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An Ecogeographic Analysis of the Herpetofauna of the Yucatan Peninsula

By
Julian C. Lee

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February 29, 1980

An Ecogeographic Analysis
of the Herpetofauna of the Yucatán Peninsula

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CONTENTS

INTRODUCTION	1
ACKNOWLEDGMENTS	1
THE ENVIRONMENT	2
Physiography	2
Climate	4
Vegetation	5
Geology	6
COMPOSITION OF THE HERPETOFAUNA	7
SECTION I. PATTERNS OF DISTRIBUTION, SPECIES DENSITY, AND ENDEMISM	8
METHODS	8
RESULTS	10
DISCUSSION	15
SECTION II. ENVIRONMENTAL CORRELATES OF SPECIES DENSITY	17
METHODS	17
RESULTS	22
DISCUSSION	24
SECTION III. EVOLUTION OF A NEOTROPICAL PENINSULAR HERPETOFAUNA	30
METHODS	31
RESULTS	31
DISCUSSION	35
SUMMARY AND CONCLUSIONS	40
RESUMEN	41
LITERATURE CITED	42
APPENDIX	47

INTRODUCTION

For several reasons the peninsula of Yucatán offers an excellent opportunity to study patterns of animal distribution and to assess the relative contributions of several factors thought to be important in setting distribution limits and thus in controlling the numbers of co-occurring species: (1) The area can be delineated objectively using natural features that constitute a barrier to dispersal of the terrestrial fauna; the peninsula is thus a relatively discrete and self-contained unit. (2) The area forms a cul-de-sac, with faunal interchange generally restricted to movement along a north-south axis; thus, although the point of origin for the various faunal elements may not be known, most of the fauna must have entered from the south and spread northward. (3) The northern end of the peninsula is comparatively young geologically, thus affording an opportunity to assess the effects of time in shaping patterns of distribution and species density. (4) Strong north-south gradients in precipitation and vegetation structure exist within the peninsula and are not seriously confounded by elevational variation.

In this study I have sought to assemble and integrate into a coherent whole certain distributional, ecological, and historical data pertaining to the herpetofauna of this restricted portion of the Neotropics. I use these data to test various hypotheses that have been invoked to explain gradients in species density, and I formulate a series of hypotheses concerning the evolution of the peninsular herpetofauna. In so doing I have found it expedient to organize the study into three sections. In section one I seek to identify recurring patterns of distribution, endemism, and species density. In section two I attempt to relate the patterns of distribution and species density to environmental features in order to evaluate the importance of various factors in setting distribution limits and in

controlling the numbers of co-occurring species. Finally, in section three I treat the historical development of the herpetofauna and its patterns of distribution through ecological and evolutionary time.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the many people who assisted in various phases of this project. For loan of specimens, answers to my written queries, and/or provision of working space, I am indebted to the following curators and their institutions: Richard G. Zweifel and Charles W. Myers, American Museum of Natural History; Clarence J. McCoy, Carnegie Museum of Natural History; Shi-Kuei Wu, University of Colorado Museum; Max A. Nickerson and Robert W. Henderson, Milwaukee Public Museum; Arnold G. Kluge and Ronald A. Nussbaum, Museum of Zoology, University of Michigan; Hymen Marx, Field Museum of Natural History; John W. Wright and Robert L. Bezy, Los Angeles County Museum; Ernest E. Williams, Museum of Comparative Zoology; David B. Wake, Museum of Vertebrate Zoology; George R. Zug and W. Ronald Heyer, National Museum of Natural History; Dorothy Smith, University of Illinois; Walter Auffenberg and John Iverson, Florida State Museum. Ernest Liner and James Knight supplied locality data from their private collections, as did Rev. Lennard Dieckmann, S. J., St. John's College, Belize City, Belize.

Collecting permits were graciously issued by Mr. E. O. Bradley, Chief Forestry Officer, Ministry of Trade and Industry, Belize; and by Dr. Antonio Landazuri Ortiz, Dirección General de la Fauna Silvestre, México. I thank the authorities of Tikal National Park for permission to measure trees there.

Field work was supported in part by a National Science Foundation grant for improving doctoral research in the field

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During various phases of this project I have benefited from discussions with many talented biologists, including Robert L. Bezy, Martha L. Crump, John D. Lynch, Clarence J. McCoy, Michael V. Plummer, Alan H. Savitzky, L. C. Stuart, Catherine A. Toft, Richard Wassersug, and John Wright. William E. Duellman, chairman of my doctoral committee, shared with me his wealth of knowledge of Neotropical biology. He also carefully read and criticized the manuscript, as did Richard F. Johnston, Norman A. Slade, and two anonymous reviewers. All errors are my responsibility.

A host of Yucatecans, Belizians, and Guatemalans aided in specimen acquisition and in other ways facilitated the field work. Richard Lacer and Michael V. Plummer provided companionship in the field.

Janet M. Lee assisted during six months of field work, often in remote areas and under unpleasant conditions. In addition to performing more than her share of maintenance activities, she recorded data, prepared voucher specimens, and identified plants. The project could not have been completed in its present form without her conscientious efforts.

Finally, I owe an obvious debt to L. C. Stuart, who anticipated by 20 to 40 years many of my conclusions. In addition to sharing with me his unparalleled knowledge of Middle American herpetology, "Don Pancho" provided accommodations at Panajachel and smoothed the way for me in many other ways. He made available to me his considerable unpublished data on peninsular amphibians and reptiles, and was, from the out-

set, enthusiastic in his support of this project.

THE ENVIRONMENT

Many authors have treated casually or in detail various aspects of the environment of the Yucatán Peninsula. Here my intent is to provide a brief overview of the physiography, climate, geology, and vegetation of the peninsula, emphasizing those features that are important for an understanding of animal distribution. Readers interested in more thorough discussions of these topics are referred to the publications cited in the following sections.

Physiography.—The Peninsula of Yucatán is a broad, flat limestone shelf jutting north-northeast into the Gulf of México and the Caribbean Sea. Bounded on the north, east, and west by water, and to the south and southwest by the highlands of Alta Verapaz, Guatemala and the Mesa Central of Chiapas, México, the area is a relatively discrete natural unit of approximately 240,000 km², and spans nearly six degrees of tropical latitude. The peninsula contains all of the Department of El Petén, Guatemala; the Republic of Belize (formerly British Honduras); and the Mexican states of Yucatán, Campeche, and Quintana Roo; as well as the eastern portion of Tabasco and the Lacandón region of Chiapas (Fig. 1).

The northern third of the peninsula is devoid of major topographic relief. Only the Sierrita de Ticul (maximum elevation 270 m; Heilprin, 1891) breaks the monotony of the countryside. (See Figure 2 for the locations of many of the place names used in this discussion). The central portion of the peninsula rises gradually to a maximum of 350 m in southeastern Campeche (West, 1964; Paynter, 1955), and is continuous with the rolling uplands of northern El Petén (Stuart, 1958). South of parallel 17°N, in central and southern El Petén, a parallel series of folded limestone ridges runs east-west and thence northwest into Chi-

apas and Tabasco, producing a more varied topography. To the south and southwest these ridges give way to highlands, the 600 m contour of which, for purposes of this work, is taken as the southern boundary of the peninsula. Commencing in northeastern El Petén and continuing through northern Belize and into southern Quintana Roo is a series of major faults which produce low limestone ridges and intervening swampy areas (West, 1964).

The most conspicuous topographic feature of the peninsula is the uplifted south-central portion of Belize, termed variously the Cockscomb or Maya Mountains. These reach a maximum elevation of 1158 m (Wadell, 1938).

The surface of much of the peninsula consists of eroded and thoroughly karsted limestone. Caves, caverns, and subterranean waterways abound, especially in the north. The porosity of the limestone precludes much accumulation of surface water; lakes are uncommon, and rivers are virtually absent from the northern third of the peninsula. Throughout much of this area natural wells (*cenotes*—from the Mayan *dzonot*), which result from collapse of the lime-

stone roofing of subterranean chambers, are important sources of fresh water and support a mesophilic biota. These caves and cenotes have been studied in detail by Cole (1910), Hatt et al. (1953), Mercer (1896), Pearse (1938), and Thompson (1897). Scattered throughout the peninsula are depressions (*aquadas*) which fill with water during the rainy months, but are frequently dry at other times. A belt of lakes extends across southern Campeche and through southern Quintana Roo. From west to east these are: Laguna Silvituc, Zoh Laguna, Laguna Chacanbacab, Laguna Om, and Lago Bacalar. Further south, at approximately 17°N, a chain of lakes lies in a major east-west fault. Among these are Laguna Perdida, Lago Macanché, Laguna Yaxhá, and Lago Petén Itzá; the latter is the largest and deepest lake in the peninsula with a depth in excess of 32 m and a surface area of 567 km² (Covich, 1976).

The northernmost river of any consequence is the Río Champotón, which drains portions of west-central Campeche and enters the Gulf of México at the town of Champotón. In southwestern Campeche several rivers flow in a northerly direction into Laguna de Términos, a large bay which is nearly cut off from the Gulf of México by Isla del Carmen. Among these is the Río Candelaria, which originates in northwestern El Petén, and the ríos Champan and Palizada. By far the largest river is the Usumacinta, which originates in the Departments of Huehuetenango and Alta Verapaz, Guatemala, and flows northward onto the Tabasco lowlands where it joins the Río Grijalva before entering the Gulf of México. Two of its major tributaries, the Río de la Pasión and the Río San Pedro Mártir, drain much of El Petén. Draining an estimated 102,828 km², and with an average annual discharge of approximately 28,118,000,000 m³, the Usumacinta is the most important river in Middle America (Tamayo, 1964). The northernmost river of the Caribbean drainage is the Río

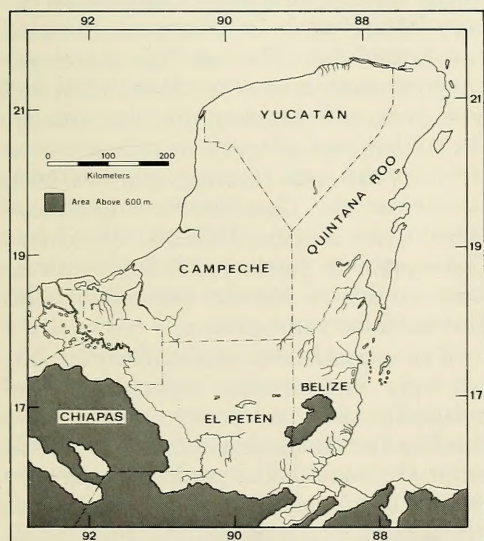


FIG. 1.—Map of the Yucatán Peninsula showing political subdivisions and major topographic features.

Hondo, the headwaters of which drain northeastern El Petén and southeastern Campeche, where the river is known as the Río Azul. The Río Hondo forms the international boundary between Belize and México as it courses northeastward, finally to enter Bahía Chetumal. Most of north-central Belize is drained by the Belize and Sibun rivers, while the southern third of the country is dissected by numerous small rivers and streams, among which are the Deep, Monkey, and Golden rivers. As it flows eastward into Bahía de Amatique, the Río Sarstoon, which originates in the depression between the Maya Mountains and the Sierra de Santa Cruz, forms the southern border between Belize and Guatemala.

The west coast of the peninsula is essentially a sandy beach, occasionally interrupted by low cliffs and rocky areas, as in the vicinity of the town of Campeche. Paralleling much of the northern margin of the peninsula, from Celestún at the northwest corner, to the vicinity of Chiquila near the Yucatán-Quintana Roo border, is a sandy barrier beach, behind which lies a series of swamps, marshes, and shallow lagoons known as *La Cienega*. Along portions of the east coast of Quintana Roo, limestone outcrops form sea cliffs and headlands with which alternate small sandy beaches, as at Tulum. Halfway down the east coast of Quintana Roo are the large shallow bays known as Bahía Ascensión and Bahía Espíritu Santo. Further south lies Bahía Chetumal, which marks the coastal boundary between Belize and México. To the north and west of the peninsula, the Campeche Banks extend up to 250 km from shore, in contrast to the east side of the peninsula where the continental shelf is narrow. Immediately off the northeast coast of Quintana Roo lie several small, sandy islands, possibly the remnants of a barrier bar (Paynter, 1955). Among these are the Islas Contoy, Cancun, and Mujeres. Beginning at the northeast corner of the peninsula and extending discontinuously southward for roughly 650 km to the Gulf of Honduras,

lies the longest coral barrier reef in the Atlantic Tropics (Edwards, 1957). Hundreds of tiny islets and atolls dot the reef, which lies approximately 40 to 60 km off shore. The protected shallow lagoon behind the reef contains numerous small mangrove islands.

Climate.—Aspects of the climate of the Yucatán Peninsula have been essayed by Page (1933, 1938), Lundell (1937), Vivó Escoto (1964), and García (1965), from whose works the following discussion is drawn.

Owing to its tropical setting, low elevation, and to strong maritime influences, the region enjoys a warm and homogeneous temperature regime, with only slight fluctuations in mean temperature from one locality to another, and from season to season. Mean annual temperatures for Progreso, Yucatán; Champotón, Campeche; and Paso de los Caballos, El Petén are 24.9, 26.2, and 27.2 C, respectively (Page, 1933, 1938). The annual range of mean monthly temperature is 6.2 C at Champotón, 4.2 C at Progreso, and 6.1 C at Paso de los Caballos. However, within a single month temperature extremes can be considerable, especially during winter and spring when variations of 22° to 28° C have been recorded at Progreso, Mérida, and Valladolid. The monthly march of temperatures is similar throughout the peninsula, with January and May usually the coldest and warmest months, respectively. Frost and freezing temperatures are unknown. The lowest temperature reported by Page (1933) is 4.0° C for Champotón in January, 1926; the maximum is 47.0° C for the same station in March of the same year.

The amount and seasonality of rainfall vary considerably throughout the peninsula, and from year to year at any one locality. In general rainfall is greatest at the base of the peninsula and decreases to the north and, especially, to the northwest. Progreso, on the northwest coast, receives an average of 500 mm of rain per annum, whereas Paso de los Caballos, in northwestern El Petén,

receives in excess of 1700 mm, and areas farther south receive somewhat more (Page, 1933, 1938). Complicating this general pattern is an area of unusually high rainfall in northern Quintana Roo, where 1200 to 1500 mm may fall in a year (García, 1965). As elsewhere in Middle America, "summer" is the rainy season, with most of the rain falling from May through October. During these six months, rainfall is bimodal, generally with peaks in June and September separated by a relatively dry July. The percentage of total annual rainfall occurring from May to October—a measure of seasonality—increases from south to northwest; in much of western Yucatán and northern Campeche 80 to 90% of the rain falls during this period. The corresponding figures for much of El Petén and eastern Quintana Roo are 60 to 70%.

In summary, the climate of the Yucatán Peninsula may be characterized as thoroughly tropical, with uniformly high temperatures and seasonal rainfall. Annual rainfall is greatest in the south and east portions of the peninsula and least at the northwest corner. Seasonality of rainfall exhibits an opposite pattern, and is greatest in the northwest portion.

Vegetation.—Several attempts have been made to describe and classify the vegetation of the Yucatán Peninsula. Lundell (1934, 1937) combined floristic, climatic, and physiographic information to recognize six phytogeographic divisions in the peninsula, none of which is especially well defined. His Southern Campeche Division includes roughly the southeast third of the state of Campeche, from about the latitude of Champotón south to the Campeche-El Petén border, and from the Campeche-Quintana Roo border west for a distance of approximately 85 km. According to Lundell, the area is a well-drained calcareous upland supporting a forest dominated by the zapote (*Achras zapota*) and the chacá (*Bursera simaruba*) both of which rarely exceed 20 m in height in this area. Palms, figs, (*Ficus* spp.), and mahogany (*Swietenia macrophylla*) are rare, and

groves of ramon (*Brosimum alicastrum*) are widely scattered. The Southwestern Campeche Division encompasses the southwestern third of the state and is characterized by Lundell as a rainforest dominated by cedar (*Cedrela mexicana*), *Swietenia macrophylla*, *Achras zapota*, and *Ficus* spp. Approximately the northern third of Campeche, together with all of Yucatán and the northern tip of Quintana Roo comprise the Northern Division of Lundell's classification. He considered the scrubby thorn forest of this area to be a subclimax resulting from centuries of shifting slash-burn agriculture practiced by the Maya. He further supposed that the region once supported a climax vegetation similar to that of southern Campeche. Embracing nearly all of Quintana Roo and the northern third of Belize is Lundell's East Coast Division, botanically a poorly known region at the time Lundell wrote. He characterized the southern two-thirds of this area, exclusive of Belize, as a vast forest dominated by *Achras zapota* and *Swietenia macrophylla*. The Northern Petén Division lies almost entirely within the Department of El Petén north of the 17th parallel. The botany of this region was treated in detail by Lundell (1937), who characterized the vegetation of these well-drained uplands as a luxuriant broadleaf evergreen quasi-rainforest, where forest giants such as *Ceiba pentandra* and *Swietenia macrophylla* may attain heights of 50 m. South and southwest of Lago Petén Itzá lies the phytogeographic division termed by Lundell (1937) the Central Petén Savanna Country. The region is characterized by a series of disconnected grassy savannas upon which are scattered low, scrubby trees, especially the nanze (*Byrsonima crassifolia*). The boundaries of this savanna country are said to coincide with the boundaries of a tongue of Cretaceous limestone (Lundell, 1937), thereby suggesting a possible edaphic explanation for the anomalous occurrence of savannas amidst the luxurious mesophytic forest. However, Lundell (1937) favored

an anthropogenic origin for the savannas.

Leopold (1950) presented a vegetation map of México, in which he attempted to reconstruct the pre-human distribution of vegetation types. He recognized five such types in the Yucatán Peninsula: rain forest, tropical evergreen forest, tropical deciduous forest, thorn forest, and savanna. Paynter (1955) devised a simple scheme involving only three vegetation zones: a scrub zone bordering the north coast and extending inland for perhaps 20 km; a deciduous forest zone extending over much of Yucatán and northern Campeche; and a rainforest zone covering central and southern Campeche, Quintana Roo, northern El Petén, and northern Belize. Paynter's scrub zone corresponds to the thorn forest type of Leopold, and his deciduous forest zone corresponds to Leopold's tropical evergreen and tropical deciduous forest types combined. Their rainforest zones are essentially the same.

Wagner (1964) utilized a structural classification devised by Beard (1955) in which plant associations are defined on the basis of floristic similarity; the associations are grouped into formations according to physiognomic similarity and are united to form formation series. Two formation series are depicted by Wagner as occurring in the Yucatán Peninsula: a dry evergreen formation series in northern and central Yucatán which also occurs as isolated patches in southwest Campeche, eastern Belize, and central Petén; and a tropical rain forest formation series occurring elsewhere.

Each of the above vegetation classifications has merit, yet no system of vegetation classification nor vegetation map can accurately reflect the complex mosaic that is the vegetation of the Yucatán Peninsula. There, vegetation types grade subtly and imperceptibly into one another, or interdigitate in intricate patterns. Slope, aspect, elevation, drainage, and edaphic factors combine to produce a heterogeneous vegetation even within limited areas. Add to this the effects of climate and long-term human disturb-

ance and the result is a vegetation so complex as to defy simple generalization. Nonetheless, it cannot be denied that both the height and luxuriousness of the forest diminish dramatically from south to north. From a structurally complex mesophytic forest in southern El Petén, the vegetation gradually gives way to a low scrubby xerophytic thorn forest at the north end of the peninsula. Nor can it be doubted that the nature of the vegetation exerts a strong influence on the composition of the herpetofauna.

Geology.—According to Sapper (1937), the Yucatán Peninsula (as defined herein) consists of two distinct orographic units named the "Yucatán Peninsula" and the "South Petén and Maya Mountains." The boundary between the two areas according to both Sapper (1937) and Wadell (1938) is the east-west fault that commences about 40 km south of Belize City on the Caribbean, skirts the northern slope of the Maya Mountains, and then passes just north of the Lakes Yaxhá, Macanché, and Petén Itzá. The boundary then swings northwest, forms the valley of the Río San Pedro Mártir, and then continues through the region of Tenosique to terminate immediately west of Laguna de Términos. North and northeast of the Sierrita de Ticul the geology is reasonably well understood. According to Sapper (1937) the area north of approximately the 21st parallel, including the barrier beach, is of Quaternary age. Southward, extending to the Sierrita lie marine limestones, mostly of Pliocene age, from which the overlying Pleistocene strata have been largely eroded, except in the vicinity of Mérida and Izamal. According to Galloway (in Hatt et al., 1953) the Sierrita is of Miocene age. Of special biogeographic importance is the conclusion of Hatt et al. (1953) that "There is indeed no geological evidence that any of the peninsula from the Serrania (= Sierrita) northwards was available to land vertebrates until late Pleistocene-Recent time. . ." Extending southwest from the Sierrita to the vicinity of Laguna de Términos and

into northern El Petén is a vast area mapped by Sapper (1937) as Miocene limestone, but which, according to the profile drawn by Galloway (in Hatt et al., 1953) should include Oligocene deposits in northern Campeche, and possible Eocene deposits in northern El Petén. The entire Tabasco-Campeche alluvial plain in the vicinity of Laguna de Términos was considered by Sapper (1937) to consist of Quaternary sediments. He considered the limestones of northern Belize and northeastern El Petén to be of Oligocene age, having been stripped of their Miocene covering (Wadell, 1938).

The area of southern El Petén, considered by Wadell (1938) a geologic-ographic continuation of Chiapas and Tabasco, consists of dolomitic limestones resting conformably upon the Lower Cretaceous limestones of northern Alta Verapaz. Wadell (1938) thus considered them to be of Upper Cretaceous age. These are overlaid by Tertiary breccias and conglomerates, generally of Eocene to Oligocene age. Quaternary deposits of gravel, sand, and clay occur along rivers and lakes, and in topographic depressions. As described by Ower (1929), the Maya Mountains of south-central Belize are an uplifted block of Upper Carboniferous granite, surrounded by Cenozoic limestones. Ower (1929) believed that the mountains arose as part of a general Pliocene orogeny, but Stuart (1966) indicated that they have been land positive since the Cretaceous.

Thus, with only local exceptions, the Peninsula of Yucatán can be viewed as a continuous block of marine limestone of various ages, sloping upward toward the south. Emergence of this unit, which apparently commenced in the Miocene (Vinson and Brineman, 1963), proceeded from south to north such that the deposits become progressively younger to the north. Throughout the late Tertiary the main portion of the peninsula together with the Maya Mountains were probably land areas in firm connection with Nuclear Central America, although marine

transgressions in the form of the Chapayal Basin and the Amatique Embayment may, in the Upper Tertiary, have severed this connection (Vinson and Brineman, 1963).

COMPOSITION OF THE HERPETOFAUNA

As presently understood, the known herpetofauna of the Yucatán Peninsula, exclusive of marine turtles and strictly insular forms, consists of 164 species representing 25 families and 93 genera (Table 1). This does not include the faunas of the hundreds of islands and atolls adjacent to the peninsula. Their treatment is beyond the scope of this study. For completeness I have included several species which, although widely distributed elsewhere, barely enter the peninsula and can scarcely be considered integral elements of the herpetofauna. Among these is *Natrix rhombifera*, which reaches its southern distribution limit in eastern Tabasco and southwest Campeche, and *Geophis carinosus*, which is generally restricted to situations at 1000 to 1500 m, but which has been taken at Palenque, Chiapas. I am aware of no specific peninsular localities for *Storeria dekayi* Holbrook (= *Storeria tropica* Cope). The type locality for *S. tropica* is "Petén, Guatemala" (Cope, 1884). Stuart (1934, 1963) considered the species present in the Department of El Petén. I consider *S. dekayi* a valid member of the peninsular herpetofauna, but exclude the species from subsequent analyses.

In comparison with other tropical

TABLE 1.—Taxonomic Composition of the Herpetofauna of the Yucatán Peninsula.

Group	Families	Genera	Species
Salamanders	1	2	5
Anurans	7	15	30
Turtles	4	8	11
Crocodylians	1	1	2
Lizards	6	22	43
Snakes	6	45	73
Total	25	93	164

areas, the peninsular herpetofauna is depauperate. For instance, the Mexican state of Michoacán, with about one-fourth the area, possesses only one less species than does the Yucatán Peninsula (Duellman, 1965b). Comparisons with Amazonia are even less favorable; a 3 km² area of Ecuadorian rainforest is

known to support 173 species of amphibians and reptiles (Duellman, 1978). The numbers of species occurring in the peninsula, and in various regions within the peninsula can be explained, at least in part, in terms of historical and ecological factors. These explanations are presented in the sections which follow.

SECTION I: PATTERNS OF DISTRIBUTION, ENDEMISM, AND SPECIES DENSITY

The task of documenting distributions and searching for patterns is the concern of descriptive (as opposed to historical or ecological) biogeography, and forms the substance of the discussion which follows. Specifically, my purposes here are to (1) ascertain the peninsular distribution of each of the 164 species of amphibians and reptiles in the Yucatán Peninsula, (2) identify areas of concordance of distribution limits, (3) identify and delineate areas of faunal homogeneity, (4) identify areas of endemism, and (5) document patterns of species density.

METHODS

Prerequisite to biogeographic analysis is accurate mapping of the geographic distributions of taxa. Minimally, such mapping requires locality records sufficient to infer distributions accurately, and some understanding of the phyletic relationships of the organism considered. At the very least one must know whether or not samples drawn from different localities represent conspecifics. These kinds of information are not uniformly available for the herpetofauna of the Yucatán Peninsula. Figure 2 identifies those areas where important collections of amphibians and reptiles have been made. Because many archeological expeditions to the peninsula included biologists among their personnel, biological investigation in the area tends, in part,

to reflect the activities of Mayanists, and the biota in the vicinity of many important Mayan centers are comparatively well known. In general Yucatán, northern Quintana Roo, central El Petén, and Belize have been well sampled, whereas portions of southern Campeche, southern Quintana Roo, and northern El Petén form an area where much remains to be learned concerning the herpetofauna.

Problems of nomenclature and alpha taxonomy persist for possibly ten percent of the 164 species here considered. Especially troublesome are members of the genera *Sphaerodactylus*, *Eleutherodactylus*, *Elaphe*, *Micrurus*, *Tantilla*, and *Phiocercus*. Additional collecting and taxonomic study will resolve these questions and refine the emerging picture of animal distribution in the peninsula. To what extent these additional data will modify the general conclusions here set forth remains to be seen, but I believe they will in no major way prove contradictory.

I assembled locality records for each species considered by me to be a valid member of the peninsular herpetofauna. In so doing I accepted published records from reliable literature sources, and I examined all major and several minor collections of Yucatecan materials in the United States. I augmented these data with approximately 2,000 specimens representing 103 species obtained during nine months of field work. These are de-

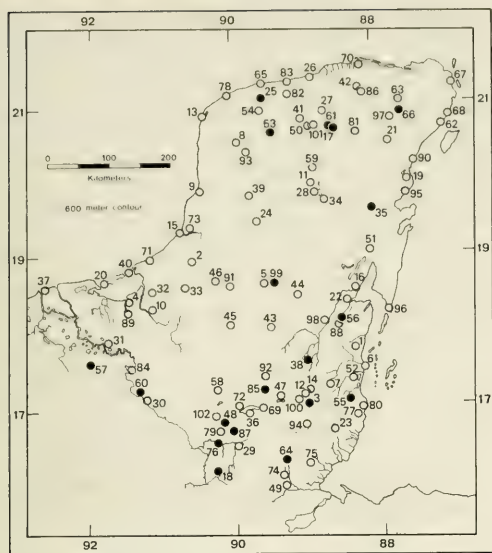


FIG. 2.—Important collecting stations in the Yucatán Peninsula. Closed circles indicate areas in which major collections have been made. Open circles represent minor collections. 1. Altun Ha, Belize; 2. Apazote, Campeche; 3. Augustine, Belize; 4. Balchacaj, Campeche; 5. Becán, Campeche; 6. Belize City, Belize; 7. Belmopan, Belize; 8. Calcehtok, Yucatán; 9. Campeche, Campeche; 10. Candelaria, Campeche; 11. Catmis, Yucatán; 12. Cayo, Belize; 13. Celestín, Yucatán; 14. Central Farm, Belize; 15. Champotón, Campeche; 16. Chetumal, Quintana Roo; 17. Chichén Itzá, Yucatán; 18. Chinajá, Alta Verapaz; 19. Chunyaxché, Quintana Roo; 20. Ciudad del Carmen, Campeche; 21. Cobá, Quintana Roo; 22. Corozal, Belize; 23. Double Falls, Belize; 24. Dzibalchén, Campeche; 25. Dzibilchaltún, Yucatán; 26. Dzilam Bravo, Yucatán; 27. Dzitás Yucatán; 28. Dziuché, Yucatán; 29. El Ceibal, El Petén; 30. El Desempeño, El Petén; 31. Emiliano Zapata, Tabasco; 32. Encarnación, Campeche; 33. Escárcega, Campeche; 34. Esmeralda, Yucatán; 35. Felipe Carrillo Puerto, Quintana Roo; 36. Flores, El Petén; 37. Frontera, Tabasco; 38. Gallon Jug, Belize; 39. Hopelchén, Campeche; 40. Isla Aguada, Campeche; 41. Kantunil, Yucatán; 42. Kikil, Yucatán; 43. Laguna Alvarado, Campeche; 44. Laguna Chacanbacab, Quintana Roo; 45. Laguna Chumpich, Campeche; 46. Laguna Silvituc, Campeche; 47. Laguna Yaxhá, El Petén; 48. La Libertad, El Petén; 49. Las Cañas, El Petén; 50. Libre Unión, Yucatán; 51. Limones, Quintana Roo; 52. Manatee, Belize; 53. Mayapan, Yucatán; 54. Mérida, Yucatán; 55. Middlesex, Belize; 56. Orange Walk, Belize; 57. Palenque, Chiapas; 58. Paso de los Caballos, El Petén; 59. Peto, Yucatán; 60. Piedras Ne-

posited in the collections of the Museum of Natural History, University of Kansas. I cannot claim to have personally examined every available museum specimen. Rather, I sought to verify peripheral or otherwise questionable records, and I accepted uncritically those records falling well within known distributions. Concerning questions of nomenclature and taxonomy, I generally have accepted the conclusions of the most recent authority to have dealt with a group in a thorough and comprehensive manner. Occasionally taxonomic decisions are based upon my own investigations, the results of which will appear elsewhere.

I summarized the locality records as spot maps—one for each species—and inferred from the maps the limits of distribution for each species (see appendix for spot maps). Though I followed no particular rule for inferring limits, I was conservative and was guided solely by the locality records, rather than by considerations of habitat. My estimates of distribution are therefore probably minimal ones. To the extent that the distribution maps reflect the distribution of the animals rather than the activity of collectors, they provide answers to a number of questions, the most funda-

gras, El Petén; 61. Pisté, Yucatán; 62. Playa del Carmen, Quintana Roo; 63. Popolná, Yucatán; 64. Poptún, El Petén; 65. Progreso, Yucatán; 66. Pueblo Nuevo X-Can, Quintana Roo; 67. Puerto Juarez, Quintana Roo; 68. Puerto Morelos, Quintana Roo; 69. Ramate, El Petén; 70. Río Lagartos, Yucatán; 71. Sabancuy, Campeche; 72. San Andres, El Petén; 73. San Jose Carpizo, Campeche; 74. San Luis, El Petén; 75. San Pedro Columbia, Belize; 76. Sayaxché, El Petén; 77. Silk Grass, Belize; 78. Sisal, Yucatán; 79. Sojio, El Petén; 80. Stann Creek, Belize; 81. Tekom, Yucatán; 82. Telchac, Yucatán; 83. Telchac Puerto, Yucatán; 84. Tenosique, Tabasco; 85. Tikal, El Petén; 86. Tizimin, Yucatán; 87. Toocog, El Petén; 88. Tower Hill, Belize; 89. Tres Brazos, Campeche; 90. Tulum, Quintana Roo; 91. Tuxpeña, Campeche; 92. Uaxactún, El Petén; 93. Uxmal, Yucatán; 94. Valentin, Belize; 95. Vigia Chico, Quintana Roo; 96. Xcalak, Quintana Roo; 97. X-Can, Yucatán; 98. Xcopen, Quintana Roo; 99. Xpujil, Campeche; 100. Xunantunich, Belize; 101. Yokdzonot, Yucatán; 102. Zotz, El Petén.

mental of which is whether or not the limits of distribution occur at random in the peninsula. To answer this, I superimposed over each map a transparent grid, the squares of which represented 50 km on a side. Grid size is a compromise between the resolution with which one hopes to perceive patterns, and the accuracy with which one can plot localities and infer distributional limits. I tallied the number of distribution limits that fell within each of the 108 grid squares, and cast the resultant values into a frequency distribution. Following the suggestion of Hagmeier and Stults (1964), I then compared it to a Poisson distribution in order to detect departures from a random distribution. Because a distribution limit in one square is not likely to be independent of the occurrence of that same limit in an adjacent square the Poisson is not precisely the expected distribution. However, it seems a reasonable approximation. I used the same grid to detect patterns of species density and endemism, and for a cluster analysis of the 108 grid squares, based upon presence or absence of species in each square. I considered a species present in a square if its distribution covered 50% or more of the land in the square. I calculated similarities for all pairwise comparisons of grid squares using the coefficient of Baroni-Urbani and Buser (1976) for binary data:

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

where A is the number of species common to both squares, B is the number present in the first but not the second, C is the number present in the second but not the first, and D is the number absent from both but present in other squares. The coefficient ranges from 0 to 1 and allows negative matches. I used the similarity coefficients to perform cluster analyses using the unweighted pair group method with arithmetic av-

erages (UPGMA). The UPGMA is an agglomerative hierarchical clustering technique which unites operational taxonomic units (OTU's) or groups of OTU's on the basis of some criterion of similarity or dissimilarity. To perform the calculations I used the TAXON program of the Numerical Taxonomy System of Multivariate Statistical Programs, version three, written by F. James Rohlf, John Kishpaugh, and David Kirk. The program also calculates cophenetic correlation coefficients which measure the distortion introduced by the clustering process. Most workers have found that cophenetic correlation coefficients generally range from 0.60 to 0.95 (Sneath and Sokal, 1973); high values indicate little distortion. Of several hierarchical clustering techniques, the UPGMA is said generally to introduce the least distortion (Rohlf, 1970). Sneath and Sokal (1973) give the algorithm for this clustering technique, and an example of its application to biogeographic data is given by Hagmeier and Stults (1964) and Hagmeier (1966). See Peters (1971) for a discussion of the limitations of this technique.

RESULTS

Distribution.—The distributions of amphibians and reptiles in the Yucatán Peninsula are summarized in the Appendix. Inspection of these figures reveals several general patterns. A number of species are restricted to the base of the peninsula, as for example: *Bolitoglossa dofleini*, *B. mexicana*, *B. rufescens*, *Oedipina elongata*, *Eleutherodactylus laticeps*, *E. loki*, *E. rugulosus*, *Syrrhophus leprus*, *Centrolenella fleischmanni*, *Kinosternon acutum*, *Anolis biporcatus*, *A. capito*, *A. uniformis*, *Sceloporus teapensis*, *Lepidophyma flavimaculatum*, *Ameiva festiva*, *Celestus rozellae*, *Adelphicos quadrivirgatus*, *Clelia clelia*, and *Coniophanes fissidens*.

Other species range through the base of the peninsula and then northward along the east side, avoiding the north-

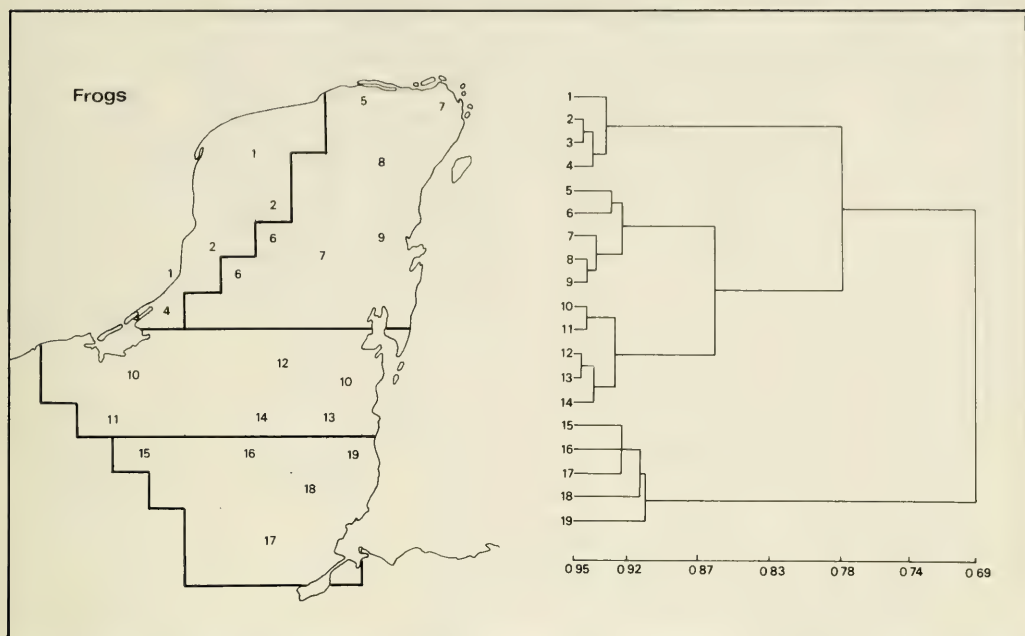


FIG. 3.—Cluster analysis of 108 grid squares on the basis of presence or absence of frog species. Squares clustered at the 0.95 level of similarity or higher are united, assigned a number, and circumscribed by a dotted line. On the map a solid line encloses major areas of faunal homogeneity. The cophenetic correlation coefficient is 0.82.

west corner. Conspicuous among these are: *Agalychnis callidryas*, *Hyla ebraccata*, *H. loquax*, *H. microcephala*, *H. picta*, *Anolis tropidonotus*, *Corytophanes hernandezii*, *Eumeces sumichrasti*, *Dendrophidion vinitor*, *Imantodes cenchoa*, *Leptophis ahaetulla*, and *Xenodon rabdocephalus*.

Still others are restricted to the north end of the peninsula, such as: *Bolitoglossa yucatanensis*, *Eleutherodactylus yucatanensis*, *Kinosternon creaseri*, *Terrapene mexicana*, *Sceloporus cozumelae*, *Leptotyphlops phenops*, *Coniophanes meridanus*, *Imantodes tenuissimus*, *Pliocercus andrewsi*, *Symphimus mayae*, *Tantilla cuniculator*, and *Bothrops yucatanicus*.

Finally there are those species which are pan-peninsular. These include: *Leptodactylus labialis*, *L. melanonotus*, *Bufo marinus*, *B. valliceps*, *Phrynohyas venulosa*, *Smilisca baudinii*, *Hypopachus variolosus*, *Rana pipiens*, *Anolis rodriguezii*, *A. sericeus*, *Basiliscus vittatus*,

Ameiva undulata, *Boa constrictor*, *Coniophanes imperialis*, *Drymarchon corais*, *Drymobius margaritiferus*, *Leptodeira frenata*, *Leptophis mexicanus*, *Mastigodryas melanolomus*, *Ninia sebae*, *Spilotes pullatus*, *Tropidodipsas sartori*, and *Micrurus diastema*.

Statistical confirmation that the limits of distribution of amphibians and reptiles do not fall randomly through the peninsula is presented in Table 2, which compares frequency distributions of numbers of distribution limits per 50 x 50 km grid square with the expected frequencies assuming a Poisson distribution. For each major taxon, and for the entire herpetofauna, the approximate chi-square values substantially exceed the expected chi-square values for the appropriate degrees of freedom at the 0.005 level. The null hypothesis that the limits of distribution follow a Poisson distribution, and thus are placed randomly, is decisively rejected in all cases. Table 2 also shows that in each case there is an

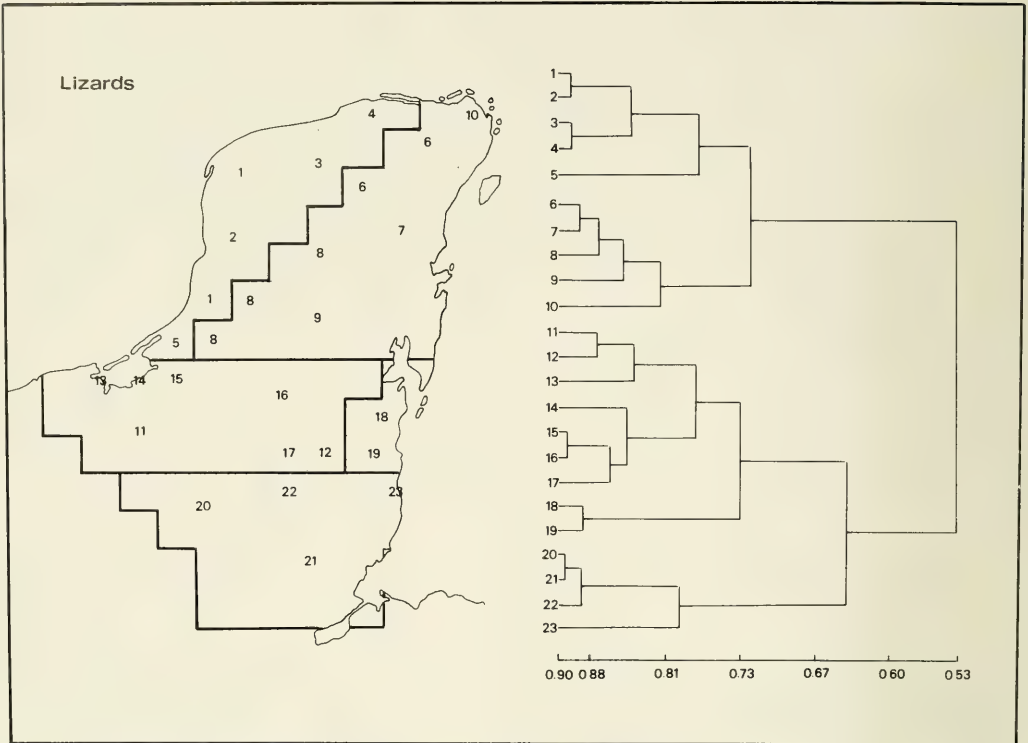


FIG. 4.—Cluster analysis of 108 grid squares on the basis of presence or absence of lizard species. Squares clustered at the 0.90 level of similarity or higher are united, assigned a number, and circumscribed by a dotted line. On the map a solid line encloses major areas of faunal homogeneity. The cophenetic correlation coefficient is 0.79.

excess of squares with few distribution limits, and an excess of squares with many limits, indicating that the limits of distribution are contagious (clumped). The coefficients of dispersion (C.D.) indicate this also, for in all cases they substantially exceed unity.

Faunal areas.—Contagious distribution limits indicate the existence of areas where distribution limits are concordant, i.e., areas of rapid faunal transition. These in turn imply the existence of areas of faunal homogeneity, the locations of which are indicated in Figures 3, 4 and 5, which summarize the results of separate cluster analyses for frogs, lizards, and snakes. What constitutes a major cluster depends upon the level of similarity used to define it, and in this I have followed no particular rule; rather I have identified clusters, and the faunal

areas they represent, by inspection of the phenograms. Some might disagree with my interpretations, but this is not a serious issue, for the clusters are usually easily recognizable. Thus, in Figure 3 four areas of faunal homogeneity are indicated for frogs: one in the northwest corner, one in the northern half of the peninsula exclusive of the northwest corner, a central area, and a southern area. A similar pattern exists for lizards, although the picture is less clear. In Figure 4 I recognize essentially the same four faunal areas identified for frogs, plus one small area in north-central Belize. A somewhat different pattern emerges for snakes, where only three major areas are apparent: a northern, central, and southern area (Fig. 5). In contrast to frogs and lizards, the north-west corner of the peninsula does not

TABLE 2.—Number of Distribution Limits per 50 X 50 km Block Fitted to a Poisson Distribution.

Anurans			Lizards			Snakes			All Species		
# limits	observed	expected	# limits	observed	expected	# limits	observed	expected	# limits	observed	expected
0	35	19.5	0	7	1.4	0	5	0.4	0	0	0.0
1	22	33.5	1	14	6.2	1	11	2.2	1	5	0.0
2	19	28.8	2	18	13.4	2	14	6.1	2	2	0.0
3	14	16.5	3	14	19.3	3	7	11.5	3	4	0.0
4	7	7.1	4	17	20.9	4	9	16.1	4	4	0.2
5	8	2.4	5	5	18.0	5	15	18.1	5	7	0.6
6	2	0.7	6	6	13.0	6	3	16.9	6	6	1.4
7	1	0.2	7	9	8.0	7	9	13.5	7	7	2.7
X ² = 37.3 x ² .005(3) = 12.8 C.D. = 1.74			8	2	4.3	8	12	9.5	8	4	4.6
			9	9	2.1	9	7	5.9	9	5	6.5
X ² = 61.3 x ² .005(5) = 16.8 C.D. = 2.30			10	2	1.0	10	3	3.3	10	2	8.6
			11	3	0.4	11	6	1.7	11	3	10.3
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			12	0	0.1	12	3	0.8	12	6	11.3
			13	2	0.0	13	0	0.3	13	7	11.5
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			14	0	0.1	14	0	0.1	14	5	10.8
			15	2	0.1	15	2	0.1	15	4	9.5
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			16	1	0.0	16	1	0.0	16	3	7.8
			17	1	0.0	17	3	6.1	17	3	6.1
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			18	2	4.5	18	2	4.5	18	2	4.5
			19	3	3.1	19	3	3.1	19	3	3.1
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			20	5	2.0	20	5	2.0	20	5	2.0
			21	3	1.3	21	3	1.3	21	3	1.3
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			22	1	0.8	22	1	0.8	22	1	0.8
			23	2	0.4	23	2	0.4	23	2	0.4
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			24	3	0.2	24	3	0.2	24	3	0.2
			25	1	0.1	25	1	0.1	25	1	0.1
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			26	2	0.1	26	2	0.1	26	2	0.1
			27	4	0.0	27	4	0.0	27	4	0.0
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			28	0	0.0	28	0	0.0	28	0	0.0
			29	0	0.0	29	0	0.0	29	0	0.0
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			30	2	0.0	30	2	0.0	30	2	0.0
			31	0	0.0	31	0	0.0	31	0	0.0
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			32	0	0.0	32	0	0.0	32	0	0.0
			33	1	0.0	33	1	0.0	33	1	0.0
X ² = 88.2 x ² .005(7) = 20.3 C.D. = 5.30			34	0	0.0	34	0	0.0	34	0	0.0
			35	1	0.0	35	1	0.0	35	1	0.0
X ² = 81.7 x ² .005(6) = 18.6 C.D. = 2.64			36	1	0.0	36	1	0.0	36	1	0.0
			37	0	0.0	37	0	0.0	37	0	0.0

emerge as a major area of faunal homogeneity for snakes. However, some indication of the distinctness of this area is apparent in the union of areas 1, 2 and 3 in Figure 5. What, if anything, is represented by the minor clusters in Figures 3, 4 and 5 is not clear, but I have confidence in the reality of the major areas, and in the existence of rather sharp faunal breaks between them, for one can intuit the areas and their approximate boundaries from inspection of Figure 6 in which for each major taxon the limits of distribution are superim-

posed on a single map. For frogs and lizards the area southwest from northern Quintana Roo to the vicinity of Laguna de Términos marks an area of faunal transition, and the same may be said for a few species of snakes. Similarly, the region of central Belize and northern El Petén is an area where limits of distribution of many species approximately coincide.

Species density.—With only two exceptions, the limits of distribution of frogs indicated in Figure 6 are the northern limits of species. From south to

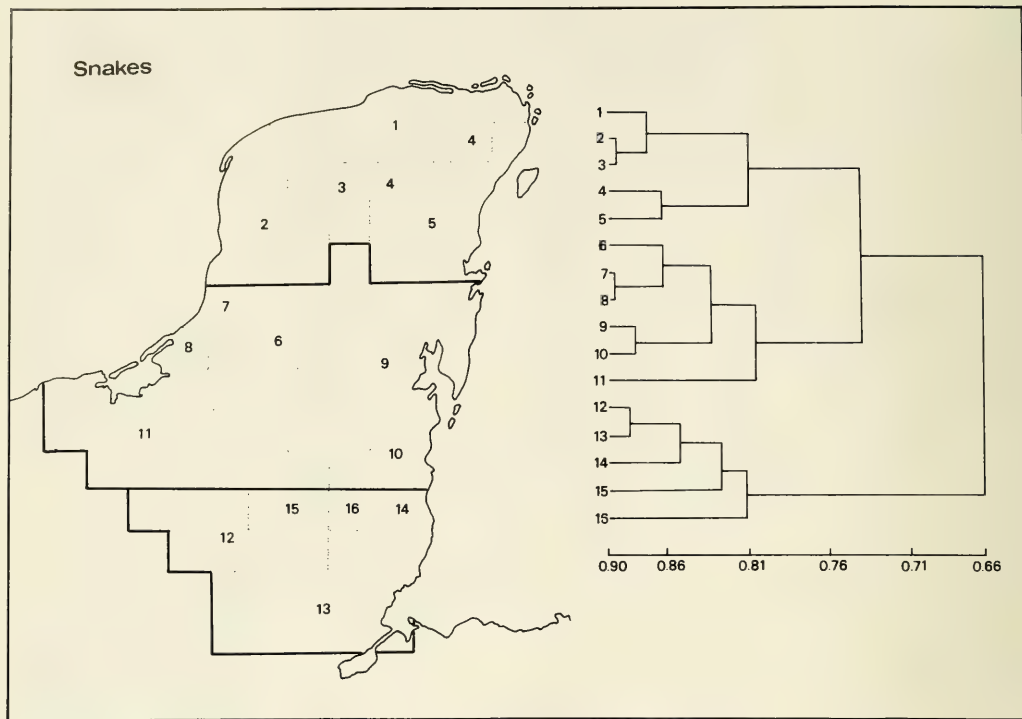


FIG. 5.—Cluster analysis of 108 grid squares on the basis of presence or absence of snake species. Squares clustered at the 0.90 level of similarity or higher are united, assigned a number, and circumscribed by a dotted line. On the map a solid line encloses major areas of faunal homogeneity. The cophenetic correlation coefficient is 0.85.

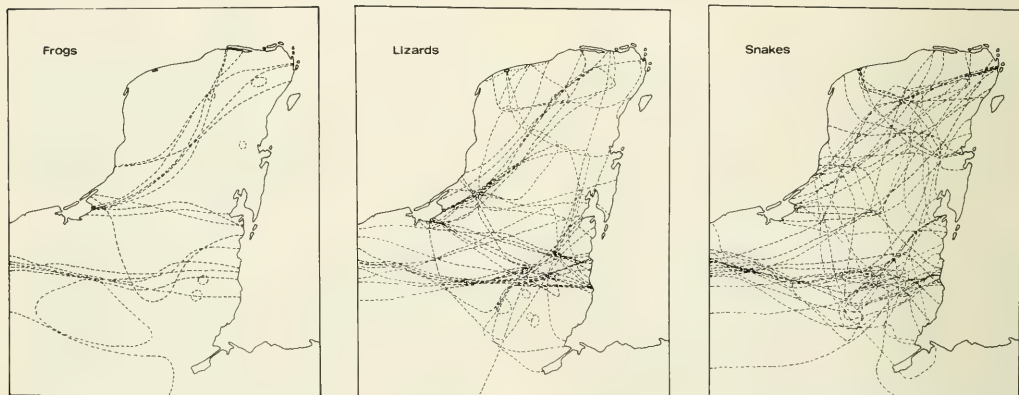


FIG. 6.—Limits of distribution of amphibians and reptiles in the Yucatán Peninsula. Each line represents the inferred limits for a single species.

northwest species drop out and are not replaced. The result is the dramatic faunal attenuation illustrated in Figure 7. The number of frog species diminishes from a maximum of 22 in southern El Petén, to a minimum of nine at the

northwest corner of the peninsula. A less dramatic decrease in species density occurs from east to west in the northern third of the peninsula. Lizards and snakes manifest a different species density pattern. For both groups species

density is greatest at the base of the peninsula, diminishes toward the center, and then increases toward the north end (Fig. 7).

Endemism.—The number of endemic species of amphibians and reptiles per grid square is indicated in Figure 8. Endemism is unquestionably greatest at the north end of the peninsula, where as many as 20 of the 26 peninsular endemics occur in a single grid square. In contrast, portions of El Petén have no endemics. Amphibians are underrepresented among the endemics: they account for 21.3% of the entire herpetofauna, but constitute only 11.5% of the total number of endemics. Lizards and snakes are overrepresented. Respectively they constitute 26.2% and 44.5% of the herpetofauna, but comprise 30.8% and 53.8% of the endemics. The single endemic turtle constitutes 3.8% of the endemic fauna.

DISCUSSION

A number of biologists have suggested that the Yucatán Peninsula could be partitioned on the basis of biological criteria. Smith (1940) utilized the distributions of lizards of the genus *Sceloporus* to define two provinces in the Yucatán Peninsula; Stuart (1943) used distributions of salamanders to recognize biotic areas in Guatemala, including El Petén; and Savage (1966) subdivided the herpetofauna of the peninsula into

two geographical assemblages. More comprehensive treatments, which combine information for many groups of organisms, include that of Goldman and Moore (1945) who recognized but a single province in the peninsula. Smith (1949) recognized provinces similar to those in his 1940 paper, but added an additional province. Stuart (1964) distinguished the northwest corner of the peninsula from the remainder of the peninsula.

One generalization that emerges from these studies is that the north and northwest portion of the peninsula represents an area biotically distinct from the central and southern portions, though there exists no consensus as to where the boundary between these areas lies. My results support the view that the northern and southern portions of the peninsula are dissimilar biotically, and they further indicate that the peninsula could be more finely divided. Yet I have chosen not to formalize the areas of herpetofaunal homogeneity by naming them. Identification of these areas is not an end in itself, but rather serves as a point of departure, for the existence of such areas raises interesting questions concerning the historical development of these areas and their faunas and the nature of their geographical limits. These historical and ecological questions are discussed in the sections which follow.

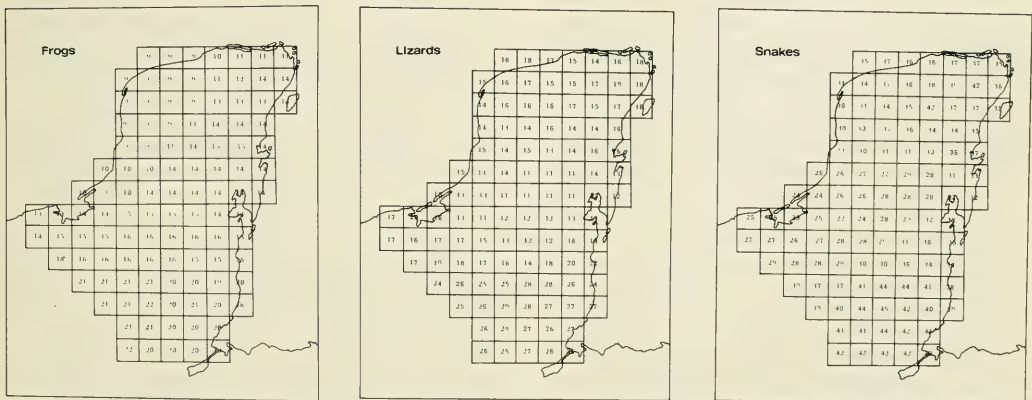


FIG. 7.—Species density patterns of amphibians and reptiles in the Yucatán Peninsula. The figures in each square represent the number of species known or presumed to occur within that square.

Reduction in species density at the ends of peninsulas—the so-called peninsula effect—has been documented in Florida for amphibians and reptiles (Keister, 1971), and in Florida, Yucatán, and Baja California for birds (MacArthur and Wilson, 1967), and mammals (Simpson, 1964). The phenomenon is thus a general one and is attributable to the isolating effects of peninsulas (Ricklefs, 1973). It is of interest therefore, that among amphibians and reptiles in the Yucatán Peninsula, only frogs exhibit this expected reduction in numbers of species. And even here something other than a peninsular effect is operating, for the reduction in numbers of species is decidedly asymmetrical (Fig. 7), a pattern not explainable solely on the basis of isolation. With fewest species in the middle of the peninsula, snakes and lizards depart even further from the expected pattern. Stuart (1958) in discussing the herpetofauna of the Tikal-Uaxactún area of northern El Petén, attributed the depauperization there in part to the fact that the area is transitional between the dry thorn forests of the outer end of the peninsula, and the wet forests of southern El Petén. Apparently the same situation obtains for much of northern El Petén, and southern Campeche and Quintana Roo. The concept of ecotone might lead one to expect more rather than fewer species in such a transitional area, but apparently this is an area which lies beyond the northernmost limits of many southern species, and beyond the southernmost limits of many northern species, especially the endemics (Fig. 8). The factors that set these limits are discussed in the next section.

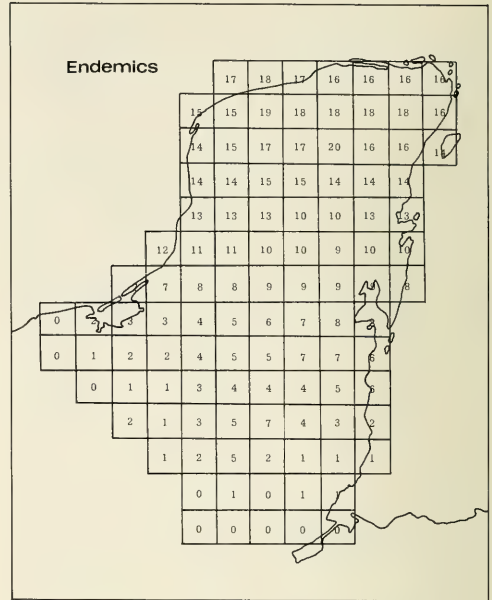


FIG. 8.—Numbers of endemic species of amphibians and reptiles in the Yucatán Peninsula. The figure in each square represents the number of endemic species known or presumed to occur within that square.

In summary, the limits of distribution of amphibians and reptiles in the Yucatán Peninsula are contiguous, indicating the existence both of areas of faunal transition and areas of faunal homogeneity. This is true for the entire herpetofauna and for all major taxonomic subdivisions. Anuran species density diminishes dramatically from south to northwest. For snakes and lizards, species density is highest at the base of the peninsula, lowest at the center, and intermediate at the northern end. The number of endemic species is greatest at the northern end and diminishes rapidly to the south.

SECTION II:

ECOLOGICAL CORRELATES OF SPECIES DENSITY

The patterns of distribution, species density, and endemism identified in the preceding section are the end products of a complex interplay of factors oper-

ating through ecological and evolutionary time. To understand these patterns and to evaluate them in the light of current ecological and biogeographic theory,

it is convenient to consider separately two aspects of the problem, namely the historical development of the patterns, and the ecological factors that are important in maintaining the patterns. This distinction between history and ecology is partly artificial and is not always easily maintained, yet it is useful because two rather different sets of questions are involved. For example, several species otherwise restricted to the dry north end of the peninsula occur as disjuncts on the savannas of El Petén and Belize (see discussion below). How these disjunctions came about is an historical question; what restricts the species to savanna regions and to the north end of the peninsula is an ecological question. Such ecological considerations form the substance of the present section. Here I seek to ascertain whether the patterns identified previously can be related to features in the environment. Specifically my purpose is to seek correlates of herpetofaunal species density, and to use the results of this analysis to weigh the merits of various hypotheses that have been invoked to explain species density gradients.

METHODS

Two sets of environmental variables change conspicuously through the Yucatán Peninsula and seem likely to be important in controlling numbers of co-occurring species of amphibians and reptiles. These are the amount and seasonality of precipitation, and the structural heterogeneity of vegetation. Unfortunately, rainfall data for the peninsula leave much to be desired; for many areas no data are available, or, where available, they are often incomplete, or span only a few years. I have relied upon the published data of Page (1933, 1938), the rainfall map of México compiled by García (1965), and unpublished data for the Xpujil, Campeche area taken by Robert Wade of the University of Wisconsin from the files of the División Hidrométricas, Península de Yucatán, Mérida, Yucatán. Quantitative data on vegetation structure in the Yucatán Peninsula are few. Consequently, I established study sites in each of seven distinct vegetation types along a rough north-south transect through the peninsula. Figure 9 gives the names and locations of the sites, each of which is described below. Each site was situated in relatively undisturbed vegetation. Using the point-quarter technique (Cottam and Curtis, 1956), I sampled woody vegetation at random points along each of ten parallel 100 m transects situated 10 m apart, except as noted below. For each plant 1 m or greater in height, I measured (or estimated) total height, height to first foliage, and plant diameter, using a clinometer when necessary. Occasionally I could identify plants to species. More often I designated apparent "species" of woody plants, and assigned sample plants to these "species" on the basis of canopy shape, growth form, leaf morphology, bark color and texture, color of wood and sap, odor of crushed foliage, and the appearance of fruits and flowers. My "species" are phena which probably correspond to taxa at or near the biological species level of differentiation. I

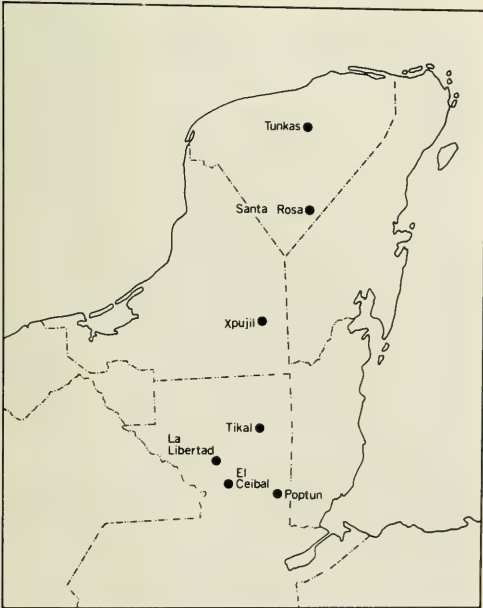


FIG. 9.—Map of the Yucatán Peninsula showing location of study sites.

made no floristic comparisons between sites.

At the Poptún site I staked out an area of 1 ha, within which I placed at random ten quadrats each 10 m square. Within each quadrat I identified and measured all woody plants 1 m or greater in height in the manner described above.

Site descriptions.—The Poptún site is located approximately 6.4 km north of the town of Poptún (16° 21' N, 89° 26' W), Department of El Petén, Guatemala, at an elevation of about 550 m. The site is in pine savanna, with *Pinus caribaea* the dominant plant, but broadleaf forest penetrates the savannas along stream channels and ravines. Grasses are the predominant herbs, and scattered shrubs and low trees dot the landscape (Fig. 10). Wadell (1938) described and illustrated the pine savanna region of Poptún. The site lies within the subtropical humid forest formation of Holdridge (1967), and has a tropical rainy climate (Af ω of the Koeppen classification; Vivó Escoto, 1964). I worked the Poptún site from 4 to 14 July 1974.



FIG. 10.—Typical pine savanna at the Poptún study site.

The El Ceibal site is located near the south bank of the Río de la Pasión, approximately 1.2 km west of the archaeological site of El Ceibal (16° 34' N, 90° 03' W), Department of El Petén, Guatemala, at an elevation of approximately 150 m. The area supports a luxurious mesophytic forest dominated by the corozo palm (*Orbignya cohune*). Trees occasionally reach a height of 50 m; many are 30 to 40 m high with interlocking crowns which produce a closed canopy through which little light penetrates to the forest floor. Lianas and bromeliads abound, and small palms and members of the genus *Piper* are common understory plants (Fig. 11). Lundell (1937) described this vegetation type, which, owing to the dominance of the corozo palm, is termed a corozal. The site lies within the tropical humid forest formation of Holdridge (1967), and has a tropical rainy climate (Af ω of the Koeppen classification; Vivó Escoto, 1964). I worked the El Ceibal site from 19 to 28 July 1974.

The La Libertad site is located approximately 4.9 km southwest of the



FIG. 11.—Interior view of forest at the El Ceibal study site.

town of La Libertad (16° 47' N, 90° 07' W), Department of El Petén, Guatemala, at an approximate elevation of 210 m. The site is situated on a savanna characterized by open expanses of grass through which are scattered small shrubby flat-topped trees, chiefly the nanze (*Byrsonima crassifolia*) (Fig. 12). Islands of typical forest edge trees such as *Bursera simaruba*, and *Cecropia* spp. dot the flat landscape. Lundell (1937) reported in detail on the botany of the central Petén savannas, and Stuart (1935) in his discussion of the herpetofauna of these savannas described and illustrated the vegetation. The La Libertad site lies within the humid tropical forest formation of Holdridge (1967), and has a tropical rainy climate (Amw of the Koeppen classification; Vivó Escoto, 1964). I worked at the La Libertad site from 15 to 20 October 1976.

The Tikal site is located approximately 4.8 km south-southwest of the famous archaeological site of Tikal (17° 20' N, 89° 39' W), Department of El Petén, Guatemala, at an approximate elevation of 283 m. The site is situated in a medium high forest, the canopy of which averages 25 to 35 m in height and is sufficiently open to permit penetration of considerable light. Common tree species include *Brosimum alicastrum*, and *Achras zapota*. Occasional *Swietenia macrophylla* are encountered. The thorny *escoba* palm (*Cryosophila argentea*) and

various species of *Piper* are common in the understory (Fig. 13). Bartlett (1935) gave a detailed account of the forest in the Tikal area. The site lies within the dry tropical forest formation of Holdridge (1967), and has a tropical rainy climate (Amw of the Koeppen classification; Vivó Escoto, 1964). I worked the Tikal site from 9 to 27 August 1974, and from 21 to 24 October 1976.

The Xpujil study site is located approximately 10.2 km west of the village of Xpujil (18° 30' N, 89° 24' W), Campeche, México, at an elevation of approximately 250 m. Vegetation in this area, which has been characterized by Duellman (1965a) as quasi-rainforest, is a lower forest than at Tikal, but many of the same species occur, including *Achras zapota*, *Cedrela mexicana*, and *Bursera simaruba*. Palms are uncommon. The canopy is partly closed and the understory is a dense tangle of small vines, shrubs and saplings. The Xpujil site lies within the dry tropical forest formation of Holdridge (1967), and has a tropical rainy climate (Amw of the Koeppen classification; Vivó Escoto, 1964). I worked the Xpujil site from 1 to 12 October 1974.

The Santa Rosa site is located approximately 12 km east-southeast of the town of Santa Rosa (19° 58' N, 88° 53' W), near the west edge of Laguna Chichancanab, Yucatán, México, at an approximate elevation of 31 m. Here the forest is comparable in height to that at Xpujil, but more open. The dominant tree is *Bursera simaruba*. Small palms, shrubs, and saplings comprise the understory, and grasses and other herbs cover the forest floor, especially where the canopy is sufficiently open to allow penetration of considerable light. The Santa Rosa site lies within the very dry tropical forest formation of Holdridge (1967), and has a tropical wet-and-dry climate (Aw of the Koeppen classification; Vivó Escoto, 1964). I worked at the Santa Rosa site from 12 to 20 November 1974.

The Tunkas site is located approximately 12.3 km west of the town of



FIG. 12.—Typical savanna in the vicinity of the La Libertad study site.

Tunkas (20° 54' N, 88° 45' W), Yucatán, México, at an approximate elevation of 33.5 m. The site is situated in a low, scrubby thorn forest, 3 to 7 m high, dominated by various species of deciduous legumes. Palms are absent. This vegetation type has been well described by Bequaert (1933), and illustrated by Paynter (1955). The Tunkas site lies within the very dry tropical forest formation of Holdridge (1967), and has a tropical wet-and-dry climate (Aw of the Koeppen classification; Vivó Escoto, 1964). I worked the Tunkas site from 25 to 31 October 1974.

To characterize the precipitation regime at each site, I inferred the amount and seasonality of rainfall from records for nearby stations. For the Tunkas site I used data from Page (1933) for Izamal, located approximately 18 km to the west. For the Santa Rosa site I used data from Page (1933) for Peto, located approximately 29 km to the northwest. For the Xpujil site I used unpublished data collected by Robert Wade for Zoh Laguna, approximately 15 km north of the village of Xpujil. For the Tikal site I used data from Page (1938) for El Paso de los Caballos, situated 67 km to the west. For both the La Libertad and El Ceibal sites I used data from Page (1938) for Paso Real, approximately 27 km south-southwest, and 14 km west of the two sites, respectively. For the Poptún site I used the data of Stuart (pers. comm.) for the village of Poptún, approximately 6.4 km to the south. These data represent records for as few as a single year (Poptún), five years (Paso Real), nine years (Izamal), ten years (Paso de los Caballos), 12 years (Peto), and 17 years (Zoh Laguna). The figures for annual precipitation are mean values. I used the percent of mean annual precipitation falling from May through October as a measure of seasonality of rainfall.

For each site I compiled a list of species of amphibians and reptiles encountered by me or presumed to occur there. Because many species are rare and/or cryptophilic, I inferred the pres-

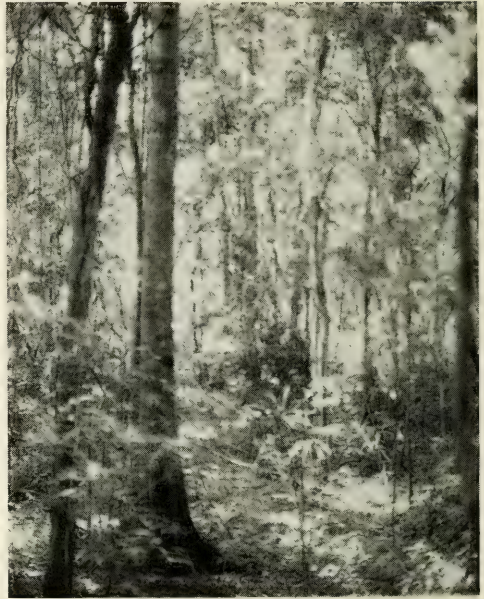


FIG. 13.—Interior view of forest at the Tikal study site.

ence of some species on the basis of collections made by me or by others in similar vegetation at nearby areas. Lists of species known or presumed to occur at each site are given in Lee (1977).

Data analysis.—Following Pianka (1971), I estimated the areal cover of each plant using the formula for the area of a circle ($A = 0.7854 d^2$, where d is the maximum diameter of the plant crown). I estimated foliage volume for each plant using the formulae for oblate

and prolate spheroids ($V = \frac{4}{3} \pi a^2 b$ and

$V = \frac{4}{3} \pi ab^2$, where a and b are the major and minor semi-axes, respectively). As a measure of heterogeneity I estimated diversity in the vegetation parameters using the information theory statistic of Shannon (Shannon and Weaver, 1949; $H = -\sum p_i \log p_i$, where p_i is the proportion of plants in the sample belonging to the i th category). This index is a composite, sensitive both to numbers of categories (richness) and to equitability of numbers of individuals among categories (evenness).

I estimated plant species diversity where in the above formula the p_i 's are the proportions of all individuals in the i th species; species cover diversity where the p_i 's are the proportions of total plant cover attributed to the i th species; and species volume diversity where the p_i 's are the proportions of total plant volume attributed to the i th species. I used the same formula to calculate plant height diversity, plant cover diversity, and plant volume diversity where the p_i 's are the proportion of all individuals within each of 20 height categories, 40 cover categories, and 100 volume categories, regardless of species. To characterize each study site on the basis of vegetation heterogeneity, I extracted principal components of variation from a matrix of correlation coefficients between the diversity indices of each site. For this I used the Biomedical Computer Program BMDP4M (Dixon, 1975). Principal component analysis constructs new orthogonal (independent) axes which are linear combinations of the original variables. The axes are oriented so as to explain maximally the dispersion in the multivariate data cloud. Thus, a large proportion of variation in the original data set can be parsimoniously explained by only a few components. OTU's can then be projected onto the component axes and their relationships assessed. See Cooley and Lohnes (1971) for further discussion of this technique.

To assess the relative contributions of variables, both singly and in combination toward explaining variation in herpetofaunal species density, I performed correlation and multiple regression analyses. For the latter I used the stepwise regression program BMDP2R of the Biomedical Computer Programs (Dixon, 1975). This program seeks that linear combination of variables that maximally explains variation in the dependent variable, in this case species density. It enters variables one at a time, in descending order of their unique contribution toward explaining variation, while simultaneously accounting for correlation be-

tween the independent variables. The program calculates a coefficient of multiple determination (R^2) which represents the proportion of variation in the dependent variable explained by the combined effects of the independent variables. I accepted as best that regression model which accounted for the greatest proportion of variation in the dependent variable (highest R^2). This is normally an unreliable criterion because R^2 can never diminish with the addition of more variables. In this instance virtually all variation is explained by only a few variables and over specification of the model does not seem to be an issue. Cooley and Lohnes (1971) give further details of this technique.

For each site the following variables were included:

1. (LAT) Latitude
2. (LONG) Longitude
3. (AMPH) Number of species of amphibians known or presumed to occur at each site
4. (SNK) Number of species of snakes known or presumed to occur at each site
5. (LZD) Number of species of lizards known or presumed to occur at each site
6. (TOTAL) Number of species of amphibians and reptiles known or presumed to occur at each site
7. (ANRN) Mean annual rainfall
8. (PCTRN) Percent of mean annual rainfall occurring from May through October
9. (PSD) Plant species diversity
10. (SCD) Species cover diversity
11. (SVD) Species volume diversity
12. (PHD) Plant height diversity
13. (PCD) Plant cover diversity
14. (PVD) Plant volume diversity

- 15. (PCI) Site scores on the first principal component
- 16. (PCII) Site scores on the second principal component

RESULTS

Species-area curves for woody plants at each site are presented in Figure 14. With the exception of El Ceibal, the curves approach the horizontal asymptote, indicating that all, or nearly all species within the sampling area are represented. The assumption of the Shannon diversity statistic that the total number of species be known (Krebs, 1972) is thus met, or only weakly violated. Figure 14 also illustrates the marked floristic impoverishment of the two savanna sites, Poptún and La Libertad.

The diversity scores and scores on the first two principal components for each site are presented in Table 3. In

general the savanna sites are the least heterogeneous both floristically and structurally. This agrees with the qualitative assessment that savannas, in contrast to the other sites, represent relatively simple environments in terms of woody vegetation.

Results of the principal component analysis are summarized in Tables 4 and 5 and in Figure 15. The first and second components subsume 59% and 38% of the variation respectively. All six diversity indices load positively on the first principal component, which is therefore interpretable as a general heterogeneity factor. On the second component, PSD, SCD, and SVD load negatively, whereas PHD, PCD, and PVD load positively. Component two thus represents a contrast between those variables which have as their richness component of diversity the number of species at each site (species-dependent indices), and those which have as their richness component of diversity the number of height, cover, and volume categories (species-independent indices). The remaining components are difficult to interpret, but are relatively unimportant, accounting for less than 3% of the variation. They are not considered further. Ordination of the study sites on the first two principal components is illustrated in Figure 15. With low scores on the first component, La Libertad and Poptún again emerge as the least heterogeneous of the seven sites; El Ceibal is most heterogeneous, followed by Santa Rosa, Xpujil, Tikal, and Tunkas. El Ceibal scores high on component two, indicating that the species-independent indices are the most important contributors to heterogeneity at that site. In contrast,

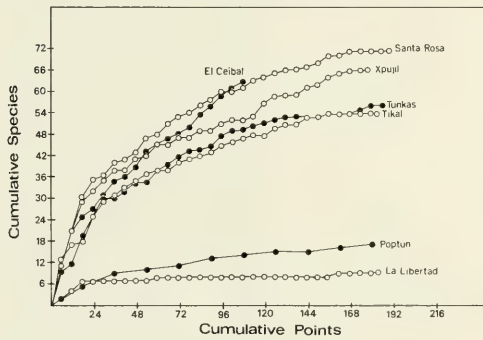


FIG. 14.—Species-area curves for woody plants at seven study sites in the Yucatán Peninsula. For Poptún the curve represents the cumulative numbers of species in ten 100 m² quadrats. For other sites the curves represent cumulative species against cumulative numbers of points.

TABLE 3.—Summary of vegetation statistics for seven sites in the Yucatán Peninsula.

Site	Variables							
	PSD	SCD	SVD	PHD	PCD	PVD	PCI	PCII
La Libertad	1.63	1.41	1.19	0.29	0.08	0.02	-1.44	0.28
Poptún	1.62	1.53	1.45	0.09	0.05	0.01	-1.42	0.07
Tikal	2.66	2.53	2.28	1.39	0.34	0.51	0.43	0.33
Tunkas	3.30	2.64	2.53	0.87	0.18	0.03	0.24	-0.68
El Ceibal	2.88	1.73	2.22	1.63	1.06	0.97	0.91	1.88
Xpujil	3.16	3.18	3.01	1.04	0.06	0.06	0.54	-1.05
Santa Rosa	3.33	3.27	3.00	1.03	0.19	0.22	0.75	-0.83

TABLE 4.—Factor loadings on the principal components extracted from a correlation matrix of six indices of structural and floristic diversity of woody vegetation at seven study sites.

Variable	Component					
	I	II	III	IV	V	VI
PSD	0.917	-0.329	0.203	0.087	-0.034	-0.008
SCD	0.695	-0.706	-0.126	-0.044	-0.038	0.018
SVD	0.870	-0.476	0.030	-0.113	0.050	-0.010
PHD	0.922	0.328	-0.157	0.125	0.036	0.003
PCD	0.525	0.831	0.161	-0.049	0.009	0.019
PVD	0.581	0.802	-0.112	-0.070	-0.042	-0.014

TABLE 5.—Tabulation of eigenvalues, percent of trace, and accumulated percent of trace for each component of principal component analysis performed on a correlation matrix. The original data matrix consisted of six indices of structural and floristic diversity of woody vegetation at seven study sites.

Principal Component	Eigenvalue	Percent of Trace	Accumulated Percent of Trace
I	3.545	59.1	59.1
II	2.279	38.0	97.1
III	0.121	2.0	99.1
IV	0.045	0.7	99.8
V	0.008	0.2	100.0
VI	0.001	0.0	100.0

for Xpujil, Santa Rosa, and Tunkas, species-dependent indices are most important. For La Libertad, Poptún, and Tikal, species-dependent and species-independent indices contribute about equally to heterogeneity.

Product-moment correlation coefficients for all pairwise comparisons of ecological variables and herpetofaunal species densities are presented in Table 6. LIZ shows a significant positive correlation with SNK, PHD, and PVD, and a highly significant positive correlation with TOTAL. AMPH shows a highly significant negative correlation with LAT, a significant positive correlation with LONG and PCII, a highly significant positive correlation with ANRN, and a significant negative correlation with PCTRN. SNK shows a significant positive correlation with LIZ, TOTAL, and PHD. Because many of the environmental variables covary, it is of interest to regress simultaneously species density on these variables. Table 7 summarizes the results of the stepwise multiple regression analyses for which AMPH, LIZ, and SNK were treated as dependent variables and a separate analysis run for each. All other variables except LAT

and LONG were entered as independent variables. Of those variables considered, the single best predictor of AMPH is ANRN (Fig. 16), which accounts for 89% of the variation, followed by PCTRN and SVD. In combination these variables explain 99% of the variation in AMPH. For SNK, PHD is the best predictor (Fig. 17), followed by PCTRN, SVD,

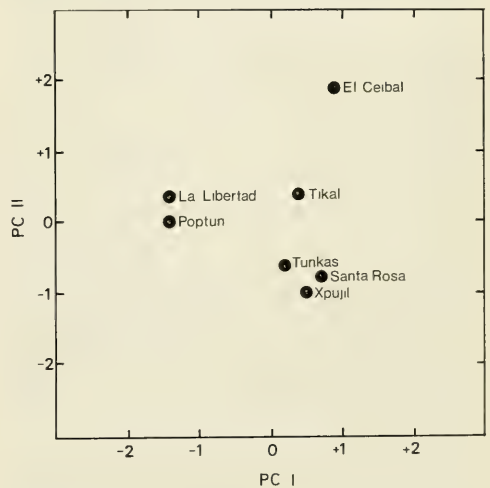


FIG. 15.—Ordination of seven study sites on the first and second principal components extracted from a matrix of correlation coefficients between indices of structural and floristic diversity.

and PVD; these four combine to explain 99% of the variation in SNK. PVD is the best predictor of LIZ (Fig. 18), followed by PCD, PCTRN, and ANRN; together these four explain 99% of the variation in LIZ.

DISCUSSION

Gradients in species density on local, regional, and global scales have long been of interest to biologists, and many hypotheses have been advanced to explain them. It is generally agreed that the processes specified in these hypotheses need not act to the exclusion of one another, but instead may operate in concert, the exact combination varying with the situation. Nonetheless it is convenient to examine each hypothesis separately before inquiring as to how they might work in combination. The various hypotheses have been summarized so often (Pianka, 1966a, 1967, 1974; Ricklefs, 1973; Krebs, 1972; Uetz, 1974) that a thorough summary is not necessary here. Instead I will examine only those hypotheses that are relevant to the present study.

The Time Hypothesis.—According to this hypothesis, biotas diversify through time, hence older communities should be more diverse (and contain more species) than younger ones. It is useful to distinguish between ecological time, which refers to the time available for dispersal and colonization, and evolutionary time, the time available for speciation. Areas that have only recently become available for colonization may be depauperate because insufficient time has elapsed for an equilibrium number of species to become established. One might argue that the northern third of the Yucatán Peninsula, which was submerged until sometime in the Pleistocene, represents such a non-equilibrium situation. Species densities of snakes, lizards, and amphibians are indeed lower at the north end than at the base of the peninsula, which has apparently remained land positive at least since the Miocene. But for snakes

TABLE 6.—Correlation coefficients (r) between ecological variables and numbers of species of amphibians and reptiles in the Yucatán Peninsula.

	LZD	AMPH	SNK	TOTAL	LAT	LONG	ANRN	PCTRN	PSD	SCD	SVD	PHD	PCD	PVD	PCI
AMPH	0.36														
SNK	0.85*	-0.15													
TOTAL	0.99**	0.41	0.84*												
LAT	-0.16	-0.97**	0.35	-0.21											
LONG	0.26	0.87*	-0.17	0.31	-0.86*										
ANRN	0.39	0.94**	-0.02	0.46	-0.89**	0.85*									
PCTRN	0.08	-0.84*	0.54	0.04	0.92**	-0.82*	-0.71								
PSD	0.34	-0.66	0.63	0.27	0.76*	-0.62	-0.70	0.78*							
SCD	0.08	-0.72	0.36	-0.01	0.75	-0.75	-0.76*	0.82*	0.84*						
SVD	0.23	-0.63	0.46	0.15	0.69	-0.66	-0.73	0.74	0.95**	0.94**					
PHD	0.86*	0.02	0.82*	0.81*	0.15	0.02	-0.04	0.29	0.72	0.42	0.63				
PCD	0.72	0.42	0.51	0.72	-0.30	0.43	0.32	-0.30	0.24	-0.24	0.07	0.73			
PVD	0.86*	0.49	0.60	0.85*	-0.35	0.44	0.40	-0.26	0.24	-0.14	0.13	0.81*	0.96**		
PCI	0.63	-0.32	0.73	0.56	0.45	-0.33	-0.41	0.53	0.92**	0.69	0.87*	0.92**	0.53	0.58	
PCII	0.56	0.78*	0.22	0.61	-0.70	0.77*	0.74	-0.68	-0.33	-0.71	-0.48	0.33	0.83*	0.80*	0.00

* Significant at the 0.05 level

** Significant at the 0.01 level

TABLE 7.—Summary of results of multiple regression analysis of ecological variables and numbers of species of amphibians and reptiles in the Yucatán Peninsula.

Amphibians			Snakes			Lizards		
Step	Variable entered	R ²	Step	Variable entered	R ²	Step	Variable entered	R ²
1	ANRN	0.89	1	PHD	0.66	1	PVD	0.73
2	PCTRN	0.95	2	PCTRN	0.76	2	PCD	0.85
3	SVD	0.99	3	SVD	0.95	3	PCTRN	0.92
			4	PVD	0.99	4	ANRN	0.99

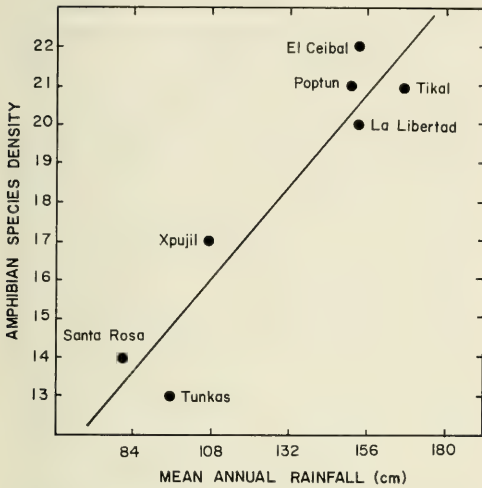


FIG. 16.—Regression of amphibian species density on mean annual rainfall for seven study sites in the Yucatán Peninsula. The regression equation is $Y = 5.25 + 0.24X$; $r = .944$; $p < .01$.

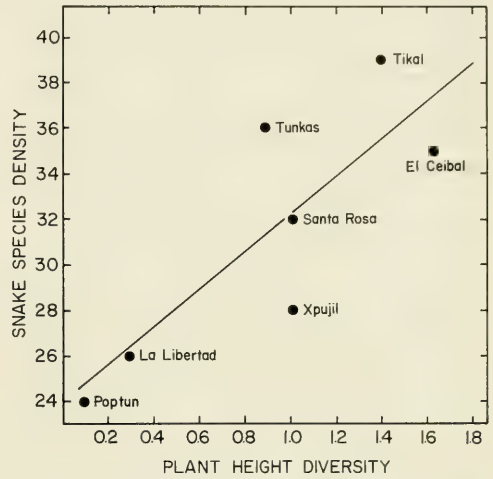


FIG. 17.—Regression of snake species density on plant height diversity for seven study sites in the Yucatán Peninsula. The regression equation is $Y = 23.97 + 8.25X$; $r = .814$; $p < .05$.

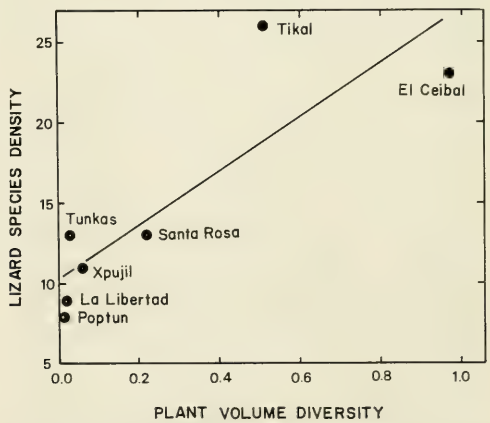


FIG. 18.—Regression of lizard species density on plant volume diversity for seven study sites in the Yucatán Peninsula. The regression equation is $Y = 10.41 + 16.63X$; $r = .864$; $p < .05$.

and lizards, the lowest numbers of species occur not in the youngest area, but rather in the somewhat older, central portion of the peninsula. And for anurans, the reduction in numbers at the north end is decidedly asymmetrical. Furthermore, so many species are pan-peninsular that it is difficult to accept the idea that more species could occur in the north, but have simply not yet made the journey. There remains the possibility that more species could co-exist at the north end, but that there has been insufficient time for the evolution of forms sufficiently specialized to partition the environment finely. The presumed recency of some of the Yucatecan endemics lends some credence to this view. Concerning *Dipsas brevifaces* and *Sibon sanniola*, and the great variation in lepidosis which obtains in those species, Peters (1960) wrote: "Since the Yucatán Peninsula was flooded for the most part during the Pliocene and Pleistocene, it is likely that both of these species are of fairly recent origin, and are quite possibly still in a state of evolutionary flux." However, the same objections may be advanced as with ecological time. The fewest species either do not occur in the youngest areas (snakes and lizards), or the pattern is asymmetrical (anurans). The existence of a substantial number of endemic species at the north end further argues against this view. Finally, the discovery of a fossil *Lepidophyma* of Pleistocene age at the northwest corner of the Peninsula (Hatt et al., 1953), far to the north of the present range of this mesophilic genus (see Appendix, Plate 15), suggests that the reduction in numbers of species at the north end may have resulted not from failure to differentiate or disperse into the area, but from failure to persist there. I conclude that the time hypothesis by itself is not adequate to explain the observed patterns of species density in the Yucatán Peninsula.

The Spatial Heterogeneity Hypothesis.—Environments that are physically complex are expected to have more spe-

cies than relatively simple environments. Here it is useful to distinguish between macro- and microspatial heterogeneity. The former refers to topographic relief on a geographic scale; the latter to habitat complexity on a local scale, such as vegetation structure, texture of substrate, etc. A number of studies (Simpson, 1964; Cook, 1969; Keister, 1971) have examined species density patterns in North America and have concluded that topographically diverse areas (mountains) support more species of mammals, birds, and amphibians than do non-montane areas at comparable latitudes. Reasons for this seem clear: topographic complexity can lead to isolation of populations that promotes speciation; such areas are also likely to contain more habitats and consequently to support more species. In the Yucatán Peninsula, major topographic relief is wanting; this aspect of spatial heterogeneity is thus not an issue and will not be considered further.

Following the successes of MacArthur and MacArthur (1961) and MacArthur (1964) who showed that bird species diversity was correlated with foliage height diversity, a number of workers have sought to quantify micro-habitat heterogeneity and to relate it to species densities or diversities of various groups of organisms. Recher (1969) found that the regression equation derived by MacArthur for North American birds accurately predicted bird species diversity in Australia, thereby suggesting generality of the relationship. But Tomoff (1974) concluded that a model that combined aspects of foliage height diversity and physiognomic cover diversity was a better predictor of bird species density in desert scrub. Using multiple regression analysis, Pianka and Huey (1971) found that plant height diversity was the best single predictor of bird species density in the Kalahari desert, followed by mean annual precipitation, numbers of species of perennial plants, mean percent cover by perennials, and plant species diversity. Rosenzweig and Winakur (1966) devised a model which incorpo-

rated qualities of soil surface, vegetation height, and vegetation density to account for species diversity in desert rodent communities. Pianka (1966b, 1967, 1971) explored the relationships between lizard species density and environmental variables in a variety of lizard communities on three continents. He found that in the deserts of western North America plant volume diversity was a good predictor of lizard species density, but that in the Kalahari desert, mean percent plant cover, and plant species diversity were the better predictors. Microspatial heterogeneity in its various forms thus has been shown to be an important correlate of species density or species diversity, but the aspects of heterogeneity that are important vary between and within vertebrate groups.

In the Yucatán Peninsula lizard species density is significantly correlated with plant volume diversity, duplicating the findings of Pianka (1966b, 1967) for North American desert lizards. However the two studies are not strictly comparable because I used many more categories in calculating plant volume diversity. Plant height diversity is also significantly correlated with lizard species density in the peninsula, but plant height diversity and plant volume diversity are themselves correlated and the multiple regression analysis indicates that plant height diversity has little or no unique explanatory power. Two aspects of vegetation structure—plant volume diversity and plant cover diversity—thus appear to be especially important, while the amount and seasonality of rainfall, which together account for only 14% of the variation, are relatively unimportant in explaining variation in lizard species density.

Of the parameters of vegetation structure considered here, only scores on the second principal component correlate significantly with amphibian species density. Apparently those sites that have high species-dependent indices of plant diversity also have large numbers of amphibian species, but the biological sig-

nificance of this relationship, if any, is not clear. Both the correlation and multiple regression analyses indicate that the amount and seasonality of rainfall are of paramount importance in accounting for variation in amphibian species density between sites, and that species volume diversity makes a small (4%) contribution. Scores on the second principal component possess little or no unique explanatory power, and are not entered into the multiple regression equation. I conclude that amphibian species density is relatively independent of habitat structure, at least as I have been able to quantify it, and that the spatial heterogeneity hypothesis need not be invoked to explain the observed pattern of amphibian species density in the Yucatán Peninsula.

Only a single variable, species height diversity, correlates with snake species density in a way suggesting possible causation. The multiple regression analysis shows that in addition, seasonality of rainfall makes a substantial contribution to explaining variation in snake species density, as does species volume diversity of vegetation. Taken as a whole, snake and lizard species density is related primarily to aspects of vegetation structure rather than to the taxonomic composition of the vegetation; amount and seasonality of rainfall appear to be of secondary importance, and I therefore conclude that the spatial heterogeneity hypothesis is in some way applicable to snakes and lizards in the Yucatán Peninsula. But what is the biological meaning of these relationships? Several explanations can be offered.

First, it seems reasonable to assume that a more complex environment can be more finely partitioned by specialists, and MacArthur and MacArthur (1961) and MacArthur (1964) have developed this argument for birds. According to these authors, organisms can exploit a complex environment either by specializing on one or a few resources, and foraging widely for these; or by utilizing a wide range of resources, and foraging over a restricted area. Only where the

resources are highly concentrated are the disadvantages of specialization outweighed by the advantages. A similar argument might apply to lizards and snakes in the Yucatán Peninsula. A number of studies, mostly involving lizards of the genus *Anolis*, have demonstrated that some lizards partition the habitat vertically, both within (Andrews, 1971; Schoener, 1967, 1969) and between (Schoener and Schoener, 1971a, 1971b; Janssen, 1973) species. In general these studies have been restricted to Antillean species which characteristically exist in much higher densities than do their mainland congeners, and among which competition for food is thought to be more intense (Andrews, 1976). My subjective impression is that in the Yucatán Peninsula population densities of snakes and lizards are low, perhaps too low for competition to promote fine habitat partitioning. Henderson and Fitch (1975) found no evidence of vertical partitioning of the habitat between *Anolis sericeus*, a pan-peninsular species, and its sympatric congeners, even where *A. sericeus* occurred in unusually high numbers. Furthermore, in the present study, the correlation between snake and lizard species densities are actually weakened if only arboreal and semiarboreal species are considered. Finally, although Pianka (1967) found that plant volume diversity correlated well with the number of lizard species in North American deserts, only three of his 15 lizard species are to any extent arboreal, and only one is highly specialized for such an existence. So although this explanation has intuitive appeal, and although the structurally complex forests of El Ceibal and Tikal do support many arboreal species, it remains to be demonstrated that mainland species of snakes and lizards partition the vertical component of the environmental mosaic.

A second possible explanation blends aspects of the spatial heterogeneity hypothesis with an hypothesis involving predation. On the basis of manipulations of intertidal invertebrates, Paine (1966)

concluded that predators can exert a regulatory force over their prey such that species are held below carrying capacity, thereby reducing competition and promoting the coexistence of more species. The best empirical evidence for this hypothesis involves structurally heterogeneous environments such as intertidal zones (Paine, 1966, 1969) and coral reefs (Porter, 1972). Such structurally complex environments should provide numerous safe sites in which individuals of prey species can avoid elimination by their predators. Experimentation (Huffaker, 1958; Huffaker et al., 1963) has shown that for some simple predator-prey systems, stable oscillations in numbers of predators and prey can be obtained only under conditions of considerable spatial heterogeneity; in structurally simple situations the systems become self-annihilating. Thus, some minimal level of environmental heterogeneity seems necessary for predation to be effective in promoting the coexistence of species; this effectiveness might vary with the degree of heterogeneity to produce the species density patterns observed for snakes and lizards in the Yucatán Peninsula. Evaluation of this suggestion requires information on the intensity of predation, information not presently at hand.

The Productivity Hypothesis.—All things being equal, areas of greater productivity can support more individuals than areas of lesser productivity. The resultant large population sizes can result in greater genetic variation, which in turn could promote speciation (Connell and Orias, 1964). Furthermore, because each species need use less of the total range of resources, the same array of resources can support more species in a productive environment (Pianka, 1974). I have no direct measure of productivity for my study sites in the Yucatán Peninsula. However, because productivity is known to be correlated with annual rainfall (Odum, 1959; Whittaker, 1970), rainfall data provide a crude index of productivity. The base of the peninsula, which receives the greatest annual rain-

fall and is thus presumably the most productive, does support the greatest numbers of species of amphibians and reptiles. But for snakes and lizards, the dry—and therefore least productive—north end of the peninsula supports more species than does the wetter and presumably more productive central portion. The species density patterns of amphibians are most consistent with the productivity hypothesis. However, the correlation between amphibian species density and amount of rainfall is open to other interpretations. Does lack of rain limit the numbers of amphibian species indirectly through control of productivity, or does it exert a more direct effect by imposing physiological demands related to problems of water balance? Although these interpretations do not exclude one another, I favor the latter for several reasons. Nearly all of those anurans occurring at the xeric northwest corner of the peninsula possess characteristics that can be interpreted as adaptations to minimize evaporative water loss. For instance, with few exceptions such species tend to be large (e.g., *Rana pipiens*, *Bufo marinus*, *Bufo valliceps*, *Phrynohyas venulosa*, *Smilisca baudinii*, *Tripurion petasatus*). Their surface to volume ratio would convey a relative advantage in terms of cutaneous evaporative water loss, in contrast to those small species which drop out along the rainfall gradient (e.g., *Hyla picta*, *H. microcephala*, *H. staufferi*, *H. ebraccata*, and *Syrhopus leprus*). *Tripurion petasatus* possess a coossified skull (Trueb, 1970), across which evaporative water loss is probably reduced, as has been shown for two other species of frogs with cranial coossification (Seibert et al., 1974); this is of obvious advantage during phragmosis (plugging holes with parts of the body) for which *Tripurion* is known to use its head (Stuart, 1935). Finally, two species, *Leptodactylus labialis* and *L. melanonotus*, construct foam nests in which the eggs hatch and the larvae undergo partial development. In *L. melanonotus* the foam nest floats on

the surface of the water, whereas in *L. labialis* the nest is constructed in burrows at the water's edge. Heyer (1969) discussed the adaptive trend toward terrestriality demonstrated by members of the genus *Leptodactylus*. He considered foam nests to be adaptations that convey a degree of independence from the aquatic environment, thereby reducing exposure to aquatic predators and the risk of desiccation of a temporary water source.

All but one of the anuran species occurring at the northwest corner of the peninsula are widely distributed throughout México and Central America. Their adaptations to xeric conditions cannot be viewed as a response to the specific conditions of aridity in Yucatán, but rather represent characteristics which preadapt them to that situation. These considerations lead me to conclude that problems of evaporative water loss and water balance have been important in setting distribution limits of amphibians in the Yucatán Peninsula and that the productivity hypothesis, although consistent with the distribution data, does not offer a compelling explanation for the observed patterns of amphibian species density.

Other Hypotheses.—Additional hypotheses and combinations of hypotheses have been advanced to explain species density gradients. They are relevant to the present discussion, but are difficult to evaluate with the data at hand. Competition, for example, is generally thought by ecologists to be a potent force in shaping community structure and it may play an important role in controlling numbers of coexisting species. How and to what extent this is so in the Yucatán Peninsula is not clear. If in fact lizards and snakes partition the structural habitat (see above), such partitioning is presumably an adjustment made in response to past competitive interactions. The complementary distribution of certain species pairs suggests competitive exclusion; e.g., *Kinosternon acutum* and *K. creaseri*, (Appendix, Plates 6, 7), *Laemanctus long-*

ipes and *L. serratus* (Appendix, Plate 12), *Sceloporus chrysostictus* and *S. teapensis* (Appendix, Plates 12, 13), *Bothrops nasutus* and *B. yucatanicus*, (Appendix, Plates 26, 27), *Bothrops asper* and *Crotalus durissus* (Appendix, Plates 26, 27). Such ecological replacement would not produce species density gradients, but more complex and diffuse competitive interactions might contribute to the observed patterns. Closely coupled with hypotheses concerning competition are ideas about climatic stability and predictability. Stable and/or predictable environments may allow finer adaptations and greater specialization because less energy is expended or held in reserve for maintenance. Evaluation of this suggestion as it applies to the Yucatán Peninsula awaits acquisition of information comparing competitive ability, reproductive performance, and energy allocation within and between species.

In conclusion, it appears that the two basic species density patterns in the Yucatán Peninsula—one manifested by amphibians, the other by snakes and lizards—have rather different underlying causes. Amphibians seem to be responsive to, and apparently are controlled by, essentially abiotic factors, of which amount and seasonality of rainfall are especially

important. These presumably act to set distribution limits through the imposition of conditions beyond the physiological tolerances of certain species. In contrast, snakes and lizards seem to be controlled, perhaps indirectly, by biotic factors, particularly features of environmental structure such as plant height, cover, and volume diversity. These conclusions can be generalized to include other tropical amphibian and reptile communities. Barbault (1976) studied herpetofaunal species diversity on savannas in the vicinity of Bouake, Ivory Coast. He found that lizard species diversity (estimated using the Shannon index) was positively related to habitat structure diversity, whereas amphibian species diversity increased as a function of both the length of the rainy season and the number of breeding sites. He felt that snake species diversity was controlled indirectly by both habitat diversity and weather acting through changes in prey community structure.

The similarity in the findings of these two studies, conducted on different continents and involving phylogenetically unrelated communities, strongly suggest that fundamental differences exist in the relative importance of biotic and abiotic factors in controlling species densities of tropical amphibians and reptiles.

SECTION III:

EVOLUTION OF A NEOTROPICAL PENINSULAR HERPETOFAUNA

In the preceding sections I found it necessary to treat the taxonomic composition and patterns of distribution of the peninsular herpetofauna as static. In reality these two attributes of the herpetofauna are in perpetual flux. New species evolve or are added to the fauna by immigration; other species become extinct locally or regionally. The effects of speciation, immigration, extinction, and emigration, all of which proceed against the background of a changing environment, insure that the herpetofauna of today is not what it was in the past, nor

what it will be in the future. Thus there remains the question of the development of the taxonomic composition and patterns of distribution through time, a subject that has long been of concern to biologists interested in the Yucatán Peninsula (e.g., Gadow, 1905) because the area has served as a notable center of vertebrate differentiation and, possibly, dispersal (Müller, 1973).

The following questions are addressed in this section: (1) To what extent is the peninsular herpetofauna autochthonous? (2) Where did the allochthonous

elements come from, and by what route? (3) Of several potential source areas, which have been most important in supplying faunal elements to the peninsula? (4) To what extent can the present-day composition and patterns of distribution be interpreted in terms of past vegetation and climatic changes? (5) How have the patterns of distribution been modified by millennia of settlement and intensive agriculture by the Maya?

METHODS

Leon Croizat's biogeography (Nelson, 1973) questions the assumption that the objective of historical biogeography is to find centers of origin and patterns of dispersal. Croizat et al. (1974) argue that to seek centers of origin and dispersal routes is to search for that which often does not exist. In those instances where they do exist, they are attributes of individual taxa having little general explanatory power. A more profitable approach, they contend, is the "vicariance" or pan-biogeographic method advocated by Croizat (1958, 1962). The method involves the compilation of the distributions of many species in order to ascertain general patterns. The distribution of a species or group of related species is circumscribed or connected by a line, producing an area termed a track. When this is done for many taxa, areas of concordant tracks may become apparent; these are known as generalized tracks. Tracks represent the geographic relationship between the members of the group and the generalized track represents an estimate of the geographical distribution of an ancestral biota which has been fragmented (vicariated) to produce the observed pattern. The method then leads to inferences concerning those historical events responsible for effecting the vicariance. These permit formulation of testable hypotheses of considerable generality. Although apparently not explicitly stated by Croizat (Ball, 1975), his followers have been quick to emphasize that the appropriate units for track anal-

ysis are monophyletic groups. Although I believe that use of the terms track, generalized track, and vicariance as applied to biogeography represents an unnecessary proliferation of jargon, I also believe that this method of analysis has two principal strengths: (1) It makes no *a priori* assumptions about centers of origin and the role of dispersal; thus the facts of distribution are allowed to speak for themselves. (2) Because the method involves the evaluation of large numbers of individual distributions, it leads to formulation of general hypotheses. The methods of "vicariance" biogeography are further discussed by Croizat et al. (1974), and by Rosen (1974). Recent examples of application of the method are those of Rosen (1975) and Wiley (1976).

Where possible I have utilized the method of Croizat, outlined above, to formulate hypotheses about the historical development of the peninsular herpetofauna, especially the origins and evolution of the endemic elements. Because the method requires information about the cladistic relationships of the taxa under consideration, and because often these relationships are very imperfectly known, this analysis must be considered a first approximation. However, the hypotheses that stem from this analysis are amenable to test. Additional distributional data and/or improved understanding of cladistic relationships may corroborate (but cannot verify) these hypotheses. More importantly, as they become available, data from paleoecology and paleoclimatology can be marshalled as potential falsifiers.

RESULTS

Of the 164 species of amphibians and reptiles in the Yucatán Peninsula, 112 (68.3%) are widespread in the Gulf and/or Caribbean lowlands of southern México and Central America. Of the 112, 54 (48.2%) also are widespread on the Pacific versant. The presence of these wide-ranging species in the penin-

sula is certainly no surprise; indeed, it is the absence of some such species (e.g. *Coniophanes picevittis*) that is noteworthy. The origin of this portion of the peninsular herpetofauna thus involves the larger question of the origins of the Middle American herpetofauna, a subject treated at length by Savage (1966). Primarily on the basis of modern distribution patterns, Savage (1966) characterized the genera of Middle American amphibians and reptiles as belonging to four historical assemblages: Old Northern, Middle American, South American, and Young Northern. He concluded that the herpetofauna of Middle America is not transitional between that of the Neotropics and the Nearctic, but rather is sufficiently distinct to stand alone as a separate major herpetofauna. If we ac-

cept Savage's interpretation, 15.1% of the peninsular genera belong to the Old Northern assemblage, 48.4% to the Middle American assemblage, 15.1% to the South American assemblage and 4.3% to the Young Northern assemblage. The remaining genera cannot be easily referred to a particular assemblage. At the specific level, 13.4% of the peninsular species show Old Northern affinities, 49.4% show Middle American affinities, 12.8% show South American affinities, and 4.9% show Young Northern affinities. Thus, at the generic and specific levels, the peninsular herpetofauna as a whole shows its greatest affinities with the Middle American assemblage, a conclusion wholly expected on the basis of geography alone. Few genera and species appear to be Nearctic or Neotropical derivatives.



FIG. 19.—South peninsular disjuncts. A. *Sceloporus chrysostictus*. B. *Cnemidophorus angusticeps*. C. *Conophis lineatus*. D. *Masticophis mentovarius*. E. *Stenorrhina freminvillei*.

INTRA-PENINSULAR PATTERNS

Southern disjuncts.—Several species occur more or less continuously through the northern portion of the peninsula, and are represented by disjunct populations to the south (Fig. 19). Several of these southern disjuncts are sufficiently differentiated to have been accorded subspecific status. Five species of reptiles that manifest this pattern are inhabitants of subhumid to xeric situations; all tend to avoid heavy forest. Those populations isolated in the south are generally associated with savannas or areas of second growth. Three additional species—*Rhinophrynus dorsalis*, *Tripurion petasatus*, and *Crotalus durissus*—are thought by some authors to conform to this pattern. However, accumulation of additional locality records suggests that they are continuously distributed throughout the region (Appendix, Plates 1, 5, 27).

Northern disjuncts.—The opposite pattern obtains for several other species. These are widely distributed through the base of the peninsula, with isolated populations to the north, and especially to the northeast (Fig. 20). In general these are mesophilic forest-dwelling species, and the disjunct populations tend to occur in an area of unusually high rainfall at the northeast corner of the peninsula (see discussion of climate in Section I above).

In summary, within the peninsula there are two complementary intraspecific patterns of distribution. Species inhabiting xeric to subhumid situations are widespread in the north and occur as disjuncts on savannas and in disturbed areas to the south; mesophilic species, wide-ranging through the base of the peninsula, occur as disjuncts to the northeast, especially in an area of high rainfall.

EXTRA-PENINSULAR PATTERNS

The Yucatán-West México Pattern.—No fewer than five species of amphibians and reptiles endemic to the peninsula have their apparent closest living relatives distributed on the Pacific versant of

México (Fig. 21). The genus *Tripurion*, with only two species, is represented by *T. petasatus* in the peninsula and by *T. spatulatus* from Jalisco to Guerrero and on the Pacific versant at the Isthmus of Tehuantepec. *Symphymus*, likewise containing only two species, is represented in Yucatán by *S. mayae* and on the Pacific versant at the Isthmus of Tehuantepec by *S. leucostomus*. Of the four species of *Enyalioides*, Duellman (1965b) considered the peninsular endemic *E. defensor* most closely related to *E. clarki* of the Tepalcatepec Valley of Michoacán. This pattern is recapitulated by *Eumeces schwartzei*, a peninsular species considered by Taylor (1935) to be most closely related to *E. altamirani* of Michoacán. Finally, *Cnemidophorus anquisticeps* of Yucatán was considered by Beargie and McCoy (1964) to be closest to *C. costatus*, a wide-ranging species in west México. Additional peninsular endemics of uncertain affinities have relatives which, if sister taxa, would further corroborate this pattern, as for example, *Dipsos brevifaces* of Yucatán and *D. gaigeae* of Colima and Jalisco. *Bothrops yucatanicus* may also reflect this pattern, for it is a member of a closely related group of four species of hog-nosed vipers, all of which are restricted to subhumid habitats, and two of which—*B. hesperis* and *B. dunni*—are restricted to western México (Campbell, 1976).

The Yucatán-East México Pattern.—Three species of reptiles occur as apparent isolates at the north end of the peninsula, and are represented by populations on the Atlantic versant of México (Fig. 22). In the case of *Sceloporus serrifer* the apparent disjunction could be a collecting artifact. Such is not the case for *Terrapene mexicana* and *Agkistrodon bilineatus*, both of which occur in Tamaulipas, far to the northwest of their Yucatecan relatives. *Agkistrodon bilineatus* is also widespread on the Pacific versant of México and Central America. The relationships between the three populations of *A. bilineatus* are unknown. If

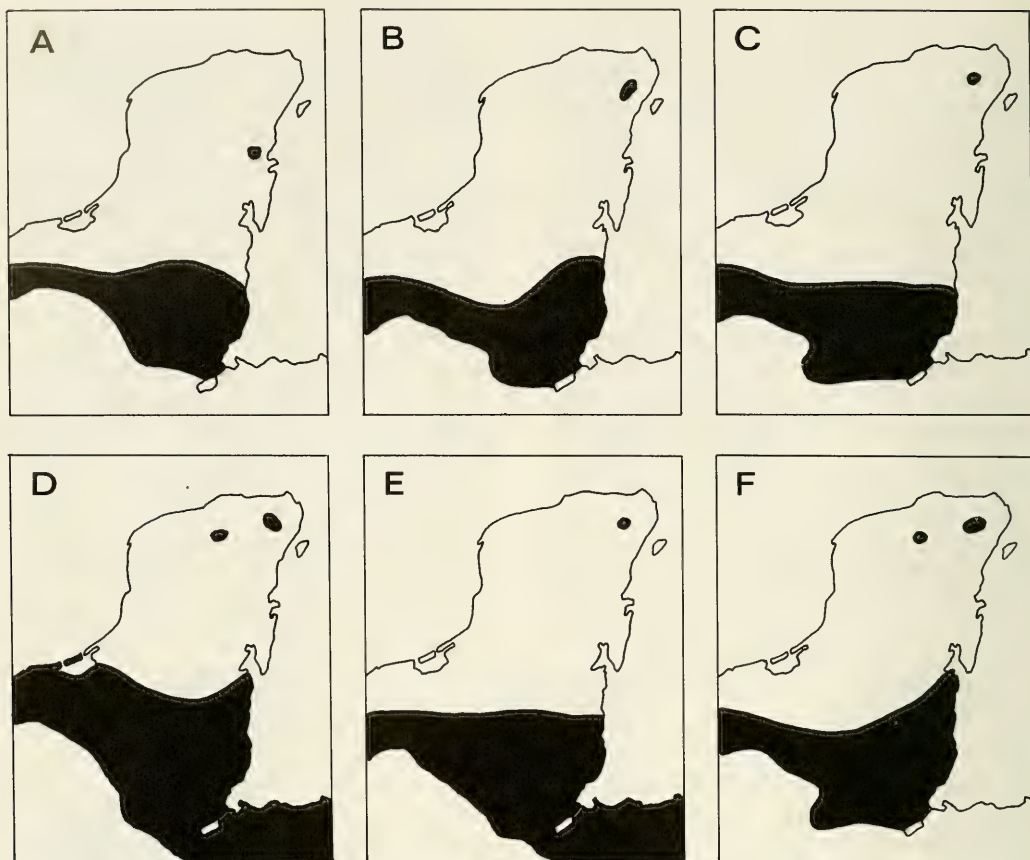


FIG. 20.—North peninsular disjuncts. Extra-peninsular distributions are rough approximations. A. *Hyla ebraccata*. B. *Corytophanes hernandezii*. C. *Eumeces sumichrasti*. D. *Sphenomorphus chieriei*. E. *Dendrophidion vinitor*. F. *Scaphiodontophis annulatus*.

the affinities of the peninsular form lie with the population on the Pacific versant, then the species represents, in modified form, an example of the Yucatán-West México pattern.

The Maya Mountain-Nuclear Central America Pattern.—The Maya Mountains of Belize support essentially a lowland fauna. However, two species of frogs known from the vicinity of the Maya Mountains, *Rana maculata* and *Agalychnis moreletii*, typically occur in montane situations. They are apparently isolated from the geographically nearest populations of their species in the highlands of Guatemala and Honduras by unsuitable lowland habitat in the Departments of El Petén and Izabal, Guatemala.

Miscellaneous Patterns.—Two endemic species of amphibians, *Bolitoglossa yucatanensis* and *Eleutherodactylus yucatanensis*, are nearly restricted to the north end of the peninsula where they occur in mesic situations such as caves and cenotes. In naming *E. yucatanensis*, Lynch (1964) acknowledged its close relationship with *E. alfredi* to the southwest. *B. yucatanensis* is one of the three members of the *dofleini* species group (Wake and Lynch, 1976); the closest living relative of *B. yucatanensis* is perhaps *B. schmidti* to the southwest (Wake, pers. comm.). The fossil *Lepidophyma arizelogyphus* is known only from a Pleistocene cave deposit in the northwest corner of the peninsula (Hatt et al., 1953), far to the north of the modern

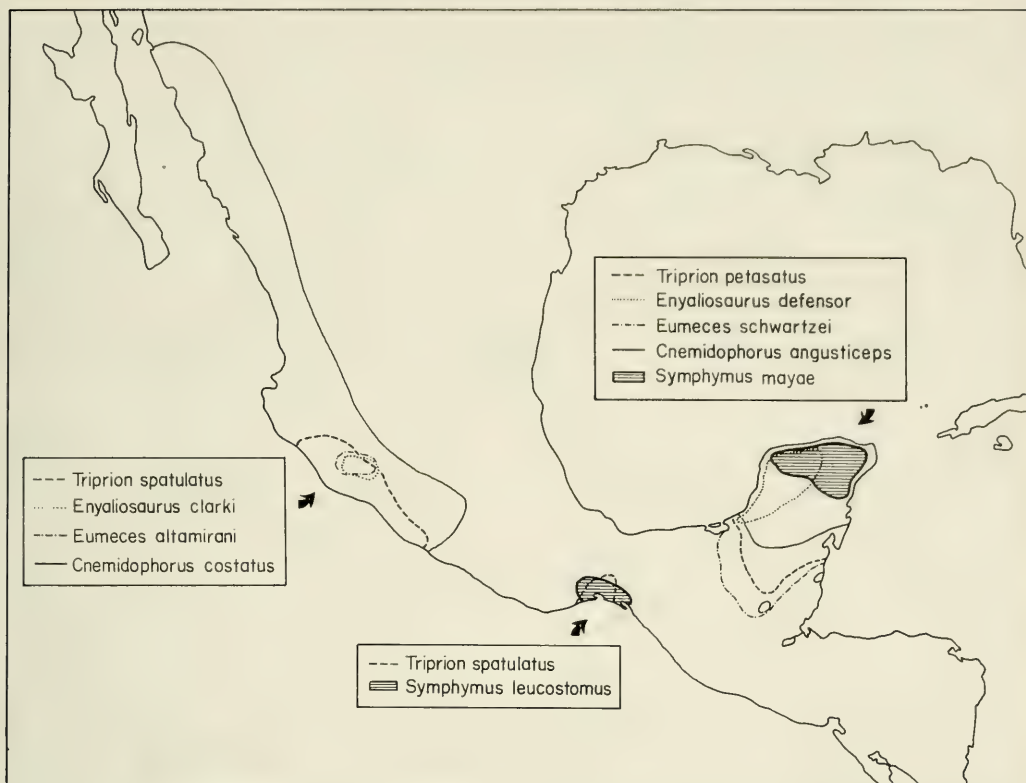


FIG. 21.—The Yucatán-West México pattern of distribution. Extra-peninsular distributions are rough approximations.

limits of this mesophilic genus. Thus, two mesic-adapted species are confined to the north end of the peninsula, but have their closest relatives in wetter areas to the south. An additional species, presumably mesophilic, existed at the north end of the peninsula until sometime in the Pleistocene.

The foregoing distribution patterns involving peninsular endemics or species with isolated populations in the peninsula can be summarized as follows: (1) Five species pairs exhibit a Yucatán-West México pattern. Two additional pairs may also exhibit this pattern. (2) Two, and perhaps three, species have a Yucatán-East México pattern of distribution. (3) Two species centered on the north end of the peninsula have their closest relatives at the base of the peninsula or immediately adjacent. (4) Within the peninsula five species are widespread

at the north end and occur as isolates to the south; six species are widespread through the base of the peninsula and occur as isolates to the north. (5) Two species are widespread through the highlands of Central America and occur in apparent isolation in the Maya Mountains of Belize.

DISCUSSION

The intra- and interspecific disjunctions identified above involve pairs of species, or sets of populations which, although separated geographically, occur in similar environments. These patterns represent the remnants of once continuous distributions that have become fragmented. In isolation, the fragmented populations have differentiated to various degrees to produce species pairs (e.g., *Triprion petasatus* and *T. spatula-*

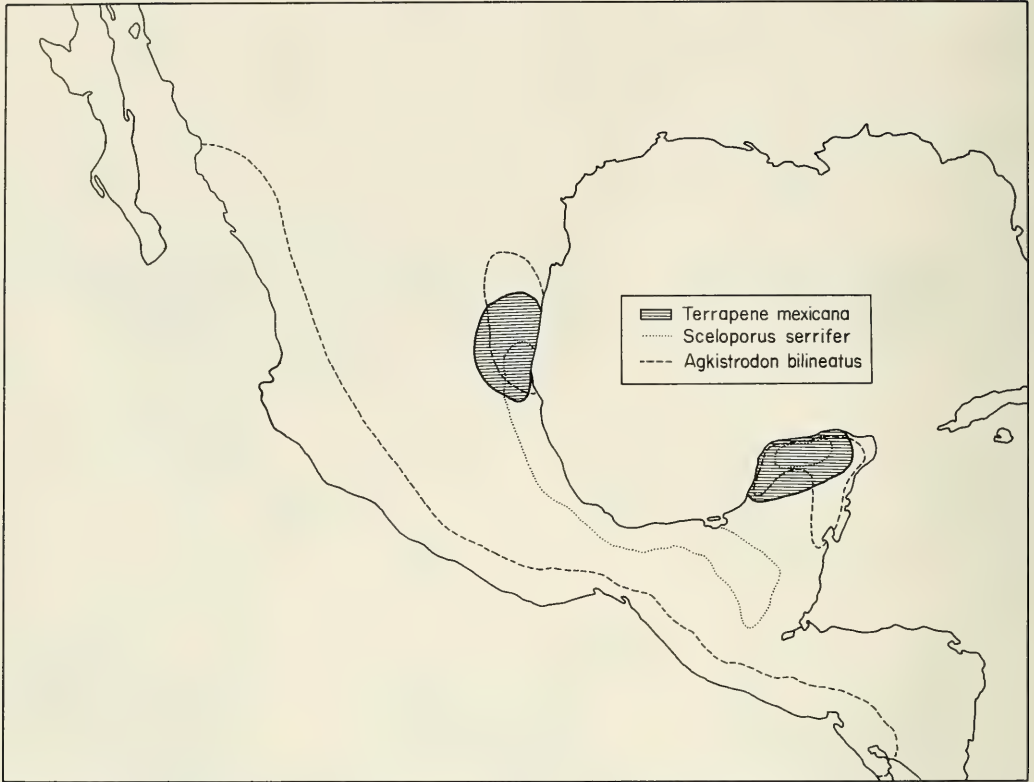


FIG. 22.—The Yucatán-East México pattern of distribution. Extra-peninsular distributions are rough approximations.

tus), subspecies pairs (e.g., *Terrapene mexicana yucatanana* and *T. m. mexicana*), and populations showing little or no differentiation (e.g., *Hyla ebraccata*). Parsimony requires the assumption that the common ancestor of each pair inhabited an environment similar to that presently occupied by its descendants. Therefore, we may infer that disjunct populations inhabiting similar habitats betoken a more widespread and continuous distribution of that habitat at some time in the past. We need to know what historical events were responsible for effecting the breakup of these habitats. I believe that two sets of events—Pleistocene changes in climate and vegetation, and pre-Columbian human influences—have been of overriding importance in shaping these patterns of distribution.

PLEISTOCENE CHANGES IN CLIMATE AND VEGETATION

The conventional view of the tropics in general, and the Neotropics in particular, as ancient and stable environments must be abandoned in the light of the paleobotanical and paleoclimatological evidence that has been accumulating steadily, especially during the past 15 years. Griscom (1942) was one of the first to advance this view when he suggested that Pleistocene climate changes resulting in the expansion and contraction of vegetation zones were important in shaping patterns of bird distribution in Central America. His idea that the montane forests of Central America were sufficiently lowered to completely pinch out the lowland rainforest is probably incorrect. However, it now seems certain.

that the Neotropics have not been exempt from the Pleistocene climatic changes that so profoundly affected the northern hemisphere.

Ideas about Neotropical climatic and vegetation change are central to theories concerning the evolution of species densities of Amazonian birds (Haffer, 1969, 1974) and frogs (Crump, 1974), and differentiation of Amazonian lizards (Vanzolini and Williams, 1970). Such ideas have also played a central role in the biogeographic analysis of Neotropic dispersal centers (Müller, 1973). Parenthetically, it is interesting to note that the two opposing views of the tropics—one that they are unchanging, the other that they have been subject to much change—are both invoked to explain the same phenomenon, namely the extraordinary numbers of species of plants and animals in the tropics.

Little evidence is at hand concerning the nature of these changes as they apply to northern Central America and southern México. However, considerable palynological data are available for tropical South America (see Van Der Hammen, 1974, for summary), and southern Central America (Bartlett and Barghoorn, 1973). Also available are paleotemperature curves calculated from deep-sea sediments in the Caribbean (Emiliani and Rona, 1969; Lynts and Judd, 1971), and documentation of long-term fluctuations in water levels of Laguna Chichancanab, Yucatán (Covich and Stuiver, 1974). Taken together these data allow a qualitative assessment of changes in the climate and vegetation in the Yucatán Peninsula, especially during Pleistocene and Holocene times.

Before pursuing this question it is appropriate to inquire as to the nature of the climatic and vegetation changes suggested by the facts of amphibian and reptile distribution. Assuming that the extent to which isolated populations have differentiated is at least roughly proportional to the length of time since they became separated (admittedly a questionable assumption, for it requires equal

rates of evolution), it is possible to suggest the nature and sequence of the environmental fluctuations which affected the separations. Thus, full species pairs presumably reflect an earlier divergence than do subspecies pairs, which in turn are older than those fragmented populations showing little or no differentiation.

Those species pairs exhibiting the Yucatán-West México pattern show a decided preference for subhumid to xeric situations. Trueb (1970) interpreted the disjunct distribution of *Tripurion* in terms of a period of Pleistocene aridity when continuous subhumid to xeric habitat may have extended from the Pacific side of México across the Isthmus of Tehuantepec to the Gulf coast, and thence into the Yucatán Peninsula. Rossman and Schaefer (1974) noted the similarity between the distributions of *Tripurion*, *Enyaliosaurus*, and *Symphymus*. The addition of the *Cnemidophorus angusticeps*-*C. costatus* and *Eumeces schwartzei*-*E. altamirani* species pairs to this pattern strengthens the argument that continuous subhumid habitat existed on both coasts of central and southern México. The subsequent onset of wetter conditions and the expansion of mesophytic vegetation, especially in the vicinity of the southern Gulf Coast, served to isolate the subhumid environment of the Yucatán Peninsula from that of west México, thereby promoting the differentiation of at least five pairs of amphibians and reptiles.

The presence of three mesic-adapted species isolated at the outer end of the peninsula, far to the north of their relatives, suggests that the peninsula was once a more mesic environment than it is today. We may suppose that under wetter conditions mesophytic forests extended northward in the peninsula, and that the progenitors of those species presently restricted to the base of the peninsula were more widely distributed. With the onset of drier conditions and the retreat of the wet forests, many species disappeared from the north end; others became restricted to small pockets

of mesic habitat associated with cenotes and caves (e.g., the ancestors of *Eleutherodactylus yucatanensis* and *Bolitoglossa yucatanensis*) where they underwent differentiation in isolation. This same sequence of events might also account for the presence of the northern disjuncts discussed above. Alternatively, they could be the result of a more recent period of humid conditions, for the isolated populations of the six species exhibiting this pattern have undergone little or no differentiation.

The Yucatán-East México pattern also involves species generally restricted to subhumid habitats, but these are differentiated only at the subspecies level. We may again hypothesize a continuous subhumid habitat around the Gulf of México uniting the Yucatán Peninsula with northeastern Mexico. Martin (1958) was first to call attention to the similarity between the faunas of Yucatán and Tamaulipas, and to suggest the existence of a dry lowland connection between the two areas. Several species thought by Martin to exhibit the Tamaulipas-Yucatán disjunction are now known to be more widely distributed through the intervening area than he supposed (e.g. *Hypopachus variolosus* and *Laemanctus serratus*). His most impressive example of a Yucatecan endemic with northern affinities was "*Opheodrys*" *mayae*, subsequently shown by Rossman and Schaefer (1974) to be a member of the Middle American genus *Symphymus* rather than of the genus *Opheodrys*. Nonetheless, the presence of *Terrapene mexicana* and *Agkistrodon bilineatus* in Tamaulipas and Yucatán argues for the existence of continuous dry forest between the two areas. Possibly this connection was coeval with the Yucatán-West México connection. Alternatively it could represent a more recent connection, for the Yucatán and Tamaulipas populations are only subspecifically distinct.

The Maya Mountain-Nuclear Central America pattern is difficult to account for in terms of Pleistocene climatic and vegetation change. Moderate depression

of montane forest might connect the Belizian population of *Agalychnis moreletii* with those in the highlands of Guatemala and Honduras, but such lowering of vegetation zones would hardly provide suitable habitat for *Rana maculata*, a species which characteristically breeds in lotic situations. The Belizian specimens referred by Lee (1976) to *Rana maculata* are peculiar in several respects, and the possibility exists that they are not conspecific with populations of *Rana maculata* to the south.

If the above interpretations are even approximately correct, two conclusions follow. First, during the late Pleistocene much of Middle America was subject to alternating periods of aridity and wetness. Second, the Yucatán Peninsula has been both drier and wetter than it is today. We now need to know to what extent these conclusions are consistent with the known facts of paleoclimatology and paleobotany. Palynological studies in northern South America (Van Der Hammen, 1974) have documented a period of aridity from about 21,000 to 13,000 B.P. when effective precipitation was less than during the Holocene (ca. the last 10,000 years), and an earlier period from about 90,000 to 21,000 B.P. when precipitation was greater than during the Holocene. In Panamá pollen from about 7,300 to 4,200 B.P. suggest a drier climate than at present (Bartlett and Barghoorn, 1973). The generalized Caribbean paleotemperature curve of Emiliani and Rona (1969) is approximately consistent with these findings if periods of low temperature are assumed to coincide with periods of aridity. Covich and Stuiver (1974) documented fluctuations of water levels in Laguna Chichancanab from about 22,000 to 8,000 B.P., culminating in a phase of reduced lake volume or perhaps complete desiccation. Thus, different lines of evidence from paleoclimatology, palynology, limnology, and zoogeography all are consistent with the idea that major changes have occurred in and adjacent to the Yucatán Peninsula with respect to

climate during the Pleistocene. Although the timing, magnitude, and sequence of these changes are imperfectly known, one may confidently assert that the alternating wet-dry periods suggested by the facts of reptile and amphibian distributions were real.

PRE-COLOMBIAN HUMAN INFLUENCES

Recent archaeological excavations in northern Belize have demonstrated the existence of an Early Formative Maya civilization at about 2500 B.C. (Hammon et al., 1976). This pushes back the beginnings of the Maya Early Formative period nearly 1500 years and establishes the Maya culture as one of the oldest in Middle America. Other studies in the vicinity of Edzna and Xpujil, in the state of Campeche, have shown that the Classic (300-900 A.D.) Maya were far more sophisticated agriculturalists than previously believed. Terraced fields (Turner, 1974) and ingenious irrigation systems (Matheny, 1976) allowed Mayan farmers to bring large areas under cultivation. Estimates of the number of people that a single Mayan farmer could support are being revised upward, and as a result ideas about population sizes and densities are being reevaluated. Whatever the impact of the Mayan civilization on the biota of the Yucatán Peninsula, the effect was of greater duration and intensity than previously thought.

Amphibians and reptiles featured prominently in Mayan thought, to judge by their representation in carvings, paintings, and masonry. Some species were evidently of mythical significance: a monstrous rattlesnake with a human emerging from its jaws is a common motif at Puuc style sites in Yucatán, especially those showing Toltec influence. The Maya undoubtedly transported living amphibians and reptiles from one locality to another for ceremonial purposes or as food items. Stuart (1958) concluded that the plastron and carapace of *Dermatemys mawii* found in a burial urn at Uaxactún were probably carried into the area from some other locale.

Such relocations were probably commonplace, but of a local nature; their effect upon general patterns of animal distribution probably was insignificant. Of far greater importance was the extensive habitat modification occasioned by Mayan agricultural practices. Present-day Mayan farmers practice the slash-burn shifting agriculture of their ancestors. As a result, the countryside is a patchwork of active and abandoned farm plots in various stages of succession, and the vegetation of nearly all of the northwestern corner of the peninsula—today the area of most intensive cultivation—is held in a subclimax stage. During the Classic period, virtually all of the Yucatán Peninsula may have been under cultivation. Lundell (1934) believed that primeval forest was either rare or nonexistent in the peninsula. It has been suggested that El Petén, which today is an area of continuous tropical forest, was, at the height of the Classic period, an area of intensive cultivation similar to present-day Ohio (Turner, quoted by La Fay, 1975). The possible anthropogenic origins of the savannas of central El Petén have been mentioned previously (see discussion of vegetation, Section I).

More subtle environmental modifications have been attributed to the extensive deforestation by ancient Mayan agriculturists. Covich (1976) documented changes in abundances of freshwater gastropods in Lago Petén Itzá which he attributed to major fluctuations in nutrient inflow and sedimentation rates caused by destruction of the surrounding forests. As discussed by Lundell (1937), the dominance of certain tree species in the vicinity of Mayan ruins is attributable to ancient Mayan horticulture. Some trees were of religious significance (e.g., *Ceiba pentandra*). Others, such as *Achras zapota* and *Brosimum alicastrum* were encouraged, if not actually cultivated, for their edible fruit.

The effects of such widespread environmental modification on the distributions of amphibians and reptiles are difficult to assess, but must have been

considerable. Those species which require open situations (e.g., *Sceloporus chrysostictus* and *Cnemidophorus angusticeps*) and which today are largely restricted to the disturbed subclimax situations at the north end of the peninsula very likely were much more widely distributed in the past. Today such species also occur in isolation on savannas and in disturbed situations to the south. Fragmentation of their once continuous distributions could have resulted from expansion of the forests following collapse of the Mayan civilization and the near-abandonment of the Petén centers at about 950 A.D. Beargie and McCoy (1964) interpreted the distribution of *Cnemidophorus angusticeps* as the result of Pleistocene aridity. In support of this view one might argue that the subspecific differentiation exhibited by several of the southern disjuncts, including *C. angusticeps*, could not have evolved in the relatively short time since the decline of the Maya. However, a millennium seems sufficient for such differentiation, especially considering the rates of evolution which could obtain in small, isolated populations under intense selection. Because these southern disjuncts are nearly always associated today with areas of human disturbance, I favor an anthropogenic explanation for this pattern of distribution.

The foregoing considerations suggest the following sequence of events has been important in shaping patterns of distribution of amphibians and reptiles in the Yucatán Peninsula. (1) Aridity was widespread and west México and Yucatán were connected by subhumid

habitat. (2) With the onset of mesic conditions, west México and Yucatán became separated; mesophilic species became more widespread in the peninsula. (3) With the return of arid conditions, northeast México and Yucatán were connected by subhumid habitat; some mesophilic species were isolated at the north end of the peninsula. (4) With the establishment of somewhat wetter, essentially modern conditions, northeastern México and Yucatán became separated by mesophytic forest through much of the Gulf lowlands. (5) Mayan agriculturists deforested much of the peninsula; non-forest species of amphibians and reptiles expanded their ranges. (6) With the collapse of Maya civilization, the forest regenerated. Non-forest species receded and became restricted to the north end of the peninsula or persisted in the south as relicts on savannas and disturbed areas.

In conclusion, the herpetofauna of the Yucatán Peninsula taken as a whole shows overwhelming affinities with the herpetofauna of Middle America. However, peninsular endemics and those species represented by disjuncts at the north end show affinities with xeric-adapted forms of western and northeastern México. The bulk of the peninsular endemics appear to have evolved *in situ* when isolated in the peninsula by changing environmental conditions during the late Pleistocene. Disjunct distributions within the peninsula are partly attributable to wet-dry alternations in climate and partly to deforestation by the Maya and subsequent reforestation following the decline of the Mayan civilization.

SUMMARY AND CONCLUSIONS

Owing to its peninsular configuration and lack of topographic relief, the peninsula of Yucatán offers an excellent opportunity to study patterns of animal distribution and to assess the relative contributions of several factors thought to be important in setting distribution

limits and controlling the numbers of co-occurring species.

The primary objectives of this study were to ascertain the taxonomic composition of the herpetofauna of the Yucatán Peninsula; to identify patterns of distribution, species density, and endemism;

and to account for these patterns in light of ecological and historical factors.

The known herpetofauna of the Yucatán Peninsula numbers 164 species representing 25 families and 93 genera. I collated locality records for each species and summarized the records as spot maps, from which I inferred the limit of distribution of each species. Statistical analyses of these data show that the limits of distribution are contagious, indicating the existence both of areas of rapid faunal change and areas of faunal homogeneity. This is true for the entire herpetofauna and for all major taxonomic subdivisions. Using cluster analysis I identified and delineated four areas of faunal homogeneity for frogs, five for lizards, and three for snakes. For frogs and lizards these areas are largely congruent; the pattern for snakes differs from that of frogs and lizards. Amphibian species density diminishes dramatically from south to north, and especially to the northwest. For snakes and lizards species density is highest at the base of the peninsula, lowest at the center, and intermediate at the north end. Endemism is greatest at the north end of the peninsula. Disproportionately few species of amphibians are endemic, whereas snakes and lizards are overrepresented among the endemics.

Measurement of vegetation structure at seven sites, each located in a distinct vegetation type, indicates that various parameters of vegetation heterogeneity, estimated using an information theory statistic, are important correlates of snake and lizard species density. For amphibians the amount and seasonality of precipitation are most important. Thus, amphibians appear to be responsive to, and limited by, abiotic factors. Snakes and lizards seem sensitive to biotic factors, especially the heterogeneity of the structural habitat.

In contrast with the results of other studies on peninsular distributions, there is no evidence that a "peninsular effect" involving isolation and distance from a source area is important in shaping spe-

cies density patterns of amphibians and reptiles in the Yucatán Peninsula. Nor is it necessary to invoke ecological or evolutionary time hypotheses to explain the observed patterns of herpetofaunal species density.

The majority of species of amphibians and reptiles in the Yucatán Peninsula are forms widely distributed throughout the mesic Gulf and Caribbean lowlands. At both the generic and specific levels, the peninsular herpetofauna shows its greatest affinities with the herpetofauna of Middle America. The xeric-adapted fauna of the north end of the peninsula exhibits affinities with the faunas of western and northeastern México. The bulk of the peninsular endemics appear to have evolved *in situ* when isolated in the peninsula by changing environmental conditions during the Pleistocene. Disjunct distributions within the peninsula are partly attributable to wet-dry alterations in climate. Those disjunctions involving non-forest species are interpretable in terms of anthropogenic influences.

RESUMEN

Debido a la configuración peninsular y a la falta de relieve topográfico, la península de Yucatán ofrece una excelente oportunidad para el estudio de las normas de la distribución animal y para evaluar las contribuciones relativas de varios factores que se consideran importantes en la asignación de límites de distribución y en el control de números de especies coexistentes.

Los principales objetivos de este estudio son varios: cerciorarse de la composición taxonómica de los anfibios y reptiles de la península de Yucatán; identificar las normas de distribución, densidad de especies y endemismo; y explicar estas normas desde el punto de vista de factores ecológicos e históricos.

En la península de Yucatán hay 164 especies conocidas de anfibios y reptiles que están representadas por 25 familias y 93 genera. He cotejado informes de

localidad por cada especie y resumido la información en mapas acotados de los cuales he deducido el límite de distribución de cada especie. Análisis estadísticos de estas referencias muestran que los límites de distribución están agrupados; esto indica la existencia de áreas de rápido cambio de fauna y áreas de homogeneidad de fauna. Esto ocurre en todos los anfibios y reptiles y en todas las subdivisiones taxonómicas.

Mediante el análisis de agrupación he identificado y delineado cuatro áreas de homogeneidad de fauna en las ranas, cinco en las lagartijas y tres en las culebras. Con respecto a las ranas y las lagartijas estas áreas son mayormente congruentes pero la norma entre las culebras difiere de la de las ranas y las lagartijas. La densidad de las especies anfibias disminuye dramáticamente de sur a norte, y en particular al noroeste. Entre las especies de culebras y de lagartijas la densidad es más alta en la base de la península, más baja en el centro e intermedia en el norte. El endemismo es mayor en la parte norte de la península. Desproporcionadamente pocas especies de anfibios son endémicas mientras que culebras y lagartijas están sobrerrepresentadas entre las endémicas.

Las medidas de estructura de vegetación en siete sitios diferentes, cada uno ubicado en un tipo de vegetación distinto, indica que varios parámetros de heterogeneidad vegetal se correlacionan con la densidad de las especies de culebras y lagartijas de una manera importante. Esto se basa en lo obtenido mediante la estadística de diversidad de Shannon. Entre los anfibios la cantidad y la periodicidad estacional de precipitación es muy importante. Por lo tanto,

parece que los anfibios reaccionan a y están limitados por factores abióticos. Las culebras y las lagartijas parecen susceptibles a factores bióticos, especialmente a la heterogeneidad del hábitat estructural.

En contraste con los resultados de otros estudios sobre la distribución peninsular, no existe prueba de que un "efecto peninsular" que abarca aislamiento y distancia desde un punto de origen es importante en moldear las normas de la densidad de especies de anfibios y reptiles en la península de Yucatán. Tampoco es necesario apelar a hipótesis de períodos evolucionarios o ecológicos para explicar las normas observadas en la densidad de dichas especies.

La mayoría de las especies de anfibios y reptiles de la península de Yucatán son formas ampliamente distribuidas a lo largo de las zonas lluviosas del Golfo y las tierras bajas del Caribe. En ambos niveles, genérico y específico, los anfibios y reptiles de la península indican su más grandes afinidades con los anfibios y reptiles de México y la América Central. La fauna xerófita de la parte norte de la península revela afinidades con las faunas del oeste y noreste de México. La gran parte de los endémicos peninsulares parece haber evolucionado en el lugar de origen cuando fueron aislados durante el pleistoceno debido a cambios ambientales. Distribuciones esporádicas dentro de la península se atribuyen en parte a las alteraciones de humedad y sequedad en el clima. Las distribuciones disyuntivas que abarcan especies en las zonas desprovistas de bosques se interpretan en términos de influencias antropógenas.

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APPENDIX

Plates 1-27 summarize the distributions of amphibians and reptiles in the Yucatán Peninsula. The index below lists the taxa in alphabetical order by genus. The star on the map for *Lepidophyma flavimaculatum* (Plate 15) indicates the fossil record of *Lepidophyma arizelogyphus*. Question marks indicate doubtful records.

INDEX TO GENERA AND SPECIES

Taxon	Plate No.	Taxon	Plate No.
<i>Adelphicos quadrivirgatus</i>	16	<i>Bufo marinus</i>	3
<i>Agalychnis callidryas</i>	3	<i>B. valliceps</i>	3
<i>A. moreleti</i>	4	<i>Celestus rozellae</i>	15
<i>Agkistrodon bilineatus</i>	26	<i>Centrolenella fleischmanni</i>	3
<i>Ameiva chaitzami</i>	14	<i>Chelydra serpentina</i>	6
<i>A. festiva</i>	14	<i>Chrysemys scripta</i>	7
<i>A. undulata</i>	14	<i>Claudius angustatus</i>	6
<i>Amistridium veliferum</i>	16	<i>Clelia clelia</i>	16
<i>Anolis biporcatus</i>	9	<i>C. scytalina</i>	16
<i>A. capito</i>	10	<i>Cnemidophorus angusticeps</i>	14
<i>A. lemurinus</i>	10	<i>C. cozumela</i>	14
<i>A. pentaprion</i>	10	<i>C. deppei</i>	15
<i>A. rodriquezi</i>	10	<i>C. rodecki</i>	15
<i>A. segrei</i>	10	<i>Coleonyx elegans</i>	8
<i>A. sericeus</i>	10	<i>Coluber constrictor</i>	16
<i>A. tropidonotus</i>	11	<i>Coniophanes bipuncatus</i>	16
<i>A. uniformis</i>	11	<i>C. fissidens</i>	17
<i>Aristelliger georgeensis</i>	9	<i>C. imperialis</i>	17
<i>Basiliscus vittatus</i>	11	<i>C. meridanus</i>	17
<i>Boa constrictor</i>	15	<i>C. quinquevittatus</i>	17
<i>Bothrops asper</i>	26	<i>C. schmidti</i>	17
<i>B. nasutus</i>	26	<i>Conophis lineatus</i>	17
<i>B. nummifer</i>	26	<i>Corytophanes cristatus</i>	11
<i>B. schlegeli</i>	26	<i>C. hernandezi</i>	11
<i>B. yucantanicus</i>	27	<i>Crocodylus acutus</i>	8
<i>Bolitoglossa doleini</i>	1	<i>C. moreleti</i>	8
<i>B. mexicana</i>	1	<i>Crotalus durissus</i>	27
<i>B. rufescens</i>	1	<i>Ctenosaura similis</i>	11
<i>B. yucatanana</i>	1	<i>Dendrophidion vintor</i>	17
		<i>Dermatemys mawii</i>	7
		<i>Dipsas brevifaces</i>	18
		<i>Drymarchon corais</i>	18
		<i>Drymobius margaritiferus</i>	18
		<i>Elaphe flavirufa</i>	18
		<i>E. triaspis</i>	18
		<i>Eleutherodactylus alfredi</i>	1
		<i>E. laticeps</i>	2
		<i>E. loki</i>	2
		<i>E. rostralis</i>	2
		<i>E. rugulosus</i>	2
		<i>E. yucantanensis</i>	1
		<i>Enyaliosaurus defensor</i>	12
		<i>Eumeces schwartzei</i>	13

Taxon	Plate No.	Taxon	Plate No.
<i>E. sumichrasti</i>	13	<i>Phrynohyas venulosa</i>	5
<i>Ficimia publia</i>	18	<i>Phyllodactylus tuberculosus</i>	9
<i>Gastrophryne elegans</i>	5	<i>Pliocercus andrewsi</i>	21
<i>Geophis carinatus</i>	19	<i>P. elapoides</i>	22
<i>Hemidactylus turcicus</i>	9	<i>Pseustes poecilonotus</i>	22
<i>Hyla ebraccata</i>	4	<i>Rhinophrynus dorsalis</i>	1
<i>H. loquax</i>	4	<i>Rana maculata</i>	6
<i>H. microcephala</i>	4	<i>R. palmipes</i>	6
<i>H. picta</i>	4	<i>R. pipiens</i>	6
<i>H. staufferi</i>	4	<i>Rhadinaea decorata</i>	22
<i>Hypopachus variolosus</i>	5	<i>Rhinoclemys areolata</i>	8
<i>Iguana iguana</i>	12	<i>Scaphiodontophis annulatus</i>	22
<i>Imantodes cenchoa</i>	19	<i>Sceloporus chrysostictus</i>	12
<i>I. gemmistratus</i>	19	<i>S. cozumelae</i>	12
<i>I. tenuissimus</i>	19	<i>S. lundelli</i>	13
<i>Kinosternon acutum</i>	6	<i>S. serrifer</i>	13
<i>K. creaseri</i>	7	<i>S. teapensis</i>	13
<i>K. leucostomum</i>	7	<i>Sibon dimidiata</i>	22
<i>K. scorpioides</i>	7	<i>S. nebulata</i>	22
<i>Laemanctus longipes</i>	12	<i>S. sanniola</i>	23
<i>L. serratus</i>	12	<i>Smilisca baudinii</i>	5
<i>Lampropeltis triangulum</i>	19	<i>S. cyanosticta</i>	5
<i>Lepidophyma flavimaculatum</i>	15	<i>Sphaerodactylus glaucus</i>	8
<i>L. mayae</i>	15	<i>S. lineolatus</i>	9
<i>Leptodactylus labialis</i>	2	<i>Sphenomorphus cherriei</i>	14
<i>L. melanonotus</i>	2	<i>Spilotes pullatus</i>	23
<i>Leptodeira frenata</i>	19	<i>Staurotypus triporcatus</i>	7
<i>L. septentrionalis</i>	20	<i>Stenorrhina degenhardti</i>	23
<i>Leptophis ahaetulla</i>	20	<i>S. freminvillei</i>	23
<i>L. mexicanus</i>	20	<i>Symphimus mayae</i>	23
<i>Leptotyphlops phenops</i>	15	<i>Syrrhophus leprus</i>	3
<i>Mabuya brachypoda</i>	13	<i>Tantilla canula</i>	23
<i>Masticophis mentovarius</i>	20	<i>T. cuniculator</i>	24
<i>Mastigodryas melanolomus</i>	20	<i>T. moesta</i>	24
<i>Micrurus diastema</i>	25	<i>T. schistosa</i>	24
<i>M. hippocrepis</i>	25	<i>Tantillita lintoni</i>	24
<i>M. nigrocinctus</i>	26	<i>Terrapene mexicana</i>	8
<i>Natrix rhombifera</i>	20	<i>Thamnophis marcianus</i>	24
<i>Ninia diademata</i>	20	<i>T. proximus</i>	24
<i>N. sebae</i>	20	<i>Thecadactylus rapicauda</i>	9
<i>Oedipina elongata</i>	1	<i>Tretanorhinus nigroluteus</i>	25
<i>Oxybelis aeneus</i>	21	<i>Triprion petasatus</i>	5
<i>O. fulgidus</i>	21	<i>Tropidodipsus fasciata</i>	25
<i>Oxyrhopus petola</i>	21	<i>T. sartorii</i>	25
<i>Physalaemus pustulosus</i>	3	<i>Typhlops microstomus</i>	16
		<i>Xenodon rabdocephalus</i>	25

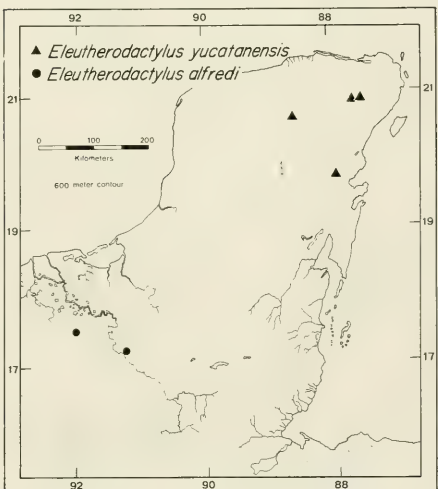
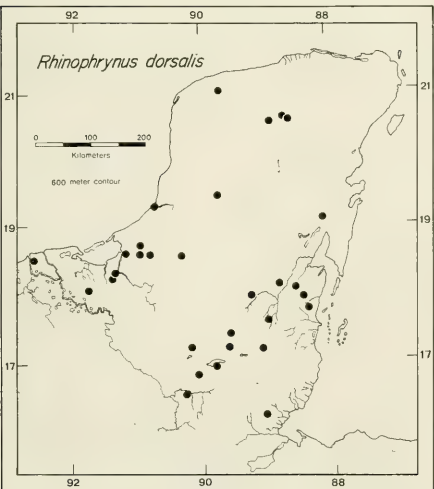
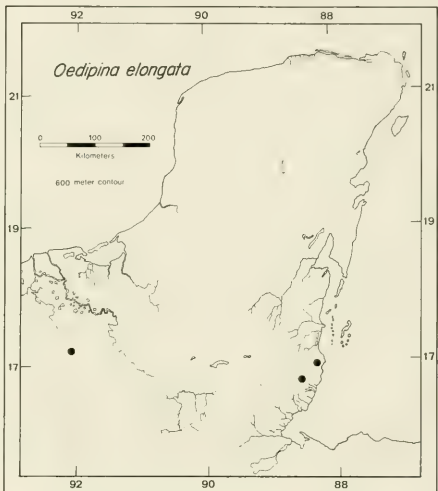
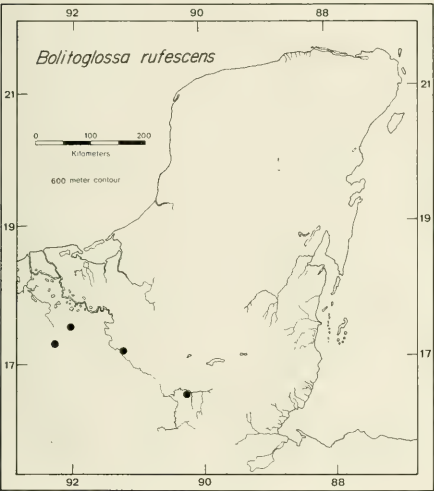
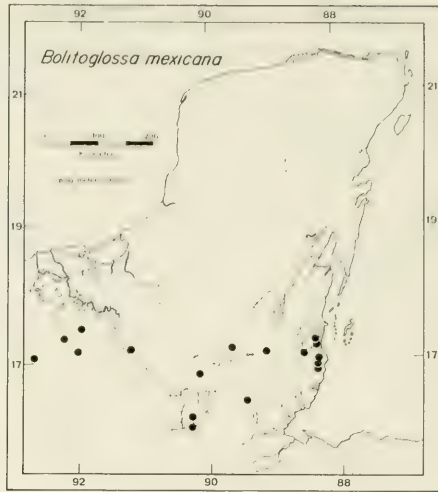
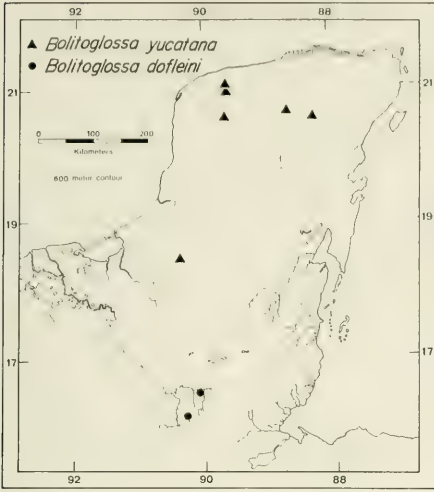


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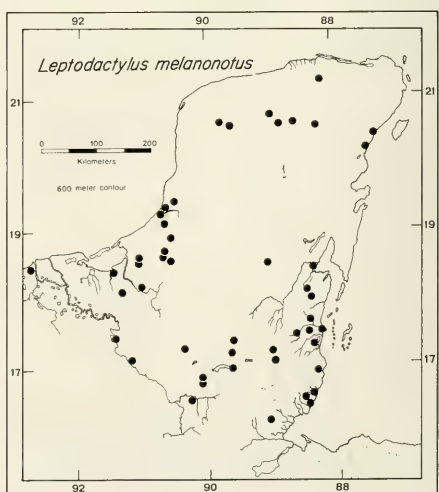
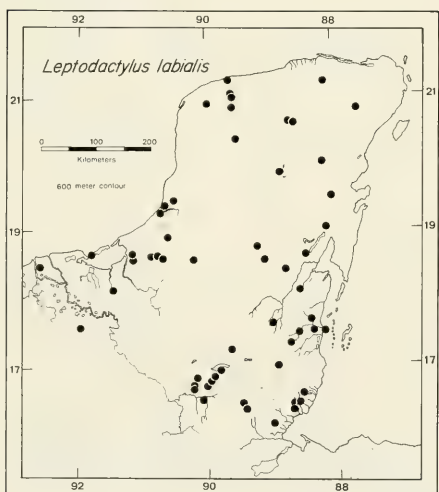
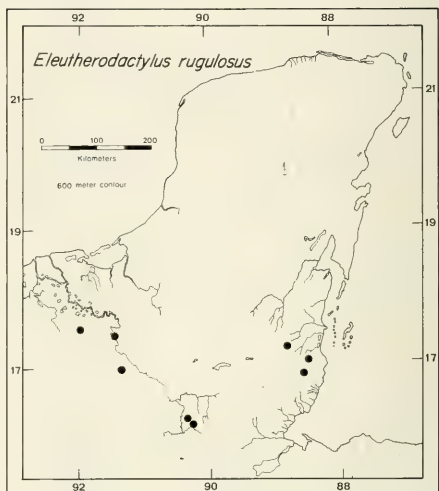
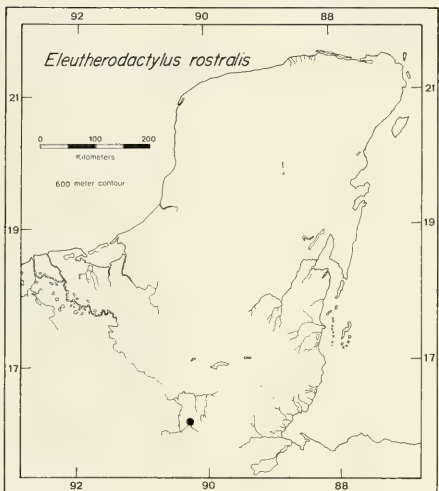
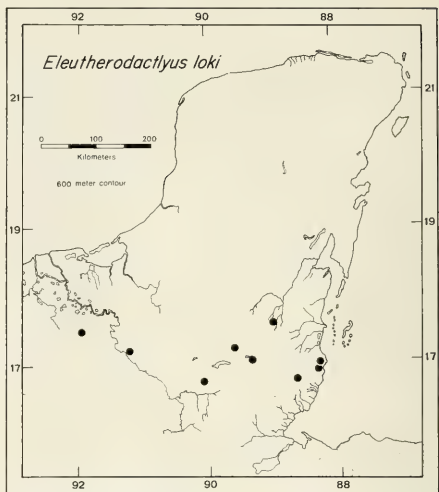
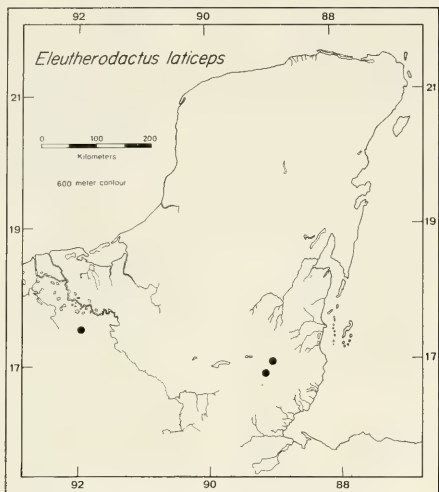


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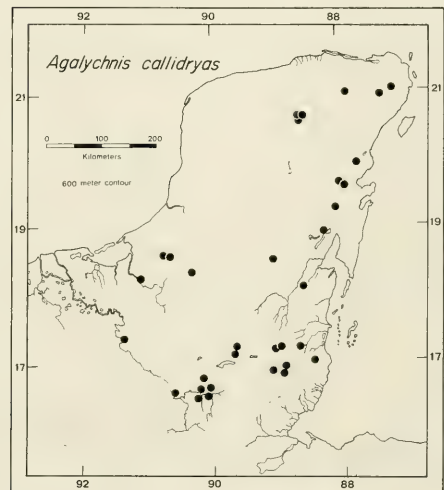
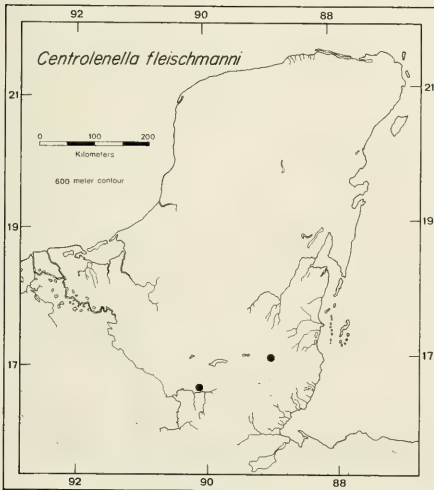
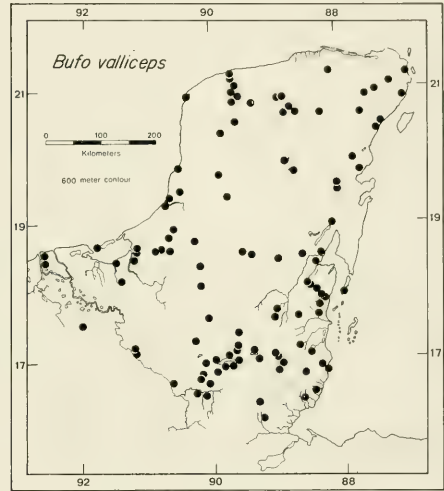
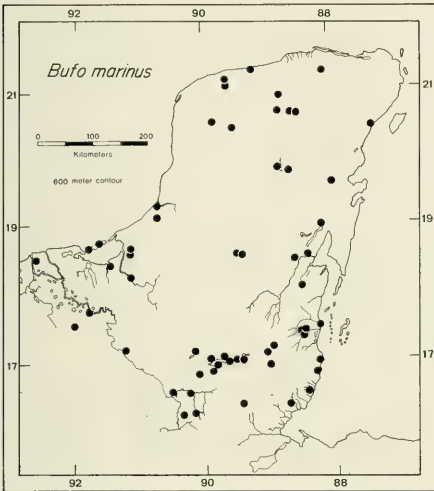
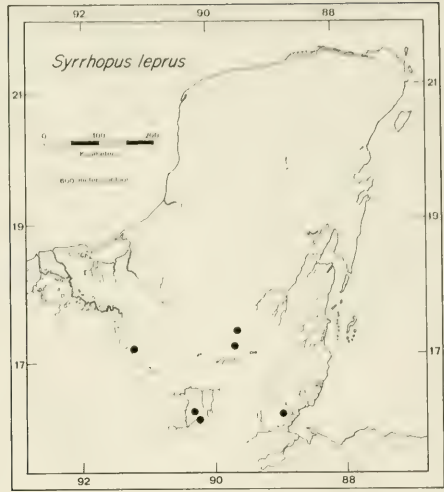
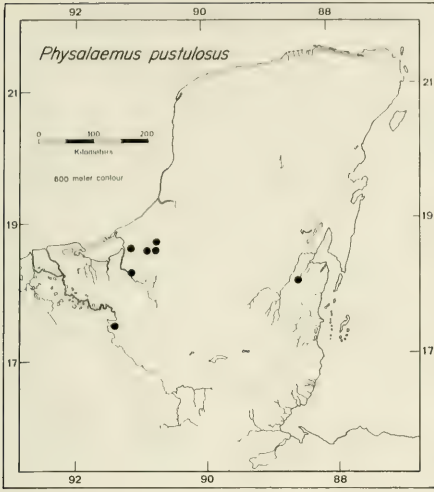


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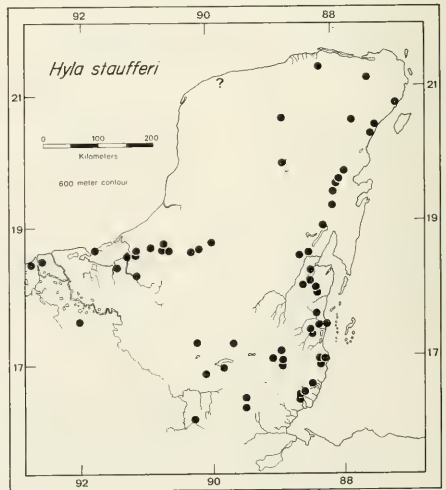
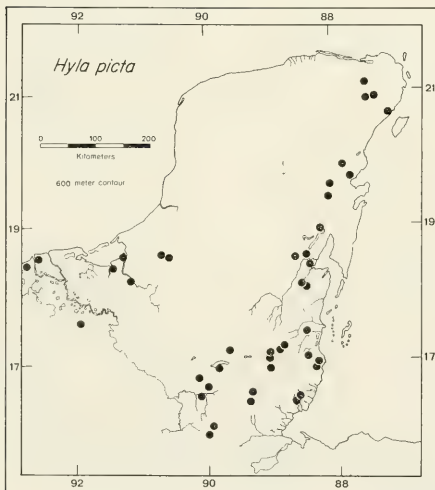
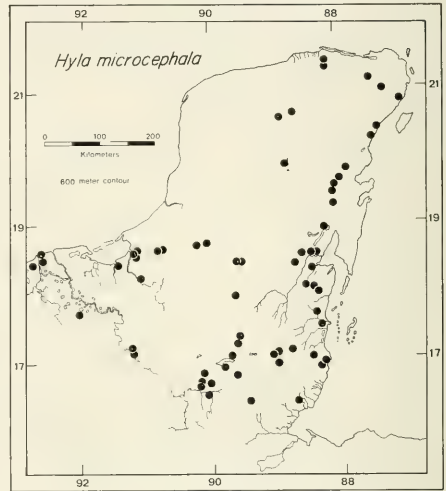
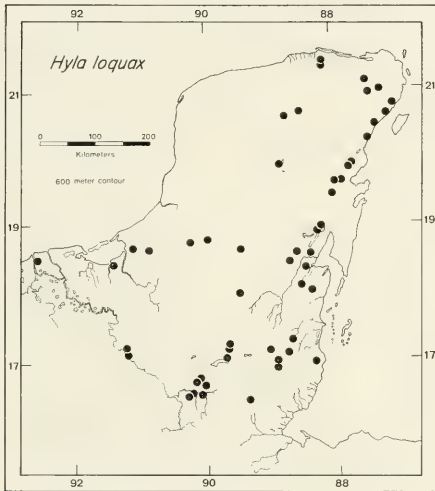
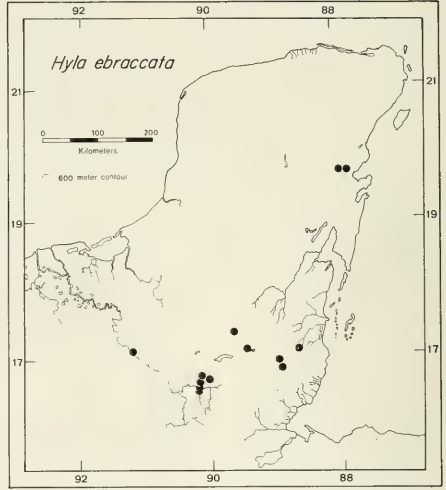
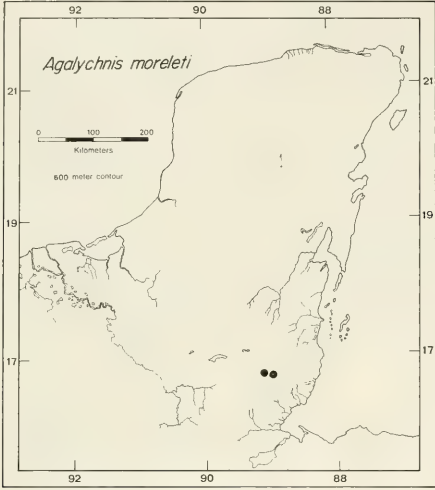


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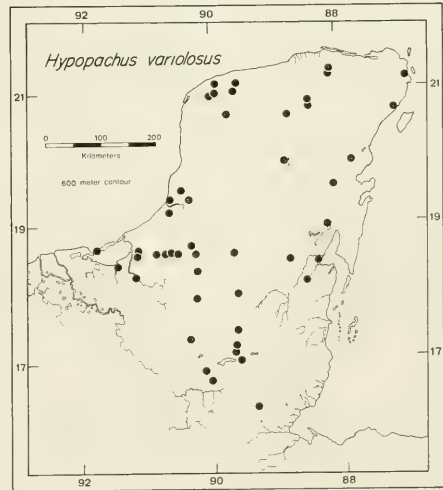
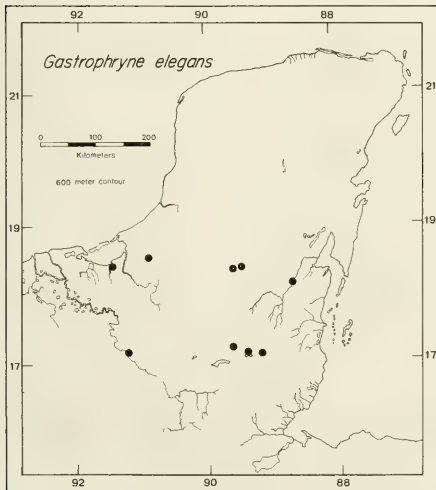
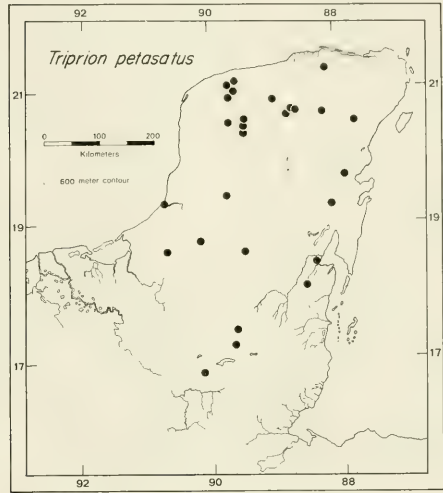
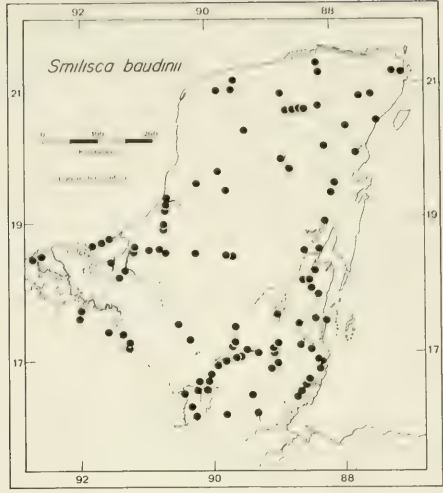
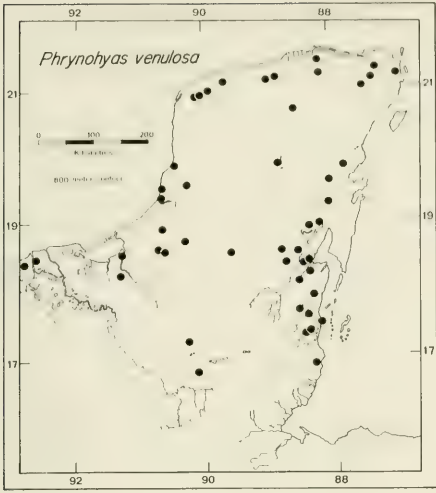


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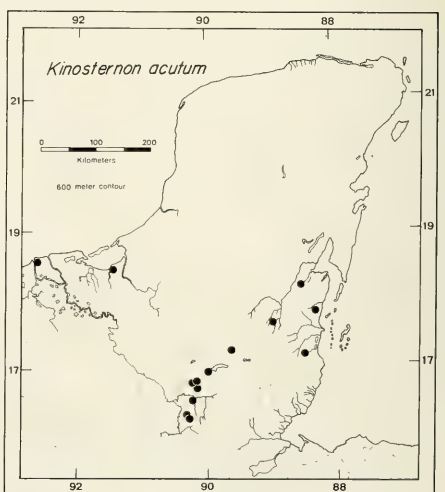
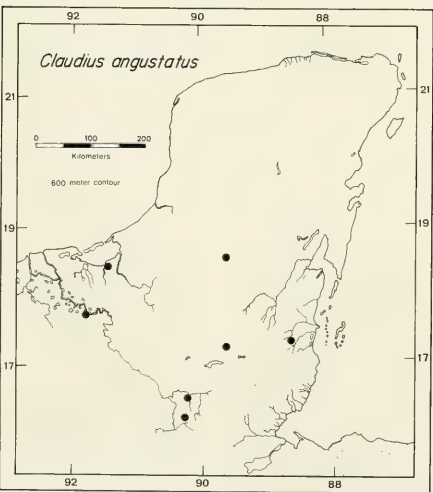
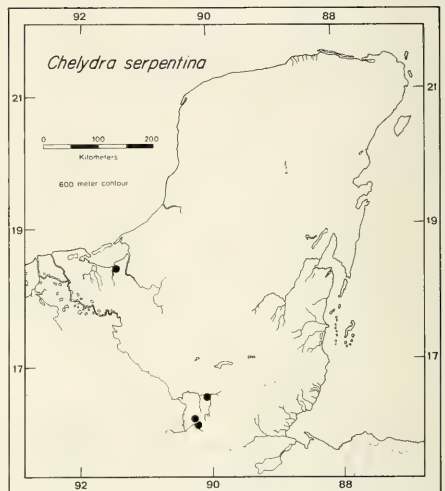
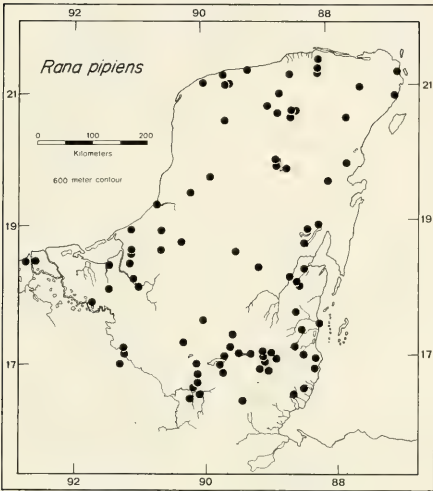
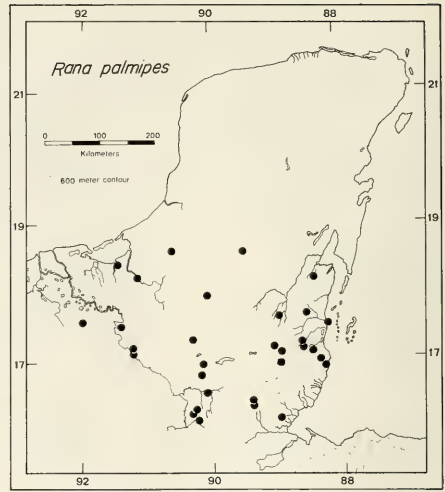
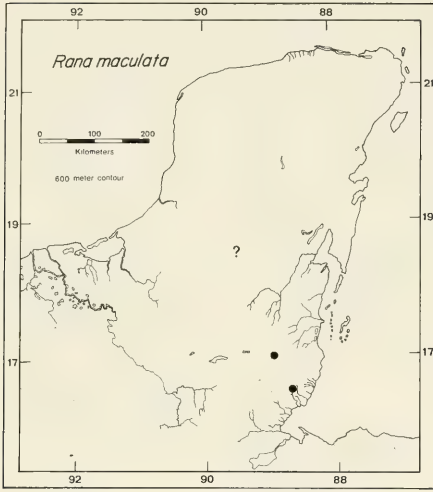


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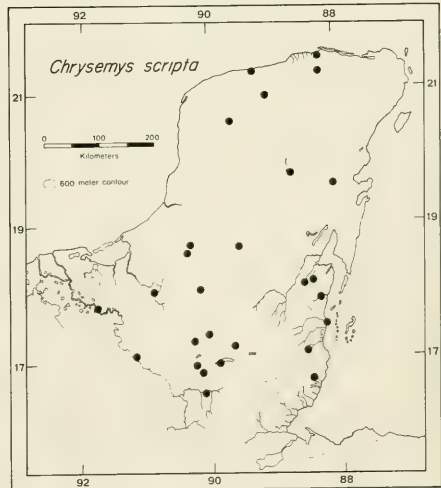
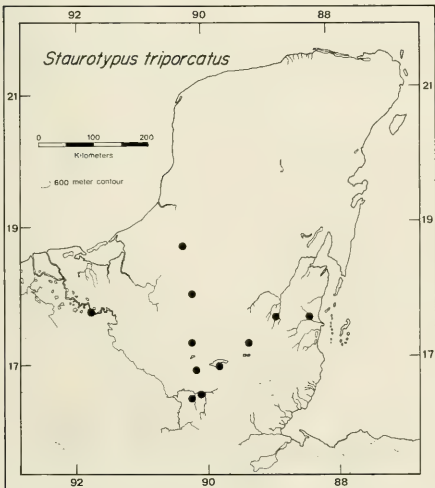
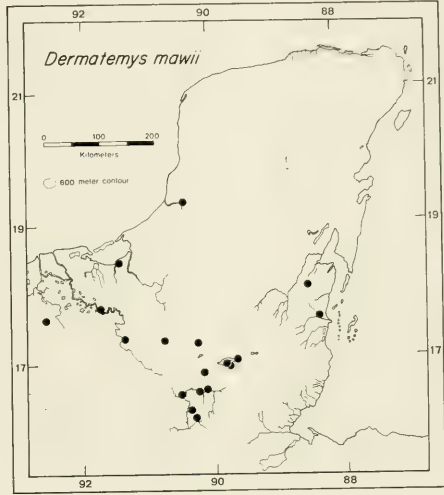
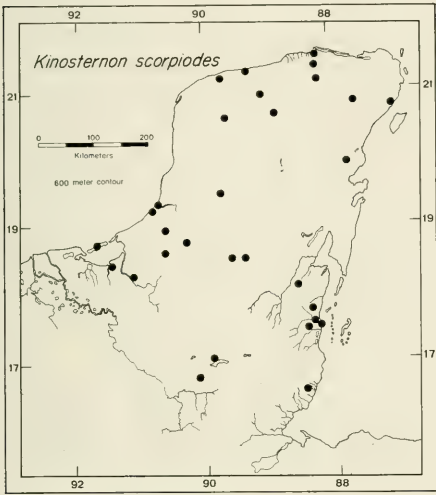
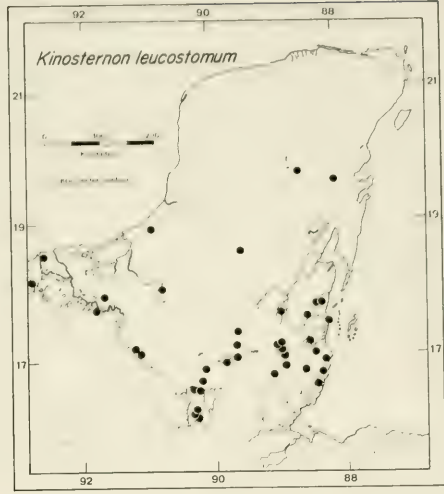
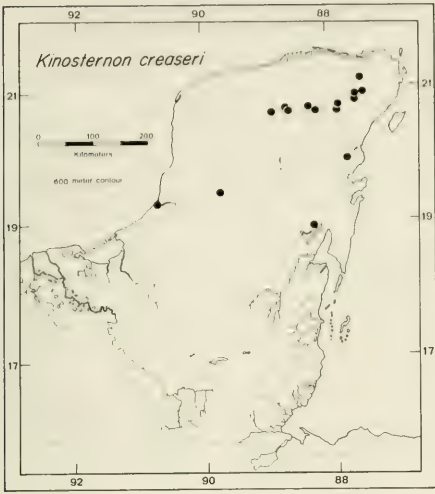


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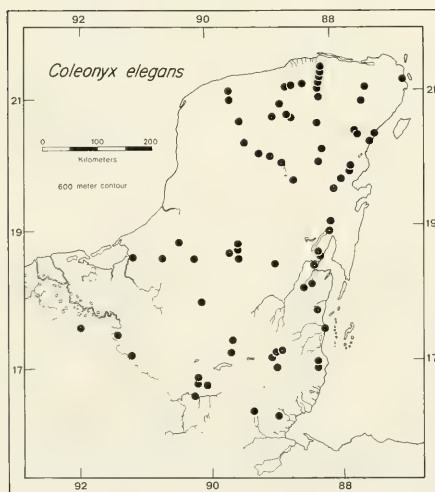
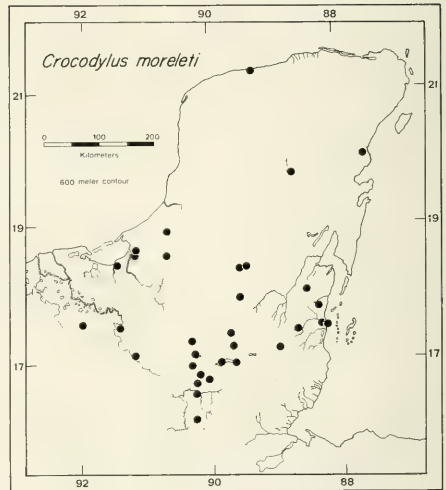
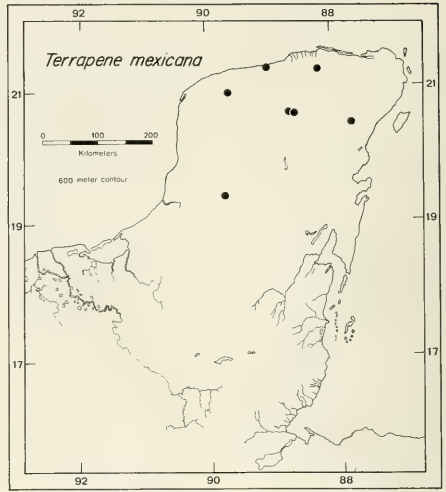
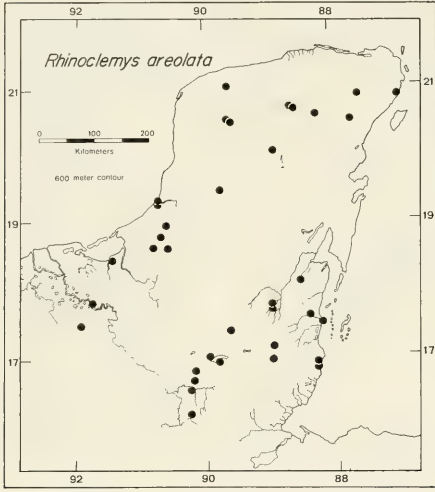


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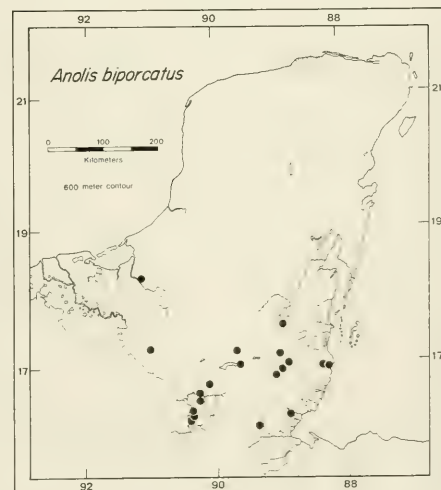
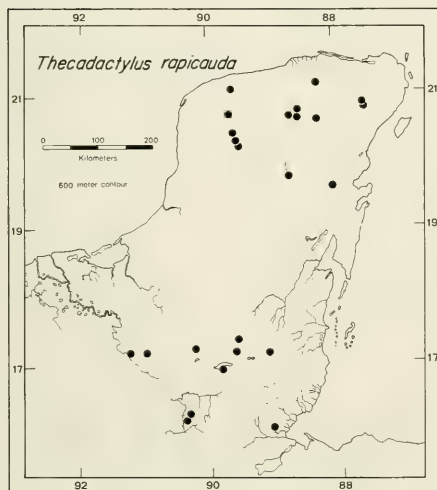
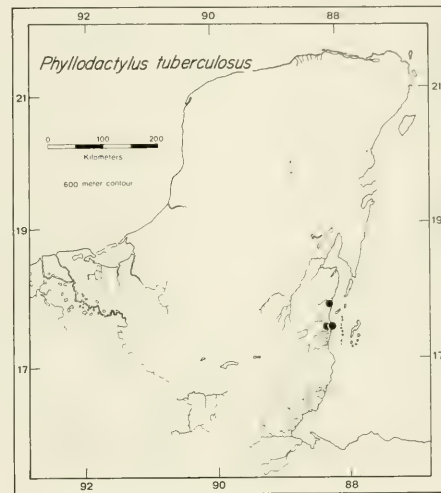
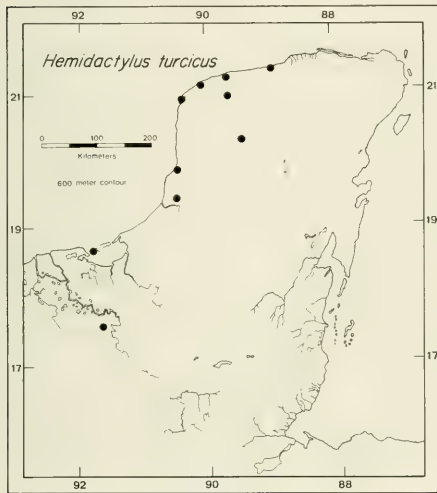
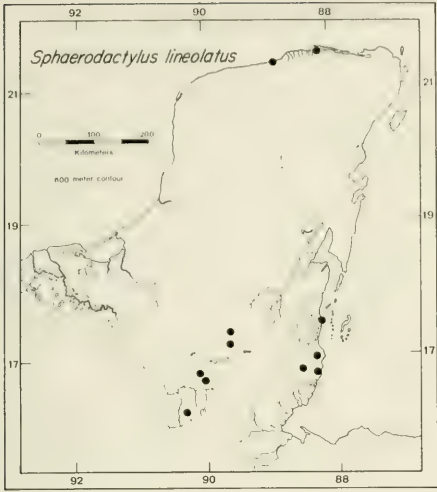
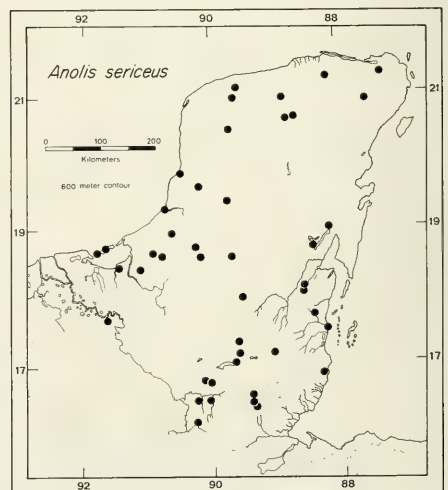
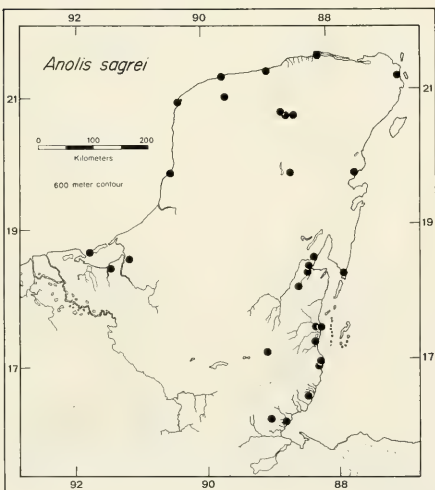
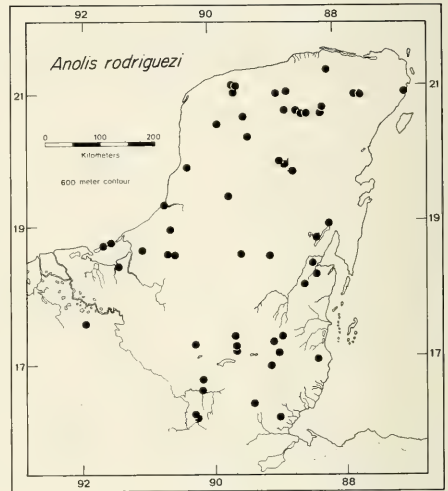
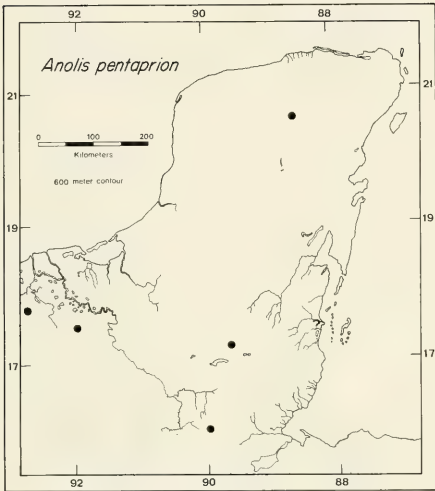
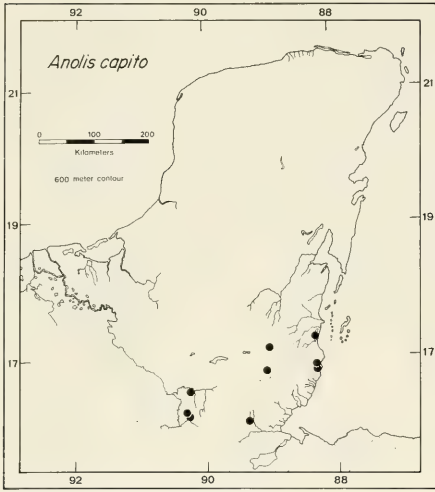
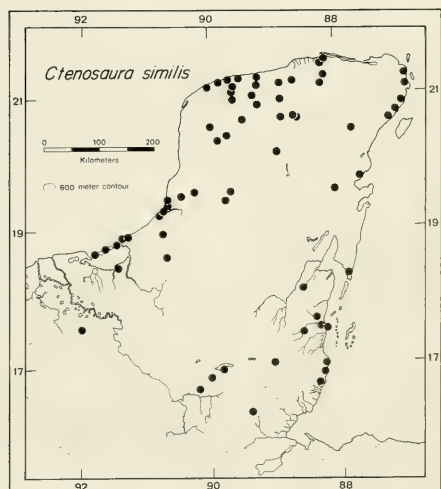
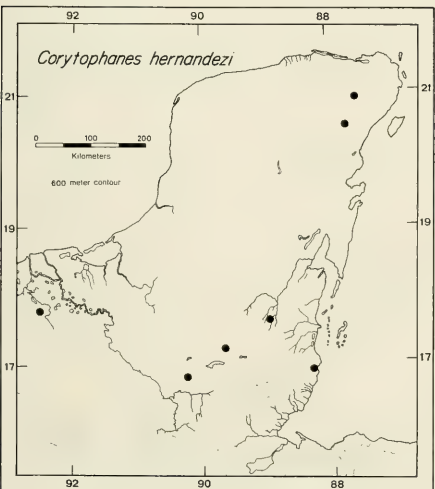
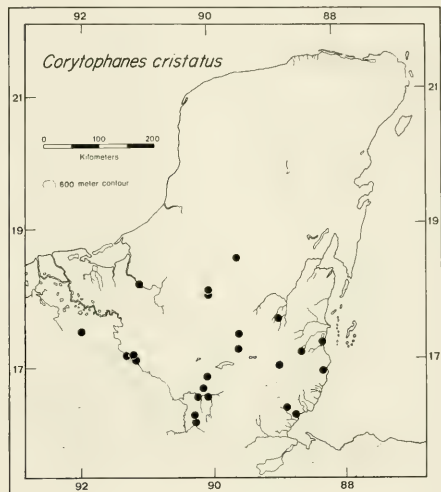
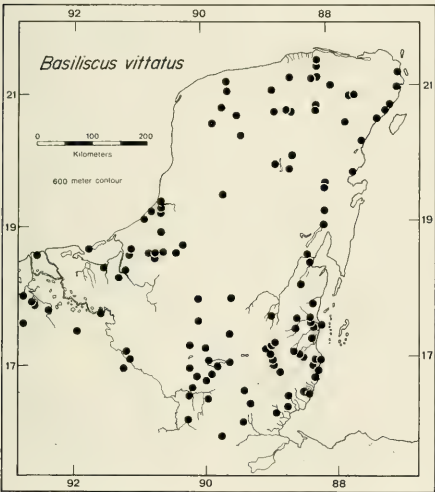
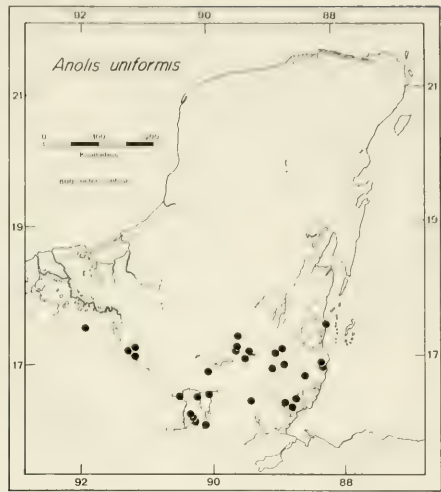
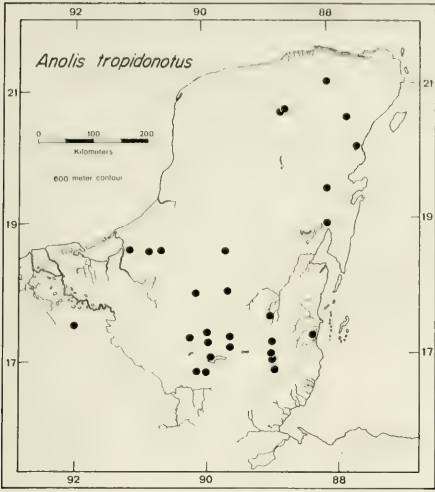


PLATE 9





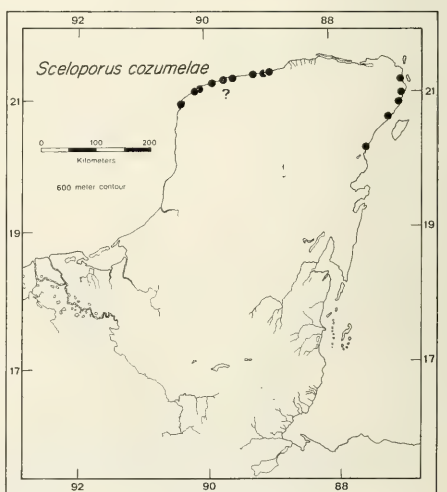
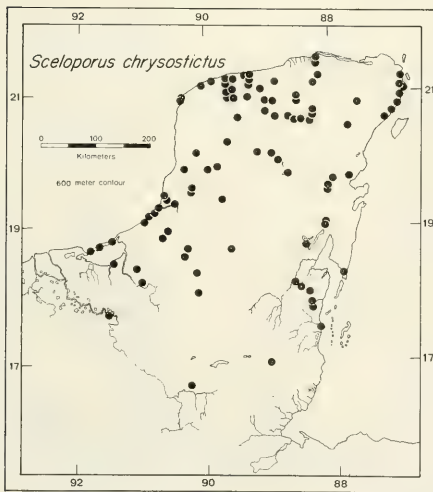
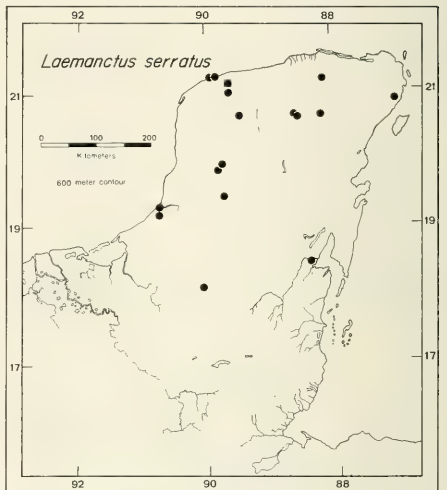
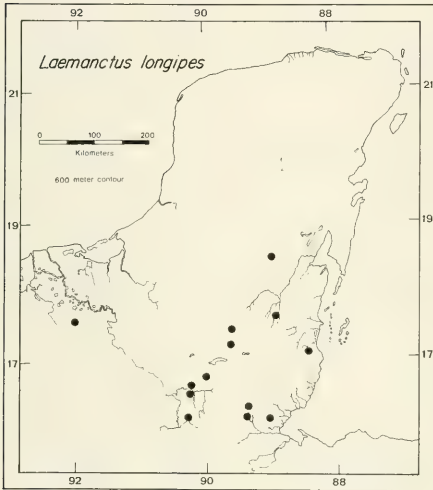
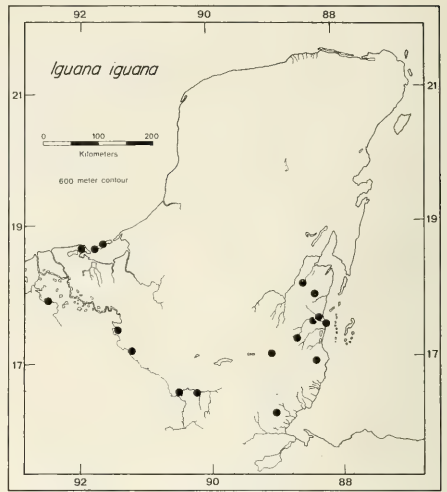
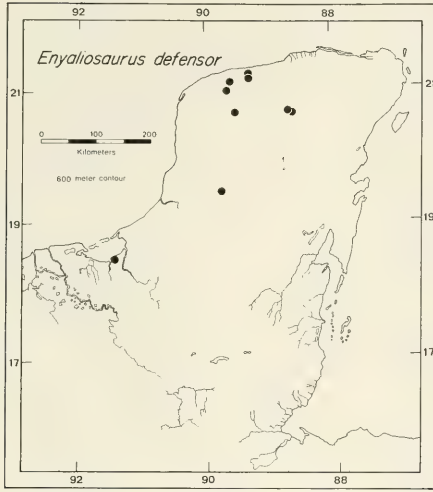


PLATE 12

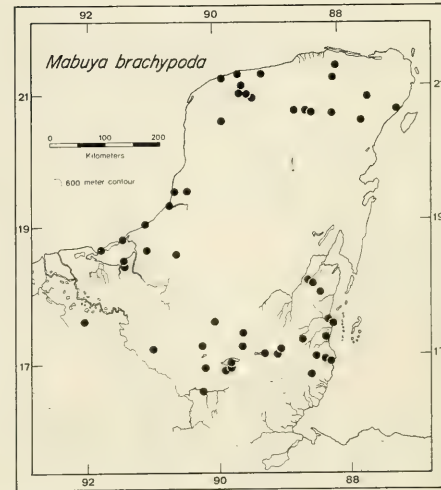
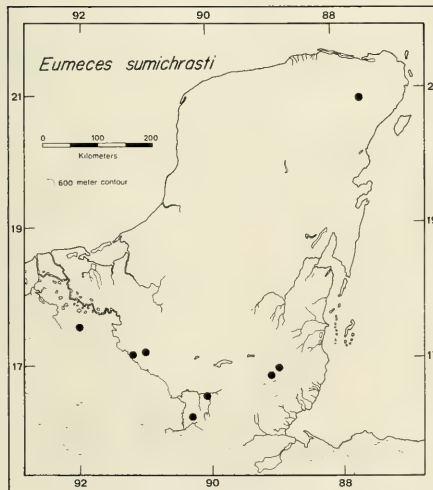
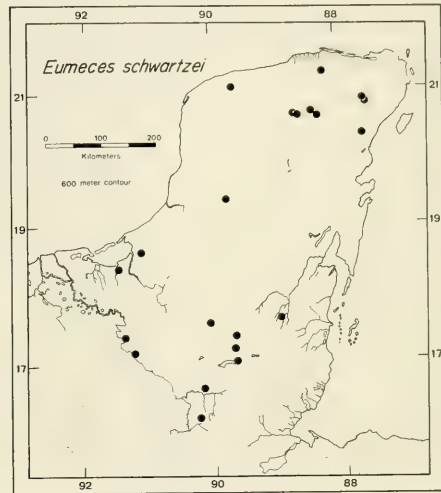
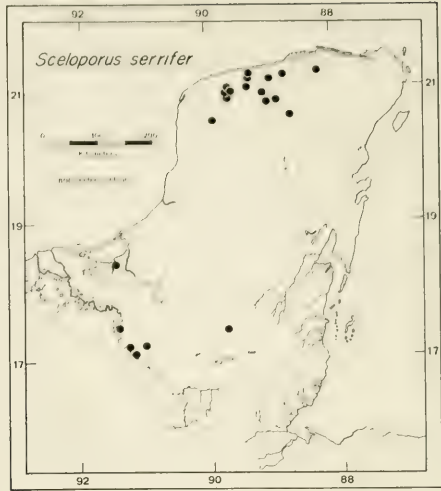
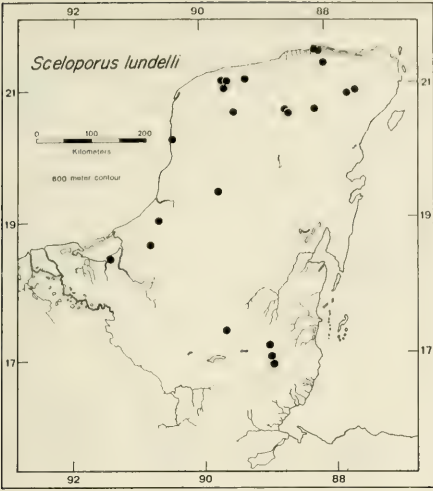
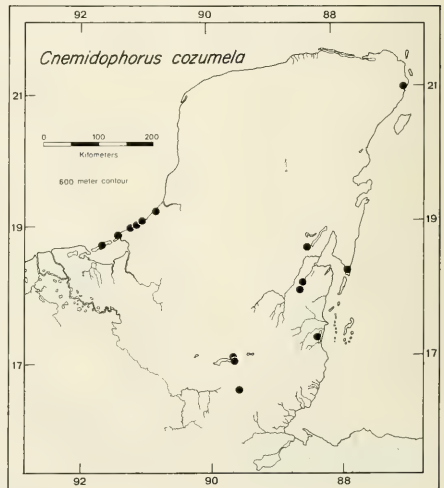
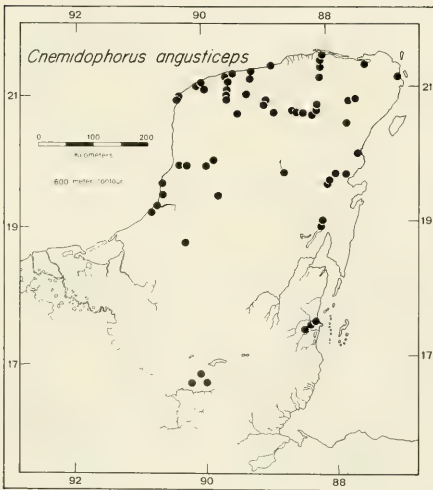
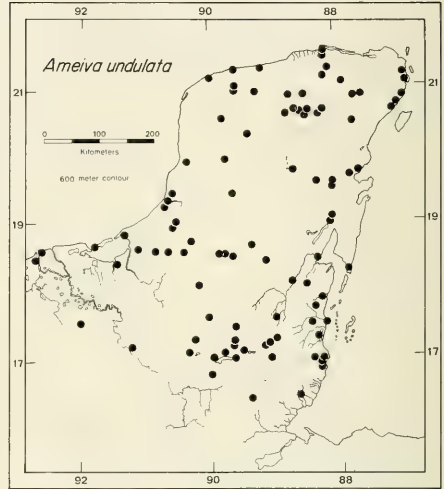
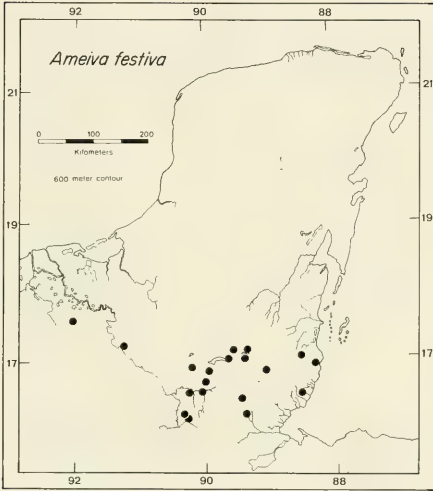
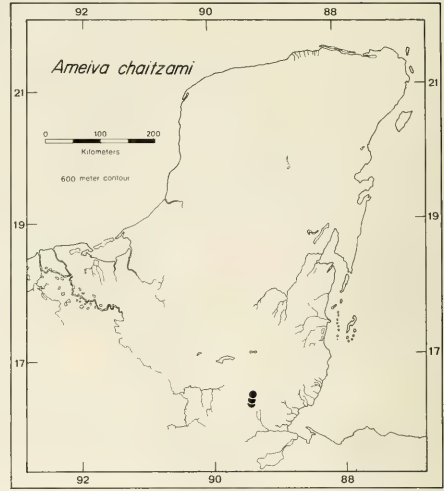
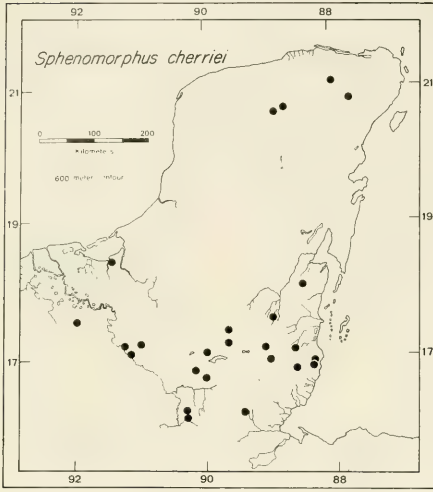
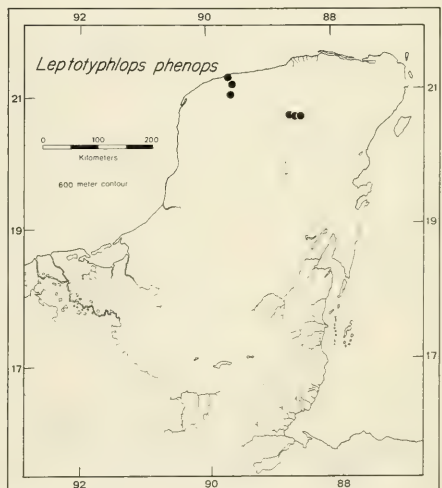
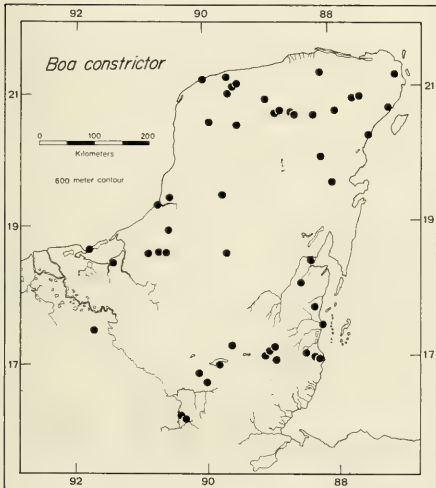
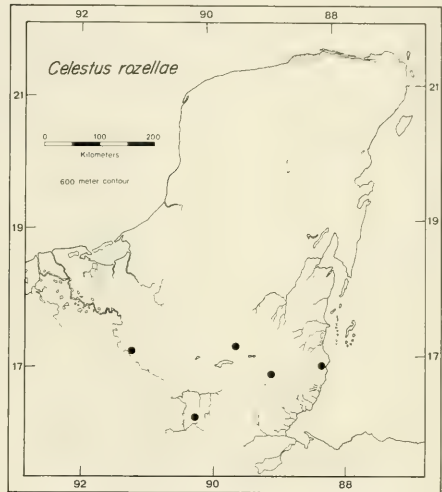
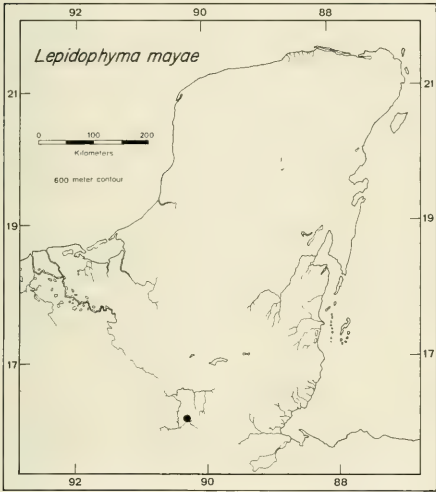
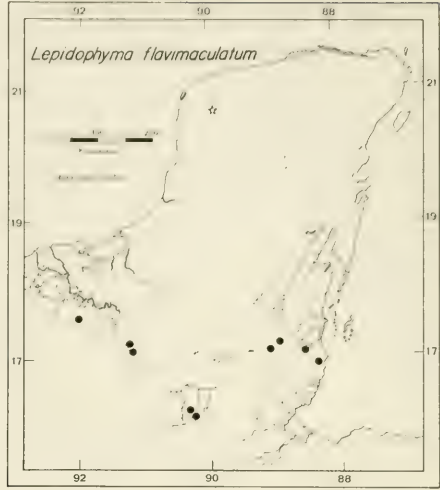
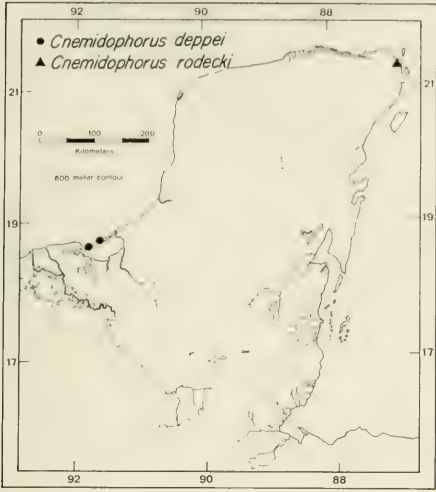
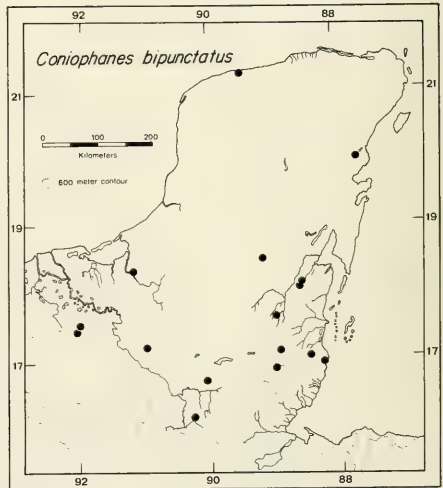
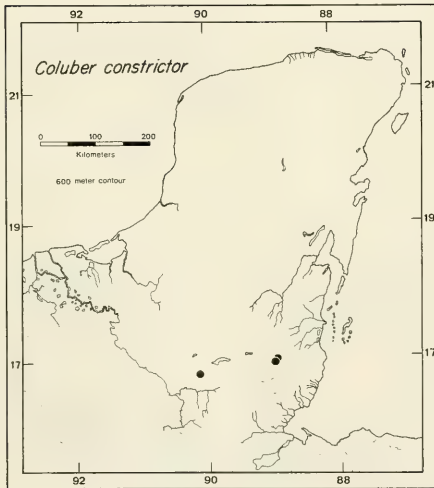
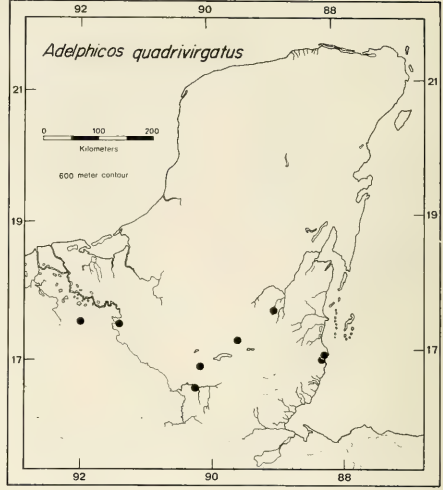
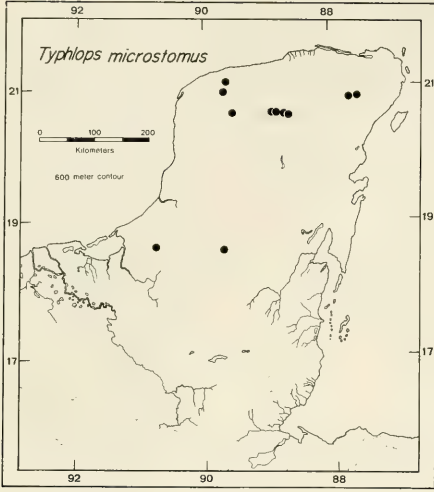


PLATE 13







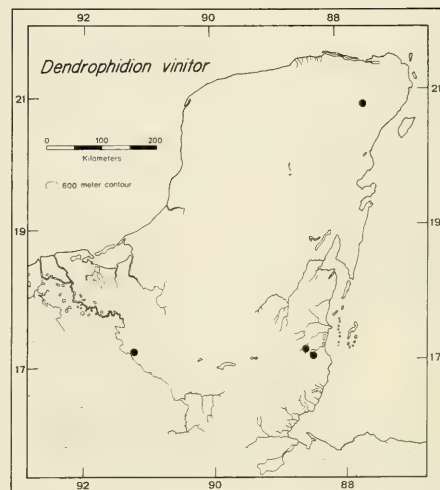
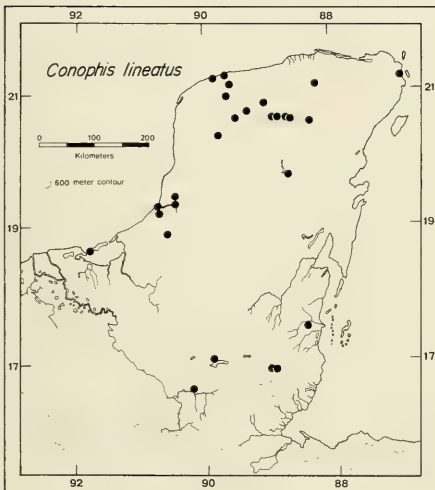
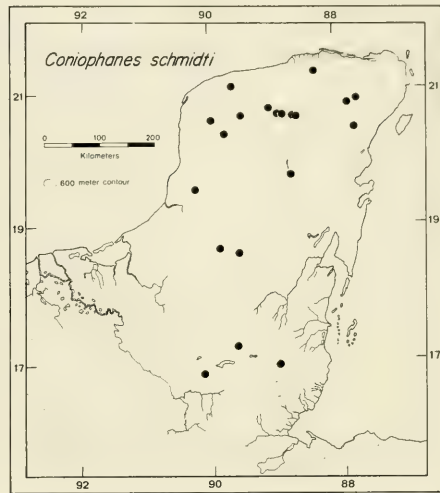
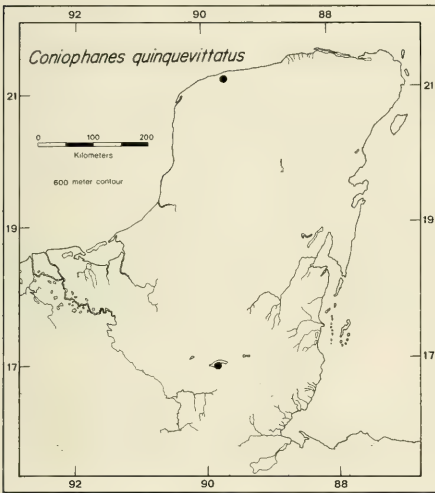
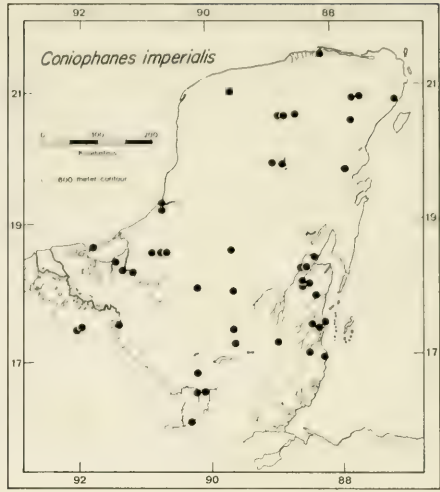
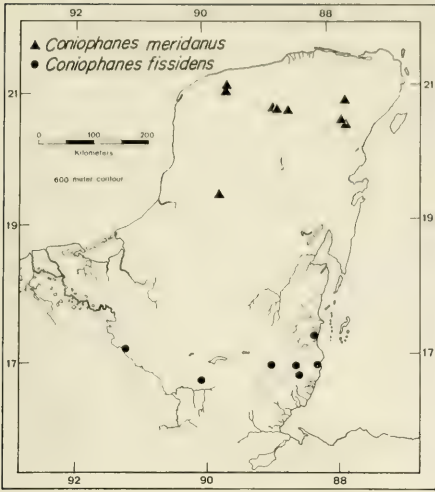


PLATE 17

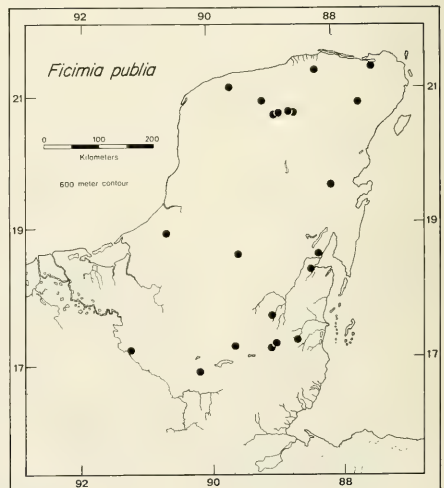
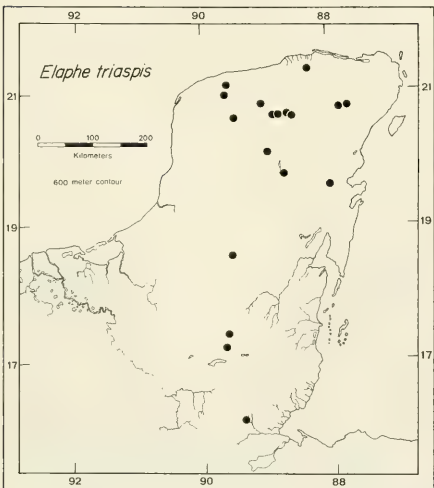
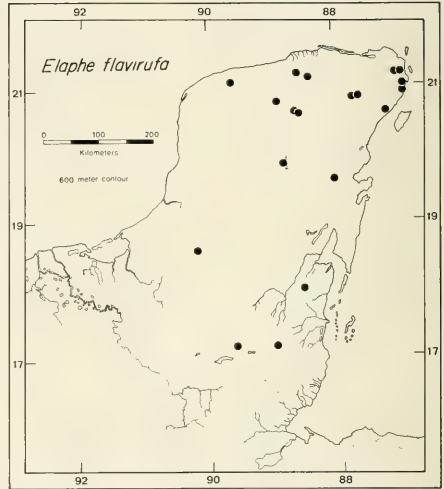
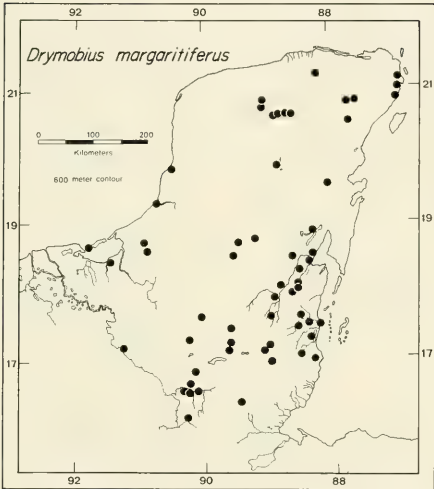
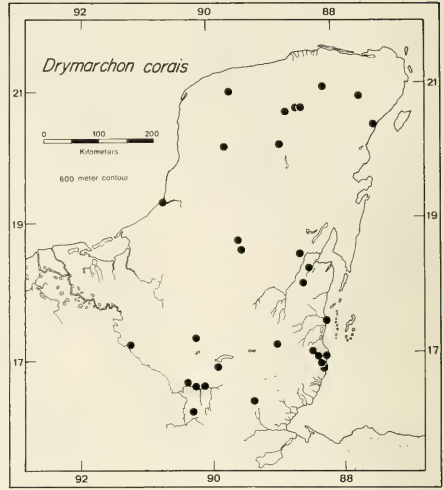
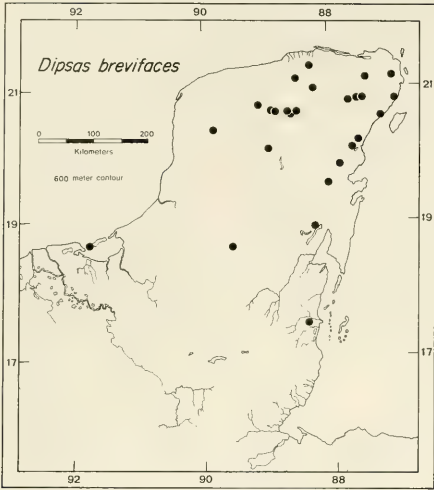


PLATE 18

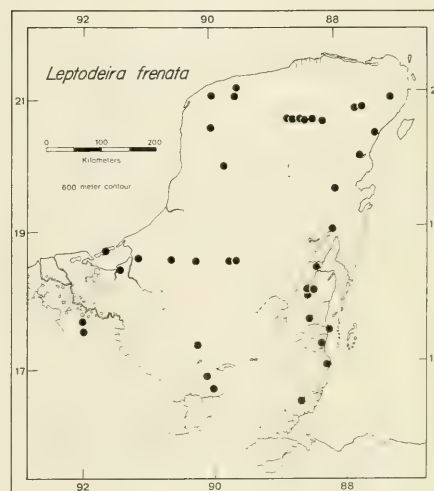
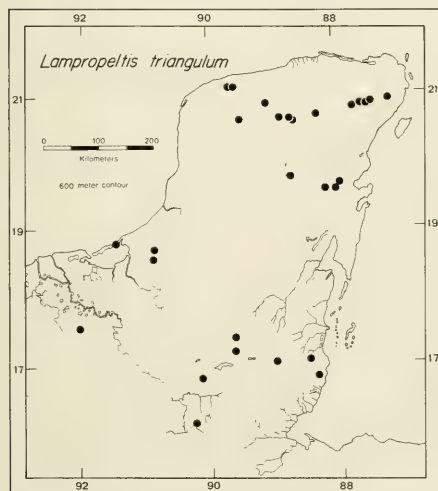
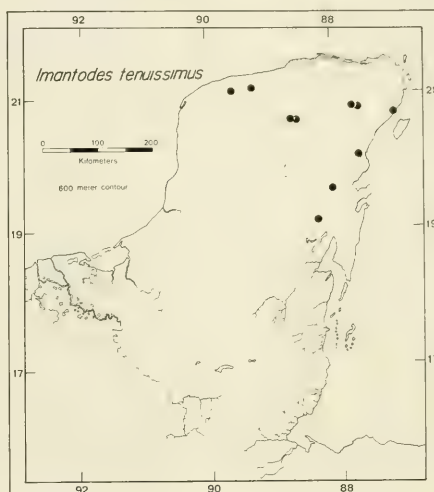
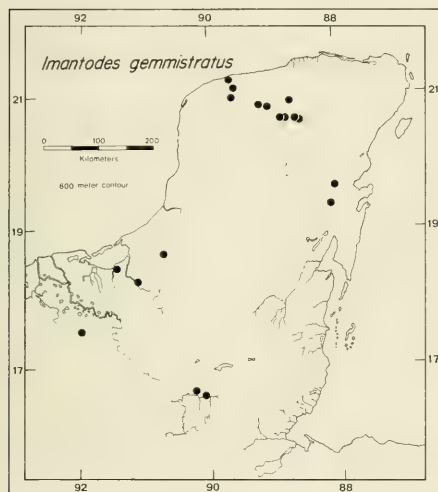
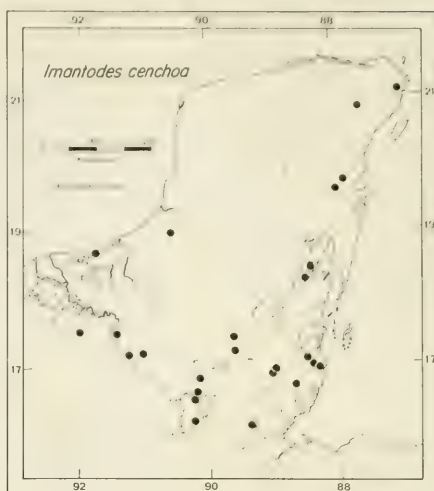
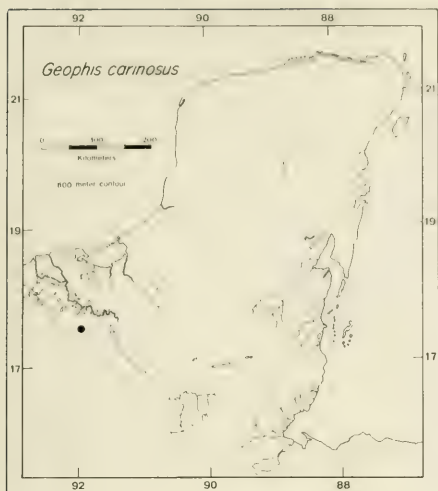
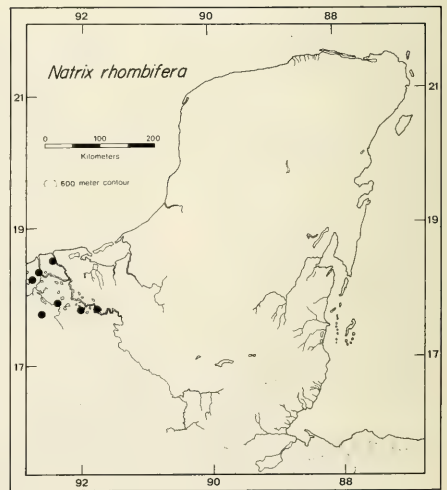
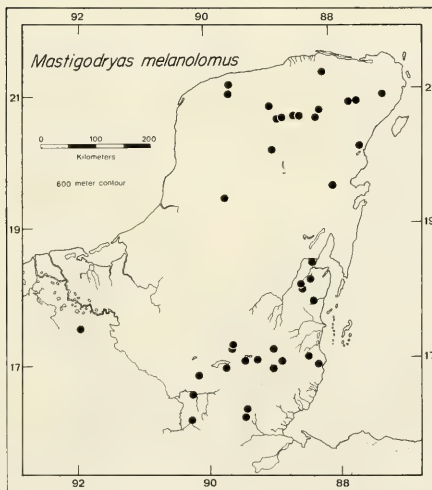
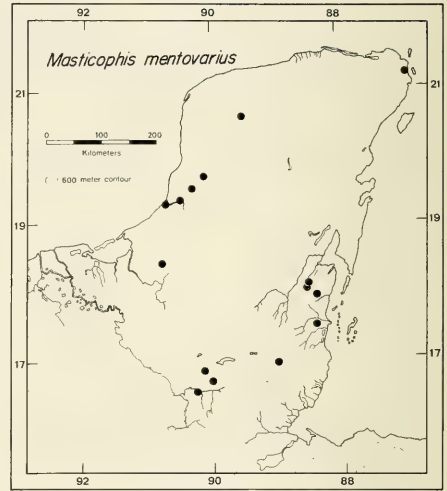
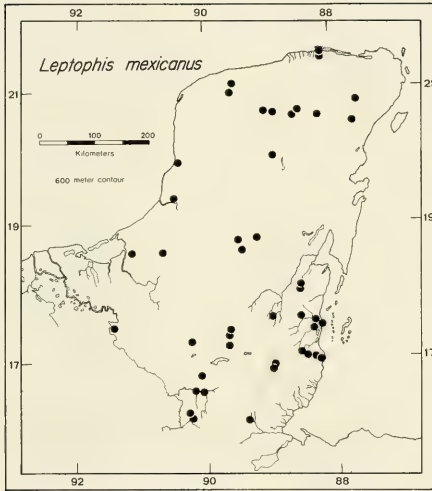
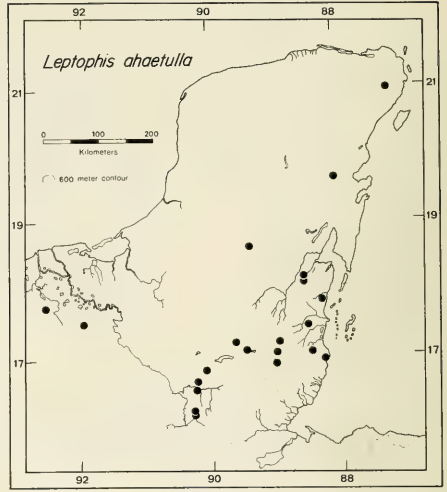
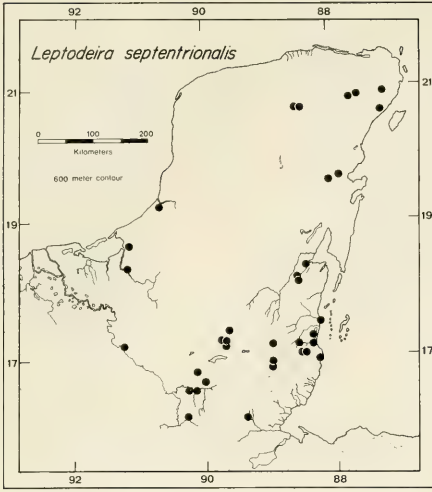
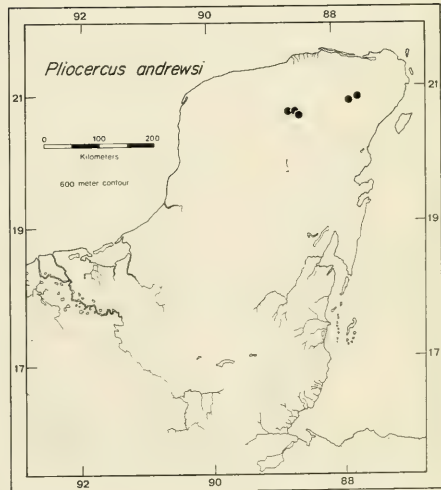
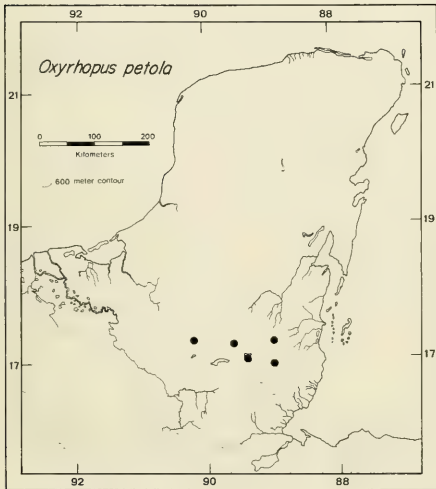
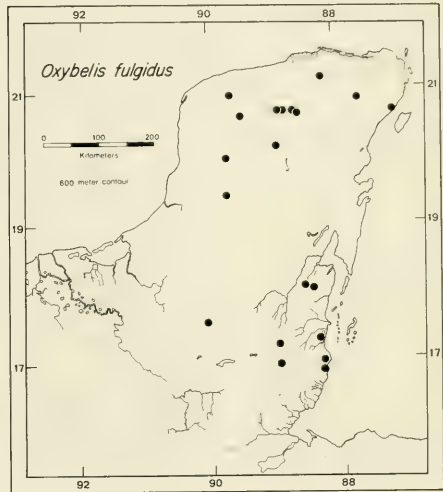
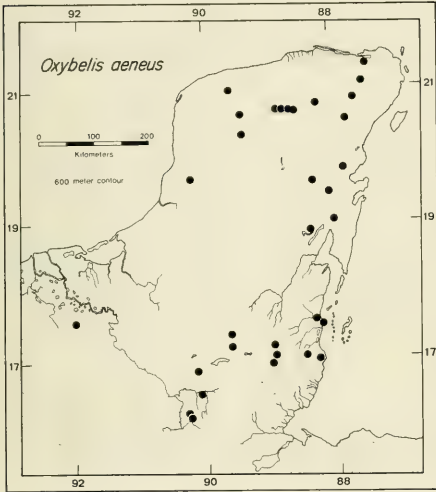
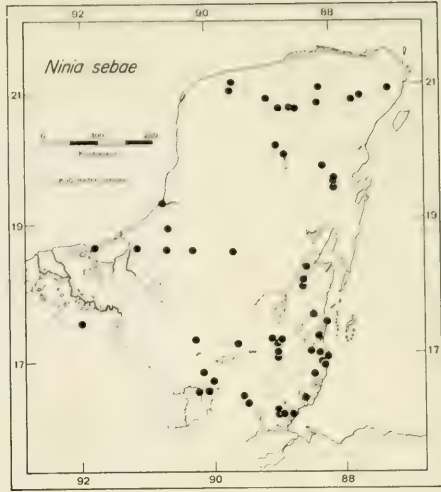
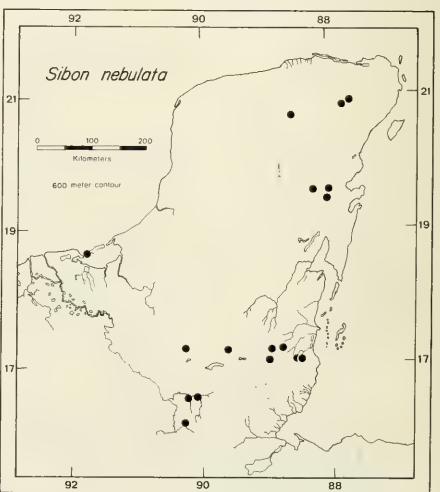
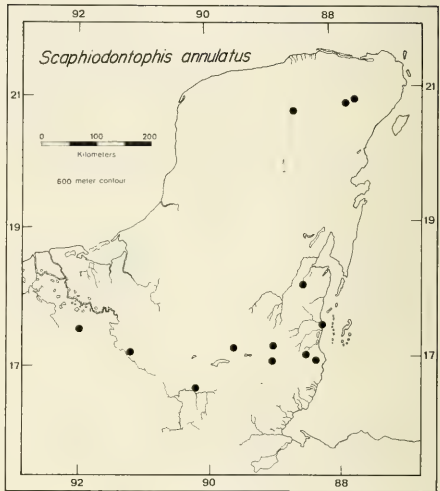
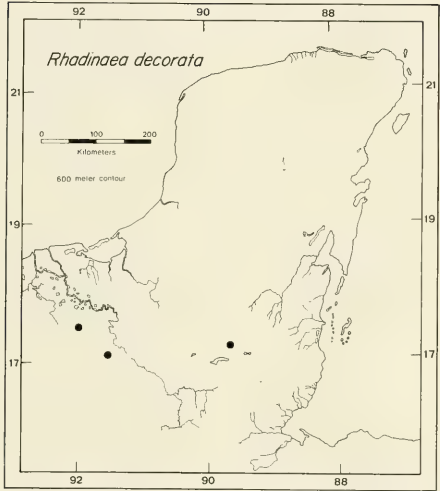
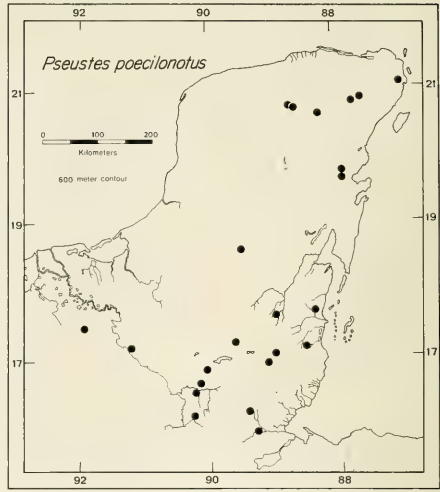
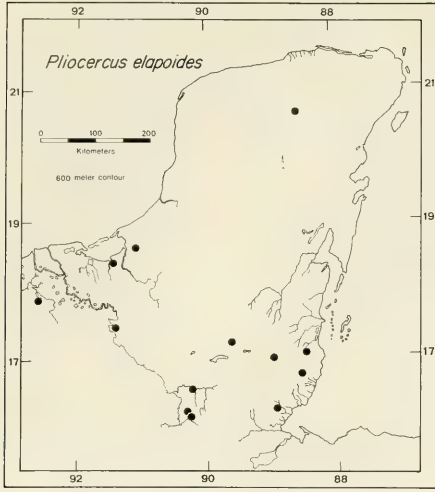
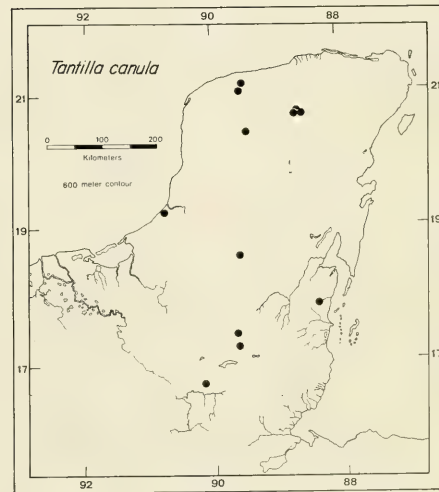
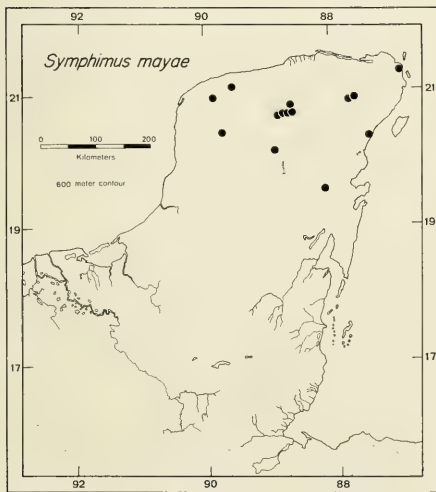
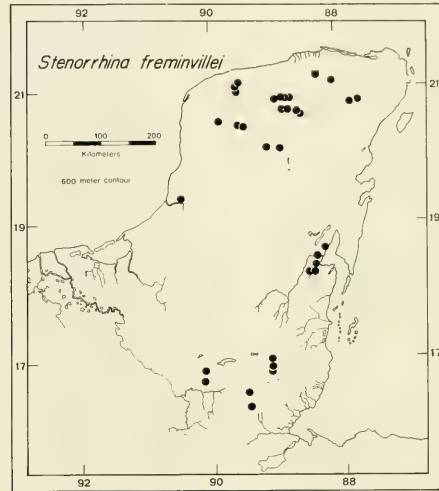
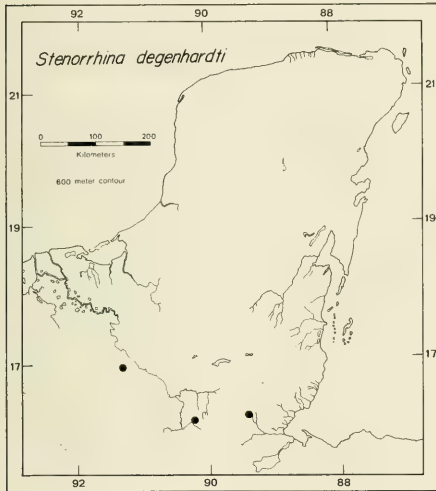
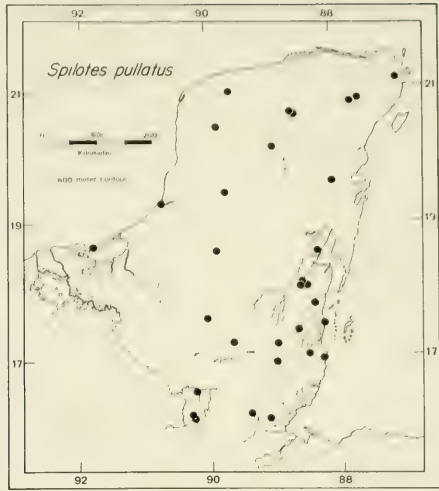


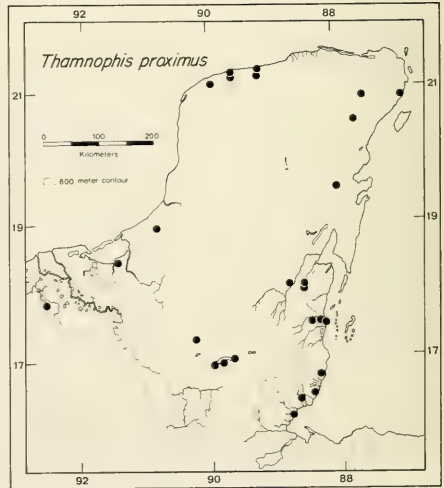
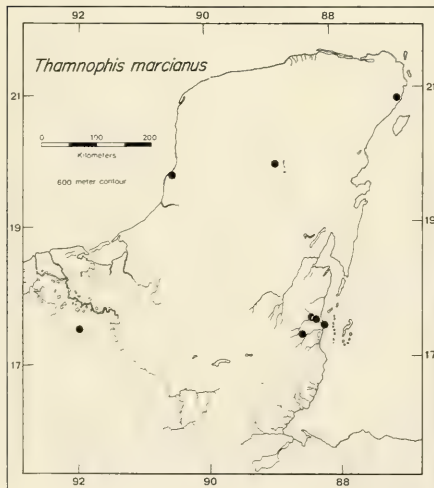
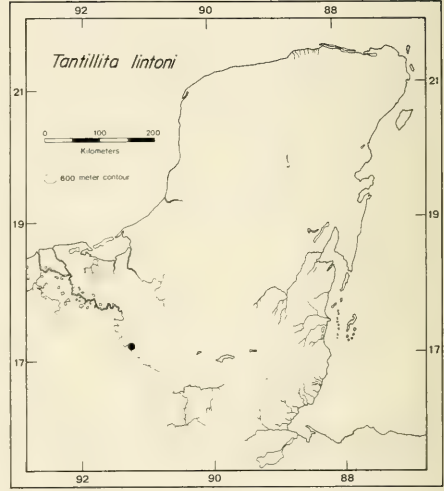
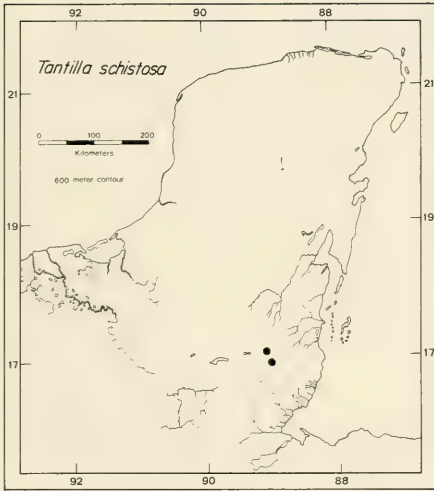
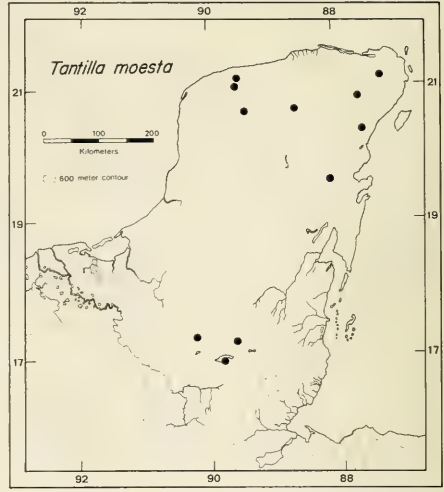
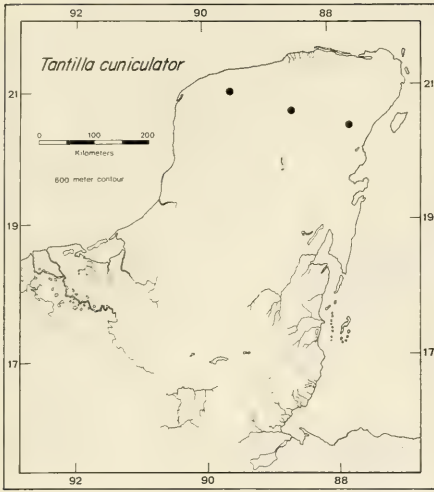
PLATE 19

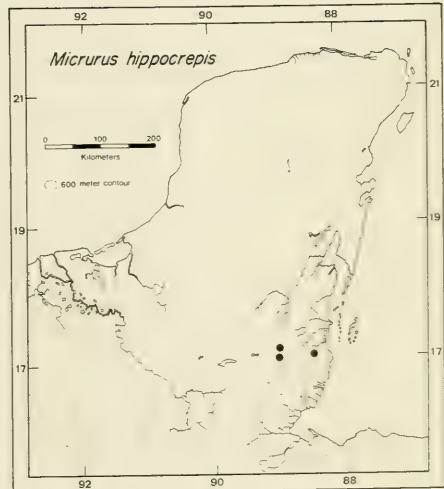
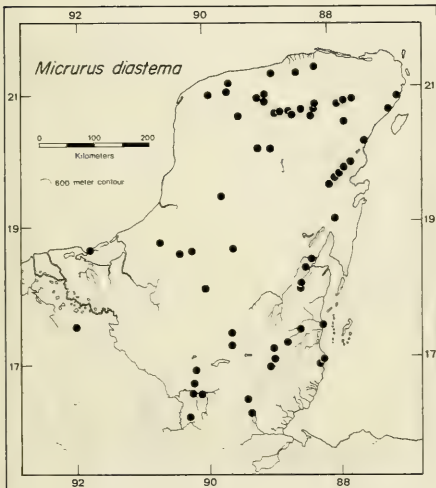
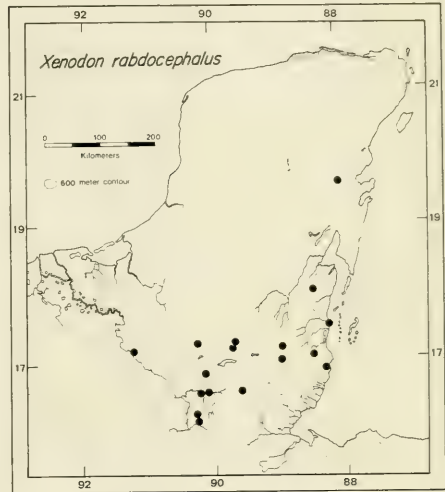
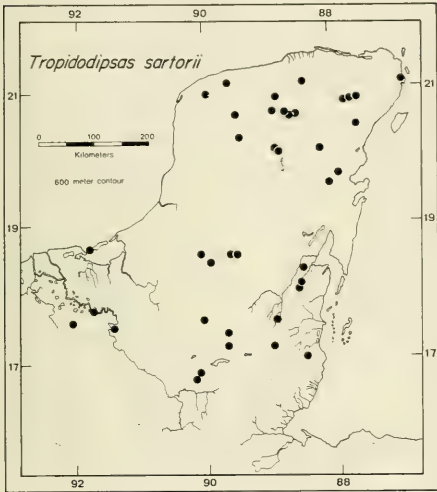
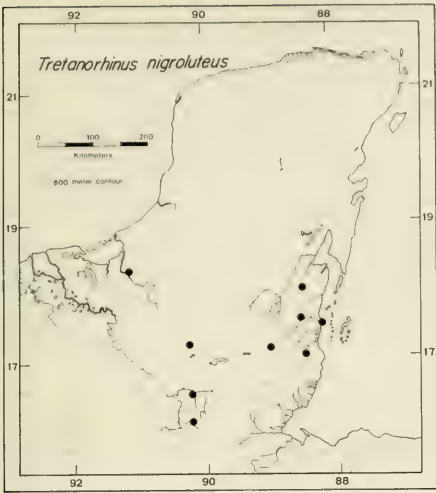


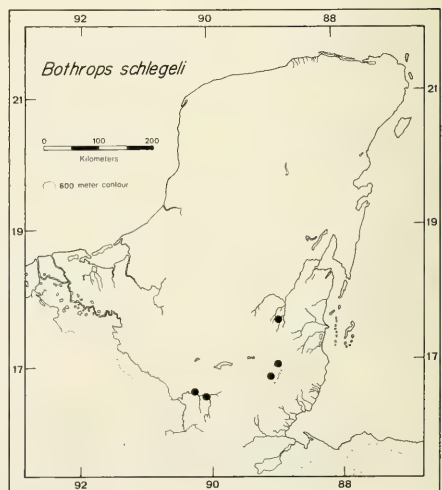
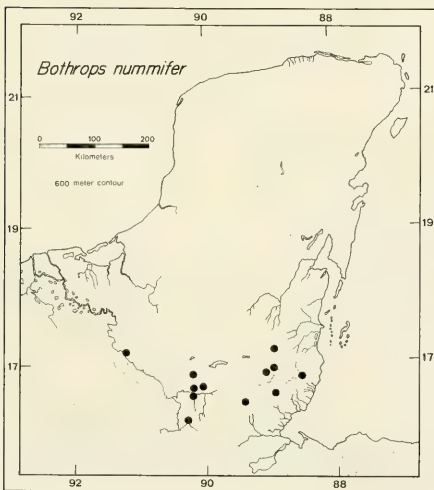
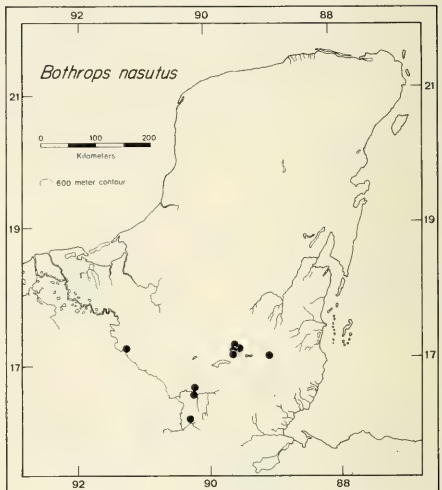
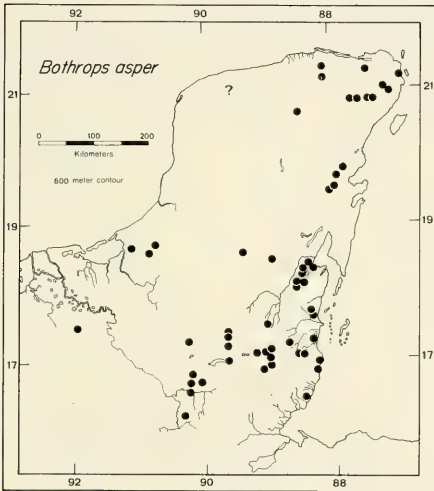
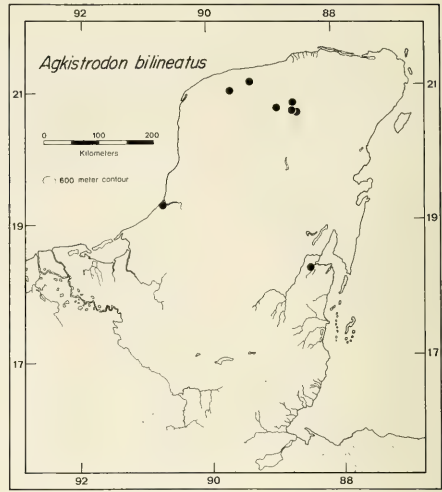
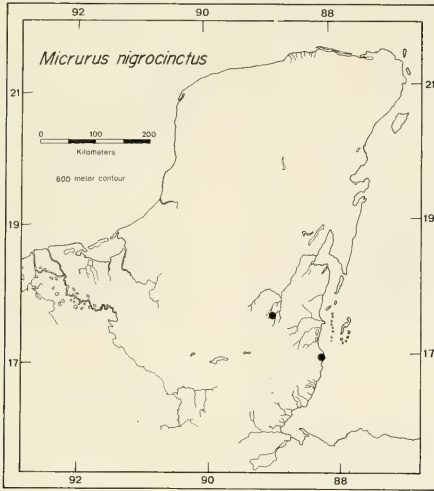


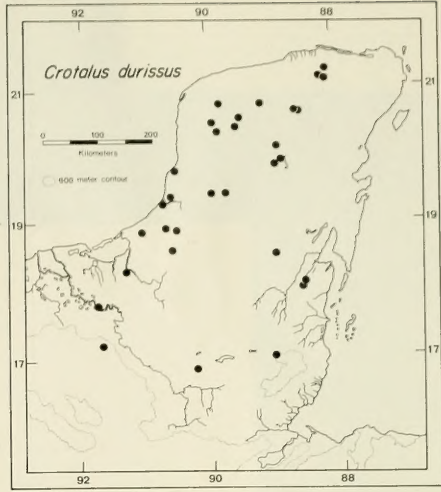
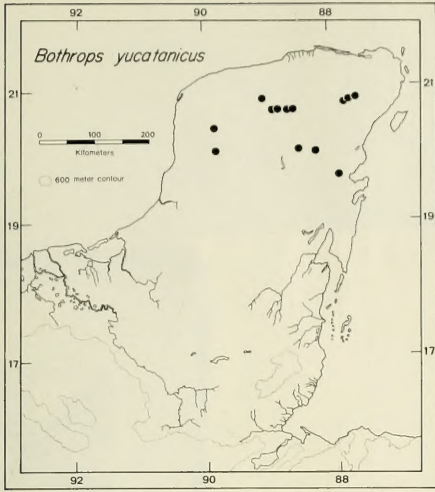












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