REPRINTED FROM ZOOGEOGRAPHY IN THE CARIBBEAN, ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA, SPECIAL PUBLICATION 13, 1978, PAGES 53-97.

ZOOGEOGRAPHY OF ANTILLEAN BATS

ROBERT J. BAKER

Department of Biological Sciences and The Museum
Texas Tech University
Lubbock, Texas 79409

AND

HUGH H. GENOWAYS

Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, Pennsylvania 15213

ABSTRACT. — Analysis of the bat fauna of the Antillean Islands suggest that the most probable source of invasion of the islands by bats is by overwater dispersal. The bat fauna of the Greater Antilles is unique, a percentage of endemism on each island being over 50 percent except for the Virgin Islands which has 33 percent endemics.

The richest bat fauna in the Antilles is on Cuba (32 species) followed by Jamaica (23 species) then Hispaniola (17 species) and Puerto Rico (16 species). The number of species found on Cuba is probably the result of the island's proximity to Central and North America and the ecological complexity of the island. Jamaica has a rich fauna because of its proximity to Central America and Cuba. The reduced fauna of Hispaniola (relative to Jamaica and Cuba) is probably because species have not reached this island with the frequency that they have reached Jamaica and Cuba (Hispaniola is as close to Cuba as is Jamaica). Puerto Rico (smaller than Cuba, Hispaniola, and Jamaica) has even a more remote position relative to the mainland and the poorest fauna of the four largest islands. Mainland species that are found on Puerto Rico and Hispaniola are also found on Jamaica and Cuba. Only two Puerto Rican species (*Brachyphylla cavernarum* and a sub-Recent fossil, *Monophyllus plethodon*) have their primary distribution in the Lesser Antilles and both of these species have counterparts in the other Greater Antillean islands.

The Bahamas are zoogeographically Antillean in nature with nine out of ten species recorded from the Bahamas being found on Cuba; the tenth is a species of *Natalus* found only in the Bahamas, which has its closest relatives in the Greater Antilles. The Bahaman bat fauna shows less affinity to the bat fauna of the southern half of Florida; two of the ten extant species but neither of the two Pleistocene fossil species from southern Florida are found in the Bahamas. The percentage of endemism of the Bahaman fauna (60 percent) is also in accordance with that characteristic of the Greater Antilles.

Whereas the Greater Antilles represent a chiropteran fauna that involves multiple invasions and subsequent radiations, the Lesser Antilles represent fewer invasions and subsequent speciation has not occurred with the frequency found in the Greater Antilles. In the Lesser Antilles only *Myotis* is represented by more than a single endemic species and the specific distinctness of these two taxa

is open to question (it is possible that both are conspecific with mainland *M. nigricans* or that both represent a single endemic species). Most of the evolutionary activity of the Lesser Antillean bat faunas has been associated with Guadeloupe. The Lesser Antilles have served as an effective filter barrier and the faunas of individual islands reflect their relative position in the chain. Although Grenada and possibly the Grenadines are in the Antillean chain, they represent a reduced mainland fauna with no Antillean endemic species. Zoogeographically, Grenada and the Grenadines are mainland islands.

From a zoogeographic and evolutionary standpoint most of the action in the Caribbean has occurred in the Greater Antilles. The bat fauna of the Greater Antilles appears to indicate that the Greater Antillean chiropteran fauna is unique, as was suggested by Simpson (1956) based upon land mammals and, as such, represents a distinctive faunal region. On the other hand, the fauna of the Lesser Antilles is less distinctive and primarily represents a depauperate attenuation of the Neotropical fauna of South America.

Although the zoogeography of Antillean bats has been discussed in several papers (Koopman and Williams, 1951; Koopman *et al.*, 1957; Koopman, 1958b, 1959, 1968, and 1976; Jones and Phillips, 1970), no overview of the chiropteran zoogeography of the entire region has been published. In the following account we discuss the available data as to species present, models of faunal origin, geographic origin of fauna, distributional patterns, endemism, and similarity of insular faunas. For this paper we have arbitrarily established the limits of the Antilles as the Bahamas to the north, Grenada to the south, and Jamaica and Cuba to the west. Koopman (1959) suggested somewhat different limits for the Antilles; however, because many of the small islands in the western Caribbean (for example, Swan, Providencia, and San Andres) have extremely depauperate bat faunas, we have not included them in our discussion. Although our discussion is limited to the bats, the interested reader will find the zoogeography of West Indian land mammals (Simpson, 1956) relevant to the following discussion.

Fossil taxa are included in the tables, figures, and computations because we wish to emphasize that these bats once occurred on the islands rather than the fact that they are extinct. Further, all fossils are believed to be late Pleistocene or Holocene in age; therefore, they are essentially a part of the modern fauna.

All computations are at the species level. The term endemic, unless otherwise indicated, refers to species, genera, or subfamilies that are found only in the Antilles. For example, if we note that Jamaica has seven endemic species then it has seven Antillean endemics, part or all of which may be found on islands other than Jamaica.

Before this report could be written it was necessary to make a number of taxonomic decisions that to some degree affected the conclusions

ultimately drawn. Unfortunately, in a number of cases such decisions had to be based on less than adequate data. Nevertheless, we feel most will prove accurate, particularly in instances when it was necessary to moderate the different standards previously applied by taxonomists — a primary source of variation in an overview of this fauna. In most cases, we have followed the most recent taxonomic revisions, but we have chosen to vary from some accounts, especially Varona, (1974) where sweeping and possibly unwarranted taxonomic changes were made. Our primary reasons for not following Varona's (1974) interpretations, for example, are that they are not in agreement with current taxonomic standards (for instance, placing members of the genus *Eumops* in the genus *Tadarida*), and because Varona gave no supporting data for his decisions. He did not, for instance, indicate which characters are shared by all members of the genus *Stenoderma* (he considered *Ariteus, Ardops,* and *Phyllops* as congeneric with *Stenoderma*) and which characters argue for *Ametrida* and *Centurio* to be regarded as generically distinct from *Stenoderma.* It may eventually prove realistic to consider all stenodermine species currently in the genera *Ardops, Ariteus, Stenoderma* and *Phyllops* (Jones and Carter, 1976) as belonging to a single genus, but we feel such decisions should be made on the basis of systematic study and that the salient characters and reasons for conclusions drawn should be documented. We are in sympathy, however, with the problems faced by Varona in compiling his checklist because we have encountered similar circumstances in preparing this paper.

In preparing our accounts, we made the following decisions concerning problem taxa and recorded instances of occurrence: considered as separate species — *Brachyphylla nana* and *B. pumila; Desmodus rotundus* and *D. stocki; Natalus stramineus, N. major, N. tumidifrons, N. macer,* and *N. micropus;* and *Phyllonycteris obtusa* and *P. poeyi;* considered as conspecific — *Tonatia bidens* and *T. saurophila; Lasiurus borealis* and all Antillean red bats; *Nycticeius humeralis* and *N. cubanus;* and all small members of the genus *Molossus* found in the Antilles; recognized as genera — *Monophyllus* distinct from *Glossophaga; Erophylla* from *Phyllonycteris; Ardops, Phyllops,* and *Ariteus* from *Stenoderma; Vespertilio* from *Eptesicus;* and *Mormopterus* from *Tadarida* and both from *Eumops;* considered erroneous or accidental records — *Lonchorhina aurita* and *Glossophaga soricina* from the Bahamas; *Eptesicus fuscus* (specimens previously reported as *E. fuscus* proved to be *E. lynni*), *Carollia perspicillata, Sturnira lilium,* and *Vampyrum spectrum* on Jamaica; and *Eptesicus fuscus* on Barbados.

Earlier records of *Myotis* from St. Martin and Grenada were ignored by LaVal (1973). On geographic grounds, we assigned specimens from St. Martin to *M. dominicensis* and those from Grenada to *M. nigricans*.

RESULTS AND DISCUSSION

All species of bats found in the Caribbean and the islands from which they are reported are listed in Table 1. The order for discussion is 1) generic accounts, 2) models of faunal origin, 3) geographic origin of fauna, 4) patterns of endemism, and 5) faunal comparisons.

GENERIC ACCOUNTS

Following are accounts of all genera of bats occurring in the Antilles in which their current taxonomic status, origin, and zoogeography are summarized.

Peropteryx

Peropteryx macrotis is the only member of the family Emballonuridae known to have reached the Antilles. This species is clearly a recent invader from South America, having been recorded only from Grenada. The family Emballonuridae is believed to be one of the oldest of extant chiropteran families (Eocene or Oligocene of Europe) and often is referred to as a stock from which several other families possibly evolved. The limited distribution of emballonurids in the Antilles would not be predicted based on the predictable geologic history of the family in the New World and the current distributional pattern (most mainland tropical and subtropical habitats worldwide and many insular areas in the Old World). Exactly why the emballonurids are not found in the Antilles is unclear to us. They are small and somewhat fragile bats, but no more so than members of the genus *Natalus,* which is one of the most successful and widespread genera in the Antilles, and as many as 10 genera and 17 species are known from Central and northern South America.

It seems doubtful to us that ecological competition has prevented emballonurids from occupying the Antilles. The two groups of insectivorous bats that might be most competitive with emballonurids are the Natalidae and the Mormoopidae. Both these families occur sympatrically with emballonurids on the mainland and we doubt that members of the three families are so competitive for food that one group would eliminate another in an island situation, particularly on large islands such as Cuba and Hispaniola. If the vicariance model for the origin of the bat fauna of the Antilles was correct, we would except this family to be well represented on the islands.

Noctilio

Noctilio leporinus is a widespread inhabitant (Davis, 1973) of the Neotropical region and is found throughout the Antilles. It could have entered the Antilles either from South America or Central America. The possibility that dual invasions occurred should not be ruled out. *Noctilio* is a strong flier and because it feeds on fish and aquatic invertebrates it spends a considerable amount of time over water. There is, therefore, a rather high probability of exchange of individuals between islands in this species.

Pteronotus

Of the five species of the genus that occur in the Antilles (Smith, 1972), *P. davyi* is the only one known from the Lesser Antilles. It has been recorded from four islands in this area (Maria Galante, Dominica, Martinique, and Grenada) and clearly entered the Antilles from the south. The remaining four species are confined to the Greater Antilles, with three (*P. macleayi, P. fuliginosus,* and *P. pristinus*) being Antillean endemics. *P. pristinus* is known only as a fossil from Cuba (Silva Taboada, 1974). The mainland species is *P. parnellii,* which is widespread from Mexico southward into South America and probably entered the islands from the general area of the Yucatan Peninsula. The ancestors of the other three species most likely originated from the Central American area.

Mormoops

The three members of this genus occurring in the Antilles are confined to the Greater Antilles, with two species (*M. megalophylla* and *M. magna*) being known only as fossils from Cuba (Silva Taboada, 1974). *Mormoops megalophylla* is widely distributed on the mainland (Smith, 1972) including the Yucatan Peninsula (Jones *et al.,* 1973). *Mormoops blainvillii* is a species endemic to the Antillean region and occurs on Cuba, Jamaica, Hispaniola, and Puerto Rico; it is known also as a fossil from the Bahamas. The ancestors of all three entered the islands from the west, probably from the region of the Yucatan Peninsula.

Micronycteris

Micronycteris megalotis is known only from Grenada in the Antillean region. It is a recent invader from South America. There is a parallel between the Emballonuridae and the subfamily Phyllostomatinae (of which *Micronycteris* is a member). The phyllostomatines are a successful group in the family Phyllostomatidae. The subfamily also is believed to be old geologically (relative to other living bat taxa), in

that it is known from the Miocene of South America (Savage, 1951), and somewhat primitive in the suite of characters by which it is recognized within the family. Yet, like representatives of the family Emballonuridae, members of this subfamily evidently have had little success in reaching or colonizing the Antilles. Only *Macrotus* has an extensive distribution in the region; at least one other genus, *Tonatia* (see generic account following), reached the islands but later became extinct there. The records of *Lonchorhina* and *Vampyrum* seem doubtful (Koopman and Williams, 1951; Goodwin, 1970). Again, why this supposedly old and successful (on the mainland) subfamily of bats has been so conspicuously unsuccessful in invading the islands is unclear to us. As is the case of the Emballonuridae, if the vicariance model explains the primary source of the Antillean bat fauna, this subfamily would be expected to be well represented on the islands.

Macrotus

The systematic relationships of members of this genus have been the subject of a number of recent studies (Anderson and Nelson, 1965; Davis and Baker, 1974; Buden, 1975b; Greenbaum and Baker, 1976). As currently understood, there are two species in the genus. *Macrotus waterhousii* occurs on the mainland and on the Antillean islands of Cuba, Jamaica, and Hispaniola, and in the Bahamas, and is known as a fossil from Puerto Rico. The species undoubtedly entered the Antilles from the west, although its distributional status on the Yucatan Peninsula is questionable (Jones *et al.*, 1973:10). The study of Greenbaum and Baker (1976) may have considerable relevance to understanding the origin of the bat fauna on the Caribbean islands. If the vicariance model as proposed by Rosen (1976) is true, then genetic divergence between the mainland and island populations of *Macrotus waterhousii* has been established since separation of the islands from the mainland. The results of electrophoresis of proteins from mainland and island populations suggest a close genetic affinity between the respective populations. Such a close genetic affinity would not be expected between mammalian populations that have been separated since the Miocene or longer. The alternative — that island populations are the result of a more recent, over water, invasion (Pleistocene or later) — is, to us, a better explanation of the data.

Tonatia

Tonatia is known from the Antilles by fossil remains of the mainland species *T. bidens* (Koopman, 1976). The ancestors of this popu-

lation reached Jamaica from the west where *Tonatia bidens* currently occurs.

Lonchorhina

The single specimen of *Lonchorhina aurita* recorded from the Bahamas is undoubtedly an accidental occurrence if the locality data are correct (Koopman *et al.*, 1957).

Glossophaga

Two species of *Glossophaga* have entered the island chain — at opposite ends. *Glossophaga soricina* is known in the Antilles only on Jamaica, which it undoubtedly reached from the mainland in the vicinity of the Yucatan Peninsula or Central America. *Glossophaga longirostris* is known from four Lesser Antillean islands (Dominica, St. Vincent, Grenadines, and Grenada). It invaded the Antilles from the South American mainland.

Monophyllus

Species of the genus *Monophyllus* are endemic to the Antillean region. One species, *M. redmani,* occurs in the Greater Antilles, whereas another, *M. plethodon,* is known at present from only the Lesser Antilles. *Monophyllus plethodon* also is known as a fossil from Puerto Rico where it occurred sympatrically with *M. redmani* (Schwartz and Jones, 1967). How ancestors of this genus reached the islands is unclear. *Monophyllus* is a genus closely related to *Glossophaga* and has been considered by some as congeneric with *Glossophaga.* At any rate, the two species of *Monophyllus* form an endemic group and clearly are more closely related to each other than either is to *Glossophaga.* Information as to the possible origin of *Monophyllus* from a living species of *Glossophaga* is not evident. We envision an earlier invasion for *Monophyllus* with subsequent speciation, and a more recent invasion for *Glossophaga longirostris* and *G. soricina.* During our field work on Jamaica (summer 1974), *Monophyllus redmani* appeared to be much more successful, as indicated by abundance in various habitats and caves than was *Glossophaga,* and in no danger of being replaced by *Glossophaga.*

Anoura

Anoura geoffroyi is known in the Antilles only from Grenada. The species has invaded the island chain from the South American mainland.

Carollia

As in *Anoura, Carollia perspicillata* occurs only on Grenada as an invader from South America. A Jamaican record for *Carollia* is believed to be inaccurate (Goodwin, 1970).

Sturnira

Two species of *Sturnira* are known from the Lesser Antilles. One, *Sturnira lilium,* is a mainland species that has been recorded from four of the Windward Islands (Dominica, Martinique, St. Lucia, and St. Vincent). *Sturnira thomasi* is an Antillean endemic that is confined to Guadeloupe. Both species have relationships to the south (Jones and Phillips, 1970; Genoways and Jones, 1975; Jones and Phillips, 1976). A record for *Sturnira lilium* from Jamaica is believed to be erroneous (Goodwin, 1970; Jones and Phillips, 1976).

Chiroderma

Chiroderma improvisum is currently known only from Guadeloupe. Geographically, the nearest place in which the genus occurs is on Trinidad. The possible relationship of *C. improvisum* to *C. doriae* (a species from southeastern Brazil) or to *C. villosum* (from Trinidad, South America, and Central America) has been proposed (Baker and Genoways, 1976).

Artibeus

Three members of the genus *Artibeus* are currently known to occur in the Antillean region. *Artibeus cinereus* and *A. lituratus* are confined to the southern portion of the Windward Islands and clearly have recently invaded the Antilles from South America. *Artibeus jamaicensis* is a common inhabitant of the Neotropics and is found throughout the Antilles. It could have entered the islands either from South America or Central America. In fact, there is evidence that both routes have been used by this species (Koopman, 1968; Jones and Phillips, 1970). The subspecies *A. j. jamaicensis* is known from the Greater Antilles (except Cuba and Bahamas where *A. j. parvipes* occurs) and the Lesser Antilles as far south as Barbados and probably entered the region from Central America. *Artibeus j. trinitatus* of Grenada appears to have its relationships with South American populations of the species. Relationships of the population on St. Vincent are unclear at present. These are additional data that we believe support an over water dispersal origin for the bat fauna. The distribution of *A. jamaicensis* is as would be predicted if different subspecies had entered at separate ends of the island chain.

Ardops

Ardops nichollsi is an Antillean endemic confined to the Lesser Antilles (Jones and Schwartz, 1967). Its relationship with *Stenoderma, Ariteus,* and *Phyllops* will be discussed in another publication. Its ancestors and route of invasion of the islands are unknown at present, but it is probable that the genera *Ardops, Phyllops, Ariteus,* and *Stenoderma* (all having a white spot on their shoulder and a shortened rostum) are the product of a single ancestral invader, with subsequent radiation and speciation on the islands. The center of this activity must have been the Greater Antilles because only *Ardops* is known from the Lesser Antilles. Three mainland genera, *Centurio, Ametrida,* and *Sphaeronycteris* (possibly also *Pygoderma*), appear to us to be the nearest relatives of the ancestral group that gave rise to the white-shouldered bats of the Antilles.

Phyllops

The genus *Phyllops* is endemic to the Antilles. Two species are known only from Cuba — *P. vetus* (a fossil species) and *P. falcatus* (an extant species). *Phyllops haitiensis* is a Recent species confined to Hispaniola. Systematic relationships among the species and ancestory of the genus are unclear at present. See account of *Ardops* for comments on origin.

Ariteus

Ariteus flavescens is known only from Jamaica and is part of the complex composed of *Stenoderma, Ardops,* and *Phyllops.* See account of *Ardops* for comments on origin.

Stenoderma

Stenoderma rufum is confined to Puerto Rico and the Virgin Islands (Jones *et al.,* 1971; Genoways and Baker, 1972). See account on *Ardops* for comments on origin.

Brachyphylla

Brachyphylla is a member of the endemic subfamily Phyllonycterinae (Silva-Taboada and Pine, 1969). Three species are currently recognized in the genus; *B. cavernarum, B. nana,* and *B. pumila. Brachyphylla cavernarum* is the most widespread member of the genus, being found on 13 of the 19 major islands in the Lesser Antilles and on Puerto Rico and the Virgin Islands in the Greater Antilles. *Brachyphylla nana* is confined to Cuba and *B. pumila* to Hispaniola (although the latter is known also as a fossil from Jamaica). We expect that

species of this genus will be found on most of the Caribbean islands (as fossils or otherwise) with the possible exception of Grenada and the Grenadines.

The fact that *B. cavernarum* has not been reported from several of the Lesser Antillean islands probably is the result of limited scientific collecting in that area. We account for the success of this species on the basis of its large, robust size and varied diet, which includes both fruits and nectar. Why the species *B. pumila* became extinct on Jamaica while other members of the genus have been so successful elsewhere in the Caribbean is an unanswered question. However, it does point up the fact that past environmental or other conditions may have caused elimination of some species even in these relatively depauperate faunas. *Brachyphylla* evidently has been isolated in the Antillean region for a long time and its route of invasion is no longer evident. Relationships of species within the genus have not been studied and still are open to question. The relationships of genera of the Phyllonycterinae (*Brachyphylla, Phyllonycteris,* and *Erophylla*) to those of other phyllostomatid subfamilies is poorly understood at present.

Phyllonycteris

Three Recent species, *P. aphylla, P. poeyi,* and *P. obtusa,* and a fossil species, *P. major,* comprise the genus *Phyllonycteris.* Originally, *P. aphylla* was described as a member of a distinct genus, *Reithronycteris.* Subsequently, however, Koopman (1952) placed the species in the genus *Phyllonycteris,* but retained *Reithronycteris* as a distinct subgenus. The genus is confined to the Greater Antilles, with each species being confined to one of the major islands (*P. poeyi,* Cuba; *P. aphylla,* Jamaica; *P. obtusa,* Hispaniola; *P. major,* Puerto Rico). The original invasion route of the ancestral stock is unclear, but all data clearly indicate that the evolution of the genus has been confined to the Greater Antilles.

Erophylla

The genus *Erophylla* is currently considered to be composed of two species (*E. bombifrons* and *E. sezekorni*), although questions concerning their specific distinctness recently have been raised. The genus is confined to the Greater Antilles: *E. sezekorni* occurs on the Bahamas, Cuba, and Jamaica, whereas *E. bombifrons* is known from Hispaniola and Puerto Rico. As a member of the subfamily Phyllonycterinae the past invasion route of *Erophylla* to the islands is unclear; however, there is no evidence to suggest that the evolutionary history of the genus has not been confined to the Greater Antilles.

Desmodus

Desmodus rotundus is known from Cuba as a fossil (Koopman, 1958a; Woloszyn and Mayo, 1974). The species undoubtedly invaded the island from the west and may not have survived because of the lack of large mammals and birds (perhaps it became extinct when the ground sloths disappeared) that would provide the blood meals necessary for this sanguivore. Varona (1974) assigned fossils of vampire bats from Cuba to the Pleistocene species *Desmodus stocki* (= *magnus*); however, Woloszyn and Mayo (1974) presented evidence that the Cuban material should be assigned to the Recent species, *Desmodus rotundus*. They did describe the fossil material as a distinct subspecies, *D. r. puntajudensis*.

Natalus

The six species of this genus that occur in the Antilles are currently divided into three subgenera of which two are endemic to the region. The endemic subgenus *Nyctiellus* contains a single species, *N. lepidus*, which occurs on Cuba (including the Isle of Pines) and the Bahamas. The other endemic subgenus, *Chilonatalus*, contains three species (*N. macer*, *N. micropus*, and *N. tumidifrons*) on the main Antillean islands and a fourth species (*N. brevimanus*) is recognized from Providencia off the coast of Nicaragua. These species are all small in size and distinguished from each other by minor characteristics; it has been suggested (Hall and Kelson, 1959:154-155) that they may represent a single species. The subgenus *Natalus* is represented by two species, *N. major* occurring in the Greater Antilles and *N. stramineus* occurring in the Lesser Antilles.

The invasion routes followed by the ancestors of the two endemic subgenera cannot be precisely documented, but their geographic position in the Greater Antilles would suggest invasion from the west. *Natalus stramineus* probably entered the Lesser Antilles from the south as suggested by Koopman (1968) and Jones and Phillips (1970), although the species does not currently occur on Trinidad and in adjacent South America. *Natalus major* is confined to the Greater Antilles and probably reached the area from the west. The parts of Mexico and Central America adjacent to the Greater Antilles are currently occupied by mainland representatives of *N. stramineus*. The relationships of *N. major* to mainland and insular populations of *N. stramineus* are unclear at present and are in need of investigation.

Myotis

Three species of this widespread genus have reached the Antillean region, and all are confined to the Lesser Antilles. Although the Neotropical *Myotis* was revised recently by LaVal (1973), the relationships of Antillean representatives remain somewhat obscure. As treated by LaVal, two of the species are endemic to the Lesser Antilles — *M. dominicensis* (Dominica) and *M. martiniquensis* (Martinique and Barbados). These populations, together with those from St. Martin and Grenada (Jones and Phillips, 1970), were previously known under the name *M. nigricans*. Specimens from the latter two islands were ignored by LaVal in his study of the group, and, therefore, present a difficult problem for us. We have assigned the one known specimen from St. Martin to the geographically nearest species — *M. dominicensis*. The specimens from Grenada have been provisionally assigned to *M. nigricans,* which occurs on Trinidad and in adjacent parts of South America. The ancestors of these species entered the region from the south; probably a single invasion was followed by later speciation.

Eptesicus

This vespertilionid genus is represented in the Antilles by two endemic species (*E. lynni* from Jamaica and *E. guadeloupensis* from Guadeloupe) and one (*E. fuscus* from the Greater Antilles except Jamaica) known from the mainland of North America, Central America, and the northern coast of South America. The stock that gave rise to *E. lynni* probably reached Jamaica from the west — from the Yucatan Peninsula or Central American mainland — where other members of the genus, such as *E. gaumeri* and *E. brasiliensis* occur. At the present, it is unclear to us which species of *Eptesicus* is the nearest relative to *E. lynni. Eptesicus lynni* may have evolved from the *E. brasiliensis* complex or it may be derived from the *E. fuscus* complex. *Eptesicus fuscus* could have entered the Antilles from the west by way of Cuba or from Florida by way of the Bahamas. We suspect that *E. guadeloupensis* represents speciation from an *E. fuscus* stock that was isolated on Guadeloupe. We believe this stock reached the island from the north, although invasion from the northern coast of South America cannot be ruled out. We have examined the specimen of *E. fuscus* previously reported from Barbados by Dobson (1878) and it is indeed a specimen of that species, but its recorded geographic origin is open to serious question.

Lasiurus

Two species of *Lasiurus* are known from the Greater Antilles. *Lasiurus intermedius* is known from Cuba and the mainland. This species could have reached Cuba from the Yucatan Peninsula or from Florida. We have (as was concluded by Varona, 1974) assigned the remaining members of the genus occurring in the Greater Antilles to *Lasiurus borealis,* although several populations have been considered as distinct species in the past. Red bats probably entered the islands from the west or possibly from the north. The relationships of Antillean populations will remain somewhat obscure until a thorough understanding is obtained of variation within mainland populations of *L. borealis* and *L. seminolus.*

Nycticeius

The one species of evening bat to reach the Antilles probably did so from the north. It is confined to Cuba. This population has been considered a distinct species (*N. cubanus*) in the past, but we have followed Varona's (1974) arrangement in which it is considered to be a subspecies of the mainland species, *N. humeralis.*

Antrozous

The species of this genus in the Antilles is *A. koopmani,* which is endemic to Cuba (Orr and Silva Taboada, 1960). The relationships of this species are poorly understood at present, but its ancestors evidently reached Cuba from the west.

Tadarida

Three mainland species (*T. brasiliensis, T. laticaudata,* and *T. macrotis*) of this genus are known from Caribbean islands. *Tadarida brasiliensis* has the widest distribution, being known from all of the Greater Antilles and 11 of the Lesser Antillean islands. We expect that it will be found on all islands except those in the southern part of the Lesser Antilles (although there is a record from Tobago). This species could have entered the area either from the north or the west. The other two species are found only in the Greater Antilles (*T. macrotis* from Cuba, Jamaica, and Hispaniola, and *T. laticaudata* from Cuba) and clearly have migrated to the islands from the west. Species of the genus *Tadarida* (as well as those of other molossid genera) are high, fast fliers and their dispersal potential is greater than that of other bats.

TABLE 1. — Occurrence of bats on Caribbean islands. Distributional data based upon Anderson and Nelson (1965), Baker and Genoways (1976), Buden (1975), Choate and Birney (1968), Davis (1973), Eger (1974), Genoways and Baker (1972, 1975), Genoways and Jones (1975), Goodwin (1959), Hall and Bee (1960), Hall and Jones (1961), Hall and Kelson (1959), Jones and Phillips (1970), Jones and Schwartz (1967), Koopman (1958a, 1958b, 1968, 1976), Koopman *et al.* (1957), Koopman and Williams (1951), LaVal (1973), Orr and Silva Taboada (1960), Schwartz and Jones (1967), Silva Taboada (1974), Silva Taboada and Koopman (1964), Smith (1972), and Varona (1974).

Species	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Bahamas	Anguilla	St. Martin	St. Bartholomew	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Maria Galante	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
Peropteryx macrotis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Noctilio leporinus	+	+	+	+	+	—	—	+	—	—	—	+	—	+	+	+	+	—	+	+	+	+	+	—	+
Pteronotus parnellii	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pteronotus fuliginosus	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pteronotus macleayi	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pteronotus davyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	—	—	—	—	+
Pteronotus pristinus	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mormoops blainvillii	+	+	+	+	—	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mormoops megalophylla	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mormoops magna	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Micronycteris megalotis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Macrotus waterhousii	+	+	+	*	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lonchorhina aurita	—	—	—	—	—	?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tonatia bidens	—	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1 (*Continued*). — Occurrence of bats on Caribbean islands.

Species	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Bahamas	Anguilla	St. Martin	St. Bartholomew	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Maria Galante	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
Glossophaga longirostris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—	+	+
Glossophaga soricina	—	+	—	—	—	?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Monophyllus plethodon	—	—	—	*	—	—	+	—	—	—	—	—	—	+	+	—	+	—	+	—	+	+	+	—	—
Monophyllus redmani	+	+	+	+	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anoura geoffroyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Carollia perspicillata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Sturnira lilium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	—	—
Sturnira thomasi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Chiroderma improvisum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Artibeus cinereus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Artibeus jamaicensis	+	+	+	+	+	+	+	+	—	+	+	+	—	+	+	+	+	—	+	+	+	+	+	—	+
Artibeus lituratus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+
Ardops nichollsi	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	+	+	—	+	+	+	+	—	—	—
Phyllops falcatus	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllops haitiensis	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllops vetus	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ariteus flavescens	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stenoderma rufum	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1 (*Continued*). — Occurrence of bats on Caribbean islands.

Species	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Bahamas	Anguilla	St. Martin	St. Bartholomew	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Maria Galante	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
Brachyphylla cavernarum	—	—	—	+	+	—	+	+	—	+	+	—	—	+	+	+	+	—	+	+	+	+	+	—	—
Brachyphylla nana	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brachyphylla pumila	—	*	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Erophylla bombifrons	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Erophylla sezekorni	+	+	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllonycteris obtusa	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllonycteris poeyi	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllonycteris aphylla	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllonycteris major	—	—	—	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Desmodus rotundus	*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natalus major	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natalus stramineus	—	—	—	—	—	—	+	—	—	+	—	—	—	—	+	+	—	—	+	—	—	—	—	—	—
Natalus lepidus	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natalus macer	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natalus micropus	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natalus tumidifrons	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Myotis dominicensis	—	—	—	—	—	—	—	(?)	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—
Myotis martiniquensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—	—

TABLE 1 (*Continued*). — Occurrence of bats on Caribbean islands.

Species	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Bahamas	Anguilla	St. Martin	St. Bartholomew	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Maria Galante	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
Myotis nigricans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Eptesicus fuscus	+	—	+	+	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	?	—	—
Eptesicus guadeloupensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Eptesicus lynii	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lasiurus borealis	+	+	+	+	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lasiurus intermedius	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nycticeius humeralis	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Antrozous koopmani	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tadarida brasiliensis	+	+	+	+	+	+	—	+	+	—	+	+	—	+	+	+	+	—	+	+	+	—	—	—	—
Tadarida laticaudata	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tadarida macrotis	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mormopterus minutus	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eumops auripendulus	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eumops glaucinus	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eumops perotis	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Molossus molossus	+	+	+	+	+	—	+	+	—	—	+	+	+	+	+	+	+	—	+	+	+	+	+	—	+

\+ = Present.
— = Absent.
* = Fossil.

Mormopterus

The relationships of the genera *Mormopterus* and *Tadarida* are currently unclear. The species *M. minutus* is confined to Cuba.

Molossus

We have considered all Antillean representatives of this genus to be a single species as suggested by Husson (1962) and Varona (1974). This is one of three species of bats that can be expected to occur on all, or nearly all, Antillean islands (*Noctilio leporinus* and *Artibeus jamaicensis* being the other two). Because *Molossus molossus* occurs both on Trinidad and in adjacent South America as well as on the Yucatan Peninsula and in adjacent parts of Middle America, the species could have entered the Antilles from either (or both) directions.

Eumops

The genus *Eumops* is represented in the Antilles by three mainland species, which occur only on Cuba (*E. glaucinus* and *E. perotis*) and Jamaica (*E. auripendulus* and *E. glaucinus*). All three mainland species obviously reached the Antilles from the west. We doubt that *Eumops glaucinus* (or any other *Eumops* for that matter) existed as such when the geographic fragmentation accounting for these islands occurred. We believe, therefore, that more recent over-water dispersal accounts for the current distributional status of the genus in the Antilles.

MODELS OF FAUNAL ORIGIN

To us, there seem to be two viable models by which faunal origin of bats in the Antillean region can be explained. The oldest, historically, is that they reached the islands by flight over the water gaps that separate each island (essentially a form of over-water dispersal that also includes rafting — but most bats hardly need a raft). This type of origin is particularly important if the islands have been relatively stable throughout time. The second model is vicariance (Bussing, 1975; Rosen, 1976), which explains "the fauna as the remnants of an ancestral biota that underwent geographical fragmentations followed by allopatric speciation (vicariance)" (Rosen, 1976). A third possible explanation of the faunal origin, land bridges, was proposed by Allen (1911), but geological evidence (Woodring, 1954) does not support this hypothesis.

If the origin of the Caribbean islands is like that described by Rosen (1976), with a geological time sequence as he suggested, then it seems likely to us that the occurrence there of some land mammals (ground

sloths and solenodons) may be accounted for by these events. However, such an explanation raises another question — mainly, why certain terrestrial mammals are not represented in the fossil or Recent faunas of these islands. Specifically, why were no marsupials, carnivores, or ungulates on these islands, along with the ground sloths, solenodons, and a select group of rodents? Marsupials, carnivores, and ungulates probably were well represented in the Central and South American fauna at the time the Antilles supposedly split away from the mainland and representatives of these groups should have survived on the islands at least long enough to have left a fossil record. The reader should see Simpson (1956) for an alternative explanation of the origin of Antillean land mammals.

At the time of the writing of this paper it is unclear to us when (geologically speaking) the islands separated from the mainland, but such an event probably occurred no later than the beginning of the Oligocene. Most modern genera of mammals did not evolve before the Miocene and most Recent species originated in the late Pliocene or Pleistocene with subspeciation occurring in the late Pleistocene. Three-fourths of the genera (24 of 32) found in the Antilles also occur on the mainland. Slightly less than half (30 of 65) of the species found in the Antilles also occur on the mainland. The point is that if vicariance is used to explain the origin of the bat fauna, the fossil evidence would suggest that the degree of morphological distinctiveness between most Antillean taxa and their mainland counterpart is what would be expected in taxa separated only since the Pliocene or more recently. There are only two New World genera (*Myotis* and *Tadarida*) that are reported from the Oligocene (both from Europe).

If part of the bat fauna has a vicariance origin, the most likely candidates are genera of the subfamily Phyllonycterinae followed by bats of the *Ariteus, Ardops, Phyllops,* and *Stenoderma* complex. If the ancestors of either group occupied the islands by this method, then there was subsequent inter-island dispersal.

However, if the bat fauna of these islands once was fairly representative of the mainland fauna, then certain obvious components now are lacking, specifically the Emballonuridae and the Phyllostomatinae (see generic accounts of *Peropteryx* and *Micronycteris*). Further, the vicariance model would not explain why Grenada, which is geologically of Antillean origin, has a bat fauna that is definitely South American in its relationships. In fact, Rosen (1976) points out that dispersal is required to explain how the fauna of the volcanic islands (essentially

the Lesser Antilles) was derived, because even though these islands are small they all support several bat species. Such data suggest that over-water dispersal has been effective in producing a fauna for the Antilles.

One point should be made relative to bat distributional patterns and the vicariance model. If the flora and associated ecology have an origin as proposed by the vicariance model — possibly prior to establishment of extensive bat faunas on the mainland (before the Eocene) — then Recent bat taxa that would be most likely to survive upon reaching the islands would be those that had evolved in similar mainland ecological associations. Therefore, the fauna surviving from over-water dispersal would appear to fit the "tracks" predictable from the vicariance model of Rosen even if the included species had not reached the Antillean islands in the way he proposed.

The fact that the vicariance model is not the best one to explain the origin of the bat fauna should not be taken as an indictment against the model. Bats are more vagile than most kinds of animals and, therefore, are more readily capable of dispersal. Additionally, the time-scale of events may have been critical; the fossil record for bats (Smith, 1976) is meager and provides little insight as to what kinds might have been present when geological fragmentation resulting in formation of the Antilles took place.

Dispersal by flight seems to us to be the most logical explanation for the present Antillean bat fauna. If dispersal from mainland to island has been the primary source of bats, then we would expect those islands adjacent to the mainland to have the richest fauna. This is the case. Further, we would expect the older endemics to be more widely distributed than the newer arrivals (those species that have conspecific mainland populations). This is also generally true. Additionally, one would predict that the faster fliers and those capable of sustained flight would have the most extensive distribution. Such species as *Tadarida brasiliensis, Molossus molossus, Artibeus jamaicensis,* and *Noctilio leporinus* are strong fliers and have extensive distributions in the Caribbean region as well as on the mainland. Finally, dispersal by flight readily explains why Grenada has a South American bat fauna even though the island is geologically Caribbean. Grenada is the Lesser Antillean island nearest Trinidad and the mainland and more South American species would be expected to reach it.

Based upon our data, we believe over-water dispersal is sufficient to explain the origin of the current bat fauna of the Antilles and the following discussion is based on this explanation of the origin of the fauna.

GEOGRAPHIC ORIGIN OF FAUNA

Routes of Dispersal from Mainland to Islands

There are three possible routes of invasion of the Antilles by bats. These routes are from South America through the Lesser Antilles chain, from North America (primarily Florida) to the Bahamas and the Greater Antilles, and from Central America to the Greater Antilles. We see little evidence for invasion of the mainland areas from the islands. *Eumops glaucinus* may be the most likely candidate (moving from Cuba to Florida), but this appears unlikely to us and we suspect that the *Eumops* in Florida is a relict from a time when *E. glaucinus* had a more widespread distribution across the southern United States (see also Rosen, 1976).

The Northern Route

Southern Florida as a source of bats on Caribbean islands deserves special comment. The bat fauna of southern Florida consist of 10 extant taxa (*Myotis austroriparius, Pipistrellus subflavus, Eptesicus fuscus, Lasiurus seminolus, L. cinereus, L. intermedius, Nycticeius humeralis, Plecotus rafinesquii, Tadarida brasiliensis,* and *Eumops glaucinus*) and two known from Pleistocene deposits (*Mormoops megalophylla* and *Desmodus stocki*). This fauna is relatively depauperate and possibly is reflective of isolation of the unique ecological association of southern Florida. However, we believe a more important factor is the absence of caves and rock outcrops that are so critical as sites for bat roosts. Southern Florida shares eight (*Myotis austroriparius, Pipistrellus subflavus, Eptesicus fuscus, Lasiurus seminolus, L. cinereus, Nycticeius humeralis, Plecotus rafinesquii,* and *Tadarida brasiliensis*) of its 10 extant species with southern Arkansas (where there are no caves or rock outcrops — Baker and Ward, 1967; Sealander and Price, 1964). Of the species found in southern Arkansas only *Lasiurus borealis* and *Lasionycteris noctivagans* are not known in Florida and we suspect that both species may eventually be found there. Five of the 10 extant species from southern Florida are known from the Greater Antilles and one of the fossils (*Desmodus*) is known from the Greater Antilles (also as a fossil, but of the species *rotundus* not *stocki*).

The point of this discussion is that the fauna of southern Florida is depauperate (although typical of the noncave areas of the Mississippi Gulf Coast) and for this reason its potential for supplying new bat taxa to the Caribbean islands is reduced. The bat fauna of southern Florida is not Caribbean in nature and we do not consider the invasion route from Florida to the Antilles as having the same importance as the route

TABLE 2. — Proposed invasion routes for the species of bats reported from the Antilles.

Mainland Species (30)			Endemic Species (35)		
Invasion from North-West	Invasion from South	Widespread	Origin Unknown	Suspected Ancestors from West-North	Suspected Ancestors from South
Mormoops megalophylla *	Peropteryx macrotis	Noctilio leporinus	Monophyllus plethodon	Mormoops blainvillii	Sturnira thomasi
Pteronotus parnellii	Pteronotus davyi	Artibeus jamaicensis	Monophyllus redmani	Mormoops magna *	Chiroderma improvisum
Macrotus waterhousii	Micronycteris megalotis	Molossus molossus	Ardops nichollsi	Pteronotus fuliginosus	Myotis dominicensis
Tonatia bidens *	Glossophaga longirostris		Phyllops falcatus	Pteronotus macleayi	Myotis martiniquensis
Glossophaga soricina	Anoura geoffroyi		Phyllops haitiensis	Pteronotus pristinus *	
Desmodus rotundus	Carollia perspicillata		Phyllops vetus *	Eptesicus lynii	
Eptesicus fuscus	Sturnira lilium		Ariteus flavescens	Eptesicus guadeloupensis	
Lasiurus borealis	Artibeus cinereus		Stenoderma rufum	Antrozous koopmani	
Lasiurus intermedius	Artibeus lituratus		Brachyphylla cavernarum		
Nycticeius humeralis	Natalus stramineus		Brachyphylla nana		
Tadarida brasiliensis	Myotis nigricans		Brachyphylla pumila		
Tadarida laticaudata			Erophylla bombifrons		
Tadarida macrotis			Erophylla sezekorni		
Eumops auripendulus			Phyllonycteris major *		
Eumops glaucinus			Phyllonycteris obtusa		
Eumops perotis			Phyllonycteris poevi		
			Phyllonycteris aphylla		
			Natalus major		
			Natalus lepidus		
			Natalus macer		
			Natalus micropus		
			Natalus tumidifrons		
			Mormopterus minutus		

* Fossil.

from Central America. Nevertheless, this northern route does exist and it probably was the source of at least some of the following species: *Nycticeius humeralis, Lasiurus intermedius, L. borealis, Eptesicus fuscus, E. guadeloupensis, Tadarida brasiliensis,* and *Eumops glaucinus.*

The Western Route

We believe this to be the most important route for bats for the Caribbean primarily because of the large number of bat species found in tropical Mexico and because the ecological differences between tropical Mexico and the Caribbean are not too great. It is difficult to know how rich the bat fauna of the Yucatan Peninsula may have been in the past, but currently 46 species are recorded from that region (Jones *et al.,* 1973; Birney *et al.,* 1974; Koopman, 1974). It is also probable that the water gap between Cuba and Jamaica and mainland Mexico has been reduced during the past (Woodring, 1954).

The Southern Route

Undoubtedly several species of bats have used this route. The number of species that occur on the northern South American mainland is not well documented, but the island of Trinidad with its 63 known species (Genoways *et al.,* 1973) is some indication of the diversity in the region. The small size of the Lesser Antillean islands probably is a primary factor explaining why more species have not reached these islands or survived on them.

PATTERNS OF ENDEMISM

Distributional Patterns

Mainland Species that Occur in the Caribbean

Table 2 summarizes the species that we believe followed each route of invasion (see above). In Table 2 we have combined the northern and western routes because in many cases it is impossible to determine whether specific taxa invaded from the west or the north. For the great majority of species listed, we believe the western route to have been the most likely. Figs. 1 and 2 give composite distributions of mainland species that we suspect invaded the Antilles from the north or west (Fig. 1) and from the south (Fig. 2). Three species (*Artibeus jamaicensis, Noctilio leporinus,* and *Molossus molossus*), which could have invaded from either the west or south, are not included in the figures because we do not know in which figure they would best fit. In fact, *Artibeus jamaicensis* probably invaded from both the west and south (Jones and Phillips, 1970). It is obvious in Fig. 1 that several

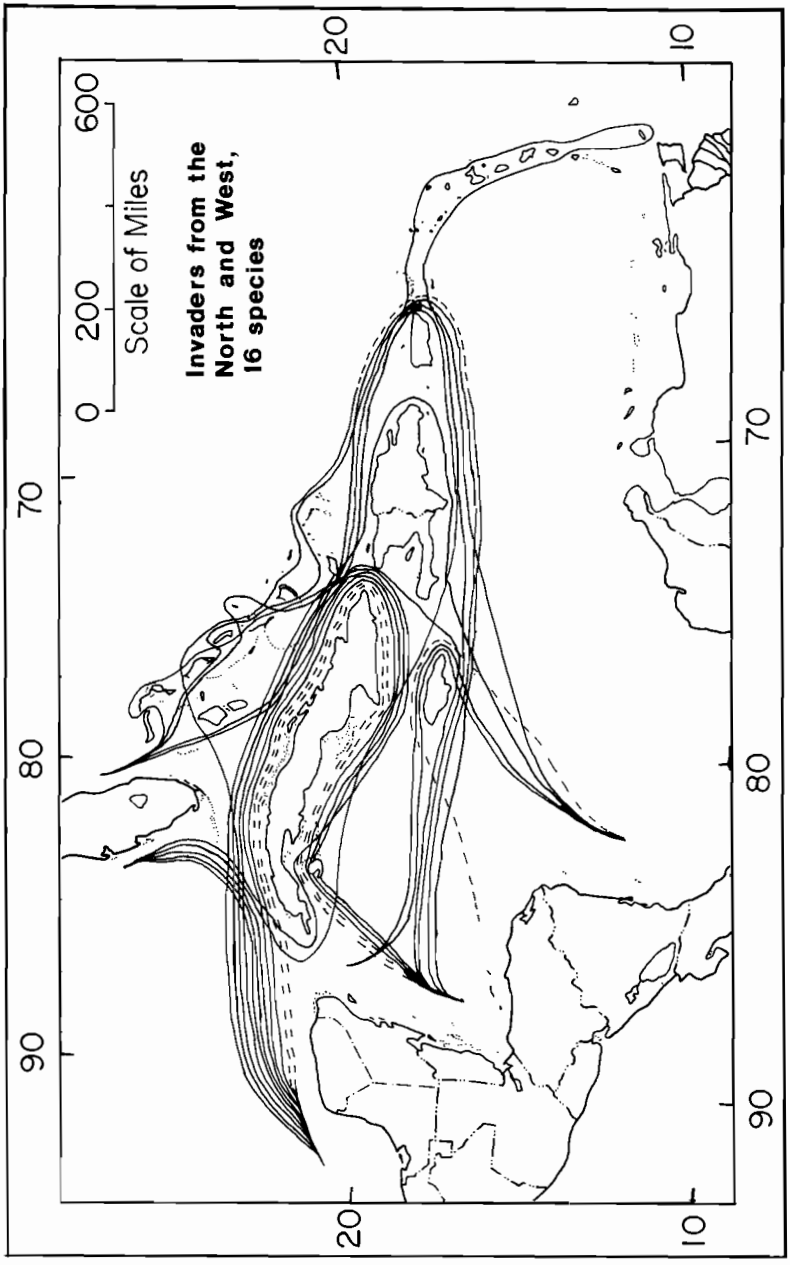

FIGURE 1. — Map showing the composite distribution of species of bats believed to have invaded the Antilles from the west or north.

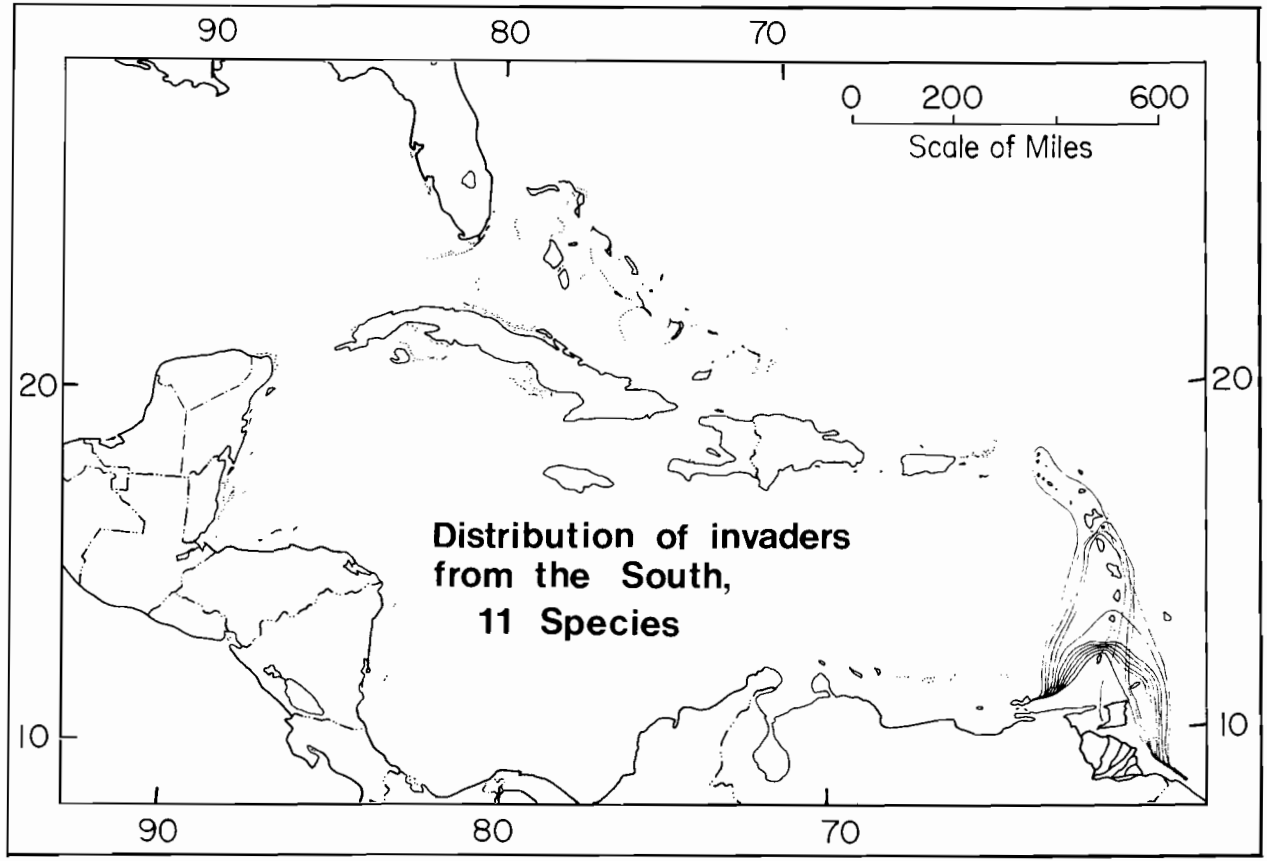

FIGURE 2. — Map showing the composite distribution of species of bats believed to have invaded the Antilles from the south.

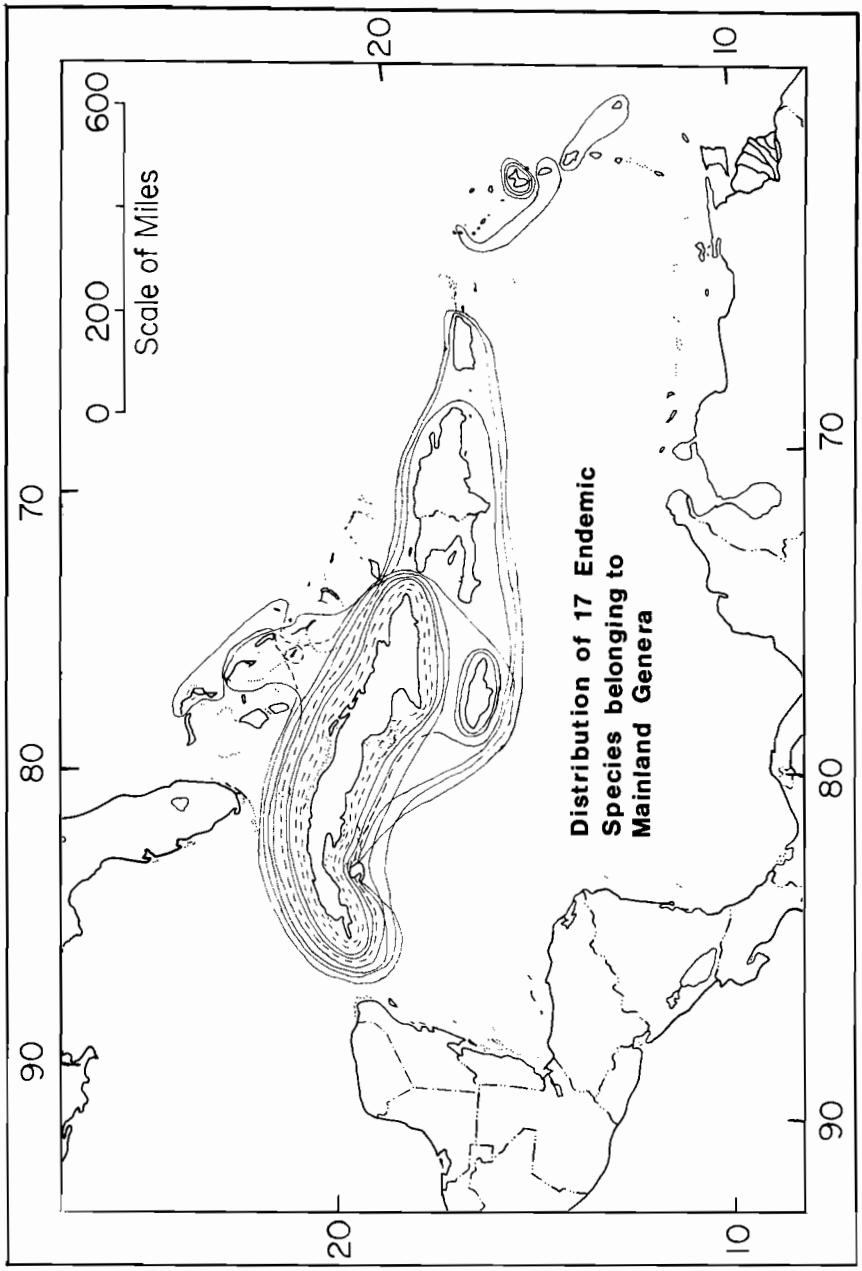

FIGURE 3.—Map showing the composite distribution of 17 endemic species of Antillean bats belonging to mainland genera.

species that probably used the northern or western route are widely distributed in the Greater Antilles and Bahamas. However, only one species (*Tadarida brasiliensis*) has an extensive distribution in the Lesser Antilles. Of the species that probably invaded from the south, none has entered the Greater Antilles (if *Artibeus jamaicensis, Noctilio leporinus,* or *Molossus molossus* used this route they, of course, would be exceptions). The southern route has been used to an extent that the fauna of Grenada (and probably also that of the Grenadines) is entirely South American in affinity with no Antillean endemics present. In both Figs. 1 and 2, it is obvious that the islands nearest the mainland have the greatest number of species and that the chain of islands has acted as a filter barrier. This is most evident in the Lesser Antilles (Fig. 2).

Endemic Species of Mainland Genera

In Fig. 3 the composite distribution is shown for 17 endemic species belonging to mainland genera. The greatest degree of speciation at this level has occurred in the Greater Antilles. Within the Greater Antilles, the greatest number of endemic species belonging to mainland genera are found on Cuba (nine); Jamaica has six, Hispaniola three, and Puerto Rico two. It should also be noted that all such species found on Hispaniola and Puerto Rico are also found on Cuba and Jamaica, but Jamaica has two endemic species from mainland genera that are not found on any other Caribbean island. In the Lesser Antilles, there are fewer endemics that are representative of mainland genera (Fig. 3). Only Guadeloupe with three has more than one species and we believe that there is some possibility that the other two species (*M. dominicensis* and *M. martiniquensis*) may be Antillean representatives of *Myotis nigricans* and perhaps should have been plotted on Fig. 2.

A careful examination of the distribution of endemic species belonging to mainland genera (Fig. 3) reveals that no speciation has occurred on those Lesser Antillean islands that are near to the mainland. A comparison of Figs. 2 and 3 shows that a relatively large number of bats has reached the southern Lesser Antilles from South America, but all data suggest that populations are conspecific with mainland species.

Based on the data summarized by Fig. 3, it is obvious that the combination of factors produced by the size, ecology, elevation, position, and age of the Greater Antilles has been much more conducive to speciation than has the equivalent combination of factors in the Lesser Antilles. However, Guadeloupe in the Lesser Antilles has been more important in this respect than has been Puerto Rico and is equal to Hispaniola.

TABLE 3. — Distributional patterns of Endemic species. A. Species restricted to Greater Antilles. B. Species restricted to Lesser Antilles. C. Species found on both Greater and Lesser Antilles.

A	B
1. Pteronotus fuliginosus	1. Sturnira thomasi
2. Pteronotus macleayi	2. Chiroderma improvisum
3. Pteronotus pristinus *	3. Ardops nichollsi
4. Mormoops blainvillii	4. Eptesicus guadeloupensis
5. Mormoops magna *	5. Myotis dominicensis
6. Monophyllus redmani	6. Myotis martiniquensis
7. Phyllops falcatus	
8. Phyllops haitiensis	
9. Phyllops vetus *	
10. Ariteus flavescens	C
11. Stenoderma rufum	1. Monophyllus plethodon **
12. Brachyphylla nana	2. Brachyphylla cavernarum
13. Brachyphylla pumila	
14. Erophylla bombifrons	
15. Erophylla sezekorni	
16. Phyllonycteris major	
17. Phyllonycteris obtusa	
18. Phyllonycteris poeyi	
19. Natalus major	
20. Natalus lepidus	
21. Natalus macer	
22. Natalus micropus	
23. Natalus tumidifrons	
24. Eptesicus lynii	
25. Antrozous koopmani	
26. Mormopterus minutus	

* Fossil species.

** Known from the Greater Antilles (Puerto Rico) from sub-Recent fossil records.

A final point of importance in Fig. 3 is that there is no overlap at this level of endemism in the faunas of the Lesser and Greater Antilles. With one exception, endemic species from mainland genera on the Greater Antilles are from different genera than have produced such species on the Lesser Antilles. The exception is *Eptesicus* in which the Greater Antillean species *Eptesicus lynni* was derived from either the *E. brasiliensis* species group or the *E. fuscus* group and the Lesser Antillean

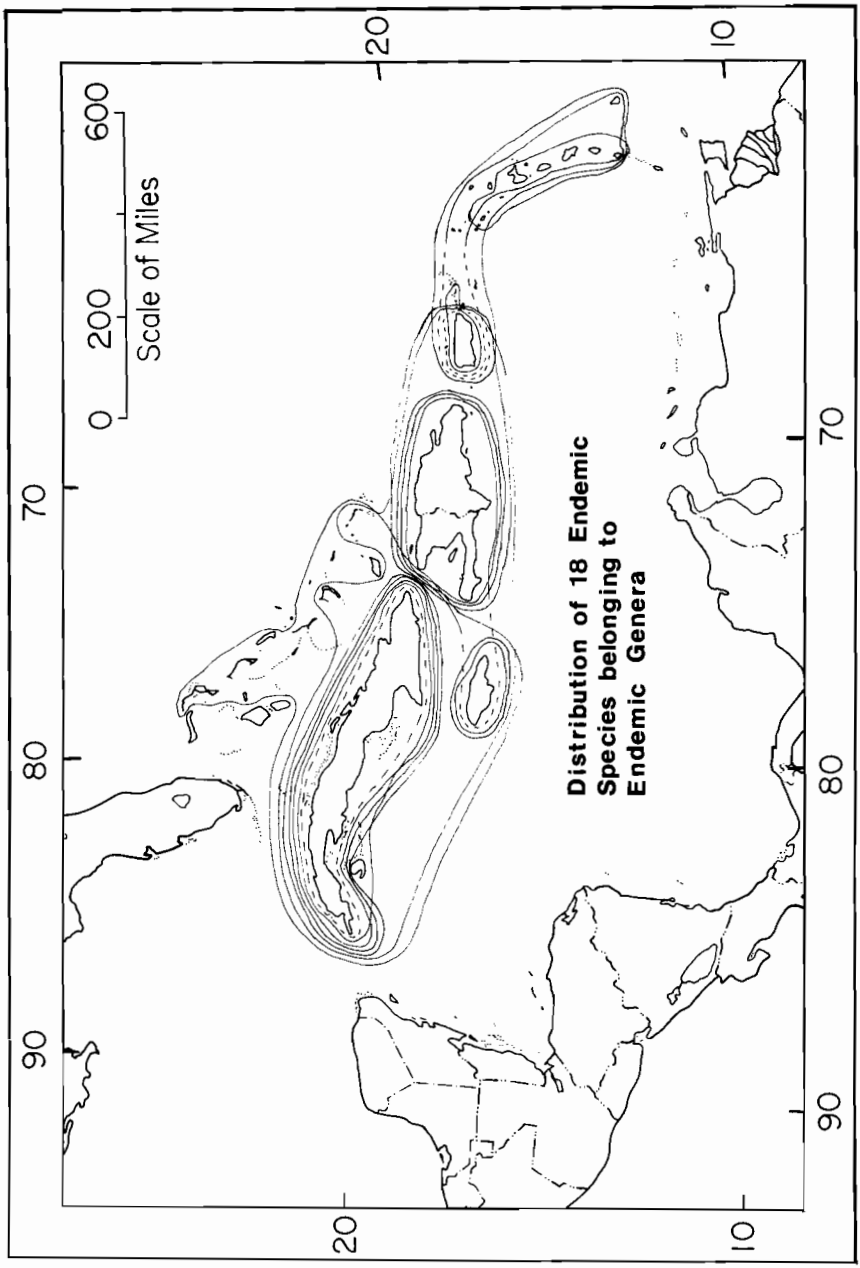

FIGURE 4.—Map showing composite distribution of 18 endemic species of Antillean bats belonging to endemic genera.

species *E. guadeloupensis* from the *E. fuscus* group. With the possible exception of *Eptesicus,* all endemics from mainland genera in the Antilles have resulted from separate invasions and not from a single invasion with subsequent speciation within the Greater and Lesser Antilles respectively. Within the Greater Antilles, three genera (*Natalus, Pteronotus,* and *Mormoops*) may have invaded the islands with independent speciation on more than one island. In the Lesser Antilles, the only genus that may have populations that arose from mainland counterparts on more than one island is *Myotis* (see comments above).

Endemic Species Belonging to Endemic Genera

The composite distribution of the 18 endemic species belonging to endemic genera is shown in Fig. 4. When Figs. 3 and 4 are compared it is obvious that Cuba, again, is the most important island relative to the endemic fauna. It is also obvious that relative to the Greater Antilles, the Lesser Antilles has a much reduced endemic fauna. Puerto Rico (with its two fossil taxa) has a fauna of endemics belonging to endemic genera as rich as that of Jamaica or Hispaniola. At this level of endemism no single Lesser Antillean island stands out as a center of importance (as Guadeloupe did at the level of endemic species belonging to mainland genera). Again, note that no Antillean endemics occur on Grenada or the Grenadines. Also, the islands of Grand Bahama and Andros (major islands of the Bahamas) have no Antillean endemics.

Cuba has seven endemics from this level, Jamaica five, Hispaniola five, and Puerto Rico six. This pattern differs from that for endemic species belonging to mainland genera. This difference can be partially explained by the amount of time the two levels of endemics have been in the Caribbean region. Endemic species belonging to mainland genera are relatively recent invaders of the islands and the islands adjacent to the mainland would be expected to have the richest fauna. The species on the more remote islands of Hispaniola and Puerto Rico appear to have arisen on Cuba or Jamaica and subsequently to have extended their distribution to more remote parts of the Caribbean. The older endemics that have had time to evolve to the point of generic or greater distinction have been in the Caribbean for a much longer time (more than ample time for all major islands in the chain to be reached) and central islands would be expected to have just as rich a fauna as peripheral islands. Cuba, with its large size and greater ecological diversity, would be expected to have a larger number of successful invaders.

TABLE 4. — Species at levels of endemism listed by endemic subfamily (Phyllonycterinae), endemic genera, and endemic species of mainland genera.

Species Belonging to Endemic Subfamily (9)	Species Belonging to Endemic Genera (9)	Endemic Species of Mainland Genera (17)
Brachyphylla cavernarum	Monophyllus plethodon	Mormoops blainvillii
Brachyphylla nana	Monophyllus redmani	Mormoops magna *
Brachyphylla pumila	Ardops nichollsi	Pteronotus fuliginosus
Erophylla bombifrons	Phyllops falcatus	Pteronotus macleayi
Erophylla sezekorni	Phyllops haitiensis	Pteronotus pristinus *
Phyllonycteris major *	Phyllops vetus *	Sturnira thomasi
Phyllonycteris obtusa	Ariteus flavescens	Chiroderma improvisum
Phyllonycteris poeyi	Stenoderma rufum	Natalus major
Phyllonycteris aphylla	Mormopterus minutus	Natalus lepidus
		Natalus macer
		Natalus micropus
		Natalus tumidifrons
		Eptesicus guadeloupensis
		Eptesicus lynii
		Myotis dominicensis
		Myotis martiniquensis
		Antrozous koopmani

* Fossils.

Smaller islands, especially as found in the Lesser Antilles, would be expected to have a poorer fauna.

Based on the above explanation Puerto Rico would be expected to have a relatively rich fauna of endemics belonging to endemic genera and this is the case. However, of the endemic species belonging to endemic genera found on the other Greater Antillean islands, only two are known from Puerto Rico (the same number of endemic species belonging to mainland genera that Puerto Rico shares with the other Greater Antillean islands). However, *Stenoderma* and a fossil *Phyllonycteris* are known only from Puerto Rico (or from Puerto Rico and the Virgin Islands). These, plus the two species that are shared with the Lesser Antillean fauna, boost the number of endemics belonging to endemic genera to six (greater than either Hispaniola and Jamaica), reflecting the central position of Puerto Rico in the Antillean chain.

Levels of Endemism

From the previous discussion it is obvious that we feel endemism of bats in the Antilles has resulted from several invasions and some groups

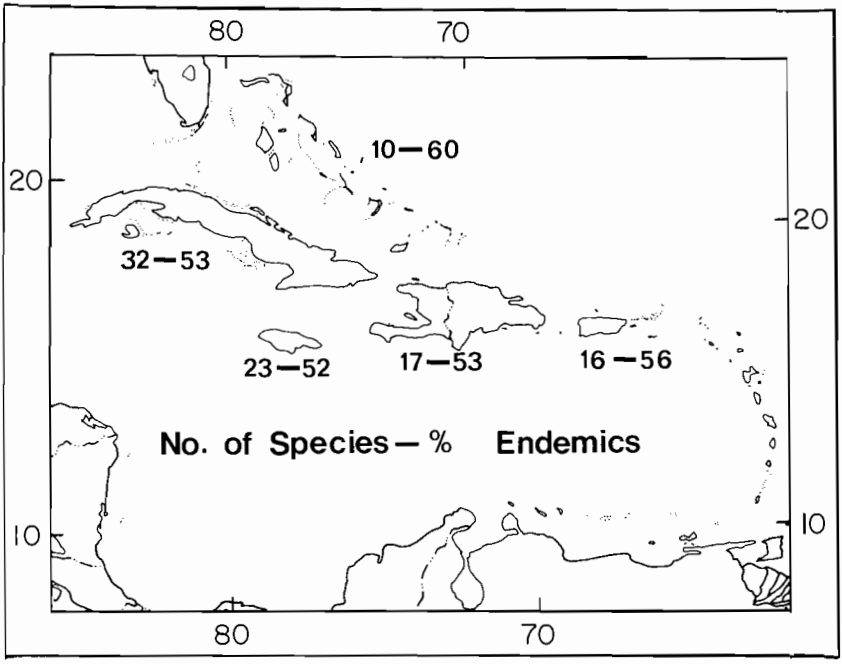

FIGURE 5. — Map of Greater Antilles showing number of species recorded from each island (number before dash) and the percentage of Antillean endemics in the bat fauna of each island (number following dash).

have been on the Caribbean islands for a long time. The oldest taxon of bats to be isolated in the Caribbean region is the subfamily Phyllonycterinae (with three genera). We believe the second oldest group to be the *Ardops, Ariteus, Stenoderma,* and *Phyllops* complex. Beyond this we do not know what the order might have been, but we suspect there have been numerous invasions.

Figs. 5 and 6 show the number of species reported for each island and the percentage of Antillean endemics. The most obvious trend is that the percentage of endemics in the fauna of the Greater Antilles (always above 50 percent except for the Virgin Islands — Fig. 5) is greater than that characteristic of the Lesser Antilles (usually 40 percent or less — Fig. 6). The two exceptions to the low perentage of endemism in the Lesser Antilles are Guadeloupe (60 percent) and Barbados (50 percent). In the case of Guadeloupe, the high percentage is a result of the presence of the endemics typical of the Lesser Antilles plus the three endemic species not found on any other Antillean islands. In the case of Barbados, the island has a reduced fauna that reflects its

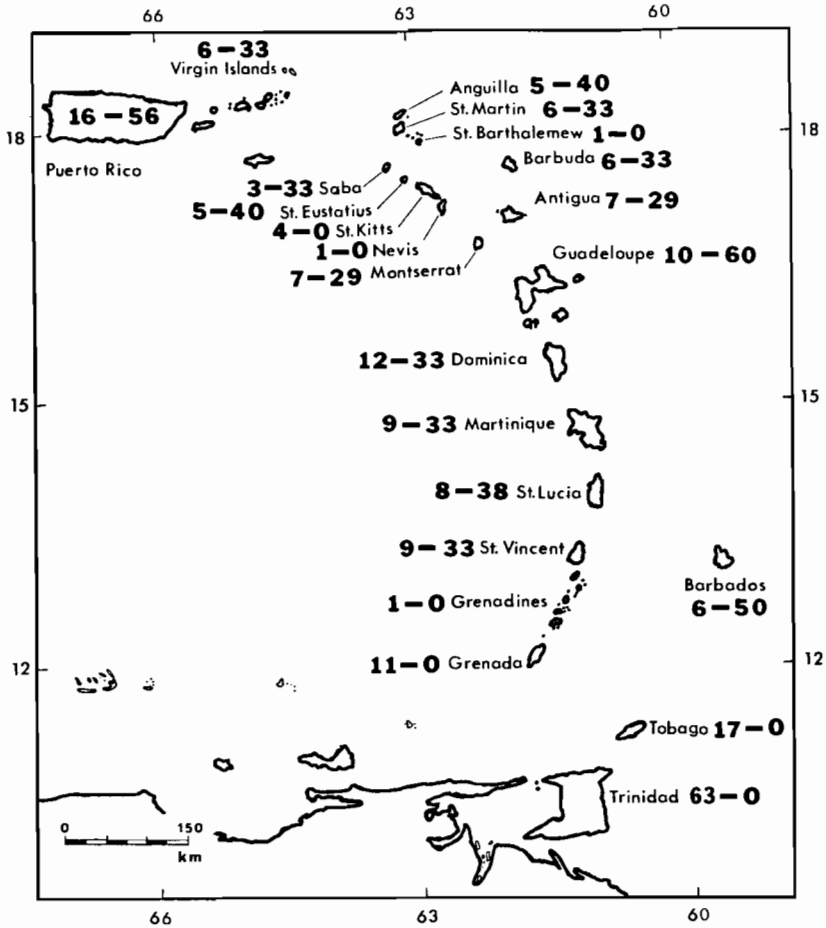

FIGURE 6. — Map of Lesser Antilles showing number of species recorded for each island (number before dash) and the percentage of Antillean endemics in the bat fauna of each island (number following dash).

somewhat isolated position relative to the other islands in the Lesser Antillean chain.

FAUNAL COMPARISON

We have compared the chiropteran faunas occurring on Antillean islands from two points of view. First, using the data in Table 1, we generated a matrix of correlation between the distribution patterns of Antillean bats using the NT-SYS program. This matrix was clustered using the UPGMA (unweighted pair-group methods using arithmetic

TABLE 5. — Faunal comparisons for Antillean bat fauna. Bold-faced numbers on the diagonal are the total number of bats occurring on the respective island. Numbers above the line of bold-faced numbers represent numbers of species common to both islands. Numbers below the line of bold-faced numbers are coefficients of community.

	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Bahamas	Anguilla	St. Martin	St. Bartholomew	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
Cuba	**32**	15	13	11	4	9	2	4	1	1	3	4	1	4	4	4	4	4	4	4	3	3	0	3
Jamaica	38	**23**	12	10	4	8	2	4	1	1	3	4	1	4	4	4	4	4	4	4	2	3	0	3
Hispaniola	36	43	**17**	12	3	7	2	4	1	1	3	4	1	4	4	4	4	4	4	4	3	3	0	3
Puerto Rico	30	34	57	**16**	6	7	4	5	1	2	4	4	1	6	6	5	6	6	5	6	5	5	0	3
Virgin Islands	12	16	15	38	**6**	2	3	5	1	2	4	4	1	5	5	5	5	5	5	5	4	4	0	3
Bahamas	26	31	33	35	13	**11**	1	2	1	1	2	2	0	2	2	2	2	2	2	2	1	1	0	1
Anguilla	6	8	10	24	38	7	**5**	3	0	3	3	2	1	4	5	4	4	5	3	4	4	4	0	2
St. Martin	12	16	21	29	71	13	38	**6**	1	2	4	4	1	5	5	5	5	5	5	5	4	4	0	3
St. Bartholomew	3	4	6	6	17	9	0	17	**1**	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0
Saba	3	4	5	12	29	8	60	29	0	**3**	2	1	0	2	3	3	2	3	2	2	2	2	0	1
St. Eustatius	9	12	16	24	57	14	43	57	20	33	**5**	3	1	4	4	4	5	5	5	5	4	3	0	2
St. Kitts	13	17	24	25	67	15	29	67	25	17	50	**4**	1	4	4	4	4	4	4	4	3	3	0	3
Nevis	3	4	6	6	17	0	20	17	0	0	20	25	**1**	1	1	1	1	1	1	1	1	1	0	1
Barbuda	12	16	21	38	71	13	57	71	17	29	57	67	17	**6**	6	5	6	6	5	6	5	5	0	3
Antigua	11	15	20	35	63	13	71	63	14	43	50	57	14	86	**7**	6	6	7	7	6	5	5	0	3
Montserrat	11	15	20	28	63	13	50	63	14	43	50	57	14	63	75	**7**	6	7	6	6	5	4	0	3
Guadeloupe	11	14	17	30	45	11	36	45	10	18	50	40	10	60	55	55	**10**	7	6	7	6	5	0	3
Dominica	10	13	16	27	38	10	42	38	8	25	42	33	8	50	58	58	47	**12**	8	8	8	5	1	5
Martinique	11	14	18	25	50	11	27	50	11	20	56	44	11	50	78	60	46	62	**9**	7	6	5	0	4
St. Lucia	11	15	19	33	56	12	44	56	13	22	63	50	13	75	67	67	64	67	70	**8**	7	5	0	3
St. Vincent	8	10	13	25	36	5	40	36	0	20	40	30	11	50	45	45	46	62	50	70	**9**	5	1	5
Barbados	9	12	15	29	50	6	57	50	0	29	38	43	17	71	63	44	45	38	50	56	50	**6**	0	3
Grenadines	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	11	0	**1**	1
Grenada	7	9	12	12	20	5	13	20	0	7	13	23	8	20	19	19	16	26	24	18	31	20	8	**12**

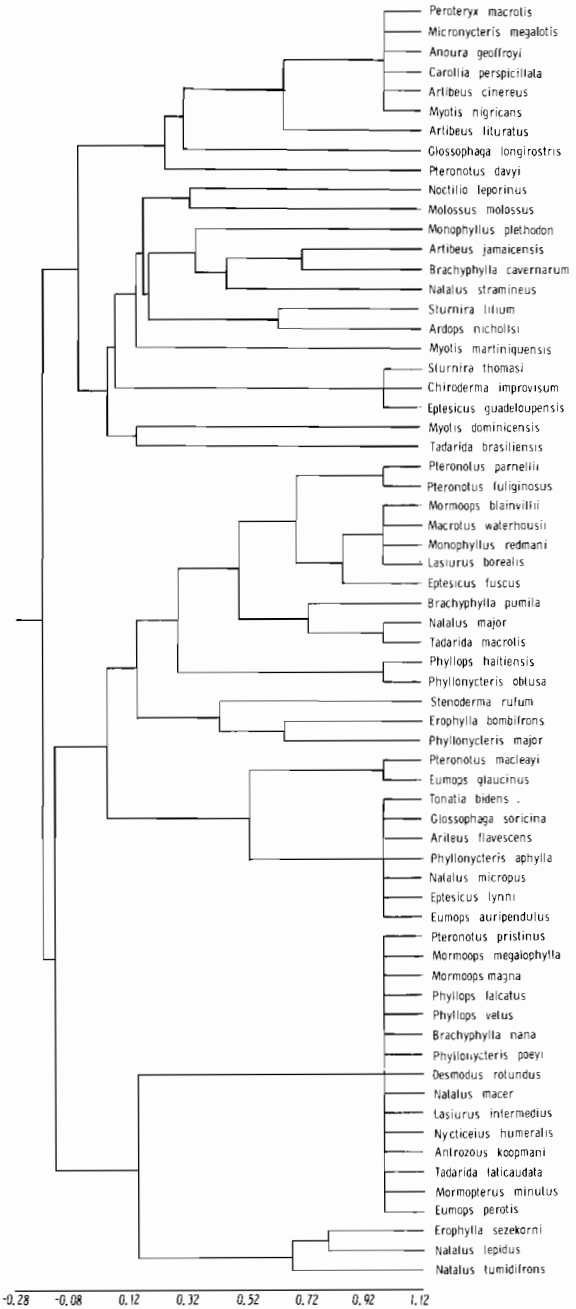

FIGURE 7. — Phenogram of Antillean bat species computed from correlation matrix based on distribution data given in Table 1 and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient is .871.

averages) method and a phenogram was generated (Fig. 7). The phenogram was compared with the original matrix and a coefficient of cophenetic correlation was computed. Secondly, the composition of the bat fauna of each island was compared using the coefficient of community (Hagmeier and Stults, 1964; Peters, 1968). The matrix of coefficients of community among all of the islands (Table 5) was clustered as above (Fig. 8).

Examination of Fig. 7 reveals that the distribution patterns for bats occurring in the Antilles fall into two major clusters. The upper cluster in this figure contains all species occurring in the Lesser Antilles including the four widespread species (*N. leporinus, A. jamaicensis, T. brasiliensis,* and *M. molossus*) and two species shared with Puerto Rico (*M. plethodon* and *B. cavernarum*). The grouping of these six species with the Lesser Antillean cluster can be explained by the greater number of islands in this region and thus a heavier weighting for this region in our analysis. The lower cluster in Fig. 7 contains those species confined to the Greater Antilles.

Within the lower cluster in Fig. 7 are two subclusters. The lower one contains those species confined to Cuba or shared between Cuba and the Bahamas. The upper subcluster reveals several interesting groupings of species. *Pteronotus parnellii* and *P. fuliginosus* have the same distributional pattern being known from the four major islands in the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico). Four other species (*Mormoops blainvillii, Macrotus waterhousii, Monophyllus redmani,* and *Lasuirus borealis*) are known from these four islands plus the Bahamas. *Eptesicus fuscus* is known from all of these islands except Jamaica. *Brachyphylla pumila* is confined to Hispaniola and Jamaica (fossil), whereas *Natalus major* and *Tadarida macrotis* are known from these two islands in addition to Cuba. *Phyllops haitiensis* and *Phyllonycteris obtusa* are endemic only to Hispaniola. Three species that occur on Puerto Rico (*Phyllonycteris major* occurs only on Puerto Rico) form the next group. Of these, *Stenoderma rufum* also occurs in the Virgin Islands and *Erophylla bombifrons* also on Hispaniola. *Pteronotus macleayi* and *Eumops glaucinus* are known only from Cuba and Jamaica, and the remaining six species in this subcluster are confined to Jamaica.

Within the upper cluster in Fig. 7, those species confined to Grenada are grouped at the top, and the three other species (*Artibeus lituratus, Glossophaga longirostris,* and *Pteronotus davyi*) shared among Grenada and other Lesser Antillean islands are also clustered there. The other species in this upper cluster are grouped in a complex pattern reflecting

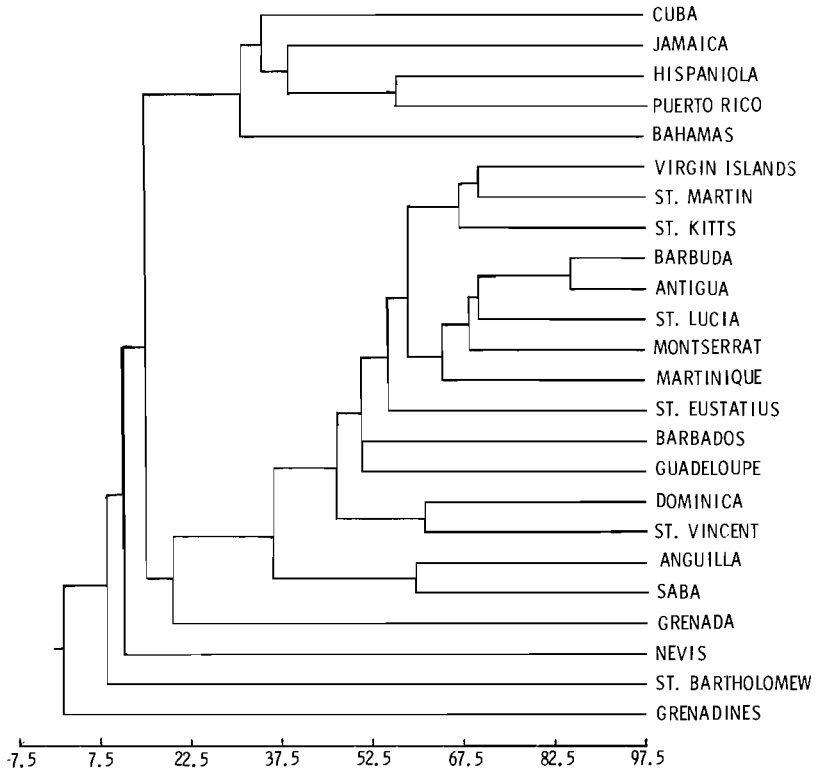

FIGURE 8. — Phenogram showing relationships among Antillean islands based upon a matrix of coefficients of community and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient is .928.

distribution of species as shown in Table 1. The three species that occur only on Guadeloupe (*Sturnira thomasi, Chiroderma improvisum,* and *Eptesicus guadeloupensis*) are grouped near the bottom of this cluster.

Clearly, based upon the distribution patterns of bats, there is little faunal overlap between the Greater and Lesser Antilles. Only six species currently are known to bridge these two areas and of these, three (four if *Tadarida brasiliensis* is included) have extensive distributions in the Neotropics of Middle and South America. Based upon the distributional patterns, it is evident that the bats of these two faunas have had almost completely separate origins.

Clustering of the coefficients of community reveals the islands falling into two major groups (Fig. 8). At the top of the figure is a group

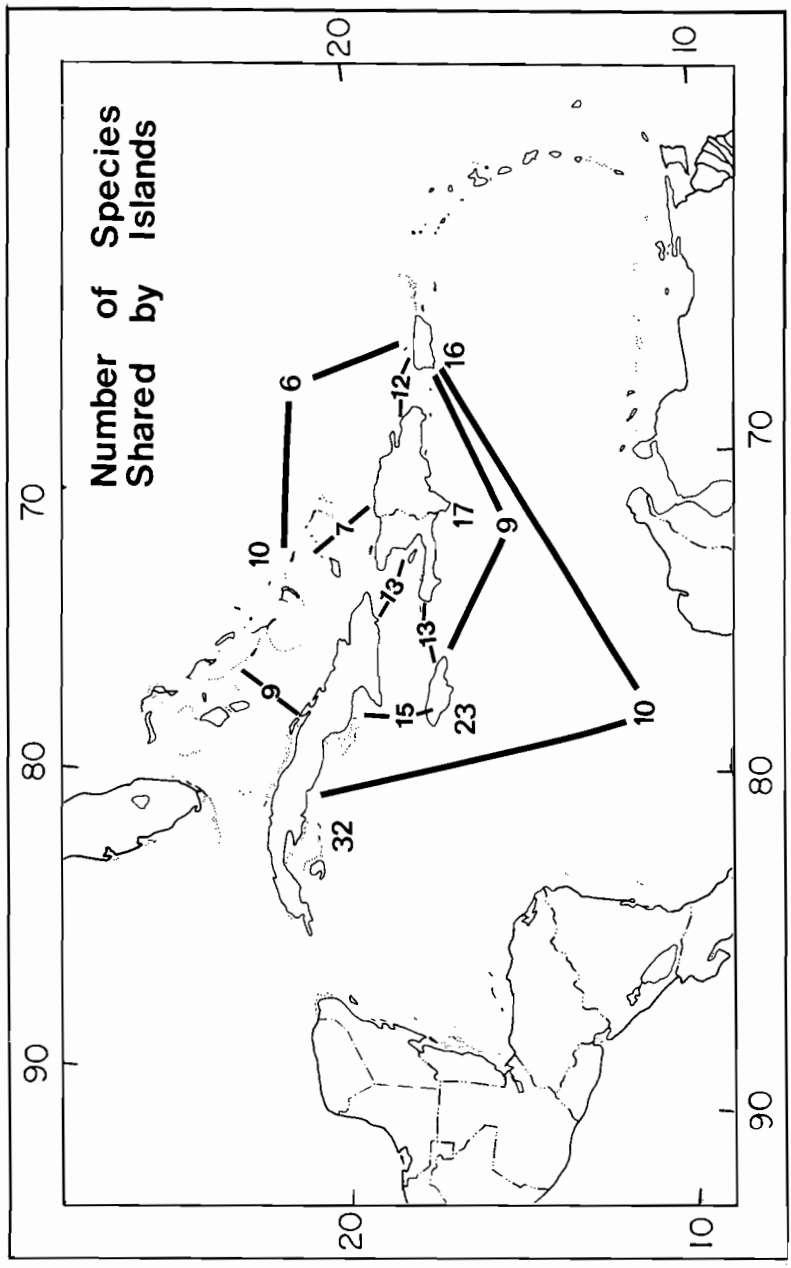

FIGURE 9. — Map of the Greater Antilles showing the number of species on each island (number adjacent to each island) and the number of species shared between islands (number between black lines connecting islands).

composed of the Greater Antillean islands of Cuba, Jamaica, Hispaniola, and Puerto Rico, and the Bahamas. In this group, the fauna of the Bahamas is the most distinct and those of Puerto Rico and Hispaniola are the least distinct. This latter finding may be changed somewhat when the relationships within the Antillean endemic genera of *Phyllonycteris, Erophylla, Brachyphylla,* and *Ardops-Phyllops-Stenoderma-Ariteus* complex are clarified. Although the internal relationships of the Greater Antillean islands may be altered by taxonomic changes, the relationship between the Greater and Lesser Antillean faunas will not be changed. Fig. 9 gives the number of species occurring on each Greater Antillean island and the number of species shared between islands. The greatest number are shared by Cuba and Jamaica (15), but this is a smaller percentage of the total faunas of the islands than that shared by Puerto Rico and Hispaniola which have 12 species in common.

The second major cluster of islands in Fig. 8 contains most of the Lesser Antilles and the Virgin Islands. Three islands at the bottom of this figure, Nevis, St. Bartholomew, and the Grenadines, currently have only one known bat species and their separation from the two major clusters is the result of their poorly known faunas. Placement of the Virgin Islands with the cluster including the Lesser Antillean islands is of interest. Geographically, the Virgin Islands are intermediate between the Greater and Lesser Antilles although geologically they are part of the Greater Antillean chain.

Six species of bats are currently known from the Virgin Islands (*Noctilio leporinus, Artibeus jamaicensis, Stenoderma rufum, Brachyphylla cavernarum, Tadarida brasiliensis,* and *Molossus molossus*). Four of these are widespread in the Antilles and give no clues as to the relationships of the Virgin Islands. *Stenoderma rufum* is known only from Puerto Rico and the Virgin Islands, whereas *B. cavernarum* is known from Puerto Rico, the Virgin Islands, and many of the Lesser Antillean islands. As pointed out by Koopman (1975), the chiropteran fauna of the Virgin Islands is a depauperate attenuation of the Puerto Rican fauna. Grouping of the Virgin Islands with the Lesser Antilles in our analysis is incorrect and probably was caused by the large number of widespread species in the fauna and the broad distribution of *B. cavernarum* in the Lesser Antilles. In the second cluster, the bat fauna of Grenada is the most distinct of any of the Lesser Antillean islands and the faunas of Antigua and Barbuda are the least distinct.

This analysis confirms that there are two distinctive chiropteran faunas in the Antillean region. The average coefficient of community

between the Greater and Lesser Antillean faunas is about 15. Excluding the three islands where the faunas are relatively unknown, Grenada has the next most distinct fauna with a coefficient of community of about 19 with other Lesser Antillean islands. This clearly indicates the distinctness of the bat fauna of Grenada, which is totally South American in origin. All remaining islands have an average coefficient of community with other islands of over 30.

CONCLUSIONS

1. Bahamas — The Bahamas are zoogeographically Antillean in nature with nine out of ten species recorded from the Bahamas being found on Cuba; the tenth, a species of *Natalus* found only in the Bahamas, has its closest relatives in the Greater Antilles. The Bahaman bat fauna shows less affinity to the bat fauna of the southern half of Florida with two of the ten extant species and neither of the two Pleistocene fossil species from southern Florida being found in the Bahamas. The percentage of endemism of the Bahaman fauna (60 percent) is also in accordance with that characteristic of the Greater Antilles.

2. Greater Antilles — The richest bat fauna in the Antilles is on Cuba (32 species) followed by Jamaica (23 species), Hispaniola (17 species), and Puerto Rico (16 species). The number of species found on Cuba is probably the result of the island's proximity to Central and North America and the ecological complexity of the island. Jamaica has a rich fauna because of its proximity to Central America and Cuba. The reduced fauna of Hispaniola (relative to Jamaica and Cuba) is probably because species have not reached this island with the frequency that they have reached Jamaica and Cuba (Hispaniola is as close to Cuba as is Jamaica). Puerto Rico (smaller than Cuba, Hispaniola, and Jamaica) has even a more remote position relative to the mainland and the poorest fauna of the four largest islands. Mainland species that are found on Puerto Rico and Hispaniola are also found on Jamaica and Cuba. Only two Puerto Rican species (*Brachyphylla cavernarum* and a sub-Recent fossil, *Monophyllus plethodon*) have their primary distribution in the Lesser Antilles and both of these species have counterparts in the other Greater Antillean islands. It is probable that those two species originated in the Greater Antilles and subsequently invaded the Lesser Antilles. The reverse, that these species may represent invaders from the Lesser Antilles, seems less probable to us. The

percentage endemism of each Greater Antillean island fauna is over 50 percent except for the Virgin Islands which has 33 percent endemics.

3. Lesser Antilles — Whereas the Greater Antilles represent a chiropteran fauna that involves multiple invasions and subsequent radiations, the Lesser Antilles represent fewer invasions and subsequent speciation has not occurred with the frequency found in the Greater Antilles. In the Lesser Antilles only *Myotis* is represented by more than a single endemic species and the specific distinctness of these two taxa are open to question (it is possible that both are conspecific with mainland *M. nigricans* or that both represent a single endemic species). Most of the evolutionary activity of the Lesser Antillean bat faunas has been associated with Guadeloupe. The Lesser Antilles have served as an effective filter barrier and the faunas of individual islands reflect their relative position in the chain. Although Grenada and possibly the Grenadines are in the Antillean chain, they represent a reduced mainland fauna with no Antillean endemic species. Zoogeographically, Grenada and the Grenadines are mainland islands.

4. Major Faunal Relationships — From a zoogeographic and evolutionary standpoint most of the action in the Caribbean has occurred in the Greater Antilles. The bat fauna of the Greater Antilles appears to indicate that the Greater Antillean chiropteran fauna is as unique as was suggested by Simpson (1956) based upon land mammals and, as such, represents a distinctive faunal region. On the other hand, the fauna of the Lesser Antilles is less distinctive and primarily represents a depauperate attenuation of the Neotropical fauna of South America.

5. All species of bats have reached the Antillean islands by over-water dispersal. There is little or no evidence of migration from the islands to the mainland.

ACKNOWLEDGMENTS

Stephen L. Williams assisted in preparing the figures and computer programs. Terry Yates assisted with the computer programs. John W. Bickham, Katrina Jarmon, J. Knox Jones, Jr., Karl F. Koopman, John C. Patton, and Donn E. Rosen critically reviewed the manuscript. Considerable original data utilized in this report is the result of field studies supported by a grant (GB-41105) from the National Science Foundation.

LITERATURE CITED

ALLEN, G. M. 1911. Mammals of the West Indies. — *Bulletin of the Museum of Comparative Zoology*, 54: 175-263.

ANDERSON, S. AND C. E. NELSON. 1965. A systematic revision of *Macrotus* (Chiroptera). — *American Museum Novitates*, 2212: 1-39.

BAKER, R. J. AND H. H. GENOWAYS. 1976. A New species of *Chiroderma* from Guadeloupe, West Indies (Chiroptera Phyllostomatidae). — *Occasional Papers of the Museum, Texas Tech University*, 39: 1-9.

BAKER, R. J. AND C. M. WARD. 1967. Distribution of bats in southeastern Arkansas. — *Journal of Mammalogy*, 48: 130-132.

BIRNEY, E. C., J. B. BOWLES, R. M. TIMM AND S. L. WILLIAMS. 1974. Mammalian distribution records in Yucatan and Quintana Roo, with comments on reproduction, structure, and status of peninsular populations. — *Occasional Papers, Bell Museum of Natural History, University of Minnesota*, 13: 1-25.

BUDEN, D. W. 1975a. *Monophyllus redmani* Leach (Chiroptera) from the Bahamas, with notes on variation in the species. — *Journal of Mammalogy*, 56: 369-377.

————. 1975b. A taxonomic and zoogeographic appraisal of the big-eared bats (*Macrotus waterhousii* Gray) in the West Indies. — *Journal of Mammalogy*, 56: 758-769.

BUSSING, W. A. 1975. Geographic distribution of the San Juan ichthyofauna of Central America with remarks on its origin and ecology. *In:* Investigations of the ichthyology of the Great Lakes of Nicaragua (T. R. Thorson, ed.). — University of Nebraska Press.

CHOATE, J. R. AND E. C. BIRNEY. 1968. Sub-Recent Insectivora and Chiroptera from Puerto Rico, with the description of a new bat of the genus *Stenoderma*. — *Journal of Mammalogy*, 49: 400-412.

DAVIS, B. L. AND R. J. BAKER. 1974. Morphometrics, evolution and cytotaxonomy of mainland bats of the genus *Macrotus* Gray (Chiroptera: Phyllostomatidae). — *Systematic Zoology*, 23: 26-39.

DAVIS, W. B. 1973. Geographic variation in the fishing bat, *Noctilio leporinus*. — *Journal of Mammalogy*, 54: 862-874.

DOBSON, G. E. 1878. Catalogue of the Chiroptera in the British Museum. London, xlii + 567 pp., 30 pls.

EGER, J. L. 1974. A new subspecies of the bat *Eumops auripendulus* (Chiroptera: Molossidae), from Argentina and eastern Brazil. — *Life Science Occasional Papers, Royal Ontario Museum*, 25: 1-8.

GENOWAYS, H. H. AND R. J. BAKER. 1972. *Stenoderma rufum*. — *Mammalian Species*, 18: 1-4.

———— AND ————. 1975. A new species of *Eptesicus* from Guadeloupe, Lesser Antilles (Chiroptera: Vespertilionidae). — *Occasional Papers, The Museum, Texas Tech University*, 34: 1-7.

GENOWAYS, H. H., R. J. BAKER AND R. S. LOREGNARD. 1973. Two species of bats new to the fauna of Trinidad. — *Mammalia*, 37: 362-363.

GENOWAYS, H. H. AND J. K. JONES, JR. 1975. Additional records of the stenodermine bat, *Sturnira thomasi*, from the Lesser Antillean island of Guadeloupe. — *Journal of Mammalogy*, 56: 924-925.

GOODWIN, G. G. 1959. Bats of the subgenus *Natalus*. — *American Museum Novitates*, 1977: 1-22.

GOODWIN, R. E. 1970. The ecology of Jamaican bats. — *Journal of Mammalogy*, 51: 571-579.

GREENBAUM, I. F. AND R. J. BAKER. 1976. Evolutionary relationships in *Macrotus* (Mammalia: Chiroptera): Biochemical variation and karyology. — *Systematic Zoology*, 25: 15-25.

HAGMEIER, E. M. AND C. D. STULTS. 1964. A numerical analysis of the distributional patterns of North American mammals. — *Systematic Zoology*, 13: 125-155.

HALL, E. R. AND J. W. BEE. 1960. The red fig-eating bat *Stenoderma rufum* Desmarest found alive in the West Indies. — *Mammalia*, 24: 67-75.

HALL, E. R. AND J. K. JONES, JR. 1961. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus *Lasiurus* Gray. — *University Kansas Publications, Museum Natural History*, 14: 73-98.

HALL, E. R. AND K. R. KELSON. 1959. The mammals of North America. — Ronald Press Company, New York, 1: xxx + 1-546 + *79*.

HUSSON, A. M. 1962. The bats of Suriname. — *Zoologische Verhandelingen*, 58: 1-282.

JONES, J. K., JR. AND D. C. CARTER. 1976. Annotated checklist, with keys to subfamilies and genera. Pp. 7-38, *in* Biology of bats of the New World family Phyllostomatidae, Part I. (R. J. Baker, J. K. Jones and D. C. Carter, eds.). — *Special Publications, The Museum, Texas Tech University*, 10: 1-218.

JONES, J. K., JR. AND C. J. PHILLIPS. 1970. Comments on systematics and zoogeography of bats in the Lesser Antilles. — *Studies on the Fauna of Curacao and other Caribbean Islands*, 32: 131-145.

———— AND ————. 1976. Bats of the genus *Sturnira* in the Lesser Antilles. — *Occasional Papers, The Museum, Texas Tech University*, 40: 1-16.

JONES, J. K., JR. AND A. SCHWARTZ. 1967. Bredin-Archbold-Smithsonian biological survey of Dominica. 6. Synopsis of bats of the Antillean genus *Ardops*. — *Proceedings of United States National Museum*, 124(3634): 1-13.

————, J. D. SMITH AND H. H. GENOWAYS. 1973. Annotated checklist of mammals of the Yucatan Peninsula, Mexico. I. Chiroptera. — *Occasional Papers, The Museum, Texas Tech University*, 13: 1-31.

KOOPMAN, K. F. 1952. The status of the bat genus *Reithronycteris*. — *Journal of Mammalogy*, 33: 255-258.

————. 1958a. A fossil vampire bat from Cuba. — *Breviora, Museum of Comparative Zoology*, 90: 1-4.

————. 1958b. Land bridges and ecology in bat distribution on islands off the northern coast of South America. — *Evolution*, 12: 429-439.

————. 1959. The zoogeographical limits of the West Indies. — *Journal of Mammalogy*, 40: 236-240.

————. 1968. Taxonomic and distributional notes on Lesser Antillean bats. — *American Museum Novitates*, 2333: 1-13.

————. 1974. Eastern limits of *Plecotus* in Mexico. — *Journal of Mammalogy*, 55: 872-873.

————. 1975. Bats of the Virgin Islands in relation to those of the Greater and Lesser Antilles. — *American Museum Novitates,* 2581: 1-7.

————. 1976. Zoogeography. Pp. 39-47, *in* Biology of Bats of the New World family Phyllostomatidae, Part I (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). — *Special Publications, The Museum, Texas Tech University,* 10: 1-218.

KOOPMAN, K. F., M. K. HECHT AND E. LEDECKY-JANACEK. 1957. Notes on the mammals of the Bahamas with special reference to the bats. — *Journal of Mammalogy,* 38: 164-174.

KOOPMAN, K. F. AND E. E. WILLIAMS. 1951. Fossil Chiroptera collected by H. E. Anthony in Jamaica, 1919-1920. — *American Museum Novitates,* 1519: 1-29.

LAVAL, R. K. 1973. A revision of the Neotropical bats of the genus *Myotis.* — *Science Bulletin, Natural History Museum of Los Angeles County,* 15: 1-54.

ORR, R. T. AND G. SILVA TABOADA. 1960. A new species of bat of the genus *Antrozous* from Cuba. — *Proceedings of Biological Society of Washington,* 73: 83-86.

PETERS, J. A. 1968. A computer program for calculating degree of biogeographical resemblance between areas. — *Systematic Zoology,* 17: 64-69.

ROSEN, D. E. 1976. A vicariance model of Caribbean biogeography. — *Systematic Zoology,* 24: 431-464.

SAVAGE, D. E. 1951. A Miocene phyllostomatid bat from Colombia, South America. — *University of California Publications in Geology,* 28: 357-366.

SCHWARTZ, A. AND J. K. JONES, JR. 1967. Bredin-Archbold-Smithsonian biological survey of Dominica. 7. Review of bats of the endemic Antillean genus *Monophyllus.* — *Proceedings of United States National Museum,* 124 (3635): 1-20.

SEALANDER, J. A., JR. AND J. F. PRICE. 1964. Free-tailed bat in Arkansas. — *Journal of Mammalogy,* 45: 152.

SILVA TABOADA, G. 1974. Fossil Chiroptera from cave deposits in central Cuba, with description of two new species (genera *Pteronotus* and *Mormoops*) and the first West Indian record of *Mormoops megalophylla.* — *Acta Zoologica Cracoviensia,* 19: 33-73.

SILVA TABOADA, G. AND K. F. KOOPMAN. 1964. Notes on the occurrence and ecology of *Tadarida laticaudata yucatanica* in eastern Cuba. — *American Museum Novitates,* 2174: 1-6.

SILVA TABOADA, G. AND R. H. PINE. 1969. Morphological and behavioral evidence for the relationship between the bat genus *Brachyphylla* and the Phyllonycterinae. — *Biotropica,* 1: 10-19.

SIMPSON, G. G. 1956. Zoogeography of West Indian land mammals. — *American Museum Novitates,* 1759: 1-28.

SMITH, J. D. 1972. Systematics of the chiropteran family Mormoopidae. — *Miscellaneous Publications, Museum of Natural History, University of Kansas,* 56: 1-132.

————. 1976. Chiropteran evolution. Pp. 49-69, Biology of bats of the New World family Phyllostomatidae, Part I. (R. J. Baker, J. K. Jones, Jr. and D. C. Carter, eds.). — *Special Publications, The Museum, Texas Tech University,* 10: 1-218.

WOLOSZYN, B. W. AND N. A. MAYO. 1974. Postglacial remains of a vampire bat (Chiroptera: Desmodus) from Cuba. — *Acta Zoologica Cracoviensia,* 19: 253-265.

WOODRING, W. P. 1954. Caribbean land and sea through the ages. — *Bulletin of Geological Society of America,* 65: 710-732.

VARONA, L. S. 1974. Catalogo de los mamiferos vivientes y extinguidos de las Antillas. — Academia de Ciencias de Cuba, Habana, viii + 139 pp.