a small median strut of bone posteriorly in *B. nigroviridis* and *B. marchi*, low, weakly bifid, and with or without the medial strut of bone in *B. lateralis*, *B. aurifer*, and *B. rowleyi*, and high, weakly bifid, and with a well developed medial strut of bone posteriorly in *B. bicolor*.

The dentary bears 12--16 relatively long, slender teeth. Generally a distinct angular and splenial are apparent, but in most specimens of *B. nigroviridis* and *B. aurifer* these bones are so tightly fused that the suture between them is obliterated. *Bothriechis rowleyi* is apparently unique in that most of the bone that borders the upper edge of the Meckelian foramen is a projection of the splenial rather than the angular. The posteroventral surface of the compound possesses a high shelf-like ridge in *B. bicolor* and *B. schlegeli*, whereas in other species the ridge is low or absent.

Compared to *Bothrops godmani*, which appears to be a rather generalized terrestrial species, the neural spines of the mid-thoracic vertebrae in *Bothriechis* are relatively low and broad, the hypapophyses are slender, and in at least one species (*B. nigroviridis*) the prezygapophyses and postzygapophyses are relatively expanded and broad laterally. The anterior edge of the bridge of bone between the zygosphenes that forms the roof of the neural canal is distinctly convex in *Bothriechis* whereas it is concave in *B. godmani*.

In *Bothriechis* the pleurapophyses of the caudal vertebrae tend to descend at a much sharper angle and are shorter than in *Bothrops*. The proximal caudal vertebrae may possess pleurapophyses that extend more laterally than the prezygapophyses in dorsal view; by mid-tail, however, none extend past the prezygapophyses. In all species of *Bothrops* I have examined, the pleurapophyses extend from the centra at a more horizontal angle, are considerably longer, and extend lateral to the prezygapophyses throughout the length of the tail.

Hemipenes.-- Species of *Bothriechis* are conservative in hemipenial morphology. The inverted organ extends the length of 6--9 subcaudals and is bifurcated with a divided sulcus spermaticus. Each lobe is subcylindrical except in one specimen of *B*. *lateralis* in which the lobes are tapered. The proximal portion of the hemipenes bears large spines with minor interspecific variation in the number. Most species have a total of 16--24 enlarged spines; however, *B*. *lateralis* possesses 10--12. Distally the organ is capitate with papillate calyces. *Bothriechis nigroviridis* and *B*. *schlegeli* have enlarged mesial spines flanking the crotch as do species of *Bothrops* I have examined.

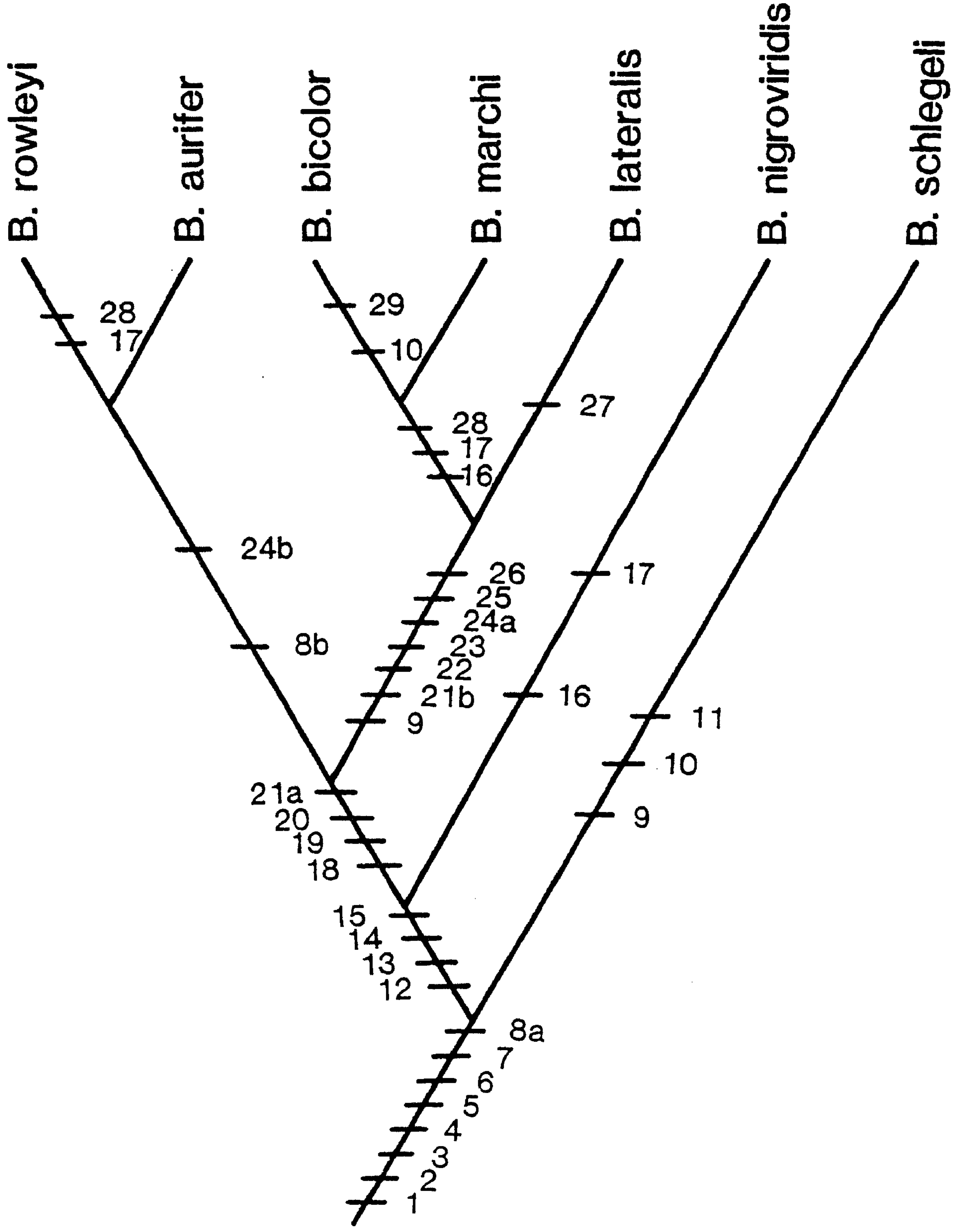
RELATIONSHIPS

The relationships of *Bothriechis* to other New World pitvipers are uncertain. I am inclined to agree with Burger (1971) that this genus seems to be more closely associated with some of the terrestrial Central American pitivipers rather than the arboreal *Bothrops* *bilineatus* group of South America. *Bothriechis* and the Central American pitvipers that includes *Bothrops* *godmani* share several characterisitics including entire subcaudals and some members of both groups have large supracephalic head scales.

The interspecific relationships of *Bothriechis* likewise remain obscure. I present a theory of relationships based on what I consider derived characters (Fig. 22). The features that unite the members of this genus into a cohesive group have been discussed previously.

Bothriechis *schlegeli* possesses a number of primitive characters, but nonetheless is distinctive in having such unique features as an

FIGURE 22. A theory of the relationships of snakes in the genus *Bothriechis*. Numbers refer to the following characters (see text for descriptions): 1, Greenish ground color (variable in *B. schlegeli*); 2, Caudal vertebrae with distinctive pleurapophyses and haemapophyses; 3, Palatine triangular; 4, Ectopterygoid broad and curved; 5, Tail spine short and blunt; 6, Subcaudals undivided; 7, Nasal pore situated deep in nostril; 8, a) Midbody scale rows 2--25, b) 17--19; 9, Scales on dorsum of snout distinctly keeled; 10, Intercanthals numerous; 11, Parietal bone expanded; 12, Increase of relative tail length in females; 13, Undersurfaces of free edges of dorsal scales black; 14, Venter generally immaculate or with few specks; 15, Supralabials generally more than 9/9; 16, Tail tip black in juveniles; 17, Lacunalabial absent; 18, Increase in relative tail length in males; 19, Sexual size dimorphism, males larger than females; 20, Reduced number and size of mesial spines on hemipenes; 21, a) Moderate increase in number of ventrals and sucaudals, b) Number of ventrals and subcaudals greatly increased; 22, Dorsum usually without zig-zag dorsal stripe or median blotches; 23, Scales in parietal region numerous with well defined keels; 24, Intrasupraoculars: a) Finely divided with individual keels, b) Secondarily fused into large, irregular plates with multiple keels; 25, Coloration of young generally reddish brown (may be variable in *B. marchi* and *B. bicolor*?); 26, Infralabials generally 11 or 12; 27, Yellow paraventral stripe; 28, Postocular stripe absent; 29, Two small scales between supraocular and canthal.


B. rowleyi
B. aurifer
B. bicolor
B. marchi
B. lateralis
B. nigroviridis
B. schlegeli
28
17
29
10
28
17
16
27
24b
8b
26
25
24a
23
22
21b
9
17
16
11
10
9
21a
20
19
18
15
14
13
12
8a
7
6
5
4
3
2
1

expanded parietal, raised superciliaries, and numerous, keeled intercanthals. This species differs from other members of the genus in having a lower number of supralabials (generally 7--8), a ventral pattern that is generall checkered or mottled, and the undersurfaces of the dorsal scales are not black. The above obviously does not apply to the so-called "oropel" or salmon color phases that are discontinuously distributed from Honduras to Panama. In some traits, such as a mottled or checkered venter, scales that that have non-black free edges, and numerous superciliaries, B. schlegeli more closely resembles the terrestrial Central American pitvipers. A study of geographical variation in B. schlegeli would be rewarding because this widespread species shows interesting clinal and individual variation in scalation, cranial osteology, pattern, and color. Southern populations tend to possess fewer ventrals, interrictals, and have poorly developed supraciliaries. This species also possesses a number of drived characters including a broader, flatter head than any other member of the genus, a high number of finely divided supracephalic scales, a prominent and extraordinarily highly raised keel on the scales of the head, particularly laterally, and a parietal bone that is expanded to form a sharp lateral ridge.

Bothriechis nigroviridis differs from other species of Bothriechis except B. schlegeli by having a relatively low number of ventrals and subcaudals, possessing large mesial spines flanking the crotch of the hemipenis, and apparently lacking sexual size dimorphism, wherein males reach significantly greater lengths than females.

The remaining five species may be divided into two groups. One group contains *B. rowleyi* and *B. aurifer* and is characterized by a low number of midbody scale rows, generally 19; a dorsal pattern, when present, of a black zig-zag stripe and/or blotches; large supracephalic plates that may be either smooth or rugose, but lack well defined keels (Fig. 20); and an intermediate number of ventrals and subcaudals (Table 14). The scales of the parietal area are large and often have multiple keels.

The other group, comprised of *B. bicolor*, *B. marchi*, and *B. lateralis*, has 19--23 midbody scale rows, a dorsal pattern, when present, of small separated paravertebral bloches; relatively small, distinctly keeled supracephalic scales; and a high number of ventrals and subcaudals. The scales in the parietal region are generally small and distinctly keeled, although in some specimens of *B. marchi* they may be moderately enlarged. The number of interrictals in these species is high relative to that in *B. aurifer* and *B. rowleyi*. The color and pattern of the young of *B. lateralis* and *B. marchi* are strikingly different from those of other species of *Bothriechis*. Juveniles generally have a light brown ground color, dark brown paravertebral blotches, and a distinctive pale paraventral stripe. In many respects, members of this group are the most derived species of *Bothriechis*.

The BOTHROPS GODMANI group

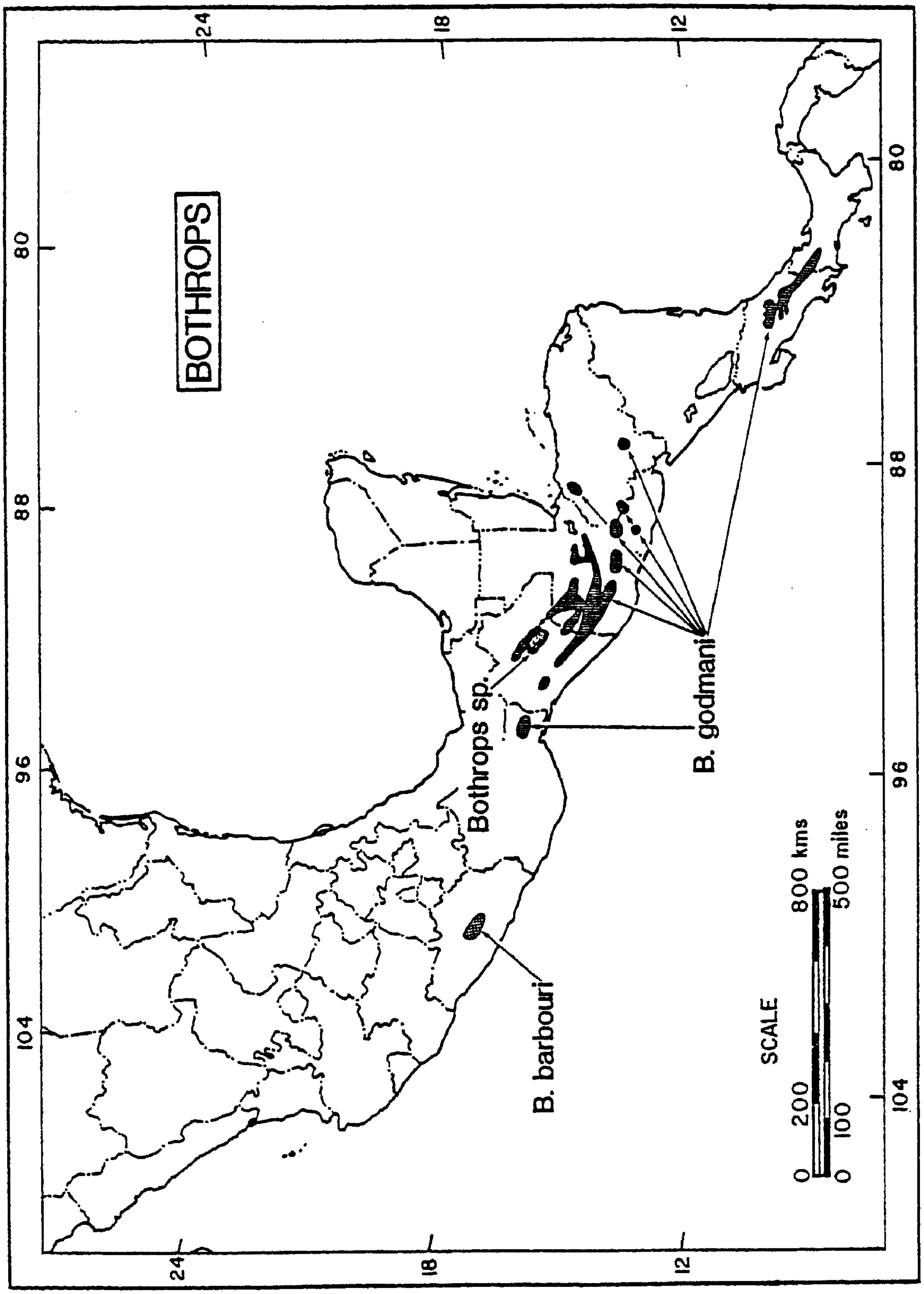
Composition and distribution.-- The *Bothrops godmani* group consists of three monotypic species of Middle American pitvipers (Fig. 23). *Bothrops barbouri* is the northernmost representative of this group and occurs in the high montane forest, including cloud forest, of the Sierra Madre del Sur of Guerrero, Mexico between 2490 and 2950 m. It is recorded from only two small areas: from the vicinity of Omilteme from where most specimens have been collected, and from the vicinity of Puerto del Gallo on the slopes of Cerro Teotepec.

The most widespread species is *B. godmani* whose distribution extends across the Nuclear Central American highlands from southeastern Oaxaca to northern Nicaragua. A major hiatus in its range occurs in the Nicaraguan lowlands, but the species is present in Isthmian Central America from the western portion of the Cordillera Central in northcentral Costa Rica to the southwestern portion of the Cordillera de Talamanca in northwestern Chiriqui Province in Panama. This species inhabits pine-oak and cloud forest at elevations of 1420--3200 m.

A third species, undescribed, occurs on the Mesa Central of Chiapas and may be sympatric with *B. godmani*. This species is known from the San Cristobal de las Casas region across the Mesa to a little east of Teopisca. It has been collected in humid pine-oak forest and almost pure stands of pine at elevations of 2200--2750 m.

Outgroup comparisons.-- For outgroup comparisons I have examined members of the predominently Central American "hognosed" viper group

FIGURE 23. Distributions of members of the *Bothrops godmani* group.


BOTHROPS
Bothrops sp.
B. godmani
B. barbouri
SCALE
0 200 800 kms
0 100 500 miles
24
18
12
80
88
96
104

that contains *B. nasutus*, members of the group that contains *B. asper*, and members of the genus *Bothriechis* (see above). There is little doubt that the genus *Bothrops* is paraphyletic; however, until the relationships of several species that inhabit the southern portions of the Mexican Plateau (*B. melanurus*, *B. undulatus*) and of the hognosed vipers, with the *B. godmani* group are better understood, less confusion is likely to be perpetrated by deferring recognition of several poorly delimited generic names that have been proposed (i.e. *Porthidium*, *Ophryacus*).

Character analysis.-- The number and arrangement of the scales covering the top of the head is extremely variable among these snakes. Most specimens of *B. barbouri* have distinctly enlarged, flattened scales arranged in a pattern resembling the typical colubrid condition. However, the condition found in *B. barbouri* differs from that of most colubrids, *Agkistrodon*, and *Sistrurus* in having an extra pair of canthals, and in that the parietals are generally separated by small scales. *Bothrops godmani* and *Bothrops* sp. generally have enlarged scales in the frontal and parietal regions, but they tend to be bordered by smaller keeled scales and overall the scales of the crown are more fragmented.

There are most frequently eight supralabials in *B. barbouri* whereas there are nine in *B. godmani* and *Bothrops* sp. Because a low number of supralabials characterizes snakes of the genus *Agkistrodon* and most members of the *B. asper* group, I consider the higher number derived. The number of scale rows at midbody is generally 21 in *B. godmani* and *Bothrops* sp. and 17 in *B. barbouri*. Whereas a number of Neotropical pitvipers have 21 midbody scale rows, 17 as a modal number is apparently unique to *B. barbouri* and seems to be derived. All species in the *B. godmani* group have relatively few ventrals and subcaudals. Only a few other stout-bodied species of *Bothrops* possess a comparable number including some members of the *B. nasutus* group and *B. nummifer* (which is possibly closely related to the *B. godmani* group). Several interesting trends relating to the number of ventrals and subcaudals in males and females of the various species in the *B. godmani* group are apparent. Most snakes are sexually dimorphic with regard to the number of ventrals and subcaudals, with females possessing more ventrals and fewer subcaudals. However, no such sexual dimorphism is present in *Bothrops godmani* with respect to the number of ventrals, and in *B. barbouri* and *Bothrops* sp. with regard to number of subcaudals; I regard the absence of sexual dimorphism as derived and possibly related to the somewhat dwarfed condition of this highland-adapted group of snakes. The mean number of ventrals is significantly less in *Bothrops* sp. than in the other two species, and is lower than any species of Neotropical viper except for *B. nummifer*. The number of teeth borne by the palatine, pterygoid, and dentary in members of the *B. godmani* group is comparable to *B. nummifer*, members of the *B. nasutus* group, and some *Bothriechis*; *Bothrops melanurus* and *B. undulatus* tend to have fewer, and the large terrestrial species of *Bothrops* tend to have more. The relatively low number of teeth in *B. barbouri* and *Bothrops* sp. seems to be plesiomorphic.

Regression equations that express the relationships between the head and body lengths of members in the *B. godmani* group are presented in Table 16. *Bothrops* sp. possesses a relatively long head and that of *B. barbouri* is short. Differences of the head to body length relationship among these three species are highly significant; however I have not calculated this relationship for other *Bothrops*. Plotting values for individual specimens of other species reveals that the heads of *B. godmani* and *Bothrops* sp. are relatively large; I consider this a derived character.

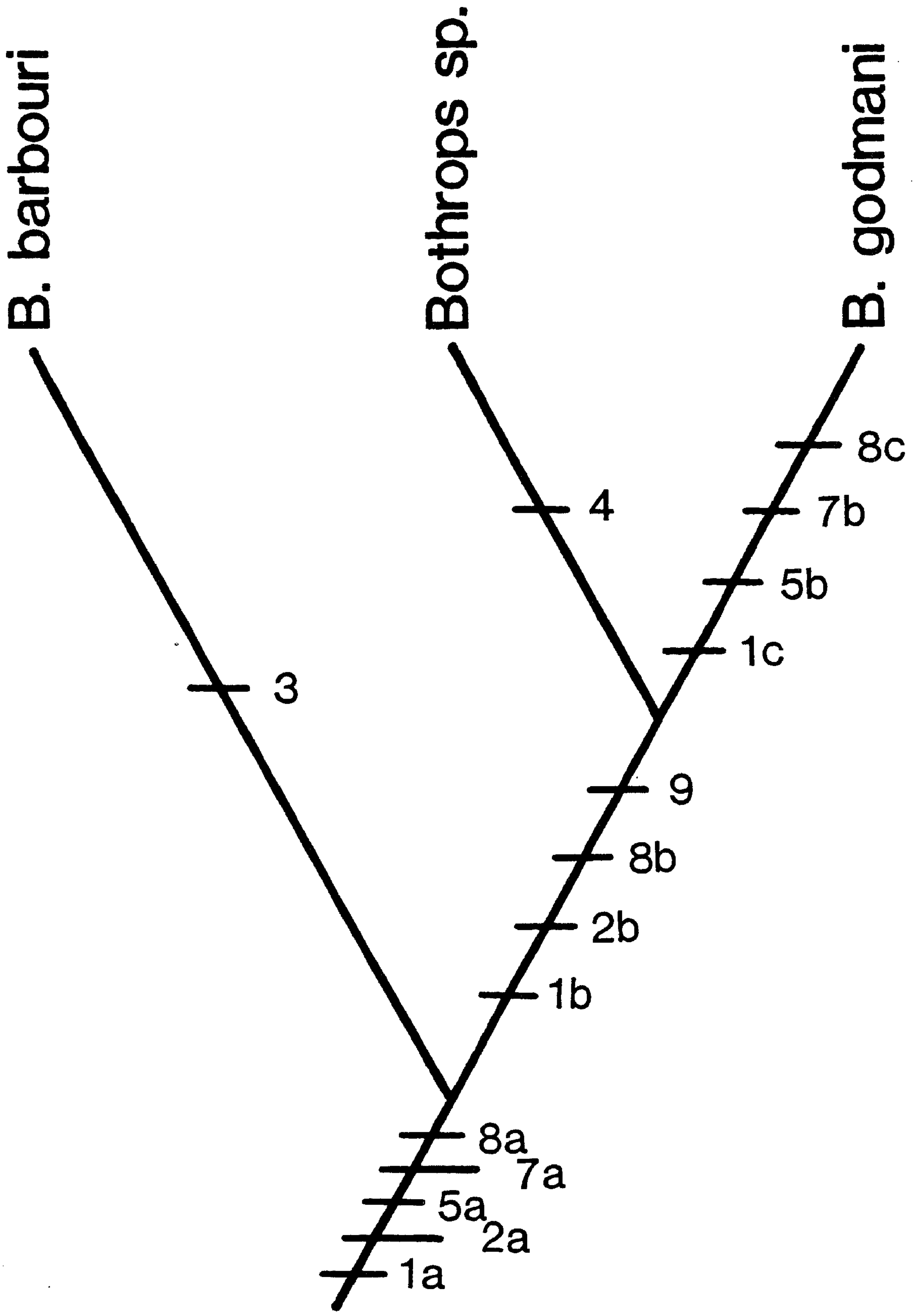
Relationships.-- The *B. godmani* group represents an endemic Middle American element and the closest relationships to the group are probably to be found in other Central American pitvipers such as the *B. nasutus* group and the monophyletic lineage considered herein as *Bothriechis*. Within the *B. godmani* group there is ample evidence that the Mexican isolate *B. barbouri* is the sister species to the widespread *B. godmani* and *Bothrops* sp. isolated on the Chiapan Plateau. The latter two species share a greater number of head plates, supralabials, and teeth; further they both have relatively long heads. A theory of the relationships of this group is presented in Figure 24.

TABLE 16. Comparison of certain features in species of the *Bothrops godmani* group. See text for details. The range of means for *B. godmani* refers to eleven samples taken from throughout its range. * indicates mode.

BOTHROPS GODMANI group

Characters	B. barbouri	B. godmani	Bothrops species
1. Head scales between supraoculars	1--4 (1*)	3--7 (5*)	3--5 (3*)
2. Supralabials	7--10 (8*)	7--13 (9*)	9--11 (9*)
3. Dorsal scale rows	21-17-15*	23-21-17*	23-21-17*
4. Ventrals (males)	130--138 (133.3)	130--148 (136--144)	120--135 (126.9)
(females)	139--145 (142.3)	130--148 (136--146)	125--134 (129.2)
5. Sexual dimorphism (females with significantly greater number of ventrals	Present	Absent	Present
6. Subcaudals (males)	27--32 (30.0)	26--36 (28--35)	27--31 (29.2)
(females)	26--30 (28.8)	23--34 (25--32)	26--32 (28.3)
7. Sexual dimorphism (males with significantly greater number of subcaudals	Absent	Present	Absent
8. Teeth (palatine)	3	4--5	4
(pterygoid)	9--12	14--18	11--13
(dentary)	8--10	13--16	13--14
9. Relationship between head and body length	$H=0.0425L+6.2007$	$H=0.0498L+5.9648$	$H=0.0444L+8.7576$

FIGURE 24. A theory of the relationships of members of the *Bothrops godmani* group. Numbers refer to characters presented in Table 16.


B. barbouri
Bothrops sp.
B. godmani
3
4
8c
7b
5b
1c
9
8b
2b
1b
8a
7a
5a
2a
1a

DISCUSSION

Gadow's (1913) often quoted statement "the key to the distribution of any group lies in the geographic configuration of that epoch in which it made its first appearance" is now generally accepted as one of the basic tenets of biogeography. Two unfortunate facts combine to hinder our understanding of the present-day distribution of the Middle American herpetofauna. First, there is a complete lack of fossils of Cenozoic amphibians and reptiles from this region. From extant distributions and fossil evidence from North America it has been shown that the region has been subjected to various "waves" or invasions of several groups (Dunn, 1931; Savage, 1966; Schmidt, 1943; Stuart, 1950, 1951). The timing of these invasions has been broadly defined, but it would be unwise to assume that all components from any one of the historical groups entered Nuclear Central America at precisely the same time and that therefore all have been subjected to the same vicariance and/or dispersal events. Similarly, the groups that comprise the Middle American (Savage, 1966) or autochthonous (Stuart, 1951) element, and which appear to have arisen in Middle America, may have had diverse histories with regard to exact area and time of origin. A second problem is that there is no general agreement on some aspects of the geological history of Central America, much less those other factors such as paleoclimates and vegetation that have contributed to the present distributional patterns.

Given that in Middle America there is no fossil evidence to establish a record of extant lineages and the geological history of the region is complicated and poorly known, is it prudent to attempt to formulate theories of the origin and evolution of its herpetofauna? I think this is a worthwhile task for the following reasons. Present patterns of distribution of cloud forest species are becoming relatively well known and may be viewed primarily as the result of recent (i.e. Pleistocene) events. As a result of this knowledge, and of preliminary theories of the relationships of various groups, an evaluation of the degree of relationship between biotas is possible. It is reasonable to assume extant distributions, and in many instances the origin of the montane species under consideration, are the direct result of vicariance or dispersal events that occurred in the Pleistocene or no earlier than the Pliocene orogenies that drastically shook Middle America. Although modern families and, in a few instances, modern genera may have been in existence by Cretaceous times (Estes, 1965;, Savage, 1966; Tihen, 1964), it is likely that most montane species in Middle America did not make an appearance until the Miocene at the earliest, the later portion of which saw the region uplifted to respectable elevations for the first time (Childs and Beebe, 1963; Dengo, 1968). Prior to the Miocene, Middle America probably possessed highlands that were not extensive, of little relief, and of relatively low elevation (Dengo, 1968; Maldonado-Koerdell, 1964). Therefore it is likely that the distributions of extant lineages, if already adapted to montane elevations at this time, were relatively restricted and their ranges were not greatly fragmented. Inferences about the evolution of species and the waxing and waning of their distributions during the more recent times are, of course, open to speculation, but it is the practice of biogeographers to propose theories that may be subsequently tested. Fortunately the geological history and its affects on the environment are relatively better known for this region during Plio-Pleistocene and Recent times. Some of the evidence of Pleistocene dispersal and climatic change in Middle America was summarized by Duellman, 1960, 1966; Martin, 1955a; Martin and Harrell, 1957; Savage, 1966; and Stuart, 1950, 1966.

In the following discussion I will identify the common patterns of distribution for cloud forest species and species groups that have representatives in the Sierra de las Minas, and subsequently address what I infer to be the vicariance and/or dispersal events that have led to these patterns. However, prior to this, it seems advantageous as a preface to subsequent discussion to summarize briefly what have been suggested to be the major episodes of the geological history of Central America.

The oldest rocks in Nuclear Central America are of Paleozoic age and occur along an east-west axis that includes the Sierra Madre de Chiapas, the Sierra de Chuacus, and the Sierra de las Minas (Dengo, 1968; McBirney, 1963; Williams, McBirney, and Dengo, 1964). This ancient core of the Central American mountain system was uplifted by a series of orogenies in the late Permian that produced an emergence of much of the area by the end of the Paleozoic (McBirney, 1963; Walper, 1960). The ancient orogenic trends across Guatemala are indicated by several serpentine belts, and although the age of the serpentine is not definitely known, it is postulated that it was extruded sometime between the middle Permian and late Jurassic (Walper, 1960). Many changes in the configuration, relief, climate, and biota must have occurred during the late Cretaceous when Middle America entered a phase of intense mountain building with the appearance of new mountain ranges in what is now Nuclear Central America and along the eastern coast of Mexico. These mountains, resulting primarily from folding, indicate Middle America was modified during the Laramide Revolution (Maldonado-Koerdell, 1964) during which time the Rocky Mountains and Sierra Madre Oriental to the north were also elevated.

Coincident with the Laramide Revolution, the Mexican Plateau and the Sierra Madre del Sur were uplifted and these landmasses have remained emergent up to the present. During Cretaceous time there was foundering of some portions of Central America and encroachment of these areas by the sea (Walper, 1960). By late Createaceous or early Tertiary the Sierra de los Cuchumatanes and Mesa Central of Chiapas had been uplifted (Anderson et al., 1973; Dengo, 1968). During this time the region has been visualized as being of relatively low topographic relief with mesic, tropical conditions and temperatures and precipitation both higher than that of today (Dorf, 1959; Savage, 1966). Whether or not a land connection existed between Central and South America during the early Tertiary is a matter of dispute. Savage (1966) favored the view that there was such a connection in his study on the herpetofauna of the region, but reversed himself in explaining the evolution of Neotropical mammals (Savage, 1974). Nevertheless, in general there is broad agreement that the Central American paleopeninsula persisted in isolation through most of the Cenozoic with an island archipelago, the Guanarivas Ridge, situated to the south of a line connecting the peninsula and South America. These islands disappeared in the Eocene, but renewed activity in the Miocene created the Talamanca Range (Lloyd, 1963). The peninsula acted as a cul-de-sac for forms dispersing into the region and increased faunal diversity (Savage, 1966; Schmidt, 1943; Smith, 1949). Independent evolution of amphibians and reptiles took place on the interjacent islands. A marine portal persisted until the Pliocene when the Isthmian land bridge became established some five to seven million years ago.

To what extent the region was elevated in the early Tertiary is also controversial, but it appears certain that after the period of mountain building ended in the early Tertiary the region underwent a long period that reduced it to a surface of low relief (McBirney, 1963). The seaways began to diminish by Eocene time and by late Eocene were probably restricted to elongate basins to the north of the Sierra de las Minas.

The time of greatest change in climate and vegetation during the Tertiary began in the late Miocene and continued into the Pliocene. It was during this time that the first of two periods of volcanism began to rock the region. These volcanoes erupted from fissures along a broad belt of some 50-70 km wide paralleling the Pacific Coast of Nuclear Central America and laid down volcanic rocks on a broad surface of rugged relief (Williams, 1960; Williams, McBirney, and Dengo, 1964). These eruptions occurred slightly to the south of the ridge of the Chuacus-Minas mountain system that was already present and produced a broad plateau in western Guatemala. Up to this time, Nuclear Central America consisted of moderately uplifted highlands and the climate was thought to have been relatively warm and moist with tropical forest interspersed with savannas (Olson and McGrew, 1941; Savage, 1966;

Stuart, 1957). However, the surface configuration prior to this volcanic activity had been eroded to one of strong relief and a ridge close to the present Continental Divide dominated the landscape along the axis formed by the Sierra de Chuacus and the Sierra de las Minas (Williams, 1960). Middle Tertiary volcanism coupled with a reduction in the temperature owing to increased elevation, created for the first time areas subjected to cold temperatures, and the distinct zonation of climates and vegetation on mountain slopes that has persisted until the present (Maldonado-Koerdell, 1964; Stuart, 1957). Similar events were also occurring to the north in Mexico; great igneous activity was building the Sierra Madre Occidental and the Mexican Plateau was raised to its present elevation (Duellman, 1965; Maldonado-Koerdell, 1964). The Cordillera Volcanica seems also to have had its beginning during this time with the great cones such as Orizaba being formed later in the Pliocene (Dengo, 1968; Maldonado-Koerdell, 1964).

A new faunal element began to mingle with the Middle American Element starting in the late Miocene and Pliocene. Northern groups such as Sceloporus, Gerrhonotus, and Thamnophis dispersed southward along the western mountain complexes of Mexico along with the Arcto-Tertiary geoflora and reached at least southern Mexico (Savage, 1966). This Northern Element subsequently evolved in conjunction with the pre-existing Middle American Element.

The question of whether a late Tertiary marine barrier existed in the Tehuantepec region remains unsettled. Durham, Arellano, and Peck (1955) concluded on the basis of sedimentary evidence that Nuclear Central America remained connected with southern Mexico throughout this period, but as pointed out by Stuart (1966), a shallow channel washed by a scouring sea might not have left any trace of itself. Certainly, the presence of fossil camels and horses of early Pliocene age in the Mejocote Valley of southwestern Honduras supports the contention that no marine barrier was present in the Isthmus of Tehuantepec at this time (Olson and McGrew, 1941). However, during the Miocene, marine waters probably reduced the Isthmus to almost half of its present width, and lacustrine deposits suggest greater local relief and heavier rainfall in the region during the Pleistocene than today (Durham, Arellano, and Peck, 1955).

The high elevations characteristic of Nuclear Central America and the Mexican Plateau were attained in the Pliocene. The occurrence of marine sediments of Miocene age at about 2300 m in Chiapas indicates that in some areas a tremendous amount of uplift elevated regions (Schuchert, 1935; Stuart, 1950). It is probable that the marine embayment of Amatique that extended through northern Guatemala, and today is indicated by Lago de Izabal, continued to be a barrier to dispersal, and to influence differentiation to the north and south (Savage, 1966). The barrier presented by the embayment across the Nicaraguan depression persisted until late Pliocene, dissecting Central America from about the Rio San Juan almost to the Gulf of Fonseca on the Pacific (Lloyd, 1963). The rugged landscape that had been carved into the older rocks was modified by inundations of Tertiary volcanism and the region became one of more moderate relief (Williams, McBirney, and Dengo, 1964). The middle Pliocene was marked by an extended period of volcanic quiescence and severe erosion, creating features in the landscape still much in evidence today in central Mexico and the highlands of Central America (Williams, McBirney, and Dengo, 1964). Remnants of a deeply weathered erosion surface in the western portion of the Sierra de las Minas at about 2000 m are indications of the broad uplift and subsequent erosion that have occurred since the Pliocene (McBirney, 1963).

By the Pliocene the young Northern Element has become widespead over the Mexican highlands (Savage, 1966). In addition to the development of altitudinal climatic zones, drastic changes in the climatic patterns of the lowlands began to develop, including increasingly arid conditions and greater seasonal temperature ranges initiated in the Pliocene and extending to Recent times. Desert vegetation developed in the Great Basin and the northern portion of the Mexican Plateau (Dorf, 1959). Subhumid vegetation types advanced southward along the Pacific Coast and in the rainshadow valleys that extend across central Nuclear Central America. This no doubt has fragmented many highland mesic forests, and may have eliminated others altogether. The effects of this drying trend on the highland forests was compounded by the effects of late Tertiary volcanism in Central America which must have had a profound influence on its biota, fragmenting the distributions of many species and eliminating others. Over 50% of the Nuclear Central American highlands are covered by extrusives from this time, and except for the Cordillera de Talamanca, the highlands of Isthmian Central America were similarly affected (Stuart, 1966).

The most recent historical events are the ones that seem to have most greatly effected the patterns of distribution of extant species. Several contibuting factors of the Pleistocene drastically modified existing distributions and molded the ranges of the biota seen today. Foremost among these were the renewal of intense and widespread volcanic activity, actually reinitiated in the late Pliocene, and fluctuations in climate brought on by advances and recessions of glaciers. Pleistocene and Recent volcanism in Nuclear Central America has been mostly restricted to a narrow belt along the southern margin of the Tertiary belt and have produced the spectacular strato-volcanoes along the Pacific slope of the western portion of the Guatemalan Plateau (McBirney, 1963; Williams, 1960). There is evidence that these Quarternary volcanoes were produced in a progressively southeastern succession from about the Chiapas border (Tacana, Tajumulco) to south of Guatemala City (Fuego, Agua, Pacaya) (Wake and Lynch, 1982). The physiography of the region was greatly modified by the heavy showers of pumice emitted from these eruptions that covered intermontane basins, especially those formed by the parallel belt of eroded, late Tertiary volcanic and sedimentary rocks lying to the north (McBirney, 1963; Williams, 1960). The formation of the more recent Quaternary volcanoes did not greatly increase the extent of the Central American highlands, but did increase elevations along the southern portion of the Guatemalan Plateau and produce numerous scattered highland "islands." They lie for the most part on a Tertiary pedestal. For example, the Volcan de Agua which rises to 3766 m lies on a Tertiary basement that ranges from about 1100 m on the south to about 1900 m on the northeast side (Williams, 1960). While the volcanoes of the southwestern Guatemalan highlands are confined to a narrow belt, those in southeastern Guatemala are more widely scattered and do not attain comparable elevations to those of the west.

Pleistocene climatic fluctuations caused vegetational shifts that undoubtedly brought about extensions, fragmentations, coalescences, and extirpations of various mesic montane forests and portions of their herpetofaunas. The development of high volcanoes along the southern Nuclear Central American highlands must have also considerably altered local wind currents and rainfall patterns of the region, especially on the Guatemalan Plateau.

The relationship between temperatures and precipitation during the various stages of glaciation during the Pleistocene are complex. Although it has been traditional to correlate the alternating climatic fluctuations of cold, moist (glacial) and warm, dry (interglacial) conditions that are supposed to have existed at northern latitudes with Middle American paleoclimates, the reverse may be true; cool, dry periods may have alternated with warm, moist ones (Martin and Harrell, 1957). Data from paleobotanical studies suggest that the glacio-pluvia periods of the more northerly latitudes in North America may have coincided with periods of aridity in the tropics (Raven and Axelrod, 1974, 1975). Duellman (1965) suggested that in Mexico and northern Central America there may have been changes in the general patterns of high and low pressure systems that modified the alternating patterns of cool-moist versus warm-dry periods that prevailed in North America during the Pleistocene. In the generalized Caribbean paleotemperature curve presented by Emiliani and Rosa (1969), low temperatures appear to coincide with the periods of aridity documented by the palynological studies of van der Hammen (1974) in northern South America.

During the height of the glacial advances, there is evidence for small glaciers throughout Middle America, and their existence has been documented for some of the highest peaks of Mexico and Costa Rica (Anderson et al., 1973; Maldonado-Koerdell, 1964; West, 1964; Weyl, 1955; White, 1960). That large vertical shifts in the environment occurred during Pleistocene fluctuations seems to be indisputable (Dorf, 1959), but the extent of these shifts remains controversial. An estimate of a downward vertical displacement of vegetation in the New World tropics for as much as 1000 m was suggested by Graham (1973), Martin (1964), and Simpson (1974, 1978). Such a drastic shift has been disputed by Stuart (1951) and Savage (1966) who contended that such a depression would eliminate all tropical habitats from the region--an event not supported by present tropical fauna distributions. Even the ameliorating influences of oceanic currents and more extensive coast exposed from a lowering of sea level as proposed by Duellman (1960, 1965) would not seem to surmount the effects of such a drastic depression of habitats. Maximum depression of mean annual temperature was suggested to have been no more than about $5^{\circ}C$ (Stuart, 1957) or $6^{\circ}C$ (Savage, 1966). Since the adiabatic lapse rate is from $6--10^{\circ}C/km$ depending on the amount of moisture in the air, it is possible that depression of vegetational belts might have approached 1000 m below those of the present day under certain conditions in some regions.

It is probable that most of the cloud forests of the major mountain systems were connected at various times in the past via narrow belts of continuous forest, especially because most were connected via ridge systems exceeding 1000 m. Duellman's (1960) contention that a cloud forest-like corridor may have existed across the Isthmus of Tehuantepec during periods of Pleistocene history seems justified. Although the ridge system connecting the westernmost extension of the Sierra Madre de Chiapas with the southern Mexican highlands descends to about 250 m, the hiatus separating the nearest 1000 m contours on either side is scarcely 60 km. Certainly if a continuous cloud forest corridor did not exist, a narrow strip of mesic forest acting as a filter barrier allowed the dispersal of some cloud forest species, particularly since some species are not restricted to cloud forest sensu strictu. It should be remembered that cloud forest formation is not necessarily dependent on large amounts of precipitation, but rather a low evapotranspiration rate. Some Middle American cloud forests receive less than 2000 m of rain annually. The depression of temperatures by 5--6°C well could have caused cloud or fog formation along the lower slopes and foothills of ridge systems that resulted in cloud forest conditions. Although I think it possible that cool, mesic forest did extend across the Isthmus of Tehuantepec, it is more difficult to explain the dispersal of montane species across the Nicaraguan Depression. Although it seems likely that a corridor of forest, more mesic than today, extended along the eastern coast of Central America from Panama to at least southern Mexico (Wake and Campbell, in press), there is no evidence to suggest there were ever cloud forest conditions spanning the Nicaraguan Depression.

Conversely, there is abundant evidence that periods in the past were severely affected by aridity. In northern South America, van der Hammen (1974) and his associates have documented several periods of aridity. Perhaps the most convincing evidence comes from consideration of the distributions of closely related species presently confined to subhumid habitats in Middle America. It is assumed that the common ancestors of these groups inhabited a comparable environment to that of its descendents and that these ancestors possessed a wider distribution at some time in the past (Lee, 1980). Numerous examples may be given of subhumid relicts. The distribution of Triprion was suggested to be the result of Pleistocene aridity followed by more mesic conditions that fragmented the range (Trueb, 1970). Other notable examples may be found in certain hognosed pitvipers of the genus Bothrops and the iguanid genus Enyaliosaurus.

It is possible to infer several important things about the past extent of cloud forests from the distributions of arid-adapted species. First, cloud forests were probably more restricted in extent and more fragmented at various times in the past than today and, secondly, many of the smaller patches of cloud forest, especially those on mountains of relatively low elevation, were probably eliminated altogether. This, in part, may explain the depauperate nature of the southeastern Guatemalan highlands, isolated highland areas in El Salvador and Honduras, and the Montanas del Mico, Guatemala. If the period of severe aridity that was documented in northern South America from about 21,000 to 13,000 B.P. was also prevalent in Middle America, it may be imagined that the highland faunas of some areas were eliminated recently and have not had the opportunity to recolonize. Shortly after this time, the last glaciation (Wisconsin) came to an end and the subtropical zone became restricted to its presently elevated distribution and various intermontane valleys and low passes became important barriers to dispersal to highland faunas, leading to the isolation of many populations.

A search for replicate patterns of these isolates reveals that the distributions of species of amphibians and reptiles inhabiting the Sierra de las Minas may be grouped into seven common patterns.

1. Endemics to the Sierra de las Minas. These include seven amphibians: *Minascaecilia sartoria*, three species of *Bolitoglossa*, two species of *Eleutherodactylus*, and *Ptychohyla panchoi*. I have included in this list *B. meliana* although its range extends west of the Sierra de las Minas into the Sierra de Chuacus. No endemic reptiles occur in the area, but apparently the wide-ranging *Coluber constrictor* enters cloud forest only in this region. The presence in Alta Verapaz of some of these presumed endemics undoubtedly would be revealed by additional collecting in that area. Some species that are not endemic to the Sierra de las Minas are conspicuously absent from most of the Alta Verapaz highlands. These include *Bufo coccifer*, *Phrynohyas venulosa*, *Hypopachus variolosus*, *Dryadophis dorsalis*, *Leptophis modestus*, *Rhadinaea godmani*, *Thamnophis fulvus*, and *Bothrops godmani*. The distribution of these species, which occur in the western portion of the Sierra de las Minas and in some instances penetrate onto the southern boundary of the Alta Verapaz highlands, is highly suggestive that they are recent immigrants and have gained access into the region via the

narrow ridge of the Sierra de Chuacus. The absence of the widespread genus *Geophis* from the Sierra de las Minas and the Alta Verapaz highlands is enigmatic. Members of the genus have evolved in practically every other highland region of Middle America and there appears to have been adequate habitat and opportunites for invasion into the northeastern Guatemalan highlands. The genus *Pseudoeurycea* reaches the southern terminus of its range in southeastern Guatemala and similarly would seem to have had time to disperse into the Sierra de las Minas.

2. Species that are shared only with Alta Verapaz. The herpetofaunal assemblage of the Sierra de las Minas has a greater affinity with that of the Alta Verapaz highlands than any other; 75 of the 80 species known to occur in the highlands of Alta Verapaz also occur in the Sierra de las Minas. Thus, the recognition of two distinct faunal districts or provinces (Stuart, 1943; Smith, 1949) seems unwarranted. Representative species that are shared between these two regions are: two species of *Bolitoglossa*, *Chiropterotriton veraepacis*, four species of *Eleutherodactylus*, *Rana* sp., *Anolis haguei*, two species of *Abronia*, *Tantilla bairdi*, and *Tropidodipsas kidderi*. Most of these species are distinct, but a few (*A. haguei*, *T. kidderi*) are only slightly differentiated from forms occuring to the west in the northwestern highlands of Guatemala and are accorded subspecific status by some authors.

3. Northern Nuclear Central American distributions. Some species range from the Sierra de las Minas through the highlands of Alta Verapaz and have disjunct populations in the Cuchumatanes (*Plectrohyla quecchi*,

Sceloporus taeniocnemis, *Adelphicos veraepacis*, *Bothriechis aurifer*), and the distributions of others continue on to the Atlantic slopes of the Mesa Central of Chiapas (*Oedipina elongata*, *Eleutherodactylus rostralis*, *Anolis cobanensis*, *Rhadinaea hempsteadae*). A few species range across the northern highlands of Guatemala and also have populations in Honduras south of the xeric Rio Motagua (*Bolitoglossa dofleini*, *Hyla bromeliacea*, *Scaphiodontophis annulatus*). *Eleutherodactylus milesi* is known only from mesic forests in the Sierra de las Minas and the Sierra de Omoa, but this species occurs at relatively low elevations.

4. Northern and Southern Nuclear Central American distributions. Species whose distributions include both Atlantic and Pacific versants in Nuclear Central America include: *Eleutherodactylus lineatus*, *Plectrohyla guatemalensis*, *P. hartwegi*, *Ptychohyla spinipollex*, *Hypopachus barberi*, *Rana maculata*, *Corytophanes percarinatus*, *Sceloporus smaragdinus*, *Sphenomorphus incertum*, *Barisia moreleti*, *Dryadophis dorsalis*, *Rhadinaea godmani*, and *Thamnophis fulvus*. These species, with the exception of *P. hartwegi*, range widely in pine-oak forest and are resricted to moderate to high elevations.

5. Nuclear Central America--trans Isthmus of Tehuantepec distributions. A fair number of species have breached the Isthmus of Tehuantepec. Some species are restricted to the Atlantic escarpments on either side (*Hyla valancifer*, *Smilisca cyanosticta*, *Typhlops tenuis*, *Micrurus diastema*, *M. elegans*), whereas others occur on both Atlantic and Pacific facing slopes (*Agalychnis moreleti*, *Anolis petersi*, *Adelphicos quadrivirgatus*, *Drymobius chloroticus*, *Ninia diademata*,

Pliocercus elapoides). Most of these species may be characterized as being restricted to cloud forest or lowland mesic forest.

6. Nuclear Central American--trans Nicaraguan Depression distributions. Almost all of the species found in mesic montane forests that flank the Nicaragua lowlands are species that range freely into lowland rainforests or other habitats. They are rather uninteresting from a biogeographic viewpoint. Examples are: *Bufo coccifer*, *Anolis humilis*, *Corytophanes cristaus*, *Ameiva festiva*, *Leptodrymus pulcherrimus*, *Oxybelis fulgidus*, and *Bothriechis schlegeli*. In some instances their ranges are fragmented in the Nicaraguan lowlands, especially in the more xeric regions (*Gymnopis multiplicata*, *Hydromorphus concolor*, *Pliocercus euryzonus*). These species also range into lowland mesic areas and lend support to the notion that more mesic conditions once prevailed allowing dispersal of species between the two highlands. Finally, a few species are restricted to relatively high elevations and therefore possess distributions that are more dificult to explain (*Ninia maculata*, *Rhadinaea godmani*, *Bothrops godmani*).

7. Widespread, occurring in México, Nuclear Central America, and Isthmian Central America. Wide-ranging species in Middle America include *Eleutherodactylus rugulosus*, *Centrolenella fleischmanni*, *Anolis biporcatus*, *Amastidium veliferum*, *Coniophanes fissidens*, *Ninia sebae*, *Pseustes poecilonotus*, *Sibon dimidiata*, *Stenorrhina degenhardti*, *Tantilla schistosa*, and *Bothrops nummifer*. Although these species enter cloud forest, invariably they range widely in lowland forests and frequently possess ranges that are continuous between isolated cloud forests.

Examination of the Prim Network connecting cloud forest assemblages with closest affinities (Fig. 6) gives some indication of possible dispersal routes used by highland faunas and/or the relative severity of the vicariance events that led to the separation of the various highland assemblages. Several points concerning cloud forest herpetofaunas seem worth emphasizing. First, the primary dispersal routes across Nuclar Central America seem to be two parallel routes, one along the northern versant and the other along the Pacific. Stuart's (1954b) subhumid corridor lying between the two routes is of primary importance in acting as a barrier to exchange of faunas between areas along these two routes, and suggests that the development of this corridor is relatively old in comparison to the origin of the species under consideration.

It is puzzling that the highlands of northwestern Honduras possess a herpetofauna that is more similar to that of the Sierra de las Minas and Alta Verapaz than southeastern Guatemala. Perusal of a topographic map suggests that montane faunal exchange in this area would be easier across the broken highlands of southeastern Guatemala than across the imposing barrier of the Motagua Valley. At least two possible explanations for the similarity of herpetofaunas of highlands flanking the Motagua Valley come to mind. The broken southeastern highlands might have served as the major dispersal route for highland faunas into Honduras during the Pleistocene, but during periods of thermal maxima and aridity much of the mesic-adapted highland fauna might have been eliminated from the region, leaving the depauperate fauna much in evidence today and relatively few endemics (_Pseudoeurycea exspectata_, _Adelphicos daryi_). This possibility seems remote because so many typical northern versant species are absent from the more extensive southwestern Guatemalan highlands. Another possibility involves direct dispersal across the lower Motagua Valley. The lower portion of the valley today is covered by mesic forests and has never been subjected to rainshadow effects as has the middle and upper portions of the valley. Possibly during times of glaciation depression of temperatures was sufficient to allow exchange of cloud forest faunas between the eastern portion of the Sierra de las Minas and the mountain ranges flanking the south of the Motagua Valley.

The isolated highlands of southeastern Oaxaca are a major pivotal point. These highlands have close affinities with the Pacific-facing slopes to the southeast, the Chiapan highlands to the northeast, and the Mexican forests to the north. The southeastern Oaxacan highlands are some of the oldest in Central America and have been an important center for the dispersal and vicariance of cloud forest herpetofaunas.

Two lowland depressions across southern Nuclear Central America that link xeric interior valleys with the Pacific Coast are important barriers to dispersal of highland, mesic-adapted species. These have received scant attention previously but I believe they are important in that they were the corridors by which many xeric species dispersed into portion of Stuart's subhumid corridor, and they fragmented highland forests to either side. The depression in which Chiquimula is situated extends to the Pacific Coast of Guatemala and El Salvador and provides an avenue between the xeric Motagua Valley and the Pacific Coast. It is presently covered with subhumid vegetation types and nowhere rises much over 600 m. The Comayagua Depression dissects Honduras from coast to coast and is probably the dispersal route taken by many of the species inhabiting the xeric Aguan, Negro, and Ulua Valleys. It is more probable that there have been multiple invasions into the dry interior valleys from the Pacific Coast and explanation of their distribution should not be based entirely on dispersal of xeric-adapted species across the fragmented corridor of Central America. Species typical of both the Pacific Coast and the interior valleys of the Motagua and Honduras include Loxocemus bicolor and Bothrops ophryomegas. These lowland areas and their faunas are important in helping to understand extant patterns of cloud forest faunas. From the level of differentiation of populations isolated from one another on the Pacific Coast and these interior valleys, I infer that their separation has been comparatively recent.

While it is possible to gain a general notion of the origin and subsequent evolution of specific groups by examination of species patterns, these are a reflection of the most recent events, and a deeper understanding of the origin of herpetological assemblages can only be gained by analysis of interrelationships of specific lineages, consideration of the historical element from which they were derived, and correlation of the distribution and evolution of the group with specific historical events in the geology, climate, and vegetation of the region they presently inhabit. I have previously proposed a theory of the relationships for seven groups. The question now becomes: do these suggested phylogenies support or contradict each other in attempting to formulate a general scenario for the evolution of cloud forest herpetofaunas in Nuclear Central America?

The seven groups for which I have proposed phylogenies are part of the Middle American Element as proposed by Dunn (1931) and elaborated on by Savage (1966). This element was derived from the generalized tropical fauna that was isolated in the Central American paleopeninsula prior to the emergence of the Isthmian Link.

The timing of the invasion of the northern element is of importance. Species and groups of species that were widespread throughout the Middle American highlands by Pliocene times would be expected to have been subjected to similar events influencing their distribution. Therefore their present distributions might be expected to broadly reflect the same general patterns of those of the Middle American Element. Thus, analyses of the relationships and distributions of such genera as <u>Bolitoglossa</u>, <u>Pseudoeurycea</u>, <u>Sceloporus</u>, and <u>Abronia</u> should reflect basic patterns evident in Middle American groups.

I have found no exceptional patterns of congruence such as those found by Rosen (1978) for poeciliid fishes and, indeed, perhaps such should not be expected for diverse groups of terrestrial vertebrates, especially those occurring in regions of complex geologies. Freshwater fishes, in general, are restricted to narrow, well defined bodies of water and their distributions can be precisely delimited in terms of drainage systems. Nevertheless, various patterns of relationships and in distributions of highland herpetofaunas can be identified that establish possible points of congruence:

1. Old vicariads across the Isthmus of Tehuantepec. Several groups possess species or groups of species on either side of the

Isthmus of Tehuantepec and appear to be the sister group to one another. Species are strongly differentiated from each other and suggest an early geographic isolation and subsequent evolution. Prominent among these are the genus *Plectrohyla* and the *H. bistincta* group, the genus *Ptychohyla* and a number of Mexican frogs including the *H. pinorum* and *H. erythromma* groups, the *Rhadinaea godmani* group and the *R. decorata* group, and *Bothrops barbouri* and the two species of the group occurring south of the Isthmus of Tehuantepec.

2. Recent vicariads across the Isthmus of Tehuantepec. Several groups provide evidence for comparatively recent dispersal and subsequent fragmentation of ancestral populations. On the Atlantic versant *Ptychohyla chamulae* and *P. ignicolor* appear to be closely related sister species on either side of the Isthmus; on the Pacific versant *Eleutherodactylus greggi* and *E. omiltemanus* likewise are closely related and show a vicariant pattern of distribution. *Ptychohyla spinipollex*, widespread throughout the Nuclear Central American highlands, has its closest relative, *P. leonhardschultzei*, on both the Atlantic and Pacific versants of southern Mexico. Three closely related species of *Rhadinaea* inhabiting the Pacific slopes of Nuclear Central America possess a close relative in eastern Mexico, and I have found a specimen belonging to this group on the Pacific escarpment of Oaxa (UTACV specimen, JAC 277). Each one of these sister taxa form, together, the sister unit to other Nuclear Central American forms that strongly suggests that direction of dispersal was from west to east across the Isthmus.

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3. Old vicariads across the Nicaraguan Depression. There appears to have been little faunal exchange at any time between the Nuclear and Isthmian Central American highlands. However several groups possibly were able to breach the Nicaraguan lowlands (or Marine barrier?) at a relatively early point in their evolution; these include the genus *Bothriechis* which possesses a southern species (*B. nigroviridis*) that may be the sister species to all other montane species of the genus in Middle America, and the genus *Eleutherodactylus* which is comprised of numerous species groups that have their main center of diversity in South America.

4. Recent vicariads across the Nicaraguan Depression. As mentioned previously, the herpetofauna of the Nuclear Central American highlands possesses little in common with those of lower Central America. This is not especially surprising given the independent histories of the two regions and lack of a highland connection between the two at any time. What is surprising and seems to lack any good explanation is the existence of isolated and poorly differentiated populations of *Ninia maculata*, *Rhadinaea godmani*, and *Bothrops godmani* in these highland regions. Furthermore, *Bothriechis marchi* and *B. lateralis* appear to be closely related and to have evolved from a recently separated common ancestral stock. Other possible examples exist. Striking similarities in adult coloration and larval morphology suggest that the *Hyla uranocHylaoa* group may ultimately prove to be derived from the same common ancestor as the *Ptychohyla schmidtorum* group. *Rhadinaea serperaster* may have evolved from an ancestor that also managed to cross the Nicaraguan Depression. As seems to be the

case across the Isthmus of Tehuantepec, the major direction of movement seems to be away from the Nuclear Central American highlands.

5. Recent Nuclear Central American Atlantic-Pacific versant vicariads. In examining relationships of northern Central American groups, a striking number of sister taxa emerge with distributions on the Atlantic and Pacific escarpments. Most frequently species are confined to one escarpment, but a few appear to have invaded across the Guatemalan Plateau. Sister species exemplifying this pattern of distribution are *Plectrohyla ixil* and *P. matudai*, *Plectrohyla quecchi* and *P. sagorum*, *Rhadinaea hannsteini* and *R. kinkelini*, and possibly *Rhadinaea hempsteadae* and *R. montecristi*. A slightly more complex pattern is shown by *Plectrohyla hartwegi-guatemalensis-species B*. It appears that *P. hartwegi* and *P. guatemalensis* may have evolved on the Sierra Madre de Chiapas and northern escarpment of the Nuclear Central American highlands, respectively. *Plectrohyla hartwegi* subsequently crossed the Guatemalan Plateau and dispersed across the northern escarpment whereas *P. guatemalensis* dispersed across most of the Guatemalan Plateau and invaded the southeastern Guatemalan highland, reaching El Salvador. The distributions of these two species thus show an interesting "crossing-over" pattern. Apparently an early stock that gave rise to the bifid prepollex group of *Plectrohyla* was isolated in the Sierra de las Minas and evolved into a distinct species (*Plectrohyla* sp. B). *Bothriechis bicolor* and *B. marchi* show the same basic Atlantic-Pacific type of distribution, but *B. marchi* rather than inhabiting the northern escarpment of the Guatemalan highlands occurs south of the Motagua Valley in Honduras, and these species probably

evolved as the result of different events. On the basis of morphological characters, color and pattern, I hypothesize that the ancestral population of *B. bicolor* was wide-ranging and occurred from the Sierra Madre de Chiapas through the southern Guatemalan highlands and across a broken highlands arc that extended into Honduras. Quaternary volcanism eliminated the species from most of the southern highlands and created a wide hiatus between eastern and western populations. Subsequently the western population of *B. bicolor* reinvaded the new highlands formed by the volcanoes, reaching only as far west as the Volcan de Agua.

6. Vicariance patterns between the Sierra de las Minas and other regions. A number of species occurring in the Sierra de las Minas have disjunct populations elsewhere, most notably in cloud forests fringing the northern escarpment of northern Central America. The most important regions with which the herpetological assemblage of the Sierra de las Minas shares species in their order of similarity are the Alta Verapaz highlands, the Cuchumatanes, the mountains of northwestern Honduras, the Mesa Central of Chiapas, and the cloud forest of southeastern Oaxaca, which is isolated from other cloud forests in the Sierra Madre de Chiapas. Several populations appear to have become isolated in the Sierra de las Minas and evolved into distinct species, whereas other portions of these lineages have become isolated and evolved into several species elsewhere in the highland regions to the west.

Eleutherodactylus daryi seems to be the sister species to the other two species in this group of frogs. Ancestral distributions of these frogs seems to have been along the ancient central mountain axis of the Sierra de las Minas, Sierra de Chuacus, and Sierra Madre de Chiapas. Subsequently the population became fragmented--on the mesic northern escarpment of the Sierra de las Minas and on the mesic southern escarpment of the Pacific highlands. Dispersal across the Isthmus of Tehuantepec into the mountains of southern Mexico followed by fragmentation of the distribution allowed independent evolution of popuations flanking the Isthmus region. Ptychohyla panchoi is a highly distinctive species that appears to represent an early offshoot of the P. schmidtorum group isolated in the Sierra de las Minas. The ancestral population that gave rise to other members of the group seems to have been widely distributed in the highlands to the west of the Sierra de las Minas. Subsequent fragmentation and reduction of ranges isolated two populations, one along the south slope of the Pacific highlands (P. schmidtorum) and the other across the northern escarpment of the mountains of northern Central America including southeastern Oaxaça (P. chamulae). Fluctuations in climate and vegetation during the Pleistocene probably account for the dispersal followed by isolation of a P. chamulae stock from the highlands of southeastern Oaxaca across the Isthmus of Tehuantepec and the evolution of P. ignicolor in the cloud forest of the Sierra Juarez.

It would seem presumptuous for anyone, especially a nongeologist, to assume it possible to ascribe with a modest degree of accuracy all of the particuar historical events that have led to modern biological patterns in Middle America. Interpretations of the geological history and paleoenvironment of the region during the Tertiary are numerous and often conflicting; so much so, in fact, that it is probably possible to devise any scenario necessary to explain the evolution and distibution of a given group, documented, of course, by the appropriate references. For this reason, Rosen (1978) deferred any search for a historical framework that would illuminate the patterns evident in two groups of Middle American live-bearing fishes until further geological data were forthcoming.

The problem of attempting to decide whether the distributional patterns displayed by several lineages are the result of some commonality or are merely a matter of geographical coincidence is partially obscured by differences in vagility (activity range) among the various groups and components of these groups. Nevertheless, unique distribution or speciation patterns are informative with regard to the history of the region inhabited by, and the ecology of, a particular monophyletic group. Allusion was made in the foregoing discussion to common patterns of distribution, various relationships of sister taxa, and possible events that brought about these relationships. In summary, I present what I perceive to be a reasonable scenario of the sequence of disintergration of ancestral populations and the location and possible historical events that produced some of these fragmentations.

Prior to the Pliocene, the ancestors of certain extant lineages were probably widespread throughout the Central American paleopeninsula. It is generally agreed that during this time only moderate elevations existed over the region. It appears that many extant sister taxa are predominantly distributed on one side of the Isthmus of Tehuantepec (e.g. Plectrohyla--Hyla bistincta group, Ptychohyla--Hyla erythromma, possibly groups of Eleutherodactylus, Rhadinaea, Pseudoeuycea, Sceloporus, and Abronia) and that their isolation from one another across this barrier is relatively old.

Present day distributional patterns of most cloud forest groups may be viewed as the result of successive expansions and recessions of cloud forests. In Nuclear Central America, most faunal exchange has occurred along the two parallel tracts of the Atlantic and Pacific versants that converge in the Cerro Baul region. Regardless of distance, contiguous cloud forests on a common escarpment tend to have more similar herpetofaunas with each other than they do with those on the opposite versant. Nevertheless, ample evidence exists of past faunal exchange between Atlantic and Pacific versants. Two of the most important areas of exchange have been in the southeastern Oaxaca highlands and across the Guatemalan Plateau.

I agree with Stuart (1951) that the late Miocene-early Pliocene orogeny probably provided the impetus for many highland lineages to become differentiated from lowland ancestors. During this time, the major center for evolution of Nuclear Central American cloud forest faunas was probably along the ancient axis formed by the Sierra de las Minas, Sierra de Chuacus, and the Sierra Madre de Chiapas. Another center were the recently elevated highlands of the Sierra de los Cuchumatanes, Mesa Central of Chiapas, and Alta Verapaz highlands. To what extent these regions were elevated and isolated from one another is speculative, but I assume that the valleys that presently separate them were not deeply incised, rainshadow effects were negligible, and cloud forest was continuous along major escarpments.

Because of the essentially linear nature of the distribution of cloud forest across Middle America at this time, the first fragmentations probably subdivided populations to the east and west. The lands uplifted during early Pliocene underwent a period of erosion during mid to late Pliocene during which time several Atlantic drainage river systems became deeply entrenched. These rivers have their headwaters in the Minas-Chuacus-Madre de Chiapas axis that are composed of hard metamorphic rocks and comprise the present-day Continental Divide. Formerly, some of these river systems appear to have flowed roughly parallel to these ranges, but owing to differential erosional properties of the regions were subsequently captured by other stream systems. Thus the headwaters of the Rio Polochic were captured by the Rio Negro and have formed the Salama Basin and the deep Rio Negro gorge that isolate the highland faunas of the Cuchumatanes from those of the Alta Verapaz highlands. The Rio Cuilco and Rio Selegua probably became deeply entrenched at this time partially isolating highland species in the Cuilco masiff (Wake and Lynch, 1982). I suspect the Rio Grijalva might have similarly changed its course, possibly at the point presently called Canon del Sumidero. From extant distributional patterns it is tempting to speculate that the deep gorge of El Sumidero was formed at about the same time as many of the other streams flowing through the Cretaceous limestone of northern Central America, dissecting the ridge that may have provided the dispersal route by which the Mesa Central of Chiapas and the western portion of the Sierra Madre de Chiapas previously exchanged faunas. Certainly, in general, the relationships of the highland fauna of the Cerro Baul region to the west of El

Sumidero is more anciently tied with the Mesa Central than to the rest of the Sierra Madre de Chiapas, from which it is isolated by low passes in the Cerro Tres Picos region. Many species are shared by the southeastern Oaxacan highlands with the portion of the Sierra Madre de Chiapas to the east, but these populations are poorly differentiated from each other and appear to be recent immigrants or vicariads (Plectrohyla hartwegi, Ptychohyla euthysanota, Bothrops godmani). The presence of distinct species or differentiated populations in the Cerro Baul region and the northern Chiapan highlands (Adelphicos, Bothriechis) suggests a relatively older connection and subsequent separation between these two regions.

The direction in which ancestral populations were fragmented is conjectural, with conflicting evidence. The relationships of the Ptychohyla schmidtorum group (including P. panchoi), the Eleutherodactlus omiltemanus group, and Bothriechis suggest that successive fragmentation proceeded from east to west; whereas in Adelphicos and the Bothrops godmani group it was from west to east. Renewed volcanic activity in the late Pliocene and continuing into the Pleistocene and Recent had a profound effect on the herpetofauna. A series of high volcanoes were produced along the Pacific Coast of Guatemala that today are connected along their lower slopes by mesic subtropical forest. The formation of this high volcanic chain along the southern margin of the previously moderately elevated highlands had a tremendous impact on the lands to the north, not only by inundating large portions of the terrain with a heavy mantle of exuvia, but also by creating drier conditions on their leeward side. These dry conditions probably fragmented any connection of the Atlantic--Pacific corridor of mesic highland forest. Nevertheless, the present seasonally harsh conditions of the Guatemalan Plateau were probably considerably altered during time of climatic fluctuations in the Pleistocene allowing at least one, and probably several, limited exchanges of Pacific--Atlantic cloud forest species. Fluctuations in degree of aridity, initiated in the Pliocene, at times seems to have severly restricted the extent of cloud forests and eliminated others.

Climatic fluctuations during the Pleistocene allowed for a corridor of mesic cool forest to be formed across the Isthmus of Tehuanepec. On the basis of the limited exchange apparent on either side of the Isthmus, the corridor acted as a filter barrier, but nevertheless permitted dispersal of some cloud forest species. The major direction of dispersal was from east to west, but the direction was reversed in a few species such as *Hyla chaneque*.

At the height of the most severe climatic fluctuations interchange was maximized between the cloud forests of Nuclear Central America, especially across the Guatemalan Plateau area, and it was possible that during this time a few species gained access across the formidable barrier of the Nicaraguan lowlands. The effects of extensive Pleistocene volcanism upon the distributions of amphibians and reptiles was suggested to have kept the environment "off balance" and may have allowed populations generally restricted to high altitudinal zones to invade the lowlands (Savage, 1966; Stuart, 1966). Thus dispersal was facilitated between a few isolated highland regions and routes were not necessarily along the "backbones" of existing ranges. I can do no better than invoke this prosthetic explanation for the trans-Nicaraguan dispersal of several species, for as Lloyd (1963) pointed out, the backbone of Middle America is missing several vertebrae in the region between Nuclear and Isthmian Central America.

It appears we are presently in a relatively mild period. At times in the past it has been much drier and at other times considerably wetter. Isolation of species such as *Plectrohyla quecchi* in the northeastern Guatemalan highlands and Cuchumatanes, and of *P. ixil* in the Cuchumatanes and Mesa Central de Chiapas suggests that the drying trend that has separated these populations may be comparatively recent relative to those events that have separated well-differentiated sister species in the same regions. The continuing drying trend that has been prevalent since the Pliocene has probably been the factor responsible for isolation and speciation of many closely related species distributed across the volcanic highlands of Nuclear Central America.

Finally, I emphasize that the ecological parameters characterizing cloud forests have been maintained for a considerable period in Middle America. These uniquely dark, damp, and cool forests have served as the matrix in which many distinctive lineages have evolved against the backdrop of historical perturbations. Cloud forests have been important centers of evolution and are conservatories of distributional relicts. In most instances, the search for the nearest relatives of a cloud forest species will lead not to the lowlands, but to other isolated cloud forests.

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APPENDIX I

All of the museum acronyms used in this study are alphabetically listed below along with their respective institutions.

AMNH--American Museum of Natural History, New York

BMNH--British Museum of Natural History, London

CAS--California Academy of Science, San Francisco

FMNH--Field Museum of Natural History, Chicago

KU--University of Kansas Museum of Natural History, Lawrence

LSU--Louisiana State University, Baton Rouge

MCZ--Museum of Comparative Zoology, Cambridge

MNHN--Museum National d'Histoire Naturelle, Paris

NMB--Naturhistorisches Museum, Basel

UIMNH--University of Illinois Museum, Urbana

USAC--Universidad de San Carlos, Guatemala

USNM--United States National Museum, Washington, D. C.

UTA--University of Texas at Arlington Collection of Vertebrates

APPENDIX II

Faunal lists for various isolated cloud forests follow. Many of the species indicated are essentially lowlanders that invade only the lower portion of the cloud forest. In preparing these lists I have relied primarily on two sources: material in the collections of the University of Kansas (KU) and the University of Texas at Arlington (UTA) and references pertaining to the region or particular groups cited below. References are given following each species. Elevations were taken from published records, data associated with museum specimens, and my field notes. Vertical distributions, where given, are rounded to the nearest 10 m. A single asterisk indicates species that probably range widely in cloud forest, but freely enter other zones; double asterisks denote species that appear largely restricted to cloud forest; no asterisk indicates species peripherally enter cloud forest.

GOMEZ FARIAS REGION, TAMAULIPAS, MEXICO

General region: A portion of the Sierra Madre Oriental immediately south of the Tropic of Cancer between 22° 48' and 23° 30' N latitude, and between 99° and 99° 30' W longitude; this was termed the Gomez Farias region by Martin (1958).

Species: Chiropterotriton chondrostega, 910--1890 m (Martin, 1955a, 1955b, and 1958; Rabb, 1958); C. multidentatus, 420--1890 m (Martin, 1955a, 1955b, and 1958; Rabb, 1958); Pseudoeurycea belli, 1050--1800 m (Martin, 1955a, 1955b, and 1958); P. cephalica, 1000--1800 m (Martin, 1955a, 1955b, and 1958); P. scandens, 1000--1800 m (Martin, 1955b and 1958); _Eleutherodactylus decoratus_, 420--1830 m (Lynch, 1967a; Martin, 1955b and 1958); _Syrrhophus cystignathoides_, 100--1200 m (Lynch, 1970a; Martin, 1955a, 1955b, and 1958); _S. longipes_, 420--1800 m (Lynch, 1970a; Martin, 1955a, 1955b, and 1958); _Bufo marinus_, 10--1200 m (Martin, 1955b and 1958); _B. valliceps_, 100--1520 m (Martin, 1955b and 1958; Porter, 1963); _Hyla miotympanum_, 120--1600 m (Duellman, 1970; Martin, 1955a, 1955b, and 1958); _Smilisca baudini_, 100--1250 m (Duellman, 1970; Martin 1955b and 1958); _Rana berlandieri_, 80--2000 m (Martin, 1955b and 1958); _Sceloporus cyanogenys_**, 1000--1400 m (Martin, 1955b and 1958); _S. variabilis_, 100--1600 m (Martin, 1955a and 1955b); _Lepidophyma flavimaculatum_, 1000--2150 m (Martin, 1955a, 1955b, and 1958); _Eumeces dicei_, 500--1800 m (Martin, 1955b and 1958); _Abronia taeniata_, 1000--2000 m (Martin, 1955a, 1955b, and 1958); _Gerrhonotus liocephalus_, 300--1600 m (Martin, 1955a and 1958); _Amastridium veliferum_**, 1050 m (Martin, 1955a, 1955b, and 1958; Wilson and Meyer, 1969); _Dryadophis melanolomus_, 100--1050 m (Martin, 1955b); _Drymobius margaritiferus_, 100--1050 m (Martin, 1955b and 1958; Wilson, 1974); _Geophis semiannulatus_*, 1050--1800 m (Downs, 1967; Martin, 1955a, 1955b, and 1958); _Leptodeira septentrionalis_, 100--1500 m (Duellman, 1958; Martin, 1958); _Leptophis mexicanus_, 100--1100 m (Martin, 1955b and 1958); _Pliocercus elapoides_**, 1000--1250 m (Martin, 1955b and 1958); _Rhadinaea gaigeae_, 1010--1830 m (Myers, 1974; Martin, 1955a, 1955b and 1958); _Storeria occipitomaculata_, 1450--1800 m (Martin, 1955a, and 1958); _Tantilla rubra_, 350--1050 (Martin, 1955b and 1958); _Tropidodipsas sartorii_, 350--1680 m (Martin, 1955a, 1955b and 1958); _Thamnophis cyrtopsis_, 1500--1800 m (Martin, 1955a and 1958); _T. mendax_, 1050--2100 m (Martin, 1955a, 1955b and 1958); Bothrops asper, 100--1000 m (Martin, 1955a, 1955b and 1958); Crotalus durissus, 700--1550 m (Martin, 1955a, 1955b and 1958); C. lepidus, 1200--1800 m (Martin, 1955a, 1955b and 1958).

NORTHERN OAXACA, MEXICO

General region: The windward escarpment of the Sierra Juarez and Sierra Mixe, including Cerro Zempoalttepec and the vicinity of Totontepec.

Species: Bolitoglossa occidentalis, 1290-1600 m (KU, UTA); B. platydactyla, low and moderate elevations (Wake and Lynch, 1976); B. rufescens, low and moderate elevations (Wake and Lynch, 1976); Chiropterotriton chiropterus, 1320--1950 m (KU); Lineatriton lineola*, 730--800 m (KU); Pseudoeurycea belli, 1830--2100 m (UTA); Pseudoeurycea juarezi*, 2520--3160 m (Lynch and Wake, 1976; Regal, 1966; KU; UTA); P. smithi*, 2800--3000 m (Wake and Lynch, 1976; KU; UTA); T. narisovalis*, intermediate elevation (UTA); Pseudoeurycea sp. A**, 1580--3160 m (KU,UTA); Pseudoeurycea sp. B**, 2100 m (UTA); Pseudoeurycea sp. C**, 2540--2590 m (UTA); Thorius macdougalli*, 2800--3160 m (Wake and Lynch, 1976; KU; UTA); T. pulmonaris*, 2350--3160 m (Wake and Lynch, 1976; KU; UTA); Thorius sp. A*, 1500--3160 m (KU,UTA); Eleutherodactylus berkenbuschii, 250--1990 m (Savage, 1975; Savage and Deweese, 1979; Smith and Laufe, 1945; KU; UTA); E. mexicanus**, 1500--2520 m (Bogert, 1968b; Lynch, 1970b; Smith and Laufe, 1945; KU; UTA); E. spatulatus*, 1000--2300 m (Lynch, 1965a, 1965b, and, 1967a and 1970b; Bogert, 1969; KU; UTA); E. werleri, 620--1800 m (KU,UTA); Syrrhopus leprus, low and moderate elevations (Lynch, 1970a); Bufo cavifrons**, 900--1600 m

(Porter, 1963; KU; UTA); _B. occidentalis_, moderate and intermediate elevations (KU; UTA); _Bufo valliceps_, 900--1300 m (Porter, 1963; KU); _Agalychnis moreleti_*, 1500--1580 m (Duellman, 1970; KU); _Anotheca spinosa_**, 800--1800 m (Duellman, 1970; KU); _Hyla arborescandens_*, 1580--2370 m (Caldwell, 1974; Duellman, 1970; KU; UTA); _Hyla chaneque_**, 680--2200 m (Duellman, 1961a, 1965b, 1965c, and 1970; KU; UTA); _H. crassa_, 1500--1600 m (UTA); _H. cyanomma_**, 2640--2780 m (Caldwell, 1974; KU; UTA); _H. dendroscarta_**, 1580--1900 m (Duellman, 1970; KU); _H. echinata_**, 1500--1580 m (Duellman, 1962 and 1970; KU); _H. erythromma_, 600--850 m (Duellman, 1970; KU); _H. hazelae_, 2300--2540 m (Duellman, 1965b and 1970; UTA); _H. mixe_**, 1280--1800 m (Duellman, 1965b and 1970; KU; UTA); _H. pentheter_, 1830 m (UTA); _H. sabrina_**, 1650--2070 m (Caldwell, 1974; KU; UTA); _H. siopela_*, 2160--2890 m (Duellman, 1970; KU; UTA); _H. thorectes_*, 2100 m (UTA); _Hyla_ sp. A, 1570 m (KU); _Ptychohyla ignicolor_**, 500--1870 m (Adler, 1965; Duellman, 1961b, 1965b, and 1970; KU; UTA); _P. leonhardschultzei_*, 540--1600 m (Adler, 1965; Duellman, 1970; Shannon, 1951; KU); _Smilisca baudini_, 50--900 m (Duellman, 1970; KU; UTA); _S. cyanosticta_*, 790--900 m (KU; UTA); _Centrolenella fleischmanni_*, 580--900 m (Duellman and Tulecke, 1960; KU); _Rana_ sp. A (_pipiens_- group), 1300--2500 m (Shannon, 1951; Smith and Laufe, 1945; KU); _Anolis biporcatus_, 900 m (UTA); _A. damulus_, 700--1860 m (KU); _A. milleri_*, moderate elevations (Smith and Laufe, 1945; Smith and Paulson, 1968; Smith and Taylor, 1950); _Anolis petersi_**, moderate and intermediate elevations (Shannon, 1951; Smith and Kerster, 1955); _A. polyrhachis_**, 1580--2160 m (Smith, 1968; KU; UTA); _Corytophanes hernandezi_, 900 m (UTA); _Sceloporus formosus_, 830--1880 m (KU; UTA); _S._

grammicus*, 2050--3300 m (Smith, 1959a; KU; UTA); S. mucronatus, intermediate elevation (Alvarez and Huerta, 1973; UTA); S. variabilis, 800--1600 m (KU,UTA); Ameiva undulata, 120--1120 m (KU,UTA); Scincella gemmingeri*, 1370--1880 m (Smith and Laufe, 1945; KU,UTA); Sphenomorphus cherriei, 900 m (UTA); Lepidophyma sawini**, 1500 m (Smith, 1973); L. tuxtlae** 1600 m (KU); Abronia fuscolabialis**, 2100 m (Campbell, 1982; Tihen, 1944; UTA); A. mitchelli**, 2750 m (Campbell, 1982; UTA); Barisia gadovi*, intermediate elevations (UTA); Barisia viridiflava*, 2650--2780 m (Bogert, 1968b; UTA); Barisia sp.**, 2000--2500 m (UTA); Celestus enneagrammus*, 1880 m (UTA); Gerrhonotus liocephalus, intermediate elevations (UTA); Xenosaurus grandis*, 1300--1600 m (King and Thompson, 1968; Shannon, 1951; KU; UTA); Typhlops tenuis, moderate to intermediate elevations (Dixon and Hendricks, 1979); Exiliboa placata**, 1700--2450 m (Bogert, 1968b; KU; UTA); Adelphicos quadrivirgatus, 900 m (UTA); Cryophis hallbergi**, 1150--1870 m (Bogert and Duellman, 1963; KU; UTA); Drymobius chloroticus*, 1750--1830 m (Wilson, 1970a and 1975a; KU,UTA); Drymobius margaritiferus, 690--1300 m (Smith and Laufe, 1945; Wilson, 1974; KU); Geophis anocularis*, 1880 m (Campbell et al., 1982; Dunn, 1920; UTA); G. duellmani**, 1570--1830 m (Campbell et al., 1982; Smith and Holland, 1969; KU; UTA); Geophis laticinctus, 730 m (Smith and Holland, 1969; KU); Imantodes cenchoa, 40--900 m (KU,UTA); Lampropeltis triangulum*, 900 m (UTA); Leptodeira annulata, 790 m (KU); Leptodeira septentrionalis*, 400--1700 m (Smith and Laufe, 1945; KU,UTA); Leptophis ahaetulla, 900 m (UTA); Ninia diademata*, 1500--1880 m (UTA); N. sebae*, 900--1300 m (Schmidt and Rand, 1957; Shannon, 1951; UTA); Oxybelis aenus, 900 m (UTA); Pliocercus elapoides*, 900--1460 m (KU,UTA);

Pseustes _poecilonotus_, 900 m (UTA); _Rhadinaea_ _bogertorum_**, 1500--2780 m (Bogert, 1968b; Myers, 1974; KU; UTA); _Sibon_ _dimidiata_, 830--1600 m (KU); _Spilotes_ _pullatus_, 900 m (UTA); _Stenorrhina_ _degenhardti_*, 900--1490 m (UTA); _Tantalophis_ _discolor_, 2440--2800 m (Duellman, 1958b; Myers and Campbell, 1981; KU); _Tantilla_ _schistosa_, 1300--1490 (Shannon, 1951; Smith, 1962; UTA); _T_. _taeniata_, low and moderate elevations (Wilson and Meyer, 1971); _Thamnophis_ _chrysocephalus_*, 1300--ca. 2000 m (Lynch and Smith, 1966; Shannon, 1951); _Thamnophis_ _scalaris_*, 2350--2950 m (Bogert, 1968b; KU; UTA); _Toluca_ _conica_, 1880--2740 m (Smith and Laufe, 1945; KU; UTA); _Tropidodipsas_ _sartori_, 210--1440 m (KU,UTA); _Xenodon_ _rhabdocephalus_, low to moderate elevations (UTA); _Micrurus_ _diastema_, low to moderate elevations (Fraser, 1973; Roze, 1967); _M_. _elegans_*, 1500--1600 m (KU,UTA); _Bothrops_ _asper_, low and moderate elevations (UTA); _Bothrops_ _nummifer_*, 900--1300 m (Burger, 1950; Shannon, 1951; UTA); _Bothrops_ _undulatus_, 2100 m (UTA); _Crotalus_ _intermedius_, 2920--3200 m (Armstrong and Murphy, 1979; Lynch and Smith, 1965a and 1966; KU); _Sistrurus_ _ravus_, 1880 (Campbell and Armstrong, 1979; USNM; UTA).

SOUTHERN VERACRUZ, MEXICO

General region: The highlands of the Sierrade los Tuxtlas including the Volcan San Martin Tuxtla, Cerro Mata Larga, Cerro Cintepec, Cerro Campanario, Volcan Santa Marta, and Volcan San Martin Pajapan.

Species: _Bolitoglossa_ _mexicana_, 200--1070 m (Shannon and Werler, 1955; Wake and Lynch, 1976; UTA); _B_. _occidentalis_, (intermediate between _occidentalis_ and _rufescens_ fide Wake and Lynch, 1976), 610 m (Shannon and Werler, 1955); *B. platydactyla*, low and moderate elevations (Perez Higareda, 1981; Werler and Smith, 1952; Wake and Lynch, 1976); *Lineatriton lineola**, 500--1220 m (Perez Higareda, 1981; Shannon and Werler, 1955); *Pseudoeurycea nigromaculata***, intermediate elevations m (Shannon and Werler, 1955); *P. werleri***, 910--1370 m (Darling and Smith, 1954); *Thorius pennatus**, 910--1220 m (Shannon and Werler, 1955); *Eleutherodactylus berkenbuschii*, 300--1220 m (Lynch, 1965; Savage, 1975; Savage and Deweese, 1979; Shannon and Werler, 1955); *E. loki**, 500--1220 m (Booth, 1959; Perez Higareda, 1978; Shannon and Werler, 1955); *E. megalotympanum**, 910--1220 m (Shannon and Werler, 1955); *E. pygmaeus**, 910--1220 m (Darling and Smith, 1954; Lynch, 1965b; Shannon and Werler, 1955; Werler and Smith, 1952); *E. rhodopis**, 910--1650 m (Booth, 1959; Darling and Smith, 1954; Shannon and Werler, 1955); *E. werleri***, moderate elevations (Lynch and Fritts, 1965); *Syrrhopus leprus*, 350--710 m (Greene, 1975; Lynch, 1970a; Shannon and Werler, 1955; Werler and Smith, 1952); *Bufo cavifrons***, 1070--1400 m (Darling and Smith, 1954; Firchein, 1950; Porter, 1963; Shannon and Werler, 1955) *B. valliceps*, 10--1300 m (Booth, 1959; Perez Higareda, 1978; Porter, 1963; Shannon and Werler, 1955; Werler and Smith, 1952 *Agalychnis moreleti**, moderate elevations (Shannon and Werler, 1955); *Anotheca spinosa***, 850 m (Duellman, 1970; Darling and Smith, 1954; Shannon and Werler, 1955; KU; UTA); *Hyla chaneque**, moderate and intermediate elevations m (UNAM); *H. dendroscarta**, moderate and intermediate elevations (Duellman, 1970); *H. miotympanum**, low, moderate, and intermediate elevations (Duellman, 1970); *H. valancifer***, 500--1180 m (Duellman, 1960b and 1970; Firschein and Smith, 1956; Perez Higareda, 1981; KU); *Plectrohyla pycnochila*, (Rabb, 1959--locality almost certainly in error, see Duellman, 1970); Smilisca baudini, low to moderate elevations (Duellman, 1970); S. cyanosticta*, 500--910 m (Duellman, 1970; Perez Higareda, 1978; Shannon and Werler, 1955; UTA); Centrolenella fleischmanni*, 350 m (Duellman and Tulecke, 1960); Rana berlandieri low and moderate elevations (Sanders, 1973; UTA); Anolis barkeri, 380 m (Kennedy, 1965; Robinson, 1962); Anolis duellmani**, 800--1150 m (Fitch and Henderson, 1973; KU); A. laeviventris*, low and moderate elevations (Fitch and Henderson, 1973); A. lemurinus, low and moderate elevations (Fitch and Henderson, 1973; UTA); A. petersi**, moderate and intermediate elevations (UTA); A. tropidonotus, low and moderate elevations (Fitch and Henderson, 1973); Corytophanes hernandezi, low to moderate elevations (Perez Higareda, 1978; UTA); Sceloporus variabilis, low to moderate elevations (Darling and Smith, 1954; Werler and Smith, 1952); Sceloporus sp. (formosus--group?), ca. 500 m (Perez Higareda, 1978); Ameia undulata, low and moderate elevations (Darling and Smith, 1954; Werler and Smith, 1952; UTA); Mabuya mabouya, low and moderate elevations (UTA); Scincella gemmingeri*, moderate and intermediate elevations (KU; UTA); S. silvicola, "base of Volcan San Martin" (Darling and Smith, 1954); Spenomorphus cherriei, 200--750 m (Booth, 1959; Greene, 1975; UTA); Lepidophyma flavimaculata*, low and moderate elevations (UTA); L. pajapanensis*, 1070 m (Werler, 1957; UTA); L. tuxtlae*, 120--910 m (Greene, 1970; Werler and Shannon, 1957; UTA); Abronia chiszari*, 360 m? (Campbell, 1982; Smith, H. M. and R. B. Smith, 1981; UTA); A. reidi**, 1640 m (Werler and Shannon, 1961); Celestus enneagramus*, intermediate elevations (UTA); Gerrhonotus liocephalus*, moderate to intermediate elevations (UTA); _Xenosaurus grandis_**, 1160--1630 m (King and Thompson, 1968; Werler and Shannon, 1961); _Typhlops tenuis_, low elevations (Dixon and Hendricks, 1979; Perez Higareda, 1980); _Leptotyphlops goudoti_, low elevations (Perez Higareda, 1980); _Adelphicos quadrivirgatus_, 500--750 m (Greene, 1975; Perez Higareda, 1978; UTA); _Amastridium veliferum_, low and moderate elevations (Perez Higareda, 1980; Wilson and Meyer, 1969; UTA); _Coniophanes fissidens_, low and moderate elevations (Perez Higareda, 1980; UTA); _Dendrophidion vinitor_, "lower slopes Volcan San Martin" (Darling and Smith, 1954; Perez Higareda, 1978); _Dryadophis melanolomus_, low and moderate elevations (Perez Higareda, 1978; UTA); _Drymobius chloroticus_*, 1350 m (Darling and Smith, 1954; Wilson, 1970a and 1975a); _D. margaritiferus_*, low and moderate elevations (Wilson, 1974; UTA); _Geophis carinosus_*, 900 m (Downs, 1967; KU); _Imantodes cenchoa_, low and moderate elevations (Perez Higareda, 1978; UTA); _Lampropeltis triangulum_*, low to moderate elevations (Perez Higareda, 1978; Williams, 1978; UTA); _Leptodeira annulata_, low and moderate elevations (Duellman, 1958; Perez Higareda, 1978); _L. septentrionalis_*, low and moderate elevations (Duellman, 1958; UTA); _Leptophis ahaetulla_, low and moderate elevations (Perez Higareda, 1978; UTA); _L. mexicana_, low and moderate elevations (Perez Higareda, 1978); _Ninia diademata_*, 350--750 m (Greene, 1975; Werler and Smith, 1952; UTA); _N. sebae_*, 350--1000 m (Greene, 1975; Schmidt and Rand, 1957; UTA); _Oxybelis aeneus_, low and moderate elevations (Keiser, 1974; Perez Higareda, 1978; UTA); _Pliocercus elapoides_*, 500--ca. 1000 m (Greene, 1969; Perez Higareda, 1978; UTA); _Pseustes poecilonotus_, low elevations (Perez Higareda, 1978); _Spilotes pullatus_, low and moderate elevations (Perez Higareda, 1978; UTA); _Stenorrhina degenhardti_*, low to moderate elevations (Perez Higareda, 1978 and 1980; UTA); _Tantilla shistosa_*, "lower slopes Volcan San Martin" (Darling and Smith, 1954; Perez Higareda, 1978; Smith, 1962); _Tropidodipsas sartorii_, low and moderate elevations (Perez Higareda, 1978; UTA); _Xenodon rhabdocephalus_, low and moderate elevations (Perez Higareda, 1978; UTA); _Micrurus diastema_, low to moderate elevations (Fraser, 1973; Perez Higareda, 1980; Roze, 1967); _M. elegans_*, low and moderate elevations (Schmidt, 1958); _M. limbatus_*, 500--1050 m (Fraser, 1964; Perez Higareda, 1980; Roze, 1967; UTA); _Bothrops asper_, 10--1100 m (Perez Higareda, 1978; UTA); _B. nummifer_*, >530 m to moderate elevations (Perez Higareda, 1978; UTA).

SIERRA MADRE DEL SUR, GUERRERO, MEXICO

General region: The highlands to the west of Chilpancingo from the vicinity of Omilteme across the Sierra Madre to Cerro Teotepec. A hiatus of the wet forest occurs in the pass between the headwaters of the Rio Yextla, a tributary of the Rio Balsas, and the Rio Papagayo, flowing to the Pacific.

Species: _Dermophis oaxacae_, low and moderate elevations (Savage and Wake, 1972); _Pseudoeurycea belli_*, 1945--2380 m (Davis and Dixon, 1965; Gadow, 1905; Smith and Taylor, 1948; KU; UTA); _Pseudoeurycea_ sp. D*, 2569 m (KU); _Pseudoeurycea_ sp. E*, 3300 m (KU); _Thorius_ sp. B*, 2560--3360 m (Myers and Campbell, 1981; KU; UTA); _Eleutherodactylus guerreroensis_, 980 m (Lynch, 1967b; KU); _E. omiltemanus_* 1500--2500 m (Davis and Dixon, 1965; Lynch, 1970b; Taylor, 1941; KU; UTA); _E. pygmaeus_*, 820--2670 m (Davis and Dixon, 1965; Lynch, 1965b Taylor, 1940; KU); _E. rugulosus_, 700--2120 m (Adler and Dennis, 1972; Davis and Dixon, 1965; Savage, 1975; KU); _E. saltator_*, 1760--2600 m (Adler and Dennis, 1972; Lynch, 1970b; Smith and Taylor, 1948; Taylor, 1942); _Eleutherodactylus_ sp. A**, 2130 m (UTA); _Syrrhopus pipilans_, 10--1800 m (Lynch, 1970a; KU); _Tomodactylus dilatus_*, 2410--2500 m (Davis and Dixon, 1955; Davis and Dixon, 1965; UTA); _Bufo occidentalis_, 1360--2440 m (Davis and Dixon, 1965; KU; UTA); _Agalychnis moreleti_*, 700 m (Duellman, 1970); _Hyla chryses_*, 2540--2600 m (Adler, 1965; Adler and Dennis, 1972; Duellman, 1970; KU); _Hyla erythromma_, 700--980 m (Davis and Dixon, 1965; Duellman, 1970; Snyder, 1972; Taylor, 1940; KU); _H. juanitae_*, 750--1070 m (Snyder, 1972; KU); _Hyla melanomma_*, 850--2000 m (Davis and Dixon, 1965; Duellman, 1970; Smith, 1941b; Taylor, 1940; KU); _H. mykter_*, 1980--2750 m (Adler and Dennis, 1972; Myers and Campbell, 1981; KU; UTA); _H. pentheter_, 2000 m (Adler and Dennis, 1972); _H. pinorum_, 700--1020 m (Duellman, 1970; Taylor, 1937; KU); _H. trux_**, 1760--2120 m (Adler and Dennis, 1972; KU); _Hyla_ sp. B (_bistincta_-group), 2600 m (Adler and Dennis, 1972; Duellman, 1970); _Ptychohyla leonhardschultzei_*, 1010 m (Adler, 1965; Duellman, 1970; Taylor, 1944); _Smilisca baudini_, 20--980 m (Duellman, 1970; KU); _Centrolenella fleischmanni_*, 740--1010 (Davis and Dixon, 1965; Duellman and Tulecke, 1960; Taylor, 1942); _Rana_* _omiltemana_*, 2220--2440 m (Davis and Dixon, 1965; KU; UTA); _Anolis dunni_, 740--1010 m (Davis and Dixon, 1961; Fitch et al., 1976; KU; UTA); _A. liogaster_**, 2410--2470 m (Davis, 1954; Davis and Dixon, 1961; Gadow, 1905 Shannon, 1951; UTA); _A. megapholidotus_, 850--1350 m (Davis and Dixon, 1961; Fitch et al., 1976); _A. omiltemanus_**, 2380 m (Davis, 1954; Davis and Dixon, 1961; KU; UTA); _A._

subocularis, 10--1500 m (Davis, 1954; Fitch et al., 1976); _Sceloporus adleri_*, 2410--3400 m (Myers and Campbell, 1981; Smith and Savitzky, 1974; KU; UTA); _S_. _formosus_*, 1700--2740 m (Davis and Dixon, 1961; Smith and Savitzky, 1974; KU; UTA); _S_. _grammicus_*, 2380--3080 m (Davis and Dixon, 1961; KU; UTA); _S_. _mucronatus_*, 1700--2560 m (Davis and Dixon, 1961; KU; UTA); _Eumeces_ _ochoterenae_*, 850--2750 m (Davis and Dixon, 1961; Myers and Campbell, 1981; UTA); _Ameiva_ _undulata_, 740--2130 m (Davis and Dixon, 1961; KU); _Abronia_ _deppei_*, 2130--2750 m (Davis and Dixon, 1961; Martin del Campo, 1939; Myers and Campbell, 1981; UTA); _Barisia_ _gadovi_*, 2320--3080 m (Davis and Dixon, 1961; Hall, 1951; Myers and Campbell, 1981; KU; UTA); _Gerrhonotus_ _liocephalus_, 850--2440 m (Davis and Dixon, 1961; Gadow, 1905); _Drymobius_ _margaritiferus_, 300--980 m (Davis and Dixon, 1961; Wilson, 1974; KU); _Geophis_ _omiltemanus_*, 2380--2440 m (Downs, 1967; Davis and Dixon, 1959; UTA); _G_. _sieboldi_, 1770 m (Downs, 1967); _Lampropeltis_ _triangulum_, 10--2110 m (Hall, 1951; Williams, 1978; KU); _Leptodeira_ _septentrionalis_, 850--1300 m (Davis and Dixon, 1961; Duellman, 1958; KU); _Oxybelis_ _aeneus_, 950--1070 m (Davis and Dixon, 1961); _Pituophis_ _lineaticollis_, 850--2500 m (Davis and Dixon, 1959; KU; UTA); _Rhadinaea_ _hesperia_, 1000--1980 m (Myers, 1974; Davis and Dixon, 1959); _R_. _omiltemana_**, 1940--2440 m (Myers, 1974; KU; UTA); _R_. _taeniata_*, 1700--2440 m (Myers, 1974; Davis and Dixon, 1959; UTA); _Rhadinophanes_ _monticola_*, 2750 m (Myers and Campbell, 1981; AMNH; UTA); _Thamnophis_ _chrysocephalus_*, 2440--2670 m (Davis and Dixon, 1959; Gadow, 1905; Hall, 1951; KU; UTA); _T_. _cyrtopsis_*, 850--2440 m (Davis and Dixon, 1959; Hall, 1951; KU; UTA); _T_. _scalaris_*, 1770--3090 m (Davis and Dixon, 1959; KU; UTA); Toluca conica, 2130--2440 m (Davis and Dixon, 1961;

UTA); *Micrurus browni*, 850--1770 m, (Roze, 1967; Schmidt and Smith, 1943; Smith and Taylor, 1945); *Bothrops barbouri**, 2380--3300 m (Campbell, 1977; Davis and Dixon, 1959; Dunn, 1919; KU; UTA); *B. undulatus**, 2010--2600 m (Campbell, 1977; Campbell and Armstrong, 1979; Davis and Dixon, 1959; KU; UTA); *Crotalus intermedius*, 2130--3000+ m (Armstrong and Murphy, 1979; Campbell, 1977; Campbell and Armstrong, 1979; KU; UTA); *Sistrurus ravus*, 1980--2290 m (Campbell and Armstrong, 1979; KU; UTA).

SOUTHEASTERN OAXACA, MEXICO

General region: The highlands extending from east of the Isthmus of Tehuantepec to Cerro Baul near the Oaxaca-Chiapas border.

Species: *Dermophis oaxacae*, low and moderate elevations (Savage and Wake, 1972); *Bolitoglossa occidentalis*, moderate elevations (Lynch and Smith, 1966; Wake and Lynch, 1976); *B. veracrucis*, 110 m (Taylor, 1951b; Wake and Brame, 1969); *Psuedoeurycea* sp. F*, intermediate elevations (Wake and Lynch, 1976); *Eleutherodactylus macdougalli**, 460--1370 m (Lynch and Smith, 1965a and 1966; Smith and Taylor, 1948; Taylor, 1942); *E. pygmaeus*, ca. 1000 m (Lynch, 1965b); *E. rhodopis**, low and moderate elevations (Lynch and Smith, 1966); *E. rugulosus*, low and moderate elevations (Lynch and Smith, 1966; Savage, 1975); *E. silvicola**, 1490 m (Lynch, 1967b); *Syrrhophus leprus*, low and moderate elevations (Lynch, 1970a); *Bufo cavifrons***, 100--1830 m (Porter, 1963; UTA); *B. valliceps*, mountains "between La Gloria and Cerro Azul" (Firschein and Smith, 1957; Lynch and Smith, 1966); *Hyla chaneque***, 1520 m (Duellman, 1970; Lynch and Smith, 1966); *Plectrohyla hartwegi***, ca. 1500 m (Duellman, 1968 and 1970); *P. matudai**, 1520 m (Bumzahem and

Smith, 1954; Duellman, 1970; Lynch and Smith, 1966); _Ptychohyla chamulae_*, moderate elevations (Duellman, 1970; Lynch and Smith, 1966); _Ptychohyla euthysanota_*, 460--2000 m (Duellman, 1970; Lynch and Smith, 1965a and 1966); _Smilisca baudini_, 10--1000 m (UTA); _Centrolenella fleischmanni_*, ca. 1500 m (Duellman and Tulecke, 1960); _Rana maculata_*, 1520 m (UTA); _Anolis barkeri_, "Cerro Azul above La Gloria" (Kennedy, 1965), "Cascajal, upper Uzpanapa River" (Schmidt, 1939); _A. biporcatus_, low to moderate elevations (Smith and Kerster, 1955); _A. breedlovei_**, 1220--1500 m (Smith and Paulson, 1968); _Anolis compressicaudus_, low and moderate elevations (Smith and Kerster, 1955); _A. cuprinus_, 270--1520 m (Fitch et al., 1976; Lynch and Smith, 1966; Smith, 1964); _A. limifrons_, low and moderate elevations (Lynch and Smith, 1966); _A. petersi_**, 1520--1830 m (Lynch and Smith, 1966; Smith and Kerster, 1955; KU; UTA); _A. pygmaeus_*, low and moderate elvations (Smith and Williams, 1963); _A. tropidonotus_, ca. 1500 m (Alvarez del Toro and Smith, 1956; Smith and Williams, 1963); _Corytophanes percarinatus_, moderate and intermediate elevations (Peters and Donoso-Barros, 1970; Stuart, 1963); _Sceloporus acanthinus_*, ca. 1500 m (Smith and Williams, 1963); _S. internasalis_, 460 m (Lynch and Smith, 1965a and 1966; Smith and Bumzahem, 1955; Stuart, 1971); _Ameiva undulata_*, 1000--1500 m (Lynch and Smith, 1965a and 1966; UTA); _Scincella gemmingeri_*, ca. 1500 m (Lynch and Smith, 1965a and 1966); _Sphenomorphus assatum_*, ca. 1000 m (Alvarez del Toro and Smith, 1956; Lynch and Smith, 1966; Stuart, 1940; Werler and Smith, 1952); _S. cherriei_, 910 m (Smith and Langebartel, 1949; Stuart, 1940); _Abronia bogerti_*, moderate elevations (Tihen, 1954); _Abronia_ sp. A**, 1520--1830 m (Campbell, in prep.; UTA); _Celestus_ rozellae, low and moderate elevations (Smith and Burger, 1955); Gerrhonotus liocephalus, 1520--1830 m (Lynch and Smith, 1966; UTA); Xenosaurus grandis*, 1370--1520 m (King and Thompson, 1968; Lynch and Smith, 1965b); Leptotyphlops goudoti, ca. 1500 m (Lynch and Smith, 1965a and 1966); Adelphicos latifasciatus**, 1500--1900 m (Campbell and Ford, 1982; Lynch and Smith, 1966; UTA); A. quadrivirgatus, low and moderate elevations (UTA); Coniophanes fissidens, 100--1500 m (Lynch and Smith, 1966; Smith and Langebartel, 1949; Smith and Williams, 1963; UTA); Dryadophis dorsalis*, moderate elevations (Lynch and Smith, 1966); D. melanolomus, 100--1500 (Smith and Langebartel, 1949; Werler and Smith, 1952 UTA); Drymobius chloroticus*, 1300--1830 m (Lynch and Smith, 1965a and 1966; Wilson, 1970a and 1975a; KU; UTA); Drymobius margaritiferus*, 10--1500 m (Smith and Lynch, 1965a; Wilson, 1974; UTA); Geophis laticinctus, moderae elevations; Geophis sp.*, 1520--1830 m (UTA); Imantodes cenchoa, 100--1500 m (UTA); Lampropeltis triangulum, 10--1500 m (Williams, 1978; UTA); Leptodeira annulata, 10--ca. 1500 m (Duellman, 1958; Lynch and Smith, 1965a); L. septentrionalis*, 100--1500 m (Duellman, 1958; Tanner,1957); Leptophis ahaetulla, 10--ca. 1500 m (Peters and Orejas-Miranda, 1970; UTA); L. mexicanus, 10--ca. 1500 m (Lynch and Smith, 1965a; Peters and Orejas-Miranda, 1970); Ninia diademata*, moderate elevations (UTA); Ninia sebae*, 800--1500 m (Lynch and Smith, 1965a; Schmidt and Rand, 1957; UTA); Pituophis lineaticollis, ca. 1500 m (Lynch and Smith, 1966; UTA); Pliocercus elapoides*, 1220--1520 m (Lynch and Smith, 1965a; Smith and Langebartel, 1949; UTA); R. godmani*, 1500--2000 m (Lynch and Smith, 1966; Myers, 1974); R. macdougalli*, 1220--1370 m (Myers, 1974; Smith and Langebartel, 1949);

_Stenorrhina degenhardti_*, 1520--1830 m (KU; UTA); _Tantilla jani_, low and moderate elevations (Wilson and Meyer, 1971); _Tantilla taeniata_, low and moderate elevations (Wilson and Meyer, 1971); _Tropidodipsas fischeri_*, 1520--1830 m (Lynch and Smith, 1966; UTA); _T. sartorii_, moderate elevation (UTA); _Micrurus browni_*, 1520--1830 m (Lynch and Smith, 1966; Roze, 1967; UTA); _M. diastema_, low and moderate elevations (Fraser, 1973; Roze, 1967); _M. elegans_**, 1520--1830 m (UTA); _M. nigrocinctus_*, 1520--1830 m (UTA); _M. nuchalis_, 300--1500 m (Lynch and Smith, 1966; Roze, 1967); _Bothriechis rowleyi_**, 1500--1830 m (Bogert, 1968a; Lynch and Smith, 1965a and 1966; Smith and Moll, 1969; UTA); _Bothrops asper_, 10--ca. 1000 m (Lynch and Smith, 1965a); _B. godmani_*, 1520--1830 m (Bogert, 1968a; Campbell, 1977; Lynch and Smith, 1965a; Smith and Williams, 1963; UTA); _B. nummifer_*, 1520--1830 m (Bogert, 1968a; Burger, 1950; Campbell, 1977; UTA).

NORTHERN CHIAPAS, MEXICO

General region: The Atlantic escarpment of the northern highlands of Chiapas.

Species: _Bolitoglossa hartwegi_*, 2040--2860 m (Wake and Brame, 1969; Wake and Lynch, 1976); _B. mexicana_, low and moderate elevations (Johnson et al., 1976; Wake and Lynch, 1976; KU); _B. occidentalis_, 500--1830 m (Johnson et al., 1976; Poglayen and Smith, 1958; Shannon, 1951; Wake and Lynch, 1976 KU); _B. resplendens_*, 2200 m (Wake and Lynch, 1976; KU); _B. rostrata_, high elevations (Wake and Lynch, 1976); _B. rufescens_, low and moderate elevations (Poglayen and Smith, 1958; Wake and Lynch, 1976); _B. stuarti_*, 1620 m (Wake and Brame, 1969; Wake and Lynch, 1976); _Nyctanolis pernix_, (Elias, in press); _Oedipina elongata_, 670 m (Smith, P. W. and H. M. Smith, 1951; Wake and Lynch, 1976); Pseudoeurycea sp. G*, moderate to high elevations (Wake and Lynch, 1976); Eleutherodactylus glaucus*, 2100 m (Lynch, 1967c); E. lineatus*, 1830 m (KU); E. rostralis*, low and moderate elevations (Stuart, 1963); E. rugulosus, 270--1690 m (Lynch, 1965c; Savage, 1975; KU); E. stuarti*, 760--1500 m (Johnson, 1973; Johnson et al., 1976; Lynch, 1970b); E. taylori*, 1690 m (Lynch, 1966; KU); Eleutherodactylus sp. B*, low to moderate elevations (KU); Eleutherodactylus sp. C*, moderate elevations (in prep); Syrrhophus pipilans, 30--1670 m (Lynch, 1970a; KU); Bufo bocourti, 2450--2900 m (KU; UTA); B. cavifrons**, 1520--1690 m (Porter, 1963; KU); B. valliceps, 300--1700 m (Porter, 1963; Smith, P. W. and H. M. Smith, 1951; Tanner, 1957); Agalychnis moreleti*, 770--1070 m (Johnson et al., 1976); Anotheca spinosa**, 760--1070 m (Johnson et al., 1976); Hyla chaneque**, 1600--1700 m (Duellman, 1965c and 1970; KU); H. melanomma*, 1550--1700 m (Duellman, 1970; Duellman and Hoyt, 1961; KU); H. miotympanum*, moderate elevations (Duellman, 1970); Plectrohyla guatemalensis*, 1550--2000 m (Booth, 1959; Duellman, 1970; KU); P. ixil*, 1550--1690 (Duellman, 1970; KU); P. pycnochila*, 2400 m (Duellman, 1970); Ptchohyla chamulae*, 1520--1690 m (Adler, 1965; Duellman, 1961b and 1970; KU); P. euthysanota*, 1520--1700 m (Duellman, 1970; Tanner, 1957; KU); Smilisca baudini, 10--1925 m (Duellman, 1970; Smith, P. W. and H. W. Smith, 1951; KU); S. cyanosticta*, moderate elevations (Johnson et al., 1976; Poglayen and Smith, 1958); Centrolenella fleischmanni*, 500 m (Duellman and Tulecke, 1960; Firschein and Smith, 1957); Hypopachus barberi, 1670--2830 m (Nelson, 1973); Rana maculata*, 1670 m (Booth, 1959; KU); Rana sp. B* (pipiens-

group), 1520--1700 m (Booth, 1959; KU); _Anolis anisolepis_*, 2150--2560 m (Fitch et al., 1976; Smith et al., 1968; KU; UTA); _A. barkeri_, 400--600 m (Alvarez del Toro, 1972; Brandon et al., 1966); _A. biporcatus_, 600--1200 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956; Booth, 1959; Johnson et al., 1976; Smith and Kerster, 1955; Tanner, 1957); _A. breedlovei_**, 1680--1740 m (Smith and Paulson, 1968); _A. capito_, low and moderate elevations (Alvarez del Toro, 1972); _A. cobanensis_**, 1520--1800 m (KU); _A. compressicaudus_, 600 m (Alvarez del Toro and Smith, 1956; Tanner, 1957); _A. crassulus_*, intermediate elevations (Alvarez del Toro, 1972); _A. humilis_, low and moderate elevations (Alvarez del Toro, 1972; Smith, P. W. and H. M. Smith, 1951); _A. laeviventris_*, 1620--1700 m (Alvarez de Toro, 1972; Alvarez del Toro and Smith, 1956; KU); _A. lemurinus_, 215--300 m (Alvarez del Toro, 1972); _A. limifrons_, 600 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956); _A. parvicirculatus_*, 1070--1200 m (Alvarez del Toro and Smith, 1956; Johnson et al., 1976); _A. petersi_**, moderate elevations (Alvarez del Toro, 1972; Johnson et al., 1976); _A. pygmaeus_, 600 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956); _A. tropidonotus_, 760--1280 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956; Johnson et al., 1976); _Corytophanes cristatus_, low and moderate elevations (Alvarez del Toro, 1972); _C. hernandezi_, 215 to ca. 1000 m (Alvarez del Toro, 1972; Johnson et al., 1976); _Sceloporus hartwegi_*, 1600--2910 m (Alvarez del Toro, 1972; Booth, 1959; Stuart, 1971; Tanner, 1957; KU); _S. internasalis_*, 500--1600 m (Alvarez del Toro, 1972; Smith and Alvarez del Toro, 1962; Stuart, 1971); _S. prezygus_*, 1000--2450 m (Alvarez del Toro, 1972; Axtell, 1960; Smith and Alvarez del Toro, 1963;

KU); S. variabilis, 10--2130 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956; KU); Lepidophyma flavimaculata*, 300--1070 m (Alvarez del Toro, 1972; Johnson et al., 1976 KU); Mabuya mabouya, low and moderate elevations (Alvarez del Toro, 1972; UTA); Sphenomorphus assatum*, 760--2100 m (Alvarez del Toro and Smith, 1956; Johnson et al., 1976); S. cherriei, 600 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956; Stuart, 1940); S. incertum*, 2130--2450 m (KU); Ameiva festiva, 300 m (KU); A. undulata*, 210--1700 m (Booth, 1959; Smith, P. W. and H. M. Smith, 1951; KU); Abronia lythrochila*, 2130--2390 m (Alvarez del Toro, 1972; Smith and Alvarez del Toro, 1962 and 1963; UTA); Barisia moreleti*, 1690--2910 m (Hartweg and Tihen, 1946; UTA); Celestus rozellae, low to moderate elevations (Alvarez del Toro, 1972); Gerrhonotus liocephalus, 1200--1700 m (Smith and Alvarez del Toro, 1963; Tanner, 1957); Xenosaurus grandis*, 1070--1500 m (Alvarez del Toro, 1972; Johnson et al., 1976; King and Thompson, 1968); Adelphicos nigrilatus*, 2200--2500 m (Alvarez del Toro, 1972; Campbell and Ford, 1982; Smith, 1942); Adelphicos quadrivirgatus, low and moderate elevations (Alvarez del Toro, 1972; Smith, 1942); Coniophanes fissidens, 300--2130 m (Alvarez del Toro, 1972; Smith and Williams, 1963; KU; UTA); Dendrophidion vinitor, 500--800 m (Alvarez del Toro, 1972; Johnson et al., 1976); Dryadophis melanolomus, 1325--1620 m (Alvarez del Toro, 1972; KU); Drymobius margaritiferus*, 215--1620 m (Alvarez del Toro, 1972; Wilson, 1974; KU); Geophis carinosus*, 1000--1500 m (Alvarez del Toro, 1972; Downs, 1967); G. laticinctus*, 760--1800 m (Alvarez del Toro, 1972; Downs, 1967; Johnson, 1979; Johnson et al., 1976; Smith and Williams, 1963; KU); G. semidolatus, moderate elevations (Alvarez del

Toro, 1972--in error for _G. laticinctus_, see Johnson, 1979 and Johnson et al. 1976); _Imantodes cenchoa_, low and moderate elevations (Alvarez del Toro, 1972; Johnson et al., 1976; KU); _Lampropeltis triangulum_, low to intermediate elevations (Alvarez del Toro, 1972; Johnson et al., 1976; Williams, 1978; KU); _L. septentrionalis_, 300--1700 m (Alvarez del Toro, 1972; Booth, 1959; Duellman, 1958; Johnson et al., 1976; Tanner, 1957; KU); _Leptophis ahaetulla_, 300--600 m (Alvarez del Toro, 1972; Smith and Alvarez del Toro, 1962; KU); _L. mexicanus_, 760--1140 m (Johnson et al., 1976; KU); _L. modestus_*, 1335 m (Alvarez del Toro, 1972; Williams and Smith, 1966); _Ninia diademata_*, 760--1700 m (Alvarez del Toro, 1972; Booth, 1959; Johnson et al., 1976; KU; UTA); _N. sebae_*, 760--1880 m (Alvarez del Toro, 1972; Johnson et al., 1976; Schmidt and Rand, 1957; Tanner, 1957; KU); _Oxybelis aeneus_, low and moderate elevations (Alvarez del Toro, 1972; Johnson et al., 1976 Keiser, 1974); _O. fulgidus_, low and moderate elevations (Alvarez del Toro, 1972); _Pituophis lineaticollis_, 1680--2140 m (Alvarez del Toro, 1972; KU); _Pliocercus elapoides_*, 1700 m (Alvarez del Toro, 1972; Booth, 1959; Tanner 1957); _Pseustes poecilonotus_, 215--760 m (Alvarez del Toro, 1972; Johnson et al., 1976; KU); _Rhadinaea godmani_*, 1500--2000 m (Myers, 1974; UTA); _R. hempsteadae_*, 2380 m (Myers, 1974); _Sibon dimidiatus_, low and moderate elevations (Alvarez del Toro, 1972; Booth, 1959; Johnson et al., 1976; Tanner, 1957); _Spilotes pullatus_, low and moderate elevations (Alvarez del Toro, 1972; Johnson et al., 1976); _Stenorrhina degenhardti_*, 760--1700 m (Booth, 1959; Johnson et al., 1976; KU); _Thamnophis fulvus_, 1880--2910 m (KU); _Tropidodipsas sartorii_, 100--2440 m (Alvarez del Toro, 1972; Johnson et al., 1976; Smith and Alvarez del

Toro, 1962; KU; UTA); *Xenodon rhabdocephalus*, low elevations (Alvarez del Toro, 1972); *Micrurus browni**, 400--2000 m (Alvarez del Toro and Smith, 1956; Blaney and Blaney, 1978); *M. diastema*, low to moderate elevations m (Alvarez del Toro, 1972; Fraser, 1973; Johnson et al., 1976; Roze, 1967); *M. elegans***, 250--1200 m (Alvarez del Toro, 1972; Alvarez del Toro and Smith, 1956; Blaney and Blaney, 1978; Johnson et al., 1976; Schmidt, 1958); *Bothriechis rowleyi***, intermediate elevations (UF); B. schlegeli, moderate elevations (Alvarez del Toro, 1972; Smith and Moll, 1969); *Bothrops asper*, 215--780 m (Alvarez del Toro, 1972; Johnson et al., 1976; KU); *Bothrops godmani**, 1900 m (Alvarez del Toro, 1972; Campbell, 1977; Martin del Campo, 1938; KU); *Bothrops nummifer**, 300--1700 m (Alvarez del Toro, 1972; Booth, 1959; Burger, 1950; Martin del Campo, 1938; Tanner, 1957).

SIERRA DE LOS CUCHUMATANES, GUATEMALA

General region: The northern versant of the Sierra de los Cuchumatanes, extending from the vicinity of the Lago de Montebello in northeastern Chiapas east into the Departamento de Quiche in Guatemala.

Species: *Bolitoglossa cuchumatana***, 1990 m (Stuart, 1943a and 1963; Wake and Brame, 1969; Wake and Lynch, 1976; UMMZ); *B. dofleini*, low elevations (Wake and Lynch, 1976); *B. lincolni***, 2450 m (Stuart, 1943a and 1963; Wake and Lynch, 1976; UMMZ); *B. mexicana*, low elevations (Stuart, 1943a; Wake and Lynch, 1976); *B. omniumsanctorum*, 2500 m (Stuart, 1952); *B. rostrata*, 2910--3480 m (Stuart, 1963; KU); *B. rufescens*, low and moderate elevations (Stuart, 1963); *Chiropterotriton cuchumatanus*, 2860 m (Lynch and Wake, 1975); *Nyctanolis pernix***, (Elias, 1982); _Pseudoeurycea rex_, 2450--3480 (Stuart, 1943a and 1963; Wake and Lynch, 1976; KU; UMMZ); _Eleutherodactylus lineatus_*, 1990 m (Stuart, 1941a, 1943a, and 1963; UMMZ); _E. rostralis_, low and moderate elevations (Stuart, 1963); _E. rugulosus_, 770--1300 (Savage, 1975; Stuart, 1943a and 1963; UMMZ); _Eleutherodactylus_ sp. D (_alfredi_- group), 1500--2000 m (LACM, UMMZ); _Bufo bocourti_, 1900--3080 m (Stuart, 1943a and 1963; KU; UMMZ); _B. marinus_, 10--1650 m (Stuart, 1963; KU); _B. valliceps_, 10--1850 m (Stuart, 1943a and 1963; KU); _Agalychnis moreleit_*, 800 m (Stuart, 1943a and 1963; UMMZ); _Hyla bromeliacea_**, 1170 m (Stuart, 1943a and 1963; UMMZ); _Plectrohyla glandulosa_*, 2900-3400 m (Stuart, 1963; KU); _P. guatemalensis_*, 1500--2200 (Duellman, 1970; Stuart, 1963; KU); _P. hartwegi_**, moderate and intermediate elevations (UMMZ); _P. ixil_*, 1180 m (Duellman, 1970; Stuart 1943a and 1963; UMMZ); _P. quecchi_*, 1000--1600 m (Duellman, 1970; Stuart, 1963); _Plectrohyla_ sp. A, 1710 m (LACM); _Ptychohyla spinipollex_*, 1700 m (Duellman, 1970; Stuart, 1963); _Smilisca baudini_, 50--1100 m (Duellman, 1970; Stuart, 1943 and 1963; KU); _S. cyanosticta_*, low and moderate elevations (Duellman, 1970; Stuart 1963); _Centrolenella fleischmanni_*, 770--1180 m (Stuart, 1943 and 1963); _Hypopachus barberi_, 1600--2010 m (Nelson, 1973; Stuart, 1943 and 1963; UMMZ); _Rana maculata_*, moderate and intermediate elevations (Stuart, 1963); _Rana_ sp. C (_pipiens_- group), 770--2500 m (Stuart, 1943 and 1963; UMMZ); _Anolis biporcatus_, low and moderate elevations (Stuart, 1963); _A. capito_, 1170 m (Stuart, 1943a and 1963; UMMZ); _A. crassulus_*, 1990--2590 m (Stuart, 1943 and 1963; UMMZ); _A. humilis_, 770 m (Stuart, 1943 and 1963; UMMZ); _A. laeviventris_*, 1550 m (KU); _A. lemurinus_, low and moderate elevations (Stuart, 1963); _A._

limifrons, 1170 m (Stuart, 1943 and 1963; UMMZ); A. petersi**, moderate elevations (Stuart, 1963); Corytophanes cristatus, low and moderate elevations (Stuart, 1963); C. percarinatus*, moderate and intermediate elevations (Stuart, 1963); Sceloporus smaragdinus*, 2400--3330 m (Stuart, 1943a and 1971; UMMZ); S. taeniocnemis*, 1200--2100 m (Stuart, 1943a and 1971; UMMZ); S. variabilis, 720--1400 m (Stuart, 1943a and 1963; UMMZ); Lepidophyma flavimaculata*, low and moderate elevations (Stuart, 1963); Mabuya mabouya, low and moderate elevations (Stuart, 1963); Sphenomorphus cherriei, low and moderate elevations (Stuart, 1940 and 1963); Ameiva festiva, 770 m (Stuart, 1943a and 1963; UMMZ); A. undulata, 720 m (Stuart, 1943a and 1963; UMMZ); Abronia ochoterenai**, 2200 m (Hartweg and Tihen, 1946; Martin del Campo, 1938; Smith and Alvarez del Toro, 1963); Barisia moreleti*, 1990--2600 m (Stuart, 1943 and 1963; KU; UMMZ); Celestus rozellae, low and moderate elevations (Stuart, 1963); Leptotyphlops goudoti low and moderate elevations (Stuart, 1963; UMMZ); Adelphicos quadrivirgatus, low and moderate elevations (Smith, 1942; Stuart, 1963); A. veraepacis*, moderate and intermediate elevations (Campbell and Ford, 1982; Stuart, 1943a and 1963; UMMZ); Coniophanes fissidens, low and moderate elevations (Stuart, 1963); Dendrophidion vinitor, low and moderate elevations (Stuart, 1963); Dryadophis dorsalis*, 1400 m (Stuart, 1943a and 1963; UMMZ); D. melanolomus, low and moderate elevations (Stuart, 1963); D. margaritiferus*, low and moderate elevations (Stuart, 1963; Wilson, 1974); Geophis carinosus*, 1000--1500 m (Downs, 1967; Stuart, 1941d, 1943 and 1963); Imantodes cenchoa, low and moderate elevations (Stuart, 1963); Lampropeltis triangulum, low to intermediate elevations (Stuart, 1963; Williams, 1978); _Leptodeira septentrionalis_*, low to intermediate elevations (Duellman, 1958; Stuart, 1963); _Leptophis ahaetulla_, low and moderate elevations (Stuart, 1963); _L. mexicanus_, low and moderate elevations (Stuart, 1963); _L. modestus_**, 2590 m (KU); _Ninia diademata_*, moderate elevations (Stuart, 1963; UMMZ); _N. sebae_*, 800--1550 m (Schmidt and Rand, 1957; Stuart, 1943a and 1963; KU; UMMZ); _Oxybelis aeneus_, low and moderate elevations (Stuart, 1963; UMZ); _O. fulgidus_, low and moderate elevations (Stuart, 1963); _Pituophis lineaticollis_, 1990 m (Duellman, 1960c; Stuart, 1943a and 1963; UMMZ); _Pliocercus elapoides_*, moderate elevations (Stuart, 1963; UMMZ; USAC); _Pseustes poecilonotus_, moderate elevations (Stuart, 1963; USAC); _Rhadinaea godmani_*, 1500--2200 m (Myers, 1974; Stuart, 1963); _R. hempsteadae_*, 1970--2600 m (Stuart, 1943a; Stuart and Bailey, 1941; UMMZ); _Scaphiodontophis annulatus_, low and moderate elevations (Peters and Orejas-Miranda, 1970; Stuart, 1963; USAC); _Spilotes pullatus_, low and moderate elevations (Stuart, 1963; USAC); _Stenorrhina degenhardti_*, low and moderate elevation (Stuart, 1963; USAC); _Tantilla schistosa_, 1170 m (Stuart, 1943a and 1963; UMMZ); _Thamnophis fulvus_*, 1990--3000 m (Stuart, 1943a and 1963; KU; UMMZ); _Tropidodipsas fischeri_*, 1900--3800 m (Stuart, 1943a and 1963; FMNH; MCZ; UMMZ); _T. sartorii_, low and moderate elevations (Stuart, 1963; USAC); _Xenodon rhabdocephalus_, low and moderate elevations (Stuart, 1963; USAC); _Micrurus diastema_, "moderate elevations" (Fraser, 1973; Roze, 1967; Stuart, 1963; USAC); _M. elegans_**, moderate elevations (Stuart, 1963; UMMZ; USAC); _Bothriechis aurifer_**, ca. 1500 m (Slevin, 1939; Martin del Campo, 1938; Smith and Moll, 1969; Stuart, 1943a and 1963; CAS); _B. schlegeli_, moderate (USAC); Bothrops asper, low and moderate elevations (Stuart, 1963; USAC); B. godmani*, intermediate and high elevations (Stuart, 1943a and 1963; UMMZ); B. nummifer*, low and moderate elevations (Stuart, 1963; USAC).

ALTA VERAPAZ, GUATEMALA

General region: The highlands of Alta Verapaz including the Sierras de Pocolha, Xucaneb, and Chama, and the highlands west of Coban.

Species: Gymnopis multiplicata*, 900 m (Savage and Wake, 1972; Stuart, 1948a; UMMZ); Bolitoglossa dofleini, 140--1000 m (Stuart, 1948a; KU); B. helmrichi**, 1300--1700 m (Schmidt, 1936a; Stuart, 1948a; Wake and Brame, 1969; CAS; UMMZ); B. mexicana, 600--1000 m (Stuart, 1948a; UMMZ); B. mulleri*, 140--1300 m (Schmidt, 1936a; Stuart, 1948a; Wake and Lynch, 1976; KU; UMMZ); B. odonelli, 600--1000 m (Stuart, 1948a; KU); B. rufescens*, 10--1300 m (Schmidt, 1936a; Stuart, 1948a; Wake and Lynch, 1976; KU; UMMZ); Oedipina elongata, 700 m (Stuart, 1948a; Wake and Lynch, 1976; UMMZ); Eleutherodactylus bocourti**, 930--1410 m (Stuart, 1948a; UMMZ); E. brocchi*, 1300--1410 m (Savage, 1975; Stuart, 1948a; UMMZ); E. daryi**, 1500--1900 m (Ford and Savage, 1982); E. lineatus*, moderate and intermediate elevations (Stuart, 1941a; UMMZ); E. rostralis*, 140--1410 m (Stuart, 1948a; UMMZ; KU); E. rugulosus, 140--1250 m (Savage, 1975; Stuart, 1948a; KU; UMMZ); E. xucanebi**, 1000--1330 m (Stuart, 1941a and 1948; KU; UMMZ); Eleutherodactylus sp. E*, moderate elevation (description in preparation); Syrrhopus leprus, 120 m (Lynch, 1970a; KU); B. valliceps, low and moderate elevations (KU; UTA); Agalychnis moreleti*, 929--1410 m (Duellman, 1970; Salvin, 1860;

Stuart, 1948a; TCWC; UMMZ); Hyla bromeliacea**, 920--1300 m (Duellman, 1970; Stuart, 1948a; KU; UMMZ); Plectrohyla guatemalensis* 1000--1410 m (Duellman, 1970; Stuart, 1948a; KU; UMMZ); P. hartwegi**, 1000 m (Duellman, 1970; Stuart, 1948a; KU; UMMZ); P. quecchi*, 1000--1410 m Duellman, 1970; Stuart, 1948a; UMMZ); Ptychohyla spinipollex*, 1000--1410 m (Adler, 1965; Duellman, 1970; Stuart, 1948a; KU; UMMZ); Smilisca baudini, 10--1300 m (Duellman, 1970; Stuart, 1948a; KU; UMMZ; UTA); S. cyanosticta*, 140 m (Duellman, 1970; KU); Centrolenella fleischmanni*, 10--1300 m (Stuart, 1948a; KU; UMMZ); Hypopachus barberi, 1000--1500 m (Nelson, 1973; Stuart, 1948a; KU; UTA); Rana maculata*, 1200--1410 m (Stuart, 1948a; KU; UMMZ); Rana sp. D (pipiens- group), 140--1410 m (Stuart, 1948a; KU; UMMZ); Anolis biporcatus, 40--290 m (Dumeril et al., 1870--1909; Stuart, 1948a; KU; UMMZ); A. capito, 140--290 m (Stuart, 1948a; KU; UMMZ); A. cobanensis**, 1000--1410 m (Stuart, 1942a and 1948; KU; UMMZ); A. haguei*, 1410 m (Stuart, 1942a and 1948; UMMZ); A. humilis, 40--400 m (Stuart, 1948a; UMMZ); A. laeviventris*, 1250--1410 m (Stuart, 1948a; UMMZ); A. lemurinus, 40--1020 m (Stuart, 1948a; KU; UMMZ); A. limifrons, 40--1325 m (Stuart, 1948a; UMMZ); A. pertersi**, 1300 m (Stuart, 1948a; UMMZ); Corytophanes cristatus, 140--930 m (Salvin, 1860; Stuart, 1948a; KU; UMMZ); C. percarinatus*, 1300--1410 m (Stuart, 1948a; KU; UMMZ); Sceloporus taeniocnemis*, 1100--1500 m (Stuart, 1948a and 1971; KU; UMMZ); S. variabilis 40--1250 m (Stuart, 1948a; KU; UMMZ); Lepidophyma flavimaculata*, 100--930 m (Stuart, 1948a; KU; UMMZ); Ameiva festiva, 40--1020 m (Stuart, 1948a; KU; UMMZ); A. undulata*, 40--1020 m (Stuart, 1948a; UMMZ); Mabuya mabouya, 40 m (Stuart, 1948a; UMMZ); Sphenomorphus _cherriei_, 920--1330 m (Stuart, 1940 and 1948; KU; UMMZ); _S. incertum_**, 1300 m (Stuart, 1940 and 1948; UMMZ); _Abronia aurita_**, intermediate elevations? (Cope, 1887; Stuart, 1948a); _A. fimbriata_**, intermediate elevations? (Bocourt, 1878; Cope, 1885); _Barisia moreleti_*, 1410 m (Stuart, 1948a; UMMZ); _Celestus rozellae_, 140 m (Stuart, 1948a and 1963; KU); _Xenosaurus grandis_**, 1220 m (King and Thompson, 1968; Stuart, 1941b and 1948; UMMZ); _Leptotyphlops goudoti_, 1330 m (Cope, 1875; Stuart, 1948a); _Typhlops tenuis_, 920--1330 m (Salvin, 1860; Stuart, 1948a; UMMZ); _Adelphicos quadrivirgatus_, 1100 m (Stuart, 1948a; CM; UMMZ); _A. veraepacis_**, 1200--1650 m (Campbell and Ford, 1982; Stuart, 1941d and 1948; UMMZ); _Amastridium veliferum_, 290 m (Stuart, 1948a; Wilson and Meyer, 1969); _Coniophanes fissidens_, 210--290 m (Cope, 1887; Stuart, 1948a; UMMZ); _Dendrophidion vinitor_, low and moderate elevations (Stuart, 1948a); _Dryadophis melanolomus_, 40--1250 m (Stuart, 1941c and 1948; KU; UMMZ) _Drymobius chloroticus_**, 1000--1700 m (Stuart, 1948a; Wilson, 1970a and 1975a; UMMZ); _D. margaritiferus_*, 10--1410 m (Salvin, 1860; Stuart, 1948a; Wilson, 1974; KU; UMMZ; UTA); _Imantodes cenchoa_, 290--1320 m (Salvin, 1860; Stuart, 1948a; KU; UMMZ); _Lampropeltis triangulum_, 10--1250 m (Stuart, 1948a; Williams, 1978; KU; UMMZ); _Leptodeira annulata_, 40--1320 m (Stuart, 1948a; Werner, 1903); _L. septentrionalis_*, 40--1320 m (Stuart, 1948a; Werner, 1903; KU; UMMZ); _Leptophis ahaetulla_, 40--990 m (Stuart, 1948a; UMMZ); _L. mexicanus_, 10--1020 m (Salvin, 1860; Stuart, 1948a; KU; UMMZ); _Ninia diademata_*, 800--1100 m (Stuart, 1948a; UMMZ); _N. maculata_*, 1300 m (Stuart, 1948a; UMMZ); _N. sebae_*, 10--1410 m (Salvin, 1860; Schmidt and Rand, 1957; Stuart, 1948a; KU; UTA); _Oxybelis aeneus_, 270--1100 m (Stuart, 1948a;

KU; UMMZ); O. fulgidus, 270--1100 m (Stuart, 1948a; UMMZ); Oxyrhopus petola, low and moderate elevations (Stuart, 1948a); Pliocercus elapoides*, 140--1000 m (Stuart, 1948a; KU; UMMZ); P. euryzonus*, 1400 m (Stuart, 1948a; TCWC); Pseustes poecilonotus, 140 m (KU); Rhadinaea hempsteadae*, 1200--1850 m (Myers, 1974; Stuart, 1948a; Stuart and Bailey, 1941; UMMZ); R. kinkelini*, 1550 m (Myers, 1974; Stuart, 1948a; Stuart and Bailey, 1941; UMMZ); Scaphiodontophis annulatus, 1000 m (Stuart, 1948a and 1963; UMMZ); Sibon dimidiatus, 120 m (Bocourt, 1884; Stuart, 1948a and 1963; KU); Spilotes pullatus, 10--1200 m (Stuart, 1948a; KU; UMMZ); Stenorrhina degenhardit*, 920--1410 m (Stuart, 1948a; KU; UMMZ); Storeria dekayi*, 990--1320 m (Salvin, 1860; Stuart, 1948a; UMMZ); Tantilla bairdi*, 1550 m (Stuart, 1941d and 1948; UMMZ); T. schistosa, 500--1300 m (Smith, 1962; Stuart, 1948a; UMMZ); Thamnophis fulvus*, 1320--1410 m (Stuart, 1948a; UMMZ); Tropidodipsas kidderi**, 1500 m (Stuart, 1942b and 1948; UMMZ); T. sartorii, 290--930 m (Stuart, 1948a; UMMZ); Xenodon rhabdocephalus, 30--1000 m (KU; USAC); Micrurus diastema, 270--1250 m (Fraser, 1973; Roze, 1967; Stuart, 1948a; Werner, 1903; KU; UMMZ); M. elegans**, 1250--1330 m (Schmidt, 1936ab and 1958; Stuart, 1948a; UMMZ); Bothriechis aurifer**, 1000--1330 m (Boulenger, 1896; Gunther, 1895; Salvin, 1860; Smith and Moll, 1969; Stuart, 1948a; UMMZ; UTA); Salvin, 1860; Stuart, 1948a; UMMZ; UTA); B. schlegeli, 100--800 m (Duellman, 1963a; KU; USAC); Bothrops asper, 10--1000 m (Stuart, 1948a; UMMZ; USAC); B. godmani*, 1410 m (Stuart, 1948a; UMMZ); B. nummifer*, 120--1410 m (Boulenger, 1896; Burger, 1950; Gunther, 1895; Stuart, 1948a; KU; UMMZ).

SIERRA DE LAS MINAS, GUATEMALA

General region: The windwards slopes of the Sierra de las Minas from near Purulha, Baja Verapaz, east to a level between Gualan, Zacapa, and El Estor, Izabal.

Species: _Minascaecilia sartoria_, 650 m (Wake and Campbell, in prep; KU); _Bolitoglossa helmrichi_**, 1300--2290 m (KU; MVZ; UTA); _B. meliana_*, 1550--2730 m (Wake and Lynch, 1982; KU;MVZ); _B. mexicana_, 100--460 m (Wake and Lynch, 1976; KU); _B. odonelli_, 150 m (KU); _B. rufescens_*, 100--770 m (KU; MVZ); _Bolitoglossa_ sp. A, 550 m (KU; MVZ); _Bolitoglossa_ sp. B* (_lincolni_- subgroup), 1900 m (Wake and Lynch, 1976); _Chiropterotriton veraepacis_**, 1610--2290 m (Lynch and Wake, 1978; KU; LACM; MVZ; UTA); _Nyctanolis pernix_**, 1610 m (KU); _Oedipina elongata_, 770 m (Wake and Lynch, 1976; KU); _Eleutherodactylus bocourti_**, 1580--1710 m (Ford, 1981; KU; UTA); _E. brocchi_*, 1460--2130 m (Ford, 1981; Savage, 1975; KU; LSU; UTA); _E. daryi_**, 1500--1900 m (Ford and Savage, 1983; KU; UTA); _E. lineatus_*, 600--1980 m (KU; UTA); _E. milesi_, 400--800 m (KU); _E. rostralis_*, 100--800 m (KU); _E. rugulosus_, 10--1200 m (Savage, 1975; KU); _E. xucanebi_**, 1520--1610 m (KU; UTA); _Eleutherodactylus_ sp. F**, 1900--2290 m (description in preparation; KU); _Eleutherodactylus_ sp. G, 100--650 m (description in preparation; KU); _Bufo coccifer_*, 1030--1610 m (KU; UMMZ; UTA); _B. valliceps_, 10--1000 m (KU; UTA); _Agalychnis moreleti_*, 550--2130 m (Salvin, 1861; KU; UTA); _Hyla bromeliacea_**, 1610--1650 m (UTA); _H. valancifer_**, 1490--1830 m (Duellman, 1978; KU; MVZ; UTA); _Plectrohyla guatemalensis_*, 1580--1900 m (KU; UTA); _P. hartwegi_**, 1460--1890 m (KU; UTA); _P. quecchi_*, 1490--1710 m (KU; UTA); _Ptychohyla panchoi_, 550--700 m

(Duellman and Campbell, 1982; KU); _P_. _spinipollex_*, 600--1890 m (Adler, 1965; Duellman, 1970; KU; UMMZ; UTA); _Smilisca_ _baudini_, 10--1610 m (KU; UTA); _S_. _cyanosticta_*, 770 m (KU); _Centrolenella_ _fleischmanni_*, 100--1610 m (KU; UTA); _Hypopachus_ _barberi_, 1500--1680 (KU; UTA); _Rana_ _maculata_*, 500--1900 m (KU, UTA); _Rana_ sp. D (_pipiens_- group), 100--1650 m (KU; UTA); _Anolis_ _biporcatus_, 500--770 m (KU); _A_. _capito_, 100--700 m (KU); _A_. _cobanensis_**, 1500--1830 m (KU; MVZ; UTA); _A_. _haguei_*, 1480--2290 m (KU; UTA); _A_. _humilis_, 100--900 m (KU); _A_. _lemurinus_, 100--700 m (KU; UTA); _A_. _limifrons_, 140--770 (KU); _A_. _petersi_**, 1520--2130 m (KU; UTA); _Corytophanes_ _cristatus_, 100--700 m (KU); _C_. _percarinatus_*, 1610--1830 m (KU; UTA); _Sceloporus_ _acanthinus_, 900--1900 m (KU; UMMZ); _S_. _smaragdinus_, 1900 m (KU); _S_. _taeniocnemis_*, 1500--2290 m (KU; UTA); _S_. _variabilis_, 10--40 m (UTA); _Lepidophyma_ _flavimaculata_*, 150--870 m (KU); _Ameiva_ _festiva_, 100--900 m (KU); _A_. _undulata_*, 250--1650 m (KU; UTA); _Mabuya_ _mabouya_, 10--910 (KU; UTA); _Sphenomorphus_ _cherriei_, 10--1300 m (KU); _S_. _incertum_**, 1520--1980 m (KU; UTA); _Abronia_ _aurita_**, 1615--1830 m (KU; UTA); _A_. _fimbriata_**, 1680 m (KU; UTA); _Barisia_ _moreleti_*, 1580--1980 m (KU; UTA); _Celestus_ _rozellae_, 150--650 m (KU); _Leptotyphlops_ _goudoti_, 1000--1610 m (UTA); _Typhlops_ _tenuis_*, 1370--1520 m (UTA); _Adelphicos_ _quadrivirgatus_, 600--650 m (KU); _A_. _veraepacis_**, 1500--1710 m (Campbell and Ford, 1982; KU; UTA); _Amastridium_ _veliferum_, 500--550 m (KU); _Coluber_ _constrictor_*, 500--800 m (KU); _Coniophanes_ _fissidens_, 150--770 m (KU) _Dendrophidion_ _vinitor_, 450--900 m (KU); _Dryadophis_ _dorsalis_*, 1350--2290 (KU; UTA); _D_. _melanolomus_, 70--950 m (KU); _Drymobius_ _chloroticus_**, 1500--1980 m (KU; UTA); _D_. _margaritiferus_*, 10--1710 m (KU; UTA); _Hydromorphus_ _concolor_, 100--650 (KU); _Imantodes cenchoa_, 10--1600 m (KU); _Lampropeltis triangulum_*, 100--1610 m (Salvin, 1861; KU; UTA); _Leptodeira annulata_, 90--1100 m (KU; UTA); _L. septentrionalis_*, 100--2290 m (KU; UTA); _Leptodrymus pulcherrimus_, 140--650 m (KU); _Leptophis ahaetulla_, 100--700 m (KU); _L. mexicanus_, 20--1360 m (KU; UTA); _L. modestus_**, 1510--1900 m (KU; UTA); _Ninia diademata_*, 1470--1500 m (KU; UTA); _N. maculata_*, 1500 m (UTA); _N. sebae_*, 10--1590 m (KU; UTA); _Oxybelis aeneus_, 100--850 m (KU; UTA); _O. fulgidus_, 100--750 m (KU); _Oxyrhopus petola_, 600--650 m (KU) _Pliocercus elapoides_*, 770--1600 m (KU); _P. euyzonus_, moderate? (Salvin, 1861); _Pseustes poecilonotus_, 650 m (KU); _Rhadinaea godmani_*, 1830--1900 m (Myers, 1974; KU; UMMZ); _R. hempsteadae_*, 1680--2300 m (KU; UTA); _R. kinkelini_*, 1300--1830 m (KU; UTA); _Scaphiodontophis anulatus_, 150--850 m (KU); _Sibon dimidiata_, 650 m (KU); _Spilotes pullatus_, 100--1200 m (KU; USAC); _Stenorrhina degenhardti_*, 100--1740 (Salvin, 1861; KU; UTA); _Storeria dekayi_*, 1400--1710 m (KU; UTA); _Tantilla bairdi_*, 1520 m (KU); _T. schistosa_, 400--650 m (KU); _T. taeniata_, 580--650 m (KU); _Thamnophis fulvus_*, 1200--2290 m (Salvin, 1860; KU; UTA); _Tropidodipsas kidderi_**, 1520--1900 m (KU; UTA); _T. sartorii_, 10--1350 m (KU; USAC; UTA); _Xenodon rhabdocephalus_, 10--400 m (KU; UTA); _Micrurus diastema_, 150--1200 m (Frazer, 1973; KU; USAC); _M. elegans_**, 1300--1620 m (KU; USAC; UTA); _Bothriechis aurifer_**, 1300--2290 m (KU; USAC; UTA); _B. schlegeli_, 400--770 m (KU; UTA); _Bothrops asper_, 10--850 m (KU; UTA); _B. godmani_*, 1520--2290 m (KU; USAC; UTA); _B. nummifer_*, 450--1520 m (KU).

PACIFIC HIGHLANDS OF GUATEMALA AND CHIAPAS, MEXICO

General region: The Pacific versant from Cerro Tres Picos in Chiapas to the Las Nubes block in southeastern Guatemala.

Species: _Dermophis mexicanus_*, 50--1550 m (KU); _Dermophis oaxacae_, 50--900 m (Savage and Wake, 1972); _Bolitoglossa brevipes_*, 1500--2500 m (Wake and Lynch, 1976); _B. engelhardti_*, 1520--2200 m (Schmidt, 1936a; Stuart, 1963; Wake and Lynch, 1976); _B. flavimembris_**, 1800--2400 m (Schmidt, 1936a; Stuart, 1963; Wake and Brame, 1969; Wake and Lynch, 1976); B. flaviventris, 10--500 m (Wake and Lynch, 1976); _B. franklini_**, 1650--2600 m (Schmidt, 1936a, Stuart, 1963; Wake and Lynch, 1976; KU); _B. morio_*, 2500--2900 m (Wake and Lynch, 1976); _B. nigroflavescens_**, 1500--2500 m (Wake and Lynch, 1976); _B. occidentalis_*, 900--1600 m (Stuart, 1963; Wake and Lynch, 1976); _B. resplendens_*, 2500--2900 m (Wake and Lynch, 1976); _B. rostrata_, 2700--3200 m (Wake and Lynch, 1976); _B. salvini_*, 600--1450 m (Stuart, 1963; Wake and Lynch, 1976); _Bolitoglossa_ sp. C* (_lincolni_- subgroup), 2200 m (Wake and Lynch, 1976); _Chiropterotriton bromeliacia_**, 1700--2700 m (Rabb, 1960; Schmidt, 1936a; Stuart, 1963; Wake and Lynch, 1976); _C. megarhinus_**, 2130 m (Rabb, 1960; Wake and Lynch, 1976); _C. xolocalcae_**, 1630--2150 m (Lynch and Wake, 1975; Rabb, 1960); _Oedipina ignea_, moderate elevations (Brame, 1968; Wake and Lynch, 1976; Stuart, 1963); _Pseudoeurycea brunnata_, 2550--2800 m (Wake and Lynch, 1976); _P. expectata_, 2530 m (Stuart, 1954c; Wake and Lynch, 1976; UMMZ); _P. goebeli_*, 2440--2800 m (Schmidt, 1936a; Stuart, 1963; Wake and Lynch, 1976); _P. rex_, 2800--3800 m (Stuart, 1963; Wake and Lynch, 1976); _Pseudoeuycea_ sp. H*, 2550--2800 (Wake and Lynch, 1976); _Eleutherodactylus greggi_**, 2000--2700 m (Bumzahem, 1955; Ford and

Savage, 1982; Savage, 1975; Stuart, 1963; KU); _E_. _lineatus_*, intermediate elevations (Stuart, 1975; Taylor, 1942); _E_. _matudai_*, 1500--2290 m (Lynch, 1965c; Savage, 1975; Smith and Taylor, 1948; Stuart, 1963; Taylor, 1941); _E_. _pygmaeus_*, 2000 m (Lynch, 1965b; Stuart, 1963; KU); _E_. _rhodopis_*, 1160--1830 m (Smith, 1959b; Smith, P. W. and H. M. Smith, 1951; Stuart, 1963); _E_. _rugulosus_, 100--1830 m (Savage, 1975; Smith, 1959b; Stuart, 1963); _E_. _sartori_**, 1830 m (Lynch, 1965b; Taylor, 1942); _Syrrhopus_ _rubrimaculatus_, 10--650 m (Lynch, 1970a; Smith, P. W. and H. M. Smith, 1951); _Bufo_ _bocourti_, intermediate and high elevations (Smith and Burger, 1955); _B_. _coccifer_, 1730 m (Stuart, 1954c and 1963); _B_. _tacanensis_*, 1500 m (Smith, P. W., 1952; Stuart, 1963; KU); _B_. _valliceps_, 10--1300 m (Firschein and Smith, 1957; Stuart, 1963; USAC; UTA); _Agalychnis_ _moreleit_*, moderate and intermediate elevations (Duellman, 1970; Stuart, 1963; USAC); _Plectrohyla_ _avia_**, 1750--2000 m (Bumzahem and Smith, 1954; Duellman, 1970; Stuart, 1952 and 1963; KU); _P_. _glandulosa_*, intermediate and high elevations (Duellman, 1970); _P_. _guatemalensis_*, 2000 m (Bumzahem and Smith, 1954; Duellman, 1970; Stuart, 1963; KU); _P_. _hartwegi_**, 1000--2050 m (Duellman, 1968 and 1970; KU); _P_. _lacertosa_**, intermediate elevations? (Bumzahem and Smith, 1954; Duellman, 1970); _P_. _matudai_*, 1070--1800 m (Bumzahem and Smith, 1954; Duellman, 1970; Hartweg, 1941; Hartweg and Orton, 1941; Lynch and Smith, 1966; Stuart, 1963; KU); _P_. _sagorum_*, 1750--2050 m (Bumzahem and Smith, 1954; Duellman, 1968 and 1970; Hartweg, 1941; Hartweg and Orton, 1941; Stuart, KU); _Ptychohyla_ _euthysanota_*, 1325 m (Adler, 1965; Duellman, 1970; Stuart, 1963; Taylor, 1942; KU); _P_. _schmidtorum_*, 500--2000 m (Adler, 1965; Duellman, 1970; Stuart, 1954c and 1963; KU); _P_.

*spinipollex**, moderate to intermediate elevations (Duellman, 1970; Schmidt, 1936a; Stuart, 1963; UTA); *Smilisca baudini*, low to moderate elevations (Duellman, 1970; Stuart, 1963); *Centrolenella fleischmanni**, ca. 1500 m (Duellman and Tulecke, 1960; Taylor, 1942); *Hypopachus barberi*, 1400--2300 m (Nelson, 1973; Stuart, 1963); *Rana maculata**, 1300--1320 m (Smith, 1959b; Stuart, 1963; KU; UTA); *Rana* sp. E (*pipiens*-group), moderate and intermediate elevations (Stuart, 1963; UTA); *Anolis crassulus**, 1500--1900 m m (Smith and Kerster, 1955; UTA); *A. cupreus*, 10--1400 m (Fitch et al, 1972; Stuart, 1955; KU); *A. dollfusianus**, 275--1500 m (Fitch et al., 1976; Smith and Kerster, 1955; Stuart, 1963); *A. laeviventris**, moderate and intermediate elevations (Smith and Kerster, 1955); *A. lemurinus*, low and moderate elevations (Smith and Kerster, 1955; Stuart, 1963); *A. matudai**, moderate? (Smith, 1956); *A. petersi***, 1320 m (Smith and Kerster, 1955; Stuart, 1963; KU); *Corytophanes percarinatus**, moderate and intermediate elevations (Alvarez del Toro, 1972; Stuart, 1963; USAC; UTA); *Sceloporus acanthinus**, ca. 1500 m (Alvarez del Toro, 1972; Stuart, 1963 and 1971); *S. internasalis**, 850--3000 m (Stuart, 1971; UMMZ); *S. smaragdinus**, 1500--4000 m (Stuart, 1963 and 1971; UTA); *Ameiva undulata**, 1160--1830 m (Smith, 1959b; Stuart, 1963); *Spenomorphus assatum**, low and moderate elevations (Alvarez del Toro and Smith, 1956; Stuart, 1940 and 1963); *S. incertum***, 1120--1680 m (Stuart, 1940 and 1963; KU); *Lepidophyma flavimaculatum*, "low elevations" (Greene, 1971; Muller, 1878; Stuart, 1963); *Abronia matudai***, 2000 m (Hartweg and Tihen, 1946); *A. vasconcelosi***, intermediate elevations (Cope, 1887; Stuart, 1963; Tihen, 1949; UTA); *Barisia moreleti**, 1500--3000 m (Alvarez del Toro, 1972; Hartweg and Tihen, 1946; Stuart, 1963; USAC); *Celestus atitlanensis**, ca. 1500 m (Smith and Taylor, 1950; Stuart, 1963); *Gerrhonotus liocephalus*, 3200 m (Alvarez del Toro, 1972; Hartweg and Tihen, 1946); *Leptotyphlops goudoti*, moderate elevations (Stuart, 1963; USAC) *Adelphicos daryi**, 1830--2130 m (Campbell and Ford, 1982; KU; UTA); *A*. *quadrivirgatus*, 610--1450 m (Greene, 1971; Landy et al., 1966; Slevin, 1939; Smith, 1942 and 1959b; Stuart, 1949 and 1963); *Adelphicos* sp.* (*veraepacis*- group), 2000 m (Campbell and Ford, 1982); *Amastridium veliferum*, moderate (Stuart, 1963; Wilson and Meyer, 1969); *Clelia scytalina*, low and moderate elevations (Slevin, 1939; Stuart, 1963); *Coniophanes fissidens*, 75--1830 m (Greene, 1971; Landy et al., 1966; Slevin, 1939; Smith, 1959b; Stuart, 1963; UTA); *Dryadophis dorsalis**, 1160--1830 m (Slevin, 1939; Smith, 1959b; Stuart, 1941c and 1963); *D*. *melanolomus*, low and moderate elevations (Slevin, 1939); *Drymobius chloroticus**, 1160--1830 m (Greene, 1971; Landy et al., 1966; Smith, 1959b; Stuart, 1963; Wilson, 1970a and 1975a; UTA); *D*. *margaritiferus**, 50--1830 m (Landy et al., 1966; Slevin, 1939; Smith, 1959b; Stuart, 1963; Wilson, 1974); *Enulius flavitorques*, low and moderate elevations (Stuart, 1963); *Geophis cancellatus**, 1030 m (Alvarez del Toro, 1972; Downs, 1967; Landy et al., 1966); *G*. *immaculatus***, 1700 m (Downs, 1967; UMMZ); *G*. *nasalis**, 600--1830 m (Downs, 1967; Landy et al., 1966; Slevin, 1939; Smith, 1959b; Smith, P. W. and H. M. Smith, 1951; Stuart, 1949; UTA); *G*. *rhodogaster**, 1500--2500 m (Downs, 1967; KU; UTA); *Imantodes cenchoa*, 610--1830 m (Landy et al., 1966; Slevin, 1939; Smith, 1959b; Stuart, 1963); *Lampropeltis triangulum**, 10--1600 m (Greene, 1971; Landy et al., 1966; Stuart, 1963; Williams, 1978; USAC);

Leptodeira annulata, 610--1500 m (Duellman, 1958; Slevin, 1939; Smith, 1959b; UTA); L. septentrionalis*, 10--1850 m (Duellman, 1958; Greene, 1971; Stuart, 1963; KU; UTA); Leptophis mexicanus, low and moderate elevations (Stuart, 1963); Ninia diademata*, 610--1830 m (Burger and Werler, 1954; Landy et al., 1966; Slevin, 1939; Smith, 1959b; Stuart, 1963); N. sebae*, 170--2000 m (Greene, 1971; Landy et al., 1966; Schmidt and Rand, 1957; Smith, 1959b; Stuart, 1940 and 1963); Oxybelis aeneus, 100--1000 m (Landy et al., 1966; Slevin, 1939; Stuart, 1963; USAC); O. fulgidus, low and moderate elevations (Stuart, 1963); Pituophis lineaticollis, 1430--1800 m (Slevin, 1939; Stuart, 1954c and 1963); Pliocercus elapoides*, 610--1830 m (Landy et al., 1966; Slevin, 1939; Smith, 1959b; Smith and Chrapliwy, 1957; Stuart, 1963; UTA); Rhadinaea godmani*, 1500--2650 m (Myers, 1974; Stuart, 1963); R. hannsteini*, 1050--1450 m (Alvarez del Toro, 1972; Landy et al., 1966; Myers, 1974; Smith, 1959b; Stuart, 1949 and 1963); R. lachrymans*, 1050--2640 m (Greene, 1971; Landy et al., 1966; Myers, 1974; Stuart, 1949 and 1963; KU); R. posadasi*, between 1160--1830 m (Myers, 1974; Slevin, 1939; Smith, 1959b); Scaphiodontophis zeteki, 610--1200 m (Landy et al., 1966; Slevin, 1939; Stuart, 1963; USAC); Sibon dimidiata, low and moderate elevations (Stuart, 1963); Spilotes pullatus, low and moderate elevations (Stuart, 1963; USAC); Tantilla brevicauda, 1750 m (Wilson, 1970b); Tantilla jani, low and moderate elevations (Slevin, 1939; Stuart, 1963; Wilson et al., 1977; Wilson and Meyer, 1971); T. mexicana, 610 m (Slevin, 1939; Stuart, 1963); Thamnophis fulvus*, 1400--2200 m (Slevin, 1939; Smith and Burger, 1955; Stuart, 1963; KU; UTA); Tropidodipsas fischeri*, 1830 m (Stuart, 1963; UTA); T. sartorii, low to intermediate elevations (Landy et al., 1966; Stuart, 1963; USAC); _Xenodon rhabdocephalus_, low and moderate elevations (Landy et al., 1966; Stuart, 1963; USAC); _Micrurus browni_, ca. 1500 m (Roze, 1967); _M. latifasciatus_*, 1160--1830 m (Landy et al., 1966; Roze, 1967; Schmidt, 1933; Schmidt and Smith, 1943; Smith, 1959b; Stuart, 1963); _M. nigrocinctus_*, 120--1830 m (Greene, 1971; Landy et al., 1966; Roze, 1967; Schmidt, 1932 and 1936b; Schmidt and Smith, 1943; Slevin, 1939; Stuart, 1963); _M. stuarti_*, 1350 m (Roze, 1967; UMMZ); _Bothriechis bicolor_**, 500--2000 m (Bocourt, 1868; Bogert, 1968; Greene, 1971; Julia Z. and Varela J., 1978; Muller, 1878; Stuart, 1963; USAC; UTA); _Bothrops asper_, 10--1070 m (Stuart, 1963; USAC); _B. godmani_*, 1500--3000 m (Campbell, 1977; Stuart, 1963; KU; USAC); _B. nummifer_*, 610--1460 m (Bocourt, 1868; Burger, 1950; Stuart, 1963; KU; USAC; UTA).

EL SALVADOR HIGHLANDS

General region: Several adjacent highland areas in El Salvador and southern Honduras, including Cerros Montecristo and El Pital, Volcanes Santa Ana and San Vicente, and the highlands in the Ahuachapan region.

Species: _Dermophis mexicanus_, 500--1000 m (Savage and Wake, 1972; KU); _Bolitoglossa dunni_*, 2200 m (Mertens, 1952; Rand, 1957; Wake and Lynch, 1976; KU); _Eleutherodactylus rhodopis_*, 670--1200 m (Mertens, 1952; Rand, 1957); _E. rugulosus_*, 100--1830 m (Mertens, 1952; Savage, 1975; KU); _B. coccifer_*, 10--2080 m (Mertens, 1952; Rand, 1957; KU); _B. valliceps_, 350--700 m (Mertens, 1952; Rand, 1957); _Agalychnis moreleti_*, ca. 1500 m (Duellman, 1970; Mertens, 1952); _Hyla salvadorensis_*, 700--1800 m (Duellman, 1970; Mertens, 1952; KU); _Plectrohyla_ _glandulosa_*, intermediate elevations (Duellman, 1970; MVZ); _P_. _guatemalensis_*, 1950--2800 m (Duellman, 1970; Mertens, 1952; Rand, 1957; KU); _P_. _sagorum_*, intermediate elevations (Duellman, 1970; MVZ); _Ptychohyla_ _euthysanota_*, 800--2200 m (Duellman, 1970; Mertens, 1952; Rand, 1957); _Smilisca_ _baudini_, 10--1200 m (Duellman, 1970; Mertens, 1952; Rand, 1957; KU); _Centrolenella_ _fleischmanni_*, 1690 m (Hidalgo, 1982b); _Hypopachus_ _barberi_, 1630--1930 m (Nelson, 1973); _Rana_ _maculata_*, 600--1830 m (Mertens, 1957; Rand, 1957; KU); _Rana_ sp. E (_pipiens_-group), 670--1830 m (Mertens, 1952; Rand, 1957; KU); _Anolis_ _crassulus_*, intermediate elevations (Mertens, 1952); _A_. _cupreus_, 10--1000 m (Fitch, et al., 1972; Mertens, 1952; Schmidt, 1928); _A_. _heteropholidotus_*, 2000--2200 m (Mertens, 1952; Rand, 1957; KU); _A_. _lemurinus_, 350--800 m (Mertens, 1952; Rand, 1957; KU); _Corytophanes_ _percarinatus_*, intermediate elevations (Mertens, 1952; Peters and Donoso-Barros, 1970; Schmidt, 1928; Stuart, 1963); _Sceloporus_ _acanthinus_, 650 m (Stuart. 1971; UMMZ); _S_. _malachiticus_*, 670--2200 m (Mertens, 1952; Rand, 1957; Schmidt, 1928; Stuart, 1971; KU); _S_. _variabilis_, low and moderate elevations (Mertens, 1952; Rand, 1957); _Ameiva_ _undulata_, 10--1000 m (Mertens, 1952; Rand, 1957; Schmidt, 1928); _Lepidophyma_ _flavimaculata_, low and moderate elevations (Mertens, 1952; KU); _Mabuya_ _mabouya_, low and moderate elevations (Mertens, 1952); _Sphenomorphus_ _assatum_, 670--1000 m (Mertens, 1952; Rand, 1957; Schmidt, 1928; Stuart, 1940 and 1963); _S_. _cherriei_, 10--1000 m (Mertens, 1952); _Abronia_ sp. B*, (Hidalgo, in press; KU); _Abronia_ sp. C*, Hidalgo, in press; KU); _Barisia_ _moreleti_, 1830--2440 m (Mertens, 1952; Rand, 1957; Schmidt, 1928; KU); _Celestus_ _atitlanensis_*, 800 m (Hidalgo, 1982a; KU); _Coniophanes_ _fissidens_, low and moderate elevations (Mertens, 1952); _Dryadophis dorsalis_*, 700--1400 m (Mertens, 1952); _Drymobius chloroticus_*, 2200 m (Uzzell and Starrett, 1958; Wilson, 1970a and 1975a; KU); _D. margaritiferus_*, 10--1200 m (Mertens, 1952; Wilson, 1974); _Enulius flavitorques_, 1100 m (Mertens, 1952); _Geophis fulvoguttatus_**, 2200 m (Downs, 1967; Mertens, 1952; KU); _G. rhodogaster_*, 2200 m (Downs, 1967; KU); _Lampropeltis triangulum_*, 10--1600 m (Mertens, 1952; Williams, 1978); _Leptodeira annulata_, 100--1200 m (Duellman, 1958; Mertens, 1952; Rand, 1957); _L. septentrionalis_*, 10--1800 m (Duellman, 1958; Mertens, 1952; Uzzell and Starrett, 1958; KU); _Leptodrymus pulcherrimus_, 700 m (Mertens, 1952); _Leptophis modestus_**, 2200 m (Hoyt, 1964; KU); _Ninia atrata_*, 1900 m (Hidalgo, 1981; Meyer and Wilson, 1971b; KU); _N. sebae_*, 10--1320 m (Mertens, 1952; Rand, 1957; KU); _Oxybelis aeneus_, 10--1000 m (Mertens, 1952; Rand, 1957); _Pliocercus elapoides_*, 1150 m (Mertens, 1952); _Rhadinaea godmani_*, 1630--2200 m (Mertens, 1952; Myers, 1974; Uzzell and Starrett, 1958); _R. kinkelini_*, 1900--2200 m (Myers, 1974; Meyer and Wilson, 1971b; KU); _R. montecristi_**, 2200 m (Mertens, 1952; Myers, 1974; Uzzell and Starrett, 1958); _R. pinicola_*, 1500 m (Mertens, 1952; Myers, 1974); _R. posadasi_, 670 m (Mertens, 1952; Rand, 1957); _Tantilla brevicauda_, 600--1510 m (Mertens, 1952; Uzzell and Starrett, 1958; Wilson, 1970b; KU); _Thamnophis fulvus_*, 1700--1900 m (Hidalgo, 1981; Meyer and Wilson, 1971b; KU); _Tropidodipsas fischeri_*, 2200 m (Uzzell and Starrett, 1958); _Micrurus nigrocinctus_, low and moderate elevations (Mertens, 1952; Roze, 1967); _Bothriechis bicolor_**, (1730--ca. 2000 m (H. Hidalgo, pers. comm.; Meyer and Wilson, 1971b); _B. godmani_*, 1830--2400 m (Campbell, 1977; Mertens, 1952; Rand, 1957; Schmidt, 1928;

Uzzell and Starrett, 1958; KU); _B. nummifer_*, 1200--2700 m (Mertens, 1952).

NORTHWESTERN HONDURAN HIGHLANDS

General region: The highlands south of the Motagua Valley from about the level of Zacapa to the Gulf of Honduras. These include the Sierra de Omoa and the Montanas de Espiritu Santo in Honduras, and several outlying highland areas to the south and southwest of La Union in southeastern Zacapa, Guatemala.

Species: _Bolitoglossa dofleini_, 1300 m (Meyer and Wilson, 1971aa; CM); _B. dunni_**, 1370--1700 m (Meyer, 1969; Meyer and Wilson, 1971a; Schmidt, 1933); _B. mexicana_*, 10--1400 m (Meyer and Wilson, 1971a; Wake and Lynch, 1976; CM); _B. occidentalis_, 850 m (CM); _B. rufescens_*, 10--1400 m (Meyer and Wilson, 1971a; Wake and Lynch, 1976; CM); _B. schmidti_, 650 m (Dunn and Emlen, 1932; Meyer, 1969; Meyer and Wilson, 1971a); _Chiropterotriton nasalis_**, 1500--2200 m (Meyer, 1969; Meyer and Wilson, 1971a; Wake and Lynch, 1976); _Eleutherodactylus gollmeri_*, 10--1600 m (Dunn and Emlen, 1932; Meyer and Wilson, 1971a; CM); _E. merendonensis_, 150--200 m (Meyer and Wilson, 1971a; Savage, 1975); _E. milesi_*, 850--1700 m (Lynch, 1965c; Meyer, 1969; Meyer and Wilson, 1971a; Savage, 1975; Schmidt, 1933; CM); _E. rugulosus_, 10--2000 m (Meyer, 1969; Meyer and Wilson, 1971a; Savage, 1975; CM); _Bufo marinus_, 10--1300 m (Meyer, 1969; Meyer and Wilson, 1971a); _Bufo valliceps_, 10--1000 m (Meyer, 1969; Meyer and Wilson, 1971a; CM); _Agalychnis moreleti_*, 800--850 m (Meyer and Wilson, 1971a; CM); _Hyla bromeliacea_**, 1500 m (Meyer, 1969; Meyer and Wilson, 1971a; Schmidt, 1933; Schmidt, 1942); _Plectrohyla dasypus_**, 1530--1660 m (McCranie and Wilson, 1981;

KU); _P_. _guatemalensis_* 1530--1660 m (McCranie and Wilson, 1981; KU); _P_. _hartwegi_**, 1530--1660 m (McCranie and Wilson, pers. comm.; KU); _P_. _matudai_*, 850 m (CM); _Ptychohyla_ _spinipollex_*, 700--1900 m (Meyer and Wilson, 1971a; McCranie and Wilson, 1981; KU); _Smilisca_ _baudini_, 10--1900 m (Duellman, 1970; Meyer, 1969; CM); _Centrolenella_ _fleischmanni_*, 10--1400 m (Meyer, 1969; Meyer and Wilson, 1971a); _Rana_ _maculata_*, 200--1900 m (Meyer, 1969; Meyer and Wilson, 1971a); _Rana_ sp. E (_pipiens_- group), 10--1900 m (Meyer, 1969; Meyer and Wilson, 1971a); _Anolis_ _biporcatus_, 10--850 m (Dunn and Emlen, 1932; Meyer, 1969; CM); _A_. _capito_, 10--500 m (Meyer and Wilson, 1973); _A_. _humilis_, 850 m (CM); _A_. _lemurinus_, 10--1100 m (Meyer, 1969; Meyer and Wilson, 1973); _A_. _limifrons_, 10--700 m (Meyer and Wilson, 1973); _A_. _tropidonotus_*, 10--1900 m (Dunn and Emlen, 1932; Meyer, 1969; Meyer and Wilson, 1973; CM); _Corytophanes_ _cristatus_, 10--1300 m (Meyer, 1969; Meyer and Wilson, 1973); _C_. _hernandezi_, 850 m (CM); _Sceloporus_ _malachiticus_*, 900--2200 m (Meyer, 1969; Meyer and Wilson, 1973; Schmidt, 1933; CM); _S_. _variabilis_, 10--1300 m (Meyer, 1969; Meyer and Wilson, 1973; CM); _Ameiva_ _festiva_, 10--1400 m (Meyer, 1969; Meyer and Wilson, 1973); _A_. _undulata_, 10--1200 m (Meyer, 1969; Meyer and Wilson, 1973; CM); _Mabuya_ _mabouya_, 10--1100 m (Meyer, 1969; Meyer and Wilson, 1973); _Spenomorphus_ _cherriei_, 10--1600 m (Dunn and Emlen, 1932; Meyer, 1969; Meyer and Wilson, 1973; CM); _Lepidophyma_ _flavimaculata_, 10--750 m (Meyer, 1969; Meyer and Wilson, 1973); _Abronia_ sp. D**, intermediate elevations (L. D. Wilson, in prep); _Celestus_ _montanus_**, 1370 m (Meyer, 1969; Meyer and Wilson, 1973; Schmidt, 1933); _Leptotyphlops_ _goudoti_, 10--700 m (Meyer, 1969); _Adelphicos_ _quadrivirgatus_, low and moderate elevations (Smith, 1942;

CM); Coniophanes fissidens, 10--1300 m (Meyer, 1969; CM); Dendrophidion percarinatum, 10--1000 m (Meyer, 1969); Dryadophis melanolomus, 10--750 m (Meyer, 1969; CM); Drymobius chloroticus**, 1100--1800 m (Wilson, 1970a and 1975a; CM); D. margaritiferus*, 10--750 m (Meyers, 1969; Wilson, 1974; CM); Enulius flavitorques, 850 m (CM); Hydromorphus concolor, 100--1400 m (Meyers, 1969; Nelson, 1966; Wilson et al, 1976); Imantodes cenchoa, 10--1500 m (Meyer, 1969; CM); Lampropeltis triangulum, 10--750 m (Dunn and Emlen, 1932; Williams, 1978; CM); Leptodeira annulata, 10--850 m (Myers, 1969; CM); L. septentrionalis*, 10--1500 m (Barbour and Loveridge, 1929; Duellman, 1958; Meyer, 1969); Leptodrymus pulcherrimus, 10--1500 m (Meyer, 1969); Leptophis ahaetulla, 10--750 m (Meyer, 1969); L. mexicanus, 10--1300 m (Meyer, 1969; CM); Ninia diademata*, 10--1300 m (Meyer, 1969; CM); N. sebae*, 10--1900 m (Meyer, 1969; Schmidt and Rand, 1957; CM); Oxybelis aeneus, 10--1500 m (Meyer, 1969; CM); O. fulgidus, 10--750 m (Meyer, 1969); Oxyrhopus petola, 10--750 m (Dunn and Emlen, 1932; Meyer, 1969); Pliocercus elapoides*, 50--1300 m (Meyer, 1969; CM); Scaphiodontophis annulatus, 10--1300 m (Meyer, 1969; CM); Sibon dimidiata*, 1300--1600 m (Meyer, 1969; CM); S. nebulata, 10--1500 m (Meyer, 1969); Spilotes pullatus, 10--900 m (Meyer, 1969; CM); Stenorrhina degenhardti* 100--1500 m (Barbour and Loveridge, 1929; Meyer, 1969; CM); Tantilla taeniata, low and moderate elevations (Wilson and Meyer, 1971); Tropidodipsas sartori, 10--850 m (Meyers, 1969; CM); Xenodon rhabdocephalus, 10--1300 m (Meyer, 1969); Micrurus diastema, 100--850 m (Fraser, 1973; Meyer, 1969; Roze, 1967; CM); M. nigrocinctus, 10--1300 m (Meyer, 1969; Roze, 1967); Bothriechis marchi**, 500?--1500 m (Barbour and Loveridge, 1929; Meyer, 1969); _B. schlegeli_, 10--1300 m (Dunn and Emlen, 1932; Meyer, 1969); _Bothrops asper_, 10--850 m (Dunn and Emlen, 1932; Meyer, 1969; CM); _B. godmani_*, 1300--1900 m (Barbour and Loveridge, 1929; Campbell, 1977; Meyer, 1969); _B. nummifer_*, 10--1300 m (Barbour and Loveridge, 1929; Burger, 1950; Meyer, 1969; CM).

EASTERN COSTA RICA

General region: Across the Cordillera Central from the Ochomogo Pass to Volcan Orosi in the Cordillera de Guanacaste.

Species: _Dermophis mexicanus_*, "premontane moist, wet, or rainforests" (Savage and Wake, 1972); _D. parviceps_, 300--1200 m (Savage and Wake, 1972); _Gymnopis multiplicata_*, 10--1400 m (Savage and Wake, 1972); _Bolitoglossa alvaradoi_*, 500--1500 m (Wake and Lynch, 1976); _B. arborescandens_*, 1000--1500 m (Wake and Lynch, 1976); _B. epimela_*, 500--1550 m (Robinson, 1976; Wake and Lynch, 1976); _B. robusta_*, 1400--1830 m (Robinson, 1976; Taylor, 1952; Van Devender, 1980; Wake and Lynch, 1976); _B. subpalmata_*, 1600--3600 m (Vial, 1966; Wake and Lynch, 1976; KU); _Chiropterotriton diminuta_**, 1550 m (Robinson, 1976); _C. picadoi_**, 1400--2200 m (Dunn, 1937a; Van Devender, 1980; Wake and Lynch, 1976); _C. richardi_*, 500--1980 m (Taylor, 1952a; Wake and Lynch, 1976); _Oedipina poelzi_*, 910--2100 m (Brame, 1968; Robinson, 1976; Wake and Lynch, 1976; KU); _O. uniformis_*, 10--2130 m (Brame, 1968; Wake and Lynch, 1976; KU); _Eleutherodactylus altae_*, 1220 m (Savage, 1980a; Taylor, 1952b); _E. andi_**, 1150--1400 m (Savage, 1974; Van Devender, 1980; KU); _E. angelicus_*, 600--1900 m (Savage, 1975 and 1980b; Van Devender, 1980; KU); _E. bransfordi_*, 100--1900 m (Van Devender, 1980; KU); _E. caryophyllaceus_*, 1200 m (Savage, 1980a; KU); _E. crassidigitus_*, 920--2000 m (Savage, 1980a; Taylor, 1952b; Van Devender, 1980; KU); E. cruentus*, 1200--1600 m (Savage, 1966b and 1980b; Van Devender, 1980; KU); E. cuaquero**, 1520 m (Savage, 1980b); E. diastema*, 10--2400 m (Dunn, 1937; Savage 1965 and 1966b and 1980b; Taylor, 1952b; Van Devender, 1980; KU); E. escoces*, 1100--2400 m (Savage, 1975; KU); E. fitzingeri, 10--1500 m (Savage, 1974; KU); E. fleischmanni*, 600--2300 m (Savage, 1975; KU); E. gollmeri, 10--1680 m (Taylor, 1952b; KU); E. hylaeformis*, intermediate elevations (Savage, 1980); E. melanostictus*, 1150--2480 m (Dunn, 1937; Savage, 1980b; Savage and Deweese, 1981; Van Devender, 1980; KU); E. moro*, 1240 m (Savage, 1965); E. podiciferus*, 780--2100 m (Savage, 1966b; Van Devender, 1980; KU); E. ridens*, 100--1520 m (Savage 1980b; Van Devender, 1980; KU); E. rugulosus*, 30--1450 m (Savage, 1975; KU); E. talamancae*, 10--1600 m (Taylor, 1952; KU); Atelopus senex*, 2070--2400 m (Savage, 1980a; Taylor, 1952b); A. varius*, 520--1520 m (Savage, 1966b; Taylor, 1952bb; Van Devender, 1980; KU); Bufo coccifer, 20--1190 m (Savage, 1980a; Taylor, 1952bb; KU); B. holdridgei*, 2100--2290 m (Savage, 1980a; Taylor, 1952bb and 1958; KU); B. marinus, 10--2130 m (Taylor, 1952bb; Van Devender, 1980; KU); B. periglenes**, 1410--1590 m (Savage, 1966b; Van Devender, 1980; KU); Agalychnis annae*, 500--1600 m (Duellman, 1970; Van Devender, 1980; KU); Anotheca spinosa*, 300--1200 m (Duellman, 1970; Savage and Heyer, 1969); Hyla angustilineata**, 1410--2200 m (Duellman, 1970; Savage, 1966b; Savage and Heyer, 1969; Van Devender, 1980); H. colymba*, 600--1400 m (Duellman, 1970; Savage and Heyer, 1969; KU); H. debilis*, 910--1700 m (Duellman, 1970; Savage and Heyer, 1969; KU); H. fimbrimembra**, 1500 m (Duellman, 1970); H. lancasteri*, 400--1920 m (Duellman, 1970; Savage and Heyer, 1969; KU); H. miliaria*, 600--1200 m (Duellman, 1970; KU); H. picadoi*, 1900--2750 m (Duellman, 1970; Savage and Heyer, 1969; KU); H. pictipes*, 1900--2800 m (Duellman, 1970; Savage and Heyer, 1969; KU); H. pseudopuma*, 1000--2400 m (Duellman, 1970; Dunn, 1937a; Savage, 1966b and 1980b; Savage and Heyer, 1969; Taylor, 1958; KU); H. rivularis*, 1200--2840 m (Duellman, 1970; Savage, 1980b; Savage and Heyer, 1969; Van Devender, 1980; KU); H. rufioculis*, 700--1600 m (Duellman, 1970; Savage, 1968; Savage and Heyer, 1969; KU); H. tica*, 830--1920 m (Duellman, 1970; Savage and Heyer, 1969; Van Devender, 1980); H. uranochroa*, 600--1720 m (Duellman, 1970; Savage, 1968 and 1980b; Savage and Heyer, 1969; Van Devender, 1980; KU); H. xanthosticta**, 2100 m (Duellman, 1968 and 1970; KU); H. zeteki*, 1200--2140 m (Duellman, 1970; Dunn, 1937a; Savage and Heyer, 1969; Taylor, 1958; KU); Phyllomedusa lemur*, 650--1600 m (Duellman, 1970; Savage and Heyer, 1969; Van Devender, 1980; KU); Smilisca baudini, 10--1600 m (Duellman, 1970; Savage and Heyer, 1969; KU); S. phaeota, 10--1200 m (Duellman, 1970; KU); Centrolenella colymbiphyllum*, 10--1600 m (Savage, 1980b; Starrett and Savage, 1973; Van Devender, 1980; KU); C. euknemos**, 1100--1500 m (Starrett and Savage, 1973); C. fleischmanni*, 10--1650 m (Starrett and Savage, 1973; Van Devender, 1980); C. prosoblepon*, 10--1920 m (Savage, 1980b; Starrett and Savage, 1973; Taylor, 1952b; Van Devender, 1980; KU); C. valerioi*, 10--1500 m (Starrett and Savage, 1973; KU); Glossostoma aterrimum*, 100--1600 m (Savage, 1980a; Taylor, 1952b; KU); Rana sp. F (pipiens- group)*, intermediate elevations (Van Devender, 1980; KU); Rana vibicaria*, 2030--2700 m (Van Devender, 1980; KU); Rana warschewitschi*, 300--1960 m (Van Devender, 1980; KU); Anolis altae**, 2130 m (Taylor, 1956; Van Devender, 1980); _A_. _biporcatus_, 10--1200 m (Taylor, 1956; KU); _A_. _cupreus_, 600--1440 m (Fitch, 1975; Fitch et al., 1972; Van Devender, 1980; KU); _A_. _godmani_**, 1500 m (Savage, 1980a; Taylor, 1956); _A_. _humilis_*, 100--1600 m (Fitch, 1975; Taylor, 1956; Van Devender, 1980; KU); _A_. _insignis_*, 10--1500 m (Cope, 1876; Fitch, 1975; Fitch et al., 1976; Savage and Talbot, 1978; Van Devender, 1980); _A_. _intermedius_*, 730--2230 m (Fitch, 1972 and 1975; Taylor, 1956; Van Devender, 1980; KU); _A_. _lemurinus_, 10--2000 m (Taylor, 1956; Van Devender, 1980; KU); _A_. _limifrons_, 10--1200 m (Taylor, 1956; KU); _A_. _lionotus_*, 100--1600 m (Fitch, 1975; Taylor, 1956; Van Devender, 1980; KU); _A_. _microtus_**, 1000--1500 m (Cope, 1876; Savage and Talbot, 1978; Taylor, 1956); _A_. _pachypus_**, 1770--2100 m (Savage, 1980a; Taylor, 1956); _A_. _tropidolepis_**, 1190--2600 m (Fitch, 1972 and 1975; Peters and Donoso-Barros, 1970; Savage, 1980b; Taylor, 1956; Van Devender, 1980; KU); _A_. _woodi_**, 1200--1680 m (Fitch, 1975; Taylor, 1956; Van Devender, 1980; KU); _Corytophanes_ _cristatus_, 10--1230 m (Taylor, 1956; KU); _Polychrus_ _gutterosus_*, low and moderate elevations (Savage, 1980a; Taylor, 1956); _Sceloporus_ _malachiticus_*, 1190--3500 m (Cope, 1876; Fitch, 1972; Savage, 1980a; Van Devender, 1980); _Ameiva_ _festiva_, 10--1200 m (Savage, 1980a; KU); _A_. _undulata_*, 10--1400 m (Van Devender, 1980; KU); _Anadia_ _ocellata_*, 1200 m (Savage, 1980a; KU); _Ptychoglossus_ _plicatus_*, 920--2450 m (Savage, 1980a; Taylor, 1956; KU); _Lepidophyma_ _flavimaculata_, low and moderate elevations (Savage, 1980a; KU); _Mabuya_ _unimarginata_, 10--1400 m (Savage, 1980a; Van Devender, 1980); _Sphenomorphus_ _cherriei_, 10--1400 m (Savage, 1980a; Van Devender, 1980; KU); _Barisia_ _monticola_*, 1950--3080 m (Fitch, 1972; Savage, 1980a; KU);

Celestus cyanochloris*, moderate and intermediate elevations (Savage, 1980a; Van Devender, 1980; KU); Diploglossus bilobatus*, 580--1600 m (Savage, 1980a; Taylor, 1956; KU); D. monotropis* 300--2000? m (Savage, 1980a; Taylor, 1956; KU); Typhlops costaricensis*, ca. 1500 m (Jimenez and Savage, 1962; Van Devender, 1980); Amastridium veliferum*, 100--1500 m (Scott, 1969; Wilson and Meyer, 1969; KU); Chironius carinatus*, 10--1600 m (Scott, 1969; Taylor, 1951a; Van Devender, 1980; KU); C. grandisquamis*, 60--1600 m (Scott, 1969; Taylor, 1951a; Van Devender, 1980; KU); Clelia scytalina*, 60--1900 m (Scott, 1969; KU); Coniophanes fissidens, 10--740 m (Scott, 1969; Taylor, 1951a; KU); Dendrophidion paucicarinatum*, 20--1700 m (Scott, 1969; Van Devender, 1980; KU); D. percarinatum, 10--1200 m (Scott, 1969; KU); Dryadophis melanolomus*, 10--1700 m (Scott, 1969; Taylor, 1951a; Van Devender, 1980; KU); Drymobius margaritiferus, 10--1450 m (Scott, 1969; Wilson, 1974; KU); D. melanotropis**, 930--1550 m (Scott, 1969; Wilson, 1970a and 1975b; KU); Erythrolamprus bizonus*, 10--1450 m (Scott, 1969; Van Devender, 1980; KU); Geophis brachycephalus*, 250--2120 m (Cope, 1876; Downs, 1967; Scott, 1969; Taylor, 1951; KU); G. godmani*, 1100--2100 m (Downs, 1967; Scott, 1969; Taylor, 1951; KU); G. hoffmani*, 10--2100 m (Cope, 1876; Downs, 1967; Fitch, 1972; Scott, 1969; Taylor, 1951a; KU); G. ruthveni*, 550--1600 m (Downs, 1967; Scott, 1969; KU); G. zeldoni*, 1600--2100 m (Downs, 1967; Scott, 1969; KU); Hydromorphus concolor, 60--1500 m (Nelson, 1966; Scott, 1969; KU); Imantodes cenchoa, 10--1830 m (Dunn, 1937a; Scott, 1969; Taylor, 1951a; Van Devender, 1980; KU); I. inornatus, 10--1500 m (Scott, 1969; Taylor, 1951; Van Devender, 1980; KU); Lampropeltis triangulum*, 10--2450 m (Dunn, 1937b; Scott, 1969;

Taylor, 1951a; Van Devender, 1980; Williams, 1978; KU); _Leimadophis epinephalus_*, 60--2100 m (Cope, 1876; Scott, 1969; Van Devender, 1980; KU); _Leptodeira annulata_, 10--1400 m (Duellman, 1958; Scott, 1969; KU); _L. septentrionalis_, 10--1150 m (Duellman, 1958; Scott, 1969; KU); _Leptodrymus pulcherrimus_, 10--800 m (Scott, 1969); _Leptophis ahaetulla_, 10--1400 m (Scott, 1969; Van Devender, 1980; KU); _L. mexicanus_, 10--1600 m (Van Devender, 1980; KU); _Ninia atrata_*, 800--1600 m (Cope, 1876; Scott, 1969; Taylor, 1951a; KU); _N. maculata_*, 10--1830 m (Cope, 1876; Scott, 1969; Taylor, 1951a; KU); _N. psephota_*, 430--1740 m (Scott, 1969; Van Devender, 1980); _N. sebae_, 40--800 m (Schmidt and Rand, 1957; Scott, 1969); _Oxybelis aeneus_, 10--800 m (Scott, 1969; KU); _O. fulgidus_, 10--1400 m (Scott, 1969; Van Devender, 1980; KU); _Oxyrhopus petola_, 10--700 m (Scott, 1969); _Plocercus euryzonus_*, 10--1680 m (Scott, 1969; Tayor, 1951a; KU); _Pseustes poecilonotus_, 10--1810 m (Fitch, 1972; Scott, 1969; Taylor, 1951a; KU); _Rhadinaea calligaster_**, 1220--2440 m (Myers, 1974; Scott, 1969; KU); _R. decorata_, 10--1200 m (Myers, 1974; Scott, 1968; KU); _R. decipiens_*, 10--2100 m (Myers, 1974; Scott, 1969); _R. godmani_, 1200--2200 m (Myers, 1974; Scott, 1969; KU); _R. guentheri_*, 60--1400 m (Myers, 1974; Scott, 1969; KU); _R. pachyura_*, 10--2400 m (Myers, 1974; Scott, 1969; KU); _R. pulveriventris_**, 1370--1600 m (Myers, 1974; Scott, 1969; Taylor, 1951a); _R. serperaster_*, 1220--2050 m (Cope, 1876; Myers, 1974; Scott, 1969; Taylor, 1951a; Van Devender, 1980; KU); _Sibon annulata_, 10--1500 m (Scott, 1969; Tayor, 1951a; KU); _S. dimidiata_*, 1450 m (Scott, 1969; Van Devender, 1980); _Spilotes pullatus_, 10--1150 m (Scott, 1969; KU); _Stenorrhina degenhardti_, 10--1050 m (Scott, 1969; KU); _Tantilla armillata_, 50--1400 m (Scott, 1969; Taylor, 1951a; KU); T. reticulata, 40--1430 m (Scott, 1969; Taylor, 1951a; Wilson and Meyer, 1971); T. schistosa, 60--1600 m (Scott, 1969; Smith, 1962; Taylor, 1951; KU); Thamnophis proximus, 10--1500 m (Scott, 1969; KU); Trimetopon gracile*, 600--2210 m (Scott, 1969; Taylor, 1951a; KU); T. pliolepis, 100--1600 m (Scott, 1969; Taylor, 1951a; KU); T. slevini, 1700 m (Scott, 1969; KU); Xenodon rhabdocephalus, 10--1170 m (Scott, 1969; KU); Micrurus mipartitus, 10--1450 m (Savage and Vial, 1974; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; Van Devender, 1980; KU); M. nigrocinctus, 10--1450 m (Savage and Vial, 1974; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; Van Devender, 1980; KU); Bothriechis lateralis*, 850--1980 m (Bogert, 1968; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; Van Devender, 1980; KU); B. nigroviridis**, 1150--2410 m (Cope, 1876; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; KU); B. schlegeli*, 10--1530 m (Scott, 1969; Taylor, 1951a; Taylor et al., 1974; KU); Bothrops asper, 10--1200 m (Scott, 1969; Taylor et al., 1974; KU); B. godmani*, 1420--2450 m (Scott, 1969; Taylor et al., 1974); B. nummifer*, 40--1400 m (Burger, 1950; Cope, 1876; Dunn, 1939; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; KU); B. picadoi*, 70--1500 m (Dunn, 1939; Scott, 1969; Taylor, 1951a; Taylor et al., 1974; KU).

APPENDIX III

```
005 PARAMETER  SPECIES=464,REGIONS=13,PRESENT=1
010 INTEGER    DATA(SPECIES,REGIONS),I,J,K,C1,C2
015 REAL       COEFF4(REGIONS,REGIONS),POSMATCH,NEGMATCH
020 CALL ATTACH(10,"/ACMATRIX;",1,0,ISTAT1)
025 CALL ATTACH(8,"/MATRIX4;",2,0,ISTAT3)
030 CALL CREATE(7,10000,0,ISTAT2)
035 DO 5 I=1,REGIONS
040 DO 10 J=1,REGIONS
045 COEFF4(I,J)=0
050 10 CONTINUE
055 5 CONTINUE
060 DO 15 I=1,SPECIES
065 READ(10,20) (DATA(I,J),J=1,REGIONS)
070 20 FORMAT(160I1)
075 15 CONTINUE
080 WRITE(7,25)
085 25 FORMAT('COEFFICIENT FOUR IS (SQRT(A*D) + A)/(
090&SQRT(A*D) + A + B + C), WHERE A'/'IS THE NUMBER
095& OF POSITIVE MATCHES, D IS THE NUMBER OF NEGATIVE
100& MATCHES,'/'AND (B + C) IS THE NUMBER OF MISMATCHES.')
105 DO 30 J=1,REGIONS - 1
110 DO 35 K=J + 1,REGIONS
115 POSMATCH=0
120 NEGMATCH=0
125 DO 40 I=1,SPECIES
```

```
130 IF (DATA(I,J) .NE. DATA(I,K)) GO TO 40
135 IF (DATA(I,J) .EQ. PRESENT) GO TO 45
140 NEGMATCH=NEGMATCH + 1
145 GO TO 40
150 45 POSMATCH=POSMATCH + 1
155 40 CONTINUE
160 COEFF4(J,K) = (SQRT(POSMATCH * NEGMATCH) + POSMATCH) / (SQRT(
165&                POSMATCH * NEGMATCH) + POSMATCH + (SPECIES -
170&                POSMATCH - NEGMATCH))
175 C1 = IFIX(POSMATCH)
180 C2 = IFIX(NEGMATCH)
185 WRITE(7,50) J,K,C1,C2,SPECIES - C1 - C2,COEFF4(J,K)
190 50 FORMAT(/'REGIONS',I4,'AND',I4,'SHARE',I4,'SPECIES.',I4,'SPECIES
195& ARE ABSENT FROM BOTH'/'REGIONS.',I4,'SPECIES ARE FOUND IN JUST ONE
200& OR THE OTHER REGION.'/'COEFFICIENT FOUR IS ',F5.3)
205 35 CONTINUE
210 30 CONTINUE
215 DO 55 J=1,REGIONS
220 WRITE(8,60) (COEFF4(J,K),K=J,REGIONS)
225 60 FORMAT(12F6.3)
230 55 CONTINUE
235 STOP
240 END
```

APPENDIX IV

The specimens of Bothriechis examined during the course of this study are listed below. I have also listed additional literature and/or museum records.

Bothriechis aurifer.-- GUATEMALA: Alta Verapaz: vicinity of Coban, ca. 1550 m (UTA R-4494); Finca El Volcan (UMMZ 91081); Baja Verapaz: E slope Cerro Quisis, Hacienda Vieja (UTA R-7039--40); E slope Cerro Quisis, ca. 1.6 km W La Union Barrios, 1829--2134 m (KU 187430, 187432, 187435--36); Cerro Quisis, 2 km SW La Union Barrios, 2134 m (KU 187437) E slope Cerro Quisis, near La Union Barrios, 1500--1829 m (UTA R-6562, 7043--45, 7763--68, 9608--09, 10434--36, KU 187440, KU 191196--99); E slope Cerro Quisis, Rio Chipilin, 1676--2134 m (UTA R-7041--42, KU 191200); Cerro Quisis, 3.2 km SE Purulha, 1524 m (UTA R-8777); Cerro Quisis, 3.8 km SE Purulha, 1615 m (UTA R-6553); Cerro Quisis, 4.1 km SE Purulha (UTA R-8778); Cerro Quisis, 4.8 km SE Purulha, 1707 m (KU 191203); Cerro Quisis, 5.4 km SE Purulha (UTA R-7716); Cerro Quisis, 7.7 km SSE Purulha, 1615 m (UTA R-6241, 6275--76, 6459, 6504--05, 6525); near La Union Barrios (UTA R-7046, 7048, 7762, 7635--36, 7788); 3.2 km NE La Union Barrios, trail to Panima, 1372 m (KU 187434); 3.5 km E La Union Barrios, Rio Sananja, 1585--1707 m (KU 191202); Cerro Verde, near La Union Barrios, 1524--1829 m (UTA R-7047, 9366, KU 187438--39); E slope Cerro Verde, 1829 m (KU 187427); NE slope Cerro Verde, 1829 m (KU 187428); W slope Cerro Verde, 1676--1829 m (KU 187429, 187431, 191192--95, 191204--05); Quiche: Finca El Soche ["El Soch" on some maps], 40 km W Coban (CAS 67049); Zacapa: Sierra de las

Minas, 7.8 km NNW San Lorenzo, 2286 m (KU 191201).

Additional Records: GUATEMALA: Alta Verapaz: vicinity of Coban (Salvin, 1860--holotype, BMNH 1946.1.17.71); MEXICO: Chiapas: Santa Rosa, near Comitan (Martin del Campo, 1938).

Bothriechis bicolor.-- GUATEMALA: Chimaltenango: Finca Pacayal, near Pochuta, 1280 m (MCZ 31941); Yepocapa (USNM 127973); Escuintla: Finca Rosario Vista Hermosa, S slope Volcan de Agua, 1372 m (UTA R-9353, Dallas Zoo--1 specimen); Suchitepequez: Olas de Moca, near Finca La Moka (FMNH 20612); MEXICO: Chiapas: "Chicharras" [probably from Cerro Chicharras, a mountain near the village of San Juan Chicharras] (USNM 46511); Cerro Ovando, 2000 m (UMMZ 94644).

Additional Records: GUATEMALA: Escuintla: Finca Rosario Vista Herosa, S slope Volcan de Agua, 457--1676 m (USAC--5 specimens); Solola: San Agustin, 610 m (Muller, 1878--syntypes, MNHN 1362 and 6137); Suchitepequez: Volcan Atitlan (holotype of B. bernoullii, NMB 2629); HONDURAS: Ocotepeque: 21.6 km E Nueva Ocotepeque, 1730 m (LSU 23821); Santa Barbara: SE slope Cerro Santa Barbara (LSU 11638). MEXICO: Chiapas: Municipio de Huixtla, Ejidal Morelos, ca. 500 m (Julia and Varela, 1978--holotype of B. ornatus, no museum or number given in original description).

Bothriecis lateralis.-- COSTA RICA: Alajuela: La Balsa (KU 140086); Villa Quesada (KU 30961); Cartago: Navarro (KU 35549); 3.2 km above Santa Cruz, Volcan Turrialba (KU 25163); Limon: Pico Blanco (KU 180261); San Jose: Patarra (UTA R-2800, 2811, 3660, 7634, 8176, KU 180262); 14 km N San Isidro el General (KU 86588); "Grosi," Central

Plateau of Costa Rica (MCZ 25211); PANAMA: Chiriqui: Rio Chiriqui Viejo (MCZ 39654); Finca Santa Clara, 1200 m (KU 112589); El Hato del Volcan (AMNH 75636); Quebrada Chevo, S slope Cerro La Pelota, 1440 m (KU 112590--95).

Additional Records: COSTA RICA: Alajuela: Isla Bonita, Volcan Poas, 1524--1829 m (Taylor, 1951); Guanacaste: Orosi [Volcan] (Picado, 1931); Tilaran area (Taylor, et al., 1974); Heredia: N Heredia (Picado, 1931); San Jose: Santa Marta de Dota (Picado, 1931); Valle Central (Taylor, et al., 1974); PANAMA: Chiriqui: Boquete (Dunn, 1947; Slevin, 1942); El Hato del Volcan [W slope Volcan Chiriqui] and Finca Lerida [E slope Volcan Chiriqui, 1615 m] (Dunn, 1947); Veraguas: "Veragua" [probably Santiago] (syntypes--Peters, 1862).

Bothriechis marchi.-- HONDURAS: Atlantida: Tela (AMNH 46949); Cortes: Sierra de Omoa, La Cumbre (AMNH 46954--57, MCZ 32029--31); Sierra de Omoa, N San Pedro Sula (UTA R-7158--59, 8175, 8258, 8333, 8336, KU 180263); "San Pedro Sula,"[probably from the Sierra de Omoa which flanks this town to the north and east] (MCZ 33334--36, 33561--64, USNM 83454); Santa Barbara: Cofradia--Santa Barbara road (paratypes--MCZ 27567--68); Quimistan (holotype--MCZ 27260); Santa Barbara (paratype--MCZ 28014); Yoro: Montanas de los Mataderos (MCZ 38785--86); Portillo Grande (MCZ 38790--91).

Additional Records: HONDURAS: Santa Barbara: Cofradia--Santa Barbara road (BMNH).

Bothriechis nigroviridis.-- COSTA RICA: Alajuela: Rio Poasito, 1 km W Poasito, 2100 m (KU 63919--20); Heredia: Volcan Barba (AMNH

17283); San Jose: Providencia, Rio Brujo, 1800 m (KU 128994); near San Isidro el General (UTA R-10432, 31954); No Specific Locality: (UTA R-7463, 9635--37); PANAMA: Bocas del Toro: N slope Cerro Pando, 1920 m (KU 112598); Chiriqui: Rio Chiriqui Viejo (MCZ 39655).

Additional Records: COSTA RICA: Alajuela: Isla Bonita, 1676 m [Volcan Poas] (Taylor, 1951); Volcan Poas (Picado, 1931); Heredia: Volcan Barba (holotype--Peters, 1959; Picado, 1931); Limon: Cerro Utyum (Savage, 1970); San Jose: La Palma (Picado, 1931); Pacific slope above San Isidro El General (Taylor, 1954); upper tributaries of Rio Sarapiqui (Picado, 1931); Taylor, et al., (1974) plot a number of unspecified localities in the Cordillera Central and the Cordillera de Talamanca; PANAMA: Chiriqui: Boquete, El Hato del Volcan [W slope Volcan Chiriqui], and Finca Lerida [E slope Volcan Chiriqui, 1615 m] (Dunn, 1947).

Bothriechis rowleyi.-- MEXICO: Chiapas: Hwy 195, 50.2 km N Bochil, or 22.1 km S Tapilula (UF 52553); Oaxaca: Cerro Baul, 1372--2134 m (UTA R-6207, 6636, 7707--09, JAC 5534); W slope Cerro Baul, 1463 m (AMNH 102894--95).

Additional Records: MEXICO: Oaxaca: 8 km W Cerro Baul, 1520 m (holotype, AMNH 100669); Pacific slope N Zanatepec, 1524 m (UIMNH 53096, 56121); Cerro Azul, ca. 16 km E La Gloria, 1524 m (UIMNH 27845).