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**THE BIOGEOGRAPHY
OF THE HERPETOFAUNA
OF THE SUBHUMID
FORESTS OF MIDDLE
AMERICA (ISTHMUS
OF TEHUANTEPEC TO
NORTHWESTERN
COSTA RICA)**

Larry David Wilson and
James R. McCranie

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THE BIOGEOGRAPHY OF THE
HERPETOFAUNA OF THE SUBHUMID FORESTS
OF MIDDLE AMERICA
(ISTHMUS OF TEHUANTEPEC TO
NORTHWESTERN COSTA RICA)

By Larry David Wilson and James R. McCranie

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Cover: Yucatecan Casque-headed Treefrog (*Triprrion petasatus*).

From 0.6 km E. Ebtún, Yucatán, Mexico.

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Contents

Abstract	1
Introduction	2
Methods	3
Limits of Study Area	3
Physiography	3
Pacific Coastal Areas	4
The Interior Valleys	5
Caribbean Coastal Areas	6
Climate	7
Factors Determining Temperature	7
Factors Determining Precipitation	7
Factors Determining Relative Humidity	10
Vegetation	11
Vegetation of Subhumid Forest Areas in Middle America	11
Composition of the Herpetofauna	13
Numerical Analysis	20
Patterns of Distribution	22
Herpetofaunal Assemblages	25
Subhumid Assemblage (SA)	25
Ubiquitous Assemblage (UA)	26
Humid Assemblage (HA)	26
Montane Assemblage (MA)	26
Historical Biogeography	28
Historical Units	28
Major Geohistorical Events	28
Origin of the Subhumid Herpetofauna	33
Analysis of Generalized Tracks and Areas of Endemism	34
Does Stuart's Subhumid Corridor Exist?	42
Acknowledgements	46
Literature Cited	47

The Biogeography of the Herpetofauna of the Subhumid Forests of Middle America (Isthmus of Tehuantepec to Northwestern Costa Rica)

Abstract

Subhumid forests in Middle America occur (or occurred until recently) in an almost uninterrupted strip along the Pacific coastal lowlands from the Plains of Tehuantepec to northwestern Costa Rica. They also occur in a much more restricted fashion in various interior river valleys in Chiapas, Mexico, in Guatemala and Honduras, and on the outer end of the Yucatan Peninsula, some of which lie on the Caribbean versant. The climate of the subhumid forest regions is characterized by a relatively high mean annual temperature of 24°C or more at elevations of sea level to ± 600 m and of 21°C or more at elevations of ± 1000 m, and a six-month-long dry season with little or no monthly precipitation. The vegetation of these regions is of relatively low height, deciduous or semi-deciduous, sparse, scrubby, and spiny. Tree cacti, acacias, jícaros, mimosas, and nances abound.

The herpetofauna of 16 subhumid forests of Middle America consists of 212 species, including 2 caecilians, 5 salamanders, 37 anurans, 11 turtles, 3 crocodilians, 59 lizards, and 95 snakes. A numerical analysis using the *Coefficient of Biogeographic Resemblance* (CBR) algorithm indicates that a relatively similar herpetofauna occurs in the Pacific coastal areas from southeastern Guatemala to northwestern Costa Rica and in two of the interior valleys of Honduras and Guatemala. The outer Yucatan Peninsula has a very distinctive herpetofauna, whereas that of the Sula Plain, the Plains of Tehuantepec, and the Central Depression of Chiapas are also relatively distinctive. The 212 taxa are placed in three distributional categories, namely, endemics (50 species), widespread forms (67 species), and peripherals (95 species). These distributional categories are used to further analyze the relationships of the 16 areas as shown by the resemblance algorithm.

Four herpetological assemblages may be recognized: the Subhumid Assemblage (96 species), the Ubiquitous Assemblage (53 species), the Humid Assemblage (54 species), and the Montane Assemblage (9 species).

There are four historical elements represented: the Old Northern, South American, Middle American, and Young Northern elements. Most Subhumid Assemblage species either belong to the Middle American or the Old Northern element.

The major geohistorical events of pertinence to an understanding of the evolution of the subhumid forest herpetofauna include: (a) concordant northward dispersal of southern groups into Middle America continuing into the Palaeocene; (b) isolation of Middle and South America by the northeastward displacement of a proto-Antillean block on the Caribbean tectonic plate beginning in the Eocene, allowing for the origin of the Middle American herpetofaunal element; (c) concordant southward dispersal of northern groups into Middle America prior to the Eocene; (d) isolation of northern groups in Middle America from related stocks in eastern North America by orogeny and cooling and drying events beginning in the Oligocene; (e) concordant northward dispersal of southern groups into Central America with reformation of an isthmian link between Central and South America in the Pliocene; (f) orogeny of main mountain masses of Mexico and Central America from the Oligocene to the Pliocene in a north-to-south sequence, segmenting the herpetofauna into eastern and western lowland assemblages and a central highland assemblage; (g) climatic and vegetational fluctuations during the Quaternary, allowing for alternating expansion and contraction of humid and subhumid forest types and of the ranges of humid- and subhumid-adapted members of the herpetofauna.

Three major areas of endemism exist within the Subhumid Assemblage (SA). These are the outer Yucatan Peninsula (21 species), the Pacific lowlands from southeastern Guatemala to northwestern Costa Rica (14 species), and the Pacific lowlands of the Isthmus of Tehuantepec (9 species). A generalized track analysis identified the following five generalized tracks for the SA species: Western Mexican Generalized Track (58 species), Eastern Mexican Generalized Track (8 species), Middle American Generalized Track (10 species), Eastern Middle American Generalized Track (9 species), and South American Generalized Track (6 species). In addition, five species could not be allocated to any of the generalized tracks identified.

In 1954, L. C. Stuart identified a subhumid corridor through the mountainous interior portion of southeastern Mexico and Guatemala (Plains of Tehuantepec–Central Depression of Chiapas–Rio Negro Valley–Motagua Valley–Pacific coastal southeastern Guatemala). Stuart proposed that this corridor was an exclusive Tertiary dispersal route for a series of “indicator species.” In an effort to test Stuart’s hypothesis, we undertook a numerical analysis of only the 96 SA species using the CBR algorithm. The analysis indicated that the same Pacific coastal areas and the same two interior valleys shown to have relatively similar herpetofaunas when the entire 212 species were analyzed also have relatively similar herpetofaunas when only the SA species are analyzed. In addition, two other Honduran interior valleys (Comayagua and Sula Plain) also share relatively similar herpetofaunas with these areas. The new analysis also demonstrates that the outer Yucatan Peninsula, the Plains of Tehuantepec, and the Central Depression of Chiapas have distinctive herpetofaunas. Four interior valleys (Otoro, Guayape-Guayambre, Aguan, and Rio Negro) have low numbers of SA species (i.e., depauperate faunas) and low CBR values. The new analysis demonstrates that the Rio Negro Valley, a central figure in Stuart’s subhumid corridor, does not show a significant CBR value with those valleys on either side (the Central Depression of Chiapas and Motagua Valley). Instead, the Rio Negro Valley shows significant CBR values with Pacific coastal areas to the south and with one interior valley in Honduras. At the same time, the Motagua Valley, another key figure in Stuart’s corridor, shows significant CBR values with several Honduran interior valleys rather than the Rio Negro Valley. Likewise, the Central Depression of Chiapas shows significant CBR values with Pacific coastal areas to the south, but not with the Rio Negro Valley. Inspection of the 16 SA species known from the Rio Negro Valley reveals that 14 presently occur in moderate elevation pine-oak forests such as presently surround the Rio Negro Valley and are continuous with such forests surrounding other subhumid valleys in the region under study. Compared to the Central Depression of Chiapas and the Motagua Valley, the Rio Negro Valley has a depauperate herpetofauna and, furthermore, the Rio Negro Valley species shared with these two valleys are also generally widespread in the interior valleys of Honduras. The conclusion reached is that Stuart’s subhumid corridor as an important exclusive Tertiary dispersal route does not exist.

Introduction

One of the most intriguing aspects of the herpetofauna of Nuclear Central America is the occurrence in interior valleys on the Caribbean versant of subhumid-adapted species with an otherwise “typical” Pacific coastal pattern of distribution. Stuart (1954a) attempted an explanation of this phenomenon in an influential paper by describing a “subhumid corridor” through the interior of northern Nuclear Central America connecting the Plains of Tehuantepec with the subhumid Pacific coastlands of Central America from southeastern Guatemala to northwestern Costa Rica. Stuart dealt with the herpetofauna of the following three subhumid interior valleys in southern Mexico and Guatemala: the Central Depression of Chiapas and the Rio Negro (and associated Salama Basin)

and Motagua River valleys. He made only vague reference to similar valleys in Honduras. We were initially drawn to the present project because of an interest in ascertaining whether Stuart’s subhumid corridor extends into Honduras. As we began our research in 1977, it became evident that the situation in Honduras was but a part of a larger problem in need of study, i.e., the composition, distribution, and biogeography of the herpetofauna of the subhumid forests of all of Middle America (as defined here), and that we would be able to understand the Honduran component only in the context of the larger problem. It was with this intent, then, that we began, some 20 years ago, the long roller-coaster ride that resulted in the production of this paper.

Methods

Initially, we delimited the study area herein under discussion based on our knowledge of the Middle American herpetofauna, as well as the work of Savage (1966) and Duellman (1966), to the area between and including the Isthmus of Tehuantepec and the Nicoya Peninsula of Costa Rica. Within these limits, we identified 16 subhumid areas, discussed below, the herpetofauna of which is sufficiently well known to allow for a meaningful analysis of biogeographic patterns. We then drew up a species list for each of the 16 areas, based on an extensive search of the literature, and circulated these lists to the knowledgeable colleagues mentioned in the Acknowledgements section. These lists have been consistently updated as necessary to the point of submission of the paper (6 July 1993).

Our Central Depression of Chiapas also includes adjacent portions of Guatemala. As such, our species list for this area differs slightly from that of Johnson (1990), who confined his records to the Mexican portion of the valley.

Hillis (1988 and in Johnson, 1990), based in part on biochemical data, used the name *Rana forreri* for the Central American Pacific coast and Central Depression of Chiapas populations of frogs of the *pipiens* group. We use *Rana berlandieri* for the frogs of this complex in this study, because no biochemical data exists for the populations of these frogs in the interior valleys of Guatemala and Honduras, and we are unable to distinguish Pacific versant specimens from Caribbean versant specimens in Honduras using traditional morphological characters.

The field work in connection with this study was carried out primarily in Honduras over the course of 25 years, but one or both of us have travelled or collected in all of the other subhumid forest areas within the study area. The majority of the Honduran material collected in subhumid forests has been previously reported elsewhere. We have not included a number of obviously introduced species, including *Crotalus atrox* from the Plains of Tehuantepec.

Limits of Study Area

Similar subhumid forests occur more or less continuously along the Pacific coast of Middle America from southern Sinaloa, Mexico, to northwestern Costa Rica, except for a significant break in southern Chiapas, Mexico, and northwestern Guatemala (Campbell and Vannini, 1988; Stuart, 1954a). The northern limits of our study area were set at the Plains of Tehuantepec and the southern at the Pacific lowlands of northwestern Costa Rica. Sixteen subhumid areas within this area were chosen for study (Fig. 1). They are (1) the Plains of Tehuantepec and associated foothills; (2) the outer Yucatan Peninsula; (3) the Central Depression of Chiapas (a small portion of which extends into Guatemala);

(4) the upper Rio Negro (= Chixoy) Valley, including the Salama Basin; (5) the upper and middle Motagua Valley; (6) the dry Pacific lowlands of Guatemala, including the low elevation subhumid portions of the Jalapan area of Campbell and Vannini (1989); (7) the Pacific lowlands of El Salvador; (8) the Pacific lowlands of Honduras; (9) the middle and upper Choluteca Valley; (10) the Comayagua Valley; (11) the Otoro Valley; (12) the Sula Plain; (13) the middle Aguan Valley; (14) the Guayape-Guayambre Valley; (15) the Pacific lowlands of Nicaragua; (16) the Pacific lowlands of northwestern Costa Rica.

Physiography

The physiography of Middle America has been discussed in general by West (1964) and Stuart (1966). The interior valleys of Honduras have been treated in some detail by Carr (1950), Johannessen (1963), Martin (1972), Meyer (1969), Monroe (1968), and Wilson and Meyer (1985); those of Guatemala by Stuart (1954a); the Central Depression of Chiapas, Mexico, by Breedlove (1981), Johnson (1990), and Stuart (1954a); and the Yucatan Peninsula by Lee (1980).

Most of the area that lies between the Isthmus of Tehuantepec and northwestern Costa Rica consists of low-

lands or areas below the 600 m contour line (Stuart, 1966). These lowland areas lie on both sides of the Continental Divide, those of the Caribbean versant being much more extensive than those of the Pacific. Between these lowland areas a complex mass of mountains extends from eastern Oaxaca, Mexico, to northern Nicaragua and from northern Costa Rica to central Panama. Within the northern portion of this mountain mass lie interior valleys and inland depressions of varying extent and elevation.

The areas under consideration here thus may be divided into three groups: (1) the Pacific coastal areas (Plains of

FIG. 1. Map of the subhumid areas of Middle America. The numbered areas refer to (1) Plains of Tehuantepec; (2) outer Yucatan Peninsula; (3) Central Depression of Chiapas; (4) upper Rio Negro Valley; (5) upper and middle Motagua Valley; (6) Pacific lowlands of Guatemala; (7) Pacific lowlands of El Salvador; (8) Pacific lowlands of Honduras; (9) middle and upper Choluteca Valley; (10) Comayagua Valley; (11) Otoro Valley; (12) Sula Plain; (13) middle Aguan Valley; (14) Guayape-Guayambre Valley; (15) Pacific lowlands of Nicaragua; (16) Pacific lowlands of northwestern Costa Rica. Though not shown in this figure, subhumid forests in areas 1-3, 5-6, and 5-7 are very narrowly connected through low mountain passes.

Tehuantepec, Pacific coastal areas of Guatemala, El Salvador, Honduras, Nicaragua [including the Great Lakes region, which is actually of Caribbean drainage], and northwestern Costa Rica); (2) the dry interior valleys (Central Depression of Chiapas [including adjacent Guatemala], upper Rio Negro, middle and upper Motagua, middle and upper Choluteca, Comayagua, Otoro, Sula Plain, middle Aguan, and Guayape-Guayambre valleys); (3) the Caribbean coastal area (Yucatan Peninsula). Within these categories, the physiography of the individual areas is described below.

PACIFIC COASTAL AREAS

The areas along the Pacific coast herein recognized are artificial divisions along country boundaries of what is, in

fact, a continuous coastal plain extending from the Plains of Tehuantepec to the Nicoya Peninsula of northwestern Costa Rica. This study includes the low-lying coastal plain and the associated low-lying foothills up to about 600 m elevation in each of these areas.

The Isthmus of Tehuantepec is a lowland depression lying between the Sierra Madre del Sur to the west and the Sierra Madre de Chiapas to the east. As pointed out by Duellman (1960), the isthmus may be divided into three sections: the Gulf coastal lowlands, the central ridges, and the Pacific coastal plain. The last area is the one included in this study and is termed the Plains of Tehuantepec (including its associated low-lying foothills). The plains are transversed by several rivers, including the Río Tehuantepec (area 1).

In Guatemala, the narrow Pacific lowlands extend the length of the country's southern border (about 320 km). It

ranges in width from 25 to 50 km (except where it penetrates into the southeastern highlands) and is transversed by several relatively short rivers that arise from the mountains of the southeastern and southwestern highlands, which, because of their height, form a dramatic backdrop to the narrow lowland strip. These rivers include the two border rivers, the Suchiate (with Mexico) and the Paz (with El Salvador), as well as the Tilapa, Samalá Nahualate, Madre Vieja, Michatoya, and Esclavos rivers (area 6).

El Salvador is the only country in Middle America that has no Caribbean seaboard and lies entirely on the Pacific versant. Much of the land of this country lies below 600 m. This monotony is alleviated by two principal mountain ranges, a disjunct coastal range and the Cordillera Apenaca (area 7). The Pacific coastline is about 310 km long. Many rivers and streams cross the country and flow into the Pacific Ocean, the principal one being the Río Lempa, the longest river on the Pacific versant of Central America. Arising in the mountains of southwestern Honduras, the Lempa cuts a swath across the width of El Salvador.

The coastal plain of Middle America skirts the Golfo de Fonseca. Its width in Honduras generally ranges from 25 to 35 km (area 8). It is transversed by three rivers of importance. The westernmost is the Río Goascorán. The Río Nacaome originates in the mountains south of Tegucigalpa and flows more or less directly southward into the Golfo de Fonseca. The Río Choluteca is the third of the major Pacific versant rivers in Honduras and is described in the following section on the interior valleys.

In Nicaragua, the lowlands extend unbroken along the Pacific coast for approximately 320 km. These lowlands are continuous with the central depression of Nicaragua that contains the two large lakes, Managua and Nicaragua, and continue around the southern end of Lake Nicaragua and join the Caribbean lowlands (area 15). Such a union is not seen again to the north until one reaches the Isthmus of Tehuantepec. The presence of the two large lakes in western Nicaragua produces the unusual hydrographic effect that the water drains to the Caribbean via the Río San Juan, which drains Lake Nicaragua. This huge lake (154 km long) is connected to the smaller Lake Managua (61 km long) by the Río Tipitapa. The two lakes together collect much of the water from the western slopes of the central mountains and shunt it to the Caribbean.

The Pacific lowlands of Costa Rica are intermittent and we can define the southern limit of our study as the point at which the Río Grande de Tárcoles flows into the Gulf of Nicoya, just north of Punta Leona in the province of Puntarenas. The area is bounded to the east by the Cordillera de Guanacaste and the west by the Pacific Ocean. This area encompasses the lowlands of Guanacaste, the Nicoya Peninsula, and the northern por-

tion of the Puntarenas lowlands (area 16). The Pacific lowlands in Costa Rica range in width from about 15 to 95 km and are drained by several rivers, the major being the Río Tempisque and its tributaries.

THE INTERIOR VALLEYS

The area between the Pacific and Caribbean coastal areas in Nuclear Central America is occupied by a complex of mountain ranges presenting some of the most striking scenery to be seen in this region. In this region a number of interior valleys are found, which, as a result of their relation to surrounding mountain masses and prevailing winds, exist in a dry climatic regime created by the "rain shadow" and "mountain valley" effects, as described in the following section. Nine such valleys are considered in this paper. Only one of these, the Middle and Upper Choluteca, lies on the Pacific versant; all others occur on the Caribbean versant.

The Central Depression of Chiapas or the Grijalva Valley (area 3) is a graben of northwest-southeast orientation. It is bounded to the north by the Northern Highlands and the Central Plateau and to the south by the Sierra Madre de Chiapas. The depression is drained by the Río Grijalva, which originates in the Guatemalan Sierra de los Cuchumatanes and empties into the Gulf of Mexico via the Tabasco lowlands. Elevations within the depression range from about 400 to 1200 m.

Two important interior valleys in Guatemala are those of the Río Negro and the Río Motagua. The Río Negro has its origin in the Sierra de los Cuchumatanes and receives several tributaries from the highlands to the south (including the Río Salamá) on its due eastward journey in its upper reaches. The river then turns northward to cut between the highlands of El Quiché and Alta Verapaz and flows onto the Tabasco lowlands as the Río Usumacinta and into the Gulf of Mexico. In its upper course, the river flows through a structural depression supporting sub-humid forest vegetation (area 4). The lower reaches are much more mesic and outside the scope of this study. Elevations of the portion of the valley of concern to us range from about 700 to 1250 m.

The Río Motagua flows through a structural depression between the Sierra de Chuacús and the Sierra de las Minas to the north and the beginnings of the southeastern highlands to the south. The upper reaches of the river have a steep gradient. In its middle reaches, the river levels out considerably and the gradient is gradual to the river's mouth. The middle and upper portions of the river valley (approximately 250 to 700 m in elevation) support sub-humid vegetation types (area 5), in marked contrast to the mesic vegetation of the lower region.

The remaining subhumid interior valleys are in

Honduras. The Otoro Valley lies about 35 km by air to the west of the Comayagua Valley. It is cut by the Río Grande de Otoro, a tributary of the Río Ulúa. It is oriented in a north-south direction and is bounded on the east by the Cordillera de Montecillos and on the west by the Sierra de Opalaca (area 11). Elevation of the valley floor is about 550 to 700 m.

The Comayagua Valley is a portion of a graben produced by north-south faulting known as the Honduran Depression, which otherwise includes the Valle de Goascorán, Valle de Humuya, and the Sula Plain. The Río Humuya runs through the Comayagua Valley from its origin in the mountains south of the valley and continues northward through the Valle de Humuya and onto the Sula Plain to join the Río Ulúa. The Comayagua Valley is oriented in a north-south direction and is bounded on the east by the Sierra de Comayagua and on the west by the Cordillera de Montecillos (area 10). Elevations within the valley range from about 550 to 800 m.

The Choluteca Valley is a narrow valley cut by the Río Choluteca, which arises in the Tegucigalpa Valley and flows into the Golfo de Fonseca. The Río Choluteca is the longest river (225 km) on the Pacific versant of Honduras, which, along with the Río Lempa in El Salvador, are the longest rivers on the Pacific coast of Central America. On course to the Pacific, the Río Choluteca passes north out of the Tegucigalpa Valley between the Montaña de Azacualpa to the south and the Sierra El Chile to the north. The river then bends southward, passing to the west of the Sierra de Dipilto and out onto the Pacific coastal plain. Only the middle and upper reaches of the valley, therefore, constitute an interior valley (area 9). Elevations of this portion of the valley range from about 650 to 930 m.

The Aguan Valley or Plain is a long, narrow structural depression in northern Honduras between the Cordillera Nombre de Dios to the north and the Montaña de Botaderos and Sierra La Esperanza to the south. It is oriented in a northeast-southwest direction and empties into the Caribbean Sea about 30 km east of Trujillo. The plain is occupied by the Río Aguan, which has its origin in the mountains north of Yoro. The plain is relatively narrow in the upper reaches of the river and broadens in its lower portion. Elevations in the subhumid middle portion of the valley (area 13) are 300 m or less.

The Guayape-Guayambre Valley is a V-shaped valley, formed by the confluence of the alluvial plains of the rivers Guayape and Guayambre (area 14). These two rivers are major tributaries of the Río Patuca, which itself is a major river of the Caribbean versant of Honduras. The Río Patuca flows in a northeasterly direction through the area of Honduras known as the Mosquitia and empties into the Caribbean Sea at Punta Patuca. The Río Guayape has

its headwaters in the Sierra El Chile and flows northeastward before bending around the end of the Montaña de Azacualpa to flow southward to its point of confluence with the Río Guayambre. The Río Guayambre originates in the Sierra de Dipilto and flows northeastward to join the Río Guayape. Elevations in the valley range from about 400 to 600 m.

The Sula Plain is an extensive north-south structural depression opening into the Gulf of Honduras and lying between the Sierra de Omoa on the west and the Cordillera Mico Quemado and Montaña El Tiburón on the east. The subhumid portion of the lower valley lies at elevations from below 100 m to about 200 m and represents the alluvial flood plain of the rivers Chamelecón and Ulúa. Together, these rivers drain most of the western and west-central portion of Honduras. The Río Chamelecón arises in the western highlands and drains the extreme western portion of Honduras. Subhumid conditions are found in the valley of this river to about 500 m (area 12). The Río Ulúa is an important Caribbean drainage river in Honduras, which, with its various tributaries, drains a large portion of western Honduras. These tributaries include the rivers Higuito, Grande de Otoro, Jicatuyo, Humuya, and Sulaco.

CARIBBEAN COASTAL AREA

The extensive Caribbean coastal plain encompasses one area of interest in this paper. The Yucatan Peninsula is a low-lying limestone platform jutting out from the eastern coastline of Middle America between the Gulf of Mexico and the Caribbean Sea. The outer end of the peninsula, north of the Sierrita de Ticul, is a mainly flat, karstic surface, with no surface streams. Instead, the surface is pockmarked with numerous sinks or *cenotes*, which, when large and deep enough, provide mesic relief from the dry, hot conditions on the surface. South of the Sierrita de Ticul, the surface of the peninsula becomes hilly and surface streams are present. The highest elevation of the peninsula is 350 m in eastern Campeche (West, 1964). The peninsula extends southward into the area of Guatemala known as the Petén and is delineated on the south by the east-west anticlinal ridges south of Lago de Petén Itzá and the Maya Mountains in Belize. Only the subhumid outer portion (area 2) of the peninsula is considered in the present analysis.

Areas 1, 2, 6, 7, 8, 12, 13, 14, 15, and 16 are typified by lowland climates and vegetation, 4 and 9 by premontane conditions, and 3, 5, 10, and 11 by lowland to premontane conditions.

Climate

The climate of the Middle American subhumid forest areas is characterized by high mean annual temperatures (24°C or more at elevations up to ± 600 m and 21°C or more at elevations of ± 1000 m) and a long dry season (November through April), during which little or no precipitation falls each month. Hence, comparatively low relative humidities prevail during this period, which are enhanced by drying winds and the paucity of cloud cover. Savage (1975) and National Academy of Sciences (1982) gave 500 m elevation as the boundary for the biotemperature of 24°C or more, although the latter noted (p. 27) "... the mean annual isotherm of 24°C may occur locally at an elevation as great as 800 m" Temperature data for three stations in subhumid forests at 536, 580, and 613 m have mean annual temperatures of 24.4 , 24.5 , and 25.1°C , respectively (Table 1); therefore, a boundary of around 600 m appears to obtain for the 24°C isotherm in the subhumid areas of Middle America.

FACTORS DETERMINING TEMPERATURE

The relative invariability of mean monthly temperatures in the subhumid forests of the areas studied (Table 1) is due to their latitudinal position, lying as they do within the tropics. The difference between the warmest months (usually May, occasionally April or June) and the coldest months (usually January, occasionally other winter months) in these areas ranges from as low as 2.7°C to as high as 7.1°C ($x = 4.4^{\circ}\text{C}$). Our data on temperature is limited for some areas, most importantly for the Rio Negro Valley. We give data for Salamá, which lies in a higher basin on a tributary of the Río Negro than areas within the Rio Negro Valley proper (e.g., Sacapulas) which would be expected to have a higher mean annual temperature.

Surface air temperature in the tropics is largely correlated with altitude. The normal lapse rate or vertical temperature gradient is 0.65°C per 100 m (Koeppé and De Long, 1958), and this roughly approximates the decrease in air temperature in the areas studied (Table 1).

FACTORS DETERMINING PRECIPITATION

As pointed out by Portig (1965:68–69), "since temperature and winds are less variable in tropical countries than in higher latitudes, precipitation is by far the most important meteorological element." The majority of the precipitation that falls on the areas under consideration results from the northeastern trade winds, bringing warm, moisture-laden

air from the Caribbean Sea and the Gulf of Mexico. During the summer months, the thermal equator migrates northward forcing the northeast trade winds to rise, where they cool and become unstable, releasing their moisture and bringing on the summer rainy season (Table 2). During the winter, when the thermal equator moves southward, Mexico and most of Central America are affected by subtropical calms or masses of descending air, which are dry and stable, and, therefore, incapable of condensation or precipitation. This brings on the typical dry season (Table 2). The descending air counteracts the trade winds, which at that time become stable and incapable of producing much precipitation except along steep, windward slopes where there are ascending winds (Vivó Escoto, 1964). In discussing this climatic regime, Carr (1950:575) pointed out that it "... is the most fundamental climatic factor operating in the region, and it may possibly constitute the single most effective agent in determining the biota."

As the warm, moisture-laden winds sweeping in from the Caribbean reach land on the Caribbean versant, much of their precipitation load is dropped there. As the winds continue to move overland toward the Pacific coast, progressively less precipitation falls, accounting for the drier climatic aspect of the majority of the Pacific coastal region, extending from the Plains of Tehuantepec to northwestern Costa Rica. Of additional importance in producing precipitation along the Pacific coast are the deflected southwestern trade winds that bring in moisture-laden air during the rainy season, especially during the months of September and October. For example, in Choluteca, on the southern coast of Honduras, the rainy months of May through October produce 1844 mm of precipitation or 94 per cent of the total annual rainfall. The distribution of rainfall during the rainy season is uneven, however (Table 2). June is a relatively rainy month during the early part of the rainy season, presumably an effect of the rising northeastern trade winds, but September and October are also relatively rainy months, an effect created by the southwestern trade winds (Table 2). These three months experience a total precipitation of 1165 mm, 63 per cent of the total for the rainy season and 60 per cent of the total annual rainfall.

The amount of rainfall, therefore, is higher on the Pacific coast of Honduras than in the interior subhumid valleys, but is far less than the amount received on the Caribbean coast (Table 2). Choluteca, on the Pacific coast has a total annual rainfall of 1954 mm, whereas Comayagua, in the subhumid interior Comayagua Valley, has only 1035 mm, and La Ceiba, on the Caribbean coast, receives 2617 mm. The same pattern holds for comparable areas in Guatemala (Wernstedt, 1972), except that the high

TABLE 1. Temperature variability at selected subhumid forest stations in Middle America. Abbreviations in headings: MMT = mean monthly temperature, MAT = mean annual temperature. Abbreviations in parenthesis following each area are used in subsequent tables.

Station	Area	Elevation (m)	Maximum MMT °C	Month	MAT °C	Minimum MMT °C	Month	Source
Tehuantepec	Plains of Tehuantepec (TEH)	38	28.9	April	27.0	25.8	February	Sapper (1932)
Mérida	Yucatan Peninsula (YUC)	22	28.0	May	25.9	22.9	January	Wernstedt (1972)
Tuxtla Gutiérrez	Central Depression of Chiapas (CDC)	536	27.2	May	24.4	20.7	December	Wernstedt (1972)
Salamá	Rio Negro Valley (RNV)	920	25.3	May	22.6	19.9	January	Sapper (1932)
Zacapa	Motagua Valley (MV)	180	30.3	May	27.4	24.5	December	Wernstedt (1972)
San José	Pacific coast of Guatemala (PG)	2	28.7	May	27.6	25.8	January	Wernstedt (1972)
San Miguel	Pacific coast of El Salvador (PES)	100	28.7	April	26.8	25.1	October	Wernstedt (1972)
Choluteca	Pacific coast of Honduras (PH)	45	30.2	April	28.4	26.9	October	Wernstedt (1972)
Tegucigalpa	Choluteca Valley (CHV)	930	23.5	May	21.7	19.5	January	Wernstedt (1972)
Comayagua	Comayagua Valley (COV)	580	26.5	May	24.5	21.6	January	Wernstedt (1972)
La Gloria	Otoro Valley (OV)	613	27.3	April+ May	25.1	23.0	January+ December	Cruz (in litt.)
San Pedro Sula	Sula Plain (SP)	100	27.9	May+ June	26.0	23.2	January	Wernstedt (1972)
Coyoles	Aguan Valley (AV)	230	27.4	June	24.9	20.3	January	Carr (1950)
Catacamas	Guayape-Guayambre Valley (GGV)	500	26.3	May	24.4	22.1	January	Wernstedt (1972)
Managua	Pacific coast of Nicaragua (PN)	61	29.4	May	27.3	26.1	December	Wernstedt (1972)
Liberia	Pacific coast of Costa Rica (PCR)	44	29.2	April	27.4	26.5	October	Wernstedt (1972)

TABLE 2. Mean monthly and total precipitation values for selected subhumid forest stations in Middle America. See Table 1 for additional characterizations of stations.

Station	J	F	M	A	M	J	J	A	S	O	N	D	Total	Source
Tehuantepec	1.0	47.0	6.0	1.0	24.0	104.0	112.0	51.0	34.0	60.0	0.0	0.0	440.0	Sapper (1932)
Mérida	30.7	16.3	19.3	26.4	81.3	150.6	141.5	129.0	154.2	102.6	31.5	29.7	913.1	Wernstedt (1972)
Tuxtla Gutiérrez	0.3	0.8	1.0	5.6	75.4	235.5	175.0	155.4	200.9	81.3	4.1	6.4	941.6	"
Salamá	0.0	0.0	12.0	48.0	80.0	233.0	102.0	81.0	79.0	92.0	34.0	4.0	764.0	Sapper (1932)
Zacapa	0.0	0.0	2.0	3.0	41.9	116.1	82.0	58.9	105.9	55.1	5.1	1.0	471.0	Wernstedt (1972)
San José	0.0	1.0	9.9	38.1	112.0	252.0	247.9	223.0	274.1	277.1	21.1	1.0	1457.1	"
San Miguel	1.0	0.0	4.1	23.1	216.9	297.9	244.1	262.9	371.1	296.9	41.9	8.1	1768.0	"
Choluteca	0.0	3.1	11.9	48.0	270.0	402.1	194.1	214.9	418.1	344.9	40.9	6.1	1954.1	"
Tegucigalpa	10.9	5.1	8.9	29.0	151.9	164.1	86.4	95.0	182.1	133.1	39.1	13.0	918.6	"
Comayagua	14.0	8.9	7.1	35.1	113.0	192.0	136.9	166.9	142.0	151.9	43.9	23.1	1034.8	"
La Gloria	8.9	5.9	4.9	34.7	130.0	175.6	147.6	158.5	214.7	110.3	27.6	13.7	1032.4	Cruz (in litt.)
San Pedro Sula	71.9	52.1	51.1	36.1	91.9	159.0	153.9	117.1	191.0	179.1	144.0	119.9	1367.1	Wernstedt (1972)
Coyoles	53.1	31.0	16.0	20.1	58.9	134.1	98.0	72.9	115.0	125.0	106.9	81.0	912.0	"
Catacamas	46.0	23.1	15.0	33.0	122.9	230.1	227.1	162.1	180.1	169.9	74.9	40.9	1325.1	"
Managua	3.0	1.0	3.0	10.9	147.0	211.0	135.9	110.0	215.9	292.1	43.9	9.9	1183.6	"
Liberia	1.8	0.3	2.5	8.6	244.6	272.8	162.3	158.8	416.3	376.9	115.1	15.7	1775.7	"

mountains of the Pacific versant of Chiapas, Mexico, and southwestern Guatemala create a barrier to the movement of moisture-laden sea breezes moving in from the west-southwest, producing atypically wet conditions on the coastal plain lying adjacent to the windward side of these mountains.

Surface configuration is important in creating local variations in rainfall, and the complicated pattern of mountains in the region under study produces an equally complicated pattern of humid and subhumid areas. The windward sides of the mountains are relatively humid, the leeward sides relatively subhumid. Where low-lying valleys sit to the leeward of high mountains, the valleys receive relatively little rainfall. Most of the rainfall is deposited on the windward side of these mountains. This is the rainshadow effect. In addition, radiation of heat from the ground during the daytime creates convectional air currents that flow up the mountain slopes surrounding the interior valleys against the barometric gradient, producing clouds and rainfall at higher elevations, leaving the lower elevations relatively dry. This is the mountain valley effect. Thus, the dry climatic conditions existing in the interior valleys of Honduras, Guatemala, and Chiapas, Mexico, are, in part, the result of a combination of the rain shadow and mountain valley effects.

Of additional, but minor, importance in rainfall pat-

terns are the westerlies that sweep across the United States and Canada during the dry season and become deflected southward into Mexico and Central America, bringing cool polar air that meets the warm northeasterlies, causing precipitation and strong northern winds. These are the so-called *nortes*.

Hurricanes develop in the Caribbean from August to October, occurring most often during September. The normal hurricane tracks pass to the north of the region under study (Vivó Escoto, 1964), but may occasionally strike the north coast of Honduras or the Yucatan Peninsula, unleashing relatively large amounts of rainfall in a short period of time. Hurricanes are infrequently recorded in the Pacific coastal areas under study and, in general, they have only a minor effect on the climate of these areas (Hubbs and Roden, 1964; Meyer, 1969).

The low, flat nature of the Yucatan Peninsula produces a climatic regime, the causative factors of which are somewhat at variance with the areas discussed above. According to Vivó Escoto (1964:201), "the northern part of the . . . Yucatan Peninsula . . . receives only moderate rainfall, with less than 1000 mm per year, for there the trade winds are not forced to rise abruptly." On the other hand, the pattern of rainfall in the Yucatan Peninsula is not uniform. The higher temperature and lower pressure regime inland produces more intense convection and con-

sequent greater rainfall than is the case along the coast. In addition, the wind velocity is greater along the coast, which tends to break up convection there (Page, 1933).

Those interior valleys that are long and narrow (Aguan, Motagua, and Central Depression of Chiapas), and lie in the path of the prevailing winds, receive more moisture in the lower portions of the valley and less in the upper portions. Stuart (1954a:9) indicated that Tuxtla Gutiérrez, in the lower portion of the Central Depression of Chiapas, "... receives almost 900 mm of rainfall annually" whereas at Motozintla, farther up the valley, the annual rainfall "... amounts to no more than 650 mm." The same situation exists in the Motagua Valley. Stuart (1954a) stated that annual rainfall in the middle Motagua Valley does not exceed 600 mm. Other data support this statement. Annual rainfall at Puerto Barrios, at the extreme lower end of the valley, averages 3075 mm, whereas that of Zacapa, in the middle portion of the valley, receives only 471 mm (Wernstedt, 1972). The pattern is the same in the Aguan Valley (pers. observ.), but we do not have the rainfall data for any localities in the lower end of the valley. However, the annual rainfall at Trujillo, just outside the mouth of the Aguan Valley, is 2716 mm, whereas, that at Coyoles, in the middle of the valley, is only 912 mm annually (Wernstedt, 1972).

FACTORS DETERMINING RELATIVE HUMIDITY

The degree of relative humidity (the actual amount of moisture in the air compared to the maximal possible amount at a given temperature) is dependent upon a large number of factors, including the following: (1) temperature regime; (2) amount of precipitation; (3) amount of cloud cover; (4) degree of exposure to the winds; (5) edaphic conditions; (6) amount of vegetative cover; and (7) microhabitat variation (exposed vs. undercover or underground). Very little data exist on variation in relative humidity in the region under study. Our limited data on variation in relative humidity for four stations in subhumid forest areas in Honduras (Table 3) shows that usually the lowest mean monthly values for relative humidity occur in March or April, at the end of the dry season, and the highest usually occur in September and October, during the latter months of the rainy season. This pattern does not apply well to San Pedro Sula, probably because of its proximity to the ocean and its vanguard position relative to the prevailing winds. Also, within a given environment and at a given time during the year, relative humidity values can vary markedly during a 24-hour period and from one microhabitat to another (Janzen, 1973a, 1973b).

TABLE 3. Relative humidity variability at selected subhumid forest stations in Honduras (Data from 1967 Almanaque Hondureño). See Table 1 for additional characterizations of stations.

Station	Elevation (m)	Mean Annual Temp. °C	Mean Annual Precip. (mm)	Mean Relative Humidity												Mean Annual Value
				J	F	M	A	M	J	J	A	S	O	N	D	
Choluteca	45	28.4	1954.1	43	42	39	42	53	71	65	68	75	68	61	48	56
Tegucigalpa	930	21.7	918.6	73	67	62	61	68	78	76	74	78	80	78	76	73
San Pedro Sula	100	26.0	1367.1	79	75	72	70	73	76	79	76	79	83	83	85	78
Catacamas	500	24.4	1325.1	76	70	63	62	67	78	81	80	79	81	81	78	75

Vegetation

The character of the vegetation in Middle America (as is the case all over Latin America) is changing rapidly under the pressure of man. These trends, however, have had a long history. The areas supporting subhumid forest have been especially altered since the arrival of the Spaniards in the Western Hemisphere (Janzen, 1988; Johannessen, 1963). The long-term use of the subhumid forest lands by man since the time of the Spanish occupation for the raising of cattle has had marked and long-lasting effects on the vegetation of the areas we are studying herein. This fact makes it difficult to categorize the natural vegetation of these areas.

Subhumid forest areas have in common the climatic features of relatively high mean annual temperature, low mean annual rainfall, and a pronounced and prolonged dry season. The soils of the interior valleys usually develop from a parent material of alluvium or basalt and consist of a sandy, moderately fertile loam to sterile clay mixed with rocky debris. These soils are sticky when wet and are hard-baked during the dry season. If the underlying soils are pervious, these soils support xeric vegetation or deciduous forest, but when an impervious dry pan is present, the area supports short-grass savannah (Carr, 1950; Johannessen, 1963; Monroe, 1968). As pointed out by Monroe (1968:16), the "soils of the Pacific coastal plains are, for the most part, shallow, sandy, and infertile. They tend to become extremely wet and marshy during the rainy season but dry out and crack deeply during the dry season."

Johannessen (1963:109), in his work on the interior valleys of Honduras, pointed out that "substantial parts . . . were covered by savannas at the time of Spanish contact. Extensive changes in the plants of the savanna association occurred with the great increase in the number of trees and shrubs, after the Spaniards introduced their livestock on these grasslands." He suggested that long dry spells and overgrazing by cattle reduced grass cover and allowed for invasion by xeric-adapted trees and shrubs, whereas prior to the introduction of cattle into Honduras by the Spaniards, luxuriant grass growth existed, and invasion of wood vegetation was forestalled by annual fires, which killed off the seedlings of such plants, but allowed for the renewal of the grasslands. Johannessen (1963:111) stated that "local inhabitants report[ed] a substantial decrease in the area of open grass savanna and a corresponding increase in the thorn-scrub and deciduous forest within the past hundred years." What the herpetofauna of these savannas was before the Spanish conquest is now, of course, difficult to know. However, such population shifts as may have occurred might still be determined by studying in detail the herpetofaunas of such savannas as still remain (e.g., the Lepaguare Valley in the Department of

Olancho), and that of areas that have been invaded by thorn-scrub vegetation (i.e., almost everywhere else in the subhumid forest areas).

It is questionable, however, whether the amphibians and reptiles make a distinction between habitats on the basis of their respective plant species composition (Duellman, 1966). In our field experience, the environmental factors that are most important in determining micropatterns of distribution are (1) annual temperature regime; (2) annual patterns of rainfall; (3) relative humidity; (4) percentage of canopy cover; (5) character of the soil; (6) amount of leaf litter; (7) structural diversity of the vegetation; (8) number and stability of hiding places; and (9) availability of water for reproduction (in anurans).

VEGETATION OF SUBHUMID FOREST AREAS IN MIDDLE AMERICA

In an effort to capitalize on the predictability and ease of use of the Holdridge (1967) system of vegetational classification, but not to become bogged down in its complexities, especially as they have come to be more recently manifested (Holdridge, 1975), we have adopted the use of the simplified system of classification based on the Holdridge system developed by Savage (1975). Savage's (1975:298) modification ". . . consists of grouping series of [Holdridge's] bioclimate into more inclusive divisions." The vegetational formations in Savage's modified system of interest to us are Lowland Thorn Woodland, Lowland Semiarid Forest, Lowland Deciduous Forest, and Premontane Deciduous Forest. We introduce one further modification of the system, namely, to broaden the Lowland altitudinal zone at its upper extreme to about 600 m in subhumid zones, for the reasons given in the section on climate.

The Lowland Thorn Woodland formation (Tropical Thorn Woodland formation of Holdridge, 1967) is characterized by occurrence at elevations ranging from sea level to about 600 m, a mean annual temperature greater than 24°C (around 27°C for the areas in Middle America that fall within this formation), and a mean annual precipitation between 250 and 500 mm. This formation is found in two areas, the Plains of Tehuantepec and the upper and middle Motagua Valley. The relatively high temperatures and low rainfall combine to create a severe climatic regime. Duellman (1960:32) stated that on the Plains of Tehuantepec "Most of the trees are deciduous, thorny, and short. During the dry season the landscape presents a barren appearance, but shortly after the first summer rains dense green foilage appears Between Juchitán and La

Ventosa few trees are more than two meters high In many areas the trees and bushes form an almost impenetrable tangle, whereas on especially rocky soils or on slopes those plants are more widely spaced." Trees of the genera *Acacia*, *Caesalpinia*, *Celtis*, *Cordia*, *Crescentia*, *Jatropha*, and *Prosopis* are widespread and abundant on these plains. Giant columnar cacti and the "tree" prickly pear are also much in evidence. Low-lying hills on slopes arising from the plains are characterized as having a "dense scrub forest" (Duellman, 1960:35). The thorn woodland of the isthmus gives way in Chiapas to more mesic types of vegetation. Breedlove (1973:151) noted that the Pacific coastal plain of Chiapas is ". . . flat and relatively dry in the north[west] and hilly and wet in the south[southeast]," with "evergreen and semi-evergreen seasonal forests . . ." in the latter region. The Motagua River Valley has been described by Stuart (1954a) and Campbell and Vannini (1988). Stuart (1954a:11) noted that "perhaps the most striking feature of the cover is the abundance of the large, *Cereus*-like cacti Rocky knolls support rank growths of spiny desert shrubs and cacti; more level plains may resemble short-grass steppe lands with scattered low trees of the acacia type or extensive thickets of mesquite . . . ; intermittent stream courses are lined with stunted deciduous trees, shrubs, and dense stands of cacti; whereas along permanent water courses a narrow band of gallery forest may prevail." Campbell and Vannini (1988:463) described the vegetational assemblage of the middle portion of the Motagua Valley as containing ". . . *Acacia*, *Busera*, *Mimosa*, spiny grasses, thorn scrub, many cacti (primarily *Pliocereus*, *Cereus*, *Opuntia*, and *Melocactus*), and agaves." The climatic features of one station in each area (Tehuantepec and Zacapa, respectively) are described in the previous section, as is the case for the other areas described below.

The Lowland Semiarid Forest formation (Tropical Arid Forest formation of Holdridge, 1967) is found between sea level and 600 m, has high mean annual temperatures greater than 24°C and relatively low annual precipitation levels of between 500 and 1000 mm. The lower elevations of the Central Depression of Chiapas, the outer end of the Yucatan Peninsula, and the middle Aguan River Valley are three areas in Middle America that support this type of vegetation. Stuart (1954a:9–10) discussed the vegetation of the Central Depression of Chiapas, noting that ". . . much of the valley supports stands of low dry forest, patches of mesquitlike thickets, occasional stands of palms, and, along the water courses, gallery forest." Patches of savannah occur ". . . dotted with stunted trees, which may occur singly or in small groves . . ." Johnson (1990:270) also discussed the Central Depression of Chiapas and stated that ". . . at the time of [his] study, most of the region had been cleared for agriculture and contained short-tree savanna or thorn woodland." Duellman

(1965a:583–585), in discussing the outer end of the Yucatan Peninsula, described localities within the arc from Champotón through Felipe Carrillo Puerto to Puerto Juárez as covered with "dense scrub forest." South and east of that arc there is a transition to what Duellman called "quasi-rainforest." The floor of the middle portion of the Aguan River Valley was briefly described by Yuncker (1939, 1940). He remarked (1939:137) that "an outstanding feature of the vegetation is the occurrence of two species of tree-like cacti often 20 or more feet in height." One is the prickly pear *Opuntia hondurensis* and the other is the columnar *Cereus junckeri*. He also noted the great burden of epiphytic plants, such as parasitic mistletoes, ferns, aroids, bromeliads, orchids, peperomias, and cacti, borne by the trees of the area. Large, ground-dwelling bromeliads and *Agave* are also common. Trees of the genera *Acacia*, *Busera*, *Celtis*, *Clusia*, *Coccoloba*, *Cupania*, *Erythrina*, and *Pithecolobium* are characteristic.

Occurring within the same elevational range as the Lowland Semiarid Forest formation and experiencing a similar temperature regime (mean annual temperature above 24°C), the Lowland Deciduous Forest formation (Tropical Dry Forest formation of Holdridge, 1967) is distinguished by a greater amount of rainfall (between 1000 and 2000 mm annually). The subhumid forest areas characterized by this formation are the Pacific coastal region of southeastern Guatemala and the terrain below 600 m extending inland to a little north of Lago de Güija, the areas of El Salvador below 600 m, the Pacific coastal area of Honduras, the Sula Plain, the Comayagua Valley below 600 m, the Otoro Valley below 600 m, the Pacific coast of Nicaragua, and the Pacific coast of northwestern Costa Rica. Land (1970:4) described the vegetation of the Pacific lowlands of Guatemala as "dry and scrubby near the coast," with good stands of gallery forest occurring near the foothills. Stuart (1943:26) noted that the ". . . vegetation was probably mixed savanna and semideciduous forest, although now it is intensively cultivated and grazed and little virgin country remains." Much of the same description can be applied to the lowlands of El Salvador (Dickey and van Rossem, 1938). Descriptions of subhumid forest areas in Honduras, western Nicaragua, and northwestern Costa Rica (Meyer, 1969; Taylor, 1963; and Scott, 1969, respectively) confirm the relative uniform physiognomy of the vegetation in these areas.

The Premontane Deciduous Forest formation (Subtropical Dry Forest formation of Holdridge, 1967) is a higher elevation counterpart of the Lowland Semiarid Forest formation, occurring between $\pm$ 600 and 1250 m in elevation, and is further characterized by mean annual temperatures of between 18 and 24°C and mean annual precipitation between 500 and 1000 mm. Two subhumid forest areas, the middle and upper Choluteca River Valley in Honduras and the Rio Negro Valley in Guatemala sup-

port this formation, as well as the upper reaches of the Central Depression of Chiapas and the upper edges of the Otoro and Comayagua valleys. Stuart (1954a:10) described the upper elevations of the Central Depression of Chiapas as having "... a vegetation cover that is almost desertic in aspect. At Canibal the valley floor was without a continuous sod cover Dense thickets of mesquite and other xeric shrubs and an abundance of *Cereus*-like cacti and prickly pears form a cover known as *espinal* Even gallery forest was lacking along the water courses." Stuart (1954a:10) also stated that "the main slopes of the depression and higher ridges within the valley support, in the main, dry forests and brushlands. At higher levels (above about 1000 m) oaks make an appearance" The vegetation of neither the Choluteca Valley nor the Rio Negro Valley has been well-described and, furthermore, has been much modified at the hands of man. Schmidt and Stuart (1941:236) indicated that in areas of the Salama Basin (cut by the Río Salamá, a tributary of the Río Negro) with "... poorer soils where the vegetation is probably more or less virgin, short grass predominates, while cactus of the prickly-pear variety is common, and low scrubby

bushes and the nance tree are all indications of aridity." Within the valley of the Río Negro itself, the vegetation is similar to that seen in the upper reaches of the Central Depression of Chiapas in the valley of the Río Cuilco. Meyer (1969:77 and 80) mentioned that the area of the upper Choluteca River Valley around Tegucigalpa is often covered with vegetation consisting of "agaves, thorny shrubs and scattered close-cropped grasses." He also mentioned the occurrence of this type of vegetation around the edges of the Comayagua and Otoro valleys.

In summary, the type of vegetation found in the sub-humid forest areas of Middle America is characterized by the presence of xeric-adapted, largely deciduous or semi-deciduous, often thorny plants. Ground cover, if present, is of short grasses occasionally relieved by terrestrial bromeliads and agaves. Spacing of the dominant trees varies widely, depending upon climatic and edaphic factors. Austere conditions exist during the prolonged dry season. Humus is generally lacking or poorly developed and leaf litter is limited. Trees of the upper story are short, 10 to 25 m in height. Broad-leaved trees are found along the water courses as components of gallery forest.

Composition of the Herpetofauna

The herpetofauna of the subhumid lowland forests of Middle America from the Plains of Tehuantepec and the Yucatan Peninsula to the Nicoya Peninsula of northwestern Costa Rica includes 212 species (Table 4). These species include 2 caecilians (0.9% of the total number of species), 5 salamanders (2.4%), 37 anurans (17.5%), 11 turtles (5.2%), 3 crocodilians (1.4%), 59 lizards (27.8%), and 95 snakes (44.8%). These figures (per cent composition) are similar to those for the native species of the sub-humid lowland forests (below 1000 m) of the Mexican states of Sinaloa and Michoacán and northern South America (Table 5).

The data in Table 4 also illustrate the herpetofaunal composition of each of the 16 subhumid areas under consideration. Within these areas, the total number of known species ranges from 23 to 93. The 16 areas are listed below in rank order according to the species number.

Plains of Tehuantepec (93)
Sula Plain (90)
Outer Yucatan Peninsula (89)
Central Depression of Chiapas (87)
Pacific coast of northwestern Costa Rica (84)
Pacific coast of Nicaragua (80)
Pacific coast of El Salvador (79)
Pacific coast of Guatemala (68)
Middle and upper Choluteca Valley (55)
Middle and upper Motagua Valley (52)
Guayape-Guayambre Valley (50)
Pacific coast of Honduras (49)
Middle Aguan Valley (37)
Upper Rio Negro Valley (37)
Comayagua Valley (36)
Otoro Valley (23)

TABLE 4. Distribution of herpetofauna in subhumid forest areas in Middle America. See Table 1 for an explanation of area abbreviations.

Species	Subhumid Forest Areas															
	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
<i>Dermophis mexicanus</i>	X		X			X	X	X				X			X	
<i>Gymnopsis multiplicata</i>												X		X		X
<i>Bolitoglossa mexicana</i>												X	X			
<i>Bolitoglossa striatula</i>															X	
<i>Bolitoglossa yucatana</i>		X														
<i>Oedipina stuarti</i>								X	X							
<i>Oedipina taylori</i>					X	X	X									
<i>Agalychnis callidryas</i>		X										X			X	
<i>Bufo canaliferus</i>	X		X			X	X									
<i>Bufo coccifer</i>	X		X	X			X	X	X					X	X	X
<i>Bufo luetkeni</i>				X	X	X	X	X	X	X	X			X	X	X
<i>Bufo marinus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Bufo marmoreus</i>	X		X													
<i>Bufo valliceps</i>		X	X	X	X					X	X	X	X	X		
<i>Eleutherodactylus bransfordi</i>																X
<i>Eleutherodactylus fitzingeri</i>															X	X
<i>Eleutherodactylus rhodopis</i>			X			X	X									
<i>Eleutherodactylus rugulosus</i>	X		X	X			X		X		X	X		X	X	X
<i>Eleutherodactylus yucatanensis</i>		X														
<i>Gastrophryne usta</i>	X		X			X	X									
<i>Hyla loquax</i>		X										X		X		
<i>Hyla microcephala</i>		X			X				X		X	X	X	X	X	X
<i>Hyla robertmertensi</i>	X		X			X	X									
<i>Hyla sumichrasti</i>	X		X													
<i>Hypopachus variolosus</i>		X	X	X	X	X	X		X	X	X	X	X	X	X	X
<i>Leptodactylus insularum</i>																X
<i>Leptodactylus labialis</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Leptodactylus melanonotus</i>	X	X	X	X	X	X	X	X	X	X				X	X	X
<i>Leptodactylus pentadactylus</i>															X	X
<i>Leptodactylus poecilochilus</i>																X
<i>Pachymedusa dacnicolor</i>	X															
<i>Phrynohyas venulosa</i>	X	X			X	X	X	X		X		X	X	X	X	X
<i>Physalaemus pustulosus</i>	X			X	X	X	X	X	X	X	X	X		X	X	X
<i>Rana berlandieri</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Rana maculata</i>				X					X							
<i>Rana vaillanti</i>	X		X									X	X	X	X	X
<i>Rhinophrynus dorsalis</i>	X	X	X			X	X					X			X	X

TABLE 4. (cont.)

[illegible]

TABLE 4. (cont.)

Species	Subhumid Forest Areas															
	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
<i>Eumeces managuae</i>								X							X	X
<i>Eumeces schwartzei</i>		X														
<i>Gerrhonotus liocephalus</i>			X													
<i>Gonatodes albogularis</i> ³						X	X	X	X					X	X	X
<i>Gymnophthalmus speciosus</i>	X		X	X	X	X	X	X	X		X		X	X	X	X
<i>Heloderma horridum</i>	X		X		X											
<i>Iguana iguana</i> ⁴	X		X		X	X	X	X	X	X		X			X	X
<i>Laemantus longipes</i>												X				
<i>Laemantus serratus</i>		X	X									X				
<i>Lepidophyma flavimaculatum</i>												X		X		
<i>Lepidophyma smithi</i>	X					X	X									
<i>Mabuya unimarginata</i>	X	X	X		X		X	X	X		X	X	X	X	X	X
<i>Norops biporcatus</i>															X	
<i>Norops cupreus</i>						X	X							X	X	X
<i>Norops cuprinus</i>	X															
<i>Norops isthmicus</i>	X															
<i>Norops laeviventris</i>			X													
<i>Norops lemurinus</i>		X				X	X					X	X			
<i>Norops pentaprion</i>		X													X	
<i>Norops rodriguezi</i>		X										X				
<i>Norops sericeus</i> ⁵	X	X	X			X	X	X	X	X	X	X	X	X	X	X
<i>Norops tropidonotus</i>		X							X			X	X	X		
<i>Phrynosoma asio</i>	X		X													
<i>Phyllodactylus muralis</i>	X															
<i>Phyllodactylus tuberculosus</i>	X		X	X	X	X	X	X	X						X	X
<i>Sceloporus acanthinus</i>				X			X									
<i>Sceloporus carinatus</i>			X	X												
<i>Sceloporus chrysostictus</i>		X														
<i>Sceloporus cozumelae</i>		X														
<i>Sceloporus edwardtaylori</i>	X															
<i>Sceloporus lundelli</i>		X														
<i>Sceloporus melanorhinus</i>	X		X													
<i>Sceloporus serrifer</i> ⁶		X	X	X												
<i>Sceloporus siniferus</i>	X		X			X										
<i>Sceloporus squamosus</i>					X	X	X	X	X	X		X			X	X
<i>Sceloporus variabilis</i>	X		X	X	X	X	X	X	X			X	X	X	X	X
<i>Sphaerodactylus dunni</i>												X				

TABLE 4. (cont.)

Species	Subhumid Forest Areas															
	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
<i>Sphaerodactylus glaucus</i>	X	X	X													
<i>Sphaerodactylus millepunctatus</i>					X				X				X	X	X	X
<i>Sphenomorphus assatus</i>	X		X				X									
<i>Sphenomorphus cherriei</i>		X										X	X	X		X
<i>Thecadactylus rapicauda</i>		X										X	X			
<i>Urosaurus bicarinatus</i>	X		X													
<i>Adelphicos quadrivirgatus</i>			X													
<i>Agkistrodon bilineatus</i>	X	X	X	X		X	X	X							X	X
<i>Atropoides nummifer</i>												X				
<i>Boa constrictor</i>	X	X	X	X	X	X	X	X	X	X		X		X	X	X
<i>Bothrops asper</i>		X										X				
<i>Clelia clelia</i>												X				X
<i>Clelia scytalina</i>			X													
<i>Coluber constrictor</i>			X		X											
<i>Coniophanes bipunctatus</i>		X													X	
<i>Coniophanes fissidens</i>	X					X	X			X		X	X	X		
<i>Coniophanes imperialis</i>	X	X	X									X				
<i>Coniophanes meridianus</i>		X														
<i>Coniophanes piceivittis</i>	X	X	X				X		X			X			X	X
<i>Coniophanes quinquevittatus</i>		X														
<i>Conophis lineatus</i>		X	X	X	X	X	X	X	X	X		X	X		X	X
<i>Conophis vittatus</i>	X		X													
<i>Crisantophis nevermanni</i>						X	X	X							X	X
<i>Crotalus durissus</i> ⁷	X	X	X	X	X	X	X	X	X	X		X			X	X
<i>Dipsas brevifacies</i>		X														
<i>Dryadophis melanolomus</i>	X	X	X				X					X	X			
<i>Drymarchon corais</i>	X	X	X	X	X	X	X		X		X			X	X	X
<i>Drymobius margaritiferus</i> ⁸	X	X	X	X	X	X	X	X	X			X	X	X	X	X
<i>Elaphe flavirufa</i>		X										X				
<i>Enulius flavitorques</i>	X		X			X	X	X	X	X		X			X	X
<i>Epicrates cenchria</i>																X
<i>Erythrolamprus bizonus</i>																X
<i>Ficimia publia</i>	X	X	X									X				
<i>Geagras redimitus</i>	X															
<i>Hydromorphus concolor</i>												X				
<i>Imantodes cenchoa</i>												X	X	X		
<i>Imantodes gemmistratus</i>	X	X	X		X	X	X	X							X	X

TABLE 4. (cont.).

Species	Subhumid Forest Areas															
	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
<i>Imantodes inornatus</i>												X				
<i>Imantodes tenuissimus</i>		X														
<i>Lampropeltis triangulum</i>	X	X	X	X	X	X	X		X			X		X	X	X
<i>Leptodeira annulata</i>	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Leptodeira frenata</i>		X														
<i>Leptodeira nigrofasciata</i>	X		X		X	X	X	X	X			X			X	X
<i>Leptodeira septentrionalis</i>		X	X									X				
<i>Leptodrymas pulcherrimus</i>					X	X			X						X	X
<i>Leptophis ahaetulla</i>									X			X		X		
<i>Leptophis diplotropis</i>	X		X													
<i>Leptophis mexicanus</i>		X										X	X	X		X
<i>Leptotyphlops goudoti</i>	X	X	X	X		X	X	X		X	X	X			X	X
<i>Leptotyphlops nasalis</i>															X	
<i>Loxocemus bicolor</i>	X		X		X	X	X	X		X		X			X	X
<i>Manolepis putnami</i>	X															
<i>Masticophis mentovarius</i>	X	X	X	X	X	X	X	X	X	X		X		X	X	X
<i>Micrurus bogerti</i>	X															
<i>Micrurus browni</i>			X													
<i>Micrurus diastema</i>		X										X				
<i>Micrurus ephippifer</i>	X															
<i>Micrurus latifasciatus</i>	X															
<i>Micrurus multifasciatus</i>																X
<i>Micrurus nigrocinctus</i>					X	X	X	X	X	X		X			X	X
<i>Ninia diademata</i>												X				
<i>Ninia sebae</i>		X							X			X	X	X	X	X
<i>Oxybelis aeneus</i>	X	X	X	X	X	X	X	X	X	X		X			X	X
<i>Oxybelis fulgidus</i>	X	X	X			X						X			X	X
<i>Oxyrhopus petola</i>							X									
<i>Porthidium dunni</i>	X															
<i>Porthidium nasutum</i>												X				
<i>Porthidium ophryomegas</i>					X	X	X	X	X	X			X	X	X	X
<i>Porthidium yucatanicum</i>		X														
<i>Pseustes poecilonotus</i>		X										X				
<i>Salvadora lemniscata</i>	X		X													
<i>Scaphiodontophis annulatus</i>		X	X				X					X				
<i>Scolecophis atrocinctus</i>							X		X						X	X
<i>Senticolis triaspis</i>	X	X	X		X	X	X		X	X		X			X	X

TABLE 4. (cont.)

Species	Subhumid Forest Areas															
	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
<i>Sibon anthracops</i>					X		X						X		X	X
<i>Sibon carri</i>					X		X	X	X							
<i>Sibon fasciata</i>	X	X	X													
<i>Sibon nebulata</i>		X					X					X				
<i>Sibon sanniola</i>		X														
<i>Sibon sartorii</i>	X	X				X	X					X			X	
<i>Spilotes pullatus</i>		X	X			X	X		X			X		X	X	X
<i>Stenorrhina degenhardti</i>												X				
<i>Stenorrhina freminvillei</i>	X	X	X	X		X	X	X	X	X		X			X	X
<i>Symphimus leucostomus</i>	X															
<i>Symphimus mayae</i>		X														
<i>Tantilla canula</i>		X														
<i>Tantilla cuniculator</i>		X														
<i>Tantilla melanocephala</i>					X	X	X	X	X					X	X	X
<i>Tantilla moesta</i>		X														
<i>Tantilla rubra</i>	X		X													
<i>Tantilla striata</i>	X															
<i>Tantilla taeniata</i>												X				
<i>Tantilla vermiformis</i>															X	X
<i>Thamnophis cyrtopsis</i>				X												
<i>Thamnophis marcianus</i>	X	X													X	
<i>Thamnophis proximus</i>	X	X	X				X	X							X	X
<i>Tretanorhinus nigroluteus</i>												X				
<i>Trimorphodon biscutatus</i>	X		X	X	X	X	X	X		X			X		X	X
<i>Typhlops microstomus</i>		X														
<i>Urotheca elapoides</i>		X										X				
<i>Xenodon rabdocephalus</i>			X									X				

¹ Sula Plain record based on captured, but not preserved individuals.² We are recognizing *Terrapene yucatana* as a species distinct from *T. carolina*, as suggested by Ward (1980).³ Guayape-Guayambre record based on sighting.⁴ Comayagua Valley record based on sighting.⁵ Otoro Valley record based on sighting.⁶ Includes *Sceloporus prezygus*.⁷ Comayagua Valley record based on live specimen seen in the Universidad Nacional Autónoma de Honduras.⁸ Pacific coast of Honduras record based on escaped individual and on another sighting.

TABLE 5. Comparisons of the number of species and per cent composition of ordinal groups of amphibians and reptiles from the subhumid forests (below 1000 m) of Middle America and selected Mexican and northern South American localities.

Group	Middle America	Sinaloa, Mexico ¹	Michoacán, Mexico ²	Northern South America ³
Caecilians	2 (0.9)	—	—	—
Salamanders	5 (2.4)	—	—	—
Anurans	37 (17.5)	28 (25.5)	23 (23.0)	42 (28.2)
Turtles	11 (5.2)	5 (4.5)	2 (2.0)	10 (6.7)
Crocodylians	3 (1.4)	1 (0.9)	1 (1.0)	4 (2.7)
Amphisbaenians	—	—	1 (1.0)	2 (1.3)
Lizards	59 (27.8)	25 (22.7)	32 (32.0)	35 (23.5)
Snakes	95 (44.8)	51 (46.4)	41 (41.0)	56 (37.6)
Total Species	212	110	100	149

¹ Information from Hardy and McDiarmid (1969) and McDiarmid et al. (1976)

² Information from Duellman (1965b) and Alvarez (1966)

³ Information from Rivero-Blanco and Dixon (1979)

Numerical Analysis

In order to determine the area relationships of the 16 areas under consideration, we used the *Coefficient of Biogeographic Resemblance* (CBR) algorithm (Duellman, 1990). We chose this formula for the reasons discussed by Duellman (1965b, 1990). The formula is

$$CBR = 2C/(N_1 + N_2),$$

where C is the number of species in common to two areas, N_1 is the number of species in the first area, and N_2 is the number of species in the second area.

The average value of the similarity matrix (Table 6) comparing the 212 species occurring in one or more of the 16 areas is 0.54. The 16 areas are listed below in rank order, according to their respective average value.

Pacific coast of El Salvador	0.62
Pacific coast of Guatemala	0.61
Middle and upper Choluteca Valley	0.61
Pacific coast of Nicaragua	0.61
Middle and upper Motagua Valley	0.59
Pacific coast of Honduras	0.59

Pacific coast of northwestern Costa Rica	0.57
Comayagua Valley	0.55
Guayape-Guayambre Valley	0.53
Upper Rio Negro Valley	0.52
Central Depression of Chiapas	0.51
Plains of Tehuantepec	0.49
Sula Plain	0.49
Middle Aguan Valley	0.46
Otoro Valley	0.44
Outer Yucatan Peninsula	0.40

Examination of this list indicates that the Pacific coastal areas from Guatemala to northwestern Costa Rica, plus the Choluteca and Motagua valleys, have relatively high average values. We interpret this to mean that these areas have relatively similar herpetofaunas. The subhumid lowlands are continuous from southeastern Guatemala to northwestern Costa Rica, as are subhumid forests from the upper portion of the Choluteca Valley to Pacific coastal Honduras (pers. observ.), and from the Motagua Valley through the lower elevations of the southeastern highlands of Guatemala to the Pacific lowlands of Guatemala and El

TABLE 6. Comparison of the herpetofaunas of the 16 subhumid forest areas. N = species at each site; N = species in common between two sites; *N* = Coefficients of Biogeographic Resemblance. See Table 1 for an explanation of area abbreviations.

	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
TEH	93	38	68	27	33	51	56	37	34	29	18	42	20	28	51	46
YUC	0.41	89	42	22	25	33	37	23	28	22	16	51	23	26	40	35
CDC	0.76	0.48	87	32	34	47	53	35	36	27	20	44	22	26	46	44
RNV	0.42	0.35	0.52	37	27	29	32	25	29	22	18	23	17	23	30	29
MV	0.46	0.35	0.49	0.61	52	42	43	35	40	29	19	34	25	31	44	42
PG	0.63	0.42	0.61	0.55	0.70	68	64	43	42	34	19	42	22	32	56	52
PES	0.65	0.44	0.64	0.55	0.66	0.87	79	47	47	35	21	46	25	34	61	58
PH	0.52	0.33	0.51	0.58	0.69	0.74	0.73	49	38	30	16	32	18	26	46	45
CHV	0.46	0.39	0.51	0.63	0.75	0.68	0.70	0.74	55	29	21	41	23	35	49	48
COV	0.45	0.35	0.44	0.60	0.66	0.65	0.61	0.71	0.64	36	17	30	18	21	34	33
OV	0.31	0.29	0.36	0.60	0.51	0.42	0.41	0.44	0.54	0.58	23	18	17	19	21	20
SP	0.46	0.57	0.50	0.36	0.48	0.53	0.54	0.46	0.57	0.48	0.32	90	30	40	48	47
AV	0.31	0.37	0.35	0.46	0.56	0.42	0.43	0.42	0.50	0.49	0.57	0.47	37	27	25	26
GGV	0.39	0.37	0.37	0.53	0.61	0.54	0.53	0.53	0.67	0.49	0.52	0.57	0.62	50	39	40
PN	0.59	0.47	0.55	0.51	0.67	0.76	0.77	0.71	0.73	0.59	0.41	0.56	0.43	0.60	80	69
PCR	0.52	0.40	0.51	0.48	0.62	0.68	0.71	0.68	0.69	0.55	0.37	0.54	0.43	0.60	0.84	84

Salvador (Stuart, 1954a, 1954b).

On the other hand, the outer Yucatan Peninsula, with its high number of species and its very low CBR value, has the most distinctive herpetofauna of the 16 areas. Distinctive herpetofaunas (with high numbers of species and low CBR values) also occur in the Sula Plain, the Plains of Tehuantepec, and the Central Depression of Chiapas. The remaining areas (Otoro, Aguan, Rio Negro, Guayape-Guayambre, and Comayagua valleys) all have relatively low numbers of species and low CBR values.

We constructed a network (Fig. 2) connecting the 16 subhumid areas at a level of significance (LS) of 0.55. We chose this value as the LS, because it is the most proximate number above the overall average value. Because of the cumbersome number of lines required to construct Figure 2, we combined Pacific coastal Guatemala with El Salvador and Pacific coastal Nicaragua with Costa Rica, thereby eliminating several lines from the figure. The areas combined are continuous with each other and have very high CBR values (0.87 for the former pair and 0.84 for the latter). Examination of Figure 2 indicates that the Pacific coastal lowlands from Guatemala to northwestern

Costa Rica are all interconnected by a CBR value of 0.71–0.77, supporting the similarity of their herpetofaunas as discussed above. Likewise, the two interior valleys with relatively high average values (Choluteca and Motagua) are each connected to one or more of these same Pacific coastal areas by a high CBR value of 0.70–0.74, while the Motagua–Choluteca CBR value is 0.75. These values indicate that the herpetofaunas of each of these two valleys are relatively similar to one another and to the Central American Pacific coastal lowlands as well. The Comayagua Valley, with an average value just above the overall value, also shows relatively high CBR values with Pacific coastal Honduras (0.71) and with the Motagua and Choluteca valleys (0.66 and 0.64, respectively). The only remaining CBR value of >0.70 is the one connecting the Plains of Tehuantepec with the Central Depression of Chiapas (0.76). Johnson (1990) has also demonstrated the similarity of the herpetofaunas of these two areas. The Plains of Tehuantepec and Central Depression of Chiapas, in turn, connect with the Pacific coastal lowlands of Guatemala and El Salvador with CBR values of 0.65 and 0.64, respectively. Otherwise, the Plains of Tehuantepec

FIG. 2. Coefficient of Biogeographic Resemblance network connecting the 16 subhumid areas at a level of significance of ≥ 0.55 . Pacific coastal Guatemala was combined with coastal El Salvador, as was Pacific coastal Nicaragua with Pacific coastal Costa Rica (see text). See Figure 1 for an explanation of the numbered areas.

and Central Depression of Chiapas have relatively distinctive herpetofaunas, only showing above-average CBR values with combined Pacific coastal Nicaragua and Costa Rica (0.59).

The Guayape-Guayambre Valley shows its two highest CBR values with the Choluteca (0.67) and Aguan (0.62) valleys, both of which are its two closest subhumid areas geographically. The Guayape-Guayambre Valley also has a higher CBR value with the Motagua Valley (0.61) than it does with any Pacific coastal area (0.60 with combined Nicaragua and Costa Rica). Likewise, the Rio Negro Valley has higher CBR values (0.60–0.63) with four other interior valleys (Choluteca, Motagua, Otoro, and Comayagua) than it does with any Pacific coastal area (0.58 with Honduras). The Aguan Valley shows significant CBR values with only the Guayape-Guayambre (0.62), Otoro (0.57), and Motagua (0.56) valleys and the Otoro Valley only with the Rio Negro (0.60), Comayagua (0.58), and Aguan (0.57) valleys. Thus the Guayape-Guayambre, Rio Negro, Aguan, and Otoro valleys, with their overall low CBR values, have their highest values with interior

valleys rather than Pacific coastal regions. Each of these interior valleys also have a relatively low number of species.

The outer Yucatan Peninsula shows a significant CBR value only with the Sula Plain (0.57), while the Sula Plain also connects via a significant value with only the value of 0.57 with the Guayape-Guayambre and Choluteca valleys and 0.56 with combined Pacific coastal Nicaragua and Costa Rica. Both the outer Yucatan Peninsula and Sula Plain have among the highest species numbers of the areas under consideration. The combination of high species numbers and few and low significant values indicates that these two areas support relatively distinctive herpetofaunas.

PATTERNS OF DISTRIBUTION

In an effort to further analyze the area relationships of the CBR algorithm, we placed each of the 212 species comprising the Middle American subhumid herpetofauna into one of three distributional categories. These categories,

their characterizations, and their memberships are outlined below. The number of areas of occurrence of each taxon arranged by these categories is indicated in parentheses.

1. ENDEMICS

Included here are 50 species that are limited to one or more (1 to 11) areas of the 16 subhumid areas listed in the previous section. Some of these species also occur marginally in more humid forests in the eastern portion and/or at the base of the Yucatan Peninsula and are indicated by an asterisk. Four species are included in this category, even though populations are known or thought to occur in areas outside the scope of this work. These species are *Cnemidophorus motaguae* (also occurs west of the Plains of Tehuantepec [Duellman and Zweifel, 1962]), *Phyllodactylus muralis* (a small isolated population also occurs in the mountains of southern Oaxaca, Mexico [Dixon, 1964]), *Micrurus bogerti* (also occurs in the coastal belt west of the Plains of Tehuantepec [Roze, 1982]), *Symphimus leucostomus* (a very questionable record for this species exists some 1045 km west-northwest of the Plains of Tehuantepec [Rossman and Schaefer, 1974]). The overall distributions of these first three species do not allow for their allocation to any of our other distributional categories. The species in this category are as follows: *Bolitoglossa yucatanica* (1), *Oedipina stuarti* (2), *O. taylori* (3), *Bufo canaliferus* (4), *B. luetkeni* (11), **Eleutherodactylus yucatanensis* (1), **Tripurion petasatus* (1), **Kinosternon creaseri* (1), *Staurotypus salvini* (3), **Terrapene yucatanica* (1), **Cnemidophorus angusticeps* (1), *C. motaguae* (8), *Ctenosaura defensor* (1), *C. palearis* (2), *C. quinquecarinata* (5), *Eumeces managuae* (3), **E. schwartzei* (1), *Norops cupreus* (5), *N. cuprinus* (1), *N. isthmicus* (1), *Phyllodactylus muralis* (1), *Sceloporus carinatus* (2), **S. chrysostictus* (1), *S. cozumelae* (1), *S. edwardtaylori* (1), **S. lundelli* (1), *S. squamosus* (9), **Coniophanes meridianus* (1), *Crisantophis nevermanni* (5), **Dipsas brevifacies* (1), *Geagras redimitus* (1), **Imantodes tenuissimus* (1), *Leptodrymus pulcherrimus* (5), *Leptotyphlops nasalis* (1), *Micrurus bogerti* (1), *Porthidium dunni* (1), *P. ophryomegas* (10), **P. yucatanicum* (1), *Scolecophis atrocinctus* (4), *Sibon anthracops* (5), *S. carri* (4), **S. sanniola* (1), *Symphimus leucostomus* (1), **S. mayae* (1), **Tantilla canula* (1), **T. cuniculator* (1), **T. moesta* (1), *T. striata* (1), *T. vermiformis* (2), *Typhlops microstomus* (1).

2. WIDESPREAD FORMS

Included in this category are 67 species that are widespread in subhumid forests of Middle America (3 to 16 areas) and also widespread in one or more adjacent vegetation zones. These species are as follows: *Dermophis mexicanus* (7), *Bufo coccifer* (9), *B. marinus* (16), *B. val-*

liceus (9), *Eleutherodactylus rugulosus* (11), *Gastrophryne usta* (4), *Hyla microcephala* (9), *Hypopachus variolosus* (14), *Leptodactylus labialis* (16), *L. melanonotus* (13), *Phrynosoma venulosa* (12), *Physalaemus pustulosus* (13), *Rana berlandieri* (16), *R. vaillanti* (7), *Rhinophrynus dorsalis* (8), *Scinax staufferi* (16), *Smilisca baudini* (16), *Kinosternon scorpioides* (11), *Rhinoclemmys pulcherrima* (11), *Trachemys scripta* (7), *Caiman crocodilus* (5), *Crocodylus acutus* (9), *Ameiva undulata* (15), *Basiliscus vittatus* (15), *Cnemidophorus deppei* (15), *Coleonyx elegans* (5), *C. mitratus* (9), *Ctenosaura similis* (14), *Gonatodes albobularis* (7), *Gymnophthalmus speciosus* (13), *Iguana iguana* (11), *Lepidophyma smithi* (3), *Mabuya unimarginata* (14), *Norops sericeus* (14), *Phyllodactylus tuberculosus* (10), *Sceloporus variabilis* (13), *Agkistrodon bilineatus* (9), *Boa constrictor* (14), *Coniophanes fissidens* (7), *C. imperialis* (4), *C. piceivittis* (8), *Conopsis lineatus* (13), *Crotalus durissus* (13), *Dryadophis melanolomus* (6), *Drymarchon corais* (12), *Drymobius margaritiferus* (14), *Enallia flavitorques* (10), *Ficimia publia* (4), *Imantodes gemmistratus* (9), *Lampropeltis triangulum* (12), *Leptodeira annulata* (15), *L. nigrofasciata* (10), *Leptophis mexicanus* (5), *Leptotyphlops goudoti* (12), *Loxocemus bicolor* (10), *Masticophis mentovarius* (14), *Micrurus nigrocinctus* (9), *Ninia sebae* (7), *Oxybelis aeneus* (13), *O. fulgidus* (7), *Senticolis triaspis* (11), *Sibon sartorii* (6), *Spilotes pullatus* (9), *Stenorrhina freminvillei* (12), *Tantilla melanocephala* (8), *Thamnophis proximus* (7), *Trimorphodon biscutatus* (11).

3. PERIPHERALS

Included in this category are 95 species that barely enter the subhumid forests of Middle America (1 to 6 areas). These species are as follows: *Gymnopsis multiplicata* (3), *Bolitoglossa mexicana* (2), *B. striatula* (1), *Agalychnis callidryas* (3), *Bufo marmoratus* (2), *Eleutherodactylus bransfordi* (1), *E. fitzingeri* (2), *E. rhodopis* (3), *Hyla loquax* (3), *H. robertmertensi* (4), *H. sumichrasti* (2), *Leptodactylus insularum* (1), *L. pentadactylus* (2), *L. poecilocheilus* (1), *Pachymedusa dacnicolor* (1), *Rana maculata* (2), *Scinax boulengeri* (1), *Smilisca sordida* (1), *Syrrhophus pipilans* (2), *Tripurion spatulatus* (1), *Chelydra serpentina* (4), *Kinosternon leucostomum* (3), *Rhinoclemmys areolata* (2), *R. rubida* (2), *Staurotypus triporcatus* (1), *Crocodylus moreleti* (1), *Ameiva chaitzami* (1), *A. festiva* (1), *Basiliscus basiliscus* (2), *Cnemidophorus guttatus* (2), *Ctenosaura pectinata* (2), *Gerrhonotus liocephalus* (1), *Heloderma horridum* (3), *Laemactis longipes* (1), *L. serratus* (3), *Lepidophyma flavimaculatum* (2), *Norops biporcatus* (1), *N. laevis* (1), *N. lemuringus* (5), *N. pentaprion* (2), *N. rodriguezi* (2), *N. tropidonotus* (5), *Phrynosoma asio* (2), *Sceloporus acanthinus* (2), *S. melanorhinus* (2), *S. serrifer* (3), *S.*

siniferus (3), *Sphaerodactylus dunni* (1), *S. glaucus* (3), *S. millepunctatus* (6), *Sphenomorphus assatus* (3), *S. cherriei* (5), *Thecadactylus rapicauda* (3), *Urosaurus bicarinatus* (2), *Adelphicos quadrivirgatus* (1), *Atropoides nummifer* (1), *Bothrops asper* (3), *Clelia clelia* (2), *C. scytalina* (1), *Coluber constrictor* (2), *Coniophanes bipunctatus* (2), *C. quinquevittatus* (1), *Conophis vittatus* (2), *Elaphe flavirufa* (2), *Epicrates cenchria* (1), *Erythrolamprus bizonus* (1), *Hydromorphus concolor* (1), *Imantodes cenchoa* (3), *I. inornatus* (1), *Leptodeira frenata* (1), *L. septentrionalis* (3), *Leptophis ahaetulla* (3), *L. diplotropis* (2), *Manolepis putnami* (1), *Micrurus browni* (1), *M. diastema* (2), *M. ephippifer* (1), *M. latifasciatus* (1), *M. multifasciatus* (1), *Ninia diademata* (1), *Oxyrhopus petola* (1), *Porthidium nasutum* (1), *Pseustes poecilonotus* (2), *Salvadora lemniscata* (2), *Scaphiodontophis annulatus* (4), *Sibon fasciata* (3), *S. nebulata* (3), *Stenorrhina degenhardti* (1), *Tantilla rubra* (2), *T. taeniata* (1), *Thamnophis cyrtopsis* (1), *T. marcianus* (3), *Tretanorhinus nigroluteus* (1), *Urotheca elapoides* (2), *Xenodon rabdocephalus* (2).

The breakdown of the total number of species in each subhumid forest area by distributional category is presented in Table 7. Examination of Table 7 will help explain the reasons why several of the areas with high species numbers and low CBR average values have distinctive herpetofaunas.

The area shown to be the most distinctive, the outer Yucatan Peninsula, has by far the highest number of species in the endemic category (21 species or 23.6% of its herpetofauna), none of which occur outside the Yucatan Peninsula. This is one of the three major areas of endemism that will be defined and discussed in a later section of this paper. Yucatan also has one of the highest number of peripheral species (26 species or 29.2%) of the 16 areas. Three of these species are not shared with any of the other 15 areas, whereas seven are shared only with the Sula Plain. The remaining 16 peripheral species are shared with one to four other areas. The combination of high numbers of endemics and peripherals in Yucatan results in this being the only one of the 16 areas with fewer than 50% of its species being widespread forms.

The Sula Plain has the highest number of peripheral species (38 species or 42.2% of its herpetofauna). Twelve of these species are not shared with any other area, whereas seven are shared only with Yucatan. The remaining 19 Sula peripherals are shared with one to four areas. The preponderance of peripherals in the Sula Plain results in its having the second lowest percentage of widespread species (56.7%) of the 16 areas. The Sula Plain also has the lowest number and percentage of species in the endemic category (1 species, 1.1%).

TABLE 7. Frequency of species of amphibians and reptiles by distributional categories in each of the 16 subhumid forest areas in Middle America. See Table 1 for an explanation of area abbreviations.

Areas	Total Species	Endemics (no. – %)	Peripherals (no. – %) Species	Widespread (no. – %)
TEH	93	12 – 12.9	25 – 26.9	56 – 60.2
YUC	89	21 – 23.6	26 – 29.2	42 – 47.2
CDC	87	3 – 3.5	31 – 35.6	53 – 60.9
RNV	37	3 – 8.1	4 – 10.8	30 – 81.1
MV	52	9 – 17.3	4 – 7.7	39 – 75.0
PG	68	10 – 14.7	3 – 4.4	55 – 80.9
PES	79	13 – 16.5	8 – 10.1	58 – 73.4
PH	49	7 – 14.3	—	42 – 85.7
CHV	55	8 – 14.5	4 – 7.3	43 – 78.2
COV	36	4 – 11.1	—	32 – 88.9
OV	23	2 – 8.7	—	21 – 91.3
SP	90	1 – 1.1	38 – 42.2	51 – 56.7
AV	37	4 – 10.8	7 – 18.9	26 – 70.3
GGV	50	3 – 6.0	10 – 20.0	37 – 74.0
PN	80	12 – 15.0	10 – 12.5	58 – 72.5
PCR	84	11 – 13.1	18 – 21.4	55 – 65.5

The Plains of Tehuantepec has a high number of peripheral species (25 or 26.9% of its herpetofauna). Six of these are not shared with any other of the 15 areas, whereas 12 are shared only with the Central Depression of Chiapas. The Plains of Tehuantepec is also one of the three major areas of endemism that will be discussed later in this paper. Of its 12 species in the endemic category (12.9%), nine do not occur outside of the Plains of Tehuantepec. The combination of the high number of peripherals and species endemic to the Plains of Tehuantepec results in a relatively low percentage of widespread species (60.2%) in this area.

The Central Depression of Chiapas has the second highest number and percentage of peripheral species (31 or 35.6%) of the 16 areas. Six species are not shared with any other of the 15 areas and 12 are shared only with the Plains of Tehuantepec. The remaining 13 peripherals are shared with only one to three areas. The preponderance of

peripherals in the Central Depression of Chiapas results in it having one of the lowest percentages of widespread species (60.9%). This area also has the second lowest percentage of species in the endemic category (3.5%).

The third major area of endemism to be discussed in more detail later on in this paper is the Pacific coastal lowlands from southeastern Guatemala to northwestern Costa Rica. Fourteen species are endemic to this area, including six and seven that also occur in the Motagua and Choluteca valleys, respectively, the two valleys with relatively high average values. This is reflected in the nearly uniform percentages of species in the endemic category in these areas as shown in Table 7. Not only does this influence the high CBR average values for these areas, but it is also indicative of the affinity of the herpetofaunas of these areas, which were demonstrated to have relatively similar herpetofaunas by the CBR algorithm.

Herpetofaunal Assemblages

We established four herpetofaunal assemblages, based on an analysis of present-day geographical and ecological distribution. These assemblages, their characterizations, and their membership are outlined below (letters in parentheses are used in the subsequent discussion).

SUBHUMID ASSEMBLAGE (SA)

Included in this assemblage are 96 species that are predominantly adapted to subhumid forests at low or low to moderate elevations in Mexico and Central America. Some of these species also occur (usually at their upper limits) in moderate elevation pine-oak forests characterized by a long dry season, and are indicated in the list below by an asterisk preceding the name. Eighteen other species also occur regularly in more humid forests along the eastern edge of and/or at the base of the Yucatan Peninsula, and are indicated in the list below by two asterisks preceding the name. All 50 species in our endemic category are in this assemblage, 26 are widespread forms, and 20 peripherals. The species in this assemblage are listed as follows (with their distributional category in parentheses): *Bolitoglossa yucatanana* (E), *Oedipina stuarti* (E), *O. taylori* (E), *Bufo canaliferus* (E), **B. luetkeni* (E), *B. marmoreus* (P), ***Eleutherodactylus yucatanensis* (E), *Gastrophryne usta* (W), **Hypopachus variolosus* (W), *Pachymedusa dacnicolor* (P), **Phrynohyas venulosa* (W), *Rhinophrynus dorsalis* (W), **Syrrhopus pipilans* (P), ***Triprrion petasatus* (E), *T. spatulatus* (P), ***Kinosternon creaseri* (E), **Rhinoclemmys pulcherrima* (W), *R. rubida* (P), *Staurotypus salvini* (E), ***Terrapene yucatanana* (E),

***Cnemidophorus angusticeps* (E), **C. deppei* (W), *C. guttatus* (P), **C. motaguae* (E), *Coleonyx elegans* (W), *Ctenosaura defensor* (E), *C. palearis* (E), *C. pectinata* (P), *C. quinquecarinata* (E), **C. similis* (W), *Eumeces managuae* (E), ***E. schwartzei* (E), **Gymnophthalmus speciosus* (W), **Heloderma horridum* (P), *Laemactus serratus* (P), **Lepidophyma smithi* (W), **Norops cupreus* (E), **N. cuprinus* (E), *N. isthmicus* (E), **N. sericeus* (W), *Phrynosoma asio* (P), **Phyllodactylus muralis* (E), **P. tuberculosus* (W), **Sceloporus carinatus* (E), ***S. chrysostictus* (E), *S. cozumelae* (E), *S. edwardtaylori* (E), ***S. lundelli* (E), *S. melanorhinus* (P), **S. serrifer* (P), **S. siniferus* (P), **S. squamosus* (E), **S. variabilis* (W), **Sphenomorphus assatus* (P), **Urosaurus bicarinatus* (P), *Agkistrodon bilineatus* (W), ***Coniophanes meridianus* (E), **C. piceivittis* (W), **Conopsis lineatus* (W), *C. vittatus* (P), *Crisantophis nevermanni* (E), **Crotalus durissus* (W), ***Dipsas brevifacies* (E), **Enulius flavitorques* (W), *Geagras redimitus* (E), **Imantodes gemmistratus* (W), ***I. tenuissimus* (E), **Leptodeira nigrofasciata* (W), *Leptodrymus pulcherrimus* (E), **Leptophis diplotropis* (P), **Leptotyphlops goudoti* (W), *L. nasalis* (E), *Loxocemus bicolor* (W), *Manolepis putnami* (P), **Masticophis mentovarius* (W), *Micrurus bogerti* (E), *Porthidium dunni* (E), **P. ophryomegas* (E), ***P. yucatanicum* (E), *Salvadora lemniscata* (P), **Scolocophis atrocinctus* (E), **Senticolis triaspis* (W), **Sibon anthracops* (E), **S. carri* (E), ***S. sanniola* (E), **Stenorrhina freminvillei* (W), *Symphimus leucostomus* (E), ***S. mayae* (E), ***Tantilla canula* (E), ***T. cuniculator* (E), ***T. moesta* (E), **T. rubra* (P), *T. striata* (E), *T. vermiformis* (E), *Trimorphodon biscutatus* (W), *Typhlops microstomus* (E).

UBIQUITOUS ASSEMBLAGE (UA)

Included in this assemblage are 53 species that occur with some regularity in both subhumid and humid forests in portions of their geographical range. Species in this assemblage may occur in low, low to moderate, or low to intermediate elevations. Forty-one species are widespread forms and 12 are peripherals. The species in this assemblage are listed as follows (with their distributional category in parentheses): *Dermophis mexicanus* (W), *Bufo coccifer* (W), *B. marinus* (W), *B. valliceps* (W), *Eleutherodactylus rugulosus* (W), *Hyla microcephala* (W), *H. robertmertensi* (P), *Leptodactylus labialis* (W), *L. melanonotus* (W), *Physalaemus pustulosus* (W), *Rana berlandieri* (W), *R. vaillanti* (W), *Scinax staufferi* (W), *Smilisca baudini* (W), *Kinosternon scorpioides* (W), *Rhinoclemmys areolata* (P), *Trachemys scripta* (W), *Caiman crocodilus* (W), *Crocodylus acutus* (W), *C. moreleti* (P), *Ameiva undulata* (W), *Basiliscus vittatus* (W), *Coleonyx mitratus* (W), *Gonatodes albogularis* (W), *Iguana iguana* (W), *Mabuya unimarginata* (W), *Norops rodriguezi* (P), *N. tropidonotus* (P), *Sphaerodactylus glaucus* (P), *Boa constrictor* (W), *Coluber constrictor* (P), *Coniophanes fissidens* (W), *C. imperialis* (W), *Dryadophis melanolomus* (W), *Drymarchon corais* (W), *Drymobius margaritiferus* (W), *Ficimia publia* (W), *Lampropeltis triangulum* (W), *Leptodeira annulata* (W), *L. frenata* (P), *Leptophis mexicanus* (W), *Micrurus browni* (P), *M. nigrocinctus* (W), *Ninia sebae* (W), *Oxybelis aeneus* (W), *O. fulgidus* (W), *Sibon fasciata* (P), *S. sartorii* (W), *Spilotes pullatus* (W), *Tantilla melanocephala* (W), *Thamnophis cyrtopsis* (P), *T. marcianus* (P), *T. proximus* (W).

HUMID ASSEMBLAGE (HA)

Included in this assemblage are 54 species predominantly adapted to humid forests of southern Mexico and Central America at low or low to moderate (to intermediate in a few cases) elevations. The distribution of these species in subhumid forests is spotty and restricted to the more mesic areas of these forests. All 54 species are peripherals as follows: *Gymnopsis multiplicata*, *Bolitoglossa mexicana*, *B. striatula*, *Agalychnis callidryas*, *Eleutherodactylus bransfordi*, *E. fitzingeri*, *E. rhodopis*, *Hyla loquax*, *Leptodactylus insularum*, *L. pentadactylus*, *L. poecilochilus*, *Scinax boulengeri*, *Smilisca sordida*, *Chelydra serpentina*, *Kinosternon leucostomum*, *Staurotypus triporcatus*, *Ameiva festiva*, *Basiliscus basiliscus*, *Laemactus longipes*, *Lepidophyma flavimaculatum*, *Norops biporcatus*, *N. lemurinus*, *N. pentaprion*, *Sphaerodactylus dunni*, *S. millepunctatus*, *Sphenomorphus cherriei*, *Thecadactylus rapicauda*, *Adelphicos quadrivirgatus*, *Atropoides nummifer*, *Bothrops asper*, *Clelia clelia*,

Coniophanes bipunctatus, *C. quinquevittatus*, *Elaphe flavirufa*, *Epicrates cenchria*, *Erythrolamprus bizonus*, *Hydromorphus concolor*, *Imantodes cenchroa*, *I. inornatus*, *Leptodeira septentrionalis*, *Leptophis ahaetulla*, *Micrurus diastema*, *M. multifasciatus*, *Ninia diademata*, *Oxyrhopus petola*, *Porthidium nasutum*, *Pseustes poecilonotus*, *Scaphiodontophis annulatus*, *Sibon nebulata*, *Stenorrhina degenhardti*, *Tantilla taeniata*, *Tretanorhinus nigroluteus*, *Urotheca elapoides*, *Xenodon rabdocephalus*.

MONTANE ASSEMBLAGE (MA)

Included in this assemblage are nine species that occur predominantly on slopes of mountains at elevations that are primarily above the subhumid forests of Middle America. *Ameiva chaitzami* is included here, even though it occurs in the pine savannahs on the lowlands of east-central Guatemala (Echternacht, 1971, and references cited therein). The reasons for including *A. chaitzami* in this assemblage are that it is a highland species around the upper tributaries of the Central Depression of Chiapas (where it occurs both in and at elevations above the valley), and that the unique overall distribution of the species does not allow for its allocation to any of our other assemblages. All nine species are peripherals as follows: *Hyla sumichrasti*, *Rana maculata*, *Ameiva chaitzami*, *Gerrhonotus liocephalus*, *Norops laeviventris*, *Sceloporus acanthinus*, *Clelia scytalina*, *Micrurus ephippifer*, *M. latifasciatus*.

In Table 8, the total number of species in each subhumid area is broken down by herpetofaunal assemblages. A number of conclusions arise from scrutiny of this table. With regard to the Subhumid Assemblage (SA), there is a north-to-south cline involving a decrease in the percentages of species in the Pacific coastal areas, with the exception of that in Honduras (see below). Of the 54 SA species found in the Plains of Tehuantepec, 32 species (or 59.3%) are found no farther south than El Salvador. Of these 32 species, 12 occur only in the Tehuantepec area and an additional 12 species occur only in the Tehuantepec and Central Depression of Chiapas areas. Thus, the cline is largely produced by a dropout of a large number of SA species in the northern portion of the Pacific coastal areas. The cline is also influenced by the relatively high percentages of Humid Assemblage (HA) species for Pacific coastal Nicaragua (12.4%) and northwestern Costa Rica (21.4%). Both of these latter areas have portions of their subhumid forests in direct contact with humid forests. Given the clinal decrease in percentages of SA species in the Pacific coastal areas, it is interesting to note the relative uniformity of percentage figures of Ubiquitous Assemblage (UA) species (38.1–46.9, $\bar{x}$ = 42.2) in these areas. The only exception is the low absolute number for Pacific coastal Honduras. This apparent anomaly is discussed below.

TABLE 8. Frequency of species of amphibians and reptiles by herpetofaunal assemblages in each of the 16 sub-humid forest areas in Middle America. See Table 1 for an explanation of area abbreviations. SA = Subhumid Assemblage; UA = Ubiquitous Assemblage; HA = Humid Assemblage; MA = Montane Assemblage.

Areas	Total Species	SA (no. – %)	UA (no. – %)	HA (no. – %)	MA (no. – %)
TEH	93	54 – 58.1	36 – 38.7	—	3 – 3.2
YUC	89	38 – 42.7	35 – 39.3	16 – 18.0	—
CDC	87	43 – 49.4	34 – 39.1	5 – 5.7	5 – 5.7
RNV	37	16 – 43.2	19 – 51.4	—	2 – 5.4
MV	52	26 – 50.0	24 – 46.2	2 – 3.8	—
PG	68	36 – 52.9	30 – 44.1	2 – 3.0	—
PES	79	40 – 50.6	33 – 41.8	5 – 6.3	1 – 1.3
PH	49	26 – 53.1	23 – 46.9	—	—
CHV	55	24 – 43.6	28 – 50.9	2 – 3.6	1 – 1.8
COV	36	19 – 52.8	17 – 47.2	—	—
OV	23	8 – 34.8	15 – 65.2	—	—
SP	90	20 – 22.2	36 – 40.0	34 – 37.8	—
AV	37	13 – 35.1	18 – 48.7	6 – 16.2	—
GGV	50	11 – 22.0	30 – 60.0	9 – 18.0	—
PN	80	35 – 43.8	35 – 43.8	10 – 12.4	—
PCR	84	34 – 40.5	32 – 38.1	18 – 21.4	—

Unusually low percentages of SA species are found in the Sula Plain and Guayape-Guayambre Valley. Both valleys have relatively high percentages of Humid Assemblage (HA) species. In fact, the Sula Plain has a very high percentage of HA species (37.8%), a little less than twice that of the next highest area. Both the Sula Plain and the Guayape-Guayambre Valley have direct contact of their subhumid forests with humid forests. The latter is also true of the outer Yucatan Peninsula and the Aguan Valley, both of which also have relatively high HA percentages.

The Central Depression of Chiapas and the Rio Negro Valley have relatively high percentages of Montane Assemblage (MA) species. Both of these valleys are relatively narrow in their upper reaches and are surrounded by high mountains, whereas the interior valleys of Honduras are relatively broad and the surrounding mountains are not so high. As a result, only a single MA species occurs in one of the valleys of the Honduras.

Compared to the other Pacific coastal areas, Pacific coastal Honduras has a known herpetofauna composed of relatively few species (49, as compared to 68–93 [$\bar{x}$ = 80.8] for the other areas; Table 8). This is also reflected in Figure 2 in which the CBR value connecting Pacific

coastal Guatemala and El Salvador with Pacific coastal Nicaragua and Costa Rica is higher (0.77) than that connecting the former pair with Pacific coastal Honduras (0.74), and in turn Pacific coastal Honduras with Pacific coastal Nicaragua and Costa Rica (0.71). Examination of the distribution of species not recorded from Pacific coastal Honduras indicates that a number likely will be eventually found there. Within the SA, there are nine species that occur in the Pacific coastal lowlands both to the northwest and south of Pacific coastal Honduras. These species are as follows: *Hypopachus variolosus*, *Rhinophrynus dorsalis*, *Ctenosaura quinquecarinata*, *Norops cupreus*, *Coniophanes piceivittis*, *Leptodrymus pulcherrimus*, *Scolecophis atrocinctus*, *Senticolis triaspis*, and *Sibon anthracops*. An additional SA species (*Cnemidophorus motaguae*) occurs in Pacific coastal lowlands to the northwest of Honduras, as well as in six interior valleys, three of which are in Honduras.

Among the UA species, there are nine that occur in Pacific coastal lowlands on both sides of Honduras. These are as follows: *Eleutherodactylus rugulosus*, *Trachemys scripta*, *Caiman crocodilus*, *Ameiva undulata*, *Drymarchon corais*, *Lampropeltis triangulum*, *Oxybelis fulgidus*, *Sibon sartorii*, and *Spilotes pullatus*. Two other

UA species (*Coniophanes fissidens* and *Dryadophis melanolomus*) range to the northwest of Pacific coastal Honduras and in several interior valleys in Honduras.

It appears likely that all 21 of these species occur in the Pacific lowlands of Honduras (*Hypopachus variolosus*, *Cnemidophorus motaguae*, *Ctenosaura quinquecarinata*, and *Leptodrymus pulcherrimus* are known to occur above 600 m east of Choluteca, Department of Choluteca). If we add these 21 species to the data in Table 8, the

adjusted figures for the area would be

Total Species	SA Species	UA Species
70	35–50.0%	35–50.0%

These figures are in alignment with those for the other Pacific coastal areas. It is obvious that there is a need for additional field work in Pacific coastal Honduras.

Historical Biogeography

Of the four herpetofaunal assemblages identified in the previous section, only the members of the Subhumid Assemblage offer much assistance in elucidating the historical events that have led to the present-day patterns of distribution in the Middle American subhumid forests. The distributions of the members of two of the assemblages, the Humid and Montane assemblages, are peripheral to the subhumid forests and those of the members of the Ubiquitous Assemblage are so broadly distributed geographically and ecologically as to offer little aid in understanding the evolution of distributional patterns in the subhumid forests. Therefore, we have focused on the Subhumid Assemblage in the following discussion.

HISTORICAL UNITS

Major advances in our understanding of historical units in the herpetofauna of Middle America have been made by Savage (1966, 1983). In those papers he delineated four such units, defined (1983:511) as follows:

1. *Old Northern Element*—"derivative stocks of originally extratropical (subtropical–warm temperate) groups distributed more or less continuously and circum-polarly in early Tertiary, but forced southward and fragmented into several more or less disjunct components as a result of increased cooling and aridity trends and mountain building in late Cenozoic."

2. *South American Element*—"derivatives of a generalized tropical American biota that evolved *in situ* in isolation in South America during most of Cenozoic."

3. *Middle American Element*—"derivative groups of a generalized tropical American biota isolated in tropical North and Central America during most of Cenozoic; developed *in situ* north of the Panamanian Portal and restricted by mountain building and climatic change in late Cenozoic to Middle America."

4. *Young Northern Element*—"derivatives from the generalized tropical American biota of early Tertiary that

responded to the challenge of physiographic and climatic revolution in the middle latitudes of western North America and Mexico; essentially an *in situ* extratropical xeric derivative of the Middle American Element."

The component taxa of Savage's (1983) historical units are genera. The 212 species under consideration are disposed among 103 genera, with 42 genera in the Old Northern unit, 37 in the Middle American unit, 21 in the South American unit, and 5 in the Young Northern unit (2 genera, *Bufo* and *Hyla*, have representatives in both the Middle American and South American units). We have extended Savage's (1983) analysis a step further to the species level in detailing the composition of these historical units in Table 9. Some minor adjustments in placement of taxa have been occasioned in the process.

MAJOR GEOHISTORICAL EVENTS

The understanding of the geohistorical events that have led to present-day patterns of distribution is still evolving. Nonetheless, the marriage of modern biogeographic theory and cladistic systematics has provided a powerful predictive tool that can illuminate in two ways, that is, to predict evolutionary relationships based on the facts of geohistory and to predict unusual geologic events from phylogenetic relationships. Unfortunately, cladistic analyses of taxa of interest to us in the current discussion are largely lacking, as is the case with Middle American taxa in general (Savage, 1983). Thus, we are left, as was Savage (1983), with analyzing concordant patterns of distribution (or generalized tracks in vicariist terminology) as a means of correlating geohistorical events with modern distributional patterns.

Savage (1983) outlined the essential geohistorical events in Middle America of importance to an understanding of present-day patterns of distribution. He predicted a series of events that would have to occur to account for these patterns and correlated these hypothetical events with demonstrable geological history. The

TABLE 9. Component species of the four historical units of the herpetofauna of the subhumid forests of Middle America (patterned after Savage, 1983).

Middle American (93)			
A. Subhumid Assemblage (39)	B. Ubiquitous Assemblage (22)	C. Humid Assemblage (28)	D. Montane Assemblage (4)
<i>Bufo canaliferus</i>	<i>Dermophis mexicanus</i>	<i>Gymnopsis multiplicata</i>	<i>Hyla sumichrasti</i>
<i>Bufo luetkeni</i>	<i>Bufo coccifer</i>	<i>Agalychnis callidryas</i>	<i>Norops laeviventris</i>
<i>Bufo marmoreus</i>	<i>Bufo valliceps</i>	<i>Eleutherodactylus bransfordi</i>	<i>Micrurus ephippifer</i>
<i>Eleutherodactylus yucatanensis</i>	<i>Eleutherodactylus rugulosus</i>	<i>Eleutherodactylus fitzingeri</i>	<i>Micrurus latifasciatus</i>
<i>Gastrophryne usta</i>	<i>Smilisca baudini</i>	<i>Eleutherodactylus rhodopis</i>	
<i>Hypopachus variolosus</i>	<i>Crocodylus acutus</i>	<i>Smilisca sordida</i>	
<i>Pachymedusa dacnicolor</i>	<i>Crocodylus moreleti</i>	<i>Basiliscus basiliscus</i>	
<i>Syrrhophus pipilans</i>	<i>Basiliscus vittatus</i>	<i>Laemactus longipes</i>	
<i>Tripurion petasatus</i>	<i>Iguana iguana</i>	<i>Norops biporcatus</i>	
<i>Tripurion spatulatus</i>	<i>Norops rodriguezi</i>	<i>Norops lemurinus</i>	
<i>Ctenosaura defensor</i>	<i>Norops tropidonotus</i>	<i>Norops pentaprion</i>	
<i>Ctenosaura palearis</i>	<i>Sphaerodactylus glaucus</i>	<i>Sphaerodactylus dunni</i>	
<i>Ctenosaura pectinata</i>	<i>Boa constrictor</i>	<i>Sphaerodactylus millepunctatus</i>	
<i>Ctenosaura quinquecarinata</i>	<i>Coniophanes fissidens</i>	<i>Adelphicos quadrivirgatus</i>	
<i>Ctenosaura similis</i>	<i>Coniophanes imperialis</i>	<i>Atropoides nummifer</i>	
<i>Laemactus serratus</i>	<i>Leptodeira annulata</i>	<i>Coniophanes bipunctatus</i>	
<i>Norops cupreus</i>	<i>Leptodeira frenata</i>	<i>Coniophanes quinquevittatus</i>	
<i>Norops cuprinus</i>	<i>Micrurus browni</i>	<i>Hydromorphus concolor</i>	
<i>Norops isthmicus</i>	<i>Micrurus nigrocinctus</i>	<i>Imantodes cenchoa</i>	
<i>Norops sericeus</i>	<i>Ninia sebae</i>	<i>Imantodes inornatus</i>	
<i>Phyllodactylus muralis</i>	<i>Sibon fasciata</i>	<i>Leptodeira septentrionalis</i>	
<i>Phyllodactylus tuberculosus</i>	<i>Sibon sartorii</i>	<i>Micrurus diastema</i>	
<i>Coniophanes meridianus</i>		<i>Micrurus multifasciatus</i>	
<i>Coniophanes piceivittis</i>		<i>Ninia diademata</i>	
<i>Conopsis lineatus</i>		<i>Porthidium nasutum</i>	
<i>Conopsis vittatus</i>		<i>Sibon nebulata</i>	
<i>Crisantophis nevermanni</i>		<i>Tretanorhinus nigroluteus</i>	
<i>Dipsas brevifacies</i>		<i>Urotheca elapoides</i>	
<i>Enallius flavitorques</i>			
<i>Imantodes gemmistratus</i>			
<i>Imantodes tenuissimus</i>			
<i>Leptodeira nigrofasciata</i>			
<i>Micrurus bogerti</i>			
<i>Porthidium dunni</i>			
<i>Porthidium ophryomegas</i>			
<i>Porthidium yucatanicum</i>			
<i>Sibon anthracops</i>			
<i>Sibon carri</i>			
<i>Sibon sanniola</i>			

TABLE 9. (cont.)

Old Northern (70)

A. Subhumid Assemblage (34)	B. Ubiquitous Assemblage (21)	C. Humid Assemblage (13)	D. Montane Assemblage (2)
<i>Bolitoglossa yucatana</i>	<i>Rana berlandieri</i>	<i>Bolitoglossa mexicana</i>	<i>Rana maculata</i>
<i>Oedipina stuarti</i>	<i>Rana vaillanti</i>	<i>Bolitoglossa striatula</i>	<i>Gerrhonotus liocephalus</i>
<i>Oedipina taylori</i>	<i>Kinosternon scorpioides</i>	<i>Chelydra serpentina</i>	
<i>Rhinophrynus dorsalis</i>	<i>Rhinoclemmys areolata</i>	<i>Kinosternon leucostomum</i>	
<i>Kinosternon creaseri</i>	<i>Trachemys scripta</i>	<i>Staurotypus triporcatus</i>	
<i>Rhinoclemmys pulcherrima</i>	<i>Coleonyx mitratus</i>	<i>Lepidophyma flavimaculatum</i>	
<i>Rhinoclemmys rubida</i>	<i>Mabuya unimarginata</i>	<i>Sphenomorphus cherriei</i>	
<i>Staurotypus salvini</i>	<i>Coluber constrictor</i>	<i>Elaphe flavirufa</i>	
<i>Terrapene yucatana</i>	<i>Dryadophis melanolomus</i>	<i>Leptophis ahaetulla</i>	
<i>Coleonyx elegans</i>	<i>Drymarchon corais</i>	<i>Pseustes poecilonotus</i>	
<i>Eumeces managuae</i>	<i>Drymobius margaritiferus</i>	<i>Scaphiodontophis annulatus</i>	
<i>Eumeces schwartzei</i>	<i>Ficimia publia</i>	<i>Stenorrhina degenhardti</i>	
<i>Heloderma horridum</i>	<i>Lampropeltis triangulum</i>	<i>Tantilla taeniata</i>	
<i>Lepidophyma smithi</i>	<i>Leptophis mexicanus</i>		
<i>Sphenomorphus assatus</i>	<i>Oxybelis aeneus</i>		
<i>Agkistrodon bilineatus</i>	<i>Oxybelis fulgidus</i>		
<i>Geagras redimitus</i>	<i>Spilotes pullatus</i>		
<i>Leptodrymus pulcherrimus</i>	<i>Tantilla melanocephala</i>		
<i>Leptophis diplotropis</i>	<i>Thamnophis cyrtopsis</i>		
<i>Loxocemus bicolor</i>	<i>Thamnophis marcianus</i>		
<i>Masticophis mentovarius</i>	<i>Thamnophis proximus</i>		
<i>Salvadora lemniscata</i>			
<i>Scolecophis atrocinctus</i>			
<i>Senticolis triaspis</i>			
<i>Stenorrhina freminvillei</i>			
<i>Symphimus leucostomus</i>			
<i>Symphimus mayae</i>			
<i>Tantilla canula</i>			
<i>Tantilla cuniculator</i>			
<i>Tantilla moesta</i>			
<i>Tantilla rubra</i>			
<i>Tantilla striata</i>			
<i>Tantilla vermiformis</i>			
<i>Trimorphodon biscutatus</i>			

TABLE 9. (cont.)

Young Northern (18)			
A. Subhumid Assemblage (17)	B. Ubiquitous Assemblage (0)	C. Humid Assemblage (0)	D. Montane Assemblage (1)
<i>Cnemidophorus angusticeps</i>			<i>Sceloporus acanthinus</i>
<i>Cnemidophorus deppei</i>			
<i>Cnemidophorus guttatus</i>			
<i>Cnemidophorus motaguae</i>			
<i>Phrynosoma asio</i>			
<i>Sceloporus carinatus</i>			
<i>Sceloporus chrysostictus</i>			
<i>Sceloporus cozumelae</i>			
<i>Sceloporus edwardtaylori</i>			
<i>Sceloporus lundelli</i>			
<i>Sceloporus melanorhinus</i>			
<i>Sceloporus serrifer</i>			
<i>Sceloporus siniferus</i>			
<i>Sceloporus squamosus</i>			
<i>Sceloporus variabilis</i>			
<i>Urosaurus bicarinatus</i>			
<i>Crotalus durissus</i>			
South American (31)			
A. Subhumid Assemblage (6)	B. Ubiquitous Assemblage (10)	C. Humid Assemblage (13)	D. Montane Assemblage (2)
<i>Phrynohyas venulosa</i>	<i>Bufo marinus</i>	<i>Hyla loquax</i>	<i>Ameiva chaitzami</i>
<i>Gymnophthalmus speciosus</i>	<i>Hyla microcephala</i>	<i>Leptodactylus insularum</i>	<i>Clelia scytalina</i>
<i>Leptotyphlops goudoti</i>	<i>Hyla robertmertensi</i>	<i>Leptodactylus pentadactylus</i>	
<i>Leptotyphlops nasalis</i>	<i>Leptodactylus labialis</i>	<i>Leptodactylus poecilochilus</i>	
<i>Manolepis putnami</i>	<i>Leptodactylus melanonotus</i>	<i>Scinax boulengeri</i>	
<i>Typhlops microstomus</i>	<i>Physalaemus pustulosus</i>	<i>Ameiva festiva</i>	
	<i>Scinax staufferi</i>	<i>Thecadactylus rapicauda</i>	
	<i>Caiman crocodilus</i>	<i>Bothrops asper</i>	
	<i>Ameiva undulata</i>	<i>Clelia clelia</i>	
	<i>Gonatodes albogularis</i>	<i>Epicrates cenchria</i>	
		<i>Erythrolamprus bizonus</i>	
		<i>Oxyrhopus petola</i>	
		<i>Xenodon rabdocephalus</i>	

events are as follows:

Dispersal I—concordant dispersal of southern groups northward into Middle America during an ancient continuity between this region and South America extending into the Palaeocene; this event established a generalized tropical herpetofauna over much of the hemisphere when warm humid climates ranged as far north as what is now the Dakotas, Montana, Wyoming, Utah, and Colorado. White (1986:179), citing numerous references to geological and biological evidence, also suggested an early Palaeocene connection for North and South America “. . . by an island series or uninterrupted dryland connection . . .” that “. . . was probably located eastward of its modern counterpart . . .”

Vicariance I—isolation of Middle America and South America beginning in the Eocene created by the north-eastward movement of a proto-Greater Antillean block on the Caribbean tectonic plate giving rise to a Middle American herpetofaunal element.

Dispersal II—concordant dispersal of northern stocks southward into Middle America prior to the Eocene allowing mixture with the Middle American element.

Vicariance II—isolation of northern groups in Middle America from allied groups in eastern North America by orogeny and cooling and drying trends instituted in the Oligocene in Middle America.

Dispersal III—concordant dispersal of southern stocks into Middle America as a result of the re-establishment of an isthmian link between Central and South America in the Pliocene.

As discussed below, other vicariance and dispersal events were of importance in producing details of present-day distributional configurations.

Savage (1983) indicated that beginning in the Oligocene and continuing through to the Pliocene, significant uplift of the main mountain masses of Mexico and Central America occurred. According to Savage (1983:520) “this process seems to have had a north to south sequence, with the Sierra Madres of Mexico present as upland areas in Oligocene, and the highlands of Nuclear Central America developing in Miocene. The final sequence of uplift was in lower Central America leading to [along with the reduction of world sea levels] the closure of the Panamanian Portal in Pliocene [probably early Pliocene].” This north-to-south sequence of mountain-building is also described by Ferrusquía-Villafranca (1984), and supported by Webb and Perrigo (1984). The latter authors pointed out that extensive block-faulting had occurred by the late Miocene, producing some of the grabens now constituting subhumid interior valleys. This uplift, as noted by Webb (1985:379) “. . . would have considerably altered the setting in the isthmian region, producing more extensive rainshadow belts for thorn scrub savanna,” which extended (Webb, 1985:380) “. . . south-

ward through North and Central America.” As suggested by Savage (1966), by the early or middle Pliocene, an Eastern Mesoamerican Complex of the Middle American Element and a Central American Complex of the Old Northern Element, both composed of humid-adapted forms, were in place in Middle America (both Nuclear and Isthmian Link segments) in the humid forests prevalent in the region since Palaeocene times. The Miocene–Pliocene uplift and associated climatic events fragmented this generalized tropical Middle American herpetofauna into three major groups: (1) an eastern lowland (humid-adapted) assemblage, (2) a western lowland (subhumid-adapted) assemblage, and (3) a central upland assemblage (Savage, 1983), and constituted another vicariance event (III).

Savage (1966:756) also suggested that by early Pliocene two historical units were poised in association with each other at the northern gateway to Nuclear Central America “. . . in position to invade the region as climate and vegetation provided opportunity in late Pliocene to the present.” These units were the Western Mesoamerican Complex (subhumid-adapted) of the Middle American Element and subhumid-adapted members of the Young Northern Element. In addition, a few members of the Western American Complex of the Old Northern Element were also apparently involved in association with the two elements to the north. Also, some members of the Northern South American Complex (subhumid-adapted) of the South American Element were poised to enter Central America from the south (Savage, 1966). Invasion of the more northerly situated units was promoted by the north-to-south mountain uplift and the attendant climatic and vegetational changes that introduced xeric lowland habitats into Middle America. “Aridity apparently influenced the Pacific Coast to the greatest extent and xeric adapted vegetation gradually moved south from the Isthmus of Tehuantepec along the lowlands. Increasingly arid conditions made possible the invasion of upland sectors of Guatemala . . . and penetration of xeric vegetation to Atlantic drainage rain-shadow valleys in eastern Guatemala and Honduras” (Savage, 1966:756).

The orogenic events of the late Tertiary produced a basic pattern of herpetological distribution in Middle America to be modified somewhat by the events of the final chapter of this story—the climatic and vegetational fluctuations of the Quaternary. Numerous lines of evidence from palaeogeology, palaeoclimatology, and palaeontology, based principally from research in South America (Haffer, 1987; Prance, 1987; van der Hammen, 1982; and references cited in each of these studies) and tropical Mexico (Toledo, 1982), have suggested that climatic and vegetational fluctuations brought about alternating expansion and contractions of xeric and humid vegetation types during the Quaternary in concert with glacial and interglacial stages in the higher latitudes. Furthermore,

as noted by Street (1981:157), “recent research has swept away the old notion that the intertropical belt experienced pluvial conditions during the glacial stages of higher latitudes. The majority of sites between latitudes 23 1/2° N and S were *drier than today during glacial maxima*” (italics ours). This statement is supported by the conclusions of Pregill and Olson (1981:92–93), who stated “through the vertebrate fossil record and related lines of evidence, we have shown that environmental conditions in the West Indies during the last Pleistocene glaciation differed from those at present by the predominance of arid savanna, grassland, and xeric scrub forest” and that “presumably the previous glacial and interglacial periods of the Pleistocene would likewise have exerted a powerful influence on zoogeographic patterns.” Webb (1985:378) further concluded that “the rich mammal record . . . [of] the interval from 2.5 to 1.5 Ma. records an extensive movement of savanna-adapted mammal faunas from north-temperate to south-temperate latitudes and in the reciprocal direction as well. The savanna elements were not incidental parts of the interchange [between North and South America], but represent the vast majority of the taxa involved The extent of savanna adaptations among the land-mammals of the interchange indicates the presence of a *continuous corridor* (italics ours) of open-country habitats or, at the very least, a moving mosaic of such habitats through the American tropics” (it should be pointed out that Webb’s use of the term “savanna” is an extremely broad one and includes all of the subhumid forest formations included in the present study). The isthmian region of Panama “. . . became a rain-forest corridor only in the late Pleistocene” (Webb, 1985:379). Finally, based on palynological studies of sediments from two lakes in the Department of Petén, Guatemala, Leyden (1984:4856) indicated that in Petén periods during the late Pleistocene were more arid and that “late Glacial vegetation consisted of marsh, savanna, and juniper scrub.”

Furthermore, Leyden (1984:4858) noted that “the Petén data are conclusive that the ‘primeval’ tropical forests [semi-evergreen seasonal forest in her terminology] are no more than 10,000 to 11,000 years old” While the possibility exists that wind-blown pollen could distort Leyden’s findings, they are, however, consistent with the other evidence presented above. In summary, current evidence supports a hypothesis of more extensive distribution of subhumid forests in the tropics during a series of Pleistocene glacial periods than at present. Likewise, mesic forest refugia would have remained at the extremes of lowered rainfall, allowing for the continuous existence of humid-adapted tropical species in southern Mexico and Central America (Prance, 1987; Toledo, 1982).

Expansion of subhumid forests in the tropics during glacial maxima would have been facilitated by the lowered sea levels occurring during the same periods, increasing the extent of the lowlands of Middle America. As noted by Haffer (1987:9) “world sea-level was about 80–100 m lower than today during the last glacial period (Wisconsin-Würm, 13,000 to 18,000 years BP).” On the other hand, “high stands of sea interglacial world sea-level compared to present sea-level decreased from about +180 and +100 m during two interglacials of the latest Pliocene, to +60, +30, and +17 m during successive Pleistocene interglacials, and to +3 (4000 a BP) and finally +1 m (2300 a BP) during the Holocene” Therefore, the above-described Pleistocene climatic and vegetational fluctuations would have allowed for a variety of dispersals of both subhumid- and humid-adapted forms within the changing environments that can collectively constitute a dispersal event IV for the associated herpetofauna. In addition, those species evolving *in situ* in various subhumid areas as a result of fragmentation and subsequent isolation from a formerly widely dispersed ancestor due to Pleistocene climatic and vegetational fluctuations constitute an additional vicariance event.

Origin of the Subhumid Herpetofauna

As we proceed to establish a set of hypotheses concerning the origin of the herpetofauna of the subhumid forests of Middle America, it is useful to recall that we have identified four herpetofaunal assemblages, most made up of contributions from all four of the historical units discussed previously (see Table 9). In addition, we consider it most elucidative to focus on the origin of the Subhumid Assemblage of this herpetofauna. It is this assemblage, as can be expected, that has been most involved with the history of the subhumid forests.

As we begin this discussion, it should be emphasized that, according to the geohistorical scenario we have

accepted, the areas included in this study now occupied by subhumid forest were mesic through the Miocene. Beginning in the Miocene, orogeny instituted farther north in Mexico in the Oligocene continued in a southward direction, producing the mountain masses of Nuclear Central America and lower Central America and, concomitantly, the climatic regimes supportive of the development of subhumid forests along the Pacific lowlands and in the interior valleys of Guatemala and Honduras. During the late Pliocene and continuing into the early Pleistocene, a more or less continuous subhumid corridor existed from northern South America into lower Central

America in areas some of which are now covered by humid forests. Furthermore, the outer portion of the Yucatan Peninsula did not become continuously land-positive until the middle to late Pleistocene (for a discussion of sea-level changes in late Tertiary and Quaternary, see Haffer, 1987:9). The subsequent discussion is predicated on this scenario and, thus, some of our comments will be at variance with some of those expressed in various systematic studies of given taxa. Some of these differences in interpretation will be discussed where pertinent.

ANALYSIS OF GENERALIZED TRACKS AND AREAS OF ENDEMISM

Savage (1983) has discussed the difficulties of generalized track analysis and set forth some principles for establishing generalized tracks. We plotted the total distribution of each of the 96 Subhumid Assemblage species. We also plotted the total distribution for closely related species of each of the 96 species when those relationships are known. Based upon a review of these distributions and following the principles set forth by Savage (1983), we were able to identify five generalized tracks for our Subhumid Assemblage species (Table 10). Three major areas of endemism occur within the subhumid areas under consid-

eration (see Fig. 16 in Savage, 1983). These are the outer Yucatan Peninsula (21 endemic species), the Pacific lowlands from southeastern Guatemala to northwestern Costa Rica (14 endemics), and the Pacific lowlands of the Isthmus of Tehuantepec (9 endemics). The phylogenetic relationships of the endemic species found in the subhumid forests of Middle America are important in expressing historical relationships among the subhumid areas that are presently separated from each other by more mesic conditions than those that prevailed in the past. Savage (1983) has provided a discussion of this "vicariist method" in determining area relationships. These phylogenetic relationships are discussed, when known, in conjunction with the generalized tracks we have developed. Five species endemic to one of the three major areas of endemism (*Crisantophis nevermanni*, *Micrurus bogerti*, *Tantilla canula*, *T. moesta*, and *T. vermiformis*) could not be allocated to a generalized track because too little is known about their relationships or the matter is in dispute.

1. WESTERN MEXICAN GENERALIZED TRACK (58 species; Table 10; Fig. 3)

The ancestors of and/or the species in this track are postulated to have reached the subhumid forests of Middle America by dispersing southward from the subhumid low-

FIG. 3. Generalized tracks of the 58 Subhumid Assemblage species belonging to the Western Mexican Generalized Track.

TABLE 10. Component species of each of the five generalized tracks identified from the 96 Subhumid Assemblage species.

Western Mexican Generalized Track (58)			
<i>Bufo marmoreus</i>	<i>Ctenosaura palearis</i>	<i>Sceloporus melanorhinus</i>	<i>Loxocemus bicolor</i>
<i>Gastrophryne usta</i>	<i>Ctenosaura pectinata</i>	<i>Sceloporus siniferus</i>	<i>Masticophis mentovarius</i>
<i>Hypopachus variolosus</i>	<i>Ctenosaura quinquecarinata</i>	<i>Sceloporus squamosus</i>	<i>Porthidium dunni</i>
<i>Pachymedusa dacinicolor</i>	<i>Ctenosaura similis</i>	<i>Sphenomorphus assatus</i>	<i>Porthidium ophryomegas</i>
<i>Rhinophrynus dorsalis</i>	<i>Eumeces managuae</i>	<i>Urosaurus bicarinatus</i>	<i>Porthidium yucatanicum</i>
<i>Syrrhophus pipilans</i>	<i>Eumeces schwartzei</i>	<i>Agkistrodon bilineatus</i>	<i>Salvadora lemiscata</i>
<i>Triprion petasatus</i>	<i>Heloderma horridum</i>	<i>Coniophanes piceivittus</i>	<i>Scolecophis atrocinctus</i>
<i>Triprion spatulatus</i>	<i>Norops cuprinus</i>	<i>Conophis vittatus</i>	<i>Senticolis triaspis</i>
<i>Rhinoclemmys pulcherrima</i>	<i>Norops isthmicus</i>	<i>Crotalus durissus</i>	<i>Sibon anthracops</i>
<i>Rhinoclemmys rubida</i>	<i>Phyllodactylus muralis</i>	<i>Enulius flavitorques</i>	<i>Stenorrhina freminvillei</i>
<i>Cnemidophorus angusticeps</i>	<i>Phyllodactylus tuberculosus</i>	<i>Geagras redimitus</i>	<i>Symphimus leucostomus</i>
<i>Cnemidophorus deppei</i>	<i>Phrynosoma asio</i>	<i>Imantodes gemmistratus</i>	<i>Symphimus mayae</i>
<i>Cnemidophorus guttatus</i>	<i>Sceloporus carinatus</i>	<i>Leptodeira nigrofasciata</i>	<i>Trimorphodon biscutatus</i>
<i>Cnemidophorus motaguae</i>	<i>Sceloporus edwardtaylori</i>	<i>Leptodrymus pulcherrimus</i>	
<i>Ctenosaura defensor</i>	<i>Sceloporus lundelli</i>	<i>Leptophis diplotropis</i>	
Eastern Mexican Generalized Track (8)			
<i>Terrapene yucatanana</i>	<i>Sceloporus chrysostictus</i>	<i>Sceloporus serrifer</i>	<i>Conophis lineatus</i>
<i>Norops sericeus</i>	<i>Sceloporus cozumelae</i>	<i>Sceloporus variabilis</i>	<i>Tantilla rubra</i>
Middle American Generalized Track (10)			
<i>Oedipina stuarti</i>	<i>Bufo luetkeni</i>	<i>Lepidophyma smithi</i>	<i>Sibon carri</i>
<i>Oedipina taylori</i>	<i>Staurotypus salvini</i>	<i>Norops cupreus</i>	<i>Tantilla striata</i>
<i>Bufo canaliferus</i>	<i>Coleonyx elegans</i>		
Eastern Middle American Generalized Track (9)			
<i>Bolitoglossa yucatanana</i>		<i>Laemantus serratus</i>	<i>Imantodes tenuissimus</i>
<i>Eleutherodactylus yucatanensis</i>		<i>Coniophanes meridianus</i>	<i>Sibon sanniola</i>
<i>Kinosternon creaseri</i>		<i>Dipsas brevifacies</i>	<i>Tantilla cuniculator</i>
South American Generalized Track (6)			
<i>Phrynohyas venulosa</i>		<i>Leptotyphlops goudoti</i>	<i>Manolepis putnami</i>
<i>Gymnophthalmus speciosus</i>		<i>Leptotyphlops nasalis</i>	<i>Typhlops microstomus</i>

lands of western Mexico. Twenty-five species are in the Middle American, 20 in the Old Northern, and 13 in the Young Northern historical units. As subhumid conditions along the Pacific coast expanded southward in the late Tertiary, some members of this track, or their ancestors, were able to disperse in two ways as follows: (1) southward along the Pacific Coast of southern Mexico and Central America and into the interior valleys of Chiapas, Mexico, Guatemala, and Honduras as early as the Pliocene with the developing subhumid forests (associated with the uplift of the main mountain axis); and/or (2) across the Isthmus of Tehuantepec to the emerging outer Yucatan Peninsula and/or northeastern Mexico during Pleistocene glacial periods (see Major Geohistorical Events above for a discussion of the evidence for these two developments). Duellman (1960:48, 1966:717) and Trueb (1970:697) have also discussed the second scenario, based upon present-day herpetofaunal distributional patterns. The three major subhumid Middle American areas of endemism (Yucatan Peninsula, Plains of Tehuantepec, and Pacific lowlands of Central America) are well represented by endemic species in this track, suggesting former continuous distributions of the ancestors of the present-day endemics. With the advent of more mesic conditions in the late Pleistocene, the xeric conditions found today on the outer Yucatan Peninsula, the Plains of Tehuantepec, and the Pacific lowlands from southeastern Guatemala to northwestern Costa Rica were isolated from each other, due to the expansion of more mesic conditions in the intervening areas. As a result, many of the endemic species in each of these major areas of endemism evolved *in situ* from a xeric-adapted ancestor that had dispersed through the previously continuous subhumid corridors. Table 11 lists examples of endemics in this track (or "syn-taxon" groups, following Kluge, 1989:316) resulting from the range fragmentation of a once-continuous, wide-ranging ancestor. Lee (1980) previously placed some of these examples in his "Yucatan–West Mexico Pattern." Two species endemic to the Pacific lowlands of Central America and some of the interior valleys of Guatemala and Honduras (*Leptodrymus pulcherrimus* and *Scolecophis atrocinctus*) have no known living close relatives. Probably the ancestors of these species were once wide ranging in western Mexico and have not survived to the present time since being isolated from their southern derivatives. Two other endemics in this track, *Norops cuprinus* and *N. isthmicus*, are restricted in distribution to the southeastern and southwestern sides of the Plains of Tehuantepec, respectively. These two species, plus *N. subocularis*, constitute the *N. subocularis* group (Lieb, 1981). Lieb (1981:247–255) postulated a western Mexico origin for this group and the *N. nebulosus* group, with the *N. subocularis* group precursor evolving in coastal Guerrero and Oaxaca and the *N. nebulosus* precursor evolving to the northwest. The *N. subocularis* group

precursor subsequently evolved into *N. cuprinus* and *N. isthmicus* at the southeastern end of the range of this group. The final endemic in this track (*Phyllodactylus muralis*—Plains of Tehuantepec) is closely related to the wide-ranging SA species *P. tuberculosus*. On the other hand, eight non-endemics (*Rhinophrynus dorsalis*, *Agkistrodon bilineatus*, *Coniophanes piceivittis*, *Crotalus durissus*, *Imantodes gemmistratus* [although Savage and Scott, 1985, have suggested that the Yucatan population might represent a distinct species], *Masticophis mentovarius*, *Senticolis triaspis*, and *Stenorrhina freminvillei*) have populations in each of the three major areas of endemism and in western Mexico as well, whereas another species (*Hypopachus variolosus*) has populations in each of these areas, except for the Plains of Tehuantepec. Each of these nine species also occurs in one or more of the interior valleys under consideration herein and eight (*S. freminvillei* the exception) also occur in eastern Mexico north of the Isthmus of Tehuantepec. Conant (1986) and Van Devender and Conant (1990) have postulated that the northeastern Mexican population of *A. bilineatus* was isolated in the Miocene from a formerly continuous coast-to-coast distribution across northern Mexico. This isolation resulted from the uplift of the Sierra Madre Oriental and Occidental and the increasing aridity of the central Mexican Plateau. These authors also believed that the northeastern population of this species has remained isolated from conspecific populations subsequent to its fragmentation (Cohn, 1965, and Morafka, 1977, have presented a more detailed discussion of this Miocene transplateau subhumid corridor). The remaining species in this group are more widely distributed throughout their respective ranges in eastern Mexico, and probably represent comparatively recent dispersalists capable of crossing relatively short stretches of more mesic vegetational formations during previously more favourable Quaternary conditions, and, therefore, capable of making periodic secondary contact with populations that were previously isolated. Another non-endemic, *Ctenosaura similis*, has populations in each of the three areas of endemism and in most of the subhumid interior valleys of Guatemala and Honduras, but does not occur north of the Isthmus of Tehuantepec, where it is replaced by its closest relatives from which it seems to be derived (see Fig. 55 in De Queiroz, 1987). Based on its overall distribution, it seems likely that *C. similis* is a good dispersalist that is also capable of making secondary contact with periodically isolated populations. Another group of 10 non-endemics (*Gastrophryne usta*, *Rhinoclemmys pulcherrima*, *Cnemidophorus deppei*, *Heloderma horridum*, *Phyllodactylus tuberculosus*, *Sphenomorphus assatus*, *Enulius flavitorques*, *Leptodeira nigrofasciata*, *Loxocemus bicolor*, and *Trimorphodon biscutatus*) has penetrated to varying degrees along the Pacific lowlands

TABLE 11. Syn-taxon groups of endemic species occurring in one or more of the three major areas of endemism.

	TEH	YUC	Pacific Central America	West Mexico	Reference
<i>Triprion petasatus</i>		X			Trueb, 1970
<i>Triprion spatulatus</i>	X			X	
<i>Cnemidophorus angusticeps</i>		X			Duellman and Zweifel, 1962
<i>Cnemidophorus motaguae</i>			X		
<i>Cnemidophorus costatus</i>				X	
<i>Ctenosaura defensor</i>		X			De Queiroz, 1987
<i>Ctenosaura palearis</i> ¹					
<i>Ctenosaura quinquecarinata</i>	X		X		
<i>Ctenosaura clarki</i>				X	
<i>Eumeces managuae</i>			X		Taylor, 1935
<i>Eumeces schwartzei</i>		X			
<i>Eumeces altamirani</i>				X	
<i>Sceloporus edwardtaylori</i>	X				Hall, <i>in</i> Sites et al., 1992
<i>Sceloporus lundelli</i>		X			
<i>Sceloporus horridus</i>				X	
<i>Sceloporus carinatus</i> ¹					Hall, <i>in</i> Sites et al., 1992
<i>Sceloporus squamosus</i>			X		
<i>Sceloporus siniferus</i>	X			X	
<i>Geagras redimitus</i>	X				Wilson and Meyer, 1981
<i>Tantilla calamarina</i>				X	
<i>Porthidium dunni</i>	X				Campbell and Lamar, 1989
<i>Porthidium ophryomegas</i>			X		
<i>Porthidium yucatanicum</i>		X			
<i>Porthidium hespere</i>				X	
<i>Sibon anthracops</i>			X		Kofron, 1987
<i>Sibon fasciata</i>	X	X		X	
<i>Sibon philippi</i>				X	
<i>Symphimus mayae</i>		X			Rossman and Schaefer, 1974
<i>Symphimus leucostomus</i>	X			X	

¹ Only known in the area under study from two interior valleys.

into Central America, but has not reached the Yucatan Peninsula (*G. usta*, *C. deppei*, and *T. biscutatus* have reached Veracruz). All of these species, except for the *Rhinoclemmys*, have been recorded from the Central Depression of Chiapas. Many of these species are also well represented in the interior valleys of Guatemala and Honduras. A final group of 12 non-endemics (*Bufo marmoreus*, *Pachymedusa dacnicolor*, *Syrhophus pipilans*, *Rhinoclemmys rubida*, *Cnemidophorus guttatus*, *Ctenosaura pectinata*, *Phrynosoma asio*, *Sceloporus melanorhinus*, *Urosaurus bicarinatus*, *Conophis vittatus*, *Leptophis diplotropis*, and *Salvadora lemniscata*) have reached the Plains of Tehuantepec and the Central Depression of Chiapas (except for *Pachymedusa*), but not the Yucatan Peninsula (*B. marmoreus* and *C. guttatus* have reached Veracruz), nor the subhumid Pacific lowlands of southeastern Guatemala southward, nor the interior valleys of Guatemala or Honduras. These 12 species probably are very recent dispersalists into the subhumid forests under study. In summary, it appears that members of this track include those that have evolved *in situ* from formerly widespread ancestors involving vicariance events and others that have dispersed into the study area rather recently.

2. EASTERN MEXICAN GENERALIZED TRACK (8 species; Table 10; Fig. 4)

The ancestors of and/or the species in this track are postulated to have reached the subhumid forests of Middle America by dispersing southward from the subhumid lowlands of northeastern Mexico. Four species are in the Young Northern, two in the Old Northern, and two in the Middle American historical units. Martin (1958:93) has discussed evidence suggesting that subhumid conditions may have been continuous at times during the Pleistocene in the coastal lowlands from northeastern Mexico to the Yucatan Peninsula (his Gulf Arc component). Three Yucatan endemics in this track appear to have arisen *in situ* after range fragmentation of their respective more widespread ancestors. These species are as follows (closest relatives are indicated parenthetically):

Terrapene yucatana (*T. carolina*)

Sceloporus chrysostictus (*S. cozumelae* and *S. variabilis*)

Sceloporus cozumelae (*S. chrysostictus* and *S. variabilis*)

Hall (see Fig. 19 in Sites et al., 1992) placed *S. chrysostictus* in a monotypic group, without providing evidence

FIG. 4. Generalized tracks of the eight Subhumid Assemblage species belonging to the Eastern Mexican Generalized Track.

for its relationships to other species (*fide* Sites et al., 1992). However, Cole (1978) placed this species in the *S. variabilis* group based on a chromosomal synapomorphy. Our proposed scenario would require *S. chrysostictus* to be derived from a *variabilis*-like ancestor. The overall historical biogeography of the genus *Sceloporus* (see Sites et al., 1992) would suggest a northeastern Mexican origin for the *variabilis* group. Larsen and Tanner (1975:14) presented a different scenario for the *S. variabilis* group, postulating the origin of the members of the group from *S. cozumelae*, an insular or coastal form on the mainland, at a time when the present-day range of this species was part of a submarine bank. *Sceloporus variabilis*, also a member of the Eastern Mexican Generalized Track, occurs from southern Texas, USA, to northwestern Costa Rica. Pleistocene dispersal southward from its region of origin in northeastern Mexico (along the east coast of Mexico to the Isthmus of Tehuantepec, across the Isthmus of Tehuantepec and southward along the Pacific coast to northwestern Costa Rica, and into the subhumid interior valleys of Mexico, Guatemala, and Honduras) is postulated for this species. Another species in this track, *Sceloporus serrifer*, belongs to a group (*S. torquatus* species group) postulated to have evolved on the Mexican Plateau (see Fig. 35 in Sites et al., 1992). The present-day range of *S. serrifer* (includes *S.*

cyanogenys; see Olson, 1987) is from southern Texas, USA, to the Yucatan Peninsula and north-central Guatemala. Another species in this track, *Tantilla rubra*, probably utilized a north-to-south dispersal along the foothills of eastern Mexico, and then across the Isthmus of Tehuantepec to the Plains of Tehuantepec and then into the Central Depression of Chiapas. Two final members of this track, *Norops sericeus* and *Conophis lineatus*, are postulated to have dispersed southward from eastern Mexico. Both have populations on the outer Yucatan Peninsula, the Pacific coastal areas, and in many of the interior valleys.

3. MIDDLE AMERICAN GENERALIZED TRACK (10 species, Table 10; Fig. 5)

The species in this track are postulated to have evolved *in situ* in the developing subhumid forests of the Pacific lowlands of southern Mexico and Central America. Six species are in the Old Northern and four are in the Middle American historical units. The events responsible for this development were the Miocene–Pliocene uplift of the main mountain axis of the area along with the associated climatic changes that gradually fragmented a generally widespread mesic Middle American herpetofauna into

FIG. 5. Generalized tracks of the 10 Subhumid Assemblage species belonging to the Middle American Generalized Track.

three groups: a western subhumid lowland assemblage, an eastern mesic lowland assemblage, and a central upland assemblage (see discussion in Major Geohistorical Events). The species in this group are as follows (closest relatives in either the eastern lowland or upland assemblages are indicated parenthetically):

Oedipina stuarti (*uniformis* subgroup of
O. uniformis group)

Oedipina taylori (*uniformis* subgroup of
O. uniformis group)

Bufo canaliferus (*B. valliceps*)

Bufo luetkeni (*B. valliceps*)

Staurotypus salvini (*S. triporcatus*)

Coleonyx elegans (*C. mitratus*)

Lepidophyma smithi (*L. flavimaculatum*)

Norops cupreus (*N. dollfusianus*)

Sibon carri (*S. fisheri*)

Tantilla striata (*T. jani* and *T. taeniata*)

All of the species in this track are in our endemic category, except for *C. elegans* and *L. smithi*. Grismer (1988) postulated an early Pliocene origin south of the Tehuantepec Portal for the *C. elegans-mitratus* ancestor. Such a scenario would allow for the *in situ* development of *C. elegans* in the evolving Pacific lowlands with subsequent Quaternary dispersal across the Isthmus of

Tehuantepec to the Yucatan Peninsula and up the east coast of Mexico.

4. EASTERN MIDDLE AMERICAN GENERALIZED TRACK (9 species; Table 10; Fig. 6)

The species in this track are postulated to have evolved *in situ* from a mesic-adapted ancestor widely distributed in Middle America from the base of the Yucatan Peninsula southward. Six species are in the Middle American and three are in the Old Northern historical units. The species in this track are as follows (closest relatives are indicated parenthetically):

Bolitoglossa yucatana (*B. dofleini*)

Eleutherodactylus yucatanensis (*E. alfredi*)

Kinosternon creaseri (*K. acutum*)

Laemactus serratus (*L. longipes*)

Coniophanes meridianus (*C. imperialis*)

Dipsas brevifacies (*D. bicolor*)

Imantodes tenuissimus (*I. cenchoa*)

Sibon sanniola (*S. dimidiata*)

Tantilla cuniculator (*T. taeniata*)

All species in this track, except for *L. serratus*, are endemic to the Yucatan Peninsula. Our generalized track analysis predicts that these Yucatan endemics arose from stocks

FIG. 6. Generalized tracks of the nine Subhumid Assemblage species belonging to the Eastern Middle American Generalized Track.

that dispersed into the emerging outer Yucatan Peninsula and evolved in association with the developing subhumid forests in the middle to late Pleistocene, or, in a few cases in humid pockets (e.g., *cenotes*) within the forest. Lang (1989), after reviewing the geological history of Mesoamerica, also postulated a Yucatan-based origin for both *Laemantus* species. Subsequently, stocks of *L. serratus* were able to disperse up the east coast of Mexico after having evolved on the outer Yucatan Peninsula. The more southern populations of this species (Central Depression of Chiapas, Sula Plain, and eastern Guatemala and Belize) could have developed *in situ* in the developing subhumid forests of these regions, or, could possibly reflect rather recent dispersal events. We are unable to find any evidence to support Lee's (1980:37) contention that the outer end of the Yucatan Peninsula "... was once a more mesic environment than it is today." He suggested such because of "the presence of three mesic-adapted species isolated at the outer end of the peninsula, far to the north of their relatives." Two extant species (*Bolitoglossa yucatanana* and *Eleutherodactylus yucatanensis*), as noted by Lee (1980), occur in cenotes and caves in the karst topography and the Holocene fossil form *Lepidophyma arizelogyphus* belongs to a genus with extant cavernicolous members. We suspect that these taxa evolved in

association with these mesic pockets as they formed rather than within widespread mesic forests that retreated "with the onset of drier conditions ..." (Lee, 1980:37).

5. SOUTH AMERICAN GENERALIZED TRACK (6 species; Table 10; Fig. 7)

The species in this track, or their ancestors, probably dispersed from south to north through a now-vanished subhumid corridor soon after the closure of the Panamanian Portal in the Pliocene. All are in the South American Historical Unit. Three of these species (*Phrynohyas venulosa*, *Gymnophthalmus speciosus*, and *Leptotyphlops goudoti*) are widespread in the area under study and in northern South America as well, and appear to be very capable dispersalists. *Manolepis putnami* is provisionally placed in this track on the basis of the molecular work of Cadle (1984). However, the present-day distribution of this snake is in the Pacific coastal lowlands of Mexico from Nayarit to the Plains of Tehuantepec, suggesting a biogeographic relationship with the final group of 12 species discussed in our Western Mexican Generalized Track. The final two species in this track, *Leptotyphlops nasalis* and *Typhlops microstomus*, are endemic to the Pacific lowlands of Nicaragua and to the Yucatan

FIG. 7. Generalized tracks of the six Subhumid Assemblage species belonging to the South American Generalized Track.

Peninsula, respectively, suggesting that these two species evolved *in situ* after isolation of their respective ancestors subsequent to crossing the Panamanian Isthmus.

DOES STUART'S SUBHUMID CORRIDOR EXIST?

In 1954, L. C. Stuart wrote a seminal paper in which he identified a subhumid corridor through the mountainous interior portion of southeastern Mexico and Guatemala. The corridor he envisioned consisted of the Plains of Tehuantepec, the Central Depression of Chiapas, the upper Rio Negro Valley (including the Salama Basin), the middle and upper Motagua valley, and the dry uplands and lowlands of southeastern Guatemala. Another arm of this corridor was thought to extend into the interior valleys of Honduras from the Motagua Valley. Stuart (1954a:24) submitted that "... herpetological indicators such as closely related species, subspecies, or populations in the genera *Hypopachus*, *Sceloporus*, *Enyaliosaurus* [= *Ctenosaura* in part], *Cnemidophorus*, and *Leptodeira* could have reached the subhumid lowlands of Honduras, Guatemala, and the Pacific versant of lower Central America *only* [italics ours] through this corridor." Stuart (1954a:23) stated that "... dry-land types probably entered the corridor shortly after its formation had begun. As uplift continued, first one species and then another was broken into populations isolated one from another by highland breaks in the corridor." Stuart's study was admittedly based on limited distributional data (he examined little material from Honduras, for example) and so it is pertinent in this paper to revisit this concept in light of the more substantial data base that has accrued in the intervening 40 years.

Portions of the subhumid segments of Stuart's interior corridor are in direct contact with its closest counterpart today. Direct contact of the Motagua Valley-Pacific coastal Guatemala subhumid areas is facilitated along river valleys through the southeastern highlands of Guatemala and adjacent El Salvador (Campbell and Vannini, 1988; Stuart, 1954a, 1954b) and that of the Plains of Tehuantepec-Central Depression of Chiapas through a "connecting portal" at the northwestern portion of the latter (Johnson, 1990:276). In addition to the late Tertiary, when the corridor was being formed, direct contact of each of these two present-day connections would have been more extensive during certain past Quaternary periods when subhumid forests were apparently more extensively distributed throughout the area. On the other hand, the Rio Negro Valley is presently separated from the Central Depression of Chiapas by an elevation of about 1900 m along the continental divide and the Rio Negro Valley is separated from the Motagua Valley by a pass at about 1400 m (Stuart, 1954a). These gaps are presently in the pine-oak

zone (Stuart, 1954a). Similar oak-pine zones separate the tributaries of the Río Motagua of Guatemala from those of the Río Chamelecón (included herein as a portion of the Sula Plain) in the central portion of the Honduran Department of Copán, where at one point (about 14°54'N, 88°54'W) near 1100 m, tributaries of these two river systems approach within one kilometre of each other.

Inasmuch as Stuart (1954a:22) proposed this corridor as "... a pathway for the dispersal of the indicators mentioned," we will utilize the data on distribution of the members of our Subhumid Assemblage for our re-examination of the importance of Stuart's subhumid corridor as an exclusive Tertiary dispersal route for the subhumid-adapted species. As we did with the 212 species, we also employed the CBR algorithm using just the 96 Subhumid Assemblage (SA) species. The average value of the similarity matrix (Table 12) comparing these 96 SA species in the 16 areas is 0.52. The 16 areas are listed below in rank order, according to their respective average value.

Pacific coast of northwestern Costa Rica	0.63
Pacific coast of Nicaragua	0.62
Pacific coast of Guatemala	0.62
Pacific coast of El Salvador	0.61
Pacific coast of Honduras	0.59
Middle and upper Choluteca Valley	0.58
Comayagua Valley	0.57
Middle and upper Motagua Valley	0.56
Sula Plain	0.55
Upper Rio Negro Valley	0.48
Central Depression of Chiapas	0.48
Middle Aguan Valley	0.44
Guayape-Guayambre Valley	0.43
Plains of Tehuantepec	0.41
Otoro Valley	0.37
Outer Yucatan Peninsula	0.31

Examination of this list indicates that the same Pacific coastal areas (those with subhumid conditions presently in continuous contact) and the same two interior valleys (each with a presently continuous contact with a Pacific coastal area) with high average values in the analysis of the total herpetofauna also have high average values when just the SA species are analyzed (although in different rank order). The Comayagua Valley, which previously had an average value just above the overall average value, now has a relatively high average value. In addition, the Sula Plain now has a relatively high average value, whereas in the analysis of the total herpetofauna, it had a relatively low value.

As shown with the total herpetofauna, the outer Yucatan Peninsula, the Plains of Tehuantepec, and the Central Depression of Chiapas, areas with high numbers of SA species, also have low average values, further

TABLE 12. Comparison of the Subhumid Assemblage species of the 16 subhumid forest areas. N = species at each site; N = species in common between two sites; *N* = Coefficients of Biogeographic Resemblance. See Table 1 for an explanation of area abbreviations.

	TEH	YUC	CDC	RNV	MV	PG	PES	PH	CHV	COV	OV	SP	AV	GGV	PN	PCR
TEH	54	12	37	10	15	26	28	18	14	14	5	16	7	7	22	22
YUC	0.26	38	16	8	8	14	15	10	9	10	4	13	5	4	14	14
CDC	0.76	0.40	43	15	16	24	26	17	16	13	7	17	8	6	21	21
RNV	0.29	0.30	0.51	16	11	14	14	12	11	9	6	8	7	6	13	13
MV	0.38	0.25	0.46	0.52	26	22	23	18	18	14	6	13	12	9	21	21
PG	0.58	0.38	0.61	0.54	0.71	36	34	23	20	18	8	18	11	11	28	28
PES	0.60	0.38	0.63	0.50	0.70	0.89	40	23	22	19	8	18	12	11	31	31
PH	0.45	0.31	0.49	0.57	0.69	0.74	0.69	26	19	15	6	15	9	9	24	24
CHV	0.36	0.29	0.48	0.55	0.72	0.67	0.69	0.76	24	14	7	15	9	9	21	21
COV	0.38	0.35	0.42	0.51	0.62	0.65	0.64	0.67	0.65	19	6	15	8	8	19	19
OV	0.16	0.17	0.27	0.50	0.35	0.36	0.33	0.35	0.44	0.44	8	5	6	5	7	7
SP	0.43	0.45	0.54	0.44	0.57	0.64	0.60	0.65	0.68	0.77	0.36	20	7	7	18	18
AV	0.21	0.20	0.29	0.48	0.62	0.45	0.45	0.46	0.49	0.50	0.57	0.42	13	7	11	11
GGV	0.22	0.16	0.22	0.44	0.49	0.47	0.43	0.49	0.51	0.53	0.53	0.45	0.58	11	11	11
PN	0.49	0.38	0.54	0.51	0.69	0.79	0.83	0.79	0.71	0.70	0.33	0.65	0.46	0.48	35	34
PCR	0.50	0.39	0.55	0.52	0.70	0.80	0.84	0.80	0.72	0.72	0.33	0.67	0.47	0.49	0.99	34

demonstrating the distinctiveness of their herpetofaunas. The remaining areas (Otoro, Guayape-Guayambre, Aguan, and Rio Negro valleys) all have low numbers of SA species and low CBR values.

The network connecting the 16 subhumid areas at a level of significance (LS) of 0.53 is shown in Figure 8. This value was chosen as the LS because it is the proximal number above the overall average value. One area, the outer Yucatan Peninsula, is omitted from Figure 8 because its highest value is only 0.45 (with the Sula Plain). Additionally, it also lies outside the subhumid corridor as envisioned by Stuart (1954a). For the same reasons expressed in the analysis of the total herpetofauna, we have combined Pacific coastal Guatemala with El Salvador (CBR value of 0.89) and Pacific coastal Nicaragua with Costa Rica (0.99) in Figure 8. Examination of Figure 8 indicates that the Pacific coastal lowlands from Guatemala to northwestern Costa Rica are all interconnected by high CBR values of 0.74–0.84, which suggests similarity of their SA herpetofauna, as was also shown in the analysis of their total herpetofauna. All four of the interior valleys with high overall average val-

ues (Choluteca, Comayagua, Motagua, and Sula Plain) are each connected to one or more of these same Pacific coastal areas by a CBR value of 0.67–0.76. The Sula Plain–Comayagua CBR value of 0.77 and the Motagua–Choluteca value of 0.72, and the fact that each of these four valleys have significant interconnecting CBR values with each other (Fig. 8) further indicates the similarities of the SA herpetofauna of these four interior valleys. The Plains of Tehuantepec–Central Depression of Chiapas similarity (CBR 0.76), as also shown in the total herpetofauna, is again demonstrated when just the SA species are considered. The Plains of Tehuantepec also shows a significant CBR value of 0.60 with combined Pacific coastal Guatemala and El Salvador, and the Central Depression of Chiapas also shows significant values of 0.63 with combined Pacific coastal Guatemala and El Salvador, 0.55 with combined Pacific coastal Nicaragua and Costa Rica, and 0.54 with the Sula Plain. Three Honduran interior valleys (Otoro, Guayape-Guayambre, and Aguan) show significant CBR values with few interior valleys (2 to 3) and no Pacific coastal areas.

Perhaps the most significant conclusion from Figure 8

FIG. 8. Coefficient of Biogeographic Resemblance network connecting the subhumid areas at a level of significance of ≥ 0.53 using only the 96 Subhumid Assemblage species. The outer Yucatan Peninsula is omitted from the figure because it shows no level of significance with any other area. Pacific coastal Guatemala was combined with coastal El Salvador, as was Pacific coastal Nicaragua with Pacific coastal Costa Rica (see text). See Figure 1 for a definition of the numbered areas.

is that the Rio Negro Valley does not show a significant CBR value with either the Central Depression of Chiapas or the Motagua Valley. The Rio Negro Valley is literally a central figure in Stuart's envisioned subhumid corridor. If this corridor was significant to the movement of much of the subhumid adapted herpetofauna, then one would expect the Rio Negro Valley to show significant CBR values with both the Central Depression of Chiapas and the Motagua Valley and to the Pacific coastal areas as well. Instead, the Rio Negro Valley only shows significant CBR values (and relatively low significant values at that) of 0.57 with Pacific coastal Honduras, 0.55 with the Choluteca Valley, and 0.54 with the combined Pacific coastal Guatemala and El Salvador (the Rio Negro–Motagua CBR value of 0.52 is just below the overall average value, while the Rio Negro–Central Depression of Chiapas CBR value of 0.46 is significantly lower). The Motagua Valley shows a significant CBR value of 0.57 with its geographically closest Honduran counterpart, the Sula Plain, but at the same time it shows

higher CBR values with three more geographically distant Honduran interior valleys (0.72 with Choluteca and 0.62 with Aguan and Comayagua). Also, as shown above, the Plains of Tehuantepec and the Central Depression of Chiapas show significant CBR values with Pacific coastal areas to the south, but not to either the Rio Negro or Motagua valleys. The above figures do not speak well for the significance of Stuart's subhumid interior corridor as a major Tertiary dispersal route for the subhumid herpetofauna found in these regions today.

With special reference to the 16 Subhumid Assemblage species in the Rio Negro Valley, there is also not much support for the idea of a subhumid corridor extending from the Tehuantepec region through Chiapas and central Guatemala to Honduras, especially as an exclusive Tertiary dispersal route.

The 16 Subhumid Assemblage species resident in the Rio Negro Valley are indicated in Table 13. Of these 16 species, 14 also occur in moderate elevation pine-oak forests, which surround the Rio Negro Valley, and are con-

TABLE. 13. The Subhumid Assemblage species recorded from the interior valleys of Stuart's subhumid corridor. An asterisk following the species name indicates that the species also occurs in moderate elevation pine-oak forests. See Table 1 for a definition of the area abbreviations.

Species	Subhumid Area			Species	Subhumid Area		
	CDC	RNV	MV		CDC	RNV	MV
<i>Oedipina taylori</i>			X	<i>Sceloporus siniferus</i> *	X		
<i>Bufo canaliferus</i>	X			<i>Sceloporus squamosus</i> *			X
<i>Bufo luetkeni</i> *		X	X	<i>Sceloporus variabilis</i> *	X	X	X
<i>Bufo marmoratus</i>	X			<i>Sphenomorphus assatus</i> *	X		
<i>Gastrophryne usta</i>	X			<i>Urosaurus bicarinatus</i> *	X		
<i>Hypopachus variolosus</i> *	X	X	X	<i>Agkistrodon bilineatus</i>	X	X	
<i>Phrynosoma venulosa</i> *			X	<i>Coniophanes piceivittis</i> *	X		
<i>Rhinophrynus dorsalis</i>	X			<i>Conophis lineatus</i> *	X	X	X
<i>Syrrhaptes pipilans</i> *	X			<i>Conophis vittatus</i>	X		
<i>Rhinoclemmys pulcherrima</i> *			X	<i>Crotalus durissus</i> *	X	X	X
<i>Rhinoclemmys rubida</i>	X			<i>Enallagma flavitorques</i> *	X		
<i>Cnemidophorus deppei</i> *	X	X	X	<i>Imantodes gemmistratus</i> *	X		X
<i>Cnemidophorus guttatus</i>	X			<i>Leptodeira nigrofasciata</i> *	X		X
<i>Cnemidophorus motaguae</i> *	X	X	X	<i>Leptodrymus pulcherrimus</i>			X
<i>Coleonyx elegans</i>	X			<i>Leptophis diplotropis</i> *	X		
<i>Ctenosaura palearis</i>			X	<i>Leptotyphlops goudoti</i> *	X	X	
<i>Ctenosaura pectinata</i>	X			<i>Loxocemus bicolor</i>	X		X
<i>Ctenosaura similis</i> *	X		X	<i>Masticophis mentovarius</i> *	X	X	X
<i>Gymnophthalmus speciosus</i> *	X	X	X	<i>Porthidium ophryomegas</i> *			X
<i>Heloderma horridum</i> *	X		X	<i>Salvadora lemniscata</i>	X		
<i>Laemactes serratus</i>	X			<i>Senticolis triaspis</i> *	X		X
<i>Norops sericeus</i> *	X			<i>Sibon anthracops</i> *			X
<i>Phrynosoma asio</i>	X			<i>Sibon carri</i> *			X
<i>Phyllodactylus tuberculatus</i> *	X	X	X	<i>Stenorrhina freminvillei</i> *	X	X	
<i>Sceloporus carinatus</i> *	X	X		<i>Tantilla rubra</i> *	X		
<i>Sceloporus melanorhinus</i>	X			<i>Trimorphodon biscutatus</i> *	X	X	X
<i>Sceloporus serrifer</i> *	X	X					

tinuous with such forests surrounding other subhumid valleys in Mexico and Honduras. The two exceptions are *Agkistrodon bilineatus* and *Trimorphodon biscutatus*, the latter of which has been collected by us in a subhumid-pine forest ecotone in Honduras. In addition, 12 of the 16 species are in our widespread distributional category (the exceptions are *Bufo luetkeni*, *Cnemidophorus motaguae*, and *Sceloporus carinatus* in the endemic category, and *Sceloporus serrifer* in the peripheral category), and, thus, are relatively broadly ecologically adapted. Furthermore, only *Sceloporus carinatus* and *S. serrifer* do not occur in

the Pacific lowlands of Guatemala southward. Finally, the Rio Negro Valley appears to have a depauperate herpetofauna, compared with the Central Depression of Chiapas and the Motagua Valley. The species numbers are, respectively, 37 (16 Subhumid Assemblage [SA] species), 87 (43 SA species), and 52 (26 SA species). If the Rio Negro Valley was part of an important and exclusive Tertiary dispersal route, one would expect that at least an intermediate number of species (compared to the valleys on either side) would occur there.

That such is not the case is evident from an examina-

tion of the SA species in the Central Depression of Chiapas (CDC) and the Motagua Valley (MV), lying on either side of the Rio Negro Valley (RNV). Forty-three species in this assemblage occur in the CDC (Table 13), including 15 of the 16 species in the RNV (the exception is *Bufo luetkeni*). The 15 species common to both valleys, however, are widespread in subhumid forests of Middle America, in general, and in interior valleys specifically. Thus, 28 species occur in the CDC, but not in the RNV (Table 13). In addition, 27 of the 43 CDC species also occur presently in pine-oak forests, providing a modern avenue for those species (Table 13). Finally, 26 of the 43 species occur today along the Pacific coast of Central America (1 reaches only Guatemala, 4 reach only El Salvador, and 21 reach Costa Rica). In sum total, 33 of the 43 species are distributed on the Pacific coast of Central America and/or occur in pine-oak forests (Table 13).

With reference to the MV, 26 SA species are known (Table 13), including 11 of the 16 species in the RNV (the exceptions are *Sceloporus carinatus*, *S. serrifer*, *Agkistrodon bilineatus*, *Leptotyphlops goudoti*, and

Stenorrhina freminvillei). Again, these 11 species are widespread in both subhumid forests in Middle America in general and in interior valleys specifically (Table 13). Thus, 15 species are found in the MV, but not in the RNV (Table 13). In addition, 21 of the 26 MV species also range presently into pine-oak forests (Table 13). Finally, 24 of the 26 species occur today along the Pacific coast of Central America (2 reach only El Salvador, 1 reaches only Honduras, and 21 reach Costa Rica). In sum total, 25 of the 26 species are known from the Pacific coast of Central America and/or pine-oak forests (Table 13).

In the final analysis, the answer to the question posed at the beginning of this section, "Does Stuart's subhumid corridor exist?" is no, at least not as an exclusive Tertiary dispersal route. The species occurring in the interior valleys in Chiapas and Guatemala (as well as in Honduras) are broadly distributed in subhumid forests in Pacific Central America and in pine-oak forests that surround the interior valleys. It is not necessary, thus, to invoke such an interior corridor to explain the distributional patterns in the Subhumid Assemblage of species.

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