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ABSTRACT

A total of 297 species of native terrestrial amphibians and reptiles are known to occur within the boundaries of northwestern Nuclear Central America, that portion of México lying east of the Isthmus of Tehuantepec, exclusive of the Yucatan Peninsula. The major environmental parameters of the area are extremely variable. The distribution of each species is discussed in relation to seven physiographic regions, 10 vegetation formations, and elevation. The herpetofaunal elements are not restricted to particular physiographic regions or vegetation formations, but most species are associated with distinct faunal areas that are defined by climate, topography, and elevation.

Groups of amphibians and reptiles are identified and classified as belonging to 13 geographic assemblages; the distribution of some species do not fit the parameters of any assemblage. Species within each group are listed. Assemblages are composed of species showing continuous or disjunct geographical ranges. Distributional analysis of the herpetofauna reveals that neither the study area nor Nuclear Central America are composed of a homogenious assemblage of amphibians and reptiles, but contain species primarily restricted to the larger Mesoamerican region. The Nuclear Central American highlands contain enough endemic species to justify a Nuclear Central American highland subregion of Mesoamerica. Only 60 species occurring within northwestern Nuclear Central America range into the Nearctic and/or Neotropical regions, and most are considered as having a Mesoamerican origin. Twenty species are regarded as having a Nearctic or Neotropical origin, with a slight majority being Nearctic forms.

Patterns of geographic distribution of the herpetofauna of northwestern Nuclear Central America necessitate the use of both vicariance and dispersal theories for explaining their historical origins. Vicariance events were primarily responsible for affecting pre-Pleistocene source biotas and Pleistocene climatic fluctuations caused the separation of disjunct assemblages described herein. Evidence also supports dispersal of species from previously vicariant populations after Pleistocene and Holocene climatic changes.

INTRODUCTION

Nuclear Central America is that portion of the Middle American land mass stretching from the Isthmus of Tehuantepec, México, to northcentral Nicaragua (Schuchert, 1935). This region is centered around the highlands of southern México, Guatemala, and Honduras. The area is bordered by the Gulf of Mexico on the north, the Caribbean Ocean on the north and east, and the Pacific Ocean on the south. For the purpose of this study, northwestern Nuclear Central America is defined as that part of southern México, exclusive of the Yucatan Peninsula, comprising the state of Chiapas (most of the area) and surrounding parts of Tabasco, Oaxaca, and Veracruz (Fig. 1). The western limit of the study area, on the Isthmus of Tehuantepec, corresponds to the transisthmian highway (Hwy. 185), which runs from Salina Cruz, Oaxaca, northward to near Coatzacoalcos, Veracruz. Location of places and geographic features of the study area mentioned in the text are shown in Figure 2.

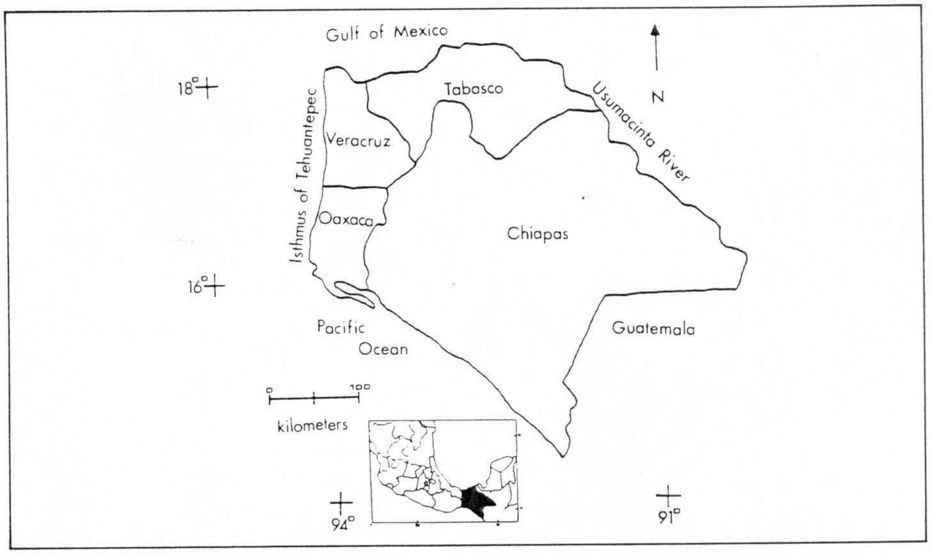


Fig. 1. Northwestern Nuclear Central America showing boundaries and Mexican states or portions thereof contained in the area.

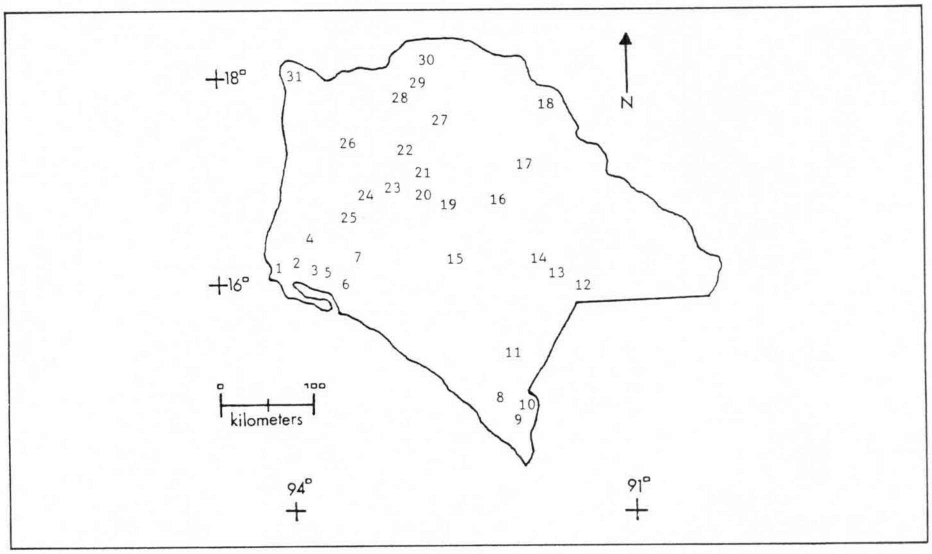


Fig. 2. Location of places and geographic features of northwestern Nuclear Central America referred to in the text. 1. Salina Cruz, Oaxaca; 2. Zanatepec, Oaxaca; 3. Tapanatepec, Oaxaca; 4. Cerro Bául, Oaxaca; 5. Arriaga, Chiapas; 6. Tonalá, Chiapas; 7. Cerro Tres Picos, Chiapas; 8. Huixtla, Chiapas; 9. Tapachula, Chiapas; 10. Volcán Tacaná, Chiapas; 11. Motozintla, Chiapas; 12. Lagos de Montebello, Chiapas; 13. La Trinitaria, Chiapas; 14. Comitán, Chiapas; 15. Presa Angostura, Chiapas; 16. San Cristóbal de las Casas, Chiapas; 17. Ocosingo, Chiapas; 18. Palenque, Chiapas; 19. Chiapa de Corzo, Chiapas; 20. Tuxtla Gutiérrez, Chiapas; 21. Sumidero Canyon, Chiapas; 22. Chicoasén Chiapas; 23. Berriozábal, Chiapas; 24. Ocozocoautla, Chiapas; 25. Cintalapa, Chiapas; 26. Presa Nezahualcóyotl, Chiapas; 27. Pueblo Nuevo Solistahuacán, Chiapas; 28. El Chichón, Chiapas; 29. Pichucalco, Chiapas; 30. Villahermosa, Tabasco; 31. Minatitlań, Veracruz.

Herpetological investigations in northwestern Nuclear Central America have increased during the last 40 years, but most collecting activity has been restricted to the most approachable localities. However, human economic development during the last 20 years (e.g., road building) has opened previously inaccessable areas for faunal sampling. For this reason, the time has come for presentation of new data that will increase our knowledge of distributional and faunal affinities of the herpetofauna of southern México.

Extensive studies of the herpetofauna of northwestern Nuclear Central America and adjacent areas began in 1941. Some important early articles include Taylor (1941a, 1941b), Smith (1942, 1943, 1944, 1947), and Smith and Taylor (1945, 1948, 1950). Both authors, especially Smith, published numerous other papers on the herpetofauna of southern México and Central America while naming and revising taxonomic groups; Smith is still doing so today.

Smith and Taylor's (1945, 1948, 1950) checklists did much to stimulate herpetological research in northwestern Nuclear Central America. Goodnight and Goodnight (1956) and Shreve (1957) made extended field trips to areas of Chiapas not extensively studied before. Alvarez del Toro and Smith (1956, 1958) and Smith and Alvarez del Toro (1962, 1963) began preliminary studies in Chiapas, which culminated in two revisions of a semipopular book by Alvarez del Toro (1960, 1973, 1982). However, Alvarez del Toro's books dealt only with reptiles, and distributional data were limited.

The region of the Isthmus of Tehuantepec has interested a few herpetologists, mainly Hartweg and Oliver (1937a, 1937b, 1938, 1940) and Duellman (1960). Stuart (1954a, 1957) commented on dispersal routes through Nuclear Central America. Stuart (1964, 1966), Duellman (1966), and Savage (1966, 1982) published a series of papers dealing with biogeography of Middle America. Those papers were most significant in outlining overall past and modern distributional patterns of the herpetofauna of southern México and Central America. Other important herpetogeographical studies of particular localities or areas were: Smith and Williams (1963), Landy *et al.* (1966), Smith and Lynch (1967), Baker *et al.* (1971), Wake and Lynch (1976), Johnson *et al.* (1977), and Campbell (1984).

This study is the culmination of about 20 man-months of field work within northwestern Nuclear Central America. The area is important zoogeographically because of the diverse climate, geology, and vegetation, the reported dispersal and vicariant patterns associated with the fauna, and as an important evolutionary center for several herpetofaunal groups (Savage, 1982). The present study is intended to describe the present ecogeographical patterns of distribution of the amphibians and reptiles of northwestern Nuclear Central America, and how they are related to herpetofaunas of other parts of Middle America, North America, and South America.

There is currently controversy regarding the role of major historical factors that have produced the distributional patterns of extant biotic communities. The controversy is centered around the development of vicariance biogeographic theory, which is supported by Croizat *et al.* (1974), Rosen (1976), Nelson and Platnick (1981), Wiley (1981), and Savage (1982), among others. Vicariance biogeographers concur that change in geologic form is the major factor governing the formation of modern distributional patterns. This contrasts with traditional dispersal theory that relates modern distributions to historical dispersal from one area to another. In this study, I examined the distributional patterns of the reptiles and amphibians of the study area, together with data from historical geology and climatology, to try and produce the best explanation as to how modern distributional patterns were attained.

DESCRIPTION OF THE STUDY AREA

Physiography, Climate, and Phytogeography

The land area defined herein as northwestern Nuclear Central America contains approximately 114,000 square km. Inasmuch as the study area includes the same seven physiographic regions recognized for Chiapas, México, I will follow Müllerried (1957) and Breedlove (1973) in describing its physiography (Fig. 3). Climatic information was gained from Vivó Escoto (1964), Wernstedt (1972), Breedlove (1973), and Miranda (1975); temperature and rainfall values are 15 year averages. The phytogeographic patterns were taken from Miranda and Hernandez X (1963), Breedlove (1973), Miranda (1975, 1976), and personal observation. Those references dealt only with the state of Chiapas, but the associated vegetation of the study area is continuous with Chiapan regions, so they are used for describing the study area. Breedlove (1973) divided the major vegetational associations into 10 formations (Table 1) based on rainfall and elevation characteristics. Optimum formations are four types of humid forests receiving enough rainfall to maintain a continuously moist leaf litter, and the seasonal vegetation is composed of four subhumid formations and two transitional (semihumid) formations whose ecological parameters fall in between humid and semihumid conditions. Breedlove (1973) also described nine restricted formations of treeless and wetland types, but no faunal assemblages can be recognized within them, so they will not be included in the ecogeographical analyses. See Breedlove (1973) and Miranda (1975) for the descriptions of all vegetation formations and the dominant plant species within each formation. It should be pointed out that human influences have drastically altered many natural ecosytems in southern México. There are still some relatively undisturbed areas existing in the Northern and Eastern Highlands and sections of the Sierra Madre de Chiapas (Fig. 3), but these are rapidly being developed for economic growth and subsistence for an ever-expanding human population. The description of the physiographic regions and their related climate and vegetation associations are as follows.

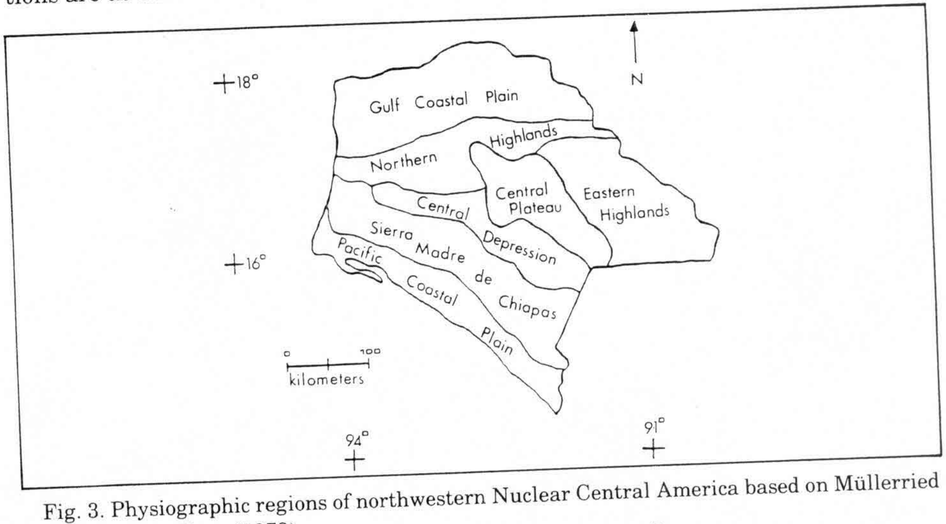


Fig. 3. Physiographic regions of northwestern Nuclear Central America based on Müllerried (1957) and Breedlove (1973).

TABLE 1

Major vegetation formations of northwestern Nuclear Central American based on Breedlove (1973) and their approximate elevational ranges and occurrence in physiorgraphic regions. PC = Pacific Coastal Plain; SM = Sierra Madre de Chiapas; CD = Central Depression; CP = Central Plateau; EH = Eastern Highlands; NH = Northern Highlands; and GC = Gulf Coastal Plain.

HUMID (WETLAND) FORMATIONS
1. Tropical rainforest: 0 - 200 m el.; EH, GC.
2. Lower montane rainforest: 100 - 800 m el.; SM, EH, NH.
3. Montane rainforest: 800 - 2500 m el.; SM, EH, NH, CP.
4. Evergreen cloud forest: 1500 - 3000 m el.; SM, CP.

SEMIHUMID (TRANSITIONAL) FORMATIONS
1. Evergreen and semi-evergreen seasonal forest: 0 - 1200 m el.; PC, SM, CD, CP, EH, NH, GC.
2. Pine-oak-*Liquidambar* forest: 1200 - 3000 m el.; SM, CP, EH, NH.

SUBHUMID (DRYLAND) FORMATIONS
1. Pine-oak forest: 700 - 2900 m el.; SM, CD, CP.
2. Tropical deciduous forest: 0 - 1200 m el.; PC, SM, CD, CP.
3. Thorn Woodland: 0 - 1200 m el.; PC, SM, CD, CP.
4. Short-tree Savanna: 0 - 1200 m el.; PC, CD.

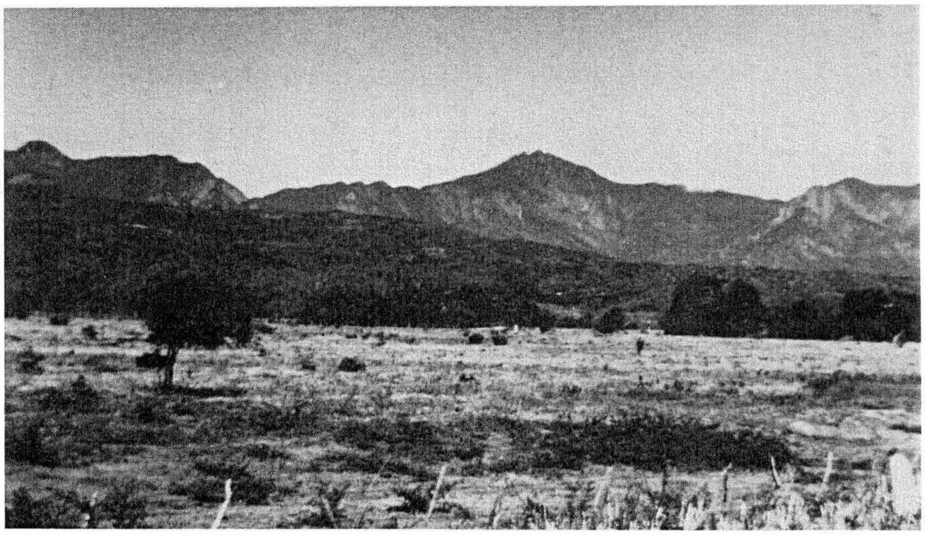


Fig. 4. The foreground pictures typical short-tree savanna of the Pacific Coastal Plain. In the distance is the Sierra Madre de Chiapas with the distinctive peak, Cerro Tres Picos, northeast of Tonalá, Chiapas.

1. *Pacific Coastal Plain* (Fig. 4). - This region is a narrow lowland strip running the entire length of the study area. It is part of a more or less continuous coastal plain that extends from northern México to Costa Rica. The region is relatively flat in the northwest and hilly in the southeast, but elevation is low (less than 200 m). The Coastal Plain is mostly composed of metamorphic strata covered by superficial deposits of Quaternary clay, sand, and cobblestones eroded from the Sierra Madre de Chiapas. Some igneous intrusive rocks (Precambrian and Paleozoic age) can also be found within the region.

The Pacific Coastal Plain is continually warm, with the northwestern portion being hottest and dryest. Average annual temperature at Tonalá, Chiapas (55 m el.) is near 25°C. Temperature is highest on the Isthmian plain. Salina Cruz, Oaxaca (55 m el.) has an average annual temperature of 26.6°C (Contreras, 1942). Annual average temperature in the southeast (Tapachula, Chiapas, 178 m el.) is 25.3°C, and is regulated somewhat by higher amounts of precipitation. High winds are common near the Isthmus of Tehuantepec, especially during the dry season (winter and spring).

Rainfall is variable along the Pacific Coastal Plain, with moist conditions occurring in the southeast. Tapachula has an average annual rainfall near 2500 mm. Rainfall decreases northwestward where subhumid conditions prevail. Tonalá receives about 1600 mm of annual rainfall and Salina Cruz about 1040 mm. Throughout the region, rainfall is seasonal, especially in the northwest. At Salina Cruz, 98% of the annual rainfall occurs from May through October. At Tonalá, the same monthly pattern is 96%. At Tapachula, 91% of the rainfall occurs from May through October, but only December, January, and February have less than 25 mm of rainfall. At Salina Cruz, less than 25 mm of rain falls during the months of Novermber through April; the same pattern is seen at Tonalá. The wettest month at Salina Cruz is July (*ca.* 330 mm), and June in Tapachula (473 mm). September is the second wettest at Salina Cruz and Tapachula (223 mm and 437 mm respectively) and July at Tonalá (302 mm). The data demonstrate the occurrence of two seasons, a summer rainy season and a dry winter.

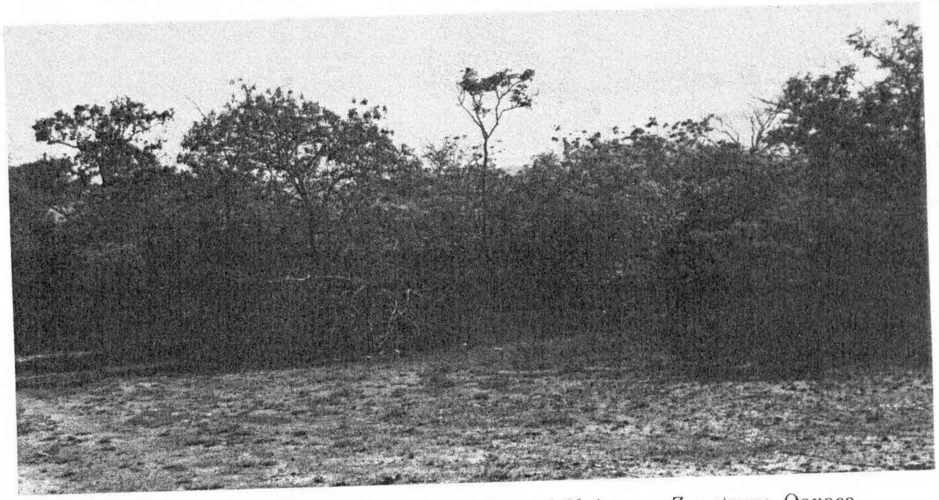


Fig. 5. Typical thorn woodland on the Pacific Coastal Plain near Zanatepec, Oaxaca.

The Pacific Coastal Plain reflects its climatic pattern in the distribution of its vegetation. Evergreen and semi-evergreen seasonal forest occurs on the southwestern portion. Tropical deciduous forest, short-tree savanna (Fig. 4), and thorn woodland are found in the subhumid northwest. Tropical deciduous forest is most common on well-drained areas and along the lower foothills of the Sierra Madre de Chiapas. Thorn Woodland is best developed on the plains of the Isthmus of Tehuantepec (Fig. 5). Today, much of the Coastal Plain has been altered by human activity and most is savanna used for grazing by cattle. Along the entire Pacific coast, a continuous stand of mangroves (a restricted formation) is found in conjunction with swamps and estuaries.

2. *Sierra Madre de Chiapas* (Fig. 4). - The Sierra Madre parallels the Pacific Coastal Plain from the Guatemalan border to the Isthmus of Tehuantepec. It is more or less a continuation of the Southwestern Highlands of Guatemala. Elevation along the continental divide is highest in the southeast (*ca.* 4000 m el. maximum), and lowest (near 300 m el.) on the Isthmus of Tehuantepec. Another low section is found from northeast of Arriaga, Chiapas, to the Chiapas-Oaxacan border (*ca.* 750 m el. minimum). From there, the Sierra Madre rises again to heights approaching 2500 m elevation to the north of Zanatepec, Oaxaca. The Sierra Madre is extremely steep on the Pacific versant and less steep on the Gulf slope (except for peaks). The region is composed of metamorphic rocks and sediments of Precambrian, Paleozoic, and Mesozoic age. The mountains, as structured today, were formed by tectonic activities that began during the mid-Cenozoic and continued through the Pliocene (Dengo, 1968; Wake and Lynch, 1982).

Climatic records are unavailable because of the absence of any sizable centers of population in the Sierra Madre. However, general patterns can be deduced from vegetation, records from adjacent areas, and personal observations. Temperature varies because of elevational factors, and much of the Pacific versant differs from the Gulf slope in rainfall and temperature. Rainfall, at least on the Pacific side and elevated Gulf ridges, is higher in the southeast than northeast of Tonalá, Chiapas, to the Oaxaca border where the Sierra Madre becomes lower in elevation. Rainfall increases again in the mountains north of Zanatepec, Oaxaca.

Rainfall is highest on the Pacific slope of Volcán Tacaná (*ca.* 4000 mm annually) near the Guatemalan border. From Volcán Tacaná northwestward, a humid to semihumid zone occurs on the Pacific slope to northeast of Tonalá. In that zone, rainfall varies from 2000 mm to 3000 mm annually. There is a sharp drop in annual rainfall from north of Tonalá to the Isthmus of Tehuantepec at lower elevations (*ca.* 1600 mm annually). In higher mountains north of Zanatepec, rainfall on the crests probably approaches 2500 mm per year.

Most of the Gulf versant of the Sierra Madre is subhumid because of the rainshadow effect. Motozintla, Chiapas, located on the southeastern sector (1240 m el.), receives approximately 787 mm of rainfall a year, with 97% occurring from May through October. This pattern is probably similar throughout the north-facing Sierra Madre adjacent to the Central Depression. Rainfall averages 2000 to 3000 mm on the Gulf slope adjacent to the humid Northern Highlands.

Rainfall is seasonal throughout the Sierra Madre, with the Pacific southwestern sector receiving more during the year. Seasonal rainfall patterns follow those of the Pacific Coastal Plain, with summer rains (May through October) and a dry winter season (November through April). The dry season is most severe along the Pacific slope from north of Tonalá to the Isthmus of Tehuantepec, and on the Gulf side (except high areas north of the continental divide) adjacent to the Central Depression.

Annual average temperatures at the highest elevations (tierra fría), above 2000 m, are 15°C or less. Days at those elevations are usually mild (15°C to 25°C), but nights are cool (less than 10°C). Frost is common during the winter months of December through January. Climate on the upper slopes of Volcán Tacaná is severe enough during the year to prevent tree growth (páramo). Moderate elevations (1000 to 2000 m el., tierra templada) in humid areas have an average annual temperature of 15°C to 25°C and subhumid areas are warmer (averages 20°C to 27°C).

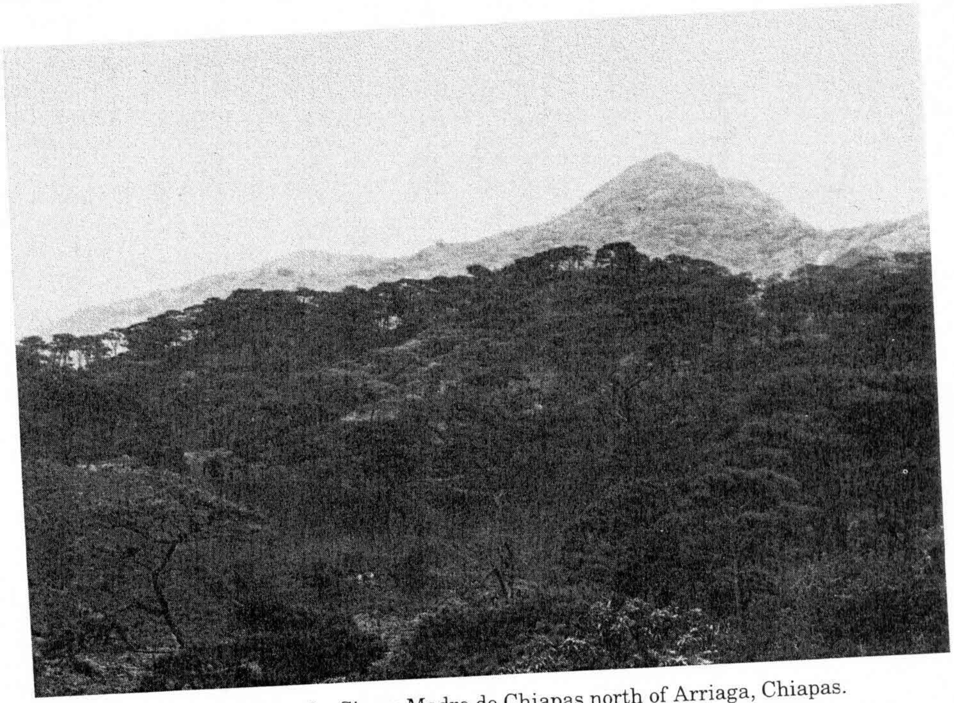


Fig. 6. Pine-oak forest on the Sierra Madre de Chiapas north of Arriaga, Chiapas.

The Sierra Madre contains humid, transitional, and subhumid plant formations. Humid formations are most common at their respective elevations on the southwestern Sierra Madre, and also in local areas in the mountains north of Zanatepec, Oaxaca. Transitional formations of evergreen and semi-evergreen seasonal forest (low and moderate elevations) and pine-oak-*Liquidambar* forest (moderate and high elevations) are found mainly on the southwestern sector of the Sierra Madre. Pine-oak forest (Fig. 6) is found at moderate and high elevations on both slopes in subhumid conditions, especially on the northwestern sector and on slopes adjacent to the Central Depression. This formation may occur as low as 700 m elevation on well drained ridges. However, at lower elevations in subhumid conditions, tropical deciduous forest (Fig. 7) is prevalent. Much of the tropical deciduous forest has been slashed and burned for agriculture.

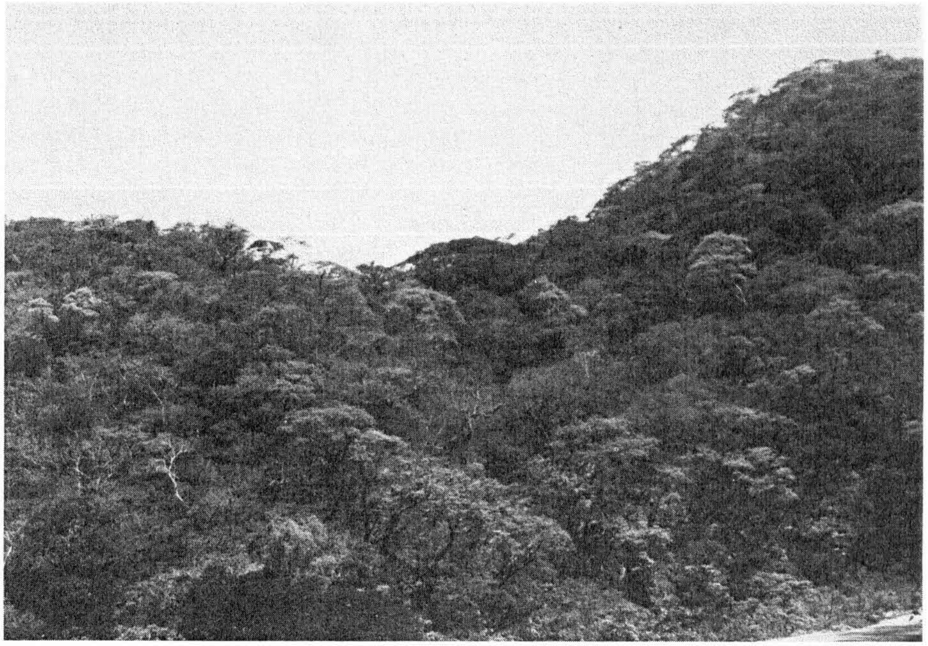


Fig. 7. Tropical deciduous forest on the Sierra Madre de Chiapas northeast of Tapanatepec, Oaxaca.

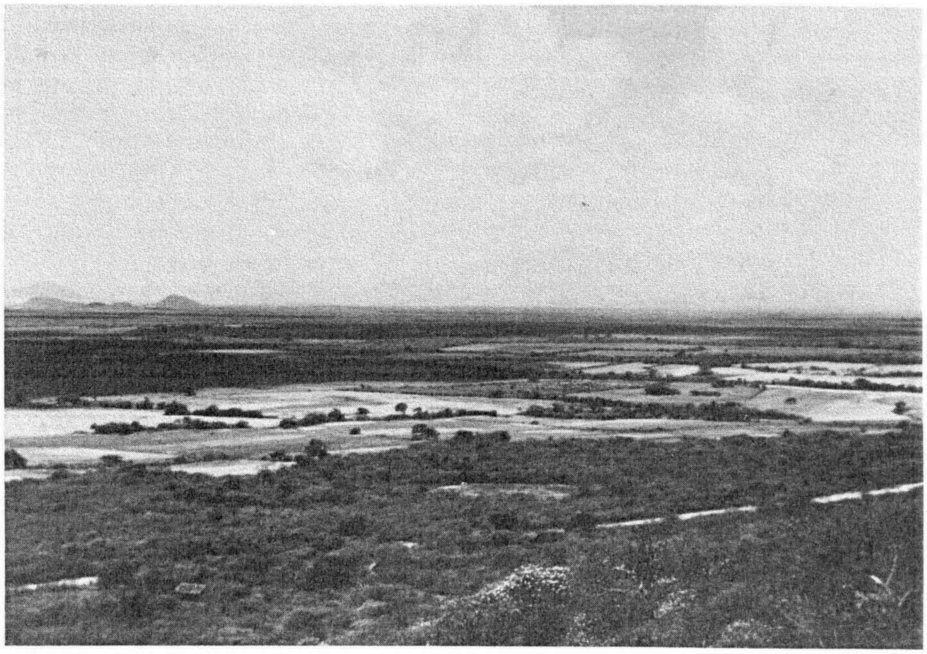


Fig. 8. The Central Depression physiographic region near Chiapa de Corzo, Chiapas.

3. *Central Depression* (Fig. 8). - The Central Depression lies between the Sierra Madre de Chiapas and Central Plateau to the east and between the Sierra Madre and Northern Highlands to the west. The region is drained by the Río Grijalva system. The valley runs northwest to southeast for approximately 250 km from the Oaxaca-Chiapas border to an area where it abuts the Sierra de los Cuchumatanes of west-central Guatemala (Stuart, 1954a). Elevations in the Depression range from about 1000 m near the Guatemalan border and 750 m near the Oaxacan border, to the lowest point near the town of Chiapa de Corzo (*ca.* 400 m) in the central part where the Río Grijalva enters Sumidero Canyon. The valley floor is uneven and moderately dissected by tributaries of the Río Grijalva. Geological strata are marine limestone (Mesozoic), slates, and conglomerate.

The Central Depression is warm (tierra caliente) and subhumid throughout, with seasonal rainfall. The average annual temperature at Tuxtla Gutiérrez, Chiapas (536 m el.), in the lower Depression, is 24°C. Rainfall averages 965 mm per year, with most falling from May through October (96%). At Cintalapa (555 m el.), in the western part of the Depression, the average yearly temperature is 23°C, with an annual rainfall of 832 mm. At that locality, 97% of the rainfall occurs from May through October. Both Tuxtla Gutiérrez and Cintalapa have maximum rainfall during June (229 mm and 207 mm, respectively). Most winter rains accompany "nortes" which sweep across the study area from north to south.

The Central Depression is climatically subhumid throughout, and the vegetation reflects the seasonal aridity. Climax plant communities are rare because the Depression is extensively farmed. Breedlove (1973) stated that the region was originally covered primarily by tropical deciduous forest. This formation is still observed at localities where farming is impractical. Much of the Depression today is covered by short-tree savanna and thorn woodland. Evergreen and semi-evergreen seasonal forest can be found adjacent to humid formations and in protected localities. Most of the Central Depression is surrounded by humid formations, with the exception of the northwestern sector of the Sierra Madre de Chiapas near the Oaxaca-Chiapas border. In that

Fig. 9. The Central Plateau physiographic region near San Cristóbal de las Casas, Chiapas.

area, there is a continuous corridor of subhumid vegetation from the Depression, through the Sierra Madre, to the Pacific Coastal Plain.

4. *Central Plateau* (Fig. 9). - The Central Plateau lies south of the Northern Highlands, east of the Central Depression, and west of the Eastern Highlands. The Plateau is more or less continuous with the Sierra de los Cuchumatanes of Guatemala, although there is an area of lower elevation between the two regions (Comitán - La Trinitaria area) that seems to mark an ecological separation between the two highland areas (at least at the present time). The Plateau is a highland mass centered near San Cristóbal de las Casas. The Plateau's summit varies from near 2100 to 2900 m in elevation on higher peaks. The region is covered with Mesozoic limestone that was uplifted during the Cretaceous or early Paleocene (Wake and Lynch, 1982). Extrusions of volcanic rocks can be found on some of the higher peaks.

The Central Plateau attains high elevations, so temperature patterns are similar to those of the Sierra Madre. Zones above 2000 m have mean annual temperatures below 15°C and winter temperatures frequently approach 0°C at night. Temperature at lower elevations (1500 to 2000 m) tend to be warmer, especially on the southern end of the Plateau. Comitán, Chiapas (1630 m el.), has an average annual temperature of about 17.6°C. Summer temperatures usually average in the low 20's degrees C, and winters average near 11°C.

Rainfall patterns vary considerable between the subhumid southern and humid northern portions of the Plateau. Comitán, on the south, has an average rainfall of about 1000 mm. San Cristóbal de las Casas (2128 m el.), on the middle Plateau, has an average annual rainfall of approximately 1168 mm and the wet northern slopes average close to 3000 mm per year. Accordingly, the north-facing slopes and higher peaks are bathed in clouds, especially at night. Seasonal rainfall shows a marked summer rainy season at Comitán where 94% of the rainfall occurs from April through October, and June (214 mm) and September (202 mm) are the wettest months. At San Cristóbal de las Casas, 95% of the rain falls between April and October, and June (250 mm) and September (247 mm) are the wettest. Although no rain-

Fig. 10. Pine-oak-*Liquidambar* forest on the Central Plateau near Pueblo Nuevo Solistahuacán, Chiapas.

Fig. 11. Evergreen cloud forest on the north-facing slope of the Central Plateau near Pueblo Nuevo Solistahucán, Chiapas.

fall data are available for seasonal rainfall patterns on the wet northern slopes, data from Pichucalco and Palenque, Chiapas (adjacent localities), indicate similar summer rains and a drier winter, but it is probable that more winter rains fall in the northern Plateau than in the middle and southern sections.

The differences in rainfall patterns between the southern end and northern end of the Plateau are reflected by the vegetation. The dry southern edge of the Plateau has tropical deciduous forest at lower elevations that grades into pine-oak forest at higher places. The northeastern escarpment contains pine-oak-*Liquidambar* forest (Fig. 10) and montane rainforest. Pine-oak forest is found throughout the Plateau in subhumid moderate and high elevations. Evergreen cloud forest (Fig. 11) occurs on the highest ridges of the northeastern slopes (the "selva negra" of Alvarez del Toro, 1973). Bunchgrass (a restricted formation) is abundant on some of the higher peaks. Few large stands of undisturbed forest remain because of human activities.

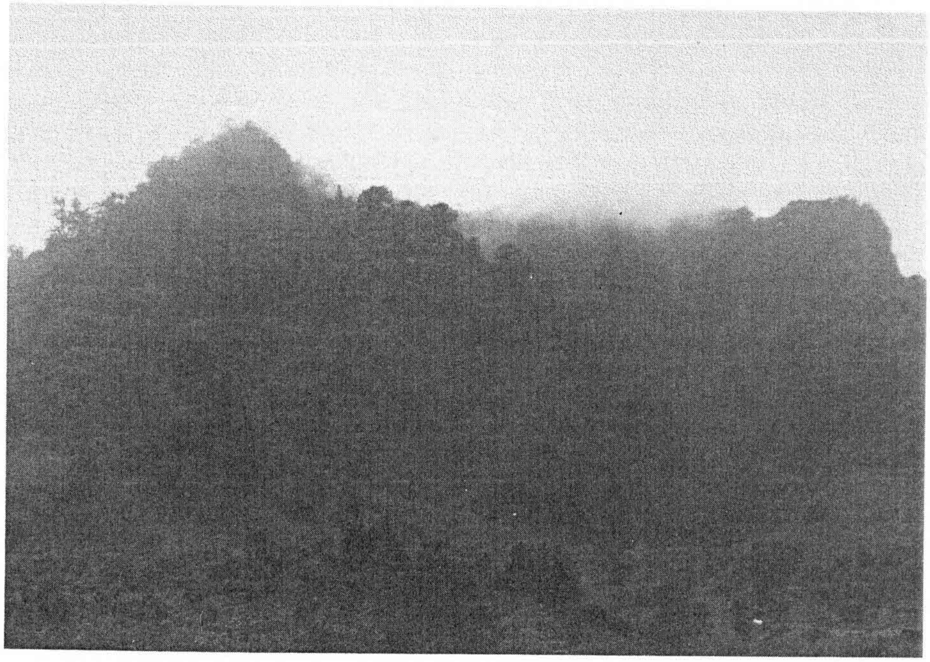


Fig. 12. The Eastern Highlands physiographic region near Ocosingo, Chiapas, showing evergreen and semi-evergreen seasonal forest.

5. *Eastern Highlands* (Fig. 12). - The Eastern Highlands region is situated east of the Central Plateau and south of the Northern Highlands. The region is composed of steep mountain ranges that slope eastward toward the Río Usumacinta. Elevations are highest on the west (*ca.* 1500 m maximum) and gradually become lower toward the east (to *ca.* 200 m), however, sites on the Río Usumacinta plain may be as low as 100 m. The region is covered mostly with uplifted marine limestone (Cretaceous) and some volcanic extrusions.

The climate of the Eastern Highlands is similar to the Northern Highlands because of corresponding elevation and rainfall patterns. Annual temperature is highest in the east (greater than 25°C) at lower elevations and least in the west (*ca.* 20°C) in higher areas. Ocosingo, Chiapas (865 m el.), is drier with an average annual temperature of 24°C. Average temperatures at Ocosingo are highest in May (26°C) and lowest in December and January (*ca.* 22°C). Rainfall is seasonal and averages between 2000 and 3000 annually throughout the region. Ocosingo receives 78% of its annual rainfall during the summer (April through September). September is the wettest month (279 mm), and June is second, averaging 254 mm of rainfall. January and February are the driest months, with rainfall averaging about 41 mm.

The Eastern Highlands region is primarily covered by lower montane rainforest and most is locally known as the Selva Lacandona (Shreve, 1957). Pine-Oak-*Liquidambar* forest is found on higher, drier, well drained ridges. Montane rainforest is found on humid high ridges. In the north, evergreen and semi-evergreen seasonal forest (Fig. 12) occurs at lower and less moist localities. Tropical rainforest occurs in the eastern portion near the Río Usumacinta. The humid forests of the Eastern Highlands are floristically similar to the El Petén rainforests of Guatemala (Breedlove, 1973).

Northern Highlands (Fig. 13). - The Northern Highlands region is situated to the north of the Sierra Madre, Central Depression, Central Plateau, and Eastern Highlands and is composed of steep volcanic ranges covered by Cretaceous limestone. The recently active volcano, El Chichón, is located in this region. Elevations are generally higher on the southern margin of the region (*ca.* 1500 m maximum), and lower in the north. However, peaks approaching the maximum elevation can be found throughout the region (e.g. El Chichón, 1260 m before eruption, 1060 m afterward; Weintraub, 1982). Lowest elevations in the region approach 200 m near the Gulf Coastal Plain.

Fig. 13. The Northern Highlands physiographic region showing lower montane rainforest 24 km north of Ocozocoautla, Chiapas. The foreground pictures a corn field commonly found within the region.

Most of the Northern Highlands can be regarded as warm and humid, but higher elevations (above 700 m) are cooler (*ca.* 20°C annual temperature), especially during winter "nortes." The only reliable annual climatic data for the region is from Palenque, Chiapas (200 m el.), located near the northern edge of the Northern Highlands (lowest and warmest area). Palenque has an average annual temperature of 26°C. Warmest months are May and June (*ca.* 28°C during both), and the coolest month is January with an average temperature of 21°C.

Rainfall patterns reveal humid conditions. Much of the region receives between 2000 and 3000 mm of rain annually, but along the north-facing slopes, rainfall approaches 4000 mm per year. Rainfall is seasonal, but with more winter rains than in subhumid regions. At Palenque, 70% of the rainfall occurs between April and October. The wettest months are September (433 mm) and October (614 mm). On the higher ridges, nocturnal fog is prevalent most of the year.

The Northern Highlands contain various humid formations, with the type dependent on elevation. Lower montane rainforest (Fig. 13) is most abundant throughout the region, with montane rainforest (Fig. 14) being common on higher ridges. At drier localities, pine-oak-*Liquidambar* forest occurs at higher elevations and evergreen and semi-evergreen seasonal forest occurs at lower elevations, especially on the southern edge. The region is rapidly being exploited for agriculture and other natural resources.

Fig. 14. Montane rainforest on the Northern Highlands 12 km northwest of Berriozábal, hiapas.

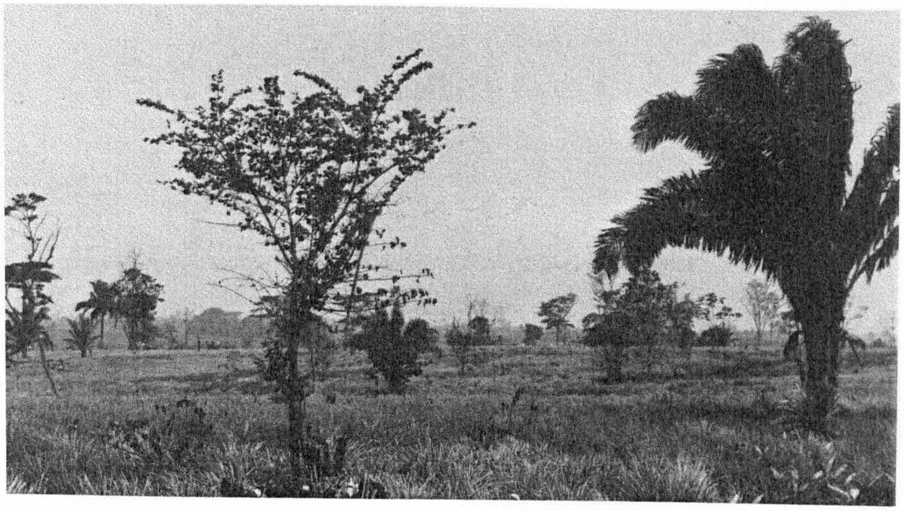


Fig. 15. The Gulf Coastal Plain physiographic region near Palenque, Chiapas.

7. *Gulf Coastal Plain* (Fig. 15). - The Gulf Coastal Plain lies north of the Northern Highlands. The region is an extension of the same physiographic region that stretches northwest and southeast of northwestern Nuclear Central America. The region is low, with maximum elevation being less than 250 m. Regional geological strata consist of late Mesozoic and early Cenozoic marine limestone overlaid with Tertiary and Quaternary fluvial deposits. Most of the coastal plain was probably covered by a sea during Pleistocene interglacial periods (Duellman, 1960, citing Cooke, 1945).

The lowlands of the Gulf Coastal Plain are warm and humid. Villahermosa, Tabasco (10 m el.), has an annual average temperature of 25.7°C. January and February are the coolest months (22°C average) and July and August are the warmest (*ca.* 28°C). Minatitlán, Veracruz (64 m el.), which is nearer the coast on the Isthmus of Tehuantepec, has an average annual temperature of 25.9°C with seasonal range averaging about 22.9°C during December and January to 28.6°C in May.

Villahermosa has an annual rainfall of approximately 2000 mm. Rainfall is seasonal, with 65% falling during the months of May through October. The wettest months are September (272 mm) and October (292 mm). The driest months are March and April, each receiving about 46 mm of rain. Minatitlán receives an annual rainfall of 2900 mm, of which 71% falls during the months of May through September. September is the wettest month (610 mm) and March and April are driest (*ca.* 38 mm each). The mean average relative humidity for the Gulf Coastal Plain is near 80%.

The Gulf Coastal Plain has been denuded of most of its natural vegetation (Fig. 16). Originally, the region was covered by tropical rainforest in the humid areas of the western portion and by evergreen and semi-evergreen seasonal forest in less humid parts of the eastern portion. Today, most of the region is covered by savanna. Stuart (1957) commented on savanna regions in Guatemala which he considered to be ephemeral and non-climatic (fluctuating). Lee (1980) thought that savannas on the Yucatan Peninsula were man-made. Beard (1953) considered savannas to be natural associations dependent on edaphic and drainage factors. The Gulf Coastal Plain also

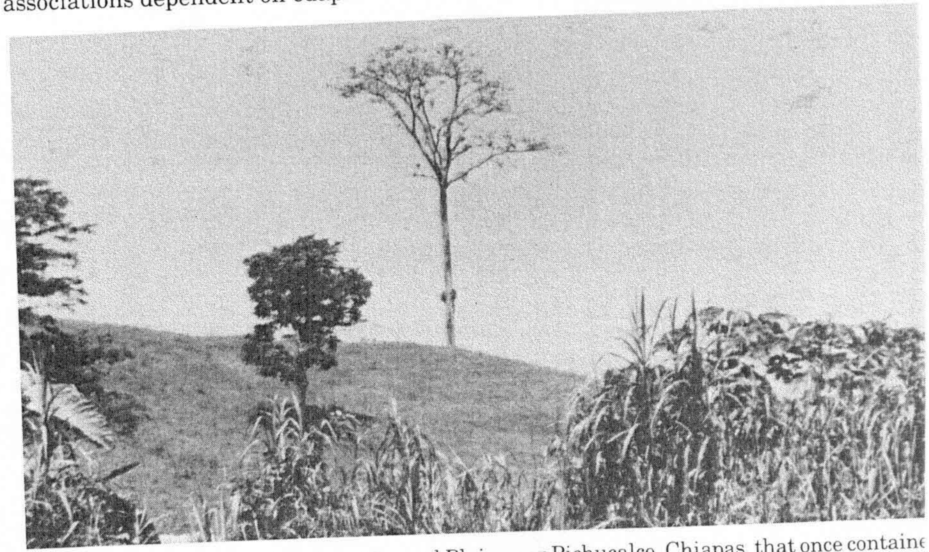


Fig. 16. A typical area of the Gulf Coastal Plain near Pichucalco, Chiapas, that once containe tropical rainforest.

has scattered palm forest, swamps, and lowland riparian forest (a restricted formation) in low areas prone to flooding. Conant (1969) described fresh water swamps near Coatzacoalcos, Veracruz, and Villahermosa, Tabasco.

In summary, temperature in northwestern Nuclear Central America is correlated with elevation. Annual temperatures range from less than 15°C above 2000 m elevation to between 15°and 25°C below 2000 m.

Rainfall is dependent on marine wind currents. The Gulf Coastal Plain, Northern Highlands, and Eastern Highlands are the most humid (above 2000 mm of annual rain). However, this amount of rainfall also occurs each year on the north slopes of the Central Plateau, Pacific slopes of the southeastern Sierra Madre de Chiapas and adjacent Pacific Coastal Plain, and the northwestern section of the high Sierra Madre. Portions of the higher elevations of the Northern Highlands and north-facing slopes of the Central Plateau are bathed in clouds during much of the year at night and during early and late hours of the day. This condition is also found locally in portions of the Sierra Madre in high areas of the southeastern and northwestern sections.

The driest portions of the study area are found in the Central Depression, northwestern Pacific Coastal Plain and adjacent slopes of the Sierra Madre. Within those areas, annual rainfall may be as low as 500 mm.

Precipitation is seasonal throughout northwestern Nuclear Central America. There is a definite wet season (May through October). During rainy season, proportionally more rain falls in subhumid areas than in humid areas. Humid areas receive enough rainfall per month to maintain evergreen forest vegetation.

Hydrography

Freshwater ecosystems in northwestern Nuclear Central America vary greatly beause of the diverse geology, topography, and climate. Information reported herein ollows Müllerried (1957), Tamayo and West (1964), personal observations, and inormation from other sources cited in the text.

The continental divide traverses the Sierra Madre de Chiapas, with drainage to the outh into the Pacific Ocean and northward into the Gulf of Mexico. The Pacific verant is steep and narrow (*ca.* 65 km maximum), until it reaches the coastal plain. The Gulf drainage area is much wider (*ca.* 400 km maximum), with gradients dependent n local topography. Natural lakes are rare throughout the area except for karst akes on the Central Plateau and Eastern Highlands. Swamps occur in lowland areas f the Gulf Coastal Plain and to a lesser extent near the Pacific coast.

Northwestern Nuclear Central America is drained primarily by two major river ystems, the Río Grijalva (Mezcalapa) and Río Usumacinta. Both systems drain nto the Gulf of Mexico in the state of Tabasco. These two river systems are the most oluminous in Middle America. Taymayo and West (1964) presented a map showing major rivers within the study area.

The Río Grijalva system drains the Sierra Madre, all of the Central Depression, most of the Northern Highlands, and the northern and western portions of the Cenral Plateau. The headwaters of the Río Grijalva occur on the Southeastern Highands and Sierra de los Cuchumatanes of Guatemala (Stuart, 1954a). The main ourse of the river runs from Guatemala into the lower Central Depression (locally nown as the Río Grande de Chiapas). The river then cuts through the southern end of the Northern Highlands to form the spectacular Sumidero Canyon. Many tributaries enter the Río Grijalva before it enters Sumidero Canyon and one major tributary (Río la Venta) enters the Río Grijalva after passing through a similar deep canyon in the Northern Highlands. After exiting Sumidero Canyon, the Río Grijalva meanders through the Northern Highlands and Gulf Coastal Plain, becoming progressively larger with confluence of other tributaries. Flooding on the Gulf Coastal lowlands is common during the summer rainy season and permanent swamps occur in less-drained areas. Because of electrical power demands, three large dams have been built on sections of the Río Grijalva. The first dam forms Presa Nezahualcóyotl (Mal Paso) of the Northern Highlands. The second dam forms Presa de la Angostura, a Central Depression lake above Sumidero Canyon. The latest dam (Chicoasén) has inundated Sumidero Canyon, destroying one of the most scenic stretches of river in México.

The Río Usumacinta headwaters in southwestern Guatemala on the eastern slope of the Sierra Madre de los Altos in the Department of Huehuetenango. All of the Eastern Highlands, the eastern slope of the Central Plateau, eastern parts of the Northern Highlands, and some of the Gulf Coastal Plain are drained by this system. The Río Usumacinta joins the Río Grijalva about 25 km from the Gulf of Mexico.

The northwestern parts of the Sierra Madre de Chiapas, Northern Highlands, and Gulf Coastal Plain drain into the Río Coatzacoalcos system in the northern part of the Isthmus of Tehuantepec.

The Pacific drainage is composed of many small, fast-flowing streams that originate in the Sierra Madre de Chiapas, and many terminate in coastal mangrove swamps and estuaries. The Pacific streams are warm and vary in flow rates (some occasionally become dry) because of seasonal rainfall.

Geological History

Nuclear Central America is part of continental North America. Some land mass has been extant in this area since the break-up of Pangea, but oceans have covered portions of modern landforms, especially during the Mesozoic (Maldonado-Koerdell, 1964). There is also evidence that Central America was separated from North America during the Cretaceous (at the Balsas Portal, Maldonado-Koerdell, 1964) and possibly again during the Quaternary at the Isthmus of Tehuantepec. However, Duellman (1960), citing Cooke's (1945) sea fluctuation data, pointed out that no seaway was present on the Isthmus during the Pleistocene.

Much of northwestern Nuclear Central America was above sea level by the start of the Cenozoic (Maldonado-Koerdell, 1964). During the Paleocene and Eocene, land relief was low, but during the Oligocene, uplift began in the area of the Chiapas highlands and continued through the Pliocene; the orogeny ended with volcanic activity in the eastern Sierra Madre (Dengo, 1968; Wake and Lynch, 1982). Therefore, modern landform patterns were essentially present from Pleistocene on.

The Central Depression was formed during the Oligocene-Pliocene orogeny when uplift on both sides created the valley (Stuart, 1954a). During the same period of time, the Río Grijalva cut through the northern uplift (Northern Highlands) to form Sumidero Canyon.

The Gulf Coastal Plain, with low relief, gradually rose from south to north, along with the montane regions to the south. This pattern was alluded to by Lee (1980), who pointed out different ages for the Cenozoic limestone on the Yucatan Peninsula and adjacent areas. Because of its low elevation, most the Gulf Coastal Plain was inundated by sea water during the Pleistocene. Pielou (1979) interpreted the magnitude of sea level fluctuation during the Pleistocene to be 230 m (160 m lower during glacial periods and 70 m higher during interglacials). If correct, much of the Gulf Coastal Plain would have been under water during interglacial times, and the central ridges of the Isthmus of Tehuantepec would have been above wáter (el. 300 m maximum, Duellman, 1960).

Composition of the Herpetofauna

Northwestern Nuclear Central America contains 297 known species of herpetofauna (203 reptiles, 94 amphibians) (Table 2; Appendix), exclusive of marine reptiles and introduced lizards. Snakes exhibit most species richness (110 species) and caecilians the least (two species). Of the total, 40 species (13%) are endemic to the area; 57% of those are reptiles. Salamanders show highest percentage of endemism (37%) and turtles, crocodilians, and caecilians have no endemic members.

TABLE 2

Taxonomic composition of the herpetofauna of northwestern Nuclear Central America.

GROUP	FAMILIES	GENERA	SPECIES	ENDEMICS SPECIES	%
AMPHIBIANS:					
Caecilians	1	1	2	0	0
Salamanders	1	5	24	9	37
Anurans	7	16	68	8	13
subtotal	9	22	94	17	18
REPTILES:					
nakes	6	51	110	9	8
izards	8	27	78	14	18
urtles	4	7	12	0	0
rocodilians	2	2	3	0	0
subtotal	20	87	203	23	11
total	29	109	297	40	13

TABLE 3

Comparison of the herpetofaunal species richness of northwestern Nuclear Central America (NNCA) with other geographical units of Middle America. The species richness value (SR) is the ratio of species/area x 100. Geographical units are arranged from northwest to southeast.

GEOGRAPHIC UNIT	SPECIES RICHNESS	AREA	SR
Sinaloa, México	121	58,000 km^2	.21
San Luis Potosí, México	147	62,848 km^2	.23
Michoacán, México	162	60,093 km^2	.27
Yucatan Peninsula	164	240,000 km^2	.07
NNCA	297	114,000 km^2	.26
Guatemala	302	108,889 km^2	.28
Honduras	238	112,087 km^2	.21
Costa Rica	362	50,900 km^2	.71

In comparison with other geographic units of Middle America, it becomes apparent that the study area has moderate herpetofaunal species richness (Table 3). Data used for comparison came from many literature sources, but primarily from the following: Sinaloa, México (Hardy and McDiarmid, 1969); San Luis Potosí, México (Taylor, 1949, 1950, 1952, 1953); Michoacán, México (Duellman, 1965); Yucatán, México (Lee, 1980); Guatemala (Stuart, 1963); Honduras (Wilson, 1983 and personal communication); and Costa Rica (Savage and Villa R, 1986). Lee reviewed hypotheses regarding maintenence of species diversity and concluded that although a number of factors contribute to diversity patterns, environmental heterogeneity is a major factor. Examination of Table 3 indicates a general increase in number of species from northwest to southeast, but there is variation in the number of species occurring within the areas of different geographic units. Comparison of the study area with the three northern México units (Table 3) shows comparable richness values. All four units are variable in geographical topography, but northwestern Nuclear Central America is much larger in area and differs in the presence of tropical humid rainforest formations. The Yucatan Peninsula is depauperate because it exhibits little variation in topography (most of the area is flat and all is under 600 m el.), an thus supports few major vegetation formations. Another factor affecting diversity on the Yucatan Peninsula is recent terrestrial age (only above sea level since the end o the Pleistocene, West, 1964). Guatemala, which is adjacent to the study area, show similar diversity values, not unexpectedly since Guatemala has similar environ ments and herpetofauna. Honduras has less richness than my study area, a puzzlin fact since that country has many of the same components of topography, climate, veg etation, and also shares many species of amphibians and reptiles. A partial explana tion is that Honduras contains less highland area above 2000 m (Wilson and Meye 1985), a zone that contains unique species in the northwestern area. Another facto may be that Honduras' middle position in Central America has prevented some sp cies from reaching the area from both the northwest and southeast. A third factor could be that Honduras is less well known herpetologically than my study area. The greatest reported species richness for a geographic area in Middle America is for Costa Rica. In Costa Rica, nearly 25 percent more species are found in an area that is less than one-half the size of northwestern Nuclear Central America. Costa Rica also has diverse environmental regimes and its close proximity to South America probably contributes to the species richness. These considerations suggest that species richness within Middle America is not primarily governed by total area of a given geographic unit, but by the environmental heterogeneity within the unit. There is also evidence that close proximity to another herpetofaunal source (e.g. South America-Costa Rica; northern México-Nuclear Central America and vice versa) contributes to species richness within a geographical unit.

Seven species of marine reptiles are omitted from biogeographical analysis herein, but have been recorded from coastal northwestern Nuclear Central America (Gulf and/or Pacific coasts). The marine reptiles include five species of turtles (*Chelonia mydas, Dermochelys coriacea, Eretmochelys imbricata, Lepidochelys kempii,* and *L. olivacea)* and two sea snakes (*Laticauda colubrina* and *Pelamus platurus*). Also omitted are three species of introduced gekkonid lizards (*Gehyra mutilata, Hemidactylus frenatus,* and *H. turcicus*). These lizards most likely arrived via cargo ship, colonized coastal areas, and then passively dispersed into interior towns and cities.

Future collecting and systematic revisions will definitely change the number of species of amphibians and reptiles known from the study area. Areas most likely containing undescribed species are higher elevations of the Sierra Madre de Chiapas, Gulf-facing slopes of the Central Plateau, and locales within the Northern and Eastern Highlands.

Habitat destruction within northwestern Nuclear Central America is extensive, and, in the absence of natural preserves, will cause extinction of many species if the current rate of activity continues. Destruction is especially acute in humid rainforest formations where species diversity is greatest. It is hoped that the Mexican people, with help from other concerned environmentalists, will take action now to preserve these natural treasures.

ECOGEOGRAPHY OF THE HERPETOFAUNA

Provincial Background

The herpetofauna of northwestern Nuclear Central America is a component of the Mesoamerican herpetofaunal region described by Savage (1966, 1982). The Mesoamerican fauna was considered part of the Neotropical fauna by Wallace (1876), Smith (1949), Darlington (1957), and Stuart (1964), and part of the Nearctic fauna by Schmidt (1954), although Schmidt also regarded it as transitional between the two regions. Savage (1966, 1982) contended that the herpetofauna of the Mesoamerican region developed mostly *in situ* and differs significantly from both Nearctic and Neotropical herpetofaunas.

Savage (1982) separated the Mesoamerican herpetofauna into the humid eastern nd western lowland, western lowland, Guatemalan highland, and Talamancan assemblages (the first three occur within the study area). These groups correspond mostly to his earlier (Savage, 1966) subregion classification. From this, it is expected that the study area contains herpetofaunal assemblages forming Gulf lowland groups, Pacific lowland groups, groups occurring on both versants in lowlands, and highland groups. It is also expected, because of the geographic position of the study area, that the species ranging outside the area will show closer relationships to areas northwest of the Isthmus of Tehuantepec than to areas southeast of Nuclear Central America.

Method of Biogeographic Analysis

The key to biogeographic analysis is that the distribution of the fauna be reasonably well known and that its taxonomy be reliable. Herpetological investigations are sufficiently advanced so that a detailed study of distributional patterns of the herpetofauna of northwestern Nuclear Central America is possible. Future systematic studies may alter my analysis somewhat, but general patterns should remain the same unless habitat destruction completely destroys our ability to investigate the natural ecosystems within the study area.

Collections were made within the study area from 1970 through 1983 (*ca.* 20 man months) during different seasons. The area of study was covered as much as possible during field work, but extensive periods were spent in several sampling areas to better understand the relationships between the species and their environmental requirements. Most sampling areas were not single localities, but larger localized areas containing similar environmental parameters listed below. *Pacific Coastal Plain* - vicinity of Zanatepec, Oaxaca (thorn woodland, *ca.* 60 m el.); vicinity of Tonalá, Chiapas (short-tree savanna, *ca.* 55 m el.); vicinity of Huixtla, Chiapas (evergreen and semi-evergreen seasonal forest, *ca.* 40 m el.). *Sierra Madre de Chiapas* - 7 km NE Tapanatepec, Oaxaca (tropical deciduous forest, *ca.* 210 m el.); Cerro Bául, Oaxaca (pine-oak forest and evergreen cloud forest, 1600-2400 m el.); 12 km N Arriaga, Chiapas (tropical deciduous forest, *ca.* 400 m el.). *Central Depression* - vicinity of Ocozocoautla, Chiapas (short-tree savanna and tropical deciduous forest, *ca.* 735 m el.); vicinity of Tuxtla Gutiérrez, Chiapas (tropical deciduous forest and thorn woodland, 500 - 600 m el.). *Central Plateau* - vicinity of Comitán, Chiapas (pine-oak forest, *ca.* 1600 m el.); Lagos de Montebello, Chiapas (pine-oak-*Liquidambar* and pine-oak forest, 1400 - 1800 m el.); vicinity of San Cristóbal de las Casas, Chiapas (pine-oak and pine-oak-*Liquidambar* forest, 2000 - 2800 m el.); vicinity of Pueblo Nuevo Solistahuacán, Chiapas (pine-oak-*Liquidambar* forest and evergreen cloud forest, 1600 - 2000 m el.). *Eastern Highlands* - vicinity of Ocosingo, Chiapas (evergreen and semi-evergreen seasonal forest, *ca.* 870 m el.). *Northern Highland* - 26 km N Ocozocoautla, Chiapas (lower montane rainforest, *ca.* 760 m el.); 12 km NW Berriozábal, Chiapas (montane rainforest, *ca.* 1060 m el.); 5 - 10 km S Palenque, Chiapas (lower montane rainforest, 250 - 300 m el.). *Gulf Coastal Plain* - vicinity of Pichucalco, Chiapas (tropical rainforest, *ca.* 100 m el.); 5 - 10 km N Palenque, Chiapas (evergreen and semi-evergreen seasonal forest, *ca.* 50 m el.). Road and field collecting (day and night) were major means of finding specimens, and numerous localities, other than those listed were randomly sampled during travel within the study area. The literature was also canvassed for reliable distributional records. Other records came from the following institutions (museum codes follow Leviton *et al.*, 1985) and the private collection of E. A. Liner (EAL): AMNH, UAZ, BYU, CAS, MVZ, CM, MCZ, FMNH, KU, LACM, LSUMZ, LSUS, UMMZ, MSUM, USNM, USB, TCWC, UTA, UTEP, MNHN, MZTG. Elevational data were taken in the field or from literature or museum records. Questionable distributional or nomenclatural data were personally scrutinized for accuracy, when possible. When taxonomic problems existed, I made decisions regarding their significance and placement of specimens into data sets. Most problems involved geographic variation (e.g. subspecies ranking) within certain taxa, therefore, my analysis is based on the species rank. In the case of the *Rana pipiens* complex, I agree with D. M. Hillis (personal communication), that several species occur in the study area. Until the group is worked out taxonomically, so the proper distributional patterns can be analyzed, I will list the group as the *R. pipiens* complex. All systematic data used for analysis herein, reflect information received before 1 January 1988.

Listed below are questions which I wanted to answer regarding biogeographic patterns of the herpetofauna of northwestern Nuclear Central America. 1. Are distinct assemblages associated with physiographic regions? 2. Are distinct assemblages associated with major vegetation formations? 3. What patterns exist with regard to elevational distribution? 4. What distributional patterns can be constructed using physiographic, vegetation, and elevational data? 5. What do the total range patterns reveal regarding relationships to the rest of Mesoamerica and to the Nearctic and Neotropical regions? 6. Can dispersal or vicariance events be used to account for present distributional patterns?

Analysis of the patterns of distribution of the herpetofauna consisted of placing each species into data sets based on its occurence in recognized physiographic regions, major vegetation formations, and known range of elevation. Similarity matrices, usng presence-absence data, were constructed to compare herpetofaunas among each of he seven physiographic regions and 10 vegetation formations. I used the similarity oefficient (SC) of Simpson (1947) for analysis: SC = C/N1, where C = the number f species common to the two herpetofaunas and N1 = the number of species in the maller of the two faunas. This coefficient compares the most similar parts of each erpetofauna and lessens the bias associated with collecting, and size of the larger auna (Simpson, 1960; Wilson and Meyer, 1985). The matrix values were also used to enerate phenograms using the unweighted pair-group method with arithmetic averges (UPGMA), as described by Sokal and Michener (1958). This method clusters hysiographic regions and vegetation formations based on heirarchial similarities etween their herpetofaunas. Some differences in the degrees of similarity shown in he matrix and the generated phenogram can be expected because of the way henograms are constructed; they cluster groups of the most similar data sets instead f simple pair-wise comparisons. Still, both methods should produce similar patterns verall. It should be pointed out that using presence-absence criteria for generating milarity information has limitations. Large heterogeneous areas may show similary with smaller homogeneous areas, even though only a portion of the larger area is milar to the smaller (especially when using Simpson's SC) and adjacent areas are xpected to show higher similarity, especially across ecotones. Therefore, the inforation gained from similarity matrices and phenograms should be used heuristically r detecting distributional patterns and for influencing the resultant conclusions garding those patterns.

Ecogeographic relationships were used to group species with similar patterns of geographic range (a faunal area) into assemblages; the assemblages contained at least five common species. Species that could not be assigned to a recognized faunal area comprise a non-assemblage group. The species groups were also compared with the rest of Nuclear Central America and with extralimital areas to the northwest (northeastern Mesoamerica and Nearctic region) and to the southeast (southeastern Mesoamerica and Neotropical region). Those comparisons were used to ascertain distributional patterns of the herpetofaunal elements with regard to their total range.

Controversy, based on either dispersal or vicariancé theory, exists in deriving explanations for present patterns of organismal distribution. I used data on the distributional patterns of the herpetofauna of the study area, together with information gleaned from present ideas concerning geological and climatic history, to test hypothesis of the two conflicting theories.

Results of Physiographic Region Analysis

Table 4 is a similarity matrix comparing herpetofaunas between all pairs of physiographic regions; Fig. 17 is a UPGMA phenogram generated from the matrix. The Sierra Madre de Chiapas contains the most species (124 reptiles, 55 amphibians) and the Eastern Highlands the fewest (59 reptiles, 19 amphibians). However, the latter region is poorest known, so future collecting should produce considerably more species, probably close to the number found in the Northern Highlands.

The similarity matrix (Table 4) reveals that the three adjacent and mostly humid regions (Eastern Highlands, Northern Highlands, Gulf Coastal Plain) all share many species, and a similar pattern is observed between the three regions containing substantial amounts of subhumid environments (Pacific Coastal Plain, Sierra Madre, Central Depression). The Central Plateau is most distinct, as it relates above the .60 level only with the Sierra Madre de Chiapas. The phenogram (Fig. 17) substantiates the above matrix relationships, except it masks the similarity between the Central Plateau and Sierra Madre. Those two regions share several highland species whose relationships are lost during the generation of the phenogram.

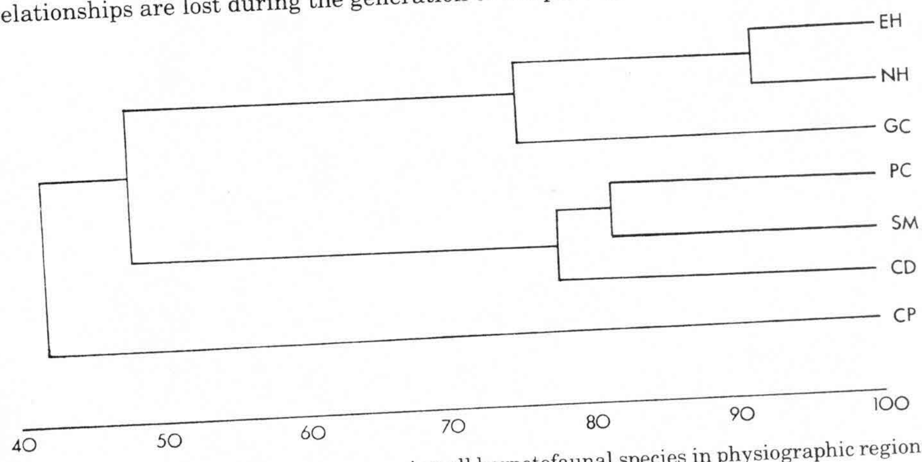


Fig. 17. A UPGMA phenogram comparing all herpetofaunal species in physiographic regions of northwestern Nuclear Central America. See Table 4 for abbreviation explanations.

TABLE 4

Similarity matrices, constructed using Simpson's (1947) similarity coefficient (SC = C/N1), which compare all herpetofaunal species, amphibians, and reptiles of physiographic regions (Müllerried, 1957) found in northwestern Nuclear Central America (C = number of species shared between two regions; N1 = smaller of the two faunas). Underlined numbers refer to the number of species in respective region, fractions are SC values; and non-underlined whole numbers refer to shared species. PC = Pacific Coastal Plain; SM = Sierra Madre de Chiapas; CD = Central Depression; CP = Central Plateau; EH = Eastern Highlands; NH = Northern Highlands; and GC = Gulf Coastal Plain.

Amphibians and Reptiles Combined

	PC	SM	CD	CP	EH	NH	GC
PC	102	83	65	30	38	44	44
SM	.81	179	69	63	50	71	51
CD	.76	.81	85	34	32	42	36
CP	.30	.62	.40	101	35	47	33
EH	.49	.64	.41	.45	78	71	60
NH	.43	.58	.49	.47	.91	123	75
GC	.43	.49	.42	.33	.77	.71	105

Amphibians

	PC	SM	CD	CP	EH	NH	GC
PC	24	20	16	07	08	10	12
SM	.83	55	18	19	11	20	13
CD	.80	.90	20	10	10	13	12
CP	.29	.53	.50	36	09	16	09
EH	.42	.58	.53	.47	19	19	17
NH	.42	.57	.65	.46	1.0	35	19
GC	.50	.45	.60	.31	.89	.66	29

Reptiles

	PC	SM	CD	CP	EH	NH	GC
PC	78	63	49	23	30	34	32
SM	.81	124	51	44	39	51	38
CD	.75	.78	65	24	22	29	24
CP	.35	.68	.37	65	26	31	24
EH	.51	.66	.37	.44	59	52	43
NH	.44	.58	.45	.48	.88	88	56
GC	.42	.50	.37	.37	.73	.74	76

In general, species richness of a physiographic region is related to the heterogeneity of its environmental regimes; topographic relief and rainfall seem to be major governing factors. There is also some evidence that rainfall is less important to species distributed in highland areas than to species occurring in lowlands. The similarity patterns between physiographic regions seem to be related to shared environmental regimes. The Central Plateau is most distinct when compared to all other physiographic regions. This is probably associated with less sharing of environmental regimes with adjacent regions or it is more isolated from other regions that do share similar regimes.

Separate comparison was done for amphibians and reptiles (Table 4; Figs. 18 and 19). The data imply that both groups have similar distributional patterns. However, the amphibian fauna of the Central Plateau is more distinct (no SC with other regions above .53).

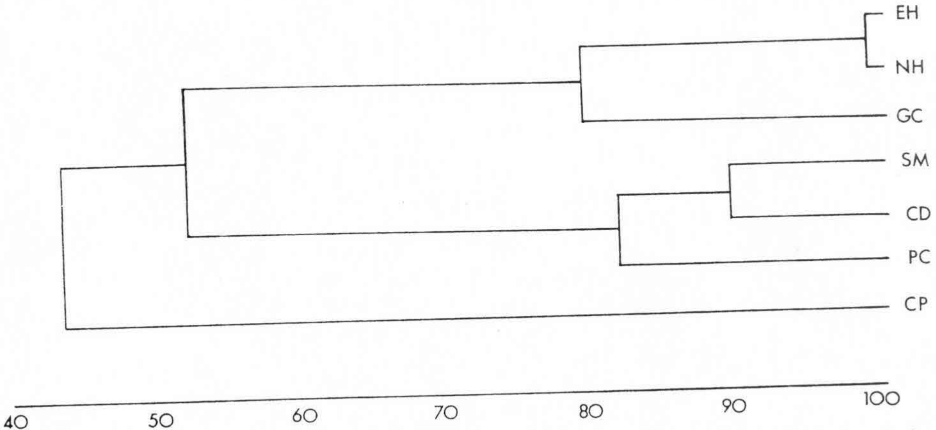


Fig. 18. A UPGMA phenogram comparing amphibians in physiographic regions of the northwestern Nuclear Central America. See Table 4 for abbreviation explanations.

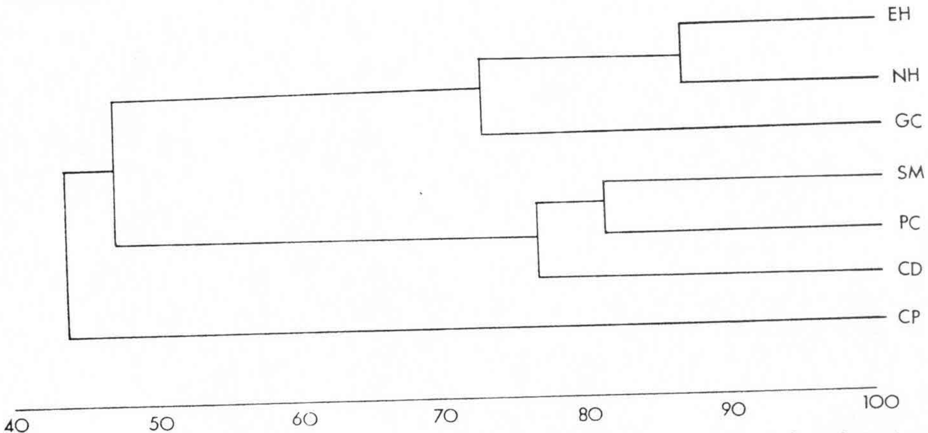


Fig. 19. A UPGMA phenogram comparing reptiles in physiographic regions of northwestern Nuclear Central America. See Table 4 for abbreviation explanations.

Results of Vegetational Formation Analysis

Moisture requirements were used to classify the vegetation formations of the study area into humid (wetland) formations, semi-humid (transitional) formations, and subhumid (dryland) formations (Table 1). This classification is not equivalent to that proposed by Holdridge (1967). It is merely a simplified description of the moisture requirements of Breedlove's (1973) vegetation formations.

The similarity patterns (Table 5; Fig. 20) show no vegetation formation containing a distinctive assemblage of amphibians and reptiles. However, four of the ten formations have substantial similarity values with only one other formation, and most of those share high similarity ($SC \geq .75$) with the other formation. Similarity is greatest between lowland subhumid formations (tropical deciduous forest, short-tree savanna, thorn woodland), between lowland humid formations (tropical rainforest, lower montane rainforest), and between humid highland formations (montane rainforest, evergreen cloud forest). The data (Table 5) also show that evergreen and semi-evergreen seasonal forest, in lowlands, share many species with both humid and subhumid formations, and pine-oak-*Liquidambar* forest is correlated on a high level only with pine-oak forest.

In general, humid mountainous regions of intermediate elevations (lower montane rainforest) contain most species richness, which again reflects topographic heterogeneity and rainfall as major factors governing species diversity. The high number of species (122) in tropical deciduous forest, a subhumid formation, reveals that rainfall requirements alone are not as important as physiognomic heterogeneity when considering the number of species inhabiting a formation. The data also agree with data presented by Martin (1955) that evergreen cloud forest contains a mixed assemblage of amphibians and reptiles common to adjacent highland formations (mostly humid elements).

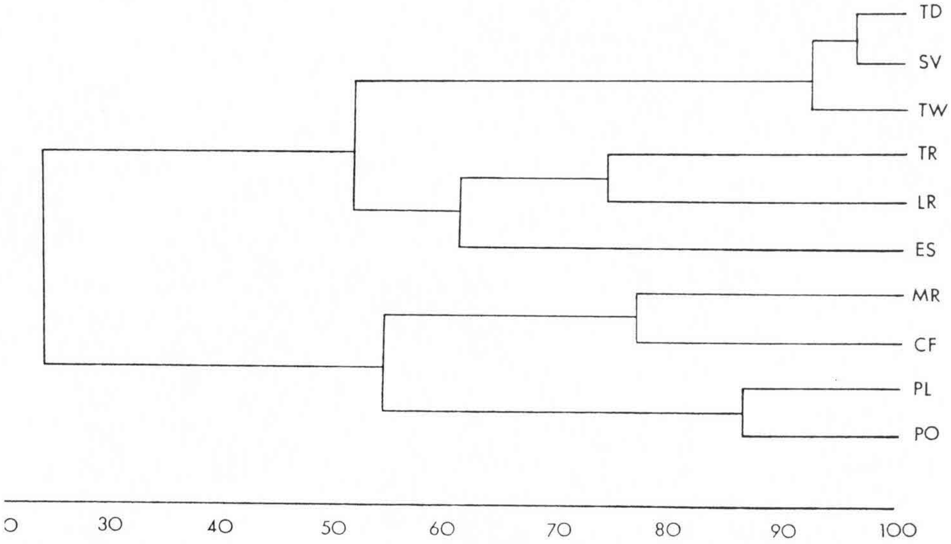


Fig. 20. A UPGMA phenogram comparing all herpetofaunal species in vegetation formations of northwestern Nuclear Central America. See Table 5 for abbreviation explanations.

TABLE 5

Similarity matrices comparing all herpetofaunal species, amphibians, and reptiles of major vegetation formations (Breedlove, 1973) found within northwestern Nuclear Central America, based on Simpson's (1947) similarity coefficient. See Table 4 for explanation of coefficient and other matrix values. TR = tropical rainforest; LR = lower montane rainforest; MR = montane rainforest; CF = evergreen cloud forest; ES = evergreen and semi-evergreen seasonal forest; TD = tropical deciduous forest; SV = short-tree savanna; TW = thorn woodland; PL = pine-oak-*Liquidambar* forest; and PO = pine-oak forest.

Amphibians and Reptiles Combined	TR	LR	MR	CF	ES	TD	SV	TW	PL	PO
TR	108	81	35	06	64	50	37	24	16	28
LR	.75	147	78	22	71	65	40	25	27	42
MR	.32	.66	119	56	44	36	15	09	39	46
CF	.09	.32	.81	69	13	08	01	01	28	32
ES	.59	.62	.39	.19	114	71	45	33	18	33
TD	.46	.53	.30	.12	.62	122	76	50	14	36
SV	.47	.51	.19	.01	.58	.97	78	50	06	23
TW	.44	.46	.17	.02	.61	.93	.93	54	05	14
PL	.27	.45	.65	.47	.30	.23	.10	.09	60	53
PO	.30	.45	.49	.46	.35	.39	.29	.26	.88	93
Amphibians										
TR	29	19	08	01	15	15	12	10	04	05
LR	.66	36	19	06	17	15	10	08	04	10
MR	.28	.53	46	28	12	10	05	03	10	14
CF	.03	.18	.85	33	05	04	01	01	05	08
ES	.52	.59	.41	.17	29	17	13	12	03	07
TD	.58	.58	.38	.15	.65	26	17	14	02	08
SV	.71	.59	.29	.06	.76	1.0	17	14	01	05
TW	.67	.53	.20	.07	.80	.93	.93	15	00	03
PL	.24	.24	.59	.29	.18	.12	.06	.00	17	15
PO	.19	.37	.52	.30	.26	.31	.29	.20	.88	27
Reptiles										
TR	79	62	27	05	49	35	25	14	12	23
LR	.78	111	59	16	54	50	30	17	23	32
MR	.37	.81	73	28	32	26	10	06	29	32
CF	.14	.44	.78	36	08	04	00	00	23	24
ES	.62	.64	.44	.22	85	54	32	21	15	26
TD	.44	.52	.36	.11	.64	96	59	36	12	28
SV	.41	.49	.16	.00	.52	.97	61	36	05	1
TW	.36	.44	.15	.00	.54	.92	.92	39	05	1
PL	.28	.53	.67	.64	.35	.28	.12	.13	43	3
PO	.35	.48	.48	.67	.39	.42	.30	.28	.88	6

Faunal similarity matrices and phenograms reveal differences when amphibians and reptiles are compared separately (Table 5; Figs. 21 and 22), although no vegetation formation has a distinct amphibian or reptile fauna. The major differences are that amphibians are more restricted in highlands than reptiles (share less similarity with other highland formations overall) and that many amphibians tolerate a wider range of moisture regimes in lowlands. Also, a higher percentage of reptile species that differ in their climatic requirements are shared between highland formations.

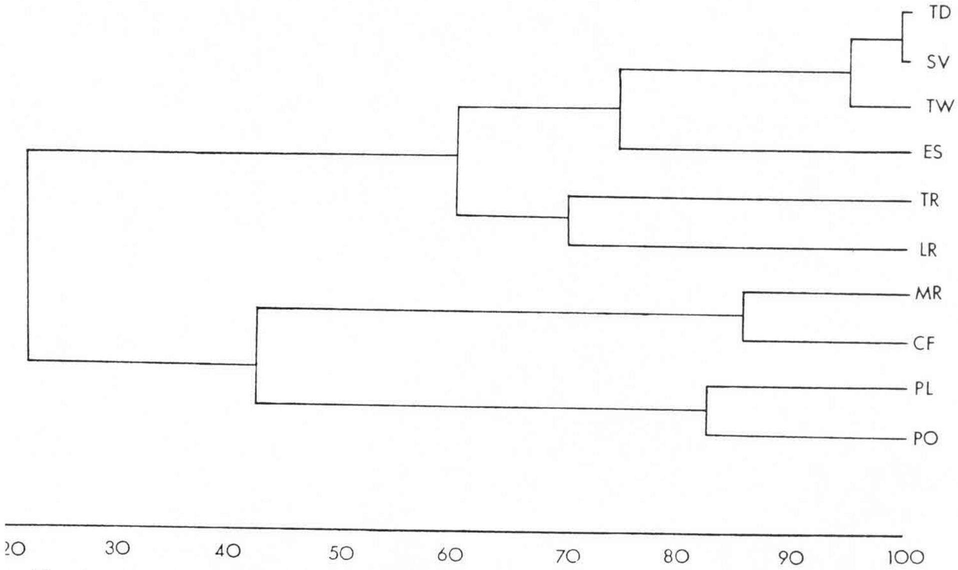


Fig. 21. A UPGMA phenogram comparing amphibians in vegetation formations of northwestern Nuclear Central America. See Table 5 for abbreviation explanations.

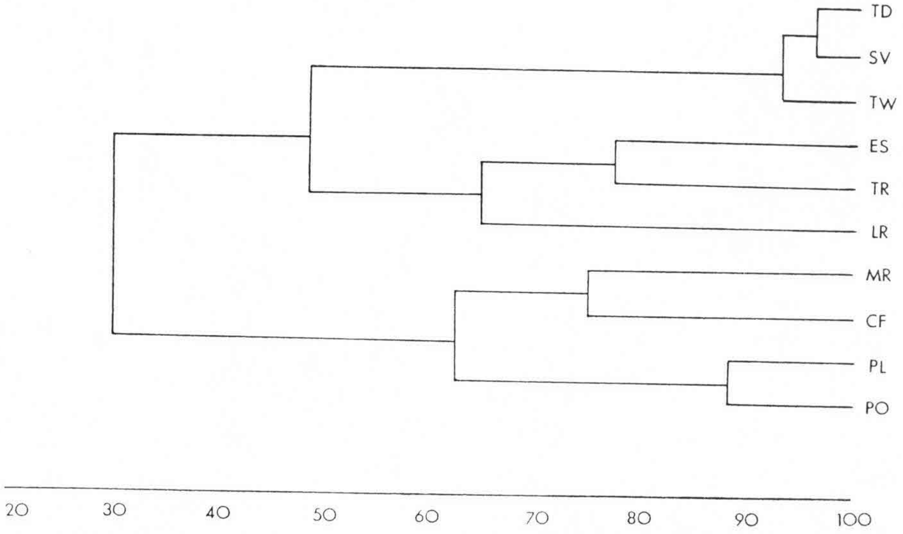


Fig. 22. A UPGMA phenogram comparing reptiles in vegetation formations of northwestern Nuclear Central America. See Table 5 for abbreviation explanations.

Results of Elevational Analysis

Table 6 shows the approximate elevational distribution of terrestrial amphibians and reptiles occurring within northwestern Nuclear Central America; the appendix shows a breakdown by species. Most species (183) are found between 700 and 800 m elevation. Fifty-six percent of the amphibians and reptiles are lowland species occurring between sea level and about 1000 m. There is a sharp drop in occurrence at intermediate elevations (1000 to 2000 m) and again in high elevations (above 2000 m). Only five species are known to occur above 3000 m, but those areas, in the Sierra Madre de Chiapas, are not well known. The sharp drop in number of species at 1000 and 2000 m elevation may be the result of sampling bias. Species distributions do not adhere to exact elevational measurements, but the fact that some vegetation formations change at approximately those elevations seems to substantiate such a pattern. Wilson and Meyer (1985) noted significant drops in number of snakes at similar elevations in Honduras. Snakes in Honduras also had a significant drop in number of species between 1400 and 1600 m elevation. In my study area, reptile abundance decreases from 69 to 57 species (43 to 33 in snakes, Table 7) at those elevations (less in amphibians). My data, as do Wilson and Meyer's (1985), refute a pronounced lowland distributional pattern of 0 through 600 m elevation as proposed by Stuart (1963). In reality, many species occurring in the lowlands range to elevations approximating 1000 m. Landform in the study area is primarily mountainous, therefore, moderate and high areas (above 1000 m el.) are regarded as highlands. Table 7 shows elevational breakdown of lower taxonomic groups of the herpetofauna.

Differences are revealed when comparing amphibians and reptiles (Table 6). Most reptile species occur in lowlands (60%), with the remainder at moderate (31%) and high (9%) elevations. Turtles and crocodilians, as expected, are basically lowland forms (Table 7) and snakes and lizards show similar patterns throughout. Amphibians are more evenly distributed with 43 percent occurring in lowlands, 39 percent at moderate elevations, and 18 percent in high areas. Of the amphibians found at higher elevations (18%), most are plethodontid salamanders, and the greatest number of those occur between 2400 and 2500 m elevation (Table 7). The evenness of distribution in low and moderate elevations is most pronounced in anurans. Anurans (Table 7) lose few species between 200 and 2000 m (34 at 200 m, 26 at 2000 m), although fluctuation takes place between those elevations (40 species at 400 m, 25 species between 1700 and 1900 m).

TABLE 6

Elevational distribution of the herpetofauna of northwestern Nuclear Central America. Numbers below taxa are those of constituent species.

ELEVATION (x 100 m)	REPTILES			AMPHIBIANS			TOTAL		
0 - 1	97	28%	60%	24	20%	43%	121	26%	56%
1 - 2	114			40			154		
2 - 3	125			44			169		
3 - 4	120			46			166		
4 - 5	122			45			167		
5 - 6	135	32%		46	23%		181	30%	
6 - 7	134			46			180		
7 - 8	138			45			183		
8 - 9	128			43			171		
9 - 10	127			44			171		
10 - 11	90	18%	31%	35	19%	39%	125	18%	33%
11 - 12	85			35			120		
12 - 13	71			31			102		
13 - 14	69			30			99		
14 - 15	69			31			100		
15 - 16	57	13%		35	20%		92	15%	
16 - 17	55			33			88		
17 - 18	51			31			82		
18 - 19	55			31			86		
19 - 20	55			32			87		
20 - 21	30	7%	9%	25	12%	18%	55	8%	11%
21 - 22	31			22			53		
22 - 23	27			19			46		
23 - 24	26			18			44		
24 - 25	26			20			46		
25 - 26	9	2%		10	6%		19	3%	
26 - 27	9			9			18		
27 - 28	9			9			18		
28 - 29	9			9			18		
29 - 30	8			8			16		
30 +	4			1			5		

TABLE 7

Elevational distribution of taxonomic groups of the herpetofauna in northwestern Nuclear Central America. Numbers below groups are those of constituent species.

ELEVATION x 100 m	CAECILIANS	SALAMANDERS	ANURANS	LIZARDS	SNAKES	TURTLES	CROCODILIANS
0 - 1	1	1	22	28	54	12	3
1 - 2	2	4	34	33	66	12	3
2 - 3	2	4	38	48	69	6	2
3 - 4	2	4	40	47	67	4	2
4 - 5	2	4	39	48	68	4	2
5 - 6	2	5	39	54	76	4	1
6 - 7	2	5	39	53	76	4	1
7 - 8	2	5	38	58	75	4	1
8 - 9	2	5	36	52	72	3	1
9 - 10	2	5	37	52	71	3	1
10 - 11	1	4	30	36	52	2	0
11 - 12	1	4	30	33	50	2	0
12 - 13	1	4	26	25	44	2	0
13 - 14	1	3	26	24	43	2	0
14 - 15	1	3	27	24	43	2	0
15 - 16	0	6	29	24	33	0	0
16 - 17	0	5	28	23	32	0	0
17 - 18	0	6	25	21	30	0	0
18 - 19	0	6	25	25	30	0	0
19 - 20	0	6	26	25	30	0	0
20 - 21	0	8	17	13	17	0	0
21 - 22	0	8	14	14	17	0	0
22 - 23	0	8	11	13	14	0	0
23 - 24	0	8	10	13	13	0	0
24 - 25	0	10	10	13	13	0	0
25 - 26	0	4	6	4	5	0	0
26 - 27	0	4	5	4	5	0	0
27 - 28	0	4	5	4	5	0	0
28 - 29	0	4	5	4	5	0	0
29 - 30	0	3	5	4	4	0	0
30 +	0	1	0	3	1	0	0

Distributional Patterns Within the Study Area and Relationships to Other Parts of Nuclear Central America

The herpetofauna of northwestern Nuclear Central America contains dynamic species, with distributions being governed by combinations of characteristics inherent in the evolution of each species. It is obvious that some species follow distinct distributional patterns, while others do not. Narrow environmental requirements govern distribution of some forms, whereas others tolerate a broad range of conditions. Different areas exhibiting similar climate and plant physiognomy may not contain the same species. Lastly, faunal areas that show distinctive groups may also contain elements of other groups and members of some assemblages may be tolerable of conditions elsewhere and occur along side other assemblages.

I used the results from similarity analysis of physiography, vegetation, and elevation to identify distributional patterns of members of the herpetofauna of the study area. Data sets were constructed utilizing species groups that exhibit similar distributional patterns. Table 8 lists the data sets and number of species present in each assemblage. Of all terrestrial amphibians and reptiles, 84 percent of the species (249) can be placed in 13 distinct assemblages. Fifty-six percent of those species are restricted to lowlands (six assemblages), 29 percent to highlands (five assemblages), and 15 percent occur in both highlands and lowlands in montane situations (two assemblages). Only 48 species (16%) are not placed in any assemblage, with a majority (60%) being lowland forms. The following species cannot be allocated to faunal assemblages (NA) because of either unknown ecological regimes, or because they are not geographically associated with five other species (asterisks indicate species endemic to the study area and plus signs indicate species endemic to Nuclear Central America).

Bolitoglossa platydactyla
*Bolitoglossa veracrucis** +
Pseudoeurycea sp. #2* +
Bufo valliceps
Hypopachus barberi +
Hypopachus variolosus
Eleutherodactylus berkenbuschii
Hyla miotympanum
*Plectrohyla hartwegi** +
Plectrohyla matudai +
Triprion spatulatus
Rana pipiens complex
Thecadactylus rapicaudus
*Lepidophyma lipetzi** +
Lepidophyma smithii +
Laemanctus serratus
*Norops cuprinus** +
*Norops pygmaeus** +
Sceloporus carinatus +
Sceloporus variabilis
Sphenomorphus assatus
Spenomorphus cherriei
Cnemidophorus sp.* +
Ameiva chatzami +
Ungaliophis continentalis
Clelia scytalina
Coluber constrictor
Coniophanes imperialis
Coniophanes schmidti +
Conophis lineatus
Conophis pulcher +
*Dipsas maxillaris** +
Ninia diademata
Ninia sebae
Oxybelis fulgidus
Senticolis triaspis
Stenorrhina freminvillei
Storeria dekayi
Tantilla jani +
Tantilla schistosa
Tantilla taeniata
Thamnophis proximus
Micrurus bogerti
Micrurus browni
Micrurus latifasciatus
Staurotypus salvinii +
Rhinoclemmys pulcherrima +
Caiman crocodylus

TABLE 8

Herpetofaunal groups of northwestern Nuclear Central America based on their d tributional patterns and numbers of species in each. Elevational ranges reflect us patterns of most species in each group. Some species will occur outside the range elevation when local conditions allow them to do so.

SPECIES GROUPS	AMPH.	REPT.	TOTAL
Lowland Assemblages (most occur below 1000 m).			
1. Continuous Assemblages:			
a. Ubiquitous Lowland (UL)	9	21	30
b. Humid Gulf Lowland (GL)	12	32	44
c. Tropical Subhumid (TS)	6	28	34
d. Gulf Coastal Plain (GC)	1	10	11
e. Moist Pacific Lowland (PL)	4	9	13
2. Disjunct Assemblage:			
Pacific Lowland-Gulf Lowland (PG)	3	4	7
subtotal	35	104	139
Highland Assemblages (most occur above 1000 m).			
1. Continuous Assemblages:			
a. Central Plateau (CP)	13	8	21
b. SE Sierra Madre (SS)	17	8	25
c. NW Sierra Madre (NS)	2	6	8
2. Disjunct Assemblages:			
a. Ubiquitous Highland (UH)	2	7	9
b. SE Sierra Madre-Central Plateau (SP)	1	8	9
subtotal	35	37	72
Mixed Elevational Assemblages			
1. Continuous Assemblage:			
Humid Gulf Montane (GM)	5	8	13
2. Disjunct Assemblage:			
Humid Para-Depression (PD)	7	18	25
subtotal	12	26	38
Non-Assemblage Species (NA)			
subtotal	12	36	48
total	94	203	297

The following are brief descriptions of each assemblage (Table 8) and their relationships to Nuclear Central America as a whole (asterisks represent species endemic to the study area and plus signs indicate species endemic to Nuclear Central America).

Continuous Lowland Assemblages:

1. Ubiquitous Lowland Assemblage (UL) (Fig. 23). - The 30 species in this assemblage typically range throughout the lowlands of the study area. The species are either habitat generalists or those living in similar habitats in different ecological areas. Most members are wide-ranging; only one species is endemic to Nuclear Central America. The assemblage, as a unit, cannot be assigned to any of Savage's (1982) herpetofaunas. Included in the assemblage are:

Dermophis mexicanus
Bufo marinus
Eleutherodactylus rhodopis
Eleutherodactylus rugulosus
Leptodactylus fragilis
Leptodactylus melanonotus
Ololygon staufferi
Smilisca baudinii
Rana vaillanti
Coleonyx elegans
Sphaerodactylus glaucus
Norops sericeus
Basiliscus vittatus
Iguana iguana
Mabuya unimarginata
Ameiva undulata
Boa constrictor
Adelphicos quadrivirgatus
Coniophanes fissidens
Drymarchon corais
Drymobius margaritiferus
Ficimia publia
Imantodes gemmistratus
Lampropeltis triangulum
Masticophis mentovarius
Dryadophis melanolomus
Oxybelis aeneus
Scaphiodontophis annulatus +
Crotalus durissus
Crocodylus acutus

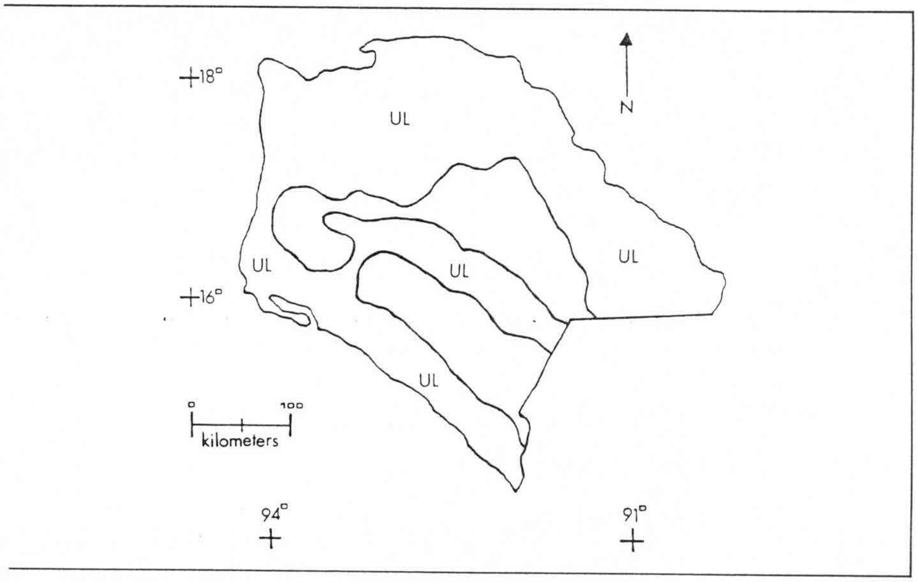


Fig. 23. The faunal area of northwestern Nuclear Central America containing the ubiquitous wland assemblage (UL).

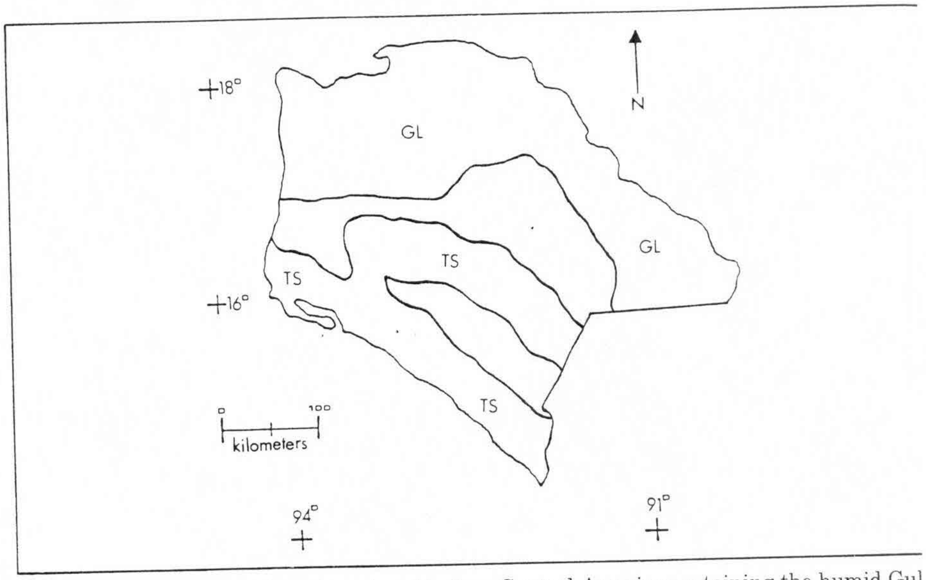


Fig. 24. Faunal areas of northwestern Nuclear Central America containing the humid Gul lowland assemblage (GL) and the tropical subhumid assemblage (TS).

2. Humid Gulf Lowland Assemblage (GL) (Fig. 24). - Forty-four species inhabi moist vegetation throughout the Gulf versant, mostly in areas less than 1000 m ele vation. However, a few species (e.g. *Bolitoglossa mexicana, Norops tropidonotus Micrurus elegans)* inhabit higher elevations locally in moist localities. Th assemblage forms a good percentage of Savage's (1982) humid eastern and wester lowland herpetofauna, but does not include species occurring on the moist Pacifi slopes of Chiapas and adjacent Guatemala (western portion of Savage' herpetofauna). Eighteen percent of the species are endemic to Nuclear Central Amer ica and 70 percent range outside that area northwestward into central Veracru Species belonging to this assemblage are:

Bolitoglossa mexicana +
Bolitoglossa rufescens
Oedipina elongata +
Eleutherodactylus alfredi
Eleutherodactylus laticeps +
Syrrhophus leprus
Agalychnis callidryas
Hyla ebraccata
Hyla loquax
Hyla microcephala
Hyla picta
Smilisca cyanosticta
Sphaerodactylus millipunctatus +
Lepidophyma flavimaculata
Lepidophyma tuxtlae
Norops barkeri
Corytophanes hernandezii
Laemanctus longipes +
Ameiva festiva
Celestus rozellae +
Clelia clelia
Coniophanes bipunctatus
Dendrophidion vinitor
Leptodeira frenata
Leptodeira ahaetulla
Oxyrhopus petola
Pseustes poecilonotus
Rhadinaea decorata
Sibon dimidiata
Stenorrhina degenhardtii
Thamnophis marcianus
Micrurus diastema

Norops capito
*Norops compressicaudus** +
Norops rodriguezii
Norops tropidonotus
Norops uniformis +
Corytophanes cristatus
Micrurus elegans
Bothrops nasuta
Dermatemys mawii
Kinosternon leucostomum
Rhinoclemmys areolata
Crocodylus moreletii

3. Tropical Subhumid Assemblage (TS) (Fig. 24). - The 34 species making up this assemblage are wide-ranging and comprise the majority of Savage's (1982) western lowland herpetofauna. Only three species are endemic to Nuclear Central America. Within Nuclear Central America, most species inhabit the subhumid or semihumid Pacific slope from the Isthmus of Tehuantepec to Nicaragua. Several forms also occur in the Central Depression and adjacent Sierra Madre de Chiapas, dry interior valleys of Guatemala, and uplands of Honduras (Wilson and Meyer, 1985). Stuart (1954a) described a subhumid corridor through Nuclear Central America using some species of this assemblage as indicators. The semihumid forest on the Pacific versant of southeastern Chiapas and adjacent Guatemala apparently does not restrict gene flow among most species. Members of the assemblage are as follows:

Bufo canaliferus +
Bufo coccifer
Bufo marmoreus
Syrrhophus pipilans
Hyla robertmertensi +
Gastrophryne usta
Phyllodactylus tuberculosus
Ctenosaura pectinata
Phrynosoma asio
Sceloporus melanorhinus
Sceloporus siniferus
Urosaurus bicarinatus
Cnemidophorus motaquae
Gymnophthalmus speciosus
Heloderma horridum
Leptotyphlops goudotii
Loxocemus bicolor
Coniophanes piceivittis
Conophis vittatus
Enulius flavitorques
Leptodeira annulata
Leptodeira nigrofasciata
Leptophis diplotropis
Manolepis putnami
Salvadora lemniscata
Sibon fasciata
Symphimus leucostomus
Tantilla rubra
*Tantillita brevissima** +
Trimorphodon biscutatus
Agkistrodon bilineatus
Bothrops dunni
Kinosternon scorpioides
Rhinoclemmys rubida

4. Gulf Coastal Plain Assemblage (GC) (Fig. 25). - This small assemblage (11 species) is restricted to areas of low relief, which characterizes the Gulf Coastal Plain. Only one species is endemic to nuclear Central America and six others are semiaquatic. Savage (1982) included these species in his humid east and west coast herpetofauna. The following are members of this assemblage:

Gastrophryne elegans
Norops sagrei
Sceloporus chrysostictus +
Typhlops tenuis
Coniophanes quinquevittatus
Nerodia rhombifera
Tretanorhinus nigroluteus
Claudius angustatus
Chelydra serpentina
Kinosternon acutum
Staurotypus triporcatus

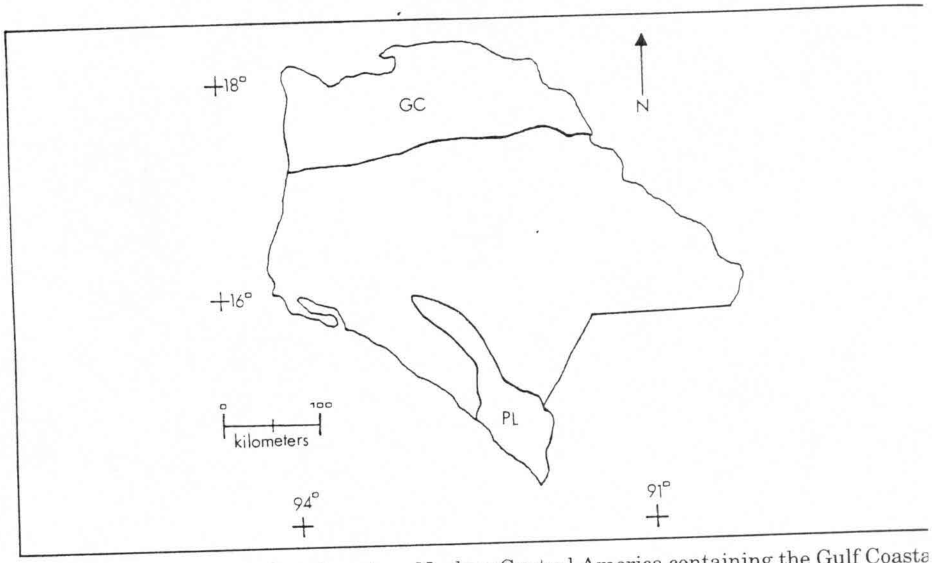


Fig. 25. Faunal areas of northwestern Nuclear Central America containing the Gulf Coasta Plain assemblage (GC) and the moist Pacific lowland assemblage (PL).

5. Moist Pacific Lowland Assemblage (PL) (Fig. 25). - This assemblage contains 1 species, eight (62%) of which are endemic to Nuclear Central America, and many oc cur only within the humid and semihumid forests of southeastern Chiapas and adja cent Guatemala. The assemblage as a unit does not conform to any of Savage's (198 groups. Species belonging to this assemblage are:

Dermophis oaxacae
*Bolitoglossa flaviventris** +
Bufo leutkenii
Syrrhophus rubrimaculatus +
Gonatodes albogularis
Norops dollfusianus +
Norops matudai +
Sceloporus squamosus
Geophis nasalis +
Rhadinaea posadasi +
*Tantilla tayrae** +
Micrurus nigrocinctus
*Bothrops ornatus** +

Disjunct Lowland Assemblage:

Pacific Lowland - Gulf Lowland Assemblage (PG) (Fig. 26). - The seven speci within this assemblage are found on both coastal plains and four also enter the Ce tral Depression (ecologically connected to the Pacific Coastal Plain). All species a wide-ranging forms (none endemic to Nuclear Central America) that tolerate humi semihumid, and subhumid conditions. The cause for disjunction is probably t uplifted central ridges of the Isthmus of Tehuantepec. During the Pleistocene, wh sea level was higher, the assemblage probably ranged continuously across t isthmus. The assemblage, as a unit, cannot be placed into any of Savage's (198 herpetofaunas. Species within the assemblage are:

Rhinophrynus dorsalis
Physalaemus pustulosus
Phrynohyas venulosus
Ctenosaura similis
Cnemidophorus deppii
Cnemidophorus guttatus
Trachemys scripta •

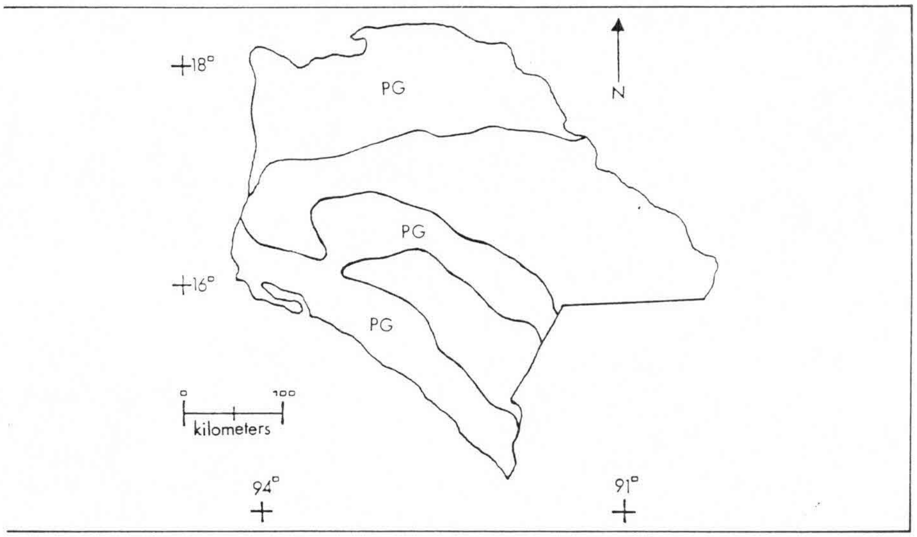


Fig. 26. The faunal area of northwestern Nuclear Central America containing the Pacific wland-Gulf lowland assemblage (PG).

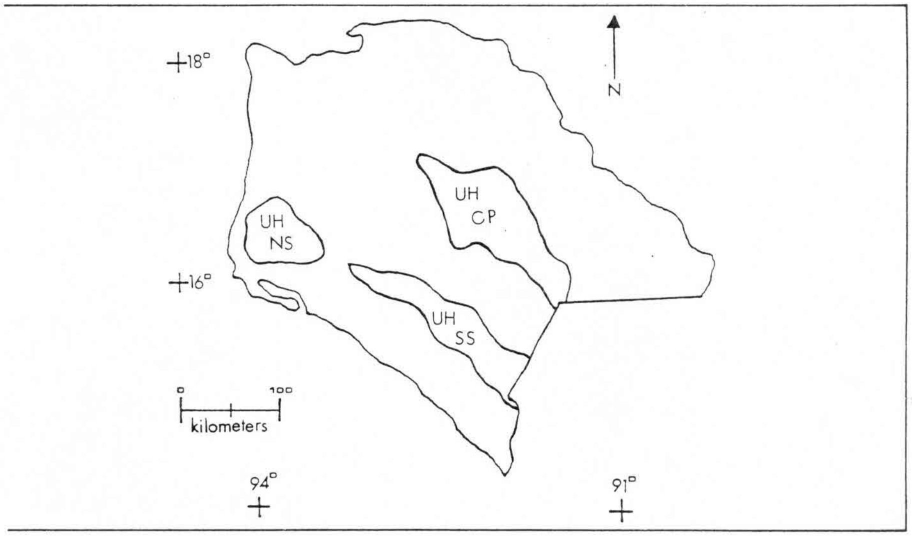


Fig. 27. Faunal areas of northwestern Nuclear Central America containing the Central ateau highland assemblage (CP), SE Sierra Madre highland assemblage (SS), NW Sierra adre highland assemblage (NS), and ubiquitous highland assemblage (UH).

ntinuous Highland Assemblages:

1. Central Plateau Highland Assemblage (CP) (Fig. 27). - Twenty-one species occur thin moderate and high elevations of the Central Plateau. Usual vegetation associed with the assemblage is pine-oak-*Liqudambar* or pine-oak forest, although a few ecies also occur in evergreen cloud forest. Ninety percent of the species are endemic Nuclear Central America; two others range northwest of the Isthmus of Tehuante-

pec. The assemblage belongs to Savage's (1982) Guatemalan highland herpetofauna. Species belonging to this assemblage are:

*Bolitoglossa hartwegi** +
Bolitoglossa lincolni +
Bolitoglossa rostrata +
Bolitoglossa stuarti +
*Nototriton alvarezdeltoroi** +
Nyctanolis pernix +
*Eleutherodactylus glaucus** +
*Eleutherodactylus taylori** +
Eleutherodactylus xucanebi +
Hyla melanomma
Hyla walkeri +
Plectrohyla ixil +
*Plectrohyla pycnochila** +
Sceloporus serrifer
Sceloporus taeniocnemis +
Abronia aurita +
*Abronia lythrochila** +
*Adelphicos nigrilatus** +
Leptophis modestus +
Rhadinaea hempsteadae +
*Bothrops tzotzilorum** +

2. SE Sierra Madre Highland Assemblage (SS) (Fig. 27). - The 25 species composin this assemblage are usually found in moist highland forests of the Sierra Madre fron approximately Cerro Tres Picos (northeast of Tonalá) southeastward to the Guate mala border. The assemblage is highly endemic to Nuclear Central America (96% one species (*Eleutherodactylus pygmaeus*) ranges northwest of the Isthmus of Te huantepec. Many of the species occur continuously in the Southeastern Highlands Guatemala (Stuart, 1951). The assemblage is a distinct subgroup of Savage's (198 Guatemalan highland herpetofauna. The following are members of the assemblag

Bolitoglossa engelhardti +
Bolitoglossa flavimembris +
Bolitoglossa franklini +
Bolitoglossa sp.* +
*Dendrotriton megarhinus** +
*Dendrotriton xolocalcae** +
Pseudoeurycea brunnata +
Pseudoeurycea goebeli +
Pseudoeurycea rex +
Bufo tacanensis +
Eleutherodactylus greggi +
Eleutherodactylus matudai +
Eleutherodactylus pygmaeus
*Eleutherodactylus sartori** +
Plectrohyla avia +
*Plectrohyla lacertosa** +
Plectorhyla sagorum +
Sceloporus acanthinus +
Sceloporus smaragdinus +
*Geophis cancellatus** +
Geophis immaculatus +
Pliocerus andrewsi +
Rhadinaea hannsteini +
Rhadinaea lachrymans +
Bothrops bicolor +

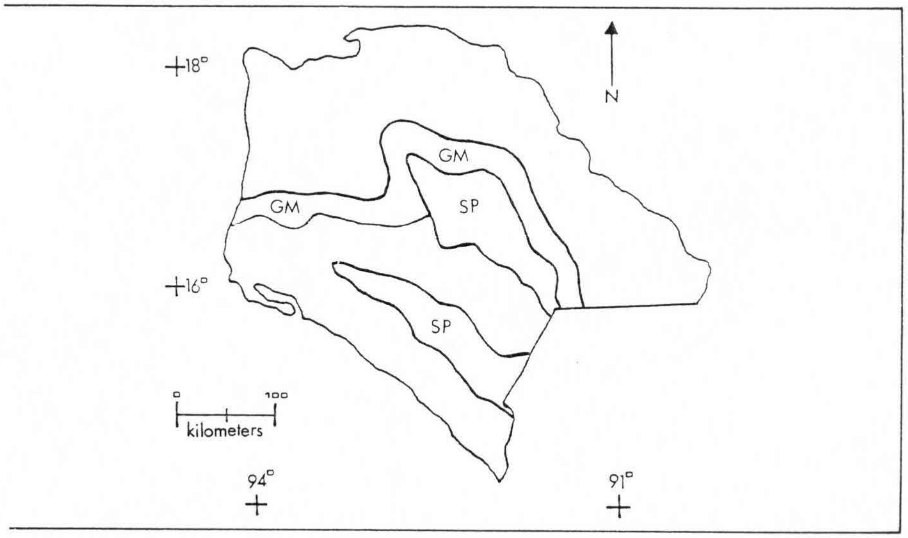
3. NW Sierra Madre Highland Assemblage (NS) (Fig. 27). - Eight species belong this assemblage, and usually inhabit pine-oak forest; a few also occur in tropical d ciduous or evergreen cloud forest. Seventy-five percent are endemic to Nuclear Ce tral America and the rest occur elsewhere in mountains northwest of the Isthmus Tehuantepec. The group as a unit does not fit into any of Savage's (1982) herpe faunas. Species belonging to this assemblage are:

Pseudoeurycea sp. #1* +
*Eleutherodactylus silvicola** +
Sphenomorphus gemmingeri
*Abronia bogerti** +
*Abronia ornelasi** +
*Adelphicos latifasciatus** +
*Ficimia ramirezi** +
Rhadinaea macdougalli

isjunct Highland Assemblages:

1. Ubiquitous Highland Assemblage (UH) (fig. 27). - The nine species contained in is disjunct assemblage are found in all highland regions of the study area above 500 m elevation (Central Plateau, northwestern Sierra Madre de Chiapas, southastern Sierra Madre de Chiapas). Therefore, these species tolerate a wide-range of osystems. Forty-four percent of the species are endemic to northwestern Nuclear entral America. *Pituophis lineaticollis, Thamnophis cyrtopsis,* and *Gerrhonotus liophalus* also range northwest of the Isthmus of Tehuantepec. The assemblage reprents species that occur throughout the Guatemalan highlands as described by avage (1982). Members are:

lectrohyla guatemalensis +
ana maculata +
errhonotus liocephalus
rymobius chloroticus +
Pituophis lineaticollis
Rhadinaea godmani
Sibon fisheri +
Thamnophis cyrtopsis
Bothrops godmani



ig. 28. Faunal areas of northwestern Nuclear Central America containing the SE Sierra dre-Central Plateau assemblage (SP) and the humid Gulf montane assemblage (GM).

2. SE Sierra Madre - Central Plateau Assemblage (SP) (Fig. 28). - Also conforming a disjunct pattern, the nine species making up this assemblage live primarily in mid areas on the Sierra Madre de Chiapas and humid to subhumid localities on the ntral Plateau. All species are endemic to Nuclear Central America and compose a tinct assemblage of Savage's (1982) Guatemalan highlands herpetofauna. Most mbers also occur in the highlands of interior and western Guatemala. Members of s assemblage are:

fo bocourti +
*rops anisolepis** +
rops crassulus +
ytophanes percarinatus +
Sphenomorphus incerta +
*Abronia matudai** +
*Abronia ochoterenai** +
Messaspis moreleti +
Thamnophis fulvus +

Elevationally Mixed Assemblages:

1. Humid Gulf Montane Assemblage (GM) (Fig. 28). - The 13 species in this assemblage have ranges that follow the upper contours (*ca.* 600 - 2000 m el.) of the Gulf slopes of the northwestern Sierra Madre, Northern Highlands, Central Plateau, and Eastern Highlands. This geographic area is typified by rugged topography, and high rainfall and humidity. At certain localities in the Northern Highlands, some species (e.g. *Bufo cavifrons, Hyla chaneque)* occur along fast-flowing mountain streams at elevations near 200 m. Six species (46%) are endemic to Nuclear Central America and six others range across the Isthmus of Tehuantepec to eastern Oaxaca and central Veracruz. The assemblage as a unit does not conform to any of Savage's (1982) herpetofaunas. Members of the assemblage are:

Bufo cavifrons
Eleutherodactylus stuarti +
Eleutherodactylus sp.* +
Anotheca spinosa
Hyla chaneque
*Norops breedlovei** +
Norops laeviventris
*Norops parvicirculata** +
Xenosaurus grandis
Geophis carinosus +
Geophis laticinctus
Bothrops nigroviridis +
Bothrops schlegelii

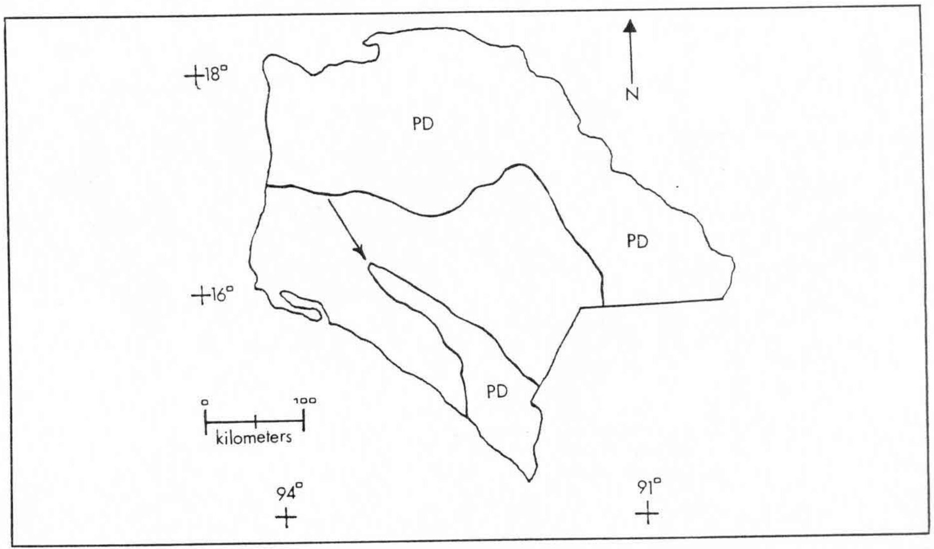


Fig. 29. The faunal area of northwestern Nuclear Central America containing the humid para-Depression assemblage (PD). The arrow indicates probable direction of historical dispersal.

2. Humid Para-Depression Assemblage (PD) (Fig. 29). - The 25 species belonging to this assemblage have ranges that nearly encircle the dry Central Depression and only 20 percent are endemic to Nuclear Central America. Today, the assemblage is mostly disjunct with members occurring on the humid Gulf slope and also on the humid and semihumid Pacific slopes of southeastern Chiapas and adjacent Guatemala (Sierra Madre and Pacific Coastal Plain). There is a hiatus between those areas located in the subhumid northwestern Sierra Madre, from Cerro Tres Picos to the Oaxaca-Chiapas

ɔorder. That area was probably more humid during a pluvial Pleistocene period. A
ew species (e.g. *Ptychohyla euthysanota, P. schmidtorum, Norpos biporcatus, Lepto-
ɔhis mexicanus)* can still be found there in protected riparian habitats. Members of
he herpetofauna typically inhabiting the area of hiatus belong to the tropical sub-
ıumid assemblage or Pacific lowland - Gulf lowland assemblage. Members of the as-
emblage were designated by Savage (1982) as belonging to his humid east and west
oast herpetofauna. The following species belong to this assemblage:

olitoglossa occidentalis +
entrolenella fleischmanni
leutherodactylus lineatus +
galychnis moreletii
yla sumichrasti
tychohyla euthysanota +
tychohyla schmidtorum +
orops biporcatus
orops lemurinus
orops pentaprion
orops petersii
*eloporus internasalis** +
Eumeces sumichrasti
Amastridium veliferum
Elaphe flavirufa
Imantodes cenchoa
Leptodeira septentrionalis
Leptophis mexicanus
Pliocercus elapoides
Sibon nebulata
Sibon sartorii
Spilotes pullatus
Xenodon rabdocephalus
Bothrops atrox
Bothrops nummifer

In summary, several conclusions can be made regarding the amphibians and rep-
es of the study area and their distributional relationships to the rest of Nuclear
ntral America. 1. - The study area does not have a distinct herpetofauna; only 13
rcent of the species are endemic to this area. Also, no assemblage discussed herein
totally restricted to northwestern Nuclear Central America. 2. The herpetofauna
es not belong primarily to geographic Nuclear Central America as only 113 species
3%) are endemic to that area (Table 9). Lowland and mixed elevational assemblages
d the lowland and mixed elevational non-assemblage species contain only 48 (16%)
demic members; lowland and mixed assemblages contain 32 endemic species
%). Therefore, Nuclear Central America does not have a homogeneous group of
ıphibians and reptiles (it is not a distinct subregion of Mesoamerica). 3. - Species
nprising highland assemblages are 86 percent endemic to Nuclear Central Amer-
(Table 9), and several occur throughout the highlands of that area. Only two spe-
s occurring primarily in highlands (*Plectrohyla hartwegi, Plectrohyla matudai)* are
members of an assemblage, but both are endemic to Nuclear Central America.
e data strongly suggest a Nuclear Central American highland subregion of Meso-
erica. 4. - The three herpetofaunas (Savage, 1982) occurring within northwestern
clear Central America are not homogeneous in species composition, as distinct
nal areas encompassing 13 assemblages can be identified. 5. - The distributional
terns of extant species comprising disjunct assemblages suggest environmental
ctuations during the Pleistocene and Holocene, and that present conditions reflect
rying trend, at least in the northwestern Sierra Madre de Chiapas.
ly data can also be used to substantiate or challenge previous theories concerning
ge scale distributional patterns of living organisms. Past biogeographical analysis
e utilized life zone concepts (Goldman, 1951), biotic provinces (Smith, 1939, 1949),
consideration of biomes as homogeneous areas (Kendeigh, 1961). Problems with
se methods were discussed by Duellman (1965) and my data reveal that areas can-
be defined by homogeneity in their flora, fauna, and geography. •

TABLE 9

Distributional patterns of the amphibians and reptiles of northwestern Nucle Central America with regard to their associations with Nuclear Central America a the Mesoamerican, Nearctic, and Neotropical regions. See the text or Table 8 for d initions of assemblages and the non-assemblage group. Distributional ranges ar Endemic to Nuclear Central America (Endemic NCA); Nearctic region to Nucle Central America (NAR-NCA); Nearctic region to southeastern Mesoamerica (NA SEM); Nearctic region to Neotropical region (NAR - NOT); northwestern Mes america to Nuclear Central America (NWM - NCA); northwestern Mesoamerica southeastern Mesoamerica (NWM-SEM); northwestern Mesoamerica to Neotropic region (NWM-NOT); Nuclear Central America to southeastern Mesoamerica (NC SEM); and Nuclear Central America to Neotropical region (NCA-NOT). Numbe refer to the number of species in each pattern.

DISTRIBUTION GROUP	ENDEMIC NCA	NAR - NCA	NAR - SEM	NAR - NOT	NWM - NCA	NWM - SEM	NWM - NOT	NCA - SEM	NCA - NOT
ASSEMBLAGE									
Lowland:									
UL	1	0	2	5	7	6	8	1	0
GL	8	0	1	0	20	6	6	1	2
TS	3	1	1	0	20	5	3	0	1
GC	1	1	1	0	6	1	1	0	0
PL	8	0	0	0	1	0	0	2	2
PG	0	0	1	1	3	0	1	1	0
subtotal	21	2	6	6	57	18	19	5	5
Highland:									
CP	19	0	0	0	2	0	0	0	0
SS	24	0	0	0	1	0	0	0	0
NS	6	0	0	0	2	0	0	0	0
UH	4	1	0	0	2	0	0	2	0
SP	9	0	0	0	0	0	0	0	0
subtotal	62	1	0	0	7	0	0	2	0
Mixed:									
GM	6	0	0	0	5	1	0	0	1
PD	5	0	0	1	7	5	5	1	1
subtotal	11	0	0	1	12	6	5	1	2
Non-Assemblage:									
NA subtotal	19	4	5	0	12	4	2	0	2
total	113	7	11	7	88	28	26	8	9

Distributional Patterns of Total Range

Biogeographic information was determined by examination of the total ranges of e herpetofaunal species found in the study area. Since Savage (1966, 1982) has con- ucted the most critical analysis concerning Middle America herpetogeography, my ata are compared primarily with his.

Table 9 shows distributional patterns based on total geographic ranges in relation- ip to the 14 groups (13 assemblages and one non-assemblage group) delimited with- the study area. Two newly defined geographic areas for use in this analysis are rthwestern Mesoamerica (between Nuclear Central America and the Nearctic Re- on) and southeastern Mesoamerica (between Nuclear Central America and the eotropical Region). The latter area was called lower Central America by Savage 982). General patterns are described as follows.

wland Assemblages:

1. Ubiquitous Lowland Assemblage (UL). - This assemblage contains many wide- nging species that occur on both versants of Mesoamerica, with 13 (43%) ranging o the Neotropics and seven (23%) into the Nearctic region. Most species occur in a riety of tropical lowland habitats.

2. Humid Gulf Lowland Assemblage (GL). - This large assemblage is composed of species (80%) restricted to Mesoamerica, with eight species (18%) ranging into the otropics, and one (2%) that ranges into the Nearctic region.

3. Tropical Subhumid Assemblage (TS). - Most members (82%) are endemic to soamerica and most of those (71%) range within Nuclear Central America and ad- ent northwestern Mesoamerica in subhumid Pacific habitats. Some are also found the Gulf lowlands in subhumid and more humid places to the northwest (Veracruz) d northeast (Yucatan Peninsula) of the study area. Four species (12%) range into uth America and two (6%) enter the Nearctic region.

. Gulf Coastal Plain Assemblage (GC). - This is a highly endemic Mesoamerican up (73%). Most species occur within the study area and to the northwest; two enter Nearctic region. One other species ranges into the Neotropics.

. Moist Pacific Lowland Assemblage (PL). - A majority (85%) of the species are en- nic to Mesoamerica; the others range into the Neotropics.

. Pacific Lowland - Gulf Lowland Assemblage (PG). - Members of this disjunct as- nblage are mostly wide-ranging and live on both versants of Mesoamerica in low- d areas. Two species enter the Nearctic region and two range into the Neotropics.

hland Assemblages:

. Central Plateau Highland Assemblage (CP). - This assemblage is totally en- nic to Mesoamerica. Two species range to the northwest of the Isthmus of Tehuan- ec.

SE Sierra Madre Highland Assemblage (SS). - Ninety-six percent of this assem- ge is endemic to Nuclear Central America. Only one species crosses the Isthmus of uantepec; it occurs on the highlands of southern Veracruz.

NE Sierra Madre Highland Assemblage (NS). - The assemblage is totally Meso- erican with six species (75%) being endemic to Nuclear Central America. Two oth- range into the highlands northwest of the Isthmus of Tehuantepec.

Ubiquitous Highland Assemblage (UH). - This disjunct assemblage is 44 percent endemic to Nuclear Central America. Three species (33%) occur to the northwest of that area, one of which enters the U.S. The other two species range into southeastern Mesoamerica.

5. Sierra Madre - Central Plateau Assemblage (SP). This disjunct assemblage is completely endemic to Nuclear Central America.

Mixed Elevational Assemblages:

1. Humid Gulf Montane Assemblage (GM). - Six species (46%) in this assemblage are endemic to Nuclear Central America. Six other species also occur in northwestern Mesoamerica on the Gulf versant and one other ranges into the Neotropical region.

2. Humid Para-Depression Assemblage (PD). - Many species (72%) in this assemblage range on the humid Gulf versant of Mesoamerica. Seven species (28%) range into the Neotropics and one of those occurs from the Nearctic to Neotropical region. Although found primarily on the Gulf slope, a disjunct community also exists on the Pacific side in southeastern Chiapas and adjacent Guatemala.

Non-Assemblage Species (NA):

Species not assignable to an assemblage are mostly endemic (73%) to Mesoamerica; six are known only from their type-localities. Two members (*Coluber constrictor, Storeria dekayi)* have highly fragmented ranges and along with six others, range into the Nearctic region. Seven species range into southeastern Mesoamerica and four others enter the Neotropics. Future collecting may place some of the species into one of the described assemblages.

Total range patterns of the herpetofauna of the study area reveal that 237 species (80%) are endemic to the Mesoamerican herpetofaunal region described by Savage (1982). Only seven species (2%) have ranges encompassing portions of all three regions (Nearctic, Mesoamerican, Neotropical; Table 9), and nearly all of those (five of seven) are part of the ubiquitous lowland assemblage. In general, lowland and mixed elevational assemblages contain species having wide-ranges in Mesoamerica (only 18% are endemic to Nuclear Central America), and highland assemblages contain species primarily (86%) restricted to Nuclear Central America. Of all the species that range outside Nuclear Central America (62% of the herpetofauna), 91 percent range to the northwest (85% of those into northwestern Mesoamerica and 15% into the Nearctic region) and 48 percent to the southeast (55% of those into southeastern Mesoamerica and 45% into the Neotropics). The above patterns disclose few species (20%) being shared between the study area and the Nearctic and/or Neotropical regions. Many species (48%) range into northwestern Mesoamerica, but only 16 percent enter southeastern Mesoamerica. Only 53 species (18%) enter either the Nearctic or Neotropical regions. Table 10 lists the 60 species that range outside Mesoamerica into the Nearctic, Neotropical, or both regions. Twenty of those species are regarded as having faunal affinities (origins) with the Nearctic (11 species) or Neotropical (9 species) regions. Inclusion into either group was based on total range of each species or the genus to which it belongs. All others are regarded as having affinities with the Mesoamerican region, or the patterns cannot be ascertained by current distributional patterns (e.g. species occurring in all three areas or widespread tropical forms).

TABLE 10

lembers of the herpetofauna of northwestern Nuclear Central America whose
nges include the Nearctic and/or Neotropical regions. The * indicates species
garded as having faunal affinities with the Nearctic region and ** indicates
finities with the Neotropics. Other species are regarded as having faunal affinities
ith Mesoamerica or affinities cannot be determined by present distributional
tterns (the latter indicated by ***).

---

inophrynus dorsalis
fo marinus ***
fo valliceps
eutherodactylus rhodopis
ptodactylus fragilis
ysalaemus pustulosus
ilisca baudinii ***
popachus variolosus
na pipiens complex *
na vaillanti
natodes albogularis **
ecadactylus rapicaudus
ana iguana ***
rops pentaprion
rops sagrei ***
loporus variabilis
eiva festiva
mnophthalmus speciosus
constrictor ***
totyphlops goudotii
lia clelia **
lia scytalina
uber constrictor *
iophanes fissidens
iophanes imperialis
marchon corais ***
mobius margaritiferus
lius flavitorques
propeltis triangulum *
ntodes cenchoa **

Leptodeira annulata
Leptodeira septentrionalis
Leptophis ahaetulla **
Masticophis mentovarius
Neorodia rhombifera *
Oxybelis aeneus
Oxybelis fulgidus
Oxyrhopus petola **
Psuestes poecilonotus **
Rhadinaea decorata
Senticolis triaspis
Sibon nebulata
Spilotes pullatus **
Stenorrhina degenhardtii
Storeria dekayi *
Tantilla rubra *
Thamnophis cyrtopsis *
Thamnophis marcianus *
Thamnophis proximus *
Trimorphodon biscutatus
Xenodon rabdocephalus **
Micrurus nigrocinctus
Bothrops atrox ***
Bothrops nasuta
Bothrops schlegelii
Crotalus durissus
Chelydra serpentina *
Trachemys scripta *
Caiman crocodylus **
Crocodylus acutus

---

he data indicate that Savage (1966, 1982) correctly demonstrated that Meso-
erica contains, to a greater extent, a distinctive herpetofauna. The data also sub-
tiate the concept of lowland assemblages composed of species occurring on the
f versant, on the Pacific versant, or both versants. Also recognizable are disjunct
land assemblages. However, the distributional patterns within all areas are
e complex than Savage (1982) described. For example, parts of the Pacific versant
outheastern Chiapas and adjacent Guatemala contain species characteristically
d in humid and semihumid vegetation on the Gulf slope of Middle America. Sav-
included those species in the western element of the humid eastern and western

lowland herpetofauna. In reality, only a few species inhabiting the Pacific side characteristic of the described herpetofauna (25 members of the humid para-Depr sion assemblage, which occur in both highland and lowland areas). A maximum 130 species would be expected on the Pacific side if the two areas indeed share same group of amphibians and reptiles. Also, the moist Pacific lowlands contain least 13 species not found on the Gulf side. The data suggest a filter barrier travers by members of the humid para-Depression assemblage from the Gulf side. Moveme across a barrier that limits many other species is also disclosed by the fact that m members of the humid para-Depression assemblage are wide-ranging forms, whi implies good dispersal ability. Members of that assemblage arrived on the Pacific si and intermingled with species that had evolved *in situ* in that area.

Another example is that the geographic area containing Savage's (1982) weste lowland herpetofauna includes 37 species not only found on the Pacific lowlands Mesoamerica, but also on the Gulf side in more humid situations (e.g. ubiquito lowland assemblage and Pacific lowland - Gulf lowland assemblage). My tropic subhumid assemblage (34 species) corresponds to Savage's western lowla herpetofauna.

Lee (1980) pointed out two subdivisions of the herpetofauna of the Yucatan Peni sula: a subhumid assemblage in the north and a mesophyllic assemblage in the sout Both assemblages contain species that can be placed into assemblages describ herein, although the northern assemblage does contain a distinct group of 19 specie Most members of the herpetofauna of the Yucatan Peninsula belong to one of the fo lowing: ubiquitous lowland, Gulf Coastal Plain, or Pacific lowland - Gulf Lowlar assemblages. Both Lee's and my data indicate that some genetic interchange is ta ing place between the Gulf and Pacific lowlands for some species, and that disjunctic has occurred for others. Because several species share the disjunct pattern, it must assumed that the hiatus has occurred within the recent past (Pleistocene to Holocer times). By examining closely related species, it is also apparent that speciation ha occurred. This suggests three explanations for those patterns: 1 - speciation has o curred more rapidly in some species than in others; 2 - some species ranges becam disjunct at earlier times than did others; or 3 - taxonomic status of some groups poorly understood (e.g. speciation has not occurred, or has, and has not been detected However, controversy surrounds the species concept (White, 1978), so the above fa tors may be affected by interpretation based on different species concepts. Also, it evident that systematic revision is needed for many taxa occurring within Meso america. For now, I prefer explanation number two: the disjunct lowland assemblage containing the same species were formed by environmental fluctuation during th Pleistocene, and disjunct areas of endemism containing closely related species by pre Pleistocene orogeny.

Savage's (1982) Guatemalan highland herpetofauna, at least in my study area, i composed of several recognizable assemblages. Only the ubiquitous highland assem blage (nine species) ranges throughout Nuclear Central America and corresponds ex actly to his Guatemalan highland group. Under modern conditions, all highlan areas within the study area are not continuous ecogeographically with respect to am phibian and reptile distribution. Some of those areas contain endemic species, where as others share common species in addition to endemics. It is probable that more tha one cause was responsible for the disjunctions: geographic barriers erected durin orogeny for endemic areas and environmental changes affecting the disjunction be tween areas containing the same species.

TABLE 11

The three distinctive areas of endemism of northwestern Nuclear Central America and their respective endemic species.

CENTRAL PLATEAU

Bolitoglossa hartwegi
Nototriton alvarezdeltoroi
Eleutherodactylus glaucus
Eleutherodactylus taylori
Plectrohyla pycnochila
Abronia lythrochila
Adelphicos nigrilatus
Bothrops tzotzilorum

SOUTHEASTERN SIERRA MADRE DE CHIAPAS

Bolitoglossa sp.
Dendrotriton megarhinus
Dendrotriton xolocalcae
Eleutherodactylus sartori
Plectrohyla lacertosa
Geophis cancellatus

NORTHWESTERN SIERRA MADRE DE CHIAPAS

Pseudoeurycea sp. *#1*
Eleutherodactylus silvacola
Abronia bogerti
Abronia ornelasi
Adelphicos latifasciatus
Ficimia ramirezi

Northwestern Nuclear Central America contains disjunct areas of endemism; all are in mountainous regions (Table 11). The Sierra Madre contains two such areas, the highlands of the southeastern sector (six endemic species) and highlands of the northwestern portion (six endemic species). Those two sectors are separated by a lower ridge of the Sierra Madre from northeast of Tonalá to near the Oaxaca-Chiapas border (Fig. 27). Future collecting may produce more endemic species as both areas have not been extensively searched. The Central Plateau with eight endemic species is the most distinctive physiographic region in northwestern Nuclear Central America. All three mountain islands hold good potential for testing vicariance biogeographic hypotheses related to patterns of historical herpetofaunal distribution. In addition, the Northern Highlands habor six endemic species, but as of now, no distinct area of endemism within the region can be defined; little is known regarding the species geographic ranges.

The only lowland region with any significant amount of endemism in the study area is the moist southeastern sector of the Gulf Coastal Plain and adjacent lower elevations of the Sierra Madre de Chiapas (contains the moist Pacific lowland assemblage, Fig. 25). Many of the species within this area are found elsewhere only in adjacent Guatemala.

HISTORICAL PERSPECTIVES

Historical biogeographic theory has been recast as a result of the development of the theory of vicariance biogeography (Croizat *et al.,* 1974: Rosen, 1976, 1978; Nelson and Rosen, 1981; Nelson and Platnick, 1981; Wiley, 1981), an outgrowth of cladistic systematics. Vicariance theory maintains that major patterns of organismic distribution are due to changes in geological form (a vicariance event) and subsequent fragmentation of a once continuous ecosystem into allopatric communities. Each new community (vicariant biota) is therefore allowed to develop genetically in isolation. A generalized track (Croizat, 1952) refers to the geographic area inhabited by a historical source biota; it encompasses all derivative vicariant biotas. The center of origin cannot be determined, therefore any concept dealing with centers of origin is invalid (Brown and Gibson, 1983). Modern ecological conditions contribute little to major distributional patterns because they may correspond to conditions not extant at the time of a vicariant event (Rosen, 1978). Vicariance biogeographers (vicariists) also conclude that speciation events were primarily pre-Quaternary, so modern distributional patterns were not affected much by climatic fluctuations during the Pleistocene (Savage, 1982).

Traditional dispersal theory states that groups of concordant species disperse from a center of origin (Darlington, 1957) along generalized tracks (dispersal routes) into areas that can accommodate them. Most disjunct patterns are caused by isolation events following dispersal, or by long distance dispersal across a barrier. Disjunction of source biotas may be caused by environmental changes or changes in geological form (Savage, 1982). Also, present patterns of distribution were greatly influenced by Pleistocene climatic fluctuations and significant amounts of speciation occurred during the Quaternary. See Savage (1982) for detailed comparison of dispersal and vicariance biogeography.

With the above tenets in mind, can dispersal or vicariance theory provide answers for explaining distributional patterns of extant amphibians and reptiles in northwestern Nuclear Central America? First of all, vicariists have developed a powerful method to test hypotheses concerning historical biogeographic patterns of related, but vicariant areas of endemism (Platnick and Nelson, 1978; Rosen, 1978; Savage, 1982). However, inherent in the method is the need for extensive systematic knowledge of the groups concerned (e.g. cladistic analysis of related taxa in vicariant biotas). To date, few analyses have been completed to show evolutionary relationships between disjunct biotas in my study area, at least with vicariance biogeography in mind. Therefore, future analyses must await more systematic knowledge and comparison between areas of endemism in Nuclear Central America. The greatest problem facing vicariists is the rampant destruction of natural ecosystems. It is feasible to think that the destruction will destroy any hope of using vicariance biogeographic approaches in many areas of Meosamerica.

The study presented here classifies the extant herpetofauna of the study area into groups of species with common geographic parameters. Vicariance biogeographical methods cannot be utilized because no schemes of cladistic analyses were presented. However, distribution of modern species can be used to predict processes that separated once continuous assemblages.

Within the study area, disjunct assemblages are found in one lowland, one mixed elevational, and two highland areas. Known geological history of the area suggests

hat ecological factors were an influence on modern herpetofaunal distribution, un-
ess long distance dispersal was a factor, which is highly remote judging by the many
pecies involved. Topographic features of the area have not been altered radically
ince the beginning of the Pleistocene (Dengo, 1968; Wake and Lynch, 1982) and can-
ot account for disjunction of assemblages containing the same species. Most uplift
nd separation of physiographic regions probably ended by mid to late Pliocene, and
is generally accepted that pre-Pleistocene orogeny produced disjunct biotas in Nu-
lear Central America. Duellman (1970), Wilson and Meyer (1971), Myers (1974),
Vake and Lynch (1976, 1982), Campbell and Ford (1982), and Larson (1983), among
thers, gave evidence of disjunct herpetofaunas of pre-Pleistocene relationship.

Modern taxa comprising disjunct assemblages of identical species have not had suf-
cient time to experience complete, or any, speciation. Therefore, what explanations
ill account for observed distributional patterns, and during what periods of time did
isjunction occur? If speciation rates were known, much information could be pro-
ssed regarding time of source biota disjunction. However, speciation rates are diffi-
ılt to assess and probably vary considerable among groups of living organisms
Vhite, 1978). It has been suggested that rates can be fast (Haffer, 1969; MacArthur,
972; Pielou, 1979), especially in small vertebrates (20,000 to 30,000 years in small
rds) and even faster in insects (1000 years for some island moths). Sea turtles sepa-
ted by the Panamanian land bridge (four to five million years) have achieved sub-
ecific status (Brown and Gibson, 1983) and may be considered full species by some
stematists. The same land bridge produced vicariant species in some fish, but not in
hers (Brown and Gibson, 1983). Haffer (1969) believed that Quaternary climatic
ıctuations influenced speciation within the South American tropics. Myers (1974)
greed that Pleistocene environmental change was a major cause for diversity in the
ake genus *Rhadinaea* in Middle America. Vicariists insist that most speciation of
odern forms took place before the Pleistocene (Savage, 1982). I agree with Mayr
970) that speciation rates vary depending on several factors and evidence shows
at many modern forms were extant by a least mid-Pleistocene (Holman, 1962, 1965,
69). Therefore, it is my opinion that disjunctions of modern assemblages containing
e same species were effected by climatic fluctuations, during at least the last half of
e Pleistocene. In one case (humid para-Depression assemblage), the hiatus between
mmunities is only now becoming complete.

Many lowland areas were probably connected ecologically during warmer periods
the Pleistocene when sea level was higher (Duellman, 1960) and some disjunct
ghland assemblages were connected during glacial periods when highland environ-
nts became depressed (Campbell, 1984; Campbell and Ford, 1982). The ecological
nection allowed some species to disperse from formally vicariant communities. I
ıbt the notion that ecological vicariance, and not dispersal, was fully responsible
forming disjunct areas containing the same species because if it were true, I would
ect many more species to be contained in the ubiquitous highland assemblage (e.g.
st species presently found in the NW Sierra Madre, SE Sierra Madre, Central Pla-
u, and SE Sierra Madre-Central Plateau highland assemblages). In other words,
highland regions of the study area did not contain a source biota, as defined by vi-
iance biogeographic theory, during the Pleistocene to Recent times. Therefore, ev-
nce suggests that the more vagile highland species dispersed between some or all
hland areas during Pleistocene ecological depression of highland habitats. After
natic conditions changed, disjunction occurred, and the disjunct communities may

become future areas of endemism if the hiatuses persist. Also, evidence reported herein and by Stuart (1954b) indicate a drying trend in the Sierra Madre de Chiapas and Southeastern Highlands of Guatemala, respectively. Restricted moist locales within those areas may be obliterated if drying continues and extinction will ensue. The above factors support the concept that ecological changes are important for shaping distributional patterns of terrestrial amphibians and reptiles.

Ecological disjunction and dispersal can be influenced by geological features. Several such features within the study area can be identified. Sumidero Canyon of the Northern Highlands most likely disrupted ecological continuity between the Central Plateau and northwestern Sierra Madre even after elevational depression of highland ecosystems during glacial periods. Only species belonging to the humid para-Depression assemblage were able to traverse the entrenchment in lowlands north of the canyon. The subhumid Central Depression separates assemblages that occur in the southeastern Sierra Madre and Central Plateau, but the area was traversed by some species during the Pleistocene. A possible recent ecological disjunction has formed between the Sierra Madre de Chiapas and the Southwestern Highlands of Guatemala (Wake and Lynch, 1982) that seems to be a xeric canyon immediately west of Volcán Tacaná. Another site of disjunction is the lower area of the Central Plateau in the vicinity of Comitán, Chiapas. This tract separates the higher Central Plateau from similar areas in the Sierra de los Cuchumatanes of Guatemala, and supports a subhumid pine-oak forest (most of which is now cleared). The central ridges of the Isthmus of Tehuantepec may be responsible for disjunction between the Gulf lowlands and Pacific Coastal Plain (Duellman, 1960), although some species range continuously across the isthmus. Another disjunct pattern involving the Isthmus of Tehuantepec is between the subhumid Pacific lowlands of México and dry areas of the Yucatan Peninsula (Lee, 1980). However, connection between those areas, in the case of many species, was likely pre-Pleistocene because of taxonomic differentiation of closely related taxa (e.g. species of *Triprion,* the *Enyaliosaurus* section of *Ctenosaura, Eumeces, Cnemidophorus,* and *Symphimus.*

Areas of ecological or faunal continuity (modern dispersal routes?) between non-adjacent regions can also be identified within the study area. The Central Depression and Pacific Coastal Plain are connected by a subhumid corridor in the northwestern Sierra Madre. Many members of the herpetofauna of the Depression are obviously Pacific versant forms that entered the region after the corridor opened. Dispersal rates have not been equal in all species. Some forms do not occur throughout the Central Depression; 17 species have been recorded only from the northwestern section near the Sierra Madre corridor. Lack of endemism in the Depression indicates faunal relationships with other areas during its history, or endemic members have since become extinct. Stuart (1954a) discussed a subhumid corridor through Nuclear Central America, with the Central Depression being a major portion of that track. Lastly, the lowland of the Isthmus of Tehuantepec afford continuity for the ranges of a few ubiquitous lowland species.

I conclude that northwestern Nuclear Central America has undergone climatic fluctuations during the Pleistocene to recent times and that species ranges have been concordantly affected. Where disjunctions have occurred, time has not been sufficient for speciation among assemblages containing the same species. However, speciation has occurred among assemblages that became disjunct before the Pleistocene. The areas of endemism located on the Central Plateau and separate areas of the Sierra

dre were probably formed by pre-Pleistocene orogenies, and some vicariant spe-
s from those areas dispersed to other areas after Pleistocene climatic changes.
Distributional patterns of the herpetofauna of the study area do not support the
esis that geological activity is the only major factor that separates homogeneous
rce biotas. I believe that two factors are involved. One factor implies source biotas
ing subjected to orogenic uplift, initiated during the Oligocene in Nuclear Central
nerica, and divided into vicariant biotas that evolved independently (strict vicari-
ce theory). The other factor involves a diverse topographic area which remained
ologically stable for a reasonable period of time, but encountered major climatic
anges (Pleistocene in Nuclear Central America). The changes caused depression or
ward (elevational) movement of ecosystems and subsequent dispersal of previously
ariant species into new areas (less vagile species remained in their respective
eas of endemism). When local ecological conditions changed following the climatic
nsformation, ecological barriers produced disruption of continuous habitats,
ereby forming separate communities. Speciation will follow if time and genetic iso-
ion permit (dispersal theory). I consider long distance dispersal, across wide barri-
, to be of little significance in continental biogeography, but it may happen under
eptional circumstances. All species or species groups formed by disjunction have a
ter of origin, but the site of origin may or may not be recognizable. Geologically vi-
iant species originate from source biotas that have been passively separated by ge-
gical features and ecologically separated species originate much the same way, but
lowing an environmental change. Dispersal may conceal any exact enter of origin
either case, if environmental conditions allow movement into new geographic
eas. More generalized species may disperse across limited barriers (filter barriers)
t restrict more specialized forms. Therefore, I believe that major biogeographic
tterns are not governed by any single process, but by particular conditions present
the area at a given time. While geological vicariance has been important in shap-
distributional patterns, especially when correlated with plate tectonics and or-
enies, ecological disjunction and dispersal cannot be dismissed as a cause of distri-
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RESUMEN

Doscientos noventa y siete especies nativas de anfibios y reptiles son reconocid dentro del límite territorial del núcleo noroeste de América Central, la zo mexicana situada al este del Itsmo de Tehuantepec y exclusiva de la Península Yucatán. La mayoría de los parámetros ambientales de dicha zona son ext madamente variables. La distribución de cada expecie herpetofáunica se discu en relación a siete regiones fisiográficas, diez formaciones vegetativas y elevación. Los elementos herpetofáunicos no se encuentran restringidos a u región fisiográfica o formación vegetativa particular, sino que la mayor de los especies están asociadas con las distintas zonas faunales las cuales s definidas por el clima, la topografía y la elevación. Grupos distribucionales anfibios y reptiles son identificados y clasificados de acuerdo a 13 conjunt geográficos o especies que no están conformadas en las dinstintas zonas faunal las especies son enlistadas dentro de cada grupo. Los conjuntos están conpuestos especies que muestran continuidad o disyunción de alineamientos geográfico Los análisis distribucionales de la herpetofauna revelan que ni el área de estud ni el núcleo Centro Americano están compuestos de un conjunto homogéneo anfibios y reptiles, sino que contienen especies restringidas primariamente a u región Mesoamericana más grande. Sin embargo, las zonas montañosas d núcleo Centro Americano contienen suficientes especies endémicas q justifican dicho núcleo como una región de Mesoamérica. Solamente 6 especies concurren dentro del nucleo noroeste Centro Americano las cuales so colocadas dentro de regiones Neoárticas y o Neotropicales y en su mayoría so consideradas de orígen Mesoamericano. Veinte especies son relacionadas con u orígen Neoártico o Neotropical, con una ligera mayoría de formas Neoárticas.

Los modelos de distribución geografica herpetofáunica del núcleo noroest Centro Americano identifican las teorias vicaria y de dispersion como la explic ción de sus origenes históricos.

Los eventos vicarios son primariamente responsables por la afectación de los r cursos bióticos del pre-Pleistoceno. Las fluctuaciones climaticas Pleistocenica causaron la separación de los conjuntos disyuntivos aquí descritos.

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APPENDIX

Extant members of the herpetofauna known to occur within northwestern Nucle Central America and their distribution within physiographic regions (Müllerrie 1957; Breedlove, 1973), vegetation formations (Breedlove, 1973), and elevation ranges. Abbreviations are as follows - Physiographic regions: PC = Pacific Coast Plain, SM = Sierra Madre de Chiapas, CD = Central Depression, CP = Centr Plateau, EH = Eastern Highlands, NH = Northern Highlands, and GC = Gu Coastal Plain. Vegetation formations: TR = tropical rainforest, LR = lower mo tane rainforest, MR = montane rainforest, CF = evergreen cloud forest, ES = ever reen and semi-evergreen seasonal forest, TD = tropical deciduous forest, SV = short-tree savanna, TW = thorn woodland, PL = Pine-oak-*Liquidambar* forest, P = Pine-oak forest.

NAME	PHYSIOGRAPHIC REGIONS	VEGETATION FORMATIONS	ELEVATIO (m)
GYMNOPHIONA:			
Dermophis mexicanus	PC,SM,CD,NH,GC	TR,LR,ES,TD,TW	0-100
Dermophis oaxacae	PC,SM	MR,ES	100-150
CAUDATA:			
Bolitoglossa engelhardti	SM	MR, CF	1500-250
Bolitoglossa flavimembris	SM	MR, CF	1500-250
Bolitoglossa flaviventris	PC, SM	LR, ES	100-100
Bolitoglossa franklini	SM	MR, CF	1500-250
Bolitoglossa hartwegi	CP	PL, PO	2000-290
Bolitoglossa lincolni	CP	PL, PO	1570-250
Bolitoglossa mexicana	CP,EH,NH,GC	TR,LR,MR,PL,PO	200-150
Bolitoglossa occidentalis	PC,SM,CP,NH	LR,MR,CF,ES,PO	150-200
Bolitoglossa platydactyla	GC	TR	50-20
Bolitoglossa rostrata	CP	PL,PO	2500-300
Bolitoglossa rufescens	EH,NH,GC	TR,LR	100-100
Bolitoglossa stuarti	CP	TD,PO	1000-150
Bolitoglossa veracrucis	GC	TR	15
Bolitoglossa sp.	SM	MR,CF	2000-250
Dendrotriton megarhinus	SM	MR,CF	2000-250
Dendrotriton xolocalcae	SM	MR,CF	1500-2500
Nototriton alvarezdeltoroi	CP	CF	1550
Nyctanolis pernix	CP	PL	1290
Oedipina elongata	EH,NH	LR	500-1000
Pseudoeurycea brunnata	SM	MR,CF	2400-3000
Pseudoeurycea goebeli	SM	MR,CF	2400-3000
Pseudoeurycea rex	SM	MR,CF	2500-3000+
Pseudoeurycea sp. 1	SM	CF,PO	1700-2000
Pseudoeurycea sp. 2	NH	MR	1000-1200
ANURA:			
Rhinophrynus dorsalis	PC,CD,GC	TR,TD,SV,TW	0-700
Bufo bocourti	SM,CP	MR,CF,ES,PL,PO	2000-3000
Bufo canaliferus	PC,SM,CD	LR,ES,TD,SV,TW	0-750
Bufo cavifrons	SM,CP,NH	LR,MR,CF,PO	300-2000

fo coccifer	PC,CD	TD	100-500
fo leutkinii	PC	ES	50-500
fo marinus	All Regions	TR,LR,ES,TD,SV TW,PO	0-1500
fo marmoreus	PC,SM,CD	TD,SV,TW	0-1000
fo tacanensis	SM	LR,MR	200-2000
fo valliceps	SM,CD,CP,EH,NH,GC	TR,LR,ES,TD,SV	0-2200
utherodactylus alfredi	EH,NH,GC	TR,LR	100-500
utherodactylus erkenbuschii	GC	TR	105
utherodactylus glaucus	CP	PO	2100
utherodactylus greggi	SM	MR,CF	2000-2500
utherodactylus laticeps	EH,NH,GC	TR,LR	200-1000
utherodactylus lineatus	SM,CP,NH	MR,CF,PO	900-2000
utherodactylus matudai	SM	MR,PL,PO	1000-2000
utherodactylus pygmaeus	SM	MR,CF,ES	200-2000
utherodactylus rhodopis	PC,SM,CD,EH,NH,GC	TR,LR,MR,ES,TD,SV	100-1200
utherodactylus rugulosus	All Regions	TR,LR,MR,ES,TD,PL,PO	100-2000
utherodactylus sartori	SM	MR	1500-2000
utherodactylus silvicola	SM	CF	1500
utherodactylus stuarti	CP,NH	LR,MR,PO	500-2300
therodactylus taylori	CP	CF	2000
therodactylus xucanebi	CP	CF,PL,PO	2000-2500
therodactylus sp.	NH	LR,MR	500-1200
todactylus fragilis	PC,SM,CD,EH,NH,GC	TR,LR,MR,ES,TD,SV,TW	0-1700
odactylus melanonotus	PC,SM,CD,EH,NH,GC	TR,LR,MR,ES,TD,SV,TW	0-1000
salaemus pustulosus	PC,SM,GC	TR,ES,TD,SV,TW	0-200
hophus leprus	NH	LR	200-1000
hophus pipilans	PC,SM,CD,CP,NH	LR,ES,TD,SV,TW,PO	100-1700
hophus rubrimaculatus	PC,SM	LR,ES	0-1000
rolenella fleischmanni	SM,NH	LR,MR	250-1500
ychnis callidryas	NH,GC	TR,LR	100-400
ychnis moreletii	SM,NH	LR,MR,ES	300-1500
heca spinosa	NH	LR,MR	500-1200
chaneque	SM,CP,NH	LR,MR,CF	200-2000
ebraccata	GC	TR,ES	0-200
loquax	GC,EH,NH	TR,LR,PL	0-1500
melanomma	CP	MR,CF,PL	1500-2100
microcephala	EH,NH,GC	TR,LR,ES	100-1000
miotympanum	CP	MR,CF	1500-2000
picta	CP,EH,NH,GC	TR,LR,ES	0-1700
robertmertensi	PC,SM,CD	ES,TD,SV,TW	0-750
sumichrasti	SM,CD,CP,NH	MR,CF,TD	200-2000
walkeri	CP	PL,PO	1500-3000
gon staufferi	All Regions	TR,LR,ES,TD,SV,TW	0-1000
ohyas venulosus	PC,SM,GC	TR,ES,TD,SV,TW	0-200
ohyla avia	SM	MR,CF	1700-2200
ohyla guatemalensis	SM,CP	MR,CF,PL,PO	2000-2500
ohyla hartwegi	SM	MR,PL,PO	1000-2200
ohyla ixil	CP	MR,CF	1500-2000
ohyla lacertosa	SM	MR,CF	1000-2000
ohyla matudai	SM,CP	MR,CF	1500-2200

Plectrohyla pycnochila	CP	PL,PO	2000-2600
Plectrohyla sagorum	SM	MR,CF	2000-3000
Ptychohyla euthysanota	SM,CP,EH,NH	LR,MR,CF,TD,PL PO	200-2000
Ptychohyla schmidtorum	SM,CP	LR,MR,CF,ES,TD	200-2000
Smilisca baudinii	All Regions	TR,LR,MR,CF,ES, TD,SV,TW,PO	0-2000
Smilisca cyanosticta	EH,NH,GC	TR,LR,MR	100-1200
Triprion spatulatus	PC	TW	0-200
Gastrophryne elegans	GC	TR,LR	0-200
Gastrophryne usta	PC,SM,CD	ES,TD,SV,TW	0-1000
Hypopachus barberi	CP,GC	TR,PO	100-2500
Hypopachus variolosus	SM,CD,CP	TD,SV,PO	100-1700
Rana maculata	NH,SM,CP	MR,ES,TD,PL,PO	200-3000
Rana pipiens complex	All Regions	TR,LR,MR,TD,SV, PL,PO	100-3000
Rana vaillanti	SM,CD,EH,NH,GC	TR,LR,TD	0-1000
SQUAMATA (Sauria):			
Coleonyx elegans	PC,SM,CD,EH,NH, GC	TR,LR,TD,SV	0-1000
Gonatodes albogularis	PC,SM	LR,ES	0-1000
Phyllodactylus tuberculosus	PC,SM,CD	TD,SV	0-800
Sphaerodactylus glaucus	PC,SM,CD,NH,GC	TR,LR,TD	200-1000
Sphaerodactylus millepunctatus	NH,GC	TR,LR	100-750
Thecadactylus rapicaudus	NH	LR	200-300
Lepidophyma flavimaculatum	NH,GC	TR,LR	100-750
Lepidophyma lipetzi	NH	LR	500
Lepidophyma smithii	PC,SM	MR,ES,TD	0-1200
Lepidophyma tuxtlae	NH	LR	750
Basiliscus vittatus	All Regions	TR,LR,ES,TD,SV, TW,PO	0-1500
Corytophanes cristatus	EH,NH	LR	200-1000
Corytophanes hernandezi	EH,NH,GC	TR,LR,MR	0-1100
Corytophanes percarinatus	SM,CP	MR,ES,TD,PL	200-2500
Ctenosaura pectinata	SM,CD	TD	200-1000
Ctenosaura similis	PC,SM,CD,GC	TR,ES,TD,SV,TW	0-1000
Iguana iguana	All Regions	TR,LR,TD,SV,TW	0-750
Laemanctus longipes	NH,GC	TR,LR,MR	200-1200
Laemanctus serratus	CD,CP,NH	LR,TD	500-1500
Norops anisolepis	SM,CP	MR,PL,PO	1500-2500
Norops barkeri	NH	LR	200-1000
Norops biporcatus	SM,CP,EH,NH	LR,MR,CF,ES,TD, PO	200-2000
Norops breedlovei	SM,CP	MR,CF,PL,PO	1500-2200
Norops capito	EH,NH,GC	TR,LR	100-1000
Norops compressicaudus	NH	LR,MR	500-1200
Norops crassulus	SM,CP	CF,PL,PO	1800-3000+
Norops cuprinus	SM	TD	200-500
Norops dolfusianus	PC,SM	LR,ES,TD	200-1200
Norops laeviventris	CD,CP,NH	LR,MR,TD,PL,PO	500-2000
Norops lemurinus	PC,SM,EH,NH,GC	TR,LR,MR,ES,TD	0-1100
Norops matudai	SM	MR,ES	200-1000
Norops parvicirculatus	NH	LR,MR	500-1200
Norops pentaprion	PC,SM,NH,GC	TR,LR,ES	0-500
Norops petersii	SM,CP,EH,NH	LR,MR,CF,PL	200-2000
Norops pygmaeus	NH	LR	750

orops rodriguezii	SM,EH,NH,GC	TR,LR,MR,CF	100-2000
orops sagrei	GC	TR	0-200
orops sericeus	All Regions	TR,LR,ES,TD,SV, TW,PO	0-1500
orops tropidonotus	CP,EH,NH,GC	TR,LR,MR,ES,PL PO	0-1700
orops uniformis	SM,EH,NH,GC	TR,LR	0-1300
hrynosoma asio	PC,CD	SV,TW	0-750
celoporus acanthinus	SM	LR,MR,ES	500-2000
celoporus carinatus	CD	TD,SV,TW,PO	500-1000
celoporus chrysostictus	GC	TR,ES	0-200
celoporus internasalis	SM,CP,NH	LR,MR,CF,PL,PO	500-2000
celoporus melanorhinus	PC,SM,CD,CP	TD,SV,TW	0-2000
celoporus serrifer	CP	PL,PO	1000-2000
celoporus siniferous	PC,SM,CD	ES,TD,SV,TW	0-1000
celoporus smaragdinus	SM	MR,CF,PL,PO	2100-3000+
celoporus squamosus	PC,SM	MR,ES,TD	0-1000
celoporus taeniocnemis	CP	MR,CF,ES,PL,PO	1500-2500
celoporus variabilis	All Regions	TR,LR,MR,ES,TD, SV,TW,PL,PO	0-2500
rosaurus bicarinatus	PC,SM,CD	TD,SV	100-1000
umeces sumichrasti	PC,SM,NH,GC	TR,LR,ES	0-1000
abuya unimarginata	PC,SM,CD,CP, NH	TR,LR,ES,TD, SV	0-1000
phenomorphus assatus	PC,SM,CD,CP, EH,NH	LR,MR,ES,TD, PL,PO	200-2500
phenomorphus cherriei	PC,SM,CP,EH, NH,GC	TR,LR,ES,PL, PO	0-2500
phenomorphus gemmingeri	SM	TD,PO	200-2000
phenomorphus incertus	SM,CP	LR,MR,PL,PO	1800-2500
meiva chaitzami	CD,CP	PL,PO	800-2000
meiva festiva	EH,NH	LR	200-1000
meiva undulata	All Regions	TR,LR,ES,TD,SV, TW,PL,PO	0-1500
nemidophorus deppii	PC,SM,CD,GC	TR,ES,TD,SV,TW, PO	0-1200
nemidophorus guttatus	PC,SM,CD,GC	TR,ES,TD,SV,TW	0-1200
nemidophorus motaguae	SM,CD	TD,SV	500-1200
nemidophorus sp.	CD,CP	TD,SV,PO	750-1500
ymnophthalmus speciosus	SM,CD	TD,SV	200-750
bronia aurita	CP	CF	1800-2000
bronia bogerti	SM	PO	700-1600
bronia lythrochila	CP	CF,PL,PO	2000-3000
bronia matudai	SM,CP	MR,CF,PL	1800-2500
bronia ochoterenai	SM,CP	MR,CF,PL,PO	1800-2500
bronia ornelasi	SM	CF	1600
elestus rozellae	NH,GC	TR,LR,MR	0-1200
errhonotus liocephalus	SM,CD,CP,NH	LR,MR,CF,TD,PL	200-2000
esaspis moreletii	SM,CP	MR,CF,PL,PO	1500-3000+
enosaurus grandis	SM,CP,EH,NH	LR,MR,PL,PO	750-1800
eloderma horridum	PC,SM,CD	TD,SV,TW	0-1000

QUAMATA (Serpentes):

oa constrictor	PC,SM,CD,EH,NH, GC	TR,LR,ES,TD,SV, TW	0-1500
oxocemus bicolor	PC,SM,CD	ES,TD,SV,TW	0-750
galiophis continentalis	PC,CP	ES,PO	100-2300
ptotyphlops goudotii	PC,SM,CD,CP,NH	LR,ES,TD,SV,TW	100-1500

Typhlops tenuis	GC	TR,ES	0-200
Adelphicos latifasciatus	SM	CF,PO	1500-2000
Adelphicos nigrilatus	CP	PL,PO	2000-2900
Adelphicos quadrivirgatus	SM,CD,EH,NH,GC	TR,LR,MR,TD,SV,PO	200-1500
Amastridium veliferum	PC,SM,NH	LR,ES	100-1000
Clelia clelia	GC	TR	0-200
Clelia scytalina	PC,SM,CD	ES,TD	100-1000
Coluber constrictor	CD	TD,SV	800
Coniophanes bipunctatus	NH,GC	TR,LR	0-300
Coniophanes fissidens	PC,SM,EH,NH,GC	TR,LR,MR,ES,TD	0-1000
Coniophanes imperialis	CD,CP,EH,NH,GC	TR,LR,TD,SV,PO	0-2000
Coniophanes piceivittis	PC,CD	TD	0-800
Coniophanes quinquevittatus	GC	TR,ES	0-200
Coniophanes schmidti	NH	LR	200
Conophis lineatus	SM	TD	250
Conophis pulcher	PC	TD,SV	0-200
Conophis vittatus	PC,SM,CD	TD,SV	0-1500
Dendrophidion vinitor	NH,GC	TR,LR	100-1000
Dipsas maxillaris	GC	TR	0-100
Dryadophis melanolomus	All Regions	TR,LR,MR,ES,TD,SV,PO	0-1500
Drymarchon corais	All Regions	TR,LR,MR,ES,TD,SV,PO	0-1500
Drymobius chloroticus	SM	LR,MR,CF,ES,PO	500-2500
Drymobius margaritiferus	All Regions	TR,LR,MR,TD,SV,TW,PO	0-2000
Elaphe flavirufa	SM,NH	LR,MR	500-1500
Enulius flavitorques	PC,SM,CD	TD,SV,TW	0-750
Ficimia publia	PC,SM,CD,NH,GC	TR,LR,ES,TD	0-1000
Ficimia ramirezi	SM	TD,PO	1000-1500
Geophis cancellatus	SM	LR,MR	500-2000
Geophis carinosus	CP,NH	LR,MR,CF,PL,PO	200-2000
Geophis immaculatus	SM	MR,CF	1500-2500
Geophis laticinctus	SM,CP,NH	LR,MR,CF,PL,PO	500-2000
Geophis nasalis	SM	LR,MR,ES,TD,SV	400-1500
Imantodes cenchoa	PC,SM,CP,EH,NH,GC	TR,LR,MR,ES,TD	0-1200
Imantodes gemmistratus	PC,SM,CD,EH,NH	LR,ES,TD,SV,TW	0-750
Lampropeltis triangulum	PC,SM,CD,EH,NH GC	TR,LR,MR,ES,TD,SV,TW	0-1000
Leptodeira annulata	PC,SM,CD	LR,MR,ES,TD,SV,TW	0-2000
Leptodeira frenata	EH,NH,GC	TR,LR	0-1000
Leptodeira nigrofasciata	PC,CD	TD,SV,TW	0-750
Leptodeira septentrionalis	PC,SM,CD,CP,NH GC	TR,LR,MR,ES,TD,PO	0-1500
Leptophis ahaetulla	EH,NH,GC	TR,LR,MR	0-1200
Leptophis diplotropis	PC,SM,CD,NH	LR,TD,SV	0-1000
Leptophis mexicanus	PC,SM,EH,NH,GC	TR,LR,ES,TD,SV,PO	50-1700
Leptophis modestus	CP	MR,CF	1500-2000
Manolepis putnami	SM	TD,PO	300-1000
Masticophis mentovarius	PC,SM,CD,GC	TR,ES,TD,SV,TW,PO	0-1500
Nerodia rhombifera	GC	TR,ES	0-200
Ninia diademata	SM,CP,EH,NH,GC	TR,LR,MR,CF,ES,PL,PO	100-2200

inia sebae	SM,CP,EH,NH,GC	TR,LR,MR,CF, ES,PL,PO	100-2200
xybelis aeneus	PC,SM,CD,EH, NH,GC	TR,LR,MR,ES, TD,SV,TW,PL	0-1500
xybelis fulgidus	PC,SM,CD,EH	LR,MR,ES,TD,SV	0-1000
xyrhopus petola	NH,GC	TR,LR	0-200
ituophis lineaticollis	SM,CP	TD,PL,PO	1500-2500
liocercus andrewsi	SM	MR,CF	1500-2000
liocercus elapoides	PC,SM,CP,EH, NH,GC	TR,LR,MR,CF, ES,TD,PL,PO	100-2000
seustes poecilonotus	EH,NH,GC	TR,LR,NH,MR	50-1200
hadinaea decorata	EH,NH,GC	TR,LR,MR,ES	50-1200
hadinaea godmani	SM,CP	CF,ES,PL,PO	1000-2500
hadinaea hannsteini	SM	LR,MR,PL,PO	500-2000
hadinaea hempsteadae	CP	CF,PL,PO	1700-3000
hadinaea lachrymans	SM	LR,MR,CF	500-3000
hadinaea macdougalli	SM	CF,PO	1500-2000
hadinaea posadasi	SM	LR	500-1000
alvadora lemniscata	PC,SM,CD	TD,SV,TW	200-1000
caphiodontophis annulatus	SM,CD,NH,GC	TR,LR,TD,SV	0-1000
enticolis triaspis	SM,CD,NH	LR,MR,TD,TW	300-1500
ibon dimidiata	EH,NH,GC	TR,LR	0-1000
ibon fasciata	SM,CD	MR,ES,TD	100-2000
ibon fisheri	SM,CP	MR,CF,PL,PO	1500-3000
ibon nebulata	SM,NH,GC	TR,LR,ES,TD	0-1000
ibon sartorii	PC,SM,CP,EH,NH	TR,LR,MR,ES	100-2000
pilotes pullatus	PC,SM,EH,NH,GC	TR,LR,ES,TD,PO	0-1500
tenorrhina degenhardtii	EH,NH	LR,MR	200-1100
tenorrhina freminvillei	PC,SM,CD,CP,EH, NH	LR,ES,TD,SV,TW, PL,PO	0-1700
toreria dekayi	CP	PO	1250
ymphimus leucostomus	SM	TD	200-1000
antilla jani	PC,SM	LR,ES,TD	0-1000
antilla rubra	PC,SM,CD	ES,TD	100-1000
antilla schistosa	PC	TW	60
antilla taeniata	PC	TW	0-100
antilla tayrae	SM	LR,MR	500-1000
antillita brevissima	SM	TD	200-1700
hamnophis cyrtopsis	SM,CP	PO	1000-2500
hamnophis fulvus	SM,CP	MR,CF,PL,PO	2000-3000 +
hamnophis marcianus	NH,GC	TR,LR,ES	0-300
hamnophis proximus	PC,CD,CP,GC	TR,TD,SV,TW,PL, PO	0-2500
etanorhinus nigroluteus	GC	TR,ES	0-200
imorphodon biscutatus	PC,SM,CD,CP,EH	LR,TD,SV,TW	0-1500
nodon rabdocephalus	PC,SM,CD,EH,NH	TR,LR,MR,ES,TD	200-1200
icrurus browni	CD,CP	TD,SV,PO	500-1500
icrurus bogerti	PC,SM	TD,SV,TW	0-300
icrurus diastema	CP,EH,NH,GC	TR,LR,MR,PL,PO	0-1500
icrurus elegans	SM,EH,NH,GC	TR,LR,MR,CF	100-1600
icrurus latifasciatus	PC,SM	LR,ES,TD,SV,TW	0-1200
icrurus nigrocinctus	PC,SM	LR,MR,ES,TD	100-1500
kistrodon bilineatus	PC,CD	TD,SV,TW	0-1000
throps atrox	PC,SM,EH,NH,GC	TR,LR,ES,TD,SV	0-1000
throps bicolor	SM	LR,MR,CF,ES	1000-2000
throps dunni	PC,SM	TD,SV,TW	0-500
throps godmani	SM,CP	MR,CF,PL,PO	1500-2500
throps nasuta	EH,GC	TR,LR	100-1000
throps nigroviridus	SM,CP,EH	LR,MR,CF,PL,PO	200-2200

Bothrops nummifer	SM,CP,EH,NH, GC	TR,LR,MR,CF, ES,TD,PL,PO	200-2000
Bothrops ornatus	SM	ES	200-500
Bothrops schlegelii	EH,NH	LR,MR	500-1200
Bothrops tzotzilorum	CP	PO	2050-2500
Crotalus durissus	PC,SM,CD,EH	LR,ES,TD,SV,TW	0-1000
TESTUDINES:			
Dermatemys mawii	EH,NH,GC	TR,LR,ES	0-300
Chelydra serpentina	GC	TR,ES	0-200
Claudius angustatus	GC	TR,ES	0-200
Kinosternon acutum	GC	TR,ES	0-200
Kinosternon leucostomum	CP,EH,NH,GC	TR,LR,ES,PL,PO	0-1500
Kinosternon scorpioides	PC,SM,CD,CP	ES,TD,SV,TW,PO	0-1500
Staurotypus salvinii	PC	ES,TD,SV	0-200
Staurotypus triporcatus	GC	TR,ES	0-200
Rhinoclemmys areolata	NH,GC	TR,LR,ES	0-300
Rhinoclemmys pulcherrima	PC	ES,TD,SV	0-200
Rhinoclemmys rubida	PC,CD	ES,TD,SV,TW	0-750
Trachemys scripta	PC,EH,GC	TR,LR,ES,TD,SV	0-1000
CROCODYLIA:			
Caiman crocodylus	PC	ES,TD,SV,TW	0-200
Crocodylus acutus	PC,CD,EH,GC	TR,LR,ES,TD,SV	0-500
Crocodylus moreletii	EH,NH,GC	TR,LR	0-1000

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